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A conspectus of the genus *Cherleria* (*Minuartia* s.l., *Caryophyllaceae*)

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Abstract: *Minuartia* s.l. (*Caryophyllaceae*) is polyphyletic, with its species belonging to eleven major clades, all of which have been recognized at the generic rank. *Cherleria* is one of these segregate genera, based on the Linnaean species *Cherleria sedoides*. Its centre of diversity is on the Balkan Peninsula, but species also occur in the European and North American high mountains and in the Arctic. The species of *Cherleria* show ecological, especially substrate, differentiation and multiple colonisations of alpine habitats. We make new combinations for the 17 (of 20) taxa in *Cherleria* that do not yet have *Cherleria* names and provide a key to all species of the genus.

Key words: nomenclature, taxonomy, *Caryophyllaceae*, *Cherleria*, *Minuartia*, Arctic, Alps, Balkan Peninsula

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Introduction

The genus *Minuartia* L. (*Caryophyllaceae*) had been defined by having three styles and three capsule teeth (Mattfeld 1922; McNeill 1962). Molecular studies have shown this circumscription of *Minuartia* to be highly polyphyletic (Fior & al. 2006; Harbaugh & al. 2010; Greenberg & Donoghue 2011; Dillenberger & Kadereit 2014). For this reason, Dillenberger & Kadereit (2014) broke *Minuartia* up into 11 different genera, based on their analyses of cpDNA and nrDNA sequence data and on having clades that were morphologically distinctive. Although they made new combinations for most species of *Minuartia*, no combinations were made for one of the segregate genera, *Cherleria* L., their Clade 6, because of ongoing work on the circumscription of its species. We present the results of that study here.

Cherleria is clearly supported with 100 percent bootstrap in the combined cpDNA and nrDNA tree and is the sister to the genus *Scleranthus* L. (Dillenberger & Kadereit 2014). It is one of two groups of *Minuartia* s.l. whose sepals have obtuse, rounded tips, instead of acute tips, a characteristic shared with its sister group *Scleranthus*. The other group of *Minuartia* s.l. with rounded sepal tips is Dillenberger & Kadereit's (2014) Clade 3, which they named *Pseudocherleria* Dillenb. & Kadereit. The two groups are separated by the presence of glandular or single-celled non-glandular hairs in *Cherleria* (versus multicellular, non-glandular hairs in *Pseudocherleria*) and by the leaves generally being linear-setaceous to subulate in *Cherleria* (versus lanceolate in *Pseudocherleria*; Dillenberger & Kadereit 2014). In the most recent monograph of *Minuartia* as a whole, Mattfeld (1922) placed most of the members of the clades 3 and 6 of Dillenberger &

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Kadereit (2014) in *M.* sect. *Spectabiles* (Fenzl) Hayek. (Table 1). *Minuartia* sect. *Spectabiles* was divided into five series: *M.* ser. *Biflorae* Mattf., *M.* ser. *Caucasicae* Mattf., *M.* ser. *Labillardiereae* Mattf., *M.* ser. *Laricifoliae* Mattf. and *M.* ser. *Laricinae* Mattf. Of these plants, all are included in *Cherleria* as here circumscribed except for *M.* ser. *Laricinae* and one of the two species in *M.* ser. *Caucasicae*, i.e. *M. aizoides* (Boiss.) Bornm. These remaining species constitute *Pseudocherleria*.

The only member of *Cherleria* as here circumscribed that Mattfeld (1922) did not include in *Minuartia* sect. *Spectabiles* is *C. sedoides* L. itself, which he placed in the unispecific *M.* sect. *Cherleria* (L.) Mattf. Although Mattfeld (1922) considered *M.* sect. *Cherleria* to be only distantly related to other sections of *Minuartia*, he hypothesized that its closest relatives were in *M.* sect. *Spectabiles*, likely in *M.* subsect. *Biflorae*.

McNeill (1962), in his work on *Minuartia* and its relatives, placed Mattfeld's *M.* sect. *Spectabiles* and *M.* sect. *Cherleria* together in his *M.* sect. *Spectabiles* (Table 1). *Minuartia* sect. *Spectabiles* was divided into three subsections: *M.* subsect. *Cherleria* (L.) McNeill (consisting only of *M. sedoides*), *M.* subsect. *Laricifoliae* (Mattf.) McNeill (consisting of Mattfeld's *M.* ser. *Caucasicae*, *M.* ser. *Labillardiereae* and *M.* ser. *Laricifoliae*) and *M.* subsect. *Spectabiles* (consisting of Mattfeld's *M.* ser. *Biflorae* and *M.* ser. *Laricinae*).

Three generic names have types that are members of Dillenberger & Kadereit's (2014) Clade 6: *Cherleria* (Linnaeus 1753), based on *C. sedoides*; *Wierzbickia* Rchb. (Reichenbach 1841), lectotypified with *Stellaria biflora* L. (McNeill 1962); and *Lidia* Á. Löve & D. Löve (Löve & Löve 1976), with *L. biflora* (L.) Á. Löve & D. Löve (≡ *S. biflora*) as type. Of these three names, *Lidia* is a nomenclatural synonym of *Wierzbickia*, as the two names have the same type. *Cherleria* has priority over *Wierzbickia*, although it has largely been overlooked because of the apparent dissimilarity of *C. sedoides* to the remaining members of *Minuartia* sect. *Spectabiles*. One member of *Cherleria* has recently received a new combination in the genus: *C. laricifolia* (L.) Iamonico.

