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Chenopodium pamiricum (Amaranthaceae) and allied species in Asia: the prolonged misapplication of names

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Up to the late 1990s and early 2000s, several small-leaved species of *Chenopodium* (Amaranthaceae *s. lato*/Chenopodiaceae *s. stricto*) were frequently misnamed in floras of central Asia and Siberia. Two widespread taxa, *C. prostratum* (now accepted as *C. karoi*) and *C. vulvaria*, were commonly recognized. However, the latter is absent from Siberia and occurs only in the southwestern central Asia. Further north the name '*vulvaria*' was misapplied to two species, *C. pamiricum* and *C. grubovii* Lomon. & Uotila *sp. nova*, characterized by procumbent stem branched mostly basally and entire, ovate leaf blade. *Chenopodium pamiricum*, distinguished by erect stem branched along the whole length and trilobate to entire, trullate leaf blade, was earlier often known by the synonymous name *C. iljinii* and misapplied to *C. grubovii*. They can be distinguished from *C. vulvaria* and *C. karoi* by their deeply divided perianth lobes and broadly ovate seeds; from each other they mostly differ in the growth habit and leaf characters. *Chenopodium karoi* is very widely distributed, from the Hindu Kush and the Himalayas to northern and northeastern Asia, *C. pamiricum* and *C. grubovii* occur on high mountains from the Hindu Kush, Pamir, and western Himalayas as far as southern Siberia, Mongolia, and central and western China, the latter species being more common in the north. *Chenopodium grubovii* grows at higher elevations than *C. pamiricum* and both species usually grow at higher elevations than *C. karoi*. A key, descriptions, drawings, and distribution maps for these species are provided.

Introduction

The widespread introduction of molecular phylogenetic methods in plant research has led to revisions of many plant groups, including *Chenopodium* (Amaranthaceae *s. lato*/Chenopodiaceae *s. stricto*). Since the recognition of several smaller genera distinct from *Chenopodium* on molecular and morphological grounds (Fuentes-Bazan *et al*. 2012b), much effort in the core genus (*Chenopodium s. stricto*) has been directed especially to *C. album* and allied species, often called the *C. album* aggregate (Mandák *et al*. 2016, 2018, and references therein). Regarding the other species of *Chenopodium s. stricto*, *C. vulvaria* was usually included in recent analysis, but other

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morphologically similar species were less frequently studied, and an incomplete understanding of their variation and taxonomy has caused additional difficulties in interpreting the results.

Chenopodium vulvaria is a well-known and widespread species with usually richly branched procumbent to ascending stems, silvery-grey colour, small ovate leaves with entire margins, and a particularly unpleasant smell, readily contaminating fingers when handling fresh plants and still perceptible even in old herbarium specimens. All major floras cited the smell for distinguishing *C. vulvaria* from other annual *Chenopodium* species. It is the only *Chenopodium* species in Europe with such a combination of characters (with exception of several rare and occasional aliens) and when fairly similar plants were found in Asia, they were also assumed to be *C. vulvaria*. However, it was gradually realised that there are other similar taxa in Asia, although the presence of *C. vulvaria* in central Asia and Siberia was not explicitly questioned.

The aim of our study was to clarify the taxonomy of the small-leaved Asian taxa resembling *C. vulvaria*, especially in central Asia and Siberia, to give morphological descriptions and distribution maps for the taxa in question, and to clarify the prolonged misapplication of the name *C. vulvaria* in central and north Asian floras. This paper supplements our earlier study of the variation and taxonomy of *C. acerifolium* and *C. karoi* (Uotila & Lomonosova 2016).

Material and methods

This study was based mainly on the rich Asian herbarium material of *Chenopodium* species in AA (Almaty), ALTB (Barnaul), B (Berlin), BIEL (Bielefeld), BM (London), C (Copenhagen), E (Edinburgh), FI (Firenze), FRU (Bishkek), G (Geneva), H (Helsinki), IRK (Irkutsk), IRKU (Irkutsk), KAS (Kassel), KRAS (Krasnoyarsk), KUH (Karachi), LD (Lund), LE (St. Petersburg), M (München), MAG (Magadan), MHA (Moscow), MW (Moscow), NSK (Novosibirsk), NS (Novosibirsk), P (Paris), PRA (Pruhonice), RAW (Rawalpindi), S (Stockholm), TASH (Tashkent), TK (Tomsk), SASY (Yakutsk), SVER (Ekaterinburg), UDU (Izhevsk), VLA (Vladivostok), W (Vienna). The herbarium acronyms follow *Index Herbariorum* (http://sweetgum.nybg.org/science/ih). In addition, images were checked of herbarium specimens identified as *C. karoi*, *C. pamiricum*, *C. iljinii* or *C. vulvaria*, and some of the large number of *C. album*, available in the Chinese Virtual Herbarium (*see* http://www.cvh.ac.cn). The data, compiled from the studied specimens and Chinese Virtual Herbarium images were used for preparing the distribution maps published by us in GBIF (https://www.gbif.org/dataset/2342ed8e-8ef4-4181-97ca-e48faa860439).

In 2013–2017, the first author paid special attention to this group during her field excursions in Siberia, the Russian Far East, and Kazakhstan. The seeds collected during these excursions were cultivated in experimental pots in the Central Siberian Botanical Garden (Novosibirsk) in 2014–2018.

The borders of central Asia have been understood in different ways. We recognize central Asia in a wide, practical sense, i.e., for the area south of Siberia and north of Iran and Afghanistan, so including western China as well as Kazakhstan, Uzbekistan, Kyrgyzstan, Turkmenistan, and Tajikistan. In the Russian literature, the area of these republics has been frequently called Middle Asia (and earlier Turkestan). Central Asia, as defined by Grubov (1959, 1963) extends from the lower Volga in the west to the Greater Khingan mountains in the east, including most of Kazakhstan, Dzungaria, Kashgaria, most of Mongolia, Tsaidam, Tibet, Qinghai, and the Eastern Pamir Mountains.

History of naming species resembling *Chenopodium vulvaria* in central Asia and Siberia

Alexander von Bunge was the first botanist to use in his "*Enumeratio Salsolacearum centrasiaticarum*" (Bunge 1880) the name *Chenopodium vulvaria* for plants from central Asia. He referred to Ledebour (1849–1851), but there the range of *C. vulvaria* was given as "*Rossia media et australi inque Tauria et provinciis caucasicis*", so it did not include central Asia. Bunge (1880) cited

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all specimens collected by A. Regel from eastern Turkestan (northwestern China) and preserved in LE. These collections include three species (*C. karoi*, *C. pamiricum*, and *C. grubovii*, described below) included in our study. Later, Bunge (in Herder 1889) described the related *C. prostratum* from northern Siberia. This name was not used before Iljin and Aellen (1936) in *Flora of the USSR*; however, they did not notice that the name was illegitimate and the correct name is *C. karoi*. Since the *Flora of the USSR* was a standard reference work for Russian botany, this illegitimate name was used continuously and became established in Russian floras and other literature until the 2010s (for details, *see* Uotila & Lomonosova 2016).

