



A broadly sampled 3-loci plastid phylogeny of *Atraphaxis* (Polygoneae, Polygonoideae, Polygonaceae) reveals new taxa: I. *Atraphaxis kamelinii* spec. nov. from Mongolia

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Abstract

Maximum Likelihood (ML) and Bayesian analyses (BI) applied for 3-plastid loci (cpDNA *trnL*^(UAA) intron, *trnL*–*trnF* IGS, and *rpl32*–*trnL*^(UAG) IGS regions) / 65 tips matrix resulted in preliminary phylogenetic reconstruction of the genus *Atraphaxis*. In combination with the morphological data the obtained phylogeny appears sufficient for recognition of challenging taxonomic entities. We found that a collection of *Atraphaxis* from the Dzungarian Gobi, which appears to be phylogenetically related to *A. pungens*, is morphologically different from the latter by the predominantly dimerous perianth and gynoeceum, shorter outer perianth segments, and the absence of the spiny shoots. It also differs from all other species of *Atraphaxis* that occur in Mongolia and neighboring countries. As a result, we described the novel endemic species *Atraphaxis kamelinii* O.V.Yurtseva sp. nov. More investigations are necessary to fully understand the origin of the newly described species.

Key words: *Atraphaxis*, molecular phylogeny, Mongolia, new species, taxonomy

Introduction

The genus *Atraphaxis* L. comprises ca. 35 species, which are distributed across North-Eastern Africa and Eurasia, ranging from South-Eastern Europe to Eastern Siberia, China and Mongolia. The genus is most diverse in South-West Asia, Central Asia, and China (Bentham & Hooker 1880, Pavlov 1936, Webb 1964, Cullen 1967, Rechinger & Schiman-Cheika 1968, Lovelius 1978, 1979, Borodina 1989, Brandbyge 1993, Czerepanov 1995, Gubanov 1996, Bao & Grabovskaya-Borodina 2003, Nikiforova 2012).

Atraphaxis includes xeromorphic shrubs with pseudoterminal or lateral thyrses, nodes with ocreas, trigonous or lenticular achenes, a perianth with 4–5 segments, and 6–8 stamens with dilatated filament bases (Bentham & Hooker 1880, Haraldson 1978, Ronse De Craene & Akeroyd 1988, Brandbyge 1993). These shrubs are distributed in stony and desert steppes and mountain scrub communities, from plains and foothills to middle mountain belts. They grow on gravelly and stony substrates such as gravel riverbeds, sand dunes, clay and chalky outcrops (Lovelius 1978).

The genus was recircumscribed by Jaubert & Spach (1844–46) by combining the genera *Atraphaxis* and *Tragopyrum* M. Bieb. The intrageneric taxonomy of *Atraphaxis* was traditionally based on the flower merosity, the position of thyrses, the shape and venation patterns of the leaf blade, and the presence of thorns. Jaubert & Spach (1844–46) recognized the subgenera: 1) *A.* subgen. “*Euatraphaxis*” Jaub. & Spach with a tetramerous perianth, six stamens and a dimerous gynoeceum; 2) *A.* subgen. *Tragopyrum* (M. Bieb.) Jaub. & Spach with a pentamerous perianth, 8–9 stamens and a trimerous gynoeceum; 3) *A.* subgen. *Tragatraphaxis* Jaub. & Spach with a single species *Atraphaxis variabilis* Jaub. & Spach demonstrating a variable flower merosity. The majority of later systematic treatments of *Atraphaxis* was based solely on morphology (Ledebour 1847–1849, Meisner 1857, Boissier 1879, Pavlov 1936, Rechinger & Schiman-Czeika 1968) and supported the two first as subgenera or sections.

Krasnov (1888) proposed the first classification of *Atraphaxis*, which included 21 species classified in five sections, and Lovelius (1979) proposed a treatment including 27 species of *Atraphaxis* split into three sections. In addition to

the sections *A. sect. Atraphaxis* and *A. sect. Tragopyrum* (M. Bieb.) Meisn., Lovelius described a monotypic section, *A. sect. Physopyrum* (Popov) Lovelius for *A. teretifolia* (Popov) Kom. with a spheroidal perianth and terete linear leaf blades. Aside from these macro-morphological characters, she used the pollen shape and fine LM-characteristics of the exine structure (Aleshina *et al.* 1978, Lovelius & Sjabrjaj 1981) as essential diagnostic traits.

The genus *Atraphaxis* is one of the most problematic taxa in the family Polygonaceae. The delimitation of *Atraphaxis* species can be difficult owing partly to phenotypic plasticity, partly to hybridization and polyploidy, and partly to the low number of morphological characters separating taxa.

A number of varieties described by Ledebour (1830, 1847–49) seemingly correspond to some species by Jaubert & Spach (1844–46), which leads to confusion and chaos in the nomenclature and identification of the taxa. A number of species were described from SW and Central Asia since the most comprehensive taxonomic treatments by Pavlov (1936) and Lovelius (1979), therefore calling for a new revision of the genus. As early as in the 19th century, Krasnov (1888) stressed the morphological uniformity of the genus and demonstrated that each of species or variety described in *Atraphaxis* has a unique combination of a few character states remaining stable in cultivation, such as the length of internodes and axes of generative shoots, the lignification level of generative shoots becoming spiny or not, the width and length of the leaf blade; the merosity of the flower and the number of stamens.

Possible hybridization events make the classification of the genus even more complicated. Based solely on morphology, Kovalevskaja (1971) suggested putative hybridization between *A. pyrifolia* Bunge and *A. seravshanica* Pavlov, *A. pungens* (M.Bieb.) Jaub. & Spach and *A. frutescens* (L.) K. Koch, *A. virgata* (Regel) Krasn. and *A. frutescens*, *A. virgata* and *A. pungens*, and described intermediate forms between *A. spinosa* L. and *A. replicata* Lam.

Large proportions (48–83%) of distorted pollen grains in some species of *Atraphaxis* (reviewed in Aleshina *et al.* 1978) may argue for the irregularities in meiosis and therefore for the processes of hybridization.

Both diploids and polyploids were detected in *Atraphaxis*, and diverse chromosome numbers were discovered in *A. frutescens* (Table 1). The variability of the pollen size was also observed in many species (Table 1). This may indicate the existence of cryptic polyploid complexes within traditionally recognized taxa (i.g. *A. billardierei* Jaub. & Spach, *A. bracteata* Losinsk., *A. laetevirens* Jaub. et Spach, *A. pungens*, *A. replicata*, *A. spinosa*).

TABLE 1. Summary of pollen size (Ryabkova 1987, Bao & Li 1993, Ge & Liu 1994, Yurtseva *et al.* 2014) and chromosome numbers for *Bactria* and *Atraphaxis*.

<i>Species</i>	Small pollen Polar axis, µm Mean (min-max)	Medium pollen polar axis, µm mean (min-max)	Large pollen polar axis, µm mean (min-max)	Chromosome number
<i>Bactria ovczinnikovii</i>		27.8 (25.5–30.0) 29.5 (28.0–30.7)		
<i>A. angustifolia</i>			35.6 (31.8–38.7)	
<i>A. ariana</i>		30.7 (28.5–32.1)		
<i>A. atraphaxiformis</i>		30.2 (29.5–31.1)		
<i>A. aucherii</i>	26.1 (23.7–27.6)			
<i>A. avenia</i>			33.5 (31.8–34.4)	
<i>A. badghysii</i>		31.3 (25.8–33.1)		
<i>A. billardierei</i>	22.2			2n ≈ 45 (Edman 1931)
<i>A. bracteata</i>		27.5 (24.3–30.7) 30	41.0 (36.1–44.3)	2n = 22 (Tian <i>et al.</i> 2009)
<i>A. caucasica</i>		30.4 (27.0–34.4)		
<i>A. canescens</i>		31.8 (25.8–35.7)		
<i>A. compacta</i>	24.0 (22.5–25.0)		35.5 (29.0–45.6) 36.3 (35.0–37.5)	
<i>A. daghestanica</i>	23.3 (22.1–24.3)	29.7 (29.0–30.1)		
<i>A. decipiens</i>		27.6 (25.0–31.3) 30.2 (28.0–32.6)	40.0 (35.0–42.5)	
<i>A. fischeri</i>	22.5 (19.8–24.2) 24.3 (22.1–25.5)			
<i>A. frutescens</i>	25.9 (20.8–31.9) 27.1 (22.5–30.0)		38.1 (35.0–41.3)	2n = 16 (Ekimova <i>et al.</i> 2009, 2012) 2n ≈ 45 (Edman 1931)
<i>A. irtyschensis</i>	20.2 (17.5–22.5)		37	
<i>A. karataviensis</i>			36.3 (31.8–40.4)	

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TABLE 1. (Continued)

<i>Species</i>	Small pollen Polar axis, μm Mean (min-max)	Medium pollen polar axis, μm mean (min-max)	Large pollen polar axis, μm mean (min-max)	Chromosome number
<i>A. kopetdagensis</i>		28.9 (25.3–35.3)		
<i>A. laetevirens</i>	24.1 (20.0–27.5)	32	36.6 (31.6–47.3)	
<i>A. lanceolata</i>			33.1 (30.9–37.5)	2n \approx 45 (Edman 1931)
<i>A. manshurica</i>			40.0 (37.5–41.3)	2n = 22 (Tian <i>et al.</i> 2009)
<i>A. muschketowi</i>	23.6 (22.5–27.5)	32.5 (27.6–35.7)		
<i>A. pungens</i>	22.4 (13.8–25.0)	27.7 (25.8–31.8) 32.8 (30–37.5)		2n = 48 (Ekimova <i>et al.</i> 2009, 2012)
<i>A. pyrifolia</i>	20	26.8 (24.0–29.2) 31.5 (30.0–33.0)	39.0 (37.5–42.5)	
<i>A. replicata</i>	21.05 (17.5–32.5)	27.1 (21.5–30.9)		
<i>A. rodinii</i>			38.5 (35.0–43.0)	
<i>A. seravshanica</i>			40.8 (39.0–42.6) 44.9 (40.0–49.0)	
<i>A. spinosa</i>	19.2 (17.5–20.0)		35.6 (31.0–39.7) 33.0 (30.1–34.6) 33.3 (30.0–37.5)	2n \approx 45, 48 (Edman 1931)
<i>A. teretifolia</i>		26.8 (25.1–28.2)		
<i>A. toktogulica</i>		28.2 (26.4–31.0)		
<i>A. tortuosa</i>		29.7 (27.5–34.0)		
<i>A. virgata</i>	20.2 (17.5–22.5)	26.3 (23.2–28.8) 26.6 (25.2–28.0)		

Irregularities in the number and location of the pollen ectoapertures are found in plant polyploids (Hong & Lee 1983; Van Leewen *et al.* 1988, Mignot *et al.* 1994, Nadot *et al.* 2000; Hong *et al.* 2005), and particularly observed in *Polygonum* (Borzova & Sladkov 1968, 1969), as well as in *Atraphaxis*. While putative diploids have small tricolporate pollen grains, a great portion of large 4-loxocolporate, 6-pantocolporate, syncolporate pollen, or pollen with ring-like shape of ectoapertures was detected in *A. laetevirens* Jaub. & Spach, *A. pyrifolia* Bunge, *A. seravschanica* Pavlov (Ryabkova 1987), *A. aucherii* Jaub. & Spach, *A. billardierei*, *A. canescens* Bunge, *A. compacta* Ledeb., *A. decipiens* Jaub. & Spach, *A. frutescens*, *A. karataviensis* Pavlov & Lipsh., *A. muschketowi* Krasn., *A. replicata*, *A. rodinii* Botsch., *A. spinosa*, *A. teretifolia*, *A. virgata* (see more in Yurtseva *et al.* 2014).

Agamospermy (diplospory) is often accompanied by hybridization and allopolyploidy in plants (Carmak 1997, Whitton *et al.* 2008, Lo *et al.* 2010) and also seems to be the way of “stabilizing” hybrids (e.g., Campbell *et al.* 1997, Fehrer *et al.* 2007, Krak *et al.* 2013). In *Atraphaxis*, this phenomenon was undoubtedly documented for *A. frutescens* (Edman 1931; Sitnikov 1986, 1991).

In the light of the nomenclatural confusion and paucity of diagnostic characters in *Atraphaxis*, a molecular phylogenetic approach in combination with morphological analysis may be useful for the delimitation of the taxa. Putative hybridization, allopolyploidy and agamospermy create certain difficulties for ITS-based phylogenetic reconstructions (Baldwin *et al.* 1993, Wendel *et al.* 1995a, b, Wendel 2000, Buckler & Holtsford 1996, Buckler *et al.* 1997, Barkman & Simpson 2002, Álvarez & Wendel 2003, Bailey *et al.* 2003, Volkov 2007; Poczai & Hyvönen 2010). Therefore, in this study, we focused mostly on plastid sequence data as well as on the analysis of morphological traits.

Recent molecular phylogenetic reconstructions based on plastid regions (*rbcL*, *matK*, *trnL-trnF*) as well as on the nuclear loci LEAFY and ITS1–2 (Lamb Frye & Kron 2003, Galasso *et al.* 2009, Sanchez *et al.* 2009, 2011, Yurtseva *et al.* 2010, Schuster *et al.* 2011a, b, 2015) showed that *Atraphaxis* is a sister of *Polygonum* s. lat. (incl. *Polygonella*) (tribe Polygoneae). These phylogenetic reconstructions led to re-evaluations of the generic circumscription of *Atraphaxis*. For example, based on the results of phylogenetic analyses, several species of *Polygonum*, with equal-sized perianth segments but the stem lignification and habit typical of *Atraphaxis*, have been transferred to *Atraphaxis* (Yurtseva *et al.* 2010, Schuster *et al.* 2011b, Yurtseva *et al.* 2012), and these results were confirmed by observations of pollen morphology (Yurtseva *et al.* 2014), life history, and other morphological characteristics (Yurtseva *et al.* 2016). The latest yet preliminary circumscription of *Atraphaxis* (Schuster *et al.* 2011a, b; Tavakkoli *et al.* 2015; Yurtseva *et al.* 2016) therefore includes the following new members: *A. ariana* (Grigorj.) T.M. Schust. & Reveal (= *Polygonum arianum* Grigorj.), *A. atraphaxiformis* (Botsch.) T.M. Schust. & Reveal (= *P. atraphaxiforme* Botsch.), *A. toktogulica* (Lazkov) T.M. Schust. & Reveal (= *P. toktogulicum* Lazkov), and *A. tortuosa* Losinsk.