For most of its history, when *Cherleria* was accepted, it was treated as a monotypic genus with only *C. sedoides*. However, various other species, now classified in several different genera, were also briefly considered to belong to *Cherleria* (Dillenberger & Kadereit 2014 and references therein).

Cherleria itself is divided into three major clades using molecular data (Table 1; Moore & Kadereit 2013), with one species, *C. rupestris* (*Minuartia labillardierei* Briq.; see Systematic treatment below) from Lebanon, having an uncertain position. *Cherleria biflora* and *C. circassica* are sister to the rest of the genus (Clade A). Although both are found in the Caucasus, *C. biflora* is also circumboreal, extending south into the Alps of Europe and the Sierra Nevada and Rocky Mountains of North America. Another clade (Clade B) contains three Arctic species (*C. arctica*, *C. obtusiloba* and *C. yukonensis*) that extend south into North America along the Rocky Mountains. These species form a polyploid complex (Löve & Löve 1976; Murray & Kelso 1997) and many questions remain in this clade, including how many times these plants colonized the C and S Rocky Mountains from the Arctic and N Rocky Mountains. This Arctic and North American clade is sister to a clade composed of European plants (Clade C) containing most of the species of *Cherleria*. Clade C is most diverse on the Balkan Peninsula (eight species) and in the Alps (four species).

Although these clades are generally geographically coherent, all three are quite morphologically heterogeneous. Therefore, we do not think they warrant taxonomic recognition at this time.

Material and methods

Species delimitations were guided in large part by our molecular work (Moore & Kadereit 2013), where most species of *Cherleria* were clearly resolved as monophyletic. In particular, the molecular work guided us in the separation of *C. biflora* from *C. obtusiloba* in the United States and the S part of Canada, contrary to most current treatments (e.g. Rabeler & al. 2005; Hartman & Rabeler 2012). The morphology of the specimens we had sequenced, clear differences between the species in the few sets of specimens when both species were collected together, and Fernald's (1919) treatment allowed us to find morphological characters to separate them.

Neither molecular nor morphological data allowed us to draw strong boundaries between the species in Clade B (containing *Cherleria arctica*, *C. obtusiloba* and *C. yukonensis*), likely due in part to polyploidy. The relationships of the species in this clade are still in flux and merit further research.

Field work was performed in Europe (focusing on the Alps and Carpathians as well as Greece and Albania). The remaining species were examined from herbarium specimens, through herbarium visits and loans, with some additional types examined online. Herbarium abbreviations follow *Index Herbariorum* (Thiers 2016+) throughout. A table of specimens examined is presented in Supplementary Material online (Table 2). Taxonomic literature was generally examined online through the Biodiversity Heritage Library (http://www.biodiversitylibrary.org/) or the websites of the respective journals.

Key for species identification

1. Sepals and pedicels glabrous, or with very fine hairs present that are not visible at 10× magnification; hairs may be present at nodes; Europe **2**
– Pedicels, and generally also sepals, moderately to densely covered with hairs (glandular or not); distri-

Table 1. The classification of members of *Minuartia* sect. *Spectabiles* according to Mattfeld (1922) and McNeill (1962) and their placement in our phylogenetic trees based on DNA sequence data. All subsections and series are part of *M.* sect. *Spectabiles* unless noted otherwise.

