

RESEARCH ARTICLE

Intergeneric relationships within the tribe Alsineae (Caryophyllaceae) as inferred from nrDNA ITS and cpDNA *rps16* sequences: A step toward a phylogenetically based generic system

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Abstract The tribe Alsineae is a large monophyletic group in the family Caryophyllaceae especially found across Eurasia and the Americas, but with a center of diversity in the Mediterranean region. Several previous molecular phylogenetic studies have focused on the delimitation of genera and tribes of Caryophyllaceae, especially the subfamily Alsinoideae or the tribe Alsineae in a broader sense than now recognized. However, there are still many open questions regarding the subdivision of the tribe and genus delimitation. In the present study, we sampled 191 (148 species) and 149 (125 species) accessions of Alsineae representing almost all (*Adenonema* and *Pseudocerastium* were not available to us) recognized genera in the tribe for nuclear DNA internal transcribed spacer (ITS) and plastid marker *rps16* sequences, respectively. A combined matrix of 103 species was built for taxa with both sequences available. Maximum parsimony and Bayesian inference analyses retrieved *Cerastium* and *Stellaria* (including *Myosoton*) as the largest monophyletic genera, while other genera were medium-sized (10–20 spp.) or small (<10 spp.). Our expanded sampling of *Pseudostellaria* and its relatives suggests a broader circumscription of this genus. Major divergence in morphology, particularly of the seeds, observed in the “Protostellaria”-clade, allows recognition of some taxonomic changes. A total of 16 genera are recognized in Alsineae including *Cerastium*, *Dichodon*, *Hartmaniella*, *Holosteum*, *Lepyrodiclis*, *Mesostemma*, *Moenchia*, *Nubelaria*, *Odontostemma*, *Pseudostellaria*, *Rabelera*, *Schizotechium*, *Shivparvatia*, and *Stellaria*, along with *Adenonema* and *Pseudocerastium* that could not be analyzed and are, therefore, kept as distinct genera. A diagnostic key to these genera, as well as notes on their relationships, distribution, and nomenclature, is provided.

Keywords *Cerastium*; Mediterranean region; phylogeny; *Stellaria*; systematics; taxonomy

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

The large family Caryophyllaceae Juss. has about 100 genera and 3000 species (Hernández-Ledesma & al., 2015), mainly distributed in the Holarctic and with a center of diversity in the Mediterranean and Irano-Turanian floristic regions; most of the tropical and Southern Hemisphere members are restricted to high altitudes (Harbaugh & al., 2010; Greenberg & Donoghue, 2011). The family has often been divided into three subfamilies (Pax & Hoffmann, 1934): Alsinoideae Burnett (= Minuartioideae DC.), Caryophylloideae Arn., and Paronychioideae A.St.-Hil. ex Fenzl (= Illecebroideae Arn.), but this treatment has been replaced by a pure tribal system classifying the family into 11 tribes following molecular phylogenetics (Harbaugh & al., 2010).

Tribe Alsineae Lam. & DC., one of the currently recognized tribes (Harbaugh & al., 2010) in the family, is defined by 4–5 free sepals, antesealous stamens usually with nectary glands at the abaxial base of the filaments, styles distinct, fruit a many-seeded (rarely few- or one-seeded) capsule or rarely a nutlet. Some representative images of these plants are presented in Fig. 1. The distribution pattern of the tribe follows the same general pattern as the family (Bittrich, 1993), but many species (e.g., *Stellaria media* (L.) Vill., *Cerastium glomeratum* Thuill.) are cosmopolitan weeds, and some are cultivated as ornamentals (e.g., *Cerastium tomentosum* L.) (Scheen & al., 2004).

Composition and rank of Alsineae have changed through time, so that the circumscription of the tribe or its genera has also varied among different classification systems. Fenzl

