

# New insights into the phylogeny and taxonomy of Chinese species of *Gagea* (Liliaceae)—speciation through hybridization

Angela Peterson · Igor G. Levichev · Jens Peterson ·  
Doerte Harpke · Martin Schnittler

Received: 5 January 2011 / Accepted: 31 August 2011 / Published online: 21 September 2011  
© Gesellschaft für Biologische Systematik 2011

**Abstract** A new region of speciation for the genus *Gagea* (Liliaceae) was investigated (Bogda-Shan and Urumqi; northwestern Xinjiang, China). Two species were recorded as new for the region (*G. rufidula*, *G. davlianidzeae*); three species are described as new to science (*G. angelae*, *G. jensii* and *G. huochengensis*). The description of *G. nigra* is emended. Sequence data (cpDNA: *trnL-trnF* IGS+*psbA-trnH* IGS, nrDNA: ITS), including representatives of all *Gagea* sections, were used to compare the new species with

closely related taxa. A nuclear single copy gene region (pCOS *At103*) was analysed for representatives of the Sects. *Minimae* and *Gagea*. Network analysis of cpDNA and nDNA indicates hybridization and recent speciation in Xinjiang. ITS and pCOS *At103* sequences reveal gene flow between *G. davlianidzeae* and *G. nigra*. A cpDNA haplotype network constructed from representatives of Sect. *Gagea* was highly informative phylogenetically. *Gagea angelae* and *G. huochengensis*, sharing gene flow, are related closely to a basal clade represented by *G. ancestralis*, *G. xiphoidea* and *G. capusii*, which may include the putative progenitor of all other taxa of the large Eurasian Sect. *Gagea*. Whereas speciation in Sect. *Minimae* seems to be driven mainly by hybridization, speciation in the Sect. *Gagea* may be influenced by both hybridization and geographical separation. We confirm the monophyly of Sects. *Bulbiferae* and *Minimae*.

**Electronic supplementary material** The online version of this article (doi:10.1007/s13127-011-0059-x) contains supplementary material, which is available to authorized users.

A. Peterson  
Martin-Luther-University of Halle-Wittenberg,  
Institute of Biology,  
Weinbergweg 10,  
06120 Halle, Saale, Germany

I. G. Levichev  
Herbarium, Komarov Botanical  
Institute of the Russian Academy of Sciences,  
Prof. Popov Str. 2,  
Saint Petersburg 197376, Russia

J. Peterson  
State Office for Environmental Protection of Saxony-Anhalt,  
Reideburger Str. 47,  
06116 Halle, Saale, Germany

D. Harpke  
Leibniz Institute of Plant Genetics and Crop Plant Research (IPK),  
06466 Gatersleben, Germany

M. Schnittler (✉)  
Ernst-Moritz-Arndt University Greifswald,  
Institute of Botany and Landscape Ecology,  
Grimmer Str. 88,  
17487 Greifswald, Germany  
e-mail: martin.schnittler@uni-greifswald.de

**Keywords** cpDNA · *Gagea* · hybridization · ITS · Liliales · pCOS *At103* · speciation

## Introduction

The genus *Gagea* Salisb. (Liliaceae) comprises 250–300 species (Peterson et al. 2008; Zarrei et al. 2011a) and many have been described during the past decade (e.g., Ali 2006; Hamazoğlu et al. 2008; Henker 2005; Levichev 2001, 2006a, b, 2008; Levichev and Ali 2006; Peruzzi et al. 2007; Tison 2004, 2009; Zhao and Zhao 2003; Zhao and Yang 2006; Zarrei et al. 2010a, b).

Highest species diversity is reported for the Western Pamir-Alai (97 species) and the Western Tien-Shan (65 species), representing two regions of ongoing speciation (Levichev 1999a; Levichev and Jezniakowsky 2008).

Speciation by neotonical divergence (Levichev 2006b) but also by hybridization and allopolyploidy (Peruzzi 2008a; Peterson et al. 2009) generates a high degree of morphological polymorphism and endemism within the genus.

The subdivision of the genus into sections varies according to the weight applied to molecular and/or morphological characters. Levichev recognized 13 (see Peterson et al. 2008) and Peruzzi et al. (2011) 14 sections. In contrast, Zarrei et al. (2011a) divided the genus into seven sections based on highly resolved major monophyletic clades, merging several monophyletic and morphologically well differentiated sections (see Peterson et al. 2008). In addition, the taxonomic status of *G. serotina* varies: the species was included within the genus *Gagea* by several authors (Peruzzi et al. 2008a; Peruzzi et al. 2011; Zarrei et al. 2009, 2011a), but was excluded by others (Levichev 2001; Peterson et al. 2008; Levichev and Jezniakowsky 2008). Our study refers generally to the infrageneric classification (see Table 1) of Levichev (and Peterson et al. 2008) and also incorporates the classification of *Gagea sensu lato* (including *Lloydia*) suggested by Zarrei et al. (2011a).

The species of *Gagea* are small bulbous plants with an ephemeroïdal cryptodicyclic development (in the 1st year every shoot grows into a subterranean storage leaf and buds, and develops into the green plant in the 2nd year, replaced again by a new shoot, Levichev 2006a). Many species reproduce by bulbils, and their form, quantity and location provide important diagnostic characters (Levichev

1999b). Bulbil formation may be limited to non-flowering stages of ontogenesis, which is crucial for the balance between sexual and asexual reproduction (Schnittler et al. 2009). Often, species possess morphologically similar juvenile stages but follow an ontogenetic pattern unique for each taxon. For example, in Sect. *Gagea*, the coalescence of the second basal leaf with the inflorescence scape is indicated by the divergence of this leaf below the first branch of the inflorescence, appearing as the lowermost and largest floral leaf. In Sect. *Minimae* the second basal leaf is usually reduced (Levichev and Ali 2006; Peterson et al. 2009). In Sect. *Gagea* the lowermost leaf of the inflorescence is arranged opposite to the basal one, whereas in Sect. *Minimae* the floral leaf (the fourth on a shoot) belongs to the inflorescence and is located above, and in line with, the first basal leaf. In addition, for the determination of species, the cross sections of basal leaves and peduncles (Ajani et al. 2010; Zarrei et al. 2010c) are very important features.

The flora of China includes 17 species of *Gagea* (Xinqi and Turland 2000). Three new species from Inner Mongolia have been described recently (Zhao and Zhao 2003, 2004; Zhao and Yang 2006). We studied *Gagea* populations around Urumqi and the eastern Tian-Shan (Bogda-Shan, Heaven Lake) using a combination of morphological and molecular methods (cpDNA and ITS sequence data). For representatives of Sects. *Gagea* and *Minimae* cpDNA haplotype networks were constructed and gene-flow between closely related species was analysed using the low

**Table 1** Infrageneric classification of *Gagea* Salisb<sup>a</sup>

Sects. according to Levichev (in Peterson et al. 2008)	Sects. according to Zarrei et al. (2011a)
<i>Gagea</i> Davlianidze, Not. Syst. Geogr. Inst. Bot. Tbilissiensis. 29: 73. 1972.	<i>Gagea</i>
<i>Didymobulbos</i> (K.Koch) Boissier, Fl. Orient 5: 204. 1882.	<i>Didymobulbos</i> K.Koch, Linnaea, 22: 229. 1849.
<i>Fistulosae</i> (Pascher) Davlianidze, Not. Syst. Geogr. Inst. Bot. Tbilissiensis. 30: 62.1973.	
<i>Minimae</i> (Pascher) Davlianidze, Not. Syst. Geogr. Inst. Bot. Tbilissiensis. 30: 62. 1973	
<i>Spathaceae</i> Levichev, Mol. Phylogenetic Evol. 46: 449. 2008.	
<i>Stipitatae</i> (Pascher) Davlianidze, Not. Syst. Geogr. Inst. Bot. Tbilissiensis. 29: 71. 1972.	
<i>Dschungaricae</i> Levichev, Mol. Phylogenetic Evol. 46: 448. 2008.	
<i>Plecostigma</i> (Turcz.) Pascher, Lotos, 24: 116. 1904.	<i>Plecostigma</i> (Turcz.) Pascher, Lotos, 24: 116. 1904.
<i>Platyspermum</i> Boissier, Fl. Orient 5: 204. 1882.	<i>Platyspermum</i> Boiss., Fl. Orient 5: 204. 1882.
<i>Graminifoliae</i> Levichev, Bot. Zhurn. 75 (2): 231. 1990.	
<i>Incrustatae</i> Levichev 1990, Bot. Zhurn. 75 (2): 232. 1990.	
<i>Bulbiferae</i> Levichev, Mol. Phylogenetic Evol. 46: 448. 2008.	
<i>Anthericoides</i> A.Terracc., Bull. Soc. Bot. France 52: 24. 1905.	<i>Anthericoides</i> A.Terracc., Bull. Soc. Bot. France 52: 24. 1905.
	<i>Tricholloydia</i> (Engl.) Zarrei & Wilkin, Phytotaxa 15: 53. 2011.
	<i>Lloydia</i> (Salisb. ex Rchb.) Peruzzi, J.-M.Tison, A.Peterson & J.Peterson, Taxon 57(4): 1212. 2008.

<sup>a</sup> For an overview of previous infrageneric classifications see Peterson et al. 2008, and Zarrei et al. 2009 (p. 126)

copy pCOS gene *At103* (Mg-p IX monomethyl ester cyclase, AGI-ID: AT3G56940; see Li et al. 2008). Three new species are described and the description of another is emended within this study.

## Materials and methods

### Sampling and morphological study

Populations of *Gagea* were collected in spring 2005, 2007 and 2009 in the foothill region around Urumqi and in the vicinity of Heaven Lake (Tianchi Lake) in the eastern Tian-Shan range. Morphological studies were carried out with living plants. At least ten individuals of each species were deposited with HAL, B and LE (<http://sciweb.nybg.org/science2/IndexHerbariorum.asp>). For *G. huochengensis* and *G. jensii*, sampling was limited by small population size. Wherever possible, individuals were collected from different sites and from all stages of ontogenesis. Vouchers for new species described were prepared in triplets and deposited in HAL (holotypes, paratypes) and B, LE, HAL (isotypes). All individuals of a given site (population) received the same Arabic number; herbarium vouchers are coded by letters A to S following this number; multiple specimens investigated within a voucher were coded by I and II, respectively (see Appendix 1).

### Genomic DNA extraction, PCR amplification, and cloning

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 with a modification for old herbarium vouchers (incubating leaves in lysis buffer for ca. 6 h). PCR was performed with 50 ng genomic DNA in 20  $\mu$ l reactions (Ready To Go™ PCR Beads, Amersham Bioscience, Piscataway, NJ) in a GeneAmp PCR System 9700 (Perkin Elmer; <http://www.perkinelmer.com>).

Primers for amplification of *trnL-trnF* intergenic spacer (IGS) and *psbA-trnH* IGS were used according to Sang et al. (1997); of the ITS region (ITS1+5.8SrRNA+ITS2) according to White et al. (1990), and of the low copy nuclear conserved ortholog set (COS) gene *At103* (partial) according to Li et al. (2008). To detect possible hybridization, fragments of *At103* were cloned for two taxa of Sect. *Minimae* (*G. nigra* 1B: Urumqi; *G. nigra* 4D and *G. davlianidzeae* 1A, 2A, 2B, 3B: Heaven Lake) and three taxa of Sect. *Gagea* (*G. huochengensis* 1H; *G. angelae* 3S, 3 M; *G. cf. xiphoides* 3I) in the pGEM-T Easy vector following the manufacturer's protocol (Promega, Mannheim, Germany). Six clones per individual were analyzed.

### Sequencing and phylogenetic analyses

Gel-purified PCR products (50–200 ng) were prepared as “u-mixes” via the StarSEQ® Sequencing Service (StarSeq, Mainz, Germany). *At103* clones were sequenced with T7 and SP6 using the Templi-Phi DNA Sequencing Template Amplification Kit following the manufacturer's protocol (Amersham Biosciences). Both strands were sequenced at least twice and combined into a single consensus sequence. All sequences have been deposited with the EMBL database (Appendix 1).

Sequence alignment was performed utilising the Clustal-W multiple alignment procedure (Thompson et al. 1994) in Bioedit software (version 7.0.9.0; Hall 1999), followed by manual adjustment. We included sequences for all sections of *Gagea*, also using data from previous studies (Peterson et al. 2004, 2008; 2009). *Tulipa cretica* was used as outgroup (see Peterson et al. 2008; Peruzzi et al. 2008a). Three ITS sequences (Appendix 1) were from EMBL. Generally, all ITS-regions are putatively functional, checked according to Harpke and Peterson (2008a, b).

Molecular analyses were performed with ITS data (ITS1+5.8SrDNA+ITS2), and the combined cpDNA data set (*trnL-trnF* IGS+*psbA-trnH* IGS). MrModeltest v2.3 (Nylander 2004; see also Posada and Crandall 1998) was used to test different models of sequence evolution. For the ITS data, the general time reversible (GTR) model with gamma-distributed (GTR+ $\Gamma$ ) was chosen, and for the cpDNA data the F81+I+ $\Gamma$  was chosen by the Akaike information criterion (AIC).

Phylogenetic relationships were reconstructed using Bayesian Analyses (BA) with MrBayes version 3.1 (Huelsenbeck and Ronquist 2001; Huelsenbeck et al. 2002). The GTR+ $\Gamma$  and F81+I+ $\Gamma$  models were applied for the ITS and cpDNA data sets. One cold and three incrementally heated Monte Carlo Markov Chains (MCMC) in two simultaneous runs were performed. The chains were run for 5 million (ITS) and 9 million (cpDNA) cycles with trees sampled every 1,000th generation, each using a random tree as a starting point. The first 25% of trees of each run were discarded as burn-in; converging log-likelihoods, potential scale reduction factors for each parameter and inspection of tabulated model parameters suggested that the stationary had been reached thereafter. Three independent runs of the MCMC analysis were performed to confirm that separate analyses converged on the same result. Each of the three independent MCMC analyses resulted in the same topology and similar nodal support. Only the results of the first analysis are shown here. Posterior probabilities (pp) were calculated from the remaining trees (ITS 3,750 trees, cpDNA 6,750 trees). Trees and data sets have been submitted to Treebase (<http://purl.org/phylo/treebase/phyloids/study/TB2:S11471>).

For representatives of Sects. *Gagea* (38 sequences, 443 bp) and *Minimae* (34 sequences, length 472 bp) cpDNA

haplotype networks were constructed using the TCS algorithm (version 1.21, Clement et al. 2000) based on a maximum parsimony approach, performing best for non-recombinant sequences (Woolley et al. 2008). For this algorithm only, gaps were reduced to a minimum length; and insertions (nine for each network) were treated as a single mutation event regardless of their length. If there were different types of insertions at one site, these were coded as one of the four nucleotides; sequences with a deletion received a 1 bp gap. Length variation at mono-nucleotide repeats (T) and indels (three in Sect. *Minimae* and four in Sect. *Gagea*) were excluded from the analyses due to uncertain homology of the sequence positions. Each haplotype was included only once.