The phylogenetic analyses of *Atraphaxis* (21 species) (Zhang *et al.* 2014) argue for the division of the genus into two major clades, with *A. teretifolia* (monotypic *A.* section *Physopyrum*) nested in one subclade, and *A.* section *Atraphaxis*, which includes the generic type *A. spinosa*, as part of the second subclade. Dual or ambiguous positions of some accessions in the plastid phylogeny of Zhang *et al.* (2014) were possibly caused by erroneous determination of the voucher specimens or reciprocal hybridization of parental species both served as maternal plants for the hybrids.

The most recent phylogenetic approach of Tavakkoli *et al.* (2015), based on 11 species of *Atraphaxis* (nrDNA ITS1–2 plus combined cpDNA *matK* and *rpl32–trnL*^(UAG) data sets), do not support the traditional sectional division of *Atraphaxis* s. str. (Jaubert & Spach 1844–46, Meisner 1857, Boissier 1879, Pavlov 1936, Lovelius 1979). Tavakkoli *et al.* (2015) also recovered *Polygonum* sect. *Spinescentia* Boiss. as a sister to *Atraphaxis* and transferred this clade to *Atraphaxis* under the name *A.* sect. *Polygonoides* Tavakkoli & Osaloo Kasempoor. According to Tavakkoli *et al.* (2015), *A.* sect. *Polygonoides* includes former *Polygonum aridum* Boiss. & Hausskn., *P. botuliforme* Mozaffarian, *P. dumosum* Boiss., *P. khajeh-jamali* Khosravi & Poormahdi, *P. salicornioides* Jaub. & Spach, and *P. spinosum* H.Gross. However, all of these species are quite different from *Atraphaxis*, as this genus is treated traditionally (Yurtseva *et al.* 2016), in habit, perianth morphology, and the ornamentation of the sporoderm. Therefore, the attribution of this group to *Atraphaxis* by Tavakkoli *et al.* (2015) is questionable from a morphological standpoint (Yurtseva *et al.* 2016).

Our phylogenetic and palynological studies placed a morphologically distinctive endemic from Pamir, *Polygonum ovczinnikovii* Czukav. (Czukavina 1962), into *Atraphaxis* (Yurtseva *et al.* 2012, 2014), which was subsequently recognized as *A. ovczinnikovii* (Czukav.) O.V.Yurtseva. This species turned out to be represented by two species, which were transferred to a new genus, *Bactria* O.V.Yurtseva & E.V.Mavrodiev (Yurtseva *et al.* 2016), due to the differences in the morphology of perianth, ochreas and sporoderm ornamentation. The last example shows that a thorough investigation of morphology combined with molecular study helps to resolve taxonomical problems.

The Herbaria of V.L. Komarov Botanical Institute, Russian Academy of Sciences (RAS), Saint Petersburg, Russia (LE) and Lomonosov Moscow State University, Faculty of Biology, Moscow, Russia (MW) keep a large number of specimens of *Atraphaxis* from Mongolia collected in 1970–1980 by V.I.Grubov, I.A.Gubanov, R.V.Kamelin and others. We found that some of those collections have been misidentified as *A. bracteata* (Losina-Losinskaya 1927) or *A. virgata* (Krasnov 1888). Grubov (1982), Borodina (1989), and Gubanov (1996) listed *A. bracteata* as present in Dzungarian Gobi, Mongolia, but their characters only weakly correspond to the morphology of the type specimen of *A. bracteata* (LE!). We therefore suggest that the presence of *A. bracteata* was erroneously indicated for the Dzungarian Gobi and some other regions of Mongolia.

Clearly, the genus *Atraphaxis* requires a taxonomic revision, and our recent work is the first step towards synthesizing the recent findings and adding new data to resolve the phylogeny of this group. Due to the number of plastid loci, our phylogeny still remains preliminary, but in combination with the morphological data it appears sufficient for recognition of challenging taxonomic entities.

In this study we aimed, 1) to obtain the best sampled phylogeny of *Atraphaxis* using three regions of the plastid genome (*trnL*^(UAA) intron, *trnL–trnF* IGS, and *rpl32–trnL*^(UAG) IGS); 2) to specify the phylogenetic placement of one of the specimens from the Dzungarian Gobi previously identified as *A. bracteata*; 3) to investigate whether there are morphological apomorphies that distinguish the latter from other species of *Atraphaxis* growing in Mongolia.

Materials & Methods

Plant Material

The morphological study involved ca. 1000 specimens of *Atraphaxis* and *Polygonum* stored in the herbaria of V.L.Komarov Botanical Institute (LE); Lomonosov Moscow State University, Moscow, Russia (MW); Tsitsin Main Botanical Garden, RAS, Moscow, Russia (MHA); and Main Botanical Garden, National Academy of Science, Bishkek, Kyrgyzstan (FRU).

The identification of the samples used in the study was conducted after examination of the type specimens of species of *Atraphaxis* and *Polygonum* (LE, MW), or their high-resolution images (P—<https://science.mnhn.fr/taxon/genus/atraphaxis>, LINN—http://linnean-online.org/linnaean_herbarium.html, B—<http://ww2.bgbm.org/herbarium/>). Taxonomic treatments of *Atraphaxis* from Turkey (Cullen 1967), Pakistan (Qaiser 2001), Iran (Rechinger & Schiman-Czeika 1968, Tavakkoli *et al.* 2015), the former USSR (Pavlov 1936, Grossheim 1930, Grossheim 1945, Krechetovitch 1937, Rzazade 1952, Drobow 1953, Kastschenko 1953, Avetisjan 1956, Bajtenov & Pavlov 1960, Kovalevskaia 1971, Kutateladze 1975, Kashina 1992, Nikiforova 2005, Grabovskaya-Borodina 2012), Central Asia (Borodina 1989),

Mongolia (Gubanov 1996), and China (Bao & Grabovskaya-Borodina 2003) were consulted for identification of our specimens.

The morphological characteristics of the specimens from the Dzungarian Gobi (Table 2) were compared to some species listed in the flora of Mongolia (Grubov 1982, Borodina 1989, Gubanov 1996, Bao & Grabovskaya-Borodina 2003): *A. bracteata*, *A. compacta* Ledeb., *A. pungens*, and *A. virgata*.

The molecular study involved 33 species (65 accessions) of *Atraphaxis*, 6 species of *Polygonum* sect. *Spinescentia*, and *Bactria ovczinnikovii*. Appendix 1 contains voucher information and GenBank accession numbers for the samples used in the study.

TABLE 2. Characteristics of *Atraphaxis pungens*, the Dzungarian Gobi collection (= *A. kamelinii*), *A. compacta*, *A. bracteata*, and *A. virgata* growing in Mongolia (own observations).

Characters	<i>A. pungens</i>	<i>A. kamelinii</i>	<i>A. compacta</i>	<i>A. bracteata</i>	<i>A. virgata</i>
Life history	Shrub	Shrub	Shrub	Shrub	Shrub
Size, cm	50–150	100–150	50	100–300	150–200
Shoots	Straight, stout, spiny	Straight, stout, unarmed	Stout, short, spiny	Straight, slender, unarmed	Straight, slender, unarmed
Bark color of second year shoot	Creamy, exfoliating	Creamy, exfoliating	Gray, fibrously disintegrating	Gray-brown, exfoliating	Gray, fibrously disintegrating
Color of annual shoot	Creamy, glabrous	Creamy, glabrous	Creamy, glabrous	Light-brown, terete, glabrous	Creamy, finely ribbed
Leaf blade shape	Broadly-elliptical, oval, oblong, lanceolate	Elliptical, rhomboid-elliptical	Circular, broadly-ovate or rhomboid-elliptical	Obovate, oval to linear	Oblong-elliptical, oblanceolate
Leaf blade size (length × width), mm	10–20 × 5–10	10–20 × 5–10	4–7 × 4–5	15–60 × 10–25	20–25 × 7–9
Leaf blade margin	Entire, flat, finely crenulate	Entire, flat or slightly revolute	Entire, flat, or slightly revolute	Strongly undulate-crenulate	Slightly revolute, finely crenulate
Leaf blade apex	Obtuse or short-pointed, acuminate	Obtuse or short-pointed	Obtuse, or short-pointed	Sharply pointed, almost subulate	Obtuse, or short-pointed
Leaf blade base	Broadly cuneate	Broadly cuneate	Broadly cuneate	Rounded	Cuneate
Leaf blade consistency	Thick	Thick	Thick	Leathery	Thick
Leaf blade color	Bluish-green	Bluish-green	Bluish-green	Green	Bluish-green
Venation	Reticulate adaxially and abaxially	Pinnate abaxially and adaxially	Pinnate abaxially and adaxially	Reticulate abaxially and adaxially	Smooth adaxially, with midvein abaxially
Thyrse, (length, cm)	Lateral (1.5–3.0)	Terminal racemes of thyrses (10.0–15.0)	Mainly lateral (1.5)	Terminal racemes of thyrses (10.0–15.0)	Terminal racemes of thyrses (10.0–15.0)
Inflorescence structure (Number of cymes in thyse)	Congested (5–6)	Spaced (5–10)	Congested (5–6)	Spaced (10)	Congested (20–23)
Petiole length, mm	3.0	1.5–3.0	1.5–3.0	3.0–6.0	0.5–1.0
Perianth tube length, mm	2.7–6.8	2.0–2.5	1.5–2.6	1.5–2.1	2.5–3.0
Perianth color	White & pinkish	Deeply pink	White & pink	White & pink	White & pink
Segments number	2 + 3	2 + 2(3)	2 + 2	2 + 3	2 + 3
Outer segments size, (length × width) mm	3.2–5.6 × 2.5–4.1	2.0–2.8 × 3.0	2.2–4.5 × 2.2–4.0	2.0–3.0 × 2.0–3.0	2.0–2.5 × 1.2–1
Inner segments size, mm	4.5–7.0 × 4.5–8.2	4.5–5.9 × 6.0–7.5	6.0–8.0 × 7.4–10.0	5.5–6.5 × 7.0–8.0	4.5–5.0 × 3.5–4.0
Inner segments shape	Circular	Circular to reniform	Circular to reniform	Circular-rhomboid	Oblong-elliptical
Achene merosity	3	2–3	2–3	3	3
Achene color	Dark-brown to black	Dark-brown to black	Light-brown	Dark-brown to black	Light-brown
Achene size, (length × width) mm	2.6–3.3 × 1.3–2.0	4.2–4.5 × 2.5	3.0–4.8 × 2.0–4.1	4.0–5.0 × 1.5–2.5	3.0–3.7 × 1.5–1.7
Achene surface	Smooth, glossy	Smooth, glossy	Smooth, dull	Smooth, glossy	Smooth, dull
Styles	Connate at the very base	Connate at the very base	Free	Free	Free
Stigmas	Capitate	Capitate	Flattened-capitate	Capitate	Capitate

DNA isolation and amplification

DNA was extracted from herbarium specimens using a NucleoSpin Plant Extraction Kit (Macherey-Nagel, Germany) with a yield of DNA ranging from 0.005 to 0.1 mg per 0.1 g of plant material.

The cpDNA *trnL*^(UAA) intron, *trnL-trnF* IGS, and *rpl32-trnL*^(UAG) IGS regions were used because of their utility in Polygonaceae and high variability (Tavakkoli *et al.* 2010, 2015, Schuster *et al.* 2011a, b). The primers of Taberlet *et al.* (1991) and Shaw *et al.* (2007) were used for amplification of these regions.

PCR was performed in a 0.02 ml mixture containing 10–20 ng DNA, 5 pmol of each primer and MaGMix (Dialat LTD, Russia), containing 0.2 mM of each dNTP, 2.0 mM MgCl₂, and 2.5 units of Smart Taq polymerase. 1.0 mM of DMSO was included for amplification of nrDNA regions with high GC content.

Amplification of nrDNA ITS and cpDNA *trnL*^(UAA) intron and *trnL-trnF* IGS regions was performed under the following cycling conditions: hold 95°C, 3 min; 94°C, 30 s; 58°C, 30 s; 72°C, 30 s; repeat 30–33 cycles; extend 72°C, 3 min. Amplification of the *rpl32-trnL*^(UAG) IGS region was performed using the following program: hold 95°C, 3 min; 94°C, 30 s; 52°C, 30 s; 72°C, 60 s; repeat 35 cycles; extend 72°C, 5 min.

Purification of PCR products and DNA sequencing

Amplification products were purified by electrophoresis (Sambrook *et al.* 1989) and one-band DNA fragments were extracted from the gel and purified using the GFX™ PCR DNA, Gel Band Purification Kit (GE HealthCare, USA) or Evrogene Cleanup Mini kit (Russia). The purified PCR products were then used as a template in sequencing reactions with the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, USA) following the standard protocol provided for a 3100 Avant Genetic Analyzer (Applied Biosystems, USA). Sanger sequences were produced at the Genome Center (Engelhardt Institute of Molecular Biology RAS, Moscow). Forward and reverse sequences were assembled and edited with BioEdit v.7.2.0. (Hall 1999).

Sequences used in phylogenetic analyses and the alignment strategy

Our present study of *Atraphaxis* incorporates the members of the genus *Atraphaxis* as circumscribed by Yurtseva *et al.* (2016), the members of *Polygonum* sect. *Spinescentia*, which rank clearly requires future clarification, and *Bactria ovezinnikovii*, which was selected as an outgroup based on the previous results (Yurtseva *et al.* 2016).

Voucher information and GenBank numbers are presented in Appendix 1.

All sequences were aligned using MAFFT (Kato *et al.* 2002; Kato & Standley 2013) following MAFFT's L-INS-i alignment strategy (Kato *et al.* 2002; Kato & Standley 2013), with the default settings set for the gap opening penalty and the offset value.

Aligned plastid matrices were manually concatenated and analyzed as a single contiguous dataset. The combined aligned chloroplast matrix for cpDNA *trnL*^(UAA) intron, *trnL-trnF* IGS, and *rpl32-trnL*^(UAG) IGS regions includes 2199 characters for a total of 72 accessions. For the cpDNA *rpl32-trnL* region 33 accessions were produced for this study, 27 were generated previously, and 11 were downloaded from GenBank (2015) <http://www.ncbi.nlm.nih.gov>. For the *trnL*^(UAA) intron, *trnL-trnF* IGS regions, 25 accessions were obtained for this study, and 27 were sequenced previously.

Phylogenetic analyses

The Maximum Likelihood (ML) analysis was performed with PhyML v. 3.0 (Guindon & Gascuel 2003, Guindon *et al.* 2010), with an estimated proportion of invariable sites and empirical nucleotide equilibrium frequencies. We took a BioNJ tree as the starting tree, and defined the strategy of the tree topology search as “best of NNIs and SPRs” following with ten random starts. The GTR + G + I model was determined as the best choice for both Bayesian and ML analyses following the automatic PhyML Smart Model Selection option (Guindon *et al.* 2010) based on Akaike information criteria. Branch supports were calculated with the approximate likelihood-ratio test (aLRT) (Guindon *et al.* 2010).