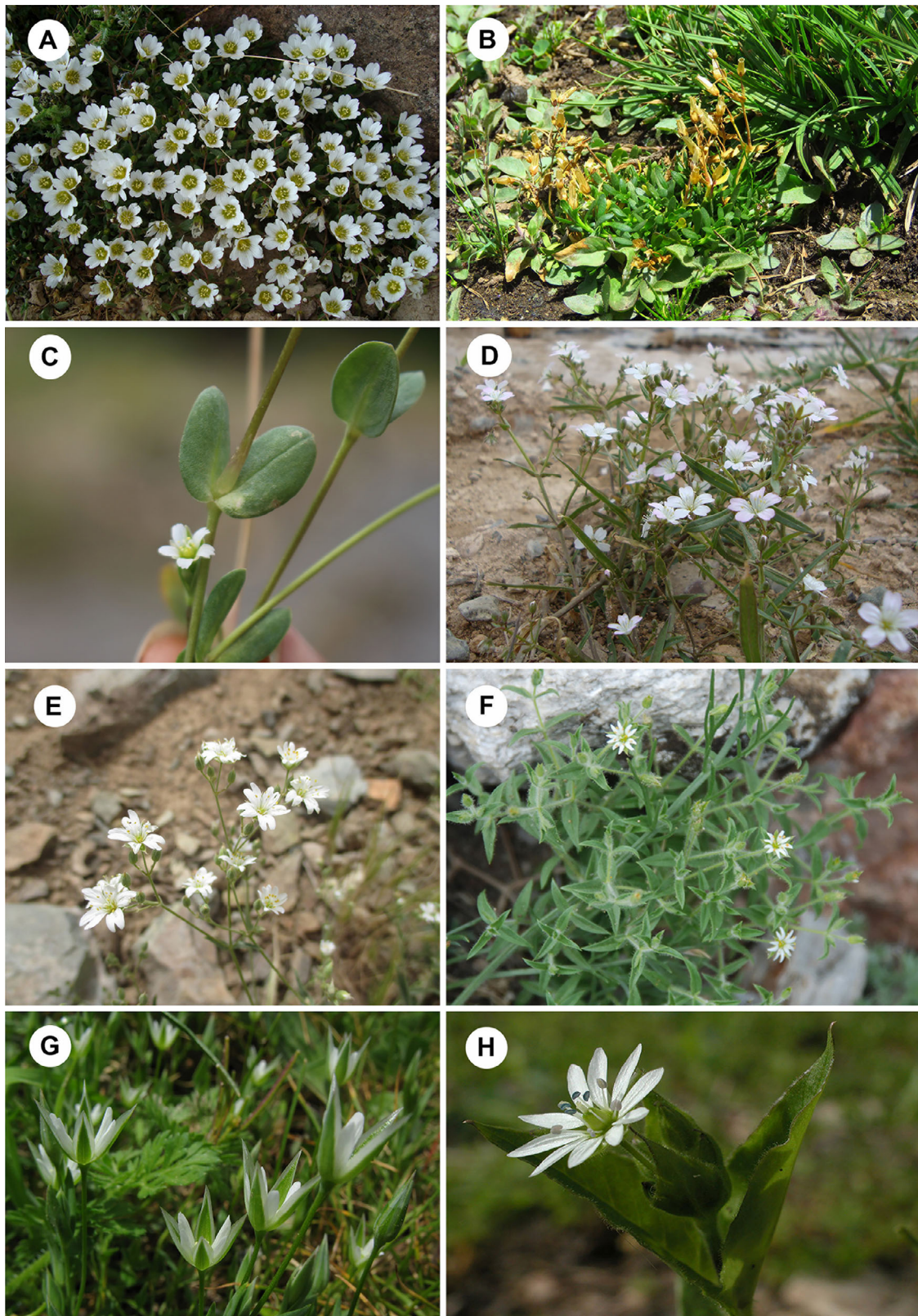


Fig. 1. Selected members of Alsineae. **A**, *Cerastium purpurascens* Adams (by A. Talebi, Iran, Mazandaran); **B**, *Dichodon persicus* (Boiss.) Ikonn. (by Z. Arabi, Iran, Hamedan); **C**, *Holosteum umbellatum* L. (by Z. Arabi, Iran, Mazandaran); **D**, *Lepyrodielis holosteoides* (C.A.Mey.) Fenzl ex Fisch. & C.A.Mey. (by A. Talebi, Iran, Mazandaran); **E**, *Mesostemma kotschyianum* (Fenzl ex Boiss.) Vved. (by Z. Arabi, Iran, Tehran); **F**, *Me. dichotomum* (L.) Arabi, Rabeler & Zarre (by M. Skotnikova, Russia, Irkutsk); **G**, *Moenchia erecta* G.Gaertn., B.Mey. & Scherb. (by V. Smith, United States, California); **H**, *Stellaria aquatica* (L.) Scop. (by D.G. Smith, United States, Vermont). (Continues)