As phylogenetic trees have their limitations in displaying reticulated evolution a neighbor network (NN) was constructed for the *At103*-region using SplitsTree version 4.6 (Huson and Bryant 2006) based on uncorrected p-distances. NN was criticized as producing false positive results (Linder and Rieseberg 2004) but simulations have also shown that it is one of the least erroneous methods when recombination is present in the data set (Woolley et al. 2008).

The number of parsimony informative sites was determined using DnaSP v5.10.01 software; excluding gap sites (Librado and Rozas 2009).

## Results

### *Gagea* taxa of Xinjiang

Four *Gagea* species occurred around Urumqi: *G. bulbifera*, *G. ova*, *G. jensii* sp. nov. and *G. nigra* (emended in this study; see Taxonomic treatment and Appendix 2 in the

Electronic supplementary material). Due to extreme over-grazing by goats, *Gagea* species occur only in steppe remnants persisting in parks and cemeteries, and rarely in rock fissures outside the city.

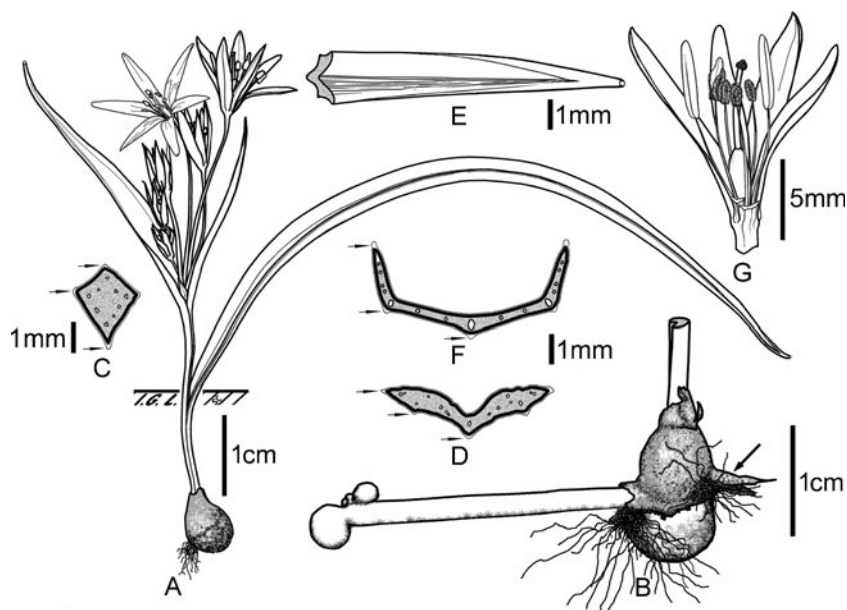
In the Bogda-Shan range of the eastern Tian-Shan, we observed *G. angelae* sp. nov., *G. rufidula*, *G. davlianidzeae*, *G. nigra* and *G. liotardii*. Within populations of *G. angelae* I. Levichev, we identified two other species of Sect. *Gagea*: *G. huochengensis* sp. nov. and *G. cf. xiphoidea*. The latter taxon was observed with only two vegetative individuals, generative samples could not be detected in our collection of over 450 samples of *G. angelae*. *Gagea huochengensis* was also found in limited numbers, but with sterile and flowering individuals. Most species had large populations, and widespread cow grazing during summer months seemed to promote their growth. *Gagea angelae*, *G. huochengensis* and *G. jensii* are described below (Taxonomic treatment, see also Figs. 1, 2 and 3 and Appendix 2 of the Electronic supplementary material for Latin descriptions). Color plates for *G. angelae*, *G. jensii*, *G. nigra*, *G. rufidula* and *G. davlianidzeae* are shown in Appendix 3 of the Electronic supplementary material.

### Taxonomic treatment

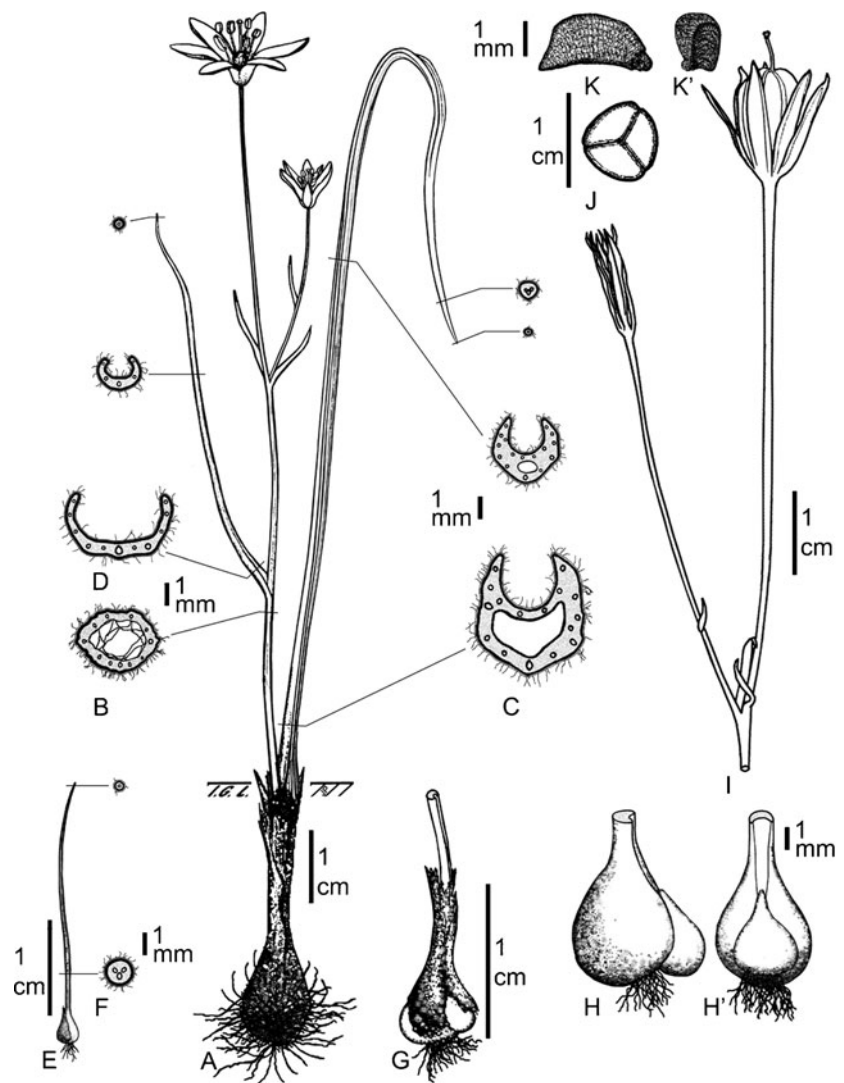
*Gagea nigra* L.Z. Shue 1980. Fl. Reipubl. Popul. Sin., 14: 282, 68, Pl. 16, emend. Schnittler, hoc loco (see Appendix 2 of Electronic supplementary material for translation of the original Chinese description)

*Diagnosis* A *G. granulosa* Turcz. et *G. davlianidzeae* Levichev plantae minutie et bulbillo vegetativo solitario differt. A *G. filiformis* (Ledeb). Kar. et Kir. (syn. *G.*

**Fig. 1 a–g** *Gagea angelae* spec. nov. **a** Whole flowering plant lacking bulbils; **b** bulb of a strong vegetative plant, developing a stolon with a group of bulbils at the tip; remnants of the stolon of the previous year are visible at the opposite side of the parent bulb (arrow); **c** tetragonal cross section of the peduncle of a flowering plant below the inflorescence; **d** cross-section of the middle part of the basal leaf; **e** tip of the basal leaf; **f** cross-section of the lower floral leaf, arrows in **c**, **d**, and **f** indicate subepidermal sclerenchyma; **g** flower, two perianth leaves removed to show the ovary



**Fig. 2 a–k** *Gagea jensii* spec. nov. **a** Flowering plant; **b** peduncle, cross-section; inner channel partly filled with dry parenchyma; **c** cross-section of basal leaves at various levels; **d** cross-section, lower part of a middle stem leaf; **e** juvenile plant originating from a bulbil in its 1st year; **f** cross-section through the single basal leaf; **g** bulb of a weak vegetative plant with one bulbil; **h, h'** the same in dorsal and lateral view, outer tunic removed; **i** inflorescence with one mature capsule, the second flower often fails to set seed; **j** capsule seen from above; **k** seed in lateral view; **k'** seed seen from the chalazial end



*sacculifera* Regel) folio pedunculo inferiore latior, perianthii segmentis basi planis (non saccatis), dorso villosis, facie exterior bulborum subnigri, nonnunquam violaceis coloribus, differt.

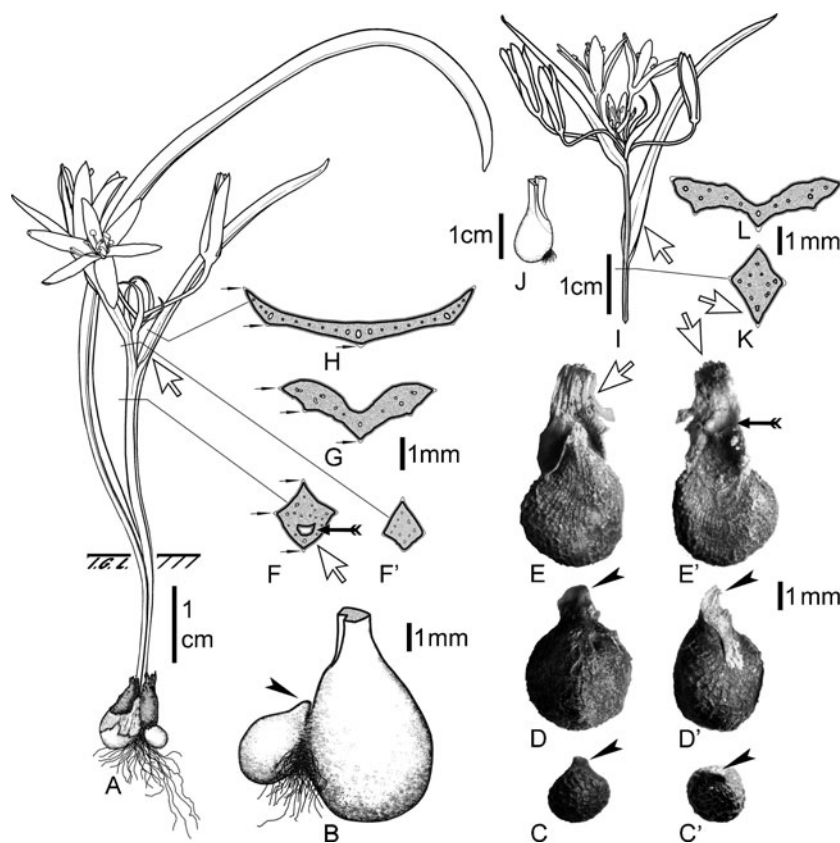
*Type* Sinkiang [Xinjiang]: Wu-lu-mu-chi [Urumqi], 14 April 1976, *L.Z. Shue* 11135 (XJBI).

*Isotypes* Xinjiang, Wu-lu-mu-chi [Urumqi], 14 April 1976, *L.Z. Shue*, 9714! (PE), 7217, 7220, 7221, 7226 (XJBI).

*Additional material* China, Xinjiang, Urumqi, at the northern fringe of the city, Bad-Shan-Di, 900 m a.s.l., 11.04.1965, *L.Z. Shue*, 650009! (PE00035658); China, Xinjiang, Urumqi, 43°43'53"N, 87°35'46"E, 987 m, 01.05.2009, *Schnittler, A. and J. Peterson*, 200904 (HAL108463, HAL108464, B100375629); China, Xinjiang, Tian-Shan, Bogda-Shan, Heaven Lake (Tianchi Lake), 43°50'17"N, 88°10'15"E, 2,250 m, 26.04.2009, *Schnittler, A. and J.*

*Peterson*, 200908 (HAL108183, B100375630); China, Xinjiang, Tian-Shan, Bogda-Shan, Heaven Lake (Tianchi Lake), 43°53'31"N, 88°06'02"E, 2,173 m, 28.04.2009, *Schnittler, A. and J. Peterson*, 200931 (HAL108460, HAL108461, B100375628).

We did not see all isotypes cited in the protologue (see also <http://www.tropicos.org/Name/18406439>), but studied specimens No. 9714 (isotype) and 650009, both from the environs of Urumqi, in Beijing (PE). These specimens from the *locus classicus* correspond in all morphological characters to our material, but contain flowering plants only. From our quantitative morphological investigations, including plants of all stages, a number of characters can now be described more precisely. First, both non-flowering and flowering plants produce only one bulbil per year. Robust flowering plants seem to delay development of the bulbil, and may still lack it at anthesis. In our data set comprising 245 flowering plants collected at various locations between 950 and 1,850 m, 215 plants were found with one bulbil; no



**Fig. 3** a–l *Gagea huochengensis* spec. nov. **a** Flowering plant with one bulbil; the second basal leaf concaulescent and nearly reaching the inflorescence (white arrow); **b** bulb of a juvenile plant with one bulbil, tunics removed; **c**, **c'** the same bulbil after 1 year, dorsal and lateral view; black arrows point towards the remnant of the second basal leaf; **d**, **d'** bulbil of a strong vegetative plant; remnants of the second basal leaf are much larger; **e**, **e'** bulbil of a weak flowering plant; the black arrow points towards the channel, remnants of the second basal leaf

surround this channel; **f**, **f'** cross-section of a peduncle below and above the second basal leaf (here developed as floral leaf), the channel is indicated by a black arrow; **g** cross-section of basal leaf; **h** cross-section of the lower leaf of an inflorescence, cross-section; little arrows in drawings **F**, **G**, **H** indicate subepidermal sclerenchyma; **i**–**I** strong generative plant without bulbils; **i** inflorescence; **j** bulb, dead tunics are removed; the basal leaf encloses the bulb; **k** cross-section of a peduncle, note the absence of a channel; **l** cross-section of basal leaf

bulbil could be detected in the remaining 30 plants, thus older plants of generative age may not form bulbils at all, or develop these later in the year. About 50% of all plants with  $4 \pm 0.25$  mm diameter of the parent bulb flower. Parent bulb diameter in flowering plants ranged from 1.7 to 11.8 mm (mean  $5.6 \pm 1.4$  mm). The bulbil of the current year is easy to recognize by its pale cream color, whereas bulbils of previous years, which often lie dormant between older tunicae of the parent bulb, have already developed the dark-brown to nearly black tunic typical for the species. Second, plants of *G. nigra* displayed large variations in plant size (especially in the size of the basal leaf) and number of flowers. Plants from higher elevations, presumably promoted by better water supply and dung due to frequent summer pasture with cows, developed much larger basal leaves and more flowers. Around Urumqi, we found also large specimens in cultivated and irrigated areas, but only small ones outside the city. The basal leaf varies from 11 to 205 mm in length, mean  $104 \pm 31$  mm; width 4.2–11.2 mm, mean  $4.3 \pm 1.4$  mm.