Olga A. Fedchenko and Boris A. Fedchenko summarized in their *Conspectus florae Turkestanicae* (Fedchenko & Fedchenko 1913) the floristic information accumulated by the early 20th century from the territory formerly called Russian Turkestan, a wide area from the Caspian region to Kul'dzha (now Yining or Ghulja/Qulja, western China). These authors used the same concept as Bunge and mentioned *C. vulvaria* as "widespread in weedy places throughout Turkestan" and in Persia (Iran and some neighboring territories), Europe, and other countries and regions as well. Boris Fedchenko's student and follower Zinaida A. von Minkwits identified many *Chenopodium* specimens in LE collected in the European part of Russia and former Turkestan as *C. vulvaria*. Porfiriy N. Krylov also accepted Bunge's concept of *C. vulvaria* in his *Flora Altaya i Tomskoi gubernii* (Krylov 1909). In the updated edition (Krylov & Sergievskaya 1930), *C. vulvaria* was described, along with other characters, as "an annual malodorous plant ...". The authors cited many specimens (in TK, LE) from the southeastern Altai (Chuya steppe, Ukok) and the Saur Mountains.

According to Iljin and Aellen (1936), the range of *C. vulvaria* in the former USSR covered southern Ukraine, southern European Russia, western Siberia "U.Tob.(?), Irt. (?)", and central Asia "Ar.-Casp.(?), Pamir-Alatau (Samarkand)". They were uncertain of the presence of *C. vulvaria* in Asia because Asian occurrences (except for Samarkand) were qualified with question marks. Furthermore, they included no locality of *C. vulvaria*, cited by Krylov and Sergievskaya (1930) in the *Flora of Western Siberia* from the Altai, but for other species of *Chenopodium s. lato* the *Flora of Western Siberia* was cited.

Paul Aellen borrowed *Chenopodium* specimens from LE for his treatment of the genus for the *Flora of the USSR* (*see* Uotila & Lomonosova 2016), and in 1933 he revised the specimens filed as *C. vulvaria.* He determined the specimens collected from the mountains of eastern Kazakhstan and western China as "*C. karoi"*, "*C. sosnowskyi* subsp. *kapelleriae* nov.", "*C. atripliciforme* Murr subsp. *kapelleriae* nov." and (one specimen) "prob. *C. sosnowskyi*". With the epithet *kapellariae*, Aellen wanted to honour Olga Antonovna Kapeller (1892–1975), who a few years earlier described from the Caucasus area one more species resembling *C. vulvaria*, namely *C. sosnowskyi* (Kapeller 1927). However, in the *Flora of the USSR* Aellen's taxon was mentioned as *C. bryoniifolium* var. *kapelleriae*, with an additional comment that "It may be assumed that this is a distinct species" (Iljin & Aellen 1936). *Chenopodium atripliciforme* was transferred into the synonymy of *C. bryoniifolium*, which explains why the infraspecific entity on the identification labels was moved to *C. bryoniifolium* in the *Flora*. Unfortunately, the new taxon remained illegitimate because of the lack of a Latin diagnosis, a requirement as from 1 January, 1935 (Turland *et al*. 2018: Art. 39.1).

In the Addenda of the *Flora of the USSR* vol. 6, Iljin (1936) described *C. pamiricum* as a new species from the Pamir. In the description he pointed out that this species has "*habitu Ch. vulvaria L., non foetida ...*", but considered it related to *C. prostratum* (= *C. karoi*). After an excursion to central Asia in the summer of 1934 Iljin wrote to Aellen that he had added this new species to the *Flora*. Aellen had already sent his manuscript of *Chenopodium* to Iljin (in February 1934; *see* Uotila & Lomonosova 2016) and did not see the final text before publication. Actually both authors of the *Chenopodium* treatment paid attention to the same taxon and described it in the flora as a novelty with different names: *C. bryoniifolium* var. *kapelleriae* and *C. pamiricum*.

Goloskokov (1950) raised Aellen's var. *kapelleriae* to the rank of species and described it as *C. iljinii*. In the protologue he cited 11

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specimens from eastern Kazakhstan and western China, eight of which were determined by Aellen as *C. atripliciforme* subsp. *kapelleriae* nov. (including the type specimen) or *C. sosnowskyi* subsp. *kapelleriae* nov.

Later Aellen identified several fragments taken from LE specimens for his herbarium (now in G) as *C.* cf. *pamiricum*. Because of several finds in Europe, *C. karoi*, *C. pamiricum* and *C. sosnowskyi* were included as casual non-established aliens in the treatment of *Chenopodium* in Hegi's *Illustrierte Flora von Mitteleuropa* (Aellen 1960). The morphological description of *C. pamiricum* and the drawing of a subhastate leaf indicate that in this flora Aellen included in *C. pamiricum* the plants that he had called "var. *kapelleriae*". But he also believed that the range of *C. sosnowskyi* extended as far as Afghanistan and Turkestan (Aellen 1960, 1967). However, it seems that Aellen was not so well aware of the group: he had seen the type material of neither *C. pamiricum* nor *C. iljinii* and very little additional material after the treatment for the *Flora of the USSR*.

Since Iljin and Aellen (1936) and Goloskokov (1950), *C. vulvaria*, *C. pamiricum* and *C. iljinii* were variously included in floras and checklists covering the territory of central Asia and Siberia. *Chenopodium vulvaria* was mentioned as the only one of these species from Turkmenistan (Iljin 1937), Uzbekistan (Bochantzev 1953) and Kyrgyzstan (Nikitina 1955), but later Nikitina (1967) recognized that the Kyrgyz report was in error and accepted *C. iljinii* and *C. prostratum* for the country. However, Gubanov (1970) soon added *C. vulvaria* to the Kyrgyz flora. Two species, *C. iljinii* and *C. vulvaria*, were included in Kazakh floras (Goloskokov & Polyakov 1955, Goloskokov 1960), *Plantae Asiae Centralis* (Grubov 1966), and the *Flora of Siberia* (Lomonosova 1992, 2003). Grubov (1966) added *C. bryoniifolium* var. *kapelleriae* in the synonymy of *C. iljini* and noted that *C. iljinii* is probably the hybrid *C. album* × *vulvaria*. Sidorenko *et al.* (1968) accepted *C. pamiricum*, *C. iljinii* and *C. vulvaria* for Tajikistan; Ikonnikov (1963, 1979) listed *C. pamiricum* and *C. vulvaria* for the Pamir; and Pratov (1972) mentioned the same species for middle Asia (i.e. Kazakhstan, Uzbekistan, Kyrgyzstan, Turkmenistan and Tajikistan). It is noteworthy that the latter placed *C. iljinii* in the synonymy of *C. album*; such incorrect synonymization was still being followed by Lazkov and Sultanova (2011).