A Bayesian analysis (BI) was conducted with MrBayes v. 3.1.2 (Ronquist & Huelsenbeck 2003) as implemented in CIPRES (Miller *et al.* 2010). Two runs with four chains each were run for 10 million generations with a burning of 2.5 million generations; the chains were sampled every 1000 generations with default parameters. At the end of the runs, the standard deviation of split frequencies between the two runs had fallen to 0.0060. Tracer ver. 1.6 (Rambaut *et al.* 2014) was used to confirm that chains had converged and a plateau in likelihoods was obtained.

We use following terminology to describe levels of statistical support—“moderate”: 0.80–0.90 aLRT/0.90–0.95 Bayesian posterior probabilities (pp) and “strong” (or well): 0.91–1.00 aLRT/0.96–1.00 pp.

Light microscopy (LM)

LM-images were made with the stereoscopic microscope Stemi 2000-C Carl Zeiss (Zeiss, Germany) using the camera AxioCam-MR and program AxioVision V. 4.8 free edition. The samples used for photographing and measurements are listed in Appendix 2.

Results

Plastid phylogeny of *Atraphaxis*

The results of ML and BI of the combined chloroplast data matrix with *Bactria ovczinnikovii*, taken as an outgroup, showed (Fig. 1) that a strongly supported clade (0.93/1.00) *Polygonum* sect. *Spinescentia* (*P. aridum*, *P. dumosum*, *P. khajeh-jamali*, *P. salicornioides*, and *P. spinosum*) is a sister to *Atraphaxis* s. str., but *P. botuliforme* is nested in the *Atraphaxis* s. str. clade and is associated with one accession (132) of *A. frutescens*.

The topology of the combined plastid phylogeny of *Atraphaxis* s. str. is as follows: *Atraphaxis* s. str. clade is strongly supported (0.90/0.99), with *A. ariana* recovered as a moderately supported sister to the rest of the genus (0.92/0.90); *A. sect. Tragopyrum* in its traditional understanding appeared as non-monophyletic, whereas the members of the type section (*A. compacta*, *A. fischeri* Jaub. & Spach, *A. karataviensis*, *A. replicata*, *A. spinosa*) plus *A. binaludensis* formed the most derived moderately supported clade (0.81/0.92). Two accessions of *A. teretifolia* (monotypic *A. sect. Physopyrum*) formed a strongly supported clade (0.95/0.99), which is recognized as a putative sister of *A. caucasica* plus well-supported (*A. rodinii* plus *A. badghysi*) (0.99/0.99) (Fig. 1).

Position of the collection from the Dzungarian Gobi in plastid topology

The collection from the Dzungarian Gobi, Mongolia (LE) was identified as most similar to *A. bracteata* by R. Kamelin, but in our plastid topology it is well-supported (0.94/0.99) as a sister to a moderately supported subclade of three accessions of *A. pungens* (0.87/0.93) (Fig. 1). *Atraphaxis bracteata* (157) from China is not closely related to the collection from the Dzungarian Gobi, nor does it belong to the Mongolian *A. virgata*, which is in a different subclade with *A. frutescens*. This result clearly demonstrates that the collection from the Dzungarian Gobi is not related to *A. bracteata* or *A. virgata* by maternal lineage. The collection from the Dzungarian Gobi is also distant from *A. spinosa* and *A. compacta*, which are likely part of the most derived subclade in *Atraphaxis* (Fig. 1).

Morphological distinctions of the collection from the Dzungarian Gobi from the other species from Mongolia

The collection from the Dzungarian Gobi is a shrub with racemes of bracteose thyrses 10–12 cm long composed of 5–10 well spaced out cymes of 1–2 flowers (Figs. 2–3), leaf blades elliptical to rhomboid-elliptical, with pinnate venation visible adaxially and abaxially (Fig. 3C–D), perianth tetramerous or pentamerous (Fig. 4A–D), achenes lenticular or triquetrous with three style branches fused at the base, and capitate stigmas (Fig. 4D–G).

The comparison of our specimen with other species growing in Mongolia (Table 2) shows that the collection from the Dzungarian Gobi has a combination of characteristics of *A. pungens*, *A. compacta*, and possibly *A. virgata*.

It resembles *A. pungens* in the creamy color of its annual shoots and the elliptical to rhomboid-elliptical leaf blades, which in *A. pungens* vary in shape from elliptical to oblanceolate, and are obtuse, shortly acuminate, or shortly pointed. In contrast to the second-year shoots of *A. pungens*, which have the gray bark, the second-year shoots in the specimens from the Dzungarian Gobi have the creamy-pinkish bark. *Atraphaxis pungens* has compact thyrses which are 1.5–3 cm long, composed of 5–6 congested cymes of 2–6 flowers; the thyrses occupy lateral positions at annual or second-year shoots, the latter later becoming spiny. The collection from the Dzungarian Gobi has unarmed shoots with elongated thyrses which are 10–15 cm long, composed of 5–10 well-spaced cymes of 2 flowers; the thyrses terminate annual shoots and axillary branchlets, which appear simultaneously with the terminal thyrse, e.g. sylleptically (Weberling 1989), so the annual shoots are terminated by the racemes of thyrses.

The collection from the Dzungarian Gobi often has a tetramerous perianth and lenticular achenes, which are characteristics of *A. sect. Atraphaxis*. Of 34 flowers examined, 62% had a tetramerous perianth and lenticular achenes, 6% had a tetramerous perianth and trigonous achenes, 6% had a pentamerous perianth and lenticular achenes, and 26% had a pentamerous perianth and trigonous achenes.

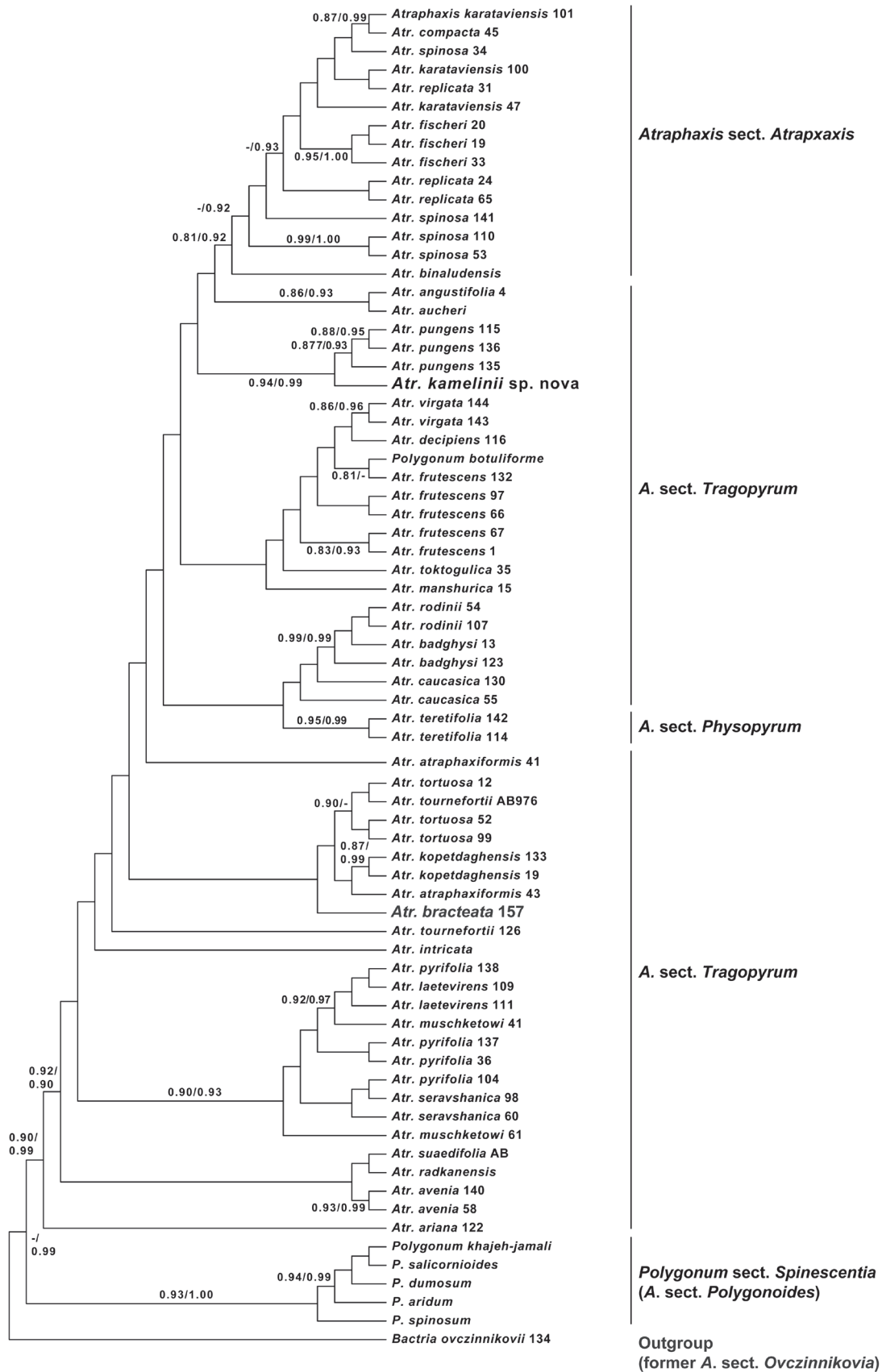


FIGURE 1. Plastid phylogeny of *Atraphaxis*, *Polygonum* sect. *Spinescentia* and outgroup (*Bactria ovczinnikovii*). The best tree from ML analysis of the combined plastid dataset: *trnL* intron, *trnL-trnF* IGS, and *rpl32-trnL*^(UAG) IGS regions of cpDNA (– log likelihood: 5639.238874). Numbers above the branches indicate the aLRT support values (equal or more than 0.8 shown) from ML analysis/posterior probabilities equal or more than 0.9 from the BI of the same matrix. The members of *A. sect. Atraphaxis*, *A. sect. Physopyrum*, and *A. sect. Tragopyrum* are indicated. *Atraphaxis kamelinii* and *A. bracteata* are shown in bold. Image: E. Mavrodiev.

The collection from the Dzungarian Gobi has circular-reniform inner segments which are 4.5–5.0 × 6.0–6.5 mm in size, outer segments of 2.0–2.5 × 3.0 mm, and a short filiform part of the perianth tube 2.0–2.5 mm long, which is equal in length to the outer segments and is joined to a pedicel with articulation (Fig. 4A–D, 5A–B). Judging by the perianth size (Table 3), this collection is close to *A. compacta* from Kazakhstan (Fig. 5C), or *A. replicata* from Kyrgyzstan (Fig. 5D).

Atraphaxis pungens has a pentamerous perianth and trimerous achenes (Fig. 5F–I). Three inner segments are rotundate-reniform, 5.0–7.0 × 4.5–8.2 mm in the fruiting stage. Two outer segments are oblong-ovate, 3.3–5.6 × 2.7–4.1 mm long. The filiform part of the perianth tube (3.0–7.0 mm long) is usually twice as long as the outer segments, and longer than in the collection from the Dzungarian Gobi. The achenes of *A. pungens* are trigonous, rhomboid-elliptical or pyriform, black and glossy, with three style branches fused at the base, and small stigmas (Fig. 5J–L).

The ratio of inner to outer segment length varies in range 1.3–1.7 in *A. pungens*, and is equal to 2.1 in the collection from the Dzungarian Gobi, varying in range 2.0–2.5 in *A. compacta* and *A. replicata* (Table 3, Fig. 5C–D). The filiform part of the perianth tube joined to a pedicel has similar length in the collection from the Dzungarian Gobi, *A. compacta*, and *A. replicata* (Table 3).

Despite the mainly tetramerous perianth with circular-reniform inner segments, the short filiform part of the perianth tube, and lenticular achenes, the collection from the Dzungarian Gobi is habitually different from *A. compacta* and *A. spinosa* from the type section of *Atraphaxis*, which occur in Mongolia. These species are small shrubs with short spiny shoots and lateral compact thyrses 1.0–1.5 cm long composed of 5–6 congested cymes of 1(2) flowers.

The specimen from the Dzungarian Gobi in the overall appearance resembles *A. bracteata* and *A. virgata*, which are shrubs with straight elongated shoots terminated by the racemes of thyrses. However, *A. virgata* differs by its oblanceolate leaf blades with a finely crenulate-papillate, slightly revolute margin, smooth or longitudinally wrinkled (when dried) at the upper surface, with a single main vein beneath. It has terminal racemes of thyrses composed of 20–23 congested cymes of 1–2 flowers; the perianth with cordate or oblong-elliptical inner segments (Fig. 5E), and light-brown trigonous achenes. *Atraphaxis bracteata* differs by its obovoid or broadly oval leaf blades which are sharply pointed and strongly undulate at margin, and its perianth with sub-equal segments, the outer ones spread horizontally in fruiting. Hence, our specimen from the Dzungarian Gobi is fairly different from both taxa.

TABLE 3. Perianth sizes in *Atraphaxis pungens*, the collection from the Dzungarian Gobi (= *A. kamelinii*), *A. compacta*, and *A. replicata*. The origin of the samples see in Appendix 2.

Species, sample	Inner segments, mm	Outer segments, mm	Ratio: IS/OS length/ IS/OS width	Filiform part of perianth tube, mm	Achene size, mm
<i>A. pungens</i> , Lomonosova & Ivanova 2408	6.0 × 7.5	3.5 × 3.0	1.7/2.5	5.3	3.5 × 2.0
<i>A. pungens</i> , Volkova & Rachkovskaya 7373	7.0 × 8.2	5.6 × 4.1	1.25/2.0	6.8	2.8 × 1.5
<i>A. pungens</i> , Gubanov 3563	4.6–5.0 × 5.7–6.4	3.3 × 2.7	1.5/2.3	2.3–2.5	2.1–2.5 × 1.1
<i>A. pungens</i> , Maltseva & Selisheva	5.5 × 5.5	3.8 × 3.4	1.4/1.6	3.2	-
<i>A. pungens</i> , Neifeld & Margasova	4.4–5.0 × 4.5–5.5	3.2–3.8 × 3.0	1.3/1.8	3.6–4.5	4.8 × 2.4
<i>A. kamelinii</i> , Daryima & Kamelin 765 (50)	4.5–5.9 × 6.0–7.5	2.0–2.8 × 3.0	2.1/2.5	2.0–2.5	4.2–4.5 × 2.5
<i>A. compacta</i> , Pavlov 160 (45)	6.0–6.3 × 7.4–7.5	2.2–2.5 × 2.2–2.5	2.5/3.0	1.5–1.7	4.8 × 4.1
<i>A. replicata</i> , Kuvaev 518-3 (31)	5.1–6.5 × 6.8–9.0	2.8 × 2.4	2.0/3.8	2.3–2.5	4.5–5.0 × 3.5–4.0

IS—inner segment of perianth, OS—outer segments of perianth. Numbers in brackets are sample numbers in Appendix 1.