Species	Mattfeld (1922)	McNeill (1962)	Molecular data (Moore & Kadereit 2013; Dillenberger & Kadereit 2014)
Minuartia sedoides	*Minuartia* sect. *Cherleria*	*Minuartia* subsect. *Cherleria*	*Cherleria*, Clade C
M. circassica	*M.* ser. *Caucasicae*	*M.* subsect. *Laricifoliae* ser. *Caucasicae* (type)	*Cherleria*, Clade A
M. aizoides (Boiss.) Bornm.	*M.* ser. *Caucasicae*	*M.* subsect. *Laricifoliae* ser. *Caucasicae*	*Pseudocherleria*
M. laricifolia	*M.* ser. *Laricifoliae*	*M.* subsect. *Laricifoliae* ser. *Laricifoliae*	*Cherleria*, Clade C
M. baldaccii	*M.* ser. *Laricifoliae*	*M.* subsect. *Laricifoliae* ser. *Laricifoliae*	*Cherleria*, Clade C
M. capillacea	*M.* ser. *Laricifoliae*	*M.* subsect. *Laricifoliae* ser. *Laricifoliae*	*Cherleria*, Clade C
M. dirphya	(not yet described)	(not yet described)	*Cherleria*, Clade C
M. doerfleri	(part of *M. baldaccii*)	(presumably part of *M. baldaccii*)	*Cherleria*, Clade C
M. garckeana	*M.* ser. *Laricifoliae*	*M.* subsect. *Laricifoliae* ser. *Laricifoliae*	*Cherleria*, Clade C
M. handelii	(not yet described)	*M.* subsect. *Laricifoliae* ser. *Laricifoliae*	*Cherleria*, Clade C
M. langii	(part of *M. laricifolia*)	(presumably part of *M. laricifolia)*	*Cherleria*, Clade C
M. parnonia	(not yet described)	(not yet described)	*Cherleria*, Clade C
M. wettsteinii	*M.* ser. *Laricifoliae*	*M.* subsect. *Laricifoliae* ser. *Laricifoliae*	*Cherleria*, Clade C
M. labillardierei	*M.* ser. *Labillardiereae*	*M.* subsect. *Laricifoliae* ser. *Laricifoliae*	*Cherleria*, unplaced as to clade
M. laricina (L.) Mattf.	*M.* ser. *Laricinae*	*M.* subsect. *Spectabiles* ser. *Laricinae* (type)	*Pseudocherleria* (not sampled)
M. brotherana (Trautv.) Woronow ex Grossh.	(part of *M. imbricata*)	*M.* subsect. *Spectabiles* ser. *Laricinae*	*Pseudocherleria* (not sampled)
M. colchica Kharadze	(not yet described)	*M.* subsect. *Spectabiles* ser. *Laricinae*	*Pseudocherleria*
M. imbricata (M. Bieb) Mattf.	*M.* ser. *Laricinae*	*M.* subsect. *Spectabiles* ser. *Laricinae*	*Pseudocherleria*
M. inamoena (C. A. Mey.) Woronow ex Grossh.	(part of *M. imbricata*)	*M.* subsect. *Spectabiles* ser. *Laricinae*	*Pseudocherleria* (not sampled)
M. kurilensis Ikonn. & Barkhalov	(not yet described)	(not yet described)	*Pseudocherleria* (not sampled)
M. macrocarpa (Pursh) Ostenf.	*M.* ser. *Laricinae*	*M.* subsect. *Spectabiles* ser. *Laricinae*	*Pseudocherleria*
M. pseudoimbricata Lazkov	(not yet described)	(not yet described)	*Pseudocherleria* (not sampled)
M. rhodocalyx (Albov) Woronow ex Grossh.	(part of *M. imbricata*)	*M.* subsect. *Spectabiles* ser. *Laricinae*	*Pseudocherleria* (not sampled)
M. trautvetteriana Sosn. & Kharadze	(not yet described)	*M.* subsect. *Spectabiles* ser. *Laricinae*	*Pseudocherleria*
M. biflora	*M.* ser. *Biflorae*	*M.* subsect. *Spectabiles* ser. *Spectabiles* (type)	*Cherleria*, Clade A
M. arctica	*M.* ser. *Biflorae*	*M.* subsect. *Spectabiles* ser. *Spectabiles*	*Cherleria*, Clade B
M. marcescens	(part of *M. obtusiloba*)	*M.* subsect. *Spectabiles* ser. *Spectabiles*	*Cherleria*, Clade B
M. obtusiloba	*M.* ser. *Biflorae*	*M.* subsect. *Spectabiles* ser. *Spectabiles*	*Cherleria*, Clade B
M. yukonensis	(not yet described)	(not yet described)	*Cherleria*, Clade B

bution various, including Europe **5**
2. Leaves 3–6 mm long, fleshy, ± triangular with obtuse tips; petals absent or rudimentary; plants of alpine to subalpine areas in European mountains, but absent from Greece . . . . . **16. *C. sedoides***
– Leaves 5–13 mm long, not fleshy, linear; petals present; Greece **3**
3. Petals < sepals; serpentine soil on island of Evvia . . . . . **6. *C. dirphya***
– Petals ≥ sepals; calcareous soils **4**
4. Plants glaucous; Crete . . . . . **17. *C. wettsteinii***
– Plants green; Mount Parnonas in Peloponnisos . . . . . **14. *C. parnonia***
5. Leaves with blunt or truncate tips, rounded in cross-section; North America or Arctic Asia **6**
– Leaves with tips acute or obtuse, but not truncate, triangular or flat in cross-section; Eurasia or North America (including Arctic regions) **7**
6. Petals 6.5–15 mm long; sepals 3–8 mm long; tundra in far-northern North America and Asia . . . **1. *C. arctica***
– Petals 4.5–8 mm long; sepals 3–4 mm long; serpentine barrens in E Canada and adjacent Vermont . . . . . **12. *C. marcescens***
7. Most leaves > 15 mm long, triangular, evenly tapered from base to tip; most leaves borne in rosettes, in which leaves diverge > 60° from axis of rosette; Caucasus . . . . . **5. *C. circassica***
– All or nearly all leaves < 15 mm long, triangular or linear; if leaves > 10 mm, borne in tufts, in which leaves diverge < 30° from axis of tuft; distribution various (including Caucasus for *C. biflora*) **8**
8. Leaves ± flat in cross-section; sepals glabrous to sparsely hairy, distinctly less hairy than pedicels (sometimes only tips of sepals glabrous in plants from non-Arctic North America); moist areas (snowbeds, streamsides), circumarctic, south to high mountains of North America (Sierra Nevada, Rocky Mountains, rarely in E Canada) and Eurasia (Alps, Caucasus, Altai Mountains) . . . . . **3. *C. biflora***
– Leaves strongly keeled and therefore triangular in cross-section; sepals with same indumentum as pedicels; generally in drier areas **9**
9. Petals pink; calcareous soils of high mountains of Lebanon . . . . . **15. *C. rupestris***
– Petals generally white; distribution various, but absent from Lebanon **10**
10. Petals 12–17 mm long, leaves borne in clusters on horizontal, creeping stems or on flowering stems; upright vegetative stems absent; serpentine soils of Greece and Albania . . . . . **2. *C. baldaccii***
– Petals < 14 mm long, some upright vegetative stems generally present; distribution various, including serpentine soils of Greece and Albania **11**
11. Indumentum consisting solely of non-glandular hairs **12**
– Indumentum with at least some glandular hairs . . . **15**
12. Vegetative stems prostrate; reproductive stems < 1 cm long, each bearing a single flower and 0–1 pairs of leaves . . . . . **9. *C. handelii***
– Vegetative stems ascending; reproductive stems > 3 cm long, generally bearing multiple flowers and > 3 pairs of leaves **13**
13. Capsules > 1.5 × sepals; plants of calcareous soils in E Alps and Carpathians . . . . . **10. *C. langii***
– Capsules < 1.5 × sepals; plants of siliceous or serpentine soils in C and W Alps, SE France and N Italy . . . . . **14** (**11. *C. laricifolia*** in part)
14. Petals 5–7 mm long (< 1.5 × sepals), plants glaucous; serpentine soils of N Apennines . . . . . **11c. *C. laricifolia*** subsp. ***ophiolitica***
– Petals 10–13 mm long (> 1.5 × sepals), plants green; siliceous or occasionally serpentine soils of C and W Alps and SE France . . . . . **11a. *C. laricifolia*** subsp. ***laricifolia***
15. Plants of North America **16**
– Plants of Europe **17**
16. Leaves straight, < 1 mm wide, with sharply pointed tips; restricted to Alaska and Yukon Territory . . . . . **18. *C. yukonensis***
– Leaves generally curved, > 1 mm wide, tips acute, but often not sharply pointed; from Alaska and Yukon Territory south to California and New Mexico . . . . . **13. *C. obtusiloba***
17. Leaves straight, not or only very slightly curved, even when borne in tufts; 2 lateral veins of sepals ending c. ½ of way to tip of sepal; open flowers bowl-shaped . . . . . **4. *C. capillacea***
– Leaves curved, both on stem and in tufts; lateral veins of sepals disappearing at c. ⅔ or more of way to tip of sepal; open flowers campanulate **18**
18. Stems densely covered with appressed tufts of leaves; plants of alpine areas with calcareous soil on Balkan Peninsula . . . . . **7. *C. doerfleri***
– Tufts of leaves not as densely packed on stem, not appressed; plants of subalpine and montane areas, generally with siliceous or serpentine soils **19**
19. Petals 5–8.5 mm long; generally of serpentine-influenced soils (but occasionally siliceous or calcareous soils) on Balkan Peninsula . . . . . **8. *C. garckeana***
– Petals 8–13 mm long; siliceous soils of Pyrenees and S Massif Central . . . . . **11b. *C. laricifolia*** subsp. ***diomedis***