We found plants with up to 13 flowers (mean  $2.9 \pm 1.9$ ). The floral leaf also varies in size (22–60 mm length, mean  $46 \pm 13$  mm; 1.0–16.6 mm width, mean  $7.3 \pm 2.4$  mm). Its base is somewhat cordate. Third, the elevation belt given by Shue (1980) seems to be too narrow: alpine meadows start in Xinjiang at 1,700 m, and we found species up to 2,400 m a.s. l. The name *G. nigra* refers to the nearly black tunicae of the bulbs, which have violaceous hues when wet.

**Similar species** Differing from *G. granulosa* Turcz. and *G. davlianidzeae* Levichev by developing only one, not several bulbils per year in adult plants. *Gagea filiformis* (Ledeb.) Kar. et Kir. forms as well one bulbil per year but has narrowly lanceolate leaves; the floral leaf is more narrow as well, lacks the nearly cordate base of that of *G. nigra* and is widest slightly below the middle, not near the base; the tunic of the bulb is pale chestnut brown, not blackish brown with violaceous tints. *Gagea filiformis* has nearly glabrous petals which may have a saccate grooving

at its base; in *G. nigra* the petals are nearly even and soft villose at its dorsal side; this species possesses a more copious pubescence in general.

*Gagea angelae* Levichev et Schnittler sp. nov. [Sect. *Gagea*]

**Diagnosis** A *Gagea calyptriifolia* Levichev inflorescentia compressa, folio radicali angusto (3–5 mm lt., nec ca. 6 mm), longe acutato, a *G. praemixta* Vved. bulbillis vegetativis aliquot stolonem longum terminantibus (nec bulbillo solitario), a alii speciebus ceteris *G. sect. Gagea* stolonem longum differt.

**Type** China, Xinjiang, Tian-Shan, Bogda-Shan, Heaven-Lake (Tianchi Lake), 43°53'38"N, 88°06'59"E, 1,980 m, 25.04.2009, *Schnittler, A. and J. Peterson*, 200913 (holotypes: HAL108470, isotypes: LE00002135, B100375627).

**Paratype** China, Xinjiang, Tian-Shan, Bogda-Shan, Heaven-Lake (Tianchi Lake), 43°53'31"N, 86°06'02"E, 2,173 m, 28.04.2009, *Schnittler, A. and J. Peterson*, 200915 (LE 00002137, HAL108471, HAL108472, HAL108473, HAL108474, HAL108475, HAL108476).

Plants solitary or in small groups, 5–8 cm tall. Bulbs of flowering plants 6–8 mm in diameter (data from 70 flowering plants: 4.5–11.5 mm, mean 7.2±1.3 mm), tunic coriaceous, pale chestnut brown. Flowering plants nearly always without bulbils. Older vegetative plants develop a horizontal, white to cream stolon of 15–50 mm length, very rarely and usually in weak plants the bulbils are nearly sessile (data from 223 non-flowering plants: stolon 0.1–79.0 mm long, mean 23.3±14.5 mm). This stolon carries at its end 2–5 (1–10, mean 3.0±2.4) globose bulbils protruding from the leaf tunic. Usually the first bulbil grows significantly larger than the surrounding bulbils. Peduncle 4–7 cm tall, tetragonal in cross section, 1–1.5 mm in diameter. Basal leaf solitary, exceeding the inflorescence but usually curved backwards; 10–17(–23) cm long and 3–5(–6) mm wide (measurements from 70 flowering plants: length 92–231 mm, mean 152±36 mm; width 2.3–7.3 mm, mean 4.3±1.0 mm). Floral leaf slightly shorter than, rarely exceeding the inflorescence, 3–7(–9) mm wide (length 14.9–75.4 mm, mean 35.6±13.4 mm; width 1.8–8.8 mm, mean 6.0±1.5 mm), narrowly lanceolate and gradually pointed into a long tip. True bracts 1–(2–3), obliquely opposite, significantly shorter. Inflorescence with 2–4 (range 1–10, mean 3.7±2.0) flowers, fasciculate, pedicels ranging from 0.7 to 2.0 cm in length. Perianth leaves narrowly lanceolate, with hooded ends, 9–11 mm long and 1.8–2.2 mm wide; inner side yellow; outer side greenish with a yellow mid rib. Ovary sessile, oblong ovate. Anthers yellow, 3.5–5 mm long and cylindrical when still closed,

after dehiscence globose, 1.5–2 mm long. Capsule barely approaching more than half of the perianth length, ovoid, sessile. Seeds terete (Fig. 1, Appendix 3 of Electronic supplementary material).

**Similar species** The species differs from *Gagea calyptriifolia* Levichev by compressed inflorescences, the very narrow basal leaf (usually 3–5 mm wide, not exceeding 6 mm) with an attenuate tip. In contrast to *G. praemixta* Vved. the new species develops several, not a single, bulbil at the end of a long stolon. This long stolon tells the species apart from all other taxa of *G. sect. Gagea*, including *G. xiphoidea* Levichev as the taxon most similar in habit.

Widespread at open, preferentially S-exp. slopes at the upper forest belt of the eastern Tien-Shan, around Heaven Lake, 1,600–1,900 m, more rarely exceeding up to 2,300 m a.s.l.

The species is named in honour of Angela Peterson (Halle/Saale, Germany), investigator of the molecular phylogeny of the genus.

*Gagea jensii* Levichev et Schnittler sp. nov. [Sect. *Plecostigma* (Turcz.) Pascher]

**Diagnosis** A *G. alberti* Regel inflorescentia angusta (non diffusa), 1(–2)-flora (non 5–7-flora), folio pedunculo infimo brevi (non inflorescentia longius).

**Type** China, Xinjiang, Urumqi, hills near a cemetery, 43°43'53"N, 87°35'46"E, 987 m, 30.04.2009, *Schnittler, A. and J. Peterson*, 200917 (holotypes: HAL108483, isotypes: HAL108481, HAL108482, LE 00002138, B100375626).

**Paratype** China, Xinjiang, Urumqi, Yamalik Hill Forest Park, 43°47'26"N, 87°34'21"E, 1,027 m, 23.04.2009, *Schnittler, A. and J. Peterson*, 200918 (HAL108480).

Plants solitary, 10–20(–22) cm tall, one- or two flowered, covered with short silvery hairs. Bulbs of flowering plants 8–10 mm in diameter and 8–15 mm long, round to elongate, with a 2–7 cm long, dull grey brown tunic extending into a long neck, lower part densely covered by numerous sclerified roots. Flowering plants do not grow bulbils, strong vegetative plants with bulbils exceeding 3 mm in diameter seem to grow one bulbil per year. Bulbils 1.5–2.5 mm in diam., 2–3 mm long, half-droplet shaped and laterally compressed, often dormant within the old tunicae of the mother plant for several years. Peduncle 10.5–21.0 cm long, round in cross section, with a blunt abaxial rib, 0.5–1.3 mm in diameter, developing 3–4(–5) alternately arranged leaves (including these of the inflorescence). Basal leaf solitary, 11.5–21.5 cm in length, as long as the inflorescence or slightly exceeding it, 0.8–1.3 mm in diameter, cross-section round, caniculate, with an expanded

base. Stem leaves alternate, the lowermost originating close to the ground, the uppermost half as long as the inflorescence, the first 1.7–7.5 cm, the second 0.6–1.5 cm in length, cross-section superficially concave. Inflorescence with 1–2 flowers, the second flower often underdeveloped or absent. Perianth leaves lanceolate with obtuse tips, 10.0–15.0 mm long and 0.8–2.2 mm wide, inner side yellow, outer side greenish, at maturity of the capsule with pale translucent margins and greenish mid-ribs. Anthers yellow, linear, 3–4 mm long, after dehiscence nearly globose, 1 mm long. Style as long as the sessile ovary, 3.5–5.0 mm tall, stigma capitate. Capsule sessile, round to bluntly triangular, 7.0–10.5 mm long and 2.5–6.0 mm in diameter, seeds crescent shaped, pale brown, with warty surfaces (Fig. 2, Appendix 3 of Electronic supplementary material).

*Similar species* *Gagea alberti* Regel has a more diffuse (not narrow) inflorescence and develops usually 5–7 flowers, lateral flowers are much smaller.

The plant was found at two steppe remnants in the outskirts of Urumqi, with small populations comprising not more than 50 individuals. We thus did not attempt quantitative measurements. Due to extreme overgrazing in the foothills around Urumqi, further searches were not successful.

The plant is named in honor of its collector, Jens Peterson (Halle/Saale, Germany).

*Gagea huochengensis* Levichev sp. nov. [Sect. *Gagea*]

*Diagnosis* A *G. brevistolonifera* Levichev, *G. ancestralis* Levichev, *G. xiphoidea* Levichev bulbillo sessili solitario, a *G. praemixta* Vved. et *G. angelae* Levichev et Schnittler stolonibus nullis, a *G. turkestanica* Pascher bulbillo vegetativo rugoso-foveolato (nec levi), a *G. fedtschenkoana* inflorescentia candelabrifirmi differt.

*Type* China, Xinjiang, eastern Tian-Shan, Boro-Choro range, Huocheng, 2,100 m, 17.04.1975, n9801 (PE00152371).

*Paratypes* China, Xinjiang, Tian-Shan, Bogda-Shan, Heaven Lake (Tianchi Lake), 43°53'38"N, 88°06'59"E, 1,980 m, leg. Schnittler, A. and J. Peterson, 200922 (HAL108465, HAL108466); China, Xinjiang, eastern Tian-Shan, Sarmin-Ula range, Chabu-Chaer, 2,100 m, Huong, 21.04.1975, n9826 (PE00035649).

Plants solitary or in small groups, up to 7–10(–13) cm tall, glabrous. Bulbs oblique drop-shaped, 6–8 mm in diameter in flowering plants, tunic pale brown (clay-coloured), thin and coriaceous. Generative plants without bulbils; in juvenile plants and rarely in early generative

stages a single vegetative bulbil per year develops. Peduncle 0.5–3.5 cm tall, in section quadrangular, 0.3–0.8 mm in diameter, with a channel in young flowering plants that develop a bulbil, but lacking this channel in older flowering plants without bulbils. Basal leaf single, linear, exceeding the inflorescence by one-third, 2–3 mm wide, cross-section angular, with a rather strong keel. Leaves of the inflorescence 4–7, nearly opposite to each other, the floral leaf (the second basal leaf) concaulescent with the peduncle, slightly exceeding the inflorescence, 9–13 mm long and 2–5 mm wide, narrowly lanceolate, gradually tapering into a long tip, the upper part arching over, nearly glabrous, sometimes with sparsely ciliate hairs. Inflorescence with (3–)5–9 flowers, short branched, candelabrum-like, with pedicels of different length. Perianth leaves narrowly lanceolate, on the ends acuminate and hooded, 1–2 cm long and 1.5–2.5 mm wide, inside yellow, outside greenish, external whorl slightly larger than the internal whorl, the latter with yellow margins at the outer side. Ovary oblong, sessile. Anthers yellow, oblong, 3–3.5 mm long, rounded after dehiscence and 1.5 mm long. Capsule barely reaching more than half of perianth length, obovate, sessile. Seeds terete (Fig. 3).

*Similar species* Differing from *G. brevistolonifera* Levichev, *G. ancestralis* Levichev, and *G. xiphoidea* Levichev by a single sessile bulbil; from *G. praemixta* Vved. and *G. angelae* Levichev et Schnittler by the absence of stolons; from *G. turkestanica* Pascher (with smooth bulbils) by the wrinkled to alveolate bulbils; from *G. fedtschenkoana* Pascher and *G. angelae* by the candelabrous inflorescence.

The plant inhabits open, sunny areas and slopes with gravelly and deep soils near or above the timberline.

## Molecular results

### ITS data

The length of the ITS regions (ITS1+5.8S+ITS2) ranged between 613 and 623 bp (640 bp in *Tulipa cretica*). The final alignment was 655 bp in length, including 270 variable positions, of which 200 were parsimony informative (Table 2). In the ITS tree (Fig. 4) based on 110 ingroup taxa five major clades were resolved (clades A–E, 0.90–1.00 pp), all separated (1.00 pp) from the early branching *G. serotina* and *G. graeca*. All representatives of Sect. *Minimae* (1.00 pp) grouped together (clade A), but *G. confusa* was found in a separate sub-clade (A-2; 1.00 pp). Within sub-clade A-1 (0.92 pp) all 16 *G. nigra* samples (from Urumqi and Heaven Lake) clustered together, separated from the other representatives of the section: *G. minima*, *G. filiformis*, *G. davlianidzeae*, *G. granulosa*, but



**Table 2** Statistics for polymorphic informative sites of ITS (ITS1+5.5S+ITS2), *At103* and cpDNA (*trnL-trnF* IGS+*psbA-trnH*-IGS) sequences

Region	Group	Number of sequences	Number of sites		
			Total <sup>a</sup>	Variable	Parsimony informative
ITS	<i>Gagea</i> +outgroup	111	655	270	200
cpDNA	<i>Gagea</i> +outgroup	107	633	50	29
cpDNA	Sect. <i>Gagea</i>	38	433	14	9
cpDNA	Sect. <i>Minimae</i>	34	464	9	3
<i>At103</i>	Sect. <i>Gagea</i>	24	405	44	31
<i>At103</i>	Sect. <i>Minimae</i>	36	363	45	37

<sup>a</sup>Sites of gaps were excluded

samples of the latter two taxa assumed different positions within sub-clade A-1. However, all branches of this sub-clade have weak support (0.52–0.75 pp). All *G. liotardii* samples grouped together (1.00 pp, sub-clade B-1 in Fig. 4). Sub-clade B-2 (1.00 pp) included *G. ova* and *G. stipitata* (Sect. *Stipitatae*). Sub-clade C-2 (1.00 pp) aggregates all our samples of Sect. *Bulbiferae*, well separated from sub-clade C-1 which consists of species of Sects. *Graminifoliae*, *Platyspermum* and *Incrustatae*. Within the section *Bulbiferae* all *G. bulbifera* (samples 1A, 1 C from Xinjiang, 2 from Russia, and 3, 4 from Iran) clustered together (0.89 pp). The three *G. rufidula* accessions from Xinjiang clustered somewhat separate from *G. rufidula* (4) from Kyrgyzstan. Within the major clade D (1.00 pp) corresponding to Sect. *Gagea* all samples of *G. angelae*, *G. huochengensis*, *G. cf. xiphoidea* (Xinjiang), *G. xiphoidea*, as well as *G. ancestralis*, were identical. Within clade E (uniting representatives of Sect. *Plecostigma*, 1.00 pp), *G. pauciflora* was found as the nearest relative of the newly described *G. jensii* (samples from two populations; 1.00 pp, sub-clade E-1 in Fig. 4).