Discussion

Plastid phylogeny of *Atraphaxis*

The results of the Maximum Likelihood and Bayesian analyses of the combined plastid data matrix confirmed *Polygonum* sect. *Spinescentia* (*Atraphaxis* sect. *Polygonoides*) as a sister of the narrowly defined *Atraphaxis* with 33 species (Tavakkoli *et al.* 2015; Yurtseva *et al.* 2016) (Fig. 1).

We also confirmed that *Atraphaxis botuliformis* (*Polygonum botuliforme*) is deeply nested in *Atraphaxis* in plastid phylogeny. This caespitose perennial herb, with sausage-shaped succulent leaves and axillary cymes of flowers at annual shoots, is a local endemic of Central Iran (Tehran region) (Mozaffarian 1988, 2012). It is morphologically quite different from other species of *Atraphaxis* but has the striate-perforate ornamentation of sporoderm (Tavakkoli *et al.* 2015), peculiar to *Atraphaxis* (Yurtseva *et al.* 2014). In ITS-based phylogeny it is however nested in *Polygonum* sect. *Spinescentia* (*A. sect. Polygonoides*) (Tavakkoli *et al.* 2015, Yurtseva *et al.* 2016). This conflict likely indicates the ancient hybrid origin of *A. botuliformis* and needs special study.

Atraphaxis sect. *Atraphaxis* is characterized by having a tetramerous perianth and a dimerous gynoecium, and it is likely the most derived clade of *Atraphaxis*, which, if *A. binaludensis* is included, has moderate support (0.81/0.92). Similarly to many members of *A. sect. Atraphaxis*, *A. binaludensis* has spinescent shoots, broadly obovate-rhomboid small (5–6 × 4–5 mm) leaf blades with abaxially prominent reticulate nervation and a slightly revolute margin, but differs by a pentamerous perianth (Tavakkoli *et al.* 2014), common in *A. sect. Tragopyrum*. A presumable hybrid origin of this taxon needs additional study. A pentamerous perianth is also usual in a presumable hybrid of *A. fischeri* and *A. frutescens*, in which a pentamerous perianth and trigonous achenes, and a tetramerous perianth and lenticular achenes can be found with the same frequency.

We confirmed the monophyly of *A. teretifolia* (monotypic *A. sect. Physopyrum*) (Zhang *et al.* 2014), which is a sister to the clade of morphologically distinct *A. caucasica*, *A. badghysi*, and *A. rodinii*, though there is no support for this relationship. As shown by Zhang *et al.* (2014), we confirm that *A. sect. Tragopyrum* is polyphyletic and requires further revisions (Fig. 1).

Placement and morphological distinctions of the collection from the Dzungarian Gobi

The collection from the Dzungarian Gobi appeared as a strongly supported sister to the *A. pungens* clade. However, the morphological characteristics of this collection only partly correspond to the morphology of *A. pungens* (Table 1, Figs. 4–5). The collection from the Dzungarian Gobi region has creamy second-year shoots, terminated by racemes of elongated thyrses with well-spaced cymes of 2 flowers, a mainly dimerous perianth with circular-reniform inner segments which are 2.0–2.5 times longer than its outer segments, the latter being equal to the filiform perianth tube, and mainly lenticular achenes (Figs. 2–4). *Atraphaxis pungens* has stout, spiny second-year shoots covered with gray bark, compact lateral thyrses with congested cymes of 2–6 flowers, a pentamerous perianth with inner segments, which are 1.3–1.7 times longer than outer segments, the latter being equal to or shorter than the filiform perianth tube, and trimerous achenes (Fig. 5F–L). Both taxa share glaucous rhomboid-elliptical or elliptical leaf blades and black shiny achenes with short styles fused at the base.

Due to the mostly maternal inheritance of plastids in Angiosperms (Hagemann & Schröder 1989), the highly supported grouping of the collection from the Dzungarian Gobi with *A. pungens* in the plastid topology of *Atraphaxis* (Fig. 1) might indicate that *A. pungens* (or any closely related taxon) served as a putative maternal plant for this collection.

The collection from the Dzungarian Gobi is also clearly distinct from all other taxa growing in Mongolia and China (Grubov 1982, Borodina 1989, Gubanov 1996). In particular, it strongly differs from *A. bracteata* (Losina-Losinskaya 1927) in various aspects (Table 2).

Atraphaxis bracteata is characterized as a 1–3 m tall shrub with racemes of thyrses, green, leathery, broadly obovate or oval leaves, sharply pointed at the tip and strongly undulate at margins. The perianth has subequal segments, three reniform-orbicular inner ones surrounding the achene, and two spreading outer segments when in fruit (Bao & Grabovskaya-Borodina 2003).

Among all of the species reported from Mongolia, the accession from the Dzungarian Gobi most corresponds to the description of *A. virgata* as “a shrub 1.5–2 m tall with gray-green oblanceolate or oblong-elliptical leaf blades with veins that are conspicuous only abaxially, margin flat or slightly downward revolute” (Krasnov 1888, Gubanov 1996, Borodina 1989, Bao & Grabovskaya-Borodina 2003). But in contrast to *A. virgata*, which is characterized by racemes of thyrses with 20–23 congested cymes of flowers, oblong-elliptical inner segments, and light-brown trigonous achenes, our plant has well-spaced 5–10 cymes, leaf blades with veins visible adaxially and abaxially, circular-reniform inner segments, often dimerous flowers, and black achenes.

In short, the collection from the Dzungarian Gobi combines the shrubby habit and the racemes of thyrses present in *A. virgata* and *A. bracteata*, the elongated thyrses with far-spaced cymes of flowers peculiar of *A. bracteata* and *A. frutescens*, the elliptical or rhomboid-elliptical leaf blades of *A. pungens* and *A. compacta*, the circular-reniform inner perianth segments and lenticular achenes of *A. sect. Atraphaxis*, and black color of achenes peculiar of *A. pungens*.

Combined with the results of the phylogenetic analysis (Fig. 1), and due to the morphological distinctiveness of

the collection from the Dzungarian Gobi, we describe it as the new species *Atraphaxis kamelinii* O.V.Yurtseva, spec. nov. The possibility of a hybrid origin of this species and its relationship with *A. pungens* (or a closely related taxon), a putative maternal parent, needs to be examined with nuclear data and cytological studies.

Conclusions

1. The preliminary 3-loci/65 tips plastid phylogeny of *Atraphaxis* showed that the morphologically distinct collection of *Atraphaxis* from the Dzungarian Gobi, which had previously been assigned by R. Kamelin (LE) to *Atraphaxis bracteata*, is actually closely related to *A. pungens*.

2. This collection is morphologically quite different from all species of *Atraphaxis* growing in Mongolia and neighbouring countries (Table 2). It combines the morphological characteristics of *A. pungens*, *A. virgata*, as well as of the species of *A. sect. Atraphaxis*, and is recognizable due to its own remarkable morphology.

3. Morphological differences of the collection from the Dzungarian Gobi from *A. pungens* and other taxa are so noticeable that it deserves to be described as a distinct species, *Atraphaxis kamelinii* O.V.Yurtseva, spec. nov.

4. The results of the phylogenetic analyses, as well as the unusual morphology of the proposed new species combining characters of several taxa, suggest a possible hybrid origin of the newly described species, but more investigations are necessary to fully understand the origin of *A. kamelinii*.

Taxonomy

Atraphaxis kamelinii O.V.Yurtseva, spec. nov. (Figs. 2–5)

Type:—MONGOLIA. [Khovd aimag]: the Dzungarian Gobi, S slope of Saertaengijin-Khuvch Uul [Mt.] near junction to Khaldzan-Ula [Mts.], 27 July 1984, Daryima & Kamelin 765 (LE! holotype).

Shrubs ca 1 m tall. Stem erect, stout, glabrous; woody shoots inclined-spreading, brown, much branched, not spiny, slightly ribbed, creamy, epidermis exfoliating and fibrously disintegrating, making light-brown or creamy wood. Current-year shoots are branched forming racemes of thyrses with branchlets departing at a nearly right angle. Annual shoots and branchlets 10–15 cm long are straight, soon lignified, slightly ribbed, glabrous, leafy with internodes 5–10 mm, or terminated by thyrses 5–10 cm long with 5–10 spaced cymes of 1–3 flowers in axils of developed or reduced leaf blades. Ocreas at vegetative shoots are tubulate, 5–6 mm, membranous, brownish at base, transparent above and cleft into two linear-lanceolate lacinulas with two faintly visible veins at both sides of leaf blade, and finely incised-serrated short middle lacinula. Ocreolas in thyrses are oblique funnel-form, 2–5 mm, membranous, brownish at base, transparent above and cleft into 2 sharp teeth. Leaf blades bluish-green or glaucous, thick, oblong-elliptic, 10–20 × 5–10 mm, gradually narrowed to a petiole 1.5–3 mm, glabrous, with prominent midvein and faint lateral veins. Margin entire, flat, or slightly revolute, glabrous, apex obtuse or short-pointed. Segments 4 or rarely 5, bright-pink; outer segments two, reflexed towards pedicel in fruit, reniform-orbicular, ca. 2.0–2.8 × 3.0 mm, prominently reticulate-veined; inner segments two or three, circular-reniform in fruit, 4.5–5.9 × 6.0–7.5 mm in diam., base nearly cordate, venation prominently reticulate, margin slightly undulate. Perianth tube 2.0–2.5 mm, filiform, joined to a pedicel (ca. 4.5 mm long) with articulation. Stamens 8, filaments subulate-lanceolate, gradually dilatated towards base. Achenes 4.2–4.5 × 2.5 mm, ovoid, gradually acuminate, lenticular or unequally-trigonous, with strongly concave faces, ribs sharp, almost winged, surface smooth, glossy, dark-brown to black.

Styles 2(3), 0.3 mm long, fused at the base, with stigmas capitate, papillate.

Fl.—May–June. **Fr.**—June–Aug.

Distribution:—Endemic of the Dzungarian Gobi in SW Mongolia, Khovd aimag (Fig. 6).

Ecology:—Mountain slopes, granites, sandy sairs.

Etymology:—The species is named after Rudolf V. Kamelin (1938–2016), famous for his studies on the flora and florogenesis of Central Asia.



FIGURE 2. Holotype of *Atraphaxis kamelinii* O.V.Yurtseva, sp. nov. Image: O. Yurtseva.

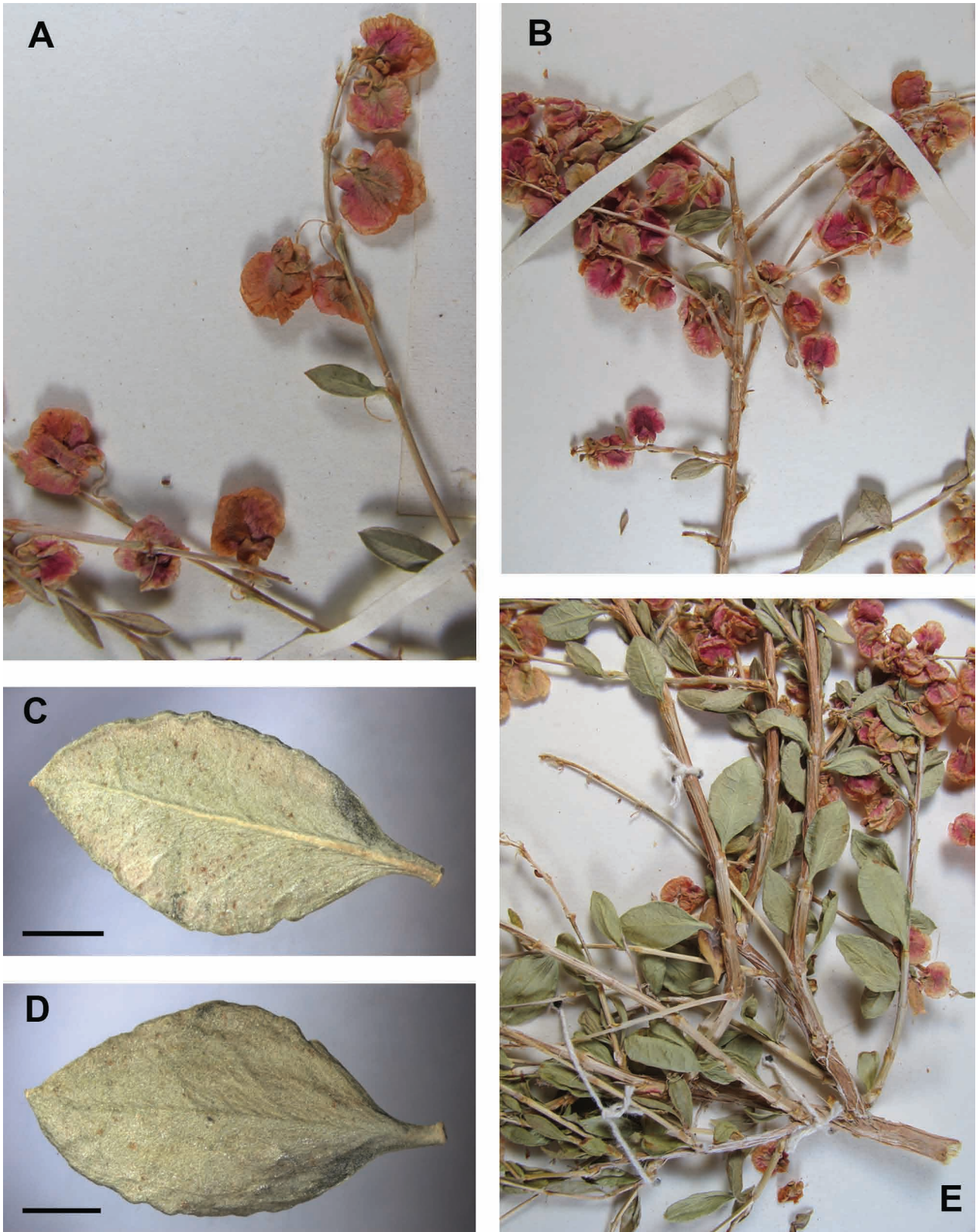


FIGURE 3. Shoots and thyrses of *Atraphaxis kamelinii* (LE! holotype, see also Fig. 2). A. Bracteose thyrses with spaced cymes of 1–2 dimerous flowers; B. Top of annual shoot with branchlets terminated by thyrses; C, D. Abaxial and adaxial view of leaf blades; E. The bases of annual shoots with axillary vegetative and generative branchlets. Scale bar = 1 mm (C–D). Images: O. Yurtseva.