Systematic treatment

Cherleria L., Sp. Pl. 1: 425. 1753 ≡ *Minuartia* sect. *Cherleria* (L.) Mattf. in Repert. Spec. Nov. Regni Veg. Beih. 15: 211. 1922 ≡ *M.* subsect. *Cherleria* (L.) McNeill in Notes Roy. Bot. Gard. Edinburgh 24: 141. 1962. – Type: *Cherleria sedoides* L.

= *Wierzbickia* Rchb., Deut. Bot. Herb.-Buch: (Nom.) 205; (Syn. Red.) 106. 1841 ≡ *Lidia* Á. Löve & D. Löve in Bot. Not. 128: 510. 1976. – Type: *Stellaria biflora* L.

1. *Cherleria arctica* (Steven ex Ser.) A. J. Moore & Dillenb., **comb. nov.** ≡ *Arenaria arctica* Steven ex Ser. in Candolle, Prodr. 1: 404. 1824 ≡ *Minuartia arctica* (Steven ex Ser.) Graebn. in Ascherson & Graebner, Syn. Mitteleur. Fl. 5(1): 772. 1918 ≡ *Lidia arctica* (Steven ex Ser.) Á. Löve & D. Löve in Bot. Not. 128: 510. 1976. – Protologue: "In littore Sibirico maris glacialis." Although a type has not been designated, Steven's collections are at H, and potential type material should be looked for there.

Cherleria arctica is present in the Asian and American Arctic. It has large white or pink petals and glandular, green or purple sepals with flattened (as opposed to hooded) tips. Its leaves have truncate (as opposed to pointed) tips, which are often purple. The leaves are generally glabrous, although a few individuals have glandular leaves, likely due to hybridization with *C. obtusiloba* or *C. yukonensis*.

2. *Cherleria baldaccii* (Halácsy) A. J. Moore & Dillenb., **comb. nov.** ≡ *Alsine baldaccii* Halácsy, Consp. Fl. Graec 1: 237. 1900 ≡ *Minuartia baldaccii* (Halácsy) Mattf. in Ascherson & Graebner, Syn. Mitteleur. Fl. 5(1): 940. 1919. – Holotype: "Epirus: in regione abietina mt. Smolika supra Palaeoseli distr. Konitza", *Baldacci 223* (WU-Halácsy-Graecum 0059782!; isotypes: G 00226883, K 000568032).

Cherleria baldaccii is a serpentine endemic restricted to Greece and Albania. It is distinctive in having larger flowers than the other Balkan species and short, creeping vegetative branches, instead of erect to ascending vegetative branches.

3. *Cherleria biflora* (L.) A. J. Moore & Dillenb., **comb. nov.** ≡ *Stellaria biflora* L., Sp. Pl. 1: 422. 1753 ≡ *Arenaria sajanensis* Willd. ex Schltdl. in Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 7: 200. 1816 [non *Arenaria biflora* L., Mant. Pl. 71. 1767] ≡ *Minuartia biflora* (L.) Schinz & Thell. in Bull. Herb. Boissier, sér. 2, 7: 404. 1907 ≡ *Lidia biflora* (L.) Á. Löve & D. Löve in Bot. Not. 128: 510. 1976. – Lectotype (Jonsell & Jarvis 1994: 159): Herb. Linn. No. 584.11 (LINN).