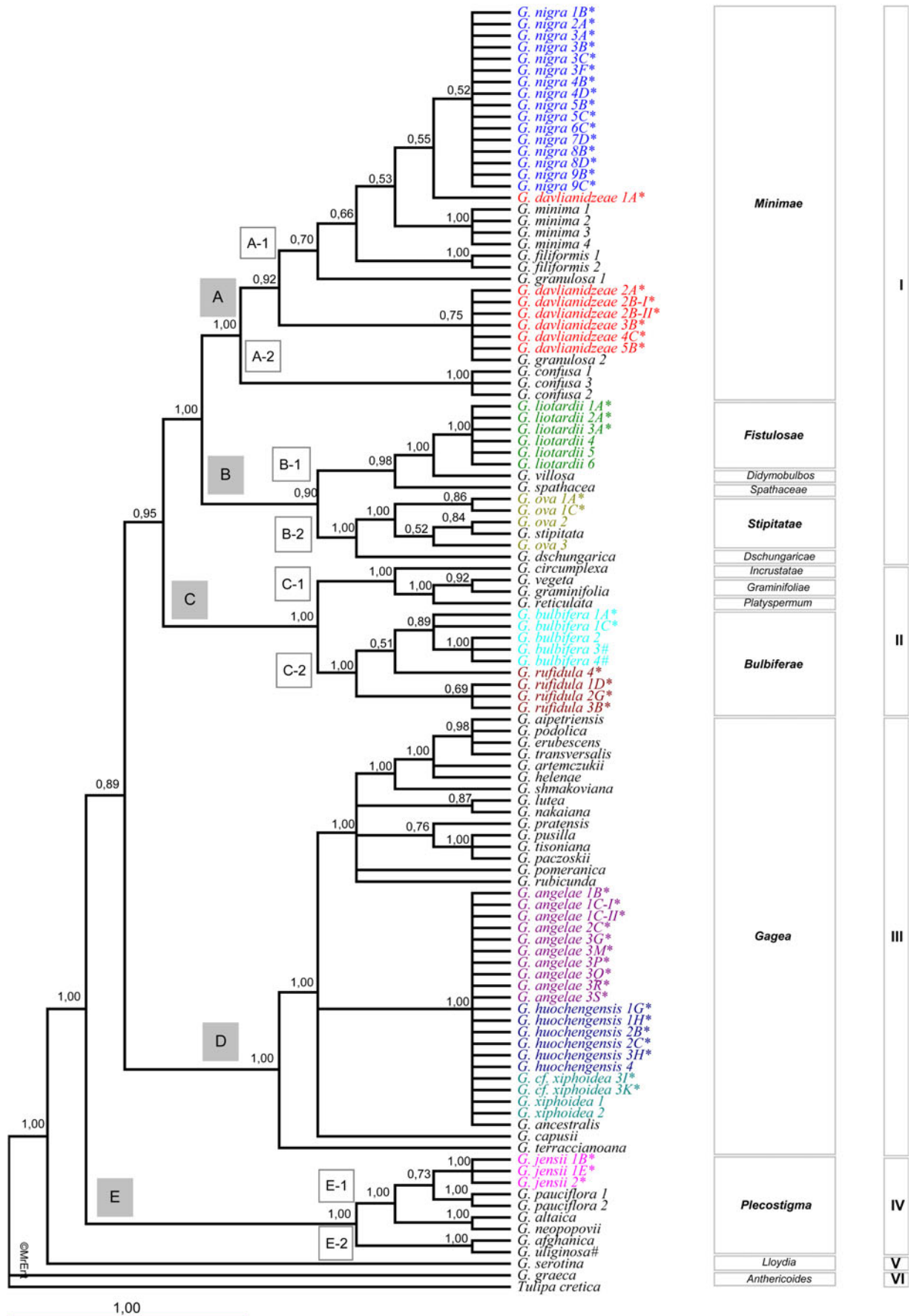
#### cpDNA data

The length of *trnL-trnF* IGS (including *T. cretica* as outgroup taxon) was 171–214 bp, the *psbA-trnH* IGS sequences ranged between 171 and 219 bp (360 bp in *T. cretica*). The final alignment (combined cpDNA data: *psbA-trnH* IGS+*trnL-trnF*-IGS) included 633 bp with 50 variable nucleotide positions, of which 29 were parsimony informative (Table 2). In the combined cpDNA tree based on 107 sequences six major clades (A–F, Fig. 5) with pp values between 0.83 and 1.00 pp were recognized. Clade A (0.99 pp) united representatives of Sect. *Minimae*; here all *G. nigra* fall into a polytomy. *Gagea granulosa* was found together with the latter species or with *G. davlianidzeae*. *Gagea filiformis*, *G. davlianidzeae*, *G. confusa* and *G. minima* were separated from *G. nigra*. Representatives of the Sect. *Stipitatae* (*G. ova*, *G. stipitata*) formed clade B (0.88 pp). The *G. liotardii* samples clustered (1.00 pp) in clade C (0.83 pp). Within clade D (1.00 pp) samples for

Sect. *Bulbiferae* (*G. bulbifera* and *G. rufidula*) are in sub-clade D-2 (0.79 pp) whereas sub-clade D-1 (1.00 pp) comprises species of Sects. *Graminifoliae*, *Platyspermum* and *Incrustatae*. In clade E (1.00 pp), representatives of Sect. *Plecostigma*, *G. jensii* and *G. pauciflora* formed a sub-clade (0.99 pp). Within the major basal clade F (0.91 pp) of Sect. *Gagea*, samples of *G. angelae*, *G. xiphoidea*, *G. cf. xiphoidea*, *G. huochengensis* and *G. ancestralis* grouped together in sub-clade F-2 (0.56 pp; see also cpDNA haplotype network, Fig. 8); *G. capusii* and *G. terraccianoana* were also assigned to this sub-clade.

#### Cloning data and networks of the low copy gene *pCOS At103*

Within representatives of Sect. *Gagea* of Xinjiang (see Tables 2 and 3) we found up to five intra-individual *At103* clones with an identity between 92 and 100%. In the Neighbour network of all clones (six clones of each *G. huochengensis* 1H, *G. angelae* 3 M, 3S and *G. cf. xiphoidea* 3I, data not shown) two distinct clades were recognized. Three clones formed a second clade (*G. cf. xiphoidea* 3I-a, d, *G. huochengensis* 1H-d). For the *At103* region of Sect. *Minimae* (see Tables 2 and 3) we differentiated up to five intra-individual *At103* clone variants in *G. nigra* (with 98–100% identity) and up to six in *G. davlianidzeae* (with 94–100% identity). In a neighbour network constructed for *G. davlianidzeae* and *G. nigra* (Fig. 6) all clones of *G. nigra* 4D (sample from Heaven Lake) form cluster I; all clones of *G. davlianidzeae* 3B, cluster II. All clones of *G. davlianidzeae* 1A, 2A, 2B, but also *G. nigra* from Urumqi (1B) were found at intermediate positions. However, the clones of *G. davlianidzeae* 2A assumed different intermediate positions, together with clones of *G. davlianidzeae* 2B, or between the latter and *G. nigra* 4D. The clones of *G. davlianidzeae* 1A were also found at two different intermediate positions; thereby four clones were closely related to *G. nigra* 1B. A relatively high number of substitutions (24–36, see Table 3) was found in *G. davlianidzeae* 2A, in *G. huochengensis* 1H and in *G. cf. xiphoidea* 3I.



**Fig. 4** General time reversible (GTR+ $\Gamma$  Bayesian Analyses (BA, 5 million cycles) of the internal transcribed spacer (ITS) region (ITS1+5.8SrdDNA+ITS2). The posterior probabilities for the clades are given above the nodes. Major clades and sub-clades are numbered. On the right side, the infrageneric classifications of *Gagea* according to Levichev (see Peterson et al. 2008; for *G. serotina* see Peruzzi 2008a and Introduction) and Zarrei et al. (2011a: I *Didymobulbos*, II *Platyspermum*, III *Gagea*, IV *Plecostigma*, V *Lloydia*, VI *Anthericoides*) are shown. Sequences of representatives of Xinjiang are indicated by an asterisk. # Sequences taken from EMBL/NCBI

#### cpDNA haplotype networks

For representatives of Sect. *Minimae* (Fig. 7, Table 2), including seven species, TCS calculated a 95% parsimony connection limit and a network of 20 haplotypes, with 11 as missing intermediate positions in the network. All samples of *G. davlianidzeae*, *G. nigra*, *G. confusa* and *G. minima* have a single haplotype. *Gagea nigra* was separated by at least one step from *G. granulosa*, and at least two steps from *G. filiformis*. The multiple haplotypes of *G. filiformis* and *G. granulosa* occupied different positions, separated by five (*G. filiformis*) or up to seven steps (*G. granulosa*).

For the representatives of Sect. *Gagea* (Fig. 8, Table 2), including 22 species, TCS calculated a 95% parsimony connection limit and showed a network of 44 haplotypes, with 30 of these as missing intermediate positions. Closest to the putative center of the network (each separated by two steps) were the haplotypes of *G. angelae*, *G. huochengensis*, *G. xiphoidea* (including *G. cf. xiphoidea*), *G. ancestralis*, and *G. capusii*. *Gagea angelae* was separated by one step from *G. xiphoidea* (including *G. cf. xiphoidea*). *Gagea huochengensis* was represented by two haplotypes, one (*G. huochengensis* 2B, 2 C, 3H) identical to *G. angelae*, the other (*G. huochengensis* 1 G, 1H, 4) identical to *G. xiphoidea*, *G. cf. xiphoidea* and *G. ancestralis*. On the outmost branches of the network *G. lutea* was separated by ten steps, *G. paczoskii* and *G. tisoniana* separated by 13 steps and *G. terraccianoana* separated by seven steps from the central position.

## Discussion

### New species of *Gagea* from Xinjiang

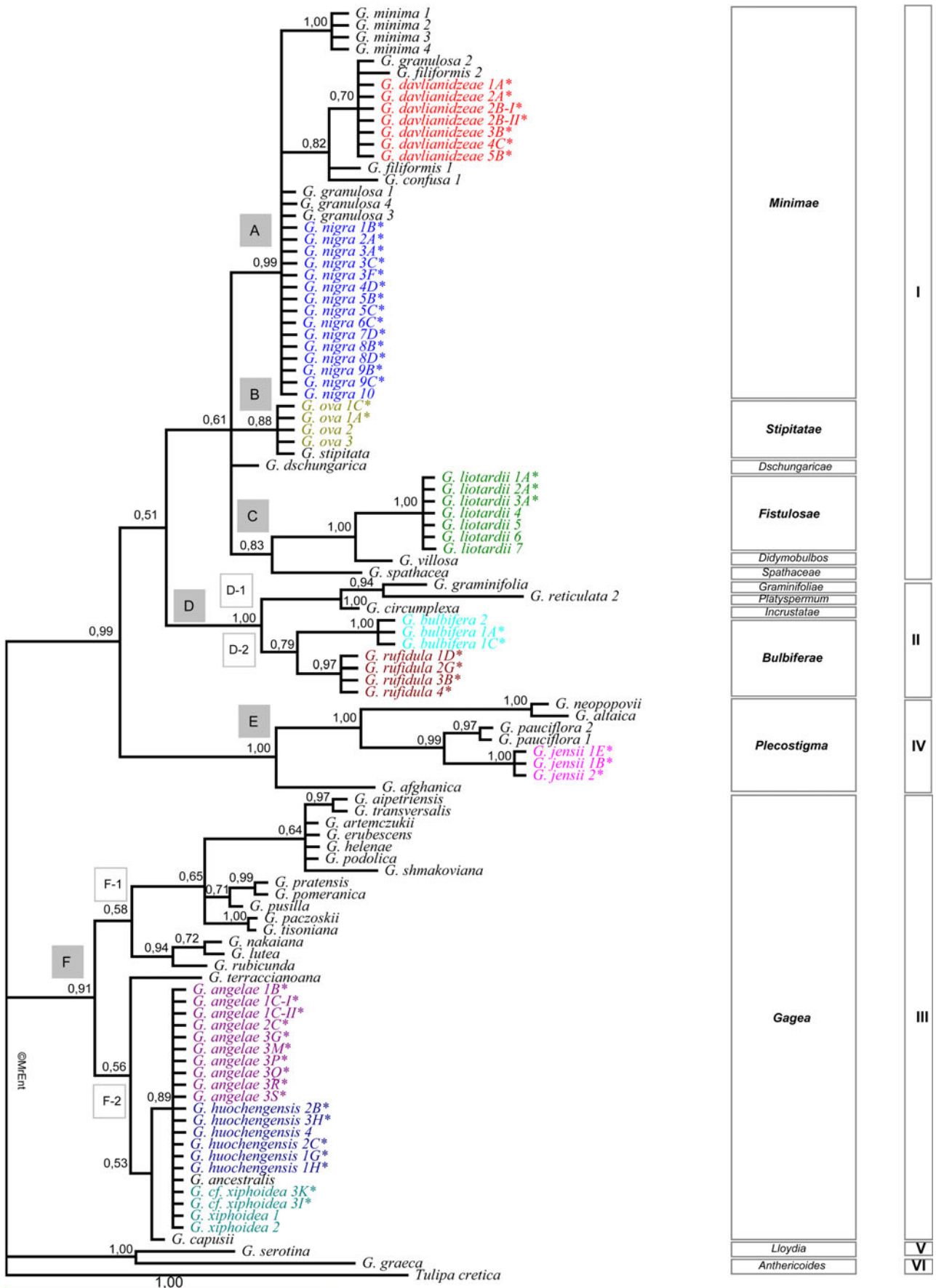
Three new species from the Chinese province of Xinjiang are described: *G. jensii* (Sect. *Plecostigma*), *G. angelae* and *G. huochengensis* (both Sect. *Gagea*). New for the region are *G. davlianidzeae* (Sect. *Minimae*) and *G. rufidula* (Sect. *Bulbiferae*). In addition, the existence of *G. bulbifera* (Sect. *Bulbiferae*), *G. nigra* (Sect. *Minimae*), *G. ova* (Sect. *Stipitatae*), and *G. liotardii* (Sect. *Fistulosae*) was confirmed for the province. These nine species represent five

different sections (according to Levichev in Peterson et al. 2008). Within Sect. *Bulbiferae*, *G. rufidula* differs from *G. bulbifera* by nodding flower buds and broader perianth leaves (*G. bulbifera* 0.8–1.8 mm; *G. rufidula* 2.0–3.2 mm); immature plants of *G. rufidula* develop clusters of bulbils around the replacement bulb. Representatives of Sect. *Minimae* (*G. nigra*: growing one bulbil per year; *G. davlianidzeae*: growing several bulbils per year) and of Sect. *Gagea* (*G. huochengensis*: producing a sessile single bulbil; *G. angelae*: producing a stolon of 1.5–5 cm length with a group of bulbils at its tip) differ as well by vegetative features.