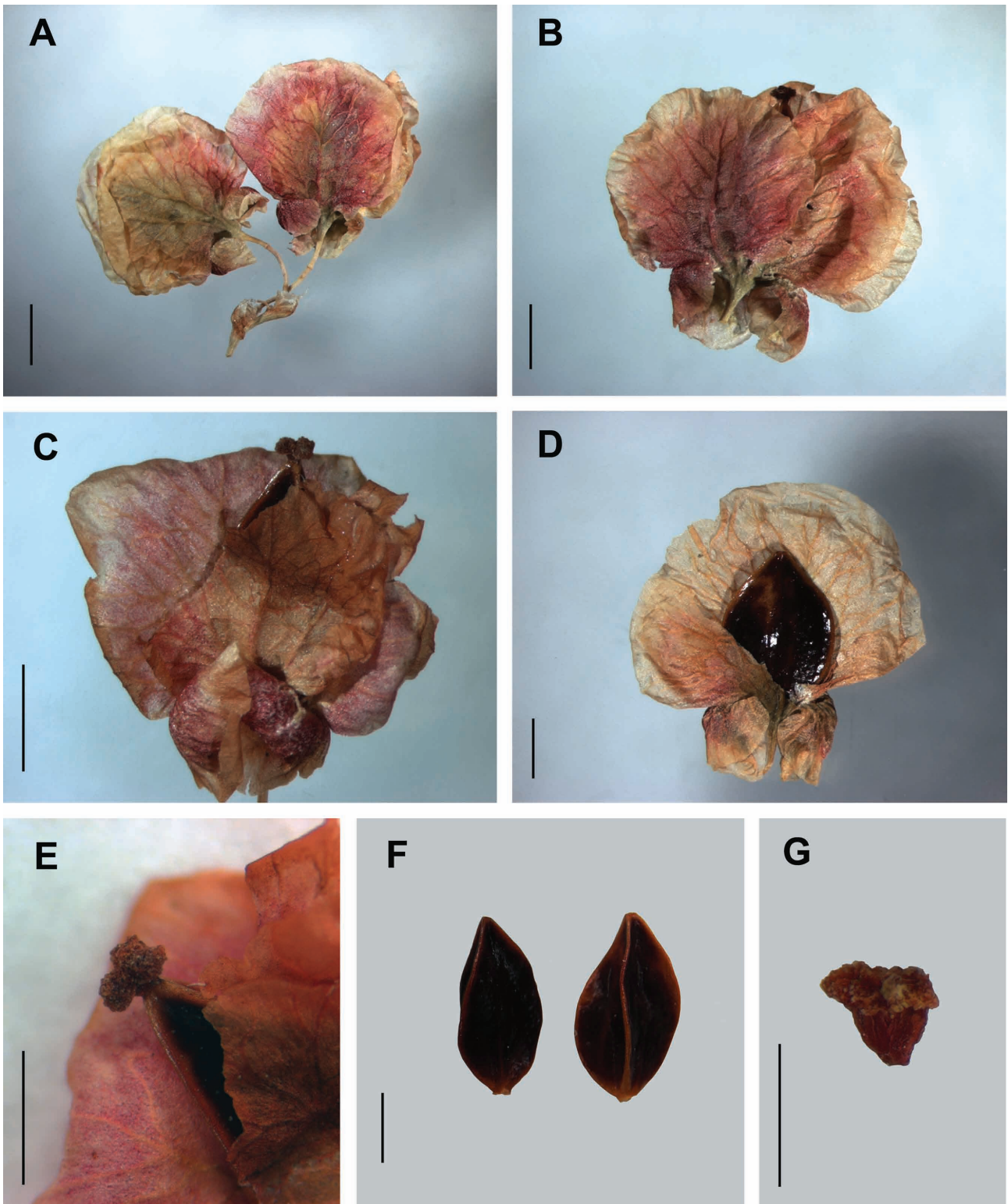


FIGURE 4. Perianths and achenes of *Atraphaxis kamelinii* (LE! holotype). A. Cyme of two flowers with tetramerous (on the left) and pentamerous (on the right) perianths; B, C. Flower with pentamerous perianth and trimerous gynoecium; D. Flower with tetramerous perianth (inner segment is removed) hiding lenticular achene; E. The top of triquetrous achene with three styles and capitate stigmas; F. Triquetrous achenes; G. Three style branches fused at the base and terminated by capitate stigmas. Scale bar = 1 mm (A–F); = 0.5 mm (G). Images: O. Yurtseva.

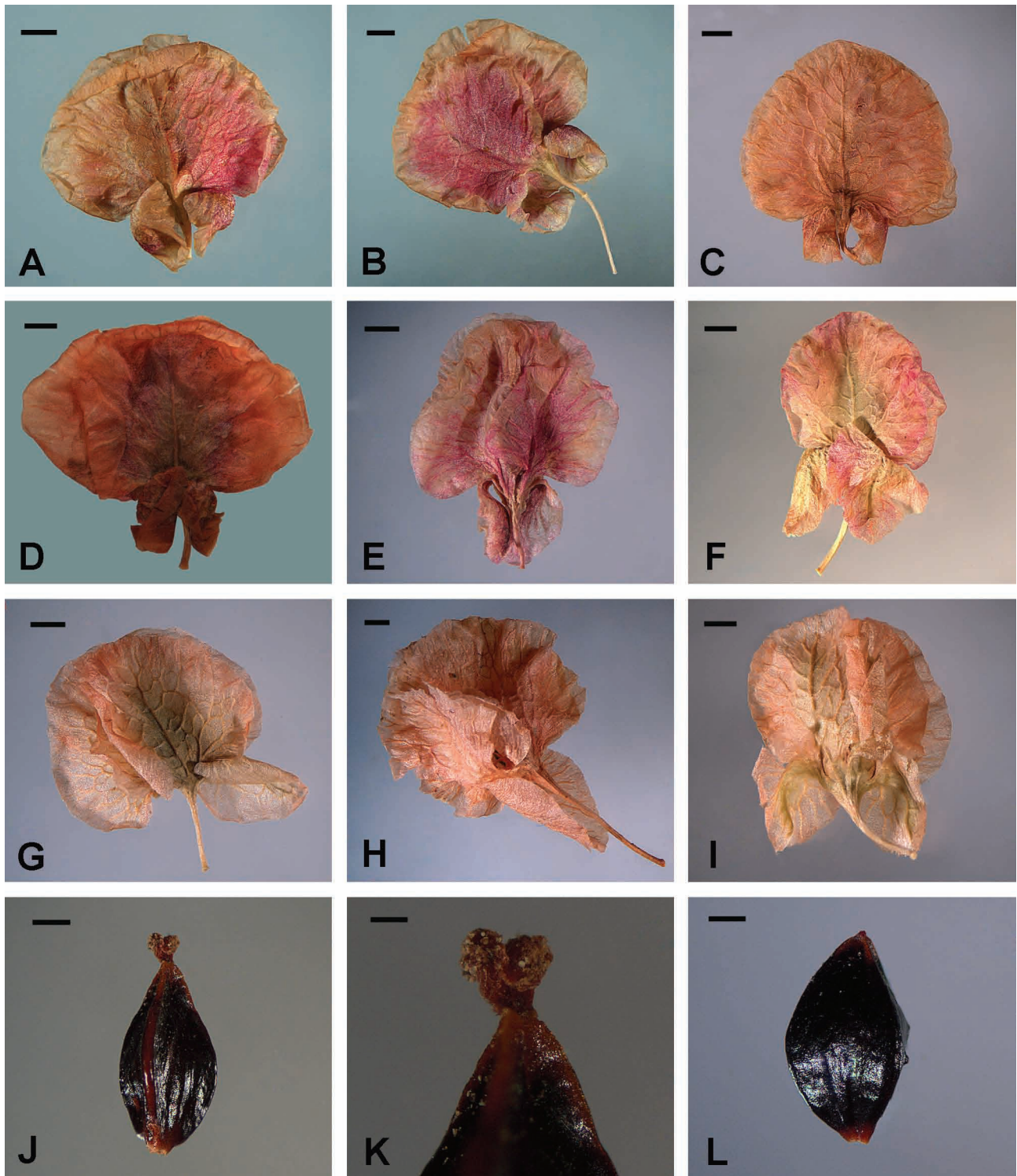


FIGURE 5. Perianths (A–I) and achenes (J–L) of *Atraphaxis kamelinii*, *A. compacta*, *A. replicata*, *A. virgata*, and *A. pungens*. A–B. *A. kamelinii* from the Dzungarian Gobi, *Daryima & Kamelin 765* (LE); C. *A. compacta*, Kazakhstan, *Pavlov 160* (MW); D. *A. replicata*, *Kuvaev 518-3* (MW); E. *A. virgata*, Mongolia, *Gubanov 2634* (MW); F, J–K. *A. pungens*, Russia, Tuva, *Neifeld & Margasova* (MHA); G. *A. pungens*, Mongolia, *Gubanov 3563* (MW); H, L. *A. pungens*, Mongolia, *Volkova & Rachkovskaya 7373* (LE); I. *A. pungens*, Russia, Tuva, *Maltseva & Selisheva* (MW). Scale bar = 1 mm (A–I); = 0.2 mm (K); = 0.5mm (J, L). Images: O. Yurtseva.

Taxonomic relationships:—The new species might be closely related to *A. pungens* as a putative maternal taxon, with which it shares the shrubby habit, branchlets of the annual shoots departing at almost right angle, elliptical or rhomboid-elliptical leaf blades, black glossy achenes, perianth size, but differs by creamy-pinkish, not spiny second-year shoots, and mainly dimerous flowers.

Atraphaxis kamelinii also resembles *A. virgata* because of the shrubby habit and racemes of thyrses, but differs

in the shape and venation of leaf blades, far-spaced cymes of flowers, circular-reniform inner segments, and black, glossy, and mainly lenticular achenes.

The new species is similar to *A. bracteata* due to the shrubby habit and racemes of thyrses, but differs by creamy annual shoots, elliptical bluish-green leaf blades entire at the margin, outer perianth segments reflected to a pedicel and mainly lenticular achenes.

It is morphologically similar to *A. spinosa* and *A. compacta* with mainly tetramerous flowers, almost reniform inner segments and lenticular achenes, but differs by lacking spiny shoots, elongated thyrses with 5–10 spaced cymes of flowers, and achenes that are almost black and glossy.

Other specimen seen (paratype):—MONGOLIA. Khovd (=Khobdo) aimag: the Dzungarian Gobi, [somon Bulgan], 15 km S of the settlement Bulgan, granites, sandy sairs, N 45°57', E 91°31', 17 June 2004, *Dyachenko & Kosachev* (ALTB!).

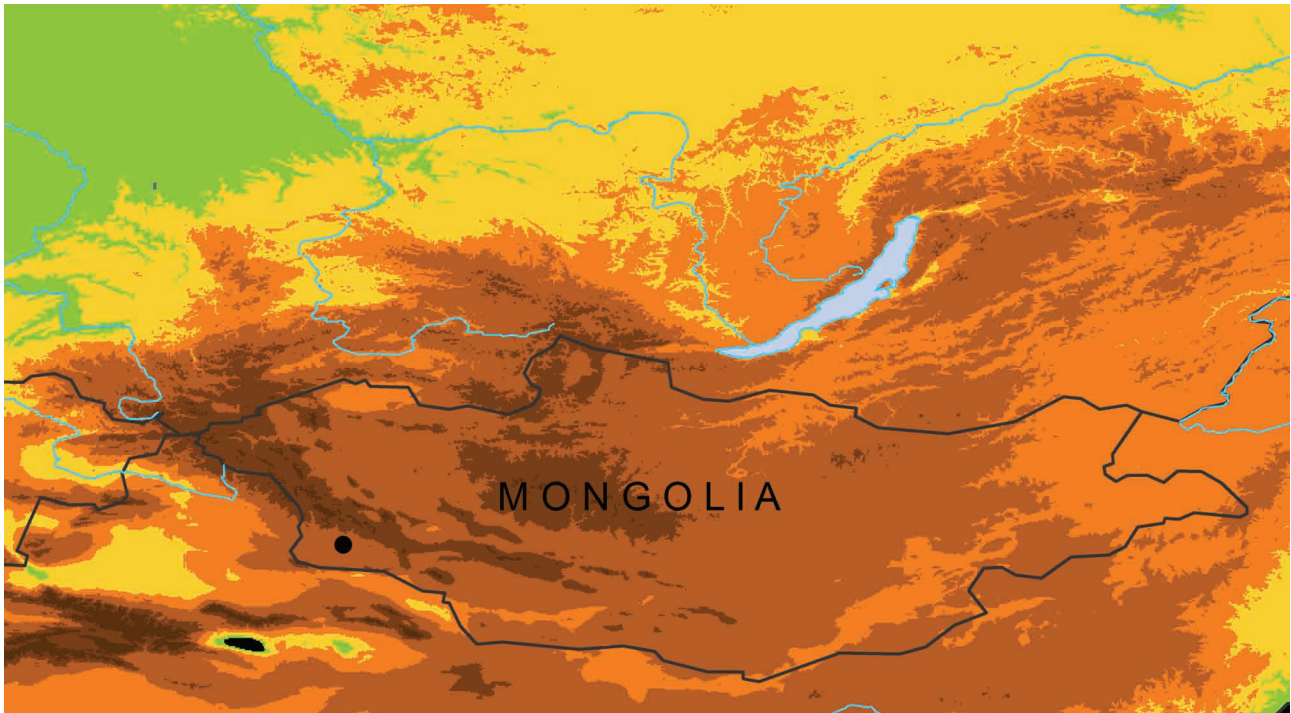


FIGURE 6. Distribution map of *Atraphaxis kamelinii*. Distribution area is indicated by black circle. Map: M. Olonova.