Cherleria biflora occurs throughout the Eurasian and American Arctic, with additional populations in high-alpine areas of the European Alps, the Asian Altai Mountains, the Caucasus, rarely in the mountains of E Canada, and the high mountains of W North America (being the only species of *Cherleria* in the Sierra Nevada of California and co-occurring with *C. obtusiloba* in the Cascades and Rocky Mountains). Throughout its range, *C. biflora* prefers mesic habitats, such as snowbanks and other areas where the soil remains moist throughout the short summer. Although it has been confused with *C. obtusiloba* in non-Arctic North America (e.g. Welsh 2003; Rabeler & al. 2005; Hartman & Rabeler 2012; Holmgren & Holmgren 2012), the two species are genetically distinct and unlikely to be able to interbreed (appearing in different major clades within *Cherleria*, Moore & Kadereit 2013) and often occur in different habitats (with *C. obtusiloba* generally occupying drier areas, where they co-occur). In addition, they can be distinguished morphologically as follows: sepals glabrescent at least at the tips and often recurved in fruit (*C. biflora*) versus glandular throughout and generally not recurved in fruit (*C. obtusiloba*); petals < 1.5 × sepals (*C. biflora*) versus > 2 × sepals (*C. obtusiloba*); leaves generally ± flat in cross-section and straight (*C. biflora*) versus clearly triangular in cross-section and generally at least somewhat curved (*C. obtusiloba*); old branches loosely covered with leaves from the previous year (*C. biflora*) versus densely covered with leaves (or their midribs) from previous years (*C. obtusiloba*); plants growing in small tufts or weak patches with small root systems (*C. biflora*) versus plants growing in dense patches with lower stems and roots clearly woody (*C. obtusiloba*).

4. *Cherleria capillacea* (All.) A. J. Moore & Dillenb., **comb. nov.** ≡ *Arenaria capillacea* All., Fl. Pedem. 2: 365, 112. 1785 ≡ *Minuartia capillacea* (All.) Graebn. in Ascherson & Graebner, Syn. Mitteleur. Fl. 5(1): 767. 1918. – Protologue [p. 112 sub *A. montana* L.]: "Legi in summo jugo *Tendae la Cola* dicto." Allioni's collections are in TO, but it is unclear if a collection for *Arenaria capillacea* exists. If not, the illustration of *A. capillacea* (Allioni, Fl. Pedem. 3: t. 89, f. 2. 1785) could be the lectotype.

Cherleria capillacea (Fig. 1A) is widespread throughout the S Alps, Balkan Peninsula, SE France and Italy, always exclusively on calcareous substrates, generally on exposed limestone bedrock or scree. In addition to its habitat, *C. capillacea* can be distinguished by having leaves that are generally straight or slightly recurved (as opposed to twisted in various directions in *C. garckeana*, *C. langii* and *C. laricifolia*), always having glandular sepals (only glandular in *C. garckeana* and *C. laricifolia* subsp. *diomedis*), and with the lateral veins of the sepals ending c. ½ of the way to the tips (instead of c. ⅔ of the way to the tips in *C. laricifolia* and all the way to the tips in *C. garckeana* and *C. langii*). The plants on the Balkan Peninsula may be genetically distinct and merit recognition as a separate species, but more extensive study is needed.

5. *Cherleria circassica* (Albov) A. J. Moore & Dillenb., **comb. nov.** ≡ *Alsine circassica* Albov in Bull. Herb. Boissier 2: 449. 1894 ≡ *Minuartia circassica* (Albov) Woronow ex Grossh., Fl. Kavkaza 2: 393. 1930. – Holotype: "Circassie: Mont Ochten, 8000 p.", 1893, *Alboff 298* (LP; isotypes: B, BP, CORD, G 00096385, JE, K, LE, LP, SI).

– "*Arenaria caucasica* Adams" in Ledebour, Fl. Ross. 1: 354. 1842, nom. inval., pro syn. sub *Alsine pinifolia* var. *robusta* Ledeb.

Cherleria circassica is endemic to the Caucasus in Armenia and Georgia. It is distinctive in having long

Fig. 1. Photographs of some species of *Cherleria*. – A: *C. capillacea* showing bowl-shaped opening of flowers and limestone habitat, Grande Roche St. Michel, Rég. Rhône Alpes, France; B: *C. laricifolia* subsp. *laricifolia* showing flowers that remain campanulate and surrounding siliceous rocks, Saas Fee, Wallis, Switzerland; C: *C. sedoides* showing rare, strap-shaped petals and creeping habit, Barcellonnette, Rég. Provence-Alpes-Côte d'Azur, France; D: *C. obtusiloba* showing dense cushion form and dry alpine habitat, Loveland Pass, Colorado, U.S.A.; E: *C. parnonia* showing flowers that open flat and relatively short petals, Paleochori, Peloponnisos, Greece; F: *C. garckeana* showing serpentine scree habitat, Mount Vorinous, Dytiki Makedonia, Greece.

(10–40 mm), triangular leaves that are evenly tapered from base to tip. The leaves are borne in rosettes, in which they are bent at the base so that they form an angle of 60° or more to the rosette axis (instead of borne in tufts, in which the leaves form angles of 30° or less to the rosette axis, which is the usual case in *Cherleria*, especially among species with leaves over 10 mm long).