When Ignatov (1988) accepted *C. vulvaria* for the Russian Far East he misidentified the only collection of '*C. prostratum*' (= *C. karoi*) from Amur Region as *C. vulvaria*. Czerepanov (1995) in *Vascular Plants of Russia and Adjacent States* and Govaerts (1999) in the *World Checklist* listed *C. iljinii*, *C. pamiricum* and *C. vulvaria* for that area. *Chenopodium iljinii* and *C. vulvaria* were accepted by Lomonosova (2012) in *Conspectus florae Rossiae Asiaticae*, by Urgamal *et al.* (2014) for Mongolia, and were listed in 2021 in the *Virtual Guide to the Flora of Mongolia* (http://floragreif.uni-greifswald.de/floragreif/).

While *C. vulvaria* was not accepted in Chinese floras, *C. iljinii* was included (e.g., Kung & Chu 1979, Mao 1994, Liu 1997, Zhu *et al.* 2003), in Zhu *et al.* (2003) with comments on the possible confusion of *C. iljinii* with *C. pamiricum*. Many digitized herbarium specimens from "Chinese Virtual Herbarium (CVH): A National Taxonomic Database" (http://www.cvh.org.cn) labelled as *C. iljinii*, were previously identified as *C. pamiricum*.

Taxonomy

The studied group of species resembling *C. vulvaria* is usually easy to distinguish from the other species of the genus. In addition to their small size and small leaves, they typically have an erect to ascending or procumbent stem with often long branches, especially in the basal parts; ± grey colour due to dense cover of vesicular hairs at least in young parts and on the lower surface of leaves; small, usually ± ovate to broadly ovate, ± entire or slightly trilobate leaves; and mostly leafy inflorescences composed of smaller or larger glomerules.

Key to the species of *Chenopodium* resembling *C. vulvaria*

1. Leaf blade (5)15–25(40) mm; perianth segments lobed at most to halfway; seeds round 2

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Fig. 1. Habit of *Chenopodium vulvaria* (Kazakhstan, Karatau, 1934 *N.V. Pavlov 141*; MW0821312).

1. Leaf blade (3)5–15(30) mm, perianth segments free to near base; seeds slightly ovate 3
2. Plant not malodorous; leaf blade slightly 3-lobed with rounded lobes, or sometimes entire; seed coat finely pitted ..... *C. karoi*
2. Plant malodorous; leaf blade entire, sometimes angled at broadest point; seed coat ± smooth ..... *C. vulvaria*
3. Stems procumbent, branched mostly basally; leaf blade entire, ovate ..... *C. grubovii*
3. Stems ± erect, branched for whole length; leaf blade trullate, with distinct angle on both sides near base .... *C. pamiricum*

Chenopodium vulvaria L. (Fig. 1)

Sp. Pl.: 220. 1753. — Lectotype (designated by Jafri & Raateb 1978): 'Habitat in Europae cultis oleraceis', Herb. Linn. No. 313/18 (LINN!).

Strongly grey-farinose annual, malodorous, smell persistent in herbarium specimens for years. Stem to 30 cm long, erect to procumbent, hard, yellowish, green striped, lacking red colour, usually divaricately much branched basally, seldom branchless; lowermost internodes short and lower branches subopposite, to 70 cm long, ascending to prostrate, secondary branches usually short. Young leaves very densely grey-farinose; petiole shorter than or equal to blade; mature blade densely farinose below, more sparsely farinose and later gla-

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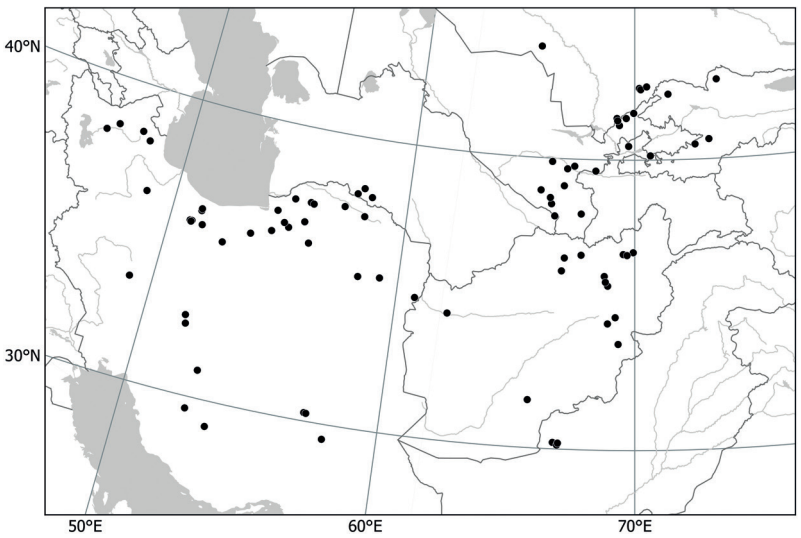


Fig. 2. Distribution of *Chenopodium vulvaria* in central Asia and *Flora Iranica* area (Iranian highlands and adjacent mountains in Iran, Afghanistan, Pakistan, Iraq, Azerbaijan and Turkmenistan) according to revised herbarium specimens (https://www.gbif.org/dataset/2342ed8e-8ef4-4181-97ca-e48faa860439; Uotila 1997).

brescent, greener above, (5)10–30 mm, ovate to broadly triangular-ovate, broadest point sometimes with a spreading lobe-like tooth or angle on both sides, base ± rounded, margins entire, apex obtuse to acute, upper leaves narrower, ovate. Inflorescence terminal and axillary, leafy, composed of loose, short thyrses; glomerules small. Flowers perfect or female; perianth lobes densely farinose, 5, connate 2/3–4/5 from base, with rounded back. Fruits falling with perianth; pericarp somewhat adherent. Seeds horizontal, brownish black, (0.9)1.0–1.2 mm in diameter, round, lenticular, margin fairly obtuse; testa almost smooth except for weak radial striae. 2n = 18 (numerous reliable counts from Europe, *see* Rice *et al.* 2015).

Habitat and distribution. In Iran, Afghanistan, Pakistan and the southern margin of central Asia, *C. vulvaria* typically grows in gardens, roadsides, field margins, wastelands in villages and towns, cattle gathering places, so almost exclusively in strongly human affected areas at 450–2500 m a.s.l. It is occasional in Iran and Afghanistan and rare further north (Fig. 2). Occurrences in southwestern and eastern Turkmenistan and southern Uzbekistan are phytogeographically connected to the Iranian and Afghan occurrences and possibly native. Further north, in Uzbekistan, Tajikistan, Kyrgyzstan and Kazakhstan, the finds most probably represent introductions, which may have become established as reported from Kyrgyzstan, Kara-Balta by Lazkov and Sennikov (2014). Mosyakin (1996) regarded *C. vulvaria* as native only in the Mediterranean area and southwestern Asia, and elsewhere introduced.