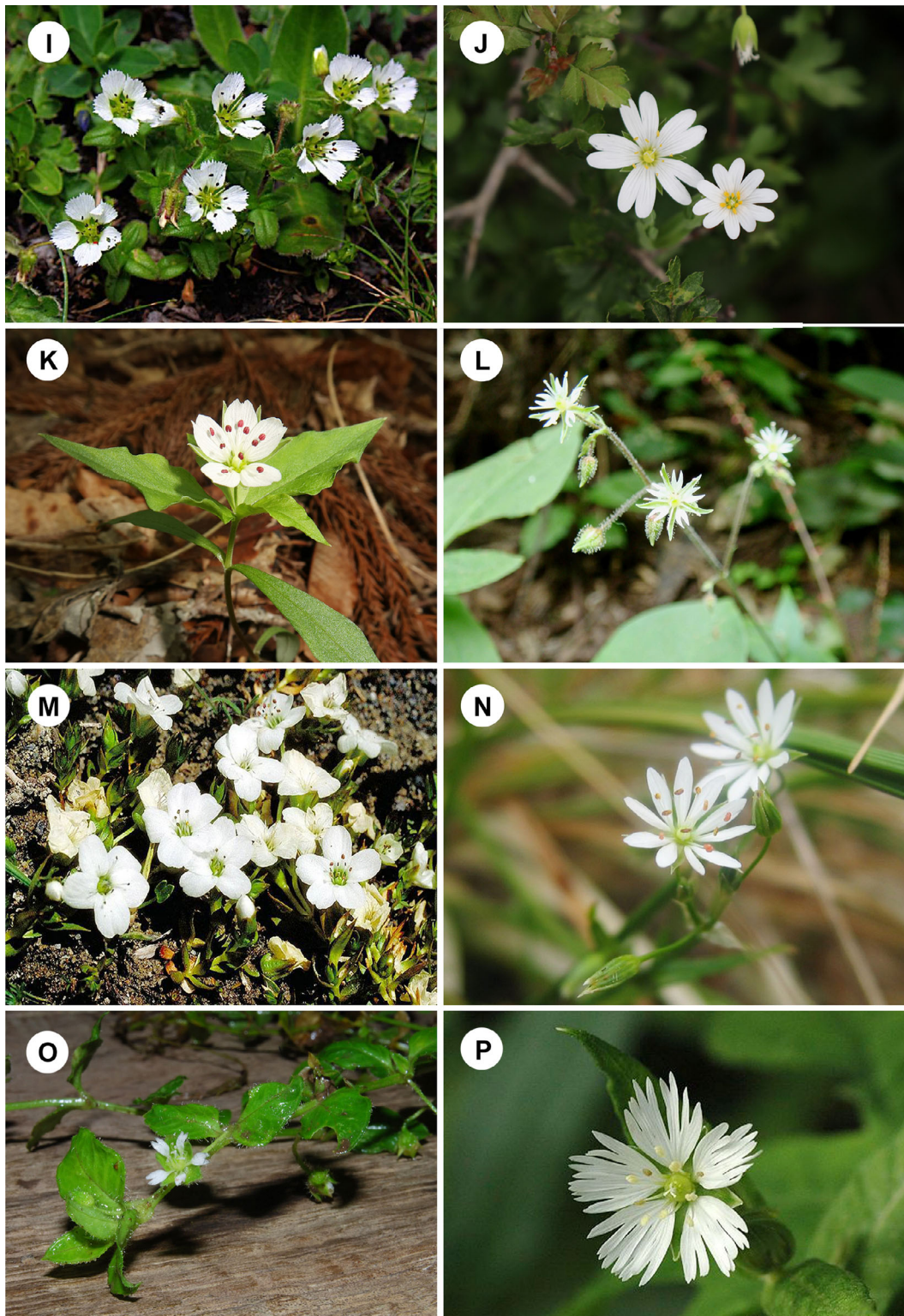


Fig. 1 (continued). I, *Odontostemma pogonanthum* (W.W.Sm.) Sadeghian & Zarre (by R.H. Ree, China, Yunnan); J, *Rabelera holostea* (L.) M.T. Sharples & E.A.Tripp (by Z. Arabi, Iran, Mazandaran); K, *Pseudostellaria heterophylla* (Miq.) Pax (https://commons.wikimedia.org/wiki/File:Pseudostellaria_heterophylla_1.JPG, Japan, Fukushima); L, *Schizotechium monospermum* (Buch.-Ham. ex D.Don) Pusalkar & S.K.Srivast. (http://www.7a.biglobe.ne.jp/~flower_world/images/Stellaria%20monosperma%20japonica/DSC09805.JPG, Japan, Mt. Takao); M, *Shivparvatia forrestii* (Diels) Rabeler (by D.E. Boufford, http://www.efloras.org/object_page.aspx?object_id=88286&flora_id=800, China, Xizang); N, *Stellaria graminea* L. (https://en.wikipedia.org/wiki/Stellaria_graminea#/media/File:%20Stellaria%20graminea_detail.jpeg, Germany, Mecklenburg-Vorpommern); O, *St. ovata* Willd. ex D.F.K.Schldtl. (by A. Monro, <https://swbiodiversity.org/seinet/imagelib/imgdetails.php?imgid=305606>); P, *St. radians* L. (by J. Liu, <https://naturelib.net/plantae/stellaria-radians/>).

(1839–1840) published the first comprehensive study on Caryophyllaceae in which Alsinoideae (as ‘Alsineae’, but should be considered as equivalent to subfamily Alsinoideae; see Art. 19.2 in Turland & al., 2018) as a “Subordo” was divided into three tribes. This treatment was followed by Boissier (1867), who, however, used Alsinoideae as equivalent to Alsinoideae. Pax & Hoffmann (1934) divided tribe Alsineae into two subtribes emphasizing the mode of capsule dehiscence, while McNeill (1962) considered that there were three “recognisable aggregations” within Alsineae that might not represent “natural” groups, i.e., *Stellaria* L.-*Cerastium* L. group, *Sagina* L. group, and *Arenaria* L. group. A summary of the Alsineae genera as classified in different systems is shown in Table 1.