6. *Cherleria dirphya* (Trigas & Iatroú) A. J. Moore & Dillenb., **comb. nov.** ≡ *Minuartia dirphya* Trigas & Iatroú in Nordic J. Bot. 23: 416. 2005. – Holotype: "[Greece, West Aegean] Nom Evvias, Ep. Chalkidos, northern slopes of Mt Dirphys, rocky slopes with *Juniperus oxycedrus* subsp. *oxycedrus* and *Genista acanthoclada* on ophiolitic substrate. Alt. 900–1000 m",

9 Sep 2000, *Trigas & Iatroú 2998* (UPA).

Cherleria dirphya is endemic to one small serpentine outcrop on the island of Evvia in Greece. It is endangered by goat grazing. It has straight, glaucous green leaves and petals that are narrower than the sepals, with flowers opening flat.

7. *Cherleria doerfleri* (Hayek) A. J. Moore & Dillenb., comb. nov. ≡ *Minuartia doerfleri* Hayek in Oesterr. Bot. Z. 70: 12. 1921 ≡ *Minuartia baldaccii* subsp. *doerfleri* (Hayek) Hayek in Repert. Spec. Nov. Regni Veg. Beih. 1: 193. 1924. – Syntypes: "Albania: In rupestribus cacuminis montis Koritnik, 2380 m", *Dörfler 961* (E 00318148!, GB 0047148, GB 0047149, MO 216552, S 07-13942, S G-7158, WU 0059964!, Z 000002654).

Cherleria doerfleri grows in alpine areas with calcareous soils in Greece and Albania. It forms mats in dense, grassy alpine vegetation. Both flowering and vegetative stems are densely covered with tufts of leaves.

8. *Cherleria garckeana* (Asch. & Sint. ex Boiss.) A. J. Moore & Dillenb., **comb. nov.** ≡ *Alsine garckeana* Asch. & Sint. ex Boiss., Fl. Orient. Suppl.: 112. 1888 ≡ *Minuartia garckeana* (Asch. & Sint. ex Boiss.) Mattf. in Bot. Jahrb. Syst. 57: 33. 1921. – Syntypes: "in glareosis montis Ida Troadis prope Kareikos", *Sintenis 457* (GOET 000609, JE 00009375, K 000395887, LD 1009141, LD 1009205, WU 0044137!, WU 0044138!).

= *Minuartia baldaccii* subsp. *skutariensis* Hayek in Repert. Spec. Nov. Regni Veg. Beih. 1: 193. 1924. – Syntypes: "Reise im Albanisch-montenegrinischen Grenzgebiete: Felsige Abhänge am Bardanjolt bei Skutari", 30 Apr 1914, *Dörfler 57* (S G-7157, WU 0060065!).

Cherleria garckeana (Fig. 1F) is endemic to the Balkan Peninsula and adjacent Turkey and appears (according to herbarium records) to be a substrate generalist, growing on calcareous, siliceous and serpentine substrates, although most occurrences seem to be on serpentine-influenced substrates. It is morphologically quite similar to its relative *C. laricifolia*, but is always glandular pubescent in the inflorescence and has a non-overlapping distribution.

9. *Cherleria handelii* (Mattf.) A. J. Moore & Dillenb., **comb. nov.** ≡ *Minuartia handelii* Mattf. in Repert. Spec. Nov. Regni Veg. 19: 193. 1923. – Holotype: "Herzegovina: Cvrsnica planina, Gesteinfluren am Ostrücken des Veliki Vilinac, Kalk, c. 2000–2050 m", 12 Jul 1909, *H. Freiherr v. Handel-Mazzetti* (WU 0044883!).

Cherleria handelii is restricted to calcareous substrates on Cvrsnica Planina in Bosnia and Herzegovina. It is distinctive in being prostrate with the flowers borne on short stems < 1 cm long.

10. *Cherleria langii* (G. Reuss) A. J. Moore & Dillenb., **comb. nov.** ≡ *Alsine langii* G. Reuss, Května Slov.: 76. 1853 ≡ *Minuartia langii* (G. Reuss) Holub in Folia Geobot. Phytotax. 9: 273. 1974. – Protologue: "Na podholách Slovenska", *Kitaibel*. No type specimen has been found, but Kitaibel's collections are in B, BM, BP, BR, G, H, M, P and PC.

= *Alsine laricifolia* subsp. *kitaibelii* Nyman, Consp. Fl. Eur. 116. 1878 ≡ *Minuartia laricifolia* subsp. *kitaibelii* (Nyman) Mattf. in Repert. Spec. Nov. Regni Veg. Beih. 15: 190. 1922 ≡ *Cherleria laricifolia* subsp. *kitaibelii* (Nyman) Iamonico in Taxon 65: 611. 2016. – Protologue: "Croat. Transs. mont. subalp." Nyman's types are generally to be looked for in S.

Cherleria langii is restricted to calcareous substrates in the E Alps and W Carpathians. It is morphologically most similar to *C. laricifolia*, and was indeed considered a subspecies of that species (as subsp. *kitaibelii*). However, they are not each other's closest relatives and colonized the Alps independently (Moore & Kadereit 2013). The two species can be distinguished by the larger petals and longer capsules of *C. langii*.