The overall more or less continuous distribution range of *C. vulvaria* covers mainly dry and warm parts of Europe, the Mediterranean area, Turkey, and the Caucasus area (*see* https://europlusmed.org/cdm_dataportal/taxon/506d11c8-a85d-4e02-9196-54cd60931324, and Groom 2015), the foothills and Mesopotamian Plain of Iraq (Sukhorukov *et al.* 2016), and Iran and Afghanistan (Uotila 1997). However, it seems to be absent from the desert areas in Iraq, central and southern Iran, and lower areas of Afghanistan, or is known there from gardens in towns. Such finds, as well as reports, from the Arabian Peninsula: Yemen and Oman (Boulos 1996), Saudi Arabia (Chaudhary 1999), and from Pakistan (Uotila 2001a), may well represent introduced plants. The species is reported as introduced at least in North America (California and several states in the east; Clemants & Mosyakin 2003), South America (Argentina and Chile; Mulgúra & Marticorena 2008) and Australia (southeastern part; Wilson 1984).

Notes. The foul smell of trimethylamine is characteristic for *C. vulvaria* (*see* also discussion below). The smell is intense in fresh plants and can be brought back in herbarium specimens several years old by slightly moistening the plant and rubbing it between finger and thumb,

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whereas the possibly similar smell in other species of the group is weaker and not easy to generate from dried herbarium specimens. However, the intensity of the smell in *C. vulvaria* can vary, and populations almost without smell when fresh were noted in the eastern Mediterranean (Sukhorukov *et al.* 2016).

In addition to the smell, several morphological characters distinguish *C. vulvaria* from the other species of the group. As in *C. karoi*, its perianth is connate to the middle or even further, and seeds are ± circular in outline, whereas in *C. grubovii* and *C. pamiricum* the perianth segments are free almost to the base and seeds are ovate in outline. In *C. vulvaria*, the leaf blade is entire with entire margins and the seed testa ± smooth; in contrast, in *C. karoi* the blade is mostly somewhat trilobate with a few small teeth on the margins, and the seed testa pitted.

The name *C. vulvaria* was misapplied to *C. pamiricum* (and *C. iljinii*) and/or *C. grubovii* in practically all central Asian and Siberian floras up to the early 2000s (*see* the chapter "History of naming species …" above). However, despite the morphological similarity, *C. vulvaria* is not related to them. In recent phylogenetic analysis, it was proved to be sister to all other *Chenopodium* species (Fuentes-Bazan *et al.* 2012a, Mandák *et al.* 2016, 2018). It was thus separated in *Chenopodium* sect. *Vulvaria* (Mosyakin & Iamonico (2017: 264). The morphologically fairly similar species *C. sosnowskyi* is probably its closest relative.

Chenopodium grubovii Lomon. & Uotila, *sp. nova* (Figs. 3 and 4)

Holotype: Russia. Altai Republic, Kosh-Agach district, 50.07379°N, 88.42288°E, 1777 m a.s.l., vicinity of Chegan-Uzun village, nomad camp "Tydtuyaryk", 8 September 2018 *E. Korolyuk & A. Korolyuk 5* (NS0000481!).

Chenopodium pamiricum auct. non Iljin: Ikonnikov, Manual of the plants of the Pamirs: 1963: 98, p.p.; Sidorenko, Kinzikaeva & Ovchinnikov in Ovchinnikov (ed.), Flora of the Tajik SSR, 3: 327. 1968, p.p.; Pratov in Bondarenko & Nabiev (eds.), Consp. Fl. As. Med. 3: 41. 1972, p.p.

Chenopodium vulvaria auct.

Etymology: The species is named in honour of Valery Ivanovich Grubov (1917–2009), an outstanding Russian botanist, who greatly contributed to knowledge of the flora of central Asia.

Annual, sometimes somewhat malodorous when fresh, smell persistent in herbarium specimens only for one or two years. Plant 4–40 cm in diameter; stem 2–20(30) cm long, procumbent, thin, yellowish to reddish, without red spots in leaf axils, much branched from base, internodes short; branches fairly equal in length, often equal to or longer than main stem, usually upward curving, lowermost subopposite, secondary branches few and short. Leaves whitish especially below because of dense vesicular trichomes, later less hairy and turning glaucous or greenish; petiole ± as long as blade, in upper leaves shorter; blade (3)5–10(20) mm, ovate to broadly ovate, entire, base short attenuate to rounded, apex ± acute, margins entire. Inflorescence paniculate, of small, fairly loose glomerules on branches and in leaf axils. Flowers perfect or female; perianth lobes 5, green, farinose, free almost to base, slightly elevated on back, midrib rather strong; stamens 5 or 0; stigmas 2. Fruits mostly falling without perianth; pericarp fairly easily removable. Seeds horizontal, black, 0.9–1.0(1.1) × 0.8–0.9 mm in diameter, broadly ovate, lenticular, margin somewhat acute, testa faintly striate, otherwise smooth. 2n = 18 (Lomonosova & Krasnikov 1994, Lomonosova *et al.* 2003; both as *C. vulvaria*).

Habitat and distribution. *Chenopodium grubovii* grows on stony, gravely or desert steppes, on clay patches at high elevations (2000–5000 m a.s.l.) of the Hindu Kush, northwestern Himalayas, Pamir, Tian Shan and Tibet, and in lower elevations further north, in the Altai and Sayan mountains, and in mountain ranges of Mongolia up to 2200 m a.s.l. (Fig. 5). Klimeš and Dickoré (2005) recorded '*C. pamiricum*' from India, Ladakh (Jammu & Kashmir) and Sukhorukov *et al*. (2019) from India (Jammu & Kashmir) and China (Tibet, Ngari Prefecture), at 3500–4500 m a.s.l. The description and distribution (map included in Sukhorukov *et al*. 2019) better match *C. grubovii* than *C. pamiricum*. All specimens of '*C. pamiricum*' for *Flora Iranica* (Uotila 1997) and *Flora of Pakistan* (Uotila 2001a) have not been rechecked recently, but they probably belong to *C. grubovii*. Aellen determined several specimens collected from Germany, Leipzig, from a spinning mill and with wool brought from Mongolia, as *C. pamiricum* or *C. karoi.* At least one of them belongs to *C. grubovii*.