Several molecular phylogenetic studies have been conducted to test the subfamilial relationships within Caryophyllaceae. The first one was published by Smitsen & al. (2002) with 15 taxa analyzed, which was followed by Fior & al. (2006), providing a more comprehensive phylogeny of the subfamilies Alsinoideae (11 spp.) and Caryophylloideae. The results of both studies were congruent in finding that the classical subfamilies of Caryophyllaceae are paraphyletic. Harbaugh & al. (2010), based on a wider sampling focused on the Alsinoideae, demonstrated not only the non-monophyly of the three subfamilies but also the paraphyly or polyphyly of many tribes traditionally recognized in Alsinoideae. This study rejected the traditional subfamilial classification of Caryophyllaceae and suggested segregating the whole family into 11 tribes. Alsineae s.str. as one of these natural tribes corresponds to one of McNeill’s (1962) artificial groups, the *Stellaria-Cerastium* aggregation, and includes the genera *Holosteum* L., *Moenchia* Ehrh., *Myosoton* Moench, *Plettkea* Mattf., *Pseudostellaria* Pax, *Arenaria* subg. *Odontostemma* (Benth. ex G.Don) F.N.Williams, and *Lepyrodiclis* Fenzl ex Endl. The morphological synapomorphies characterizing most members of Alsineae s.str. are: petals deeply cleft (rarely jagged or nearly entire or absent), and capsules dehiscing by twice as many valves as styles (except *Lepyrodiclis* with an equal number of capsule valves and styles).

In order to confidently resolve the relationships within Caryophyllaceae, Greenberg & Donoghue (2011) expanded the sampling within the family and retrieved the same tribes as Harbaugh & al. (2010). Both investigations indicated the non-monophyly of the larger genera of Alsineae, i.e., *Cerastium* and *Stellaria*. Similar results were obtained for other large genera traditionally assigned to Alsineae, viz. *Arenaria* (Sadeghian & al., 2015) and *Minuartia* Loefl. (Dillenberger & Kadereit, 2014). Sadeghian & al. (2015) confirmed the exclusion of the majority of *Arenaria* spp. (as *Arenaria* s.str.) from Alsineae as reported by Harbaugh & al. (2010) and Greenberg & Donoghue (2011), but raised *Arenaria* subg. *Solitaria* McNeill and *Ar.* subg. *Odontostemma* to genus rank, maintaining them as members of Alsineae. *Minuartia*, also treated as a member of Alsineae in traditional systems (Pax & Hoffmann, 1934; Schischkin, 1936; Bittrich, 1993), turned out to be polyphyletic with members placed in both tribes

Sagineae J.Presl and Scleranthae DC. (Dillenberger & Kadereit, 2014). A recent study of *Pseudostellaria* retrieved this genus as a member of the *Odontostemma* clade, and the new genus *Hartmaniella* M.L.Zhang & Rabeler was proposed for two American species formerly assigned to *Pseudostellaria* (Zhang & al., 2017). In addition, the isolated position of members of the genus *Dichodon* (Bartl. ex Rchb.) Rchb. from *Cerastium* was recently confirmed (Arabi & al., 2018). A comprehensive molecular phylogenetic study using selected cpDNA markers identified the main clades within *Cerastium* (Scheen & al., 2004), but due to poor outgroup sampling, the correct position of *Cerastium* (ca. 180 spp.) within Alsineae could not be clarified adequately. Other phylogenetic studies that covered several representatives of *Cerastium* have shown that *C.* subg. *Dichodon* deserved to be recognized as a distinct genus (Greenberg & Donoghue, 2011; Arabi & al., 2018).

Molecular phylogenetics of *Stellaria*, the second-largest genus of Alsineae (112–120 spp., according to Morton, 2005; Sharples, 2019), have shown that the initially designated type of the genus, i.e., *St. holostea* L., should be replaced since it was not retrieved in the main clade containing the majority of species (Greenberg & Donoghue, 2011). More recently, based on a broad sampling of *Stellaria*, Sharples & Tripp (2019a) and Sharples (2019) recovered five major clades in the genus. Sharples & Tripp (2019a) also revised the generic boundaries around the core group of *Stellaria* and suggested several novel taxonomic changes in Alsineae, including the segregation of two new genera, *Nubelaria* M.T. Sharples & E.A.Tripp and *Rabelera* M.T.Sharples & E.A. Tripp. Furthermore, Sharples & Tripp (2019b) provided a significant contribution on the delimitation of some challenging species of *Stellaria*, using RAD sequencing technology. A recent phylogenomic study of Alsineae using several plastid markers along with nrDNA ITS reduced the generic name *Pseudocerastium* to a synonym of *Cerastium* (Yao & al., 2021).