11. *Cherleria laricifolia* (L.) Iamonico in Taxon 65: 611. 2016 ≡ *Arenaria laricifolia* L., Sp. Pl. 1: 424. 1753 ≡ *Minuartia laricifolia* (L.) Schinz & Thell. in Bull. Herb. Boissier, sér. 2, 7: 403. 1907. – Lectotype (Iamonico 2016: 611): Herb. Linn. No. 585.42 (LINN).

= *Arenaria striata* L., Cent. Pl. II: 17. 1756 ≡ *Minuartia striata* (L.) Mattf. in Ascherson & Graebner, Syn. Mitteleur. Fl. 5(1): 940. 1919. – Lectotype (Iamonico 2016: 614): Herb. Burser XI: 129 (UPS – see photograph of specimen in Iamonico 2016).

Cherleria laricifolia is restricted to siliceous and occasionally serpentine substrates in the Alps (subsp. *laricifolia*), Apennines (subsp. *ophiolitica*), Pyrenees (subsp. *diomedis*) and SE France (subsp. *diomedis* and subsp. *laricifolia*). Although it is not restricted to scree or bedrock as are *C. capillacea* and *C. langii*, it appears to be entirely absent from soils with influence of calcareous rocks.

11a. *Cherleria laricifolia* (L.) Iamonico subsp. ***laricifolia***

Subsp. *laricifolia* (Fig. 1B) is the most widespread subspecies of *Cherleria laricifolia*, growing throughout the Alps and in most of SE France. It has larger flowers than the other two subspecies, and the sepals and inflorescence axes are generally non-glandular.

11b. *Cherleria laricifolia* subsp. ***diomedis*** (Braun-Blanq.) A. J. Moore & Dillenb., **comb. nov.** ≡ *Minuartia diomedis* Braun-Blanq. in Annuaire Conserv. Jard. Bot. Genève 21: 30. 1919 ≡ *Minuartia laricifolia* subsp. *diomedis* (Braun-Blanq.) Mattf. in Repert. Spec. Nov. Regni Veg. Beih. 15: 192. 1922. – Type: "France, Cévennes, Pic de la Fajerle [Fageole?], 1300m", 20 Jul 1913, *Braun-Blanquet s.n.* (G 00226885).

Subsp. *diomedis* is restricted to the Pyrenees and adjacent SE France and is distinguished by having glandular sepals and inflorescence axes. Although some populations appear to be mixed between subsp. *diomedis*

and subsp. *laricifolia* and the morphological distinction between the two subspecies is somewhat equivocal (L. Sáez Gonyalons, Universitat Autònoma de Barcelona, pers. comm.), populations belonging to this subspecies are clearly genetically distinct within *C. laricifolia* (A. J. Moore & J. W. Kadereit, unpublished data).

11c. *Cherleria laricifolia* subsp. ***ophiolitica*** (Pignatti) Iamonico in Taxon 65: 611. 2016 ≡ *Minuartia laricifolia* subsp. *ophiolitica* Pignatti in Giorn. Bot. Ital., n.s., 107: 208. 1973. – Holotype: Italy, "M. Murlo", 29 Jul 1933, *Pichi-Sermolli* (FI).

Subsp. *ophiolitica* is restricted to serpentine soils of the N Apennines in Italy. It differs from the typical subspecies in having smaller flowers and more glaucous leaves, but is not completely distinct genetically and likely experienced significant gene flow during its divergence from subsp. *laricifolia* (Moore & al. 2013).

12. *Cherleria marcescens* (Fernald) A. J. Moore & Dillenb., **comb. nov.** ≡ *Arenaria marcescens* Fernald in Rhodora 21: 15. 1919 ≡ *Minuartia marcescens* (Fernald) House in Amer. Midl. Naturalist 7: 132 1921. – Holotype: Canada, Western Newfoundland, "Region of Bay of Islands: Serpentine and magnesian limestone barrens, northeastern bases and slopes of Blomidon ('Blow-me-down') Mts.", 24 Jul 1901, *Fernald*, *Wiegand & Kittredge 3365* (GH 00037601! ["Type sheet 1"] and GH 00037602! ["Type sheet 2"]).

Cherleria marcescens is endemic to serpentine substrates in Newfoundland, Labrador, Quebec, Canada, and one location in Vermont, U.S.A. Its leaves generally have the truncate tips typical of its relative *C. arctica*, but its flowers are much smaller and the plants are sprawling. The only species with which it slightly overlaps in distribution is *C. biflora*.

13. *Cherleria obtusiloba* (Rydb.) A. J. Moore & Dillenb., **comb. nov.** ≡ *Alsinopsis obtusiloba* Rydb. in Bull. Torrey Bot. Club 33: 140. 1906 ≡ *Arenaria obtusa* Torr. in Ann. Lyceum Nat. Hist. New York 2: 170. 1828 [non *Arenaria obtusa* All., Auct. Syn.: 35. 1773] ≡ *Arenaria obtusiloba* (Rydb.) Fernald in Rhodora 21: 14. 1919 ≡ *Minuartia obtusiloba* (Rydb.) House in Amer. Midl. Naturalist 7: 132. 1921 ≡ *Lidia obtusiloba* (Rydb.) Á. Löve & D. Löve in Bot. Not. 128: 510. 1976. – Protologue: [of *Arenaria obtusa* Torr.] "On the higher parts of the Rocky Mountains." as part of a set of plants collected by Edwin P. James. The only possible specimen of *Minuartia* s.l. collected by James in NY (where Torrey's types should be) is NY 342403! (Holmgren & Holmgren 2012); however, it does not correspond to Torrey's description, so the type material is either elsewhere or (more likely) has been lost, in which case a neotype must be designated.