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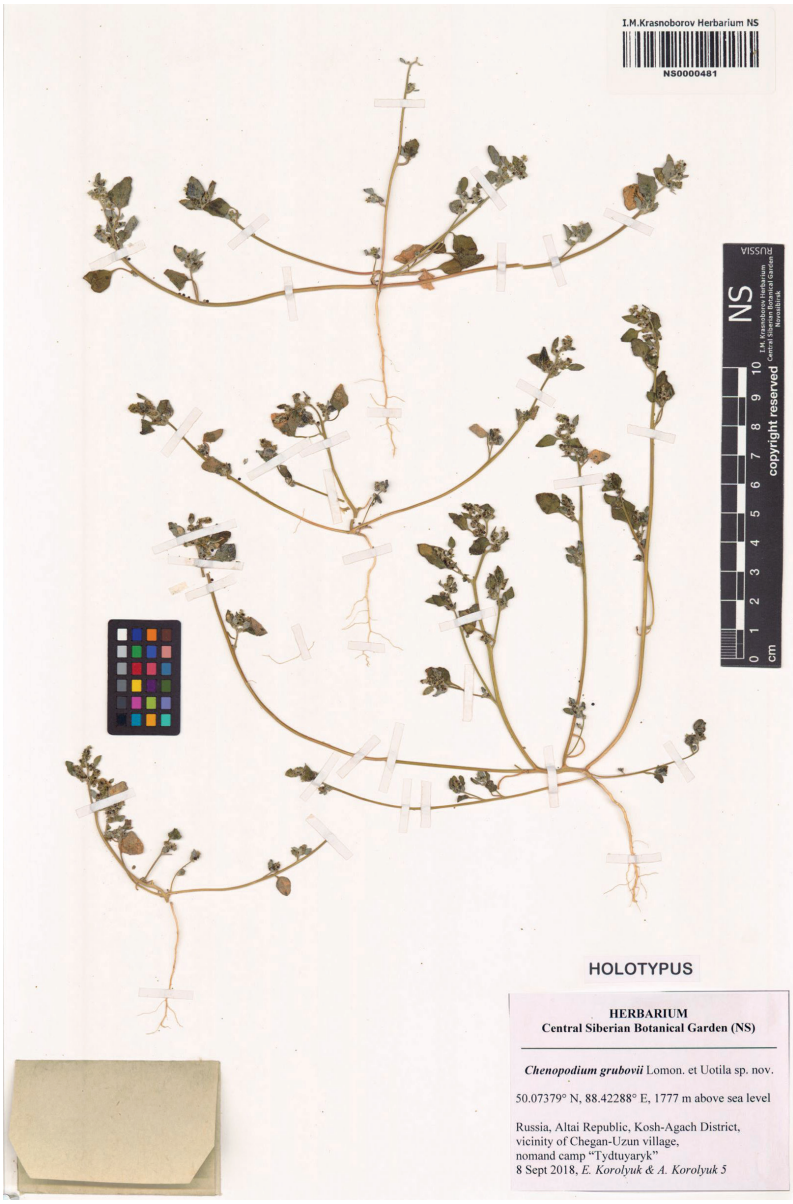


Fig. 3. Holotype of *Chenopodium grubovii* (NS0000481).

NOTES. In general, perianth and seed characters easily distinguish *C. grubovii* from small specimens of *C. karoi* and *C. vulvaria*. However, its morphological variation is quite wide and northern taller plants resemble *C. vulvaria* in habit more than the southern ones. Furthermore, plants of *C. grubovii* from the Altai may have a foul smell similar to that of *C. vulvaria*, although weaker. *Chenopodium grubovii* and *C. pamiricum* have similar flowers but seeds of slightly different sizes. The best characters to separate them are the leaf shape and colour. *Chenopodium grubovii* has ovate, entire leaves, whereas those of *C. pamiricum* are more or less trullate, mostly with spreading small lobes in the broadest part and elongated apical part; if without lobes the leaves have distinct angles in the lower parts. At high elevations, those two and *C. karoi* may be very small and rather similar in habit. *Chenopodium grubovii* typically grows at higher elevations than *C. pamiricum* and *C. karoi*, and it is more southern than *C. pamiricum*.

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Fig. 4. Habit of *Chenopodium grubovii* (Russia, Tyva, 1982 *I. Krasnoborov & L. Mironova s.n.*; NS).

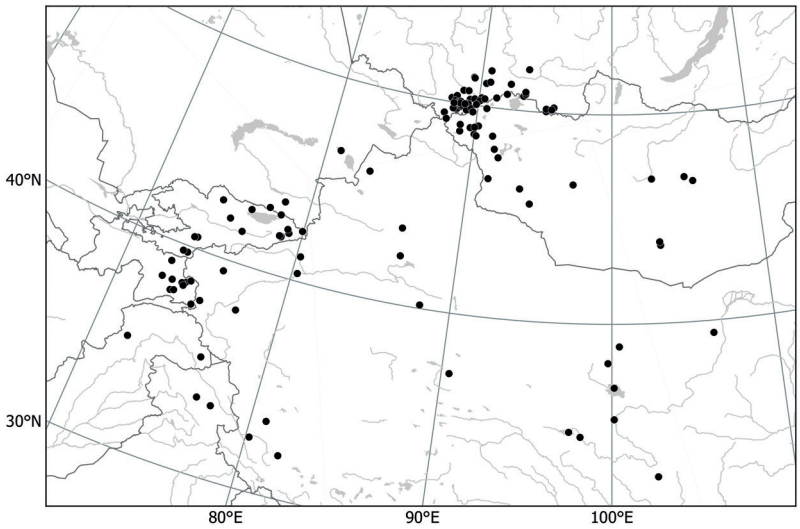


Fig. 5. Distribution of *Chenopodium grubovii* according to revised herbarium specimens (https://www.gbif.org/dataset/2342ed8e-8ef4-4181-97ca-e48faa860439).

Chenopodium pamiricum Iljin (Figs. 6 and 7)

Fl. RSSS 6: 70, in obs., 873. 1936 — Holotype: [Tajikistan] Declivia ad confluentes Baital et Murgab, 1 November 1923 *I. Raikova* (TASH0000487!); isotype (fragment from TASH; LE!).

Chenopodium iljinii Golosk., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 13: 65. 1950. — Holotype: [Kyrgyzstan] Tian-schan centralis, fl. Kochkor [systema fl. Czu (Tschu)], 8 August 1928 *E. Nikitina & I. Vykhodtsev* (LE!).

Chenopodium bryoniifolium var. *kapellariae* Aellen *ex* Iljin & Aellen, Fl. URSS 6: 67. 1936, *nom. inval*. (Turland *et al*. 2018: Art 39.1; no Latin description).

Chenopodium album auct. non L.; Pratov, Consp. Fl. As. Med. 3: 41. 1972, *p.p. min*.

Chenopodium vulvaria auct.