The morphological characters (e.g., number of capsule valves and styles) used in traditional taxonomy have been shown to be homoplasious, and divergent classifications were based on the rather subjective emphasis on individual characters or suites of characters. A more comprehensive study covering all genera of the tribe Alsineae with an adequate sampling of the larger genera is required to improve our understanding of genus limits and relationships between genera. The objectives followed in the present study are: (1) defining generic boundaries, (2) proposing a new phylogeny-based classification, (3) resolving nomenclatural issues with genus names, (4) inferring the position of the genera recognized in the tribe, and (5) presenting an updated identification key to these genera.

■ MATERIALS AND METHODS

Taxon sampling. — In order to provide sufficient sampling, we tried to incorporate more representatives of all genera

Table 1. Generic concepts in Alsineae as mostly applied in previous literature.

Lamarck & Candolle (1806)	Fenzl (1839–1840)	Bentham & Hooker (1862)	Boissier (1867)	Pax & Hoffmann (1934)	Schischkin (1936)	Bittrich (1993)	Takhtajan (2009)	Harbaugh & al. (2010)
<i>Ortega</i>	Sabulineae	<i>Holosteum</i>	Sabulineae	Stellariinae	<i>Stellaria</i>	<i>Arenaria</i>	<i>Arenaria</i>	<i>Lepyrodiclis</i>
<i>Polycarpon</i>	<i>Sagina</i>	<i>Cerastium</i>	<i>Sagina</i>	<i>Goorlingia</i>	<i>Krascheninikowia</i>	<i>Thylacospermum</i>	<i>Dichodon</i>	<i>Pseudostellaria</i>
<i>Bufoia</i>	<i>Bufoia</i>	<i>Stellaria</i>	<i>Bufoia</i>	<i>Arenaria</i>	(= <i>Pseudostellaria</i>)	<i>Moehringia</i>	<i>Eremogone</i>	<i>Moenchia</i>
<i>Sagina</i>	<i>Queria</i>	<i>Brachystemma</i>	<i>Lepyrodiclis</i>	<i>Holosteum</i>	<i>Malachium</i>	<i>Brachystemma</i>	<i>Thylacospermum</i>	<i>Holosteum</i>
<i>Alsine</i>	<i>Alsine</i>	<i>Arenaria</i>	<i>Alsine</i>	<i>Pseudostellaria</i>	<i>Cerastium</i>	<i>Thurya</i>	<i>Moehringia</i>	<i>Cerastium</i>
<i>Moehringia</i>	<i>Triplateia</i>	<i>Bufoia</i>	<i>Queria</i>	<i>Thylacospermum</i>	<i>Holosteum</i>	<i>Bufoia</i>	<i>Brachystemma</i>	<i>Odontostemma</i>
<i>Elatine</i>	<i>Honkenja</i>	<i>Sagina</i>	<i>Thurya</i>	<i>Brachystemma</i>	<i>Sagina</i>	<i>Lepyrodiclis</i>	<i>Thurya</i>	<i>Stellaria</i>
<i>Spergula</i>	<i>Lepyrodiclis</i>	<i>Colobanthus</i>	Stellariinae	<i>Moehringia</i>	<i>Bufoia</i>	<i>Cerastium</i>	<i>Bufoia</i>	<i>Pletkea</i>
<i>Cerastium</i>	Merckieae	<i>Thylacospermum</i>	<i>Arenaria</i>	<i>Stellaria</i>	<i>Lepyrodiclis</i>	<i>Moenchia</i>	<i>Lepyrodiclis</i>	<i>Myosoton</i>
<i>Cherleria</i>	<i>Merckia</i>	<i>Schiedea</i>	<i>Stellaria</i>	<i>Moenchia</i>	<i>Queria</i>	<i>Stellaria</i>	<i>Cerastium</i>	
<i>Arenaria</i>	<i>Dolophragma</i>	<i>Queria</i>	<i>Moehringia</i>	<i>Malachium</i>	<i>Minuartia</i>	<i>Pseudostellaria</i>	<i>Stellaria</i>	
<i>Stellaria</i>	Stellariinae	<i>Spergula</i>	<i>Holosteum</i>	<i>Cerastium</i>	<i>Ammoenia</i>	<i>Holosteum</i>	<i>Mesostemma</i>	
	<i>Thylacospermum</i>	<i>Spergularia</i>	<i>Moenchia</i>	Sabuliniinae	<i>Arenaria</i>	<i>Myosoton</i>	<i>Tythostemma</i>	
	<i>Arenaria</i>	<i>Spergularia</i>	<i>Cerastium</i>	<i>Schiedea</i>	<i>Moehringia</i>	<i>Minuartia</i>	<i>Fimbripetalum</i>	
	<i>Moehringia</i>	<i>Malachium</i>	<i>Malachium</i>	<i>Sagina</i>	<i>Merckia</i>	<i>Wilhelmsia</i>	<i>Pseudostellaria</i>	
	<i>Krascheninikowia</i>		Sperguleae	<i>Colobanthus</i>	<i>Thylacospermum</i>	<i>Honkenya</i>	<i>Moenchia</i>	
	(= <i>Pseudostellaria</i>)		<i>Spergula</i>	<i>Honkenya</i>		<i>Sagina</i>	<i>Holosteum</i>	
	<i>Brachystemma</i>		<i>Spergularia</i>	<i>Reicheella</i>		<i>Colobanthus</i>	<i>Myosoton</i>	
	<i>Odontostemma</i>			<i>Lyallia</i>		<i>Alsinidendron</i>	<i>Minuartia</i>	
	<i>Holosteum</i>			<i>Hectorella</i>		<i>Schiedea</i>	<i>Queria</i>	
	<i>Stellaria</i>			<i>Minuartia</i>		<i>Reicheella</i>	<i>Wilhelmsia</i>	
	<i>Cerastium</i>			<i>Thurya</i>		<i>Pletkea</i>	<i>Honkenya</i>	
	<i>Malachium</i>			<i>Lepyrodiclis</i>		<i>Pycnophyllopsis</i>	<i>Sagina</i>	
				<i>Bufoia</i>		<i>Colobanthus</i>	<i>Colobanthus</i>	
				<i>Merckia</i>		<i>Alsinidendron</i>	<i>Alsinidendron</i>	
				<i>Pycnophyllopsis</i>		<i>Schiedea</i>	<i>Schiedea</i>	
						<i>Reicheella</i>	<i>Reicheella</i>	
						<i>Pletkea</i>	<i>Pletkea</i>	
							<i>Pycnophyllopsis</i>	