In the Tian-Shan region, taxa of the Sect. *Gagea* frequently occur in mixed populations, and a species with many flowering plants may be associated with a second represented by juvenile plants only. For example, for *G. cf. xiphoidea* we did not find corresponding generative samples. These plants may represent a further species differing from *G. xiphoidea* (Levichev 2001) by its vegetative features (with a short stolon of 0.7–1.3 cm length and two bulbils at the opposite sites of the stolon).

Except for the representatives of Sect. *Gagea*, all species can be distinguished by their ITS and/or cpDNA sequences. We encountered numerous cases of polytomy within the Sect. *Gagea* (Figs. 4 and 5): *G. paczoskii* and *G. tisoniana* (see also Peruzzi et al. 2008b); or *G. podolica* and *G. erubescens*. Polytomy was also found in the *G. reticulata* species complex of Sect. *Platyspermum* (Zarrei et al. 2010d) or within Sect. *Didymobulbos* (Peruzzi et al. 2008b). Several further examples where morphologically differentiated species shared identical chloroplast regions (e.g. Jakob and Blattner 2006; *Hordeum*) or ITS regions (Gurushidze et al. 2008; *Allium*) can be found in the literature.

In contrast to its original description, *Gagea nigra* (Sect. *Minimae*) grows a single vegetative bulbil in all stages of ontogenesis except for seedlings; the sometimes extremely large plants possess a flat, rather fleshy basal leaf. Since the number of vegetative bulbils formed within different stages of ontogenesis is highly diagnostic for the genus, we emended the description of *G. nigra* at this point. One isotype of *G. nigra* investigated by us (Urumqi, at the northern fringe of the city, Bad-Shan-Di, 900 m a.s.l., leg L. Z. Shue) corresponds in all morphological characters to our material from Xinjiang (samples from Urumqi and Heaven Lake). In spite of large variations in size, leaf width and number of flowers, all samples from *G. nigra* from Urumqi and Heaven Lake were found to be molecularly uniform but to differ from both *G. filiformis* and *G. davlianidzeae*. The morphological variability encountered within *G. nigra* could be due to a hybridogenous origin, but is more likely caused by the different habitats colonized, ranging from steppe to alpine meadows.



**Fig. 5** F81+I+Γ Bayesian Analyses (BA, 9 million cycles) of the cpDNA (*psbA-trnH* IGS+*trnL-trnF* IGS). The posterior probabilities for the clades are given above the nodes. Major clades and sub-clades are numbered. For infrageneric classifications shown on the right side, cf. Fig. 4. Sequences of representatives of Xinjiang are marked by an asterisk

The correct name for *G. liotardii* is still under debate (named *G. fragifera* by Bayer and López González 1989; see e.g., Tison 2001; Zarrei et al. 2011a but *G. liotardii* by Levichev 2006a; Gutermann 2009). The taxonomic status of *Gagea ova* has also been questioned. According to Zarrei et al. (2007), the latter taxon is considered as a synonym of *G. stipitata*, and *G. stipitata* was seen as synonymous with *G. kunawurensis* (Zarrei et al. 2011b). Morphological studies of these species (I.G.L. unpublished data) do not support the suggestions made by Zarrei et al. (2007, 2011b). *G. kunawurensis* is morphological clearly differentiated from *G. ova* and *G. stipitata* by the absence of sclerified roots. *Gagea ova* is characterized by small, white- to straw-coloured perianth leaves, black tunicae and densely crowded groups of bulbils in all stages. In *G. stipitata*, perianth leaves are brilliant yellow, tunicae are brown; juvenile plants possess loose groups of bulbils, adult ones develop only a single bulbil.

#### Evolution and speciation in Sect. *Gagea*

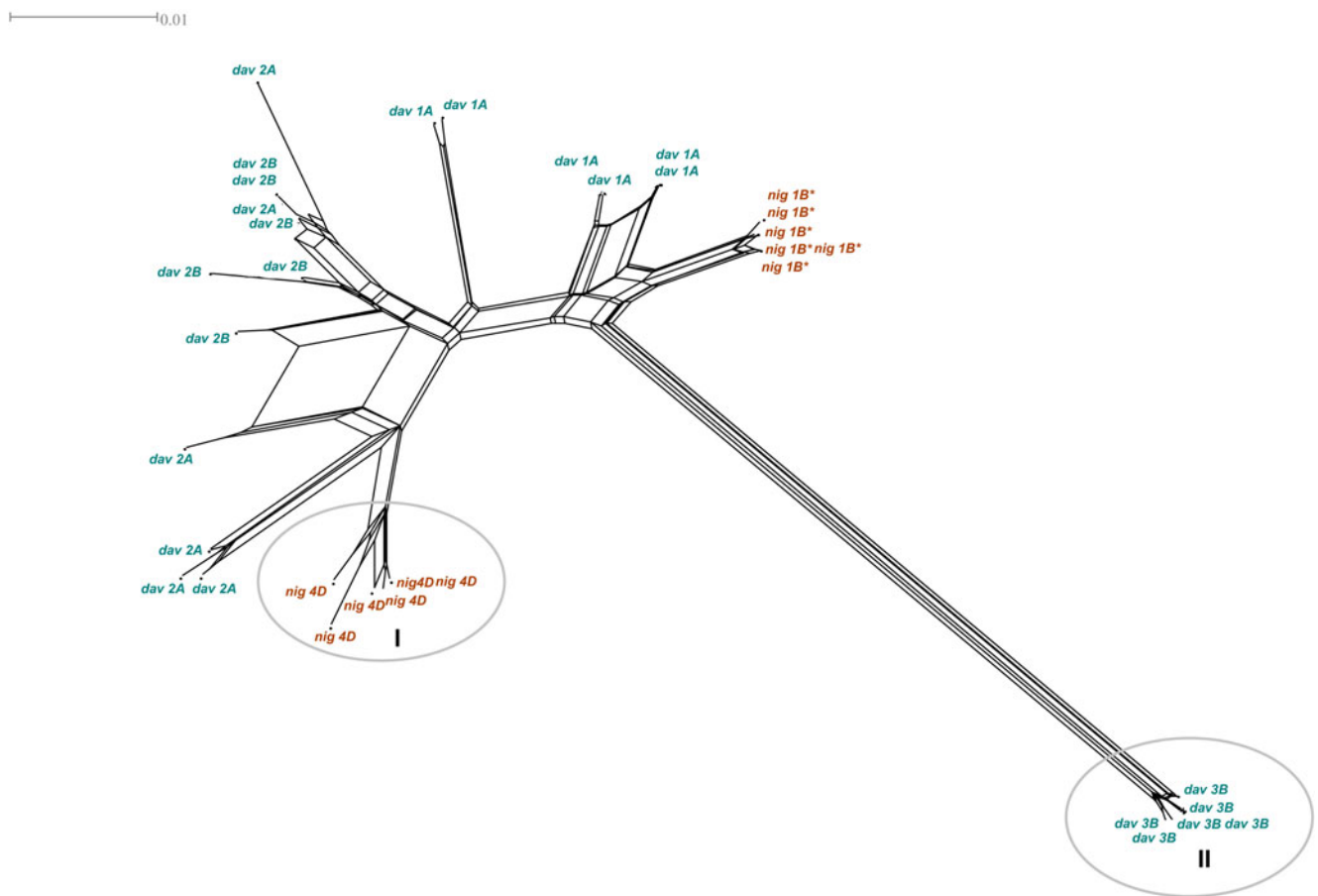
According to our nrDNA data and cpDNA haplotype network, we hypothesize that *G. angelae*, *G. huochengensis* and *G. cf. xiphoidea* have had gene flow over a long period with a common origin. The combined cpDNA data resulted in one haplotype each for *G. angelae* and *G. xiphoidea* (including *G. cf. xiphoidea*). However, the samples of *G.*

*huochengensis* matched both types, indicating the hybridogenic origin of the latter. In addition, at the the 3' end of the *psbA* gene (5'>STNG3') we found a mutation for asparagine ("AAT" in *G. ancestralis*, *G. huochengensis* 1 G, 1H, *G. xiphoidea* and *G. cf. xiphoidea*, and "AAC" in all other representatives of Sect. *Gagea*). Asparagine at this position seldom occurs in *Gagea* (e.g., *G. chlorantha*: EU939231) but is always present as "AAT" in the genera *Tulipa* (e.g., *T. cretica*: AM49257; *T. chusiana*: AM085140) and *Lilium* (e.g., *L. candidum*: AJ431692). This mutation appears to be symplesiomorphic.

According to our cpDNA haplotype network (Fig. 8) *G. angelae*, *G. huochengensis*, *G. ancestralis*, *G. xiphoidea* and *G. capusii* form a basal group of taxa. All these Central Asian species are separated from the putative center of the network by two steps. Species distributed outside Central Asia, such as *G. lutea* (Europe, Mediterranean region, southwestern Asia), *G. nakaiana* (eastern Asia), *G. aipe-triensis* (Crimea), and *G. paczoskii* (Europe) occur at the tips of the network. This agrees with the low degree of neotonical divergence in *G. ancestralis*, a species from the Altai Mountains, which could be the putative progenitor for *G. lutea*, *G. nakaiana* and other taxa of this section within Eurasia (Levichev and Maassoumi 2005). Adult plants of this species possess flat bifacial basal and floral leaves without unifacial leaf tips. In addition, cpDNA (Fig. 4) and ITS (Fig. 5) trees placed *G. capusii* and *G. terraccianoana* on basal positions in the clade including *G. ancestralis*, *G. angelae*, *G. huochengensis* and *G. xiphoidea*. According to ITS data of Sect. *Gagea* (see Peterson et al. 2009) three major clusters were detected in the NN: one of these included most of the diploid species, whereas the other two included both diploids and polyploids. *G. capusii* and *G. terraccianoana* formed the diploid cluster (see Peterson et al. 2009).

**Table 3** Statistics of intra-individual *At103* variability in *G. nigra*, *G. davlianidzeae*, *G. huochengensis*, *G. angelae* and *G. cf. xiphoidea* specimens from Xinjiang

Species	code	Length variants (bp)	Identity	Number of Genotypes	Substitutions	Indels
Sect. <i>Minimae</i>						
<i>G. nigra</i>	1B	396	99–100%	3	2	–
<i>G. nigra</i>	4D	433, 434, 435	98–100%	5	6	1
<i>G. davlianidzeae</i>	1A	397, 433	96–100%	5	13	2
<i>G. davlianidzeae</i>	2A	420, 454, 461	94–99%	6	24	3
<i>G. davlianidzeae</i>	2B	453, 454, 456, 461	97–100%	6	15	2
<i>G. davlianidzeae</i>	3B	428	99–100%	2	2	–
Sect. <i>Gagea</i>						
<i>G. huochengensis</i>	1H	425, 434	92–100%	5	33	3
<i>G. angelae</i>	3S	418, 434	98–100%	5	9	1
<i>G. angelae</i>	3 M	418, 434, 495	96–100%	4	14	3
<i>G. cf. xiphoidea</i>	3I	425, 434	92–100%	5	36	3



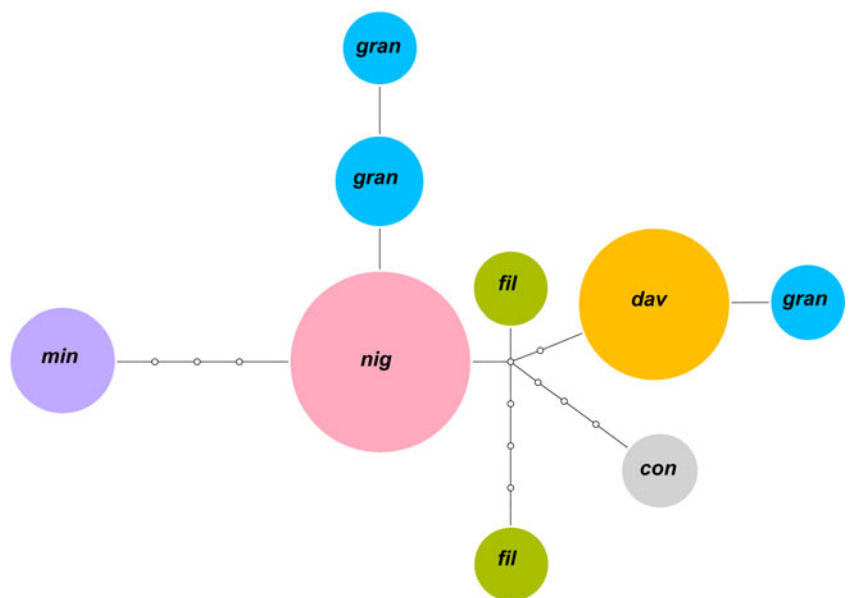
**Fig. 6** Neighbor net (NN) splits graph of pCOS *At103* clones of *G. davlianidzeae* 1A, 2A, 2B, 3B (dav) and *G. nigra* 1B, 4D (nig) of *Gagea* sect. *Minimae*. For further taxon information see Appendix 1.