Annual, not malodorous, densely grey-farinose when young, later turning more glabrescent. Stem 10–30 cm long, erect, sometimes ascending from base, thickish, hard, weakly green-striped, usually without red colour but sometimes later turning red, branched along entire stem or in middle part; branches shorter than or equal to main stem and thinner, ascending to almost spreading, straight. Leaf blade

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Fig. 6. Holotype of *Chenopodium pamiricum* (TASH0000487). By courtesy of the National Herbarium of Uzbekistan, Academy of Sciences, Uzbekistan.

7–13(30) mm, usually shallowly trilobate, basal lobes distinct, spreading, midlobe narrowly triangular, lobes entire, sometimes blade entire, trullate with basal angles, base widely cuneate or rounded, apex obtusish to acute, margins entire. Inflorescence paniculate, mostly fairly compact, terminal and axillary, sometimes laxer on elongated stems and branches; glomerules small. Flowers perfect or female; perianth lobes 5, free to below middle to near base, ± farinose, back slightly elevated, midrib rather distinct inside. Pericarp fairly easily scraped off. Seeds 1.0–1.2(1.25) × 0.9–1.0 mm, broadly ovate, margin slightly acute; testa radially faintly furrowed and slightly rugose to almost smooth, almost identical with *C. grubovii*. 2n = 18 (Mandák *et al.* 2018, Lomonosova *et al.* 2003; both as *C. iljinii*).

Habitat and distribution. *Chenopodium pamiricum* grows on stony and sandy slopes, steppes, along roadsides and in fallows and

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wastelands at 300 m a.s.l. (northernmost location in the Minusinsk basin) to 1000–1500 m a.s.l. further south in intermontane basins, and up to 4500 m a.s.l. in the Mongolian Altai, Nanshan, Tian Shan, and Pamir. Its total range extends from the Himalayas, Karakoram, northern Hindu Kush and Pamir to the Alay, Altai and Sayan mountains, western Mongolia, and western China (Fig. 8). Geographically, it is widely sympatric with *C. grubovii*, but *C. pamiricum* seems to be somewhat more northern and is less frequent.

NOTES. *Chenopodium pamiricum* is rather variable. Typically it is silvery-grey or whitish because of dense indumentum of vesicular trichomes, and has an erect stem with branches along the whole stem or in the middle part. Older and smaller plants are less silvery. The leaf shape is characteristic and different from that in the other species of the group: almost always trilobate with rather small basal lobes or, if not lobed, leaves are more or less trullate. To some extent, the erect habit and leaf shape resemble those of small plants of *C. album*, and the name *C. album* was sometimes misapplied to *C.* '*pamiricum*'. It is particularly difficult to distinguish small, slender high-mountain specimens of *C. pamiricum* and *C. grubovii* from the Pamir, where many plants were collected as weeds in irrigated fields. In such habitats, they had an unnatural appearance with several ± prostrate stems and often with sterile flowers; there only leaf shape differentiates *C. pamiricum* and *C. grubovii*.

Goloskokov (1950) considered *C. iljinii* to be related to *C. bryoniifolium* and Grubov (1966) accepted *C. iljinii* and included *C. bryoniifolium* var. *kapellariae* in its synonymy. However, differences between *C. pamiricum* and *C. bryoniifolium* are clear: *C. bryoniifolium* is taller, with larger, glabrous, triangular-ovate leaves and larger seeds.

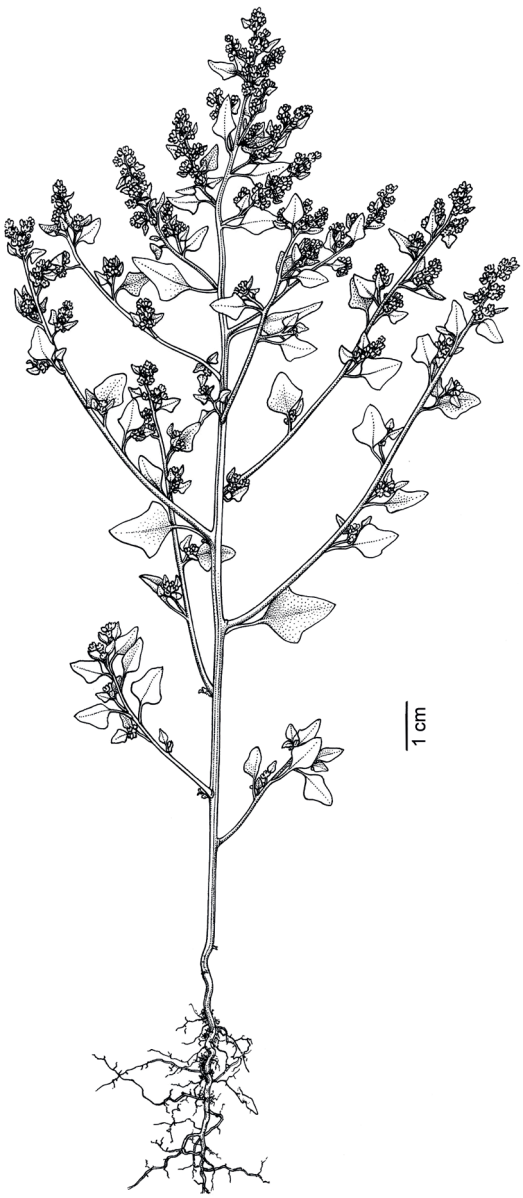


Fig. 7. Habit of *Chenopodium pamiricum* (Russia, Krasnoyarsk Territory, Minusinsk District, 1964 *I. Krasnoborov & V. Chaika s.n.*; NS).

Chenopodium karoi (Murr) Aellen (Fig. 9)

Feddes Repert. Spec. Nov. Regni Veg. 26: 149. 1929. — *Chenopodium album* subsp. *karoi* Murr, Neu. Übers. Bl.-Pfl. Vorarlberg 1: 97. 1923. — *Chenopodium prostratum* subsp. *karoi* (Murr) Lomon., Konspekt Fl. Irkutsk Obl.: 111. 2008; Fl. Sibir. 5: 147. 1992, without basionym. — LECTOTYPE (designated by Sukhorukov *et al.* 2019; earlier cited as "holotype" by Uotila and Lomonosova 2016: 226; *see* comments in Mosyakin & Mandák 2020: 422): [Russia] Plantae Dahuricae No. 169 *Chenopodium album α integrifolium* Fenzl. Nerczynsk. Wüste Orte, gartenland. 1892 *F. Karo* [G00405813 (Herbarium of Paul Aellen no. 20473)!].

Chenopodium prostratum Bunge *ex* Herder, Acta Horti Petrop. 10: 594. 1889, *nom. illeg., non* Pall. & Schult. 1820, *non* Jacquem. *ex* Moq. 1849, *non* Roxb. *ex* Hook. f. 1886. — LECTOTYPE (designated by Uotila and Lomonosova 2016): [Russia.] Nischne-Kolymsk, 6 July 1832 *Scharypoff 20* (LE01015991!).