In Fenzl (1839–1840), “Alsineae” (which is in fact equal to subfam. Alsinoidae) was treated as a “Subordo” (i.e., subfamily, cf. Art. 19.2) and divided into three “tribi”, albeit with modern subtribe terminations, while Boissier (1867), who treated “Alsineae” as a family (“Ordo”, cf. Art. 18.2), changed the composition of the three tribes. Harbaugh & al. (2010) transferred many of the genera that earlier authors had placed in Alsineae or Alsinoidae (or Alsinaceae) to their Sagineae and Sclerantheae. Tribes and subtribes, when available, are indicated in bold.

recognized in tribe Alsineae as currently circumscribed (Harbaugh & al., 2010). We sampled richly from the large genera *Cerastium* (31 spp.) and *Stellaria* (including *Mesostemma* Vved., *Nubelaria*, *Schizotechium* Rchb., and *Rabelera*; 65 spp.). In the sampling strategy, we tried to cover all morphological groups known to represent different sections and the entire distribution range of these large genera. We also sampled 16 species of *Pseudostellaria*, one of the most challenging taxonomic groups in Alsineae. The genera *Dichodon* (5 spp.), *Hartmaniella* (2 spp.), *Holosteum* (4 spp.), *Lepyrodiclis* (2 spp.), *Moenchia* (2 spp.), *Myosoton* (1 sp.), *Odontostemma* (3 spp.) and *Shivparvatia* Pusalkar & D.K.Singh (3 spp.) were also sampled sufficiently. Twelve species were selected as outgroups to recover all main clades and tribes already recognized in Caryophyllaceae (Harbaugh & al., 2010; Greenberg & Donoghue, 2011). A list of voucher specimens used for this study is presented in Appendix 1.

DNA extraction, amplification, and sequencing. — The selected taxa were sequenced for their nuclear ribosomal internal transcribed spacer (nrITS) and the plastid *rps16* gene, known as the most informative and effective molecular markers in phylogenetic inference of Caryophyllaceae (Oxelman & Petri, 2011; Pirani & al., 2014; Sadeghian & al., 2015; Madhani & al., 2018). A total of 82 and 83 sequences were generated for nrDNA ITS and cpDNA *rps16*, respectively. In addition, 175 sequences were obtained from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>).

Leaf materials were obtained from fresh collected silica-dried samples as well as herbarium sheets held at the herbaria B, M, MSB, T, and TUH. Genomic DNA was extracted using a NucleoSpin Plant DNA Extraction kit (Macherey-Nagel, Düren, Germany) according to the manufacturer's protocol. The ITS region was amplified using primer pair ITS1/ITS4 (White & al., 1990). For amplification of the complete intron of the plastid *rps16* gene, we alternatively used primer pair *rpsF*/*rpsR2R* (Oxelman & al., 1997; Petri & Oxelman, 2011; Kool & al., 2012) or *rpsF*/*rpsR3R*. PCR reactions were performed according to Salmaki & al. (2012).