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References

- Aleshina, L.A., Lovelius, O.L. & Sjabrjaj, S.V. (1978) Exploraciones morfologiae pollinis specierum generis *Atraphaxis* L. florum URSS. *Novitates systematicae plantarum vascularium et non vascularium* 1977: 108–122. [in Russian]
- Álvarez, I. & Wendel, J.F. (2003) Ribosomal ITS sequences and plant phylogenetic inference. *Molecular Phylogenetics and Evolution* 29: 417–434.
[http://dx.doi.org/10.1016/S1055-7903\(03\)00208-2](http://dx.doi.org/10.1016/S1055-7903(03)00208-2)
- Avetisjan, E.M. (1956) *Atraphaxis* L. In: Takhtajan, A.L. (Ed.) *Flora Armenii*, vol. 2. Akademia Nauk Armjanskoj SSR, Erevan, pp. 420–426. [in Russian]
- Bailey, C.D., Carr, T.G., Harris, S.A. & Hughes, C.E. (2003) Characterization of angiosperm nrDNA polymorphism, paralogy, and pseudogenes. *Molecular Phylogenetics and Evolution* 29 (3): 435–455.
<http://dx.doi.org/10.1016/j.ympev.2003.08.021>
- Bajtenov, M.B. & Pavlov, N.V. (1960) *Atraphaxis* L. In: Pavlov, N.V. (Ed.) *Flora of Kazakhstan*, vol. 3. Akademia Nauk Kazahskoj SSR, Alma-Ata, pp. 110–118. [in Russian]
- Baldwin, B.G., Sanderson, M.J., Porter, J.M., Wojciechowski, M.F., Campbell, Ch.S. & Donoghue, M.J. (1995) The ITS region of nuclear ribosomal DNA: a valuable source of evidence on Angiosperm phylogeny. *Annals of the Missouri botanical garden* 82: 247–277.
<http://dx.doi.org/10.2307/2399880>
- Bao, B. & Grabovskaya-Borodina, A.E. (2003) *Atraphaxis* L. In: Wu, Z.Y., Raven, P.H. & Hong, D.Y. (Eds.) *Flora of China*, vol. 5. Science Press, Beijing; Missouri Botanical Garden Press, St. Louis, pp. 328–332.
- Bao, B.-J. & Li, A.-J. (1993) A study of the genus *Atraphaxis* in China and the system of *Atraphaxideae* (*Polygonaceae*). *Acta Phytotaxonomica Sinica* 31 (2): 127–139. [in Chinese]
- Barkman, T.J. & Simpson, B.B. (2002) Hybrid origin and parentage of *Dendrochilum acufiferum* (Orchidaceae) inferred in a phylogenetic context using nuclear and plastid DNA sequence data. *Systematic Botany* 27: 209–220.
- Bentham, G. & Hooker, J.D. (1880) Polygonaceae. In: Bentham, G. & Hooker, J.D. (Eds.) *Genera plantarum*, vol. 3(1). Reeve & Co, London, pp. 88–105.
- Boissier, E. (1879) *Flora Orientalis sive enumeratio plantarum in Oriente a Graecia et Aegypto ad Indiae fines hucusque observatorum*, vol. 4. H.Georg Bibliopolam, Genevae et Basileae, pp. 1–1276.
- Borodina, A.E. (1989) Polygonaceae. In: Borodina, A.E., Grubov, V.I., Grudzinskaja, I.A. & Menitsky, J.L. (Eds.) *Plantae Asiae Centralis*, vol. 9. Nauka, Leningrad, pp. 77–129. [in Russian]
- Borzova, L.M. & Sladkov, A.N. (1968) Pollen of some species of the genus *Polygonum* L. 1. Three-, four- and hexacolporate pollen grains. *Nauchnye doклады vysshey shkoly. Biologicheskie nauki* 8: 54–58. [in Russian]
- Borzova, L.M. & Sladkov, A.N. (1969) Pollen morphology and system of the genus *Polygonum* L. s. l. of Tajikistan Flora. *Vestnik Moscovskogo Universiteta, Seria Biologia* 4: 47–54. [in Russian]
- Brandbyge, J. (1993) Polygonaceae. In: Kubitzki, K., Rohwer, J. G. & Bittrich, V. (Eds.) *The families and genera of vascular plants*, vol. 2. Springer-Verlag, Berlin, pp. 531–544.
http://dx.doi.org/10.1007/978-3-662-02899-5_63
- Buckler, E.S.I. & Holtsford, T.P. (1996) Zea ribosomal repeat evolution and substitution patterns. *Molecular Biology and Evolution* 13: 623–632.
<http://dx.doi.org/10.1093/oxfordjournals.molbev.a025622>
- Buckler, E.S. IV, Ippolito, A. & Holtsford, T.P. (1997) The Evolution of Ribosomal DNA Divergent Paralogues and Phylogenetic Implication. *Genetics* 145: 821–832.
- Campbell, C.S., Wojciechowski, M.F., Baldwin, B.G., Alice, L.A. & Donoghue, M.J. (1997) Persistent nuclear rribosomal DNA sequence polymorphism in the *Amelanchier* agamic complex (Rosaceae) *Molecular Biology and Evolution* 14 (1): 81–90.
<http://dx.doi.org/10.1093/oxfordjournals.molbev.a025705>
- Carmak, J.G. (1997) A synchronous expression of duplicate genes in angiosperms may cause apomixis, bispory, tetraspory, and polyembryony. *Biological Journal of the Linnean Society* 61: 51–94.
<http://dx.doi.org/10.1111/j.1095-8312.1997.tb01778.x>
- Chukavina, A.P. (1962) The undershrub species of the genus *Polygonum* from Tajikistan. *Izvestija Akademii Nauk Tadzhikskoi SSR. Otdel. Biol. Nauk* 2 (9): 62–68. [in Russian]
- Cullen, J. (1967) *Atraphaxis* L. In: Davis, P.H. (Ed.) *Flora of Turkey and the East Aegean Islands*, vol. 2. Edinburgh University Press, Edinburgh, pp. 266–267.
- Czerepanov, S.K. (1995) *Vascular Plants of Russia and adjacent states (within the former USSR)*. Mir – I – Semia-95, St. Petersburg, pp. 1–990.
- Drobow, V.P. (1953) *Atraphaxis* L. In: Korovin, E.P. (Ed.) *Flora Uzbekistana*, vol. 2. Academia Nauk Uzbekskoj SSR, Taschkent, pp. 120–127. [in Russian]
- Edman, G. (1931) Apomeiosis and Apomixis bei *Atraphaxis frutescens* C.Koch. *Acta horti bergiani* 11 (2): 11–66.
- Ekimova, N.V., Hrolenko, Yu.A., Muratova, E.N. & Silkin, P.P. (2009) Chromosome numbers and karyotypes of some species of the

- family Polygonaceae. *Botanichesky Zhurnal* 94 (2):148–153. [in Russian]
- Ekimova, N.V., Muratova, E.N. & Silkin, P.P. (2012) The role of Polyploidy in Adaptation and settling of Steppe Shrubs in Central Asia. *Russian Journal of Genetics: Applied Research* 2 (2): 105–109.
<http://dx.doi.org/10.1134/S2079059712020037>
- Fehrer, J., Gemeinholzer, B., Chrtek, J. & Bräutigam, S. (2007) Incongruent plastid and nuclear DNA phylogenies reveal ancient intergeneric hybridization in *Pilosella* hawkweeds (*Hieracium*, Cichorieae, Asteraceae). *Molecular Phylogenetics and Evolution* 42: 347–361.
<http://dx.doi.org/10.1016/j.ympev.2006.07.004>
- Ge, X.-J. & Liu, G.-J. (1994) Studies on the pollen shape of *Atraphaxis* L. in China. *Arid zone research* 11 (4): 8–13. [in Chinese]
- Grabovskaya-Borodina, A.E. (2012) *Atraphaxis* L. In: Takhtajan, A.L. (Ed.) *Conspectus Florae Caucasi*, vol. 3 (2). Consociatio editorium scientiarum KMK, Petropoli-Mosquae, pp. 270–271. [in Russian]
- Grossheim, A.A. (1930) *Flora Kavkaza*, vol. 2. *Trudy Tiflisskogo Botanicheskogo Sada*. Erevan, Tiflis, pp. 1–438. [in Russian]
- Grossheim, A.A. (1945) *Flora Kavkaza*, vol. 3. 2 ed. Akademia Nauk Azerbajanskoj SSR, Baku, 521 pp. [in Russian]
- Grubov, V.I. (1982) *Opredelitel sosudistykh rasteniy Mongolii (Key to the vascular plants of Mongolia, with atlas)*. Nauka, Leningrad, 442 pp. [in Russian]
- Gubanov, I.A. (1996) *Conspectus of Flora of Outer Mongolia: Vascular Plants*. Valang, Moscow, 136 pp. [in Russian]
- Guindon, S. & Gascuel, O. (2003) A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* 52: 696–704.
<http://dx.doi.org/10.1080/10635150390235520>
- Guindon, S., Dufayard, J.F., Lefort, V., Anisimova, M., Hordijk, W. & Gascuel, O. (2010) A new algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Systematic Biology* 59: 307–321.
<http://dx.doi.org/10.1093/sysbio/syq010>
- Hagemann, R. & Schröder, M.-B. (1989) The cytological basis of the plastid inheritance in angiosperms. *Protoplasma* 152: 57–64.
<http://dx.doi.org/10.1007/BF01323062>
- 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.
- Haraldson, K. (1978) Anatomy and Taxonomy in Polygonaceae subfam. Polygonoideae Meisn. emend. Jaretsky. *Symbolae Botanicae Upsaliensis* 22 (2): 1–95.
- Hong, S.-P. & Lee, S.-T. (1983) A palynological study of the Korean Polygonaceae. *Korean Journal of Plant Taxonomy* 13 (2): 63–76.
- Hong, S.-P., Oh, I.-C. & Ronse Decraene, L.-P. (2005) Pollen morphology of the genera *Polygonum* s. str. and *Polygonella* (Polygonaceae). *Plant Systematics and Evolution* 254: 13–30.
<http://dx.doi.org/10.1007/s00606-005-0334-4>
- Jaubert, H.-F.C. & Spach, E. (1844–1846) *Atraphaxis* L. In: *Illustrationes Plantarum Orientalium*, vol. 2. Roret, Paris, tab. 110–115.
- Kashina, L.I. (1992) *Atraphaxis* L. In: Lomonosova, M.N., Bolshakov, N.M. & Krasnoborov, I.M. (Eds.) *Flora Sibiriae*, vol. 5. Nauka, Sibir. otdel., Novosibirsk, pp. 108–109. [in Russian]
- Kastschenko, L.I. (1953) *Atraphaxis* L., *Polygonum* L. In: Vvedensky, A.I. (Ed.) *Flora Kyrgyzskoj SSR*, vol. 4. Akademia nauk Kyrgyzskoj SSR, Frunze, pp. 116–123, 124–147. [in Russian]
- Katoh, K. & Standley, D.M. (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780.
<http://dx.doi.org/10.1093/molbev/mst010>
- Katoh, K., Misawa, K., Kuma, K. & Miyata, T. (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30: 3059–3066.
<http://dx.doi.org/10.1093/nar/gkf436>
- Kovalevskaja, S.S. (1971) *Atraphaxis* L. In: Kovalevskaja, S.S. (Ed.) *Conspectus Florae Asiae Mediae*, vol. 2. Editio Academiae Scientiarum UzSSR, Tashkent, pp. 176–182. [in Russian]
- Krak, K., Caklova, P., Chrtek, J. & Fehrer, J. (2013) Reconstruction of phylogenetic relationship in a highly reticulate group with deep coalescence and recent speciation. *Heredity* 110: 138–151.
<http://dx.doi.org/10.1038/hdy.2012.100>
- Krasnov, A.N. (1888) Opyt istorii razvitiya flory yuzhnoi chasti Vostochnogo Tyan'Shanya (An Essay of the history of development of the Flora in the Southern Part of Eastern Tien Shan). *Zapiski Russkogo Geograficheskogo obschestva po obschey geografii* 19: 1–413. [in Russian]
- Krechetovitch, V.I. (1937) *Atraphaxis* L., *Polygonum* L. In: Fedchenko, B.A. (Ed.) *Flora Turkmenii*, vol. 2 (1). Akademia nauk SSSR, Turkmenskij Filial, Aschkehabad, Leningrad, pp. 47–55, 79–97. [in Russian]
- Kutateladze, Sh.I. (1975) *Atraphaxis* L. In: Ketskhoveli, N.N. (Ed.) *Flora Gruzii*, vol. 5. Metsniereba, Tbilisi, pp. 131–133. [in Georgian]
- Ledebour, C.F. (1830) *Flora Altaica*, vol. 2. G. Reimer, Berlin, pp. 1–464.
- Ledebour, C.F. (1847–1849) *Flora Rossica*, vol. 3. E. Schwiezerbart, Stuttgart, pp. 1–866.
- Lo, E.Y.Y., Stefanovič, S. & Dickinson, T.A. (2010) Reconstructing reticulation history in a phylogenetic framework and the potential of allopatric speciation driven by polyploidy in agamic complex in *Grataegus*. *Evolution* 64 (12): 3593–3608.