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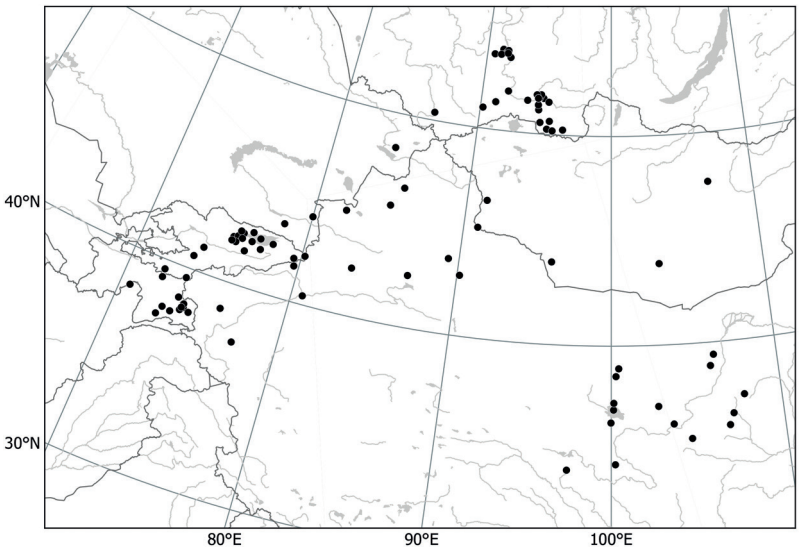


Fig. 8. Distribution of *Chenopodium pamiricum* according to revised herbarium specimens (https://www.gbif.org/dataset/2342ed8e-8ef4-4181-97ca-e48faa860439).



Fig. 9. Habit of *Chenopodium karoi* (Russia, Trans-Baikal Territory, Onon district, 2008 *M. Isaikina & N. Pazdnikova 24547*; NS).

Chenopodium jenissejense Aellen & Iljin, Fl. USSR 6: 873. 1936. — LECTOTYPE (designated by Uotila and Lomonosova 2016): [Russia.] Turukhansky Krai, Eniseiysk Gub., Ust'e r. Kureyka, 66°30´N, 87°17´E, 7 September 1914 *N. I. Kusnezov & W. Reverdatto 4102* (LE01015992!).

Not malodorous, annual. Stem (5)10–25(40) cm long, ascending to erect, sometimes procumbent, brownish green-striped, sometimes turning reddish, but without red spots in leaf

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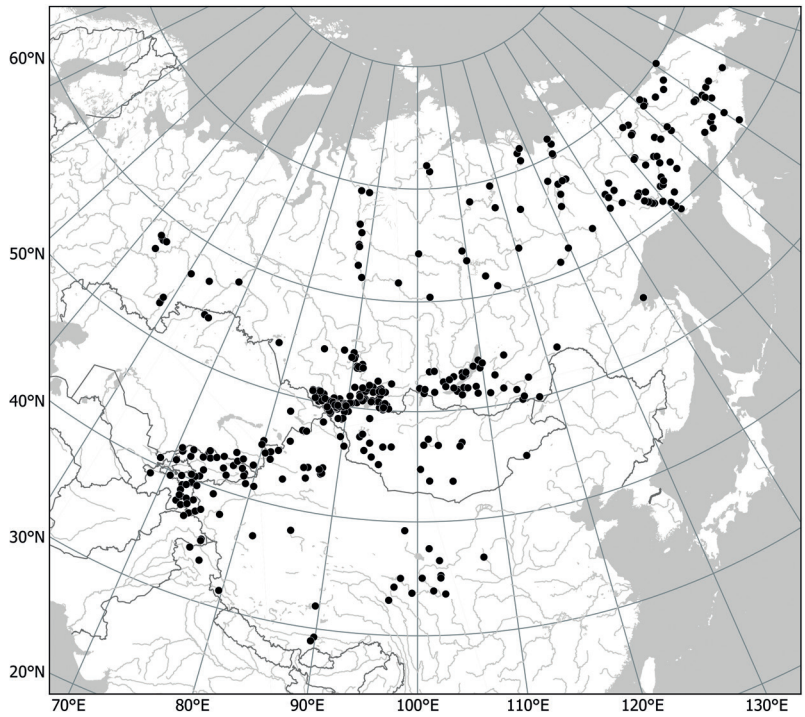


Fig. 10. Distribution of *Chenopodium karoi* according to revised herbarium specimens (https://www.gbif.org/dataset/2342ed8e-8ef4-4181-97ca-e48faa860439).

axils, usually basally branched, lowermost internodes short, branches subopposite, ascending, long but usually shorter, sometimes as long as or even longer than main axis, upper branches short, secondary branches few; sometimes without branches and with typically curved stem base. Leaves bluish to dirty green, sometimes turning pale yellow or reddish; blade 1.3–2 × as long as the petiole, ± farinose especially below, (12)20–30(40) × (5)15–25(35) mm, ovate to broadly ovate to sometimes elliptic, usually somewhat longer than broad, seldom as long as broad, usually at least slightly shallowly trilobate, base short attenuate, lateral lobes mostly in middle of blade, sometimes below middle, rounded, rarely with 2 teeth, apical lobe often fairly abruptly narrowing to usually obtuse apex, margins entire or with a few teeth; uppermost leaves narrower, apex more acute and sometimes shortly acuminate. Inflorescence paniculate, mostly leafy and on fairly short branches; glomerules fairly closely set, small, loose to dense. Flowers perfect or female; perianth lobes 5, green, farinose, connate to middle, keeled on back. Pericarp fairly easily removable, reticulate-foveate, pits with ± straight walls. Seeds horizontal, black, 1.0–1.2(1.3) × 1.0–1.25 mm, ± round in outline, margin somewhat acute; testa with radial furrows and shallow pits especially near margin. 2n = 36 (Mandák *et al.* 2018, Lomonosova *et al.* 2019).

Habitat and distribution. Montane steppe often disturbed by cattle, semi-deserts, in the north often on pebble and sandy riverbanks; as a weed by roadsides, field margins, in pastures and wastelands near buildings. In the west it is usually spreading along railways. In high mountains in the south, *C. karoi* reaches 3000–4250 m a.s.l., but in the north and in low mountains it occurs at 40–1000 m a.s.l. It has a very wide distribution range from the Hindu Kush in northeastern Afghanistan (Uotila 1997, Breckle *et al*. 2013), northern Pakistan (Uotila 2001a) and the Himalayas (Yonekura 2008, Sukhorukov & Kushunina 2014, Sukhorukov *et al.* 2019) and Tibet (Li & Ma 1983) to Siberia (Lomonosova 1992), northern China, Mongolia and the Russian Far East (Fig. 10). In spite of the vast area, all parts of the range possibly have a rather similar continental climate with warm summers and cold winters, but towards the north the day length increases during the growing period and the summers are shorter. The species seems common in most of the range;

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this is also reflected in the rather frequent casual finds from the southern Urals and from Europe, at least from east-European Russia (Mosyakin 1996), Germany, Norway and Sweden (Aellen 1960, Uotila 2001b).