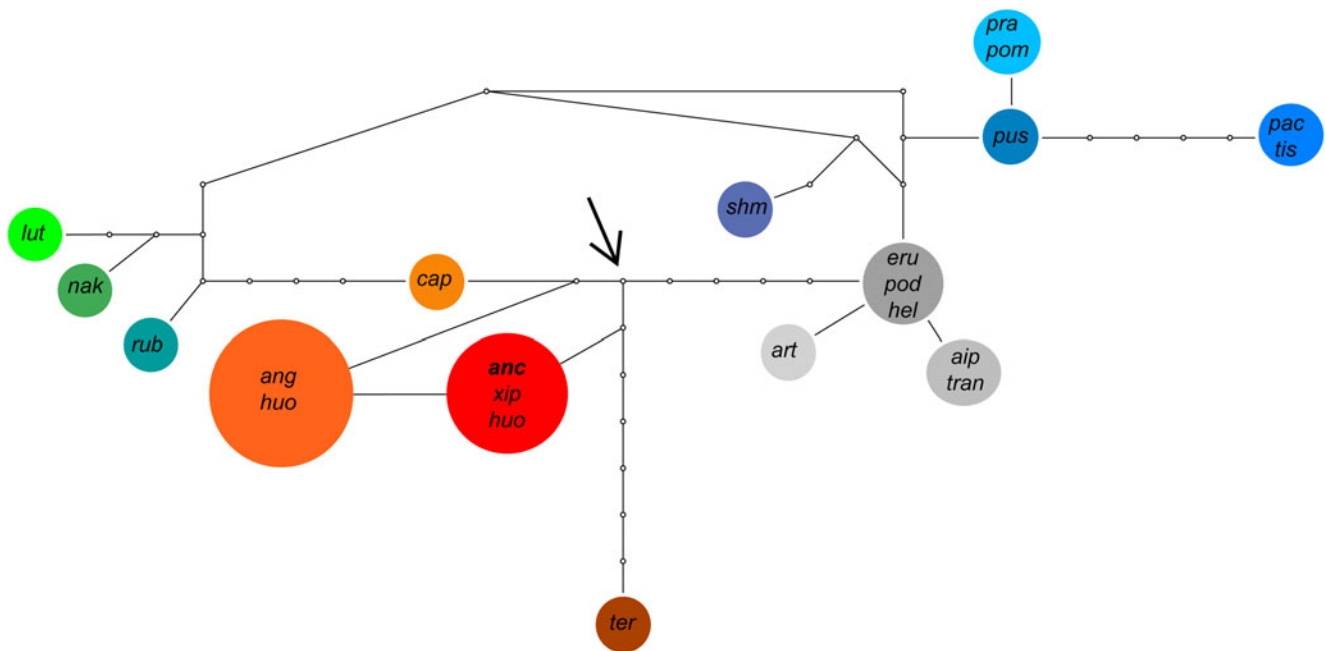
Edge lengths are proportional to the uncorrected p-distances. Clusters are labelled (I–II). Clones of *G. nigra* from Urumqi (1B) are indicated by an asterisk

We hypothesize that speciation and evolution of sect. *Gagea*, colonizing large areas of temperate Eurasia, was

influenced by mainly migration and subsequent polyploidization, hybridization, and introgression (discussed in

**Fig. 7** Haplotype network for 20 cpDNA haplotypes (*psbA-trnH* IGS+*trnL-trnF* IGS) including 33 sequences of representatives of *Gagea* sect. *Minimae*: *G. confusa* (con), *G. davlianidzeae* (dav), *G. filiformis* (fil), *G. granulosa* (gran), *G. minima* (min), and *G. nigra* (nig, for further details, see Appendix 1 and Table 2). Circle size corresponds to the number of taxa possessing the haplotype. Empty circles refer to missing intermediates not found in the analyzed sequences





**Fig. 8** Haplotype network for 44 cpDNA haplotypes (*psbA-trnH* IGS+*trnL-trnF* IGS) including 38 sequences of representatives of *Gagea* sect. *Gagea*: *G. aipetriensis* (aip), *G. ancestralis*, *G. angelae* (ang), *G. artemczukii* (art), *G. capusii* (cap), *G. erubescens* (eru), *G. helenae* (hel), *G. huochengensis* (huo), *G. lutea* (lut), *G. nakaiana* (nak), *G. paczkoskii* (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. xiphoidea* and *G. cf. xiphoidea* (xip, for further details see Appendix 1 and Table 2). Circle size corresponds to the number of taxa possessing the haplotype. Empty circles refer to missing intermediates not found in the analyzed sequences. The putative ancestral haplotype is indicated by an arrow. *Gagea ancestralis* as the putative progenitor for all other Eurasian taxa of this section is indicated in bold

Peterson et al. 2009), and that recent speciation is in progress.

#### Hybridization drives speciation in Sect. *Minimae*

In the region around Heaven Lake we found large populations with thousands of individuals of *G. nigra* co-occurring with *G. davlianidzeae*, although the latter is more shade-tolerant. For this study, we could clearly delimit *G. davlianidzeae* and *G. nigra* using cpDNA and ITS data, but we also found strong evidence for gene flow and hybridization between both taxa. The putative hybrid plant *G. davlianidzeae* 1A assumed an intermediate position in the ITS tree (Fig. 4) and the At103 Neighbour net (Fig. 6) although it could not be morphologically differentiated from other samples of *G. davlianidzeae*. Although the capsules did not reach maturity at the time of our field studies, seeds in *G. davlianidzeae* appeared aborted—an indication of its putative hybridogenic origin presumably accompanied by polyploidization. In our study, *G. elegans* (2889 LE; India, Punjab, Bashar State, Simla district, 3,400 m) corresponded in the *trnL-trnF* IGS (FR690255) to *G. nigra*. *Gagea davlianidzeae* was found on different positions in the ITS tree, thus indicating its possible hybridogenic origin. In the cpDNA tree *G. granulosa* was found with different haplotypes, similar to *G. nigra* or to *G.*

*davlianidzeae*. Our cpDNA haplotypes display sometimes morphologically different taxa sharing the same haplotype (*G. nigra* and *G. elegans*), but also single species with multiple haplotypes (e.g., *G. granulosa*, *G. filiformis*). This provides further evidence for hybridization between representatives of this section. Several species of this section were found with different ploidy levels probably caused by hybridization, such as *G. granulosa* with  $2n=24$  and 72 chromosomes, or *G. elegans* with  $2n=72$ , 96 chromosomes (see literature cited in Peruzzi 2003, 2008b). The species complex of *G. elegans*, *G. filiformis* and *G. granulosa* (all belonging to Sect. *Minimae*) is taxonomically difficult (e.g., Pascher 1904, 1905, 1907; Terracciano 1905–1906; Vvedensky 1971; Dasgupta and Deb 1986; Levichev 1990; Ali and Levichev 2007). Morphological studies revealed many intergrading forms. Several species of Sect. *Minimae* occur frequently sympatric, for example *G. granulosa*, *G. filiformis* and *G. davlianidzeae* in the Dshungarian region, *G. davlianidzeae* and *G. lowariensis* in the Himalayas, or *G. filiformis*, *G. davlianidzeae* and *G. lowariensis* in the Tian-Shan range (Ali and Levichev 2007; I. G.L. personal observation), and *G. nigra* and *G. davlianidzeae* in Xingjiang (this study).

For a better understanding of speciation via hybridization it would be desirable to estimate the relative impor-

tance of sexual and asexual reproduction in different taxa and to prove if hybrids are capable of sexual reproduction by carrying out comparative studies using genotyping methods like AFLP (Pfeiffer et al. 2011).

#### New insights into infrageneric classification

Molecular analyses of further representatives of Sects. *Minimae* and *Bulbiferae* provide further evidence to separate these sections. Therefore we do not agree with Zarrei et al. (2011a) to include Sect. *Bulbiferae* within Sect. *Platyspermum* and Sect. *Minimae* in a major Sect. *Didymobulbos* (see also Table 1). Molecular data from *G. rufidula* and *G. bulbifera* confirm the monophyly of Sect. *Bulbiferae* (ca. 7 species; Levichev in Peterson et al. 2008). Anatomical characters (Zarrei et al. 2010c) also do not support the placement of *G. bulbifera* within Sect. *Platyspermum*.

Species of Sect. *Minimae* (ca. 8 species, Levichev in Peterson et al. 2008; Levichev and Jezniakowsky 2008) share a similar ontogeny. The isolation of this section within *Gagea* agrees with our molecular data (see also Peterson et al. 2008). The monophyly of the proposed Sect. *Didymobulbos* sensu Zarrei et al. (2011a) is supported only by ITS data and not by cpDNA data, which confirms results of this study and that of Peterson et al. (2008). The Sects. *Minimae* and *Bulbiferae* are also accepted by Peruzzi et al. (2008a, 2011). In contrast, the inclusion of Sect. *Fistulosae* within Sect. *Didymobulbos* suggested by Peruzzi et al. (2008a, 2011) is in agreement with our opinion (except for Levichev) and supported by molecular results (Peterson et al. 2008; 2009; Peruzzi et al. 2008a, b, 2011).

Except for the position of Sects. *Plecostigma* and *Gagea*, trees based on ITS and cpDNA data are in agreement. However, in the cpDNA tree proximal branches were sometimes insufficiently resolved. To produce a sound infrageneric classification, both further markers (e.g. pCOS *At103*) and the inclusion of a higher number of representatives from all suggested sections of the genus are essential.

#### Conclusion

Our results support the hypothesis that, beside the Pamir Alai and western Tien-Shan, the eastern Tian-Shan represents a third region of high, but yet insufficiently documented species diversity and that, also in this region, lowland areas are less species-rich than mountainous ones (see Levichev 1999a).

Hybridization is evident in several sections of *Gagea* (here shown for Sect. *Minimae*) and speciation is in process, thus complicating the delimitation of species (see also discussion in Peterson et al. 2009). Field studies,

examining the morphology of fresh plants from all life stages together with molecular investigations are essential to detect hybrid taxa and to determine species borders (see also Peruzzi et al. 2008a, 2011; Peterson et al. 2010).

We confirm the high potential of network analyses to display the relationship between closely related taxa of *Gagea* (see also Peterson et al. 2009, 2010; Peruzzi et al. 2011). Our haplotype network of Sect. *Gagea* indicates that the European species of this section have their origin in Central Asia, which is also supported by the morphological investigations of Levichev and Maassoumi (2005).

Since biparentally inherited ribosomal markers (often undergoing concerted evolution), but also uniparentally inherited plastide markers, have limitations for phylogenetic studies (e.g., Jakob and Blattner 2006; Álvarez and Wendel 2003). Recent studies have aimed to identify single copy nuclear genes with a high phylogenetic potential (reviewed in Li et al. 2008 and Duarte et al. 2010). In our study, the results of such a gene region (pCOS *At103*) were in agreement with the results of ITS and cpDNA data.

**Acknowledgments** We are grateful for the logistical support of the group of Nurbay Abdusalih, Institute of Natural Resources and Environment, Xinjiang University. Anne Petzold and Gymeniaz Saidahmet helped with field work. Niels Thevs kindly provided the translation of the Chinese description of *G. nigra*. Petra Oswald (IPK Gatersleben) is gratefully acknowledged for cloning and sequencing *At103*. We are grateful to M. Zarrei for providing *Gagea* material from Iran. Morphological research was supported by the Russian Foundation of Basic Research (grant 08-04-00670 to I.G.L.). We also thank three anonymous reviewers for very detailed and helpful comments.

#### Appendix 1

Sources of the studied material and EMBL/NCBI accession numbers. **Taxon** (sample code)<sup>a</sup>: origin: voucher: (number of collection site)<sup>b</sup>: *trnL-trnF* IGS, *psbA-trnH* IGS, ITS region: ITS1+5.8SrDNA+ITS2, pCOS *At103* region (#sequences taken from EMBL/NCBI)

*Gagea afghanica* A. Terracc.: Iran, Province Khorasan: 52/04DNALevichev (LE)/ HAL101785: (Zarrei & Ajani 830): AJ890373, AJ973160, AM087953, -. *G. aipetriensis* Levichev: Ukraine, Crimea: 15/04DNALevichev (LE), HAL01801: AJ970178, AM049259, AM087955, -. *G. altaica* Schischk. & Sumnev.: Kazakhstan: 51/04DNALevichev (LE), HAL101786: AJ890374, AJ973159, AM162670, -. *G. ancestralis* Levichev: Russia, Republic Altai: 144/10DNA Levichev (LE): FR690249, FR690844, FR691052, -. *G. artemczukii* Krasnova: Ukraine, Crimea: 19/04DNALevichev (LE), HAL101481: AM180470, AM409339, AM409331, -. *G. angelae* Levichev et Schnittler sp. nov.: (1B): China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'38" N, 88°06'59"E, 1,980 m: LE 00002135: (200913): FR690259, FR691028, FR690104, -. (1 C-I): China,



- Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'38"N, 88°06'59"E, 1,980 m: HAL108470: (200913, generative sample): FR690260, FR691029, FR690105, -. (1 C-II): China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'38"N, 88°06'59"E, 1,980 m: HAL108470: (200913, vegetative sample): FR690261, FR691030, FR690106, -. (2 C): China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°50'17"N, 88°10'15"E, 2,250 m: HAL108477: (200914): FR690262, FR691031, FR690107, -. (3 G): China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'31"N, 86°06'02"E, 2,173 m: HAL108476: (200915): FR690263, FR691032, FR690108, -. (3 M): China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'31"N, 86°06'02"E, 2,173 m: HAL108475: (200915): FR690264, FR691033, FR690109, FR691334-FR691339 (3P) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'31"N, 86°06'02"E, 2,173 m: HAL108474: (200915): FR690265, FR691034, FR690110, -. (3Q) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'31"N, 86°06'02"E, 2,173 m: HAL108473: (200915): FR690266, FR691035, FR690111, -. (3R) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'31"N, 86°06'02"E, 2,173 m: HAL108472: (200915): FR690267, FR691036, FR690112, -. (3S) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'31"N, 86°06'02"E, 2173 m: HAL108471: (200915): FR690268, FR691037, FR690113, FR691328-FR691333. *G. bulbifera* (Pall.) Salisb.: (1A) China, Xinjiang, Urumqi, Yamalik Hill Forest Park, 43°48'00"N, 87°34'51"E, 942 m: HAL107953: (200930): FR690234, FR690829, FR689753, -. (1 C) China, Xinjiang, Urumqi, Yamalik Hill Forest Park, 43°48'00"N, 87°34'51"E, 942 m: HAL107952: (200930): FR690235, FR690830, FR689754, -. (2) Russia, District Astrakhan: 2/04DNALevichev (LE), HAL101840: AJ969119, M049260, AM162669, -. (3)<sup>#</sup> Iran: Zarrei & al. TUH-E BOT.EXP. 35713 (TUH)(Kew 23140): -, -, EU912027, -. (4)<sup>#</sup> Iran: Zarrei & al. TUH-E BOT.EXP. 35709 (TUH)(Kew 23166): -, -, EU912028, -. *G. capusii* A. Terracc.: Uzbekistan: 24/04DNALevichev (LE), HAL101839: AJ969123, AM085143, AM422455, -. *G. chlorantha* (Bieb.) Schult. et Schult. f. <sup>#</sup>: -: -, EU939231, -, -. *G. circumplexa* Vved.: Uzbekistan: 30/04DNALevichev (LE), HAL101795: AJ969122, AJ973172, AM265529, -. *G. confusa* A. Terracc.: (1) Iran, Tehran: 13/04DNALevichev (LE), HAL101803: AJ890369, AJ973173, AM087949, -. (2)<sup>#</sup>Iran: Zarrei & Zarrei 35266 (TUH)(Kew 23137): -, -, EU912040, -. (3)<sup>#</sup>Iran: TUH-E BOT.EXP. 35712 (TUH)(Kew 23169): -, -, EU912041, -. *G. davlianidzeae* Levichev: (1A) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'52"N, 88°08'08"E, 1,928 m: HAL107948: (200925): FR690236, FR690831, FR689755, FR691346-FR691351 (2A) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°50'17"N, 88°10'15"E, 2,250 m: HAL107946: (200926): FR690237, FR690832, FR689756, FR691352- FR691357 (2B-I) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°50'17"N, 88°10'15"E, 2,250 m: HAL107945: (200926): FR690238, FR690833, FR689757, -. (2B-II) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°50'17"N, 88°10'15"E, 2,250 m: HAL107945: (200926): FR690239, FR690834, FR689758, FR691358-FR691363 (3B) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'51"N, 88°07'51"E, 1,928 m: HAL107943: (200927): FR690240, FR690835, FR689759, FR691364- FR691369. (4 C) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°54'44"N, 88°07'00"E, -: HAL107941: (200928): FR690241, FR690836, FR689760, -. (5B) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°54'15"N, 88°06'51"E, -: HAL107939: (200929): FR690242, FR690837, FR689761, -. *G. dschungarica* Regel: Kyrgyzstan: 14/04DNALevichev (LE), HAL101802: AJ970175, AJ973164, AM087952, -. *G. elegans* Wall. ex D. Don in Royle: India, Punjab, Bashar State, Simla District: 2889 (LE): FR690255, -, -, -. *G. erubescens* (Besser) Besser: Ukraine, near Charkow: 25/04DNALevichev, G-103 (LE), HAL103861: AM180469, AM238516, AM493953, -. *G. filiformis* (Ledeb.) Kar. et Kir.: (1) Kazakhstan: 12/04DNALevichev (LE), HAL101804: AM084904, AM161459, AM180457, -. (2) Western Tian-Shan, 1550 m: 72/09DNALevichev (LE): FR690250, FR690845, FR689768, -. *G. graeca* (L.) Irmisch.: Greece, Crete, Ori Thriptis, HAL105185: AM939645, AM939648, AM939649, -. *G. graminifolia* Vved.: Kyrgyzstan, 114/09DNALevichev (LE): FR690251, FR690846, FR689769, -. *G. granulosa* Turcz.: (1) 11a/04DNALevichev (LE), HAL101805: AM180462, AM238518, AM265533, -. (2) Kazakhstan: 11b/04DNALevichev (LE), HAL101836: AM180463, AM238517, AM287278, -. (3) Ukraine, Poltava: 100/09DNALevichev (LE): FR690252, FR690847, -, -. (4) Russia, Sibiria, near Tomsk: 141/09DNALevichev(LE): FR690253, FR690848, -, -. *G. helenae* Grossh.: Russia, Dagestan: 22/04DNALevichev (LE), HAL101798: AJ969120, AM161461, AM265531, -. *G. huochengensis* Levichev sp. nov.: (1 G) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'38"N, 88°06'59"E, 1,980 m: HAL108466: (200922): FR690269, FR691038, FR690114, -. (1H) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'38"N, 88°06'59"E, 1,980 m: HAL108465: (200922): FR690270, FR691039, FR690115, FR691322-FR691327. (2B) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°50'17"N, 88°10'15"E, 2,250 m: HAL108467: (200923): FR690271, FR691040, FR690116, -. (2 C) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°50'17"N, 88°10'15", 2,250 m: HAL108469: (200923): FR690273, FR691043, FR690119, -. (3H) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'31"N, 86°06'02"E, 2,173 m: HAL108468: (200924): FR690272, FR691041, FR690117, -. (4) Kazakhstan, 1,550 m: 132/09DNALevichev (LE),