Cherleria obtusiloba (Fig. 1D) is restricted to North America, ranging from the Arctic south along the Cascades and Rocky Mountains to New Mexico. Outside of the Arctic, it grows in alpine and subalpine habitats, often occupying rockier and drier sites than *C. biflora*. It appears to be entirely absent from California and the western two-thirds of Utah, but overlaps with *C. biflora* in the Cascades, Rocky Mountains and eastern mountain ranges of Utah. See the discussion of the differences between the two species under *C. biflora*.

14. *Cherleria parnonia* (Kamari) A. J. Moore & Dillenb., **comb. nov.** ≡ *Minuartia wettsteinii* subsp. *parnonia* Kamari in Strid & Tan, Fl. Hellen. 1: 182. 1997 ≡ *Minuartia parnonia* (Kamari) Iatroú & al. in Tan & Iatroú, Endemic Pl. Greece, Peloponnese: 85. 2001. – Holotype: Greece, Peloponnisos, "Nom. Arkadias, Ep. Kinourias, Mt Parnonas, 1 km from Paliohori to Ag. Vassilis", 700 m, 17 Jun 1989, *Kit Tan & al. 6256* (C).

Cherleria parnonia (Fig. 1E) is endemic to calcareous substrates on Mount Parnonas in Greece, where it is threatened by grazing. Like its relatives *C. dirphya* and *C. wettsteinii*, *C. parnonia* has straight, glaucous leaves and flowers that open flat with petals narrower than the sepals.

15. *Cherleria rupestris* (Labill.) A. J. Moore & Dillenb., **comb. nov.** ≡ *Arenaria rupestris* Labill., Icon. Pl. Syr. 4: 8. 1812 ≡ *Minuartia labillardierei* Briq. in Annuaire Conserv. Jard. Bot. Genève 13–14: 385. 1911 [non *Minuartia rupestris* (Scop.) Schinz & Thell. in Bull. Herb. Bossier, sér 2, 7: 403. 1907]. – Holotype: [protologue: "Habitat in Libano"], *Labillardière* (G; isotype: FI 005962).

Cherleria rupestris grows on calcareous substrates in alpine areas of the mountains of Lebanon. It has straight, glaucous leaves and flowers with pink petals. Genetically, it appears to be rather isolated within *Cherleria*, although chloroplast sequence data place it near to *C. dirphya*, *C. parnonia* and *C. wettsteinii*, which it resembles vegetatively (A. J. Moore, F. J. Valtueña, M. S. Dillenberger, J. W. Kadereit and C. D. Preston, in prep.).

16. *Cherleria sedoides* L., Sp. Pl. 1: 425. 1753 ≡ *Arenaria sedoides* (L.) Druce in Rep. Bot. Soc. Exch. Club Brit. Isles 8: 109. 1927 [non *Arenaria sedoides* (Froel. ex W. D. J. Koch) B. D. Jacks., Index Kew. 1: 181. 1893] ≡ *Minuartia sedoides* (L.) Hiern. in J. Bot. 37: 321. 1899. – Lectotype (López González in Jarvis & al. 1993: 33): [icon] "*Cherleria*" in Haller, Enum. Meth. Stirp. Helv. 1: 391, t. 6. 1742.

Cherleria sedoides (Fig. 1C) is widespread throughout the European high mountains and in Scotland, but is absent from the Arctic. It is distinctive in having lanceolate (versus linear or linear-lanceolate) leaves with obtuse tips and petals that are reduced or most often entirely absent.

17. *Cherleria wettsteinii* (Mattf.) A. J. Moore & Dillenb., **comb. nov.** ≡ *Minuartia wettsteinii* Mattf. in Bot. Jahrb. Syst. 57, Beibl. 127: 62. 1922. – Holotype: "Kreta: Felsritzen in der Gipfelregion (1400 m) des Aphendi

Kavusi bei Hieraptera", 2 Aug 1904, *Dörfler 1048* (WU-Halácsy-Graecum 0059781!; isotypes: B 10 9005638!, WU 0060040!).

Cherleria wettsteinii is restricted to calcareous substrates on Mount Thriptis (Afendis Kavousi) in E Crete. It is greatly threatened by sheep and goat grazing and is likely close to extinction.

18. *Cherleria yukonensis* (Hultén) A. J. Moore & Dillenb., **comb. nov.** ≡ *Minuartia yukonensis* Hultén in Ark. Bot., n.s., 7: 52. 1968 ≡ *Lidia yukonensis* (Hultén) Á. Löve & D. Löve in Bot. Not. 128: 510. 1976. – Holotype: "Yukon Territory: Canada, Yukon Terr., near mouth of Klondike River near Dawson", 28 Jun 1949, *Calder & Billard 3359* (S G-7150; isotype: W 1955-9230!).

Cherleria yukonensis grows in far-northern North America and is distinguished from the other species in its range (*C. arctica*, *C. biflora* and *C. obtusiloba*) by its long, straight leaves with sharply pointed tips. Before it was described, specimens of *C. yukonensis* were annotated as *Minuartia* (or *Arenaria*) *laricifolia*, to which it is not closely related. The boundary between *C. yukonensis* and its close relative *C. obtusiloba* is unclear, and it is possible that further study will show that some of the non-Arctic plants treated here as *C. obtusiloba*, particularly those in the Canadian Rockies and Cascade Mountains, belong to *C. yukonensis*.

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