Notes. The variation in *C. karoi* and its relationships to *C. acerifolium* as well as the identity of the northern plants were discussed in detail by Uotila and Lomonosova (2016). The species is not uniform throughout its very wide range. Most problematic are specimens from Yakutia and the Russian Far East, which are often very slender, with narrow and long leaves with indistinct lobes or no tendency to lobing. Typical *C. karoi* with broader and ± trilobate leaves is very rare there. According to the map and specimens cited in Sukhorukov *et al.* (2019), *C. karoi* is rather widespread in the Himalayas and Tibet. However, their species description and the few specimens seen by us from the area do not fully match *C. karoi* from central Asia, and indicate that also in the south the variation is marked or that other taxa may be involved. The same concerns some specimens from Pakistan, included in Uotila (2001a). Distinct morphotypes can occur over such a wide area and under strongly differing day-length conditions, and in-depth molecular research is required to elucidate the background of the variability.

Chenopodium karoi differs from the other species of the group in its leaf shape, as well as in its shallowly pitted seed surface, the other species having almost smooth seeds. Pitted seeds led Aellen (1960) to include *C. karoi* together with *C. acerifolium* and *C. suecicum*, which have similar shallowly pitted seed coat testa, in a different subsection from *C. pamiricum*. Seeds of *C. karoi* are larger and rounder and the perianth lobes more connate than in *C. grubovii* and *C. pamiricum*. It is less mealy than *C. vulvaria*, the leaf blade is usually trilobate, and the margins have small teeth. Furthermore, *C. karoi* is tetraploid (2n = 4x = 36) whereas *C. vulvaria*, *C. pamiricum* and *C. grubovii* are diploids (2n = 2x = 18).

Discussion

The characteristic unpleasant smell caused by the presence of trimethylamine has been used as a character to distinguish *C. vulvaria* from other chenopods. Its importance can be seen in most of the central Asian and Siberian floras: the smell is mentioned for *C.* '*vulvaria*' in almost all of them. However, it is a matter of doubt if all authors had really detected the smell in the field: the information on its presence might have just been copied from other floras. The smell was probably an important reason for misapplication of the name in this area, however, since it was not realized that other morphologically similar species could have a similar smell, at least when fresh. Correspondingly, in New Zealand the alien *C. vulvaria* was often confused with the morphologically fairly similar endemic *C. detestans* (local vernacular name "fish-guts plant"), which has a similar foetid odour (Wilson 1983, Webb *et al*. 1988).

The foul smell of trimethylamine is not a character of *C. vulvaria* and *C. detestans* only. Strong smell has been mentioned for the Australian *C. desertorum* (Wilson 1983; for two of the three subspecies recognized) and the North African *C. hoggarense* (Chatelain *et al*. 2022), and weaker, less persistent smell has been noted in some other species of *Chenopodium*, such as Caucasian *C. sosnowskyi* (Kapeller 1927) and *C. nidorosum* (Otschiauri 1981), and *C. grubovii*, as well as morphologically unrelated *C. acerifolium*, Siberian *C. frutescens*, South American *C. hircinum* and some other American taxa. A similar smell was also noted in germinating seeds of *C. acerifolium* and even *Suaeda corniculata*, *S. glauca* and *S. heteroptera* (the first author), as well as in small amounts in the tissues of many plants from other families (Cromwell 1950).

There seems to be variation in the intensity of the smell among populations, or as a result of ecological conditions. Regarding *C. grubovii*, the smell was noted at least in plants from the Altai; S. Mosyakin (pers. comm.) reported some faint trimethylamine smell in some (but not all) fresh specimens of *C. acerifolium* from the sands of the Dnipro River near Kyiv, Ukraine; Kapeller (1927) mentioned the smell in one of the three forms of *C. sosnowskyi* she described, but Habibi *et al.* (2018) did not find the smell in *C. sosnowskyi* in extensive cultivation experiments; and, finally, Sukhorukov *et al*. (2016) reported a *C. vulvaria* population almost lacking such a

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smell. Aellen, who did not study fresh plants of *C.* '*pamiricum*' and *C. sosnowskyi*, stated that they have no smell (Aellen 1960), since in these species this smell disappears in dry specimens.

The smell of trimethylamine has some taxonomic importance, but because of presence in unrelated species from different continents and unknown biochemical background of this character, its phylogenetic importance remains obscure; Mosyakin and Iamonico (2017), concluded that "the trimethylamine smell seems to occur mainly in early-branching clades of *Chenopodium*".

In the study of the genome size of *Chenopodium* species (Vít *et al*. 2016, Mandák *et al.* 2016), it was possible to distinguish difficult pairs of species such as *C. vulvaria* and *C. karoi*, and *C. vulvaria* and '*C. pamiricum*' (i.e. *C. grubovii*) + '*C. iljinii*' (i.e. *C. pamiricum*), but the latter species did not differ from each other. In molecular studies it was found that typical *C. vulvaria* (together with *C. sosnowskyi*) formed a sister lineage to the rest of *Chenopodium* (e.g. Mandák *et al*. 2016). Similarly, using nrDNA ITS and three cpDNA regions that included samples of '*C. pamiricum*' (i.e. *C. grubovii*) and '*C. iljinii*' (i.e. *C. pamiricum*), the results revealed no differences between them (Mandák *et al.* 2016, 2018).

Recently, Belyaev *et al*. (2020) explored low-coverage NGS data to infer satellite DNA evolution of diploid species of the *C. album* aggregate. Among the others, '*C. iljinii*' (i.e., *C. pamiricum*) from China and '*C. pamiricum*' (i.e., *C. grubovii*) from Tajikistan were included in the analysis. It was shown that the genomes of the analysed diploid species of the *C. album* aggregate could be divided into high-microsatellite-copy-number genomes such as that of '*C. pamiricum*' (i.e., *C. grubovii*) and low-copy-number genomes, such as that of as '*C. iljinii*' (i.e., *C. pamiricum*).

In this study of extensive morphological material, we clarified the taxonomy and distribution of the group of small-leaved *Chenopodiums* in Asia and confirmed some assumptions proposed earlier on grounds of molecular studies (Mandák *et al.* 2016, Belyaev *et al.* 2020). However, considering the morphological variation noted in the taxa studied and the fact the molecular phylogenetic analyses of this group was carried out on single samples, further study on a large amount of material is necessary, especially from the Altai-Mongolian region.

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