DNA sequence alignment and phylogeny reconstruction. — All sequences were first aligned in Mafft v.7 (Katoh & Standley, 2013) using default parameters, and the alignment errors were identified and manually edited in Mesquite v.2.75 (Maddison & Maddison, 2010). The beginning and end of the alignments, where the majority of taxa did not provide complete data, were excluded (see the alignments in suppl. Appendices S1 & S2). Indels in the alignments were not coded. Phylogenetic reconstruction analyses were performed with Bayesian inference (BI) and maximum parsimony (MP) approaches. The analyses were performed separately on each dataset, as the taxon composition of cpDNA (149 accessions) and nrDNA (191 accessions) matrices was not identical. However, a combined matrix (151 accessions representing 127 species) was built for taxa for which both sequences were available. Bayesian analyses of the individual matrices were conducted using the Markov chain Monte-Carlo (MCMC) algorithm of MrBayes v.3.2. (Ronquist & al., 2012) on the

CIPRES Gateway (Miller & al., 2010). The best nucleotide substitution model was selected using the Akaike information criterion (AIC) in jModelTest v.2.1.6 (Darriba & al., 2012). The general time reversible model of nucleotide substitution with gamma-shaped rate variation and a proportion of invariable sites (GTR+I+ Γ) was the estimated best-fit model for ITS, and a simpler model, GTR+ Γ , was chosen for *rps16*. We set the generation number in MCMC to 10, 10, and 4 million generations for the ITS, *rps16*, and combined datasets, respectively. Trees were sampled every 1000 generations, and the runs were stopped when the average standard deviation of split frequencies fell below the critical value of 0.01; the burn-in fraction was set to 10%. Posterior probabilities (PPs) were calculated on the basis of the remaining trees. MP analysis of the individual genes was performed using PAUP* v.4.0b10 (Swofford, 2002). An initial analysis was conducted with 1000 random addition cycles, tree bisection-reconnection (TBR) branch swapping, and retaining the five most parsimonious trees in each replicate. A second heuristic search with the same settings followed, starting from the trees in memory (Davis & al., 2004), retaining a maximum of 20,000 trees. To assess branch support, 5000 bootstrap replicates were generated with one tree held per replicate. The bootstrap supports were shown on the obtained trees. FigTree v.1.4 (Rambaut, 2012) was used for tree presentation.

■ RESULTS

In total, we generated 165 new sequences including 83 nrDNA ITS and 82 plastid *rps16* sequences of tribe Alsineae and outgroup taxa. Our nrDNA ITS alignment consisted of 836 sites for 191 accessions. The *rps16* alignment included 1121 sites for 149 accessions (suppl. Fig. S1). The combined matrix of nrDNA ITS and cpDNA *rps16*, which included only those taxa having sequences of both markers, had 1957 aligned positions and 137 accessions. Analysis of the nrDNA ITS region resulted in a higher proportion of variable (55.98%) and potentially parsimony-informative (48.69%) positions compared to the *rps16* dataset (52.45% and 34.79%, respectively).

The MP and BI analyses of both the ITS and *rps16* datasets show similar topologies; therefore, we only show the BI trees (Fig. 2, suppl. Fig. S1). The tree gained from the BI analysis of the combined dataset is presented in Fig. 3. It shows essentially the same topology as the nrDNA ITS trees but is not discussed in detail here since it includes a smaller number of accessions, and there are residual doubts with regards to the combination of plastid and nuclear markers in phylogenetic analyses (Pirie, 2015). The nrDNA ITS sequences (Fig. 2) provide a more resolved phylogeny than the *rps16* dataset (suppl. Fig. S1). Some species traditionally known as members of *Stellaria*, i.e., *St. howardii* Maguire, *St. minutifolia* Maguire, and *St. ovata* Willd. ex D.F.K.Schldl., are placed in the same clades as outgroups in both trees. The genera of Alsineae fall into two well-supported monophyla “Alsineae A” (ITS: PP 1.00, BS 70%; *rps16*: PP 1.00, BS 92%) and