<http://dx.doi.org/10.1111/j.1558-5646.2010.01063.x>

- Losina-Losinskaya, A.S. (1927) Mongolian species of the genus *Atraphaxis*. *Izvestiya Glavnogo Botanicheskogo sada Akademii Nauk SSSR* 26 (1): 39–47. [in Russian]
- Lovelius, O.L. & Sjabrjaj, S.V. (1981) Evolution of the genus *Atraphaxis* L. on morphological data. In: Sytnik, K.M. (Ed.) *Problemy evolucionnoi morfologii i biohimii v sistematike i filogenii rastenii*. Naukova dumka, Kiev, pp. 100–104. [in Russian]
- Lovelius, O.L. (1978) Compositio specierum, Distributio geographica et cohaerentia oecologica generis *Atraphaxis* L. (Polygonaceae) *Novitates systematicae plantarum vascularium et non vascularium* 1977: 85–108. [in Russian]
- Lovelius, O.L. (1979) Synopsis generis *Atraphaxis* L. (Polygonaceae). *Novitates systematicae plantarum vascularium* 15: 114–128. [in Russian]
- Marschall von Bieberstein, L.B.Fr. (1819) *Flora Taurico-Caucasica*, vol. 3. Typis Academicis, Charkov, pp. 1–654.
- Meisner, C.F. (1857) Polygonaceae. In: Candolle, A.P. de (Ed.) *Prodromus Systematis Naturalis Regni vegetabilis*, vol. 14. V. Masson, Paris, pp. 1–186.
- Mignot, A., Hoss, C., Dajoz I., Leuret, C., Henry, J.-P., Dreuillaux, J.-M., Heberle-Bors, E. & Till-Bottraud, I. (1994) Pollen aperture polymorphism in the Angiosperms: importance, possible causes and consequences. *Acta Botanica Gallica* 141 (2): 109–122.
<http://dx.doi.org/10.1080/12538078.1994.10515144>
- Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Pirece, M. (Ed.) *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 Nov. 2010. New Orleans, LA, pp. 1–8.
<http://dx.doi.org/10.1109/GCE.2010.5676129>
- Mozaffarian, V. (1988) New species and new plant records from Iran. *Iranian Journal of Botany* 4 (1): 61–70.
- Mozaffarian, V. (2012) A revision of *Polygonum* L. sensu lato (Polygonaceae) in Iran. *Iranian Journal of Botany* 18 (2): 159–174.
- Nadot, S., Ballard, H.E., Creach, J.B. & Dajoz, I. (2000) The evolution of pollen heteromorphism in *Viola*: A phylogenetic approach. *Plant Systematics and Evolution* 223: 155–171.
<http://dx.doi.org/10.1007/BF00985276>
- Nikiforova, O.D. (2012) *Atraphaxis* L. In: Baikov, K.S. (Ed.) *Conspectus Florae Rossiae asiaticae: Plantae vasculares*. The Siberian branch of the Russian Acad. Sci., Novosibirsk, p. 115. [in Russian]
- Pavlov, N.V. (1936) *Atraphaxis* L. In: Komarov, V.L. (Ed.) *Flora URSS*, vol. 5. USSR Academy of Sciences, Moscow & Leningrad, pp. 501–527. [in Russian]
- Poczai, P. & Hyvönen, J. (2010) Nuclear ribosomal spacer regions in plant phylogenetics: problems and prospects. *Molecular Biology Reports* 37: 1897–1912.
<http://dx.doi.org/10.1007/s11033-009-9630-3>
- Qaiser, M. (2001) Polygonaceae. In: Ali, S.I. & Qaiser, M. (Eds.) *Flora of Pakistan*, vol. 205. University of Karachi, Karachi; Missouri Bot. Garden, St. Louis, pp. 1–190.
- Rambaut, A., Suchard, M.A., Xie, D. & Drummond, A.J. (2014) Tracer v.1.6. Available from: <http://tree.bio.ed.ac.uk/software/tracer/> (accessed 1 July 2016)
- Rechinger, K.H. & Schiman-Czeika, M. (1968) Polygonaceae. In: Rechinger, K.H. (Ed.) *Flora Iranica*, vol. 56. Akademische Druck-u.-Verlagsanstalt, Graz, Austria, pp. 1–88.
- Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.
<http://dx.doi.org/10.1093/bioinformatics/btg180>
- Ronse De Craene, L.-P. & Akeroyd, J.R. (1988) Generic limits in *Polygonum* and related genera (Polygonaceae) on the Basis of floral Characters. *Botanical Journal of the Linnean Society* 98 (4): 321–371.
<http://dx.doi.org/10.1111/j.1095-8339.1988.tb01706.x>
- Ryabkova, L.S. (1987) *Palinography of the flora of Tajikistan. Cyperaceae—Portulacaceae*. Academy of Sciences of Tajikistan SSR, Institut of Botany; Nauka, Leningrad, 1–108 pp. [in Russian]
- Rzazade, R.Ya. (1952) *Atraphaxis* L. In: Karjagin, I.I. (Ed.) *Flora Azerbajjana*, vol. 3. Akademia Nauk Azerbajskoj SSR, Baku, pp. 163–164. [in Russian]
- Sanchez, A., Schuster, T.M. & Kron, K.A. (2009) A large-scale phylogeny of Polygonaceae based on molecular data. *International Journal of Plant Sciences* 170 (8): 1044–1055.
<http://dx.doi.org/10.1086/605121>
- Sanchez, A., Schuster, T.M., Burke, J.M. & Kron, K.A. (2011) Taxonomy of Polygonoideae (Polygonaceae): a new tribal classification. *Taxon* 60(1): 151–160.
- Schuster, T.M., Reveal, J.L. & Kron, K.A. (2011b) Phylogeny of *Polygonoideae* (Polygonaceae: polygonoideae). *Taxon* 60 (6): 1653–1666.
- Schuster, T.M., Wilson, K.L. & Kron, K.A. (2011a) Phylogenetic relationships of *Muehlenbeckia*, *Fallopia*, and *Reynoutria* (Polygonaceae) investigated with chloroplast and nuclear sequence data. *International Journal of Plant Sciences* 172 (8): 1053–1066.
<http://dx.doi.org/10.1086/661293>
- Schuster, T.M., Reveal, J.L., Bayly, M.J. & Kron, K.A. (2015) An updated molecular phylogeny of Polygonoideae (Polygonaceae): Relationships of *Oxygonum*, *Pteroxygonum*, and *Rumex*, and a new circumscription of *Koenigia*. *Taxon* 64 (6): 1188–1208.
<http://dx.doi.org/10.12705/646.5>

- Shaw, J., Lickey, E.B., Schilling, E.E. & Small, R.L. (2007) Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: the tortoise and the hare III. *American Journal of Botany* 94: 275–288. <http://dx.doi.org/10.3732/ajb.94.3.275>
- Sitnikov, A.P. (1986) Pseudogamy in *Atraphaxis frutescens* (Polygonaceae) in Tatar SSR. Gametogenesis, fertilization and embryogenesis of seed plants, ferns and mosses. In: Chebotar, A.A. (Ed.) *IX Vsesoyuznoye Soveshaniye po embriologii rasteniy*. Shtiintsa, Kishinev, 1986, pp. 167–168. [in Russian]
- Sitnikov, A.P. (1991) *Variability of reproductive structures in the genus Polygonum L. and other members of Polygonaceae Juss.* Dissertation cand. biol. nauk, Kasan, 179 pp. [in Russian]
- Taberlet, P., Gielly, L., Pautou, G. & Bouvet, J. (1991) Universal primers for amplification of three regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1191. <http://dx.doi.org/10.1007/BF00037152>
- Tavakkoli, S., Kazempour Osaloo, S. & Maassoumi, A.A. (2010) The phylogeny of *Calligonum* and *Pteropyrum* (Polygonaceae) based on nuclear ribosomal DNA ITS and chloroplast trnL-F sequences. *Iranian Journal of Biotechnology* 8 (1): 7–15.
- Tavakkoli, S., Kazempour Osaloo, Sh. & Mozaffarian, V. (2014) *Atraphaxis binaludensis* (Polygonaceae), a new species from Northeastern Iran. *Iranian Journal of Botany* 20 (1): 1–3.
- Tavakkoli, S., Kazempour Osaloo, Sh., Mozaffarian, V. & Maassoumi, A. (2015) Molecular phylogeny of *Atraphaxis* and the woody *Polygonum* species (Polygonaceae): taxonomic implications based on molecular and morphological evidence. *Plant Systematics and Evolution* 301 (4): 1157–1170. <http://dx.doi.org/10.1007/s00606-014-1140-7>
- Tian, X.-M., Liu, R.R., Tian, B. & Liu, J.-Q. (2009) Karyological studies of *Parapteropyrum* and *Atraphaxis* (Polygonaceae). *Caryologia* 62 (4): 261–266.
- Van Leeuwen, P., Punt, W. & Hoen, P.P. (1988) The Norwest European Pollen Flora. 43: Polygonaceae. *Review of Palaeobotany and Palynology* 57: 81–151.
- Volkov, R.A., Komarova, N.Y. & Hemleben, V. (2007) Ribosomal DNA in plant hybrids: inheritance, rearrangement, expression. *Systematics and Biodiversity* 5 (3): 261–276.
- Webb, D.A. (1964) *Atraphaxis* L. In: Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M. & Webb, D.A. (Eds.) *Flora Europaea*, vol. 1. Cambridge University Press, Cambridge, p. 89.
- Weberling, F. (1989) *Morphology of flowers and inflorescences*. (Transl. by Punkhurst, R.J.). Cambridge University Press, Cambridge, 405 pp.
- Wendel, J.F. (2000) Genome evolution in polyploids. *Plant Molecular Biology* 42: 225–249.
- Wendel, J.F., Schnabel, A. & Seelanan, T. (1995a) Bidirectional interlocus concerted evolution following allopolyploid speciation in cotton (*Gossypium*). *Proceedings of the National Academy of Sciences of the United States of America* 92: 280–284.
- Wendel, J.F., Schnabel, A. & Seelanan, T. (1995b) An unusual ribosomal DNA sequence from *Gossypium gossypioides* reveals ancient, cryptic, intergenomic introgression. *Molecular Phylogenetics and Evolution* 4: 298–313.
- Whitton, J., Sears, C.J., Baack, E.J. & Otto, S.P. (2008) The dynamic nature of apomixis in the angiosperms. *International Journal of Plant Sciences* 169 (1): 169–182.
- Yurtseva, O.V., Troitsky, A.V., Bobrova, V.K. & Voylokova, V.N. (2010) On taxonomical revision of *Polygonum* L. s.str. (Polygonaceae): phylogenetic and morphological data. *Botanichesky Zhurnal* 95 (2): 226–247. [in Russian]
- Yurtseva, O.V., Kuznetsova, O.I., Severova, E.E. & Troitsky, A.V. (2012) Taxonomy and morphology of *Atraphaxis* (Polygoneae, Polygonaceae). In: Timonin, A.K., Sukhorukov, A.P., Harper, G.H. & Nilova, M.V. (Eds.) *Caryophyllales: New Insights into the Phylogeny, Systematics and Morphological Evolution of the Order. Proceedings of the Symposium held on 24–27 September 2012 at Moscow MV Lomonosov State University*. Grif & Co, Tula, pp. 114–118.
- Yurtseva, O.V., Severova, E.E. & Bovina, I.Yu. (2014) Pollen morphology and taxonomy of *Atraphaxis* (Polygoneae, Polygonaceae). *Plant Systematics and Evolution* 300 (4): 749–766. <http://dx.doi.org/10.1007/s00606-013-0917-4>
- Yurtseva, O.V., Kuznetsova, O.I., Mavrodiya, M.E. & Mavrodiya, E.V. (2016) What is *Atraphaxis* L. (Polygonaceae, Polygoneae): cryptic taxa and resolved taxonomic complexity instead of the formal lumping and the lack of morphological synapomorphies *PeerJ* 4:e1977. <http://dx.doi.org/10.7717/peerj.1977>
- Zhang, M.-L., Sanderson, S.C., Sun, Y.-X., Byalt, V.V. & Hao, X.-L. (2014) Tertiary montane origin of the Central Asian flora: evidence inferred from cpDNA sequences of *Atraphaxis* (Polygonaceae). *Journal of Integrative Plant Biology* 56 (12): 1125–1135.

APPENDIX 1. Taxa, voucher information, current sample and GenBank accession numbers used in the study. Herbarium acronyms according to Index Herbariorum. Asterisked are sequences obtained from Genbank.

Taxon	Locality, voucher information (herbarium code)	Sample num-ber	<i>rpl32-trnL</i> ^(UAG)	<i>trnL-trnF</i>
<i>Atraphaxis angustifolia</i> Jaub. & Spach	Armenia, Megri d. Zangezour Ridge. 1.06.1973. <i>Shvedchikova</i> (MW)	4	KU724453	KU508756
<i>A. ariana</i> (Grigorj.) T.M. Schust. & Reveal	Turkmenistan, [Badghys], v. Morgunovsky. 25.04.1988. <i>Gorelova</i> (LE)	122	KU724454	KU508757
<i>A. atraphaxiformis</i> (Botsch.) T.M. Schust. & Reveal	Kyrgyzstan, Alay Ridge, Kadamzhay. 19.07.2005. <i>Lazkov</i> (FRU) <i>Yurtseva et al.</i> 2010	41	KU724455	KU508758
<i>A. atraphaxiformis</i> (Botsch.) T.M. Schust. & Reveal	Uzbekistan, Alay, Turkestan Ridge, the Isphara. 07.1970. <i>Kamelin</i> 532 (LE)	43	KU724456	KU508759
<i>A. avenia</i> Botsch.	Kyrgyzstan, Alay Ridge, the Gulcha basin, Irgailysu, Sufi-Kurgan. 16.07.1987. <i>Pimenov & Klujkov</i> 407 (MW)	58	KU724457	KJ690694
<i>A. avenia</i> Botsch.	Kyrgyzstan, Osh reg., Kara-Kulzha d., Alay Ridge, basin of the Gulcha river, 2 km N of v. Gulcha. 10.08.2011. <i>Lazkov</i> (MW)	140	KX192201	KX192173
<i>A. aucherii</i> Jaub. & Spach	Tavakkoli <i>et al.</i> 2015		AB976694*	—
<i>A. badghysi</i> Kult.	Turkmenistan, Er Oylan-Duz. 21.04.1965. <i>Meschcheryakov</i> (LE)	13	KU724458	KU508760
<i>A. badghysi</i> Kult.	Turkmenistan, Badkhyz, fixed sands to S of saline Namaksaar. 25.06.1976. <i>Botschantsev</i> 259 (LE)	123	KX192202	KX192174
<i>A. binaludensis</i> S.Tavakkoli, Mozaff. & Kaz. Osaloo	Tavakkoli <i>et al.</i> 2015		AB976695*	—
<i>A. bracteata</i> Losinsk.	China, Inner Mongolia, Ikodzhoumen. 10.08.1957. <i>Petrow</i> (MW)	157	KU724459	KU508761
<i>A. caucasica</i> (Hoffm.) Pavlov	Georgia, Akhaltsihe. 26.05.1973. <i>Schvedchikova</i> (MW)	55	KX192203	KX192175
<i>A. caucasica</i> (Hoffm.) Pavlov	Russia, Daghestan, v. Untsukul, 7-8.07.1967. <i>Bekova</i> (MHA)	130	KX192204	KX192176
<i>A. compacta</i> (Hoffm.) Pavlov	Kazakhstan, Dzambul reg., Chu-Ili Mts., Sunkar-Tube (Khan-Tau). 14.05.1951. <i>Pavlov</i> 160 (MW)	45	KX192205	KX192177
<i>A. decipiens</i> Jaub. & Spach	Kazakhstan, Karaganda reg., Ulu-Tau Mts. 9.08.1957. <i>Karamysheva</i> 1979 (LE)	116	KX192206	KJ690701
<i>A. fischeri</i> Jaub. & Spach	Russia, Volgograd reg., Kirov d., Bolshaya Otrada. 7.05.09. <i>Klinkova & Suprun</i> 4 (MW)	19	KX192208	KX192179
<i>A. fischeri</i> Jaub. & Spach	Russia, Volgograd reg., Kirov d., Bolshaya Otrada. 7.05.09. <i>Klinkova & Suprun</i> 2 (MW)	20	KX192207	KX192180
<i>A. fischeri</i> Jaub. & Spach	West Kazakhstan, Atyrau reg. Inder. 04.05.2011. <i>Onipchenko</i> (MW)	33	KU724460	KJ690713
<i>A. frutescens</i> (L.) K.Koch	West Mongolia, Mongol Altay, Bayan-Olygiy aimag, the Bulgan river basin, Ikh-Dzhergalanta. 27.07.1988. <i>Kamelin et al.</i> 2298 (MW)	1	KX192209	KX192181
<i>A. frutescens</i> (L.) K.Koch	Russia, Saratov reg., Khvalynsky d., Elshanka. 04.07.2011. <i>Bulany</i> (MW)	66	KX192210	KJ690700
<i>A. frutescens</i> (L.) K.Koch	China, Xinjiang. 2010. <i>Olonova</i> (MW)	67	KU724461	KJ690702
<i>A. frutescens</i> (L.) K.Koch	Russia, Orenburg gub., Chkalovsk reg., Guberlinsky hills, 15 km W of Guberlinskaya. 23.06.1950. <i>Kirikov</i> (MW)	97	KX192211	KX192182
<i>A. frutescens</i> (L.) K.Koch	Russia, Orenburg reg., Saraktash d., 7 km SE of v. Gavrilovka. S. part of Sambula hills. 31.05.2011. <i>Abramova</i> (MW)	132	KX192212	KX192183
<i>A. intricata</i> Mozaff.	Tavakkoli <i>et al.</i> 2015		AB976698*	—
<i>A. kamelinii</i> O.V.Yurtseva	Mongolia, [Hovd (=Kobdo) aimag], the Dzungarian Gobi, S slope of Saertaengijin-Khuvch Uul (Mts.) near junction to Khaldzan-Ula (Mts.), 27.07.1984. <i>Daryima & Kamelin</i> 765 (LE)	50	KX192213	KJ690709