- HAL107949: FR690274, FR691042, FR690118, -. *G. jensii* Levichev et Schnittler sp. nov.: (1B) China, Xinjiang, Urumqi, hills near cemetery, 43°43'53"N, 87°35'46"E, 987 m: HAL108482: (200917): FR690256, FR691025, FR690101, -. (1E) China, Xinjiang, Urumqi, hills near cemetery, 43°43'53"N, 87°35'46"E, 987 m: HAL108483: (200917): FR690257, FR691026, FR690102, -. (2) China, Xinjiang, Urumqi, Yamalik Hill Forest Park, 43°47'26"N, 87°34'21"E, 1,027 m: HAL108480: (200918): FR690258, FR691027, FR690103, -. *G. liotardii* (Sternberg) Schult. et Schult. f. (= *G. fragifera* (Vill.) Ehr. Bayer & G. López González): (1A) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°50'54"N/ 88°09'47"E, 2,146 m: HAL107898: (200919): FN868226, FN868198, FN868162, -. (2A) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°50'17"N/ 88°10'15"E, 2,250 m: HAL107896: (200920): FN868227, FN868199, FN868163, -. (3A) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°58'10"N/ 88°05'28"E, 2,350 m: HAL107894: (200921): FN868228, FN868200, FN868164, -. (4) Bulgaria, Pirin Mountains: HAL070407: AJ890368, AJ973158, AM162677, -. (5) Kazakhstan: 29b/04DNA Levichev (LE), HAL101796: AM161467, AM238521, AM180455, -. (6) Ukraine, Crimea: 29a/04DNA Levichev (LE), HAL101797: AM161466, AM238522, AM265532, -. (7) Switzerland, Canton Graubünden: ZT10726: AJ890375, AM238531, -. *G. lutea* Ker Gawl.: Germany, Saxony-Anhalt: -: AJ419165, AJ416368, AJ427544, -. *G. minima* (L.) Ker Gawl.: (1) Italy, Calabria (Pollino Massif), 1,860 m: CLU 12698: AM283109, AM282996, AM287273, -. (2) Ukraine, Carpathians: 9/04DNA Levichev (LE), HAL101808: AM238539, AM238524, AM087948, -. (3) Russia, Republic Tatarstan, Nizhnyaya Kama: 10/04DNA Levichev (LE), HAL101806: AM180471, AM238519, AM180459, -. (4) Germany, Saxony-Anhalt: -: AJ419164, AJ416374, AJ427546, -. *G. nakaiana* Kitag.: Russia, Khabarovsk Territory: 17/04DNA Levichev/55 (LE), HAL101799: AM110256, AM161457, AM180454, -. *G. neopopovii* Golosk.: Eastern Kazakhstan, Za-Iliskii Altai: 120/09DNA Levichev (LE): FR690254, FR690849, FR689770, -. *G. nigra* L.Z. Shue, emend. Schnittler: (1B) China, Xinjiang, Urumqi, 43°43'53"N, 87°35'46"E, 987 m: HAL108464: (200904): FR690123, FR691010, FR690081, FR691056-FR691061. (2A) China, Xinjiang, Urumqi, 43°38'50"N, 87°39'04"E: HAL108462: (200905): FR690124, FR691011, FR690082, -. (3A) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'27"N, 88°06'46"E: HAL108459: (200906): FR690125, FR691012, FR690083, -. (3B) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'27"N, 88°06'46"E: HAL108458: (200906): -, -, FR690084, -. (3 C) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'27"N, 88°06'46"E: HAL108181: (200906): FR690126, FR691013, FR690085, -. (3 F) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'27"N, 88°06'46"E: HAL108182: (200906): FR690127, FR691014, FR690086, -. (4B) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'31"N, 88°06'02"E, 2,173 m: HAL108461: (200931) -, -, FR690087, -. (4D) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'31"N, 88°06'02"E, 2,173 m: HAL108460: (200931): FR690128, FR691015, FR690088, FR691062-FR691067. (5B) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°52'35"N, 88°07'41"E, 1,950 m: HAL108456: (200907): FR690129, FR691016, FR690089, -. (5 C) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°52'35"N, 88°07'41"E, 1,950 m: HAL108455: (200907): FR690130, FR691017, FR690090, -. (6 C) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°50'17"N, 88°10'15"E, 2,250 m: HAL108183: (200908): FR690131, FR691018, FR690091, -. (7D) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'51"N, 88°08'23"E, 1,900 m: HAL108457: (200909): FR690132, FR691019, FR690092, -. (8B) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'38"N, 88°06'59"E, 1,980 m: DNAAP8B 2010 Levichev (LE): (200910): FR690133, FR691020, FR690093, -. (8D) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'38"N, 88°06'59"E, 1,980 m: HAL108184: (200910): FR690134, FR691021, FR690094, -. (9B) China, Xinjiang, Urumqi, Yamalik Hill Forest Park, 43°47'47"N, 87°34'38"E, 941 m: HAL108452: (200911): FR690135, FR691022, FR690095, -. (9 C) China, Xinjiang, Urumqi, Yamalik Hill Forest Park, 43°47'47"N, 87°34'38"E, 941 m: HAL108451: (200911): FR690136, FR691023, FR690096, -. (10) China, Xinjiang, Urumqi, (N9714, Sichuan Univ., Chengdu / 134/10DNA Levichev, LE): FR690137, FR691024, -. *Gagea ova* Stapf: (1A) China, Xinjiang, Urumqi, Yamalik Hill Forest Park, 43°47'44"N, 87°34'29"E, 938 m: HAL107951: (200912): FR690243, FR690838, FR689762, -. (1 C) China, Xinjiang, Urumqi, Yamalik Hill Forest Park, 43°47'44"N, 87°34'29"E, 938 m: HAL 107950: (200912): FR690244, FR690839, FR689763, -. (2) Iran, Province Golestan: 39b/04DNA Levichev (LE)/ HAL10183: (Zarrei 899): AM180466, AM265588, AM287277, -. (3) Iran, Province Khorasan: 39a/04DNA Levichev (LE), HAL101834: AM180465, AM238526, AM287276, -. *G. paczoskii* (Zapal.) Grossh.: Italy: HAL104323: AM903072, AM903061, AM903051, -. *G. pauciflora* Turcz. ex Ledeb.: (1) Mongolia, Ulan Bator: HAL070423: AJ890372, AJ973168, AM409330, -. (2) Russia, District Krasnoyarsk: 1/04DNA Levichev (LE), HAL103857: AM161468, AM287266, AM493952, -. *G. podolica* Schult. et Schult. f.: Ukraine: 21/04DNA Levichev (LE), HAL101832: AM084903, AM238525, AM409334, -. *G. pomeranica* Ruthe: Germany: Saxony-Anhalt HAL095842: AJ419167, AJ416375, AJ427543, -. *G. pratensis* (Pers.) Dumort.: Germany, Saxony-Anhalt: HAL095847:

AJ419162, AJ416372, AJ427542, -. *G. pusilla* (F.W. Schmidt) Sweet: cultivated: 18/04DNALevichev (LE): HAL101831: AM180464, AM161458, AM422453, -. *G. reticulata* (Pall.) Schult. et Schult.: (1) Israel, Central Negev: Z34650: -, -, AM087954, -. (2) Armenia, near Erivan: 35b/04DNALevichev (LE), HAL103856: AM238532, AM238528, -, -. *G. rubicunda* Meinsh. emend. Levichev: Estonia: 26/04DNA-Levichev (LE), HAL103855: AM238541, AM409338, AM493954, -. *G. rufidula* Levichev: (1D) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'38"N, 88°07'02"E, 1,950 m: HAL107929: (200901): FR690245, FR690840, FR689764, -. (2 G) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'31"N, 88°06'02"E, 2,173 m: HAL107924: (200902): FR690246, FR690841, FR689765, -. (3B) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°54'27"N, 88°06'46"E: HAL107922: (200903): FR690247, FR690842, FR689766, -. (4) Kyrgyzstan: 149/09DNALevichev (LE): FR690248, FR690843, FR689767, -. *G. shmakoviana* Levichev: Russia, Altai: 23/04DNALevichev (LE), HAL101830: AM265520, AM287265, AM422454, -. *G. serotina* (L.) Ker Gawl. (= *L. serotina*): Kazakhstan: 45a/04DNALevichev (LE), HAL101789: AJ890376, AM238530, AM087956, -. *G. spathacea* (Hayne) Salisb.: Germany, Saxony-Anhalt: HAL095844: AJ419166, AJ416369, AJ427541, -. *G. stipitata* Merckl. ex Bunge: Iran, Province Khorasan: 49/04DNALevichev (LE)/ HAL101828: (Zarrei & Ajani 816): AM265519, AM265594, AM409336, -. *G. terraccianoana* Pascher: Russia: 55/04DNALevichev (LE), HAL103853: AM287280, AM287268, AM493955, -. *G. tisoniana* Peruzzi, Bartolucci, Frignani & Minutillo: Italy CLU14920: AM409358, AM409349, AM422466, -. *G. transversalis* Steven: Ukraine, Crimea: 56/04DNALevichev, 365 (LE), HAL101783: AJ890370, AJ973167, AM162671, -. *G. uliginosa* Siehe & Pascher: #Iran: Zarrei et al. TUH-E BOT.EXP. 35304, (TUH)(Kew 23153): -, -, EU912089, -. *G. vegeta* Vved.: Uzbekistan: 32/04DNALevichev, 339a (LE), HAL103691: -, -, AM287275, -. *G. villosa* (Bieb.) Sweet: Germany, Saxony-Anhalt: -: AJ419163, AJ416373, AJ427545, -. *G. xiphoidea* Levichev (1) cultivated in (LE): Russia, Republic Altai, district Kosch-Agaczensis, 1,620 m: 71/09DNALevichev (LE): (G271-topotypus): FR690138, FR691044, FR690097, -. (2) Russia, Republic Altai, district Kosch-Agaczensis, 1,620 m: 102/09DNALevichev (LE): FR690139, FR691045, FR690098, -. *G. cf. xiphoidea* (3I) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'31"N, 86°06'02"E, 2,173 m: HAL108479: (200916): FR690140, FR691046, FR690099, FR691340-FR691345 (3 K) China, Xinjiang, Tian-Shan, Bogda-Shan, Tianchi Lake, 43°53'31"N, 86°06'02"E, 2,173 m: HAL108478: (200916): FR690141, FR691047, FR690100, -. *Lilium candidum* L.: -: -, AJ431692, -, -. *Tulipa clusiana* D.C.: -: HAL101864: - AM085140, -, -. *T. cretica* Boiss. &

Heldr.: Greece, Crete: HAL099934: AJ810118, AM049257, AM180461, -.