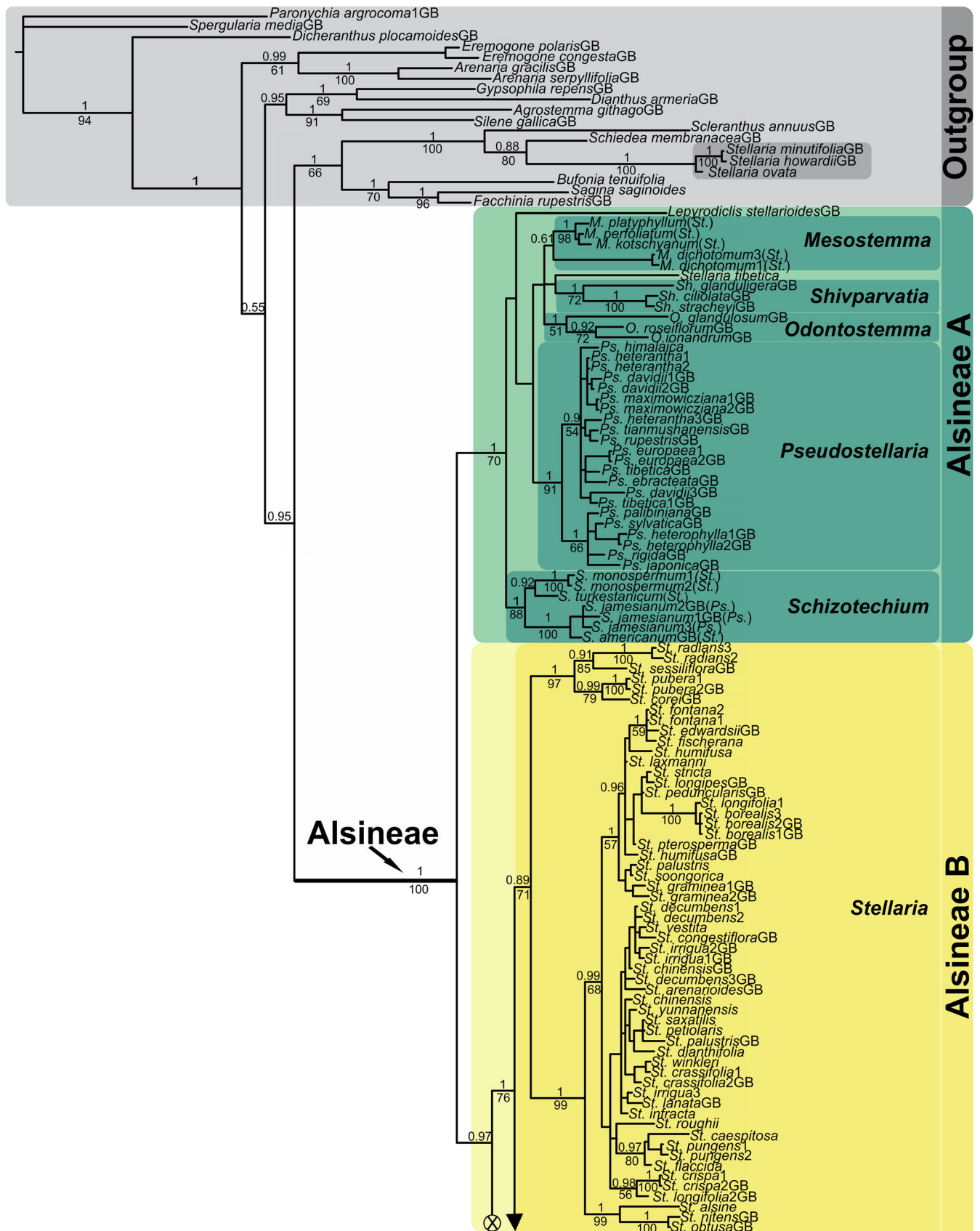


Fig. 2. For caption, see p. 615.

“Alsineae B” (ITS: PP 0.97, BS < 50%; *rps16*: PP 0.99, BS 78%). “Alsineae A” comprises the genera *Lepyrodiclis*, *Mesostemma*, *Odontostemma*, *Pseudostellaria*, *Shivparvatia*, *Schizotechium* as well as a few *Stellaria* spp., but does not include *St. holostea*, formerly the type of the generic name, and the majority of the *Stellaria* clade, which is placed in “Alsineae B”. Species assigned to *Stellaria* in “Alsineae A” appear to be best accommodated by inclusion into the genera listed above, except for *St. tibetica*. “Alsineae B” encompasses the majority of *Stellaria* as well as the genera *Cerastium*, *Dichodon*, *Holosteum*, *Moenchia*, *Hartmaniella*, *Nubelaria*, and *Rabelera*.

The first diverging clade in “Alsineae A” is *St. tibetica* Kurz in the *rps16* trees (suppl. Fig. S1: PP 0.52, BS < 50%) and *Lepyrodiclis* in the combined trees (Fig. 3: PP 0.72, BS < 50%). Members of *Odontostemma* form a monophylum in the ITS topology (Fig. 2: PP 1.00, BS 51%), but *O. glandulosum* is not recovered on the same branch with the other two species in the *rps16* tree (suppl. Fig. S1). Representatives of the genus *Mesostemma* form a clade with high support in both gene trees (Fig. 2: PP 1.00, BS 98%; suppl. Fig. S1: PP 1.00, BS 97%), but the sister group of this clade differs among the two phylogenies: *St. dichotoma* L. forms the sister to *Mesostemma* in