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APPENDIX 1. (Continued)

Taxon	Locality, voucher information (herbarium code)	Sample num-ber	<i>rpl32-trnL</i> ^(UAG)	<i>trnL-trnF</i>
<i>A. karataviensis</i> Pavlov & Lipsch.	Kazakhstan, Syr-Darya-Kara-Tau, Tersakkan, rocks. 4.07.1974. <i>Kamelin 1489</i> (LE)	47	KX192215	KX192184
<i>A. karataviensis</i> Pavlov & Lipsch.	Kyrgyzstan, Ichkem-Tau Mts., Orlovka. 07.1973. <i>Kamelin</i> (LE)	100	KU724462	KU508762
<i>A. karataviensis</i> Pavlov & Lipsch.	Kazakhstan, Syr-Darya, Kara-Tau, in cliff Kantagy. 3.07.1974. <i>Kamelin 1444</i> (LE)	101	KX192214	KX192185
<i>A. kopetdagensis</i> Kovalevsk.	Turkmenistan, the Central Kopet Dagh, Geok-Tepe d., Kara-Agach. 30.05.1972. <i>Mesheryakov</i> (LE)	19	KX192216	KX192186
<i>A. kopetdagensis</i> Kovalevsk.	Turkmenistan, Kazandzhik d. Trgoy Mts. 11–15.05.1981. <i>Proskuryakova</i> (MHA)	133	KU724463	KU508763
<i>A. laetevirens</i> Jaub. & Spach	Kazakhstan, Dzhungar Alatau, Kaikan Mts, Glinovka. 18.06.1959. <i>Goloskokov</i> (MW)	109	KU724464	KU508764
<i>A. laetevirens</i> Jaub. & Spach	Kazakhstan, Talas Alatau, Aksu-Dzabagly, pass Kshy-Kaindy, Akshy-Aksu. 11.08.1948. <i>Kultiasov</i> (MW)	111	KX192217	KX192187
<i>A. manshurica</i> Kitag.	NE China, Manchzhuriya, E slope of Khingan, Kogusten-Golt. 14.07.1899. <i>Potanin & Soldatov</i> (LE)	15	KX192218	KX192188
<i>A. muschketowi</i> Krasn.	Kazakhstan, Tian Shan, Zaily Alatau, Alma-Ata d., Mt. Kok-Tebe. 24.05.1998. <i>Majorov 98-246</i> (MW)	41	KU724465	KJ690697
<i>A. muschketowi</i> Krasn.	Kazakhstan, Zaily Alatau, Bolshaya Alma-Atinka, 1.06.1967. <i>Radugin</i> (LE)	61	KX192219	KX192189
<i>A. pungens</i> (M.Bieb.) Jaub. & Spach	Mongolia, Uver-Khangay, S of Tugrek, Bajangyin-Nuru (spurs of Dzegest-Ula). 27.07.1983. <i>Gubanov 7471</i> (MW)	115	KX192220	KJ690710
<i>A. pungens</i> (M.Bieb.) Jaub. & Spach	Russia, Khakassia, Shira d., Borets, right board of the river Son. 15.08.1993. <i>Pimenov & Vasilieva</i> (MW)	135	KX192221	KX192191
<i>A. pungens</i> (M.Bieb.) Jaub. & Spach	Mongolia, Central aimag, Telengyim-Baishin, Mt. Dzamryn-Ula. 23.06.1988. <i>Budantsev et al.</i> 27 (MW)	136	KU724466	KU508765
<i>A. pyrifolia</i> Bunge	Tadjikistan, Badakhshan, Schugnan d. the Gunt, Vozh × Shtamm. 02.08.2011. <i>Klujkov et al.</i> 26 (MW)	36	KU724467	KJ690696
<i>A. pyrifolia</i> Bunge	Tadjikistan, Central Pamir, Bokhud-river, cliff Bokhud. 16.07.1986. <i>Fedorov</i> (MW)	104	KX192222	KJ690695
<i>A. pyrifolia</i> Bunge	Kyrgyzstan, Chatkal Ridge, basin of Aflatun, 7.06.2011. <i>Lazkov</i> (MW)	137	KX192223	KX192192
<i>A. pyrifolia</i> Bunge	Kyrgyzstan, Alay Ridge, Osh d., the Ak-Bura river, influent Kyrk-Kege. 12.08.2011. <i>Lazkov</i> (MW)	138	KX192224	KX192193
<i>A. radkanensis</i> S. Tavakkoli, Kaz. Osaloo & Mozaff.	Tavakkoli <i>et al.</i> 2015		AB976701*	—
<i>A. replicata</i> Lam.	Kazakhstan, Usturt, Mangistau reg., Beyneu. 3.06.2003. <i>Sukhorukov</i> (MW)	24	KU724468	KJ690714
<i>A. replicata</i> Lam.	Kyrgyzstan, Alay, the Gulcha, Kyzyl-Kurgan. 08.07.1986. <i>Kuvaev 518-3</i> (MW)	31	KU724469	KJ690716
<i>A. replicata</i> Lam.	Russia, Saratov reg., Krasnoarmeysk d., between Belogorskoye and Nizhnaya Bannovka 21.07.2011. <i>Arhipova</i> (MW)	65	KX192225	KJ690711
<i>A. rodinii</i> Botsch.	Turkmenistan, Badhyz, Pynhangeshme Ridge. 27.04.1978. <i>Gorelova</i> (LE)	54	KX192226	KX192194
<i>A. rodinii</i> Botsch.	Turkmenistan, Badhyz, Akar-Cheshme. 11.05.1976. <i>Botchantsev 679</i> (LE) Isotypus	107	KX192227	KX192195
<i>A. seravschanica</i> Pavlov	Kyrgyzstan, Susamyr Mts, Chichkan valley, Toktogul. 7.06.1996. <i>Pimenov & Klujkov K96-59</i> (MW)	60	KX192228	KJ690692

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APPENDIX 1. (Continued)

Taxon	Locality, voucher information (herbarium code)	Sample num-ber	<i>rpl32-trnL</i> ^(UAG)	<i>trnL-trnF</i>
<i>A. seravschanica</i> Pavlov	Kyrgyzstan, Chatkal Ridge, Alabuksay, Alabuk. 2.09.1982. <i>Borodina, Philatova</i> (LE)	98	KU724470	KJ690693
<i>A. spinosa</i> L.	West Kazakhstan, Mangystau reg. Beyneu. 07.05.2011. <i>Onipchenko</i> (MW)	34	KU724471	KJ690715
<i>A. spinosa</i> L.	Armenia, Azizbeck d., Gerger forest, East Arpa-Tchay. 4.09.1951. <i>Surova</i> (MW)	53	KX192229	KX192196
<i>A. spinosa</i> L.	Daghestan, Usukh-Tchay, the Samur valley. 9.07.1940. <i>Elenevsky</i> (MW)	110	KX192230	KX192197
<i>A. spinosa</i> L.	Armenia, Ararat reg. Gorevan. 13.08.2012. <i>Lyskov</i> (MW)	141	KU724472	KU508766
<i>Atraphaxis suaedifolia</i> Jaub. & Spach	Tavakkoli <i>et al.</i> 2015		AB976705*	—
<i>A. teretifolia</i> (Popov) Kom.	Kazakhstan, Karaganda reg. Navaly-Sora, Mointy. 29.05.1951. <i>Pavlov 382</i> (MW)	114	KX192231	KX192198
<i>A. teretifolia</i> (Popov) Kom.	Kazakhstan, Karaganda reg., Dzheskazgan × Ula-Tau. 23.06.1958. <i>Rachkovskaya 6185</i> (LE)	142	KU724473	KU508767
<i>A. toktogulica</i> (Lazkov) T.M.Schust. & Reveal	Kyrgyzstan, Susamyrd Ridge, Kara-Dzhigach. 7.07.2005. <i>Lazkov</i> (FRU)	35	KU724474	KU508768
<i>A. tortuosa</i> Losinsk.	Mongolia, South Gobi aimag, SE of Nomgon, Shilt-Ula Mt. 19.07.1974. <i>Rachkovskaya & Volkova 6525</i> (LE)	12	KU724475	KU508769
<i>A. tortuosa</i> Losinsk.	Mongolia, East Gobi aimag, SW of Khuvsgul. 30.07.1971. <i>Isachenko & Rachkovskaya 1891</i> (LE)	52	KU724476	KU508770
<i>A. tortuosa</i> Losinsk.	Mongolia, South Gobi aimag, SE of Khan-Bogd.. 1972. <i>Rachkovskaya & Guricheva 21581</i> (LE)	99	KU724477	KU508771
<i>A. tournefortii</i> Jaub. & Spach	Turkey, Yozgat. 13.06.1975. <i>Browicz & Zielinski 582</i> (LE)	126	KU724478	KU508772
<i>A. tournefortii</i> Jaub. & Spach	Tavakkoli <i>et al.</i> 2015		AB976706*	—
<i>A. virgata</i> (Regel) Krasn.	Kazakhstan, South-Kazakhstan reg., Tulkubass d., the riverheads of Mashat, 29.09.2012. <i>Sagalaev</i> (MHA)	143	KX192232	KX192199
<i>A. virgata</i> (Regel) Krasn.	Kyrgyzstan, Kyrgyz Ridge, environs of Bishkek. 18.06.2011. <i>Lazkov</i> (MW)	144	KX192233	KX192200
<i>Polygonum aridum</i> Boiss. & Hausskn. ex Boiss.	Tavakkoli <i>et al.</i> 2015		AB976693*	—
<i>P. botuliforme</i> Mozaff.	Tavakkoli <i>et al.</i> 2015		AB976696*	—
<i>P. dumosum</i> Boiss.	Tavakkoli <i>et al.</i> 2015		AB976697*	—
<i>P. khajeh-jamali</i> Khosravi & Poormahdi	Tavakkoli <i>et al.</i> 2015		AB976700*	—
<i>P. salicornioides</i> Jaub. & Spach	Tavakkoli <i>et al.</i> 2015		AB976702*	—
<i>P. spinosum</i> H.Gross	Tavakkoli <i>et al.</i> 2015		AB976699*	—
<i>Bactria ovezinnikovii</i> (Czhukav.) O.V. Yurtseva & E.V. Mavrodiev (= <i>Polygonum ovezinnikovii</i> Czukav.)	Tajikistan, Khablon reg. Shuroabad d. the Piandzh, Bakhorak × Bag. 25.07.2013. <i>Ukrainskaya et al. 12.</i> (MW)	134	KU724452	KU508754

APPENDIX 2. Origin of the material used for LM micrographs and measurements in Table 3.

Atraphaxis compacta (Hoffm.) Pavlov. Kazakhstan, Dzambul reg., Chu-Ili Mts., Sunkar-Tube (Khan-Tau). 14.05.1951. Pavlov 160 (MW)

Atraphaxis kamelinii O.V.Yurtseva. Mongolia, [Khovd (=Kobdo) aimag], the Dzungarian Gobi, S slope of Saertaengijin-Khuvch Uul (Mts.) near junction to Khaldzan-Ula (Mts.), 27.07.1984. *Daryima & Kamelin* 765 (LE)

Atraphaxis replicata Lam. Kyrgyzstan, Alay, the Gulcha, Kyzyl-Kurgan. 08.07.1986. *Kuvaev* 518-3 (MW)

Atraphaxis pungens (M.Bieb.) Jaub. & Spach. Russia, Tuva Republic, Ulug-Khem d., Eastern slope of Tuva Basin to the river Senek. 25.06.1977. *Neifeld & Margasova* (MHA)

Atraphaxis pungens (M.Bieb.) Jaub. & Spach. Mongolia, The south of Bulgan aimag, Northern spurs of Khangay, 90 km to SEE of Kharkhorin, southern macroslope of Mt. Tsetserleg, near the former Buddhist monastery. 3.07.1980. *Gubanov* 3563 (MW)

Atraphaxis pungens (M.Bieb.) Jaub. & Spach. Russia, Tuva Republic, Ulug-Khem d., Uyük ridge, southern slope, near Bayan-Kol ferry, stony steppe. 6.08.1976. *Lomonosova & Ivanova* 2408 (MHA)

Atraphaxis pungens (M.Bieb.) Jaub. & Spach. Mongolia, Khovd aimag, 90 km to S of somon Bulgan, foothill plain of Baytag-Bogdo ridge. 9.08.1977. *Volkova & Rachkovskaya* 7373 (LE).

Atraphaxis pungens (M.Bieb.) Jaub. & Spach. Russia, Tuva Republic, Ulug-Khem d., environs of Shagonar, stony slope of hills. 15.06.1977. *Maltseva & Selisheva* (MW)

Atraphaxis virgata (Regel) Krassn. Mongolia, Transaltay Gobi, Gobi-Altay aimag, Atas-Bogdo-Ula Mts. In hollows on the slopes at an altitude of 1300-1600 m. a.s.l. 1.08.1978. *Gubanov* 2634 (MW).