<sup>a</sup>Sample codes were used only if more than one individual was studied for a species (see explanation under Materials and methods)

<sup>b</sup>Number of collection sites are given for all species collected by us in Xinjiang

## References

- Ajani, Y., Noroozi, J., & Levichev, I. G. (2010). *Gagea alexii* (Liliaceae), a new record from subnival zone of southern Iran with key and notes on sect. *Incrustatae*. *Pakistan Journal of Botany*, 42 Special Issue SI, 67–77.
- Ali, S. I. (2006). Two new species of *Gagea* Salisb. (Liliaceae) from Pakistan. *Pakistan J Botany*, 38, 43–46.
- Ali, S. I., & Levichev, I. G. (2007). *Gagea*. In Ali, S. I., & Qaiser, M. (Eds.) *Flora of Pakistan No. 215 Liliaceae*. (pp. 17–82). Department of Botany, University of Karachi & Missouri Botanical Press.
- Álvarez, I., & Wendel, J. F. (2003). Ribosomal ITS sequences and plant phylogenetic inference. *Molecular Phylogenetic Evolution*, 29, 417–434.
- Bayer, E., & López González, G. (1989). Nomenclatural notes on some names in *Gagea* Salisb. (Liliaceae). *Taxon*, 38, 643–645.
- Clement, M., Posada, D., & Crandall, K. A. (2000). TCS: a computer program to estimate gene genealogies. *Molecular Ecology*, 9, 1657–1660.
- Dasgupta, S., & Deb, D. B. (1986). Taxonomic revision of the genus *Gagea* Salisb. (Liliaceae) in India and adjoining regions. *Journal of the Bombay Natural History Society*, 83, 78–97.
- Duarte, J. M., Wall, P. K., Edger, P. P., Landherr, L. L., Ma, H., Pires, J. C., et al. (2010). Identification of shared single copy nuclear genes in *Arabidopsis*, *Populus*, *Vitis* and *Oryza* and their phylogenetic utility across various taxonomic levels. *BMC Evolutionary Biology*, 10, 61.
- Gurushidze, M., Fritsch, R. M., & Blattner, F. R. (2008). Phylogenetic analysis of *Allium* subgenus *Melanocrommyum* infers cryptic species and demands a new sectional classification. *Molecular Phylogenetics and Evolution*, 49, 997–1007.
- Gutermann, W. (2009). Notulae nomenclaturales 29–40. *Phyton Horn, Austria*, 49, 77–92.
- Hall, T. A. (1999). BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, 41, 95–98.
- Hamazoğlu, E., Budak, Ü., & Aksoy, A. (2008). A new species of *Gagea* Salisb. (Liliaceae) from Sivas (Central Anatolia, Turkey). *Turkish Journal of Botany*, 32, 261–264.
- Harpke, D., & Peterson, A. (2008a). 5.8S motifs for the identification of pseudogenetic ITS regions. *Botany*, 86, 300–305.
- Harpke, D., & Peterson, A. (2008b). Extensive 5.8S nrDNA polymorphism in *Mammillaria* (Cactaceae) with special reference to the identification of pseudogenetic ITS regions. *Journal of Plant Research*, 121, 261–270.
- Henker, H. (2005). Goldsterne und Stinsenpflanzen in Mecklenburg-Vorpommern. *Botanische Rundbrief Mecklenburg-Vorpommern*, 39, 3–108.
- Huelsenbeck, J. P., & Ronquist, F. (2001). MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics*, 17, 754–755.
- Huelsenbeck, J. P., Ronquist, F., Nielsen, R., & Bollback, J. P. (2002). Bayesian inference of phylogeny and its impact on evolutionary biology. *Science*, 294, 2310–2314.

- Huson, D. H., & Bryant, D. (2006). Application of phylogenetic networks in evolutionary studies. *Molecular Biology and Evolution*, *23*, 254–267.
- Jakob, S. S., & Blattner, F. R. (2006). A chloroplast genealogy of *Hordeum* (Poaceae): long-term persisting haplotypes, incomplete lineage sorting, regional extinction, and the consequences for phylogenetic inference. *Molecular Biology and Evolution*, *23*, 1602–1612.
- Levichev, I. G. (1990). Quid est *Gagea pseudoerubescens* Pasch. (Liliaceae)? *Novitates systematicae plantarum vascularium* (Leningrad), *27*, 22–25. [In Russian]
- Levichev, I. G. (1999a). Phytogeographical analysis of the genus *Gagea* Salisb. (Liliaceae). *Komarovia St Petersburg*, *1*, 47–59 [In Russian].
- Levichev, I. G. (1999b). Zur Morphologie in der Gattung *Gagea* Salisb. (Liliaceae). I. Die unterirdischen Organe. *Flora*, *194*, 379–392.
- Levichev, I. G. (2001). New species of the genus *Gagea* Salisb. (Liliaceae) from western regions of Asia. *Turczaninowia*, *4*, 5–35.
- Levichev, I. G. (2006a). A review of the *Gagea* (Liliaceae) species in the flora of Caucasus. *Bot Zhurn (Leningrad)*, *91*, 917–951 [In Russian].
- Levichev, I. G. (2006b). Four new species of the genus *Gagea* Salisb. (Liliaceae) from Western Himalayas and the adjoining regions. *Pakistan Journal of Botany*, *38*, 47–54.
- Levichev, I. G. (2008). New species of genus *Gagea* Salisb (Liliaceae) from the Crimean Yaila. *Novitates systematicae plantarum vascularium St Petersburg*, *40*, 39–46 [In Russian].
- Levichev, I. G., & Ali, S. I. (2006). Seven new species of the genus *Gagea* Salisb. (Liliaceae) from Western Himalayas and adjoining regions. *Pakistan Journal of Botany*, *38*, 55–62.
- Levichev, I. G., & Jezniakowsky, S. A. (2008). *Historia Gagearum*. [<http://www.binran.ru/infsys/gagea/index-eng.html>], accessed 20 July 2010].
- Levichev, I. G., & Maassoumi, S. M. (2005). Comparison of sporoderm features of *Gagea lutea* and *G nakaiana* (Liliaceae). *Bot Zhurn (Leningrad)*, *90*, 874–878 [In Russian].
- Li, M., Wunder, J., Bissoli, G., Scarponi, E., Gazzani, S., Barbaro, E., et al. (2008). Development of COS genes as universally amplifiable markers for phylogenetic reconstructions of closely related plant species. *Cladistics*, *24*, 1–19.
- Librado, P., & Rozas, J. (2009). DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, *25*, 1451–1452.
- Linder, C. R., & Rieseberg, L. H. (2004). Reconstructing patterns of reticulate evolution in plants. *American Journal of Botany*, *91*, 1700–1708.
- Nylander, J. A. A. (2004). *MrModeltest v2. Program distributed by the author*. Uppsala: Evolutionary Biology Centre, Uppsala Univ.
- Pascher, A. A. (1904). Übersicht über die Arten der Gattung *Gagea*. Sitzungsberichte des Deutschen Naturwissenschaftlich-Medizinischen Vereins für Böhmen. *Lotos (NF)*, *24*, 109–131.
- Pascher, A. A. (1905). Neue Arten und Varietäten der Gattung *Gagea*. *Fedd Repert*, *1*, 190–196.
- Pascher, A. A. (1907). Conspectus *Gagearum Asiae*. *Bulletin de la Societe Imperiale des Naturalistes de Moscou*, *19*, 353–375.
- Peruzzi, L. (2003). Contribution to the cytotoxicological knowledge of *Gagea* Salisb (Liliaceae) sect. *Foliatae* A. Terracc. and synthesis of karyological data. *Caryologia*, *56*, 115–128.
- Peruzzi, L. (2008a). Hybridity as a main evolutionary force in the genus *Gagea* Salisb (Liliaceae). *Plant Biosystems*, *142*, 179–184.
- Peruzzi, L. (2008b). Contribution to the cytotoxicological knowledge of the genus *Gagea* Salisb. (Liliaceae). III. New karyological data from the central Mediterranean area. *Caryologia*, *61*, 92–106.
- Peruzzi, L., Bartolucci, F., Frignani, F., & Minutillo, F. (2007). *Gagea tisoniana*, a new species of *Gagea* Salisb sect *Gagea* (Liliaceae) from Central Italy. *Botanical Journal of the Linnean Society*, *155*, 337–347.
- Peruzzi, L., Tison, J.-M., Peterson, A., & Peterson, J. (2008a). On the phylogenetic position and taxonomic value of *Gagea trinervia* (Viv.) Greuter and *Gagea* sect. *Anthericoides* A. Terracc. (Liliaceae). *Taxon*, *57*, 1201–1214.
- Peruzzi, L., Peterson, A., Tison, J.-M., & Peterson, J. (2008b). Phylogenetic relationships of *Gagea* Salisb (Liliaceae) in Italy, inferred from molecular and morphological data matrices. *Plant Systematics and Evolution*, *276*, 219–234.
- Peruzzi, L., Peterson, A., Tison, J.-M., & Harpke, D. (2011). New light on phylogeny and taxonomy of the Eurasian *Gagea villosa*—*G. fragifera* complex (Liliaceae). *Nordic Journal of Botany*, in press.
- Peterson, A., John, H., Koch, E., & Peterson, J. (2004). A molecular phylogeny of the genus *Gagea* (Liliaceae) in Germany inferred from non-coding chloroplast and nuclear DNA sequences. *Plant Systematics and Evolution*, *245*, 145–162.
- Peterson, A., Levichev, I. G., & Peterson, J. (2008). Systematics of *Gagea* and *Lloydia* (Liliaceae) and infrageneric classification of *Gagea* based on molecular and morphological data. *Molecular Phylogenetics and Evolution*, *46*, 446–465.
- Peterson, A., Harpke, D., Peruzzi, L., Levichev, I. G., Tison, J.-M., & Peterson, J. (2009). Hybridization drives speciation in *Gagea* (Liliaceae). *Plant Systematics and Evolution*, *278*, 133–148.
- Peterson, A., Harpke, D., Peruzzi, L., Tison, J.-M., John, H., & Peterson, J. (2010). *Gagea bohémica* (Liliaceae), a highly variable monotypic species within sect. *Didymobulbos*. *Plant Biosystems*, *144*, 308–322.
- Pfeiffer, T., Klahr, A., Heinrich, A., & Schnittler, M. (2011). Does sex make a difference? Genotypic diversity and spatial genetic structure in two co-occurring *Gagea* species with contrasting reproductive strategies (*G lutea*, *G. spathacea*, Liliaceae). *Plant Systematics and Evolution*, *281*, 189–201.
- Posada, D., & Crandall, K. A. (1998). Modeltest, testing the model of DNA substitution. *Bioinformatics*, *14*, 817–818.
- Sang, T., Crawford, D. J., & Stuessy, T. F. (1997). Chloroplast DNA phylogeny, reticulate evolution, and biogeography of *Paeonia* (Paeoniaceae). *American Journal of Botany*, *84*, 1120–1136.
- Schnittler, M., Pfeiffer, T., Harter, D., & Hamann, A. (2009). Bulbils contra seeds: reproductive investment in two species of *Gagea* (Liliaceae). *Plant Systematics and Evolution*, *279*, 29–40.
- Shue, L. Z. (1980). *Gagea nigra* L. Z. Shue. *Fl Reipubl Popularis Sin*, *14*, 282.
- Terracciano A. (1905–1906). *Gagearum species florum orientalis ad exemplaria imprimis in herbariis Boissier et Barbey servata*. *Bull Herb Boissier* T. 5(11). P. 1061–1076; T. 5(12). P. 1113–1128; T. 6(2). P. 105–120.
- Thompson, J. D., Higgins, D. G., & Gibson, T. J. (1994). Clustal-W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research*, *22*, 4673–4680.
- Tison, J.-M. (2001). Typification de *Gagea cossoniana* Pascher, de *Gagea fragifera* (Vill.) Ehr. Bayer & G. López et de *Gagea maroccana* (A. Terracc.) Sennen & Mauricio. *Candollea*, *56*, 197–202.
- Tison, J.-M. (2004). *Gagea polidorii* J. -M. Tison, espèce méconnue du sud-ouest des Alpes et des Apennins. *Acta Bot Gallica*, *151*, 319–326.
- Tison, J.-M. (2009). Update of the genus *Gagea* Salisb. (Liliaceae). *Lagascalia*, *29*, 7–22.
- Vvedensky, A. I. (1971). *Determination handbook of the plants of Central Asia*, vol 2. Tashkent. [In Russian]
- White, T. J., Bruns, T., Lee, S., & Taylor, J. (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In M. A. Innis, D. H. Gelfand, J. J. Sninsky, & T. J. White (Eds.), *PCR Protocols: A Guide to Methods and Applications* (pp. 315–322). San Diego: Academic.

- Woolley, S. M., Posada, D., & Crandall, K. A. (2008). A comparison of phylogenetic network methods using computer simulation. *PloS One*, 3, e1913. doi:10.1371/journal.pone.0001913.
- Xinqi, C., & Turland, N. J. (2000). *Flora of China* 24, 117–121. [<http://flora.huh.harvard.edu/china/PDF/PDF24/gagea.pdf>, accessed 20 February 2010].
- Zarrei, M., Zarre, S., Wilkin, P., & Rix, M. (2007). Systematics revision of the genus *Gagea* (Liliaceae) in Iran. *Botanical Journal of the Linnean Society*, 154, 559–588.
- Zarrei, M., Wilkin, P., Fay, M. F., Ingrouille, M. J., Zarre, S., & Chase, M. W. (2009). Molecular systematics of *Gagea* and *Lloydia* (Liliaceae; Liliales): implications of analyses of nuclear ribosomal and plastid DNA sequences for infrageneric classification. *Annals of Botany*, 104, 125–142.
- Zarrei, M., Wilkin, P., Ingrouille, M. J., & Chase, M. W. (2010a). *Gagea calcicola* (Liliaceae), a new species from southwestern Iran. *Kew Bulletin*, 65, 89–96.
- Zarrei, M., Wilkin, P., Ingrouille, M. J., & Chase, M. W. (2010b). *Gagea robusta* (Liliaceae), a new species from *Flora Iranica* area. *Kew Bulletin*, 65, 327–336.
- Zarrei, M., Wilkin, P., Ingrouille, M. J., Leitch, I., Buerki, S., Fay, M. F., & Chase, M. W. (2010d). Species relationships in the *Gagea reticulata* species complex utilizing nucleotide sequences of the low-copy nuclear gene malate synthase and flow cytometry data. Poster in SPNHC & CBA-ABC Joint Conference, p. 102, Ottawa, Canada.
- Zarrei, M., Wilkin, P., Ingrouille, M. J., Zarre, S., & Chase, M. W. (2010c). The systematic importance of anatomical data in *Gagea* (Liliaceae) from the *Flora Iranica* area. *Botanical Journal of the Linnean Society*, 164, 155–177.
- Zarrei, M., Wilkin, P., & Chase, M. W. (2011b). *Gagea Salisb* (Liliaceae) in Iran: an updated species checklist. *Phytotaxa*, 15, 3–43.
- Zarrei, M., Wilkin, P., Ingrouille, M. J., & Chase, M. W. (2011a). A revised infrageneric classification for *Gagea* (Tulipeae; Liliaceae): insights from DNA sequence and morphological data. *Phytotaxa*, 15, 44–56.
- Zhao, L.-Q., & Yang, J. (2006). *Gagea daqingshanensis* (Liliaceae), a new species from Inner Mongolia, China. *Annales Botanici Fennici*, 43, 223–224.
- Zhao, Y.-Z., & Zhao, L.-Q. (2003). A new species of *Gagea* (Liliaceae) from Nei Mongol, China. *Acta Phytotaxonomica Sinica*, 41, 393–394.
- Zhao, Y.-Z., & Zhao, L.-Q. (2004). *Gagea chinensis* (Liliaceae), a new species from Inner Mongolia, China. *Annales Botanici Fennici*, 41, 297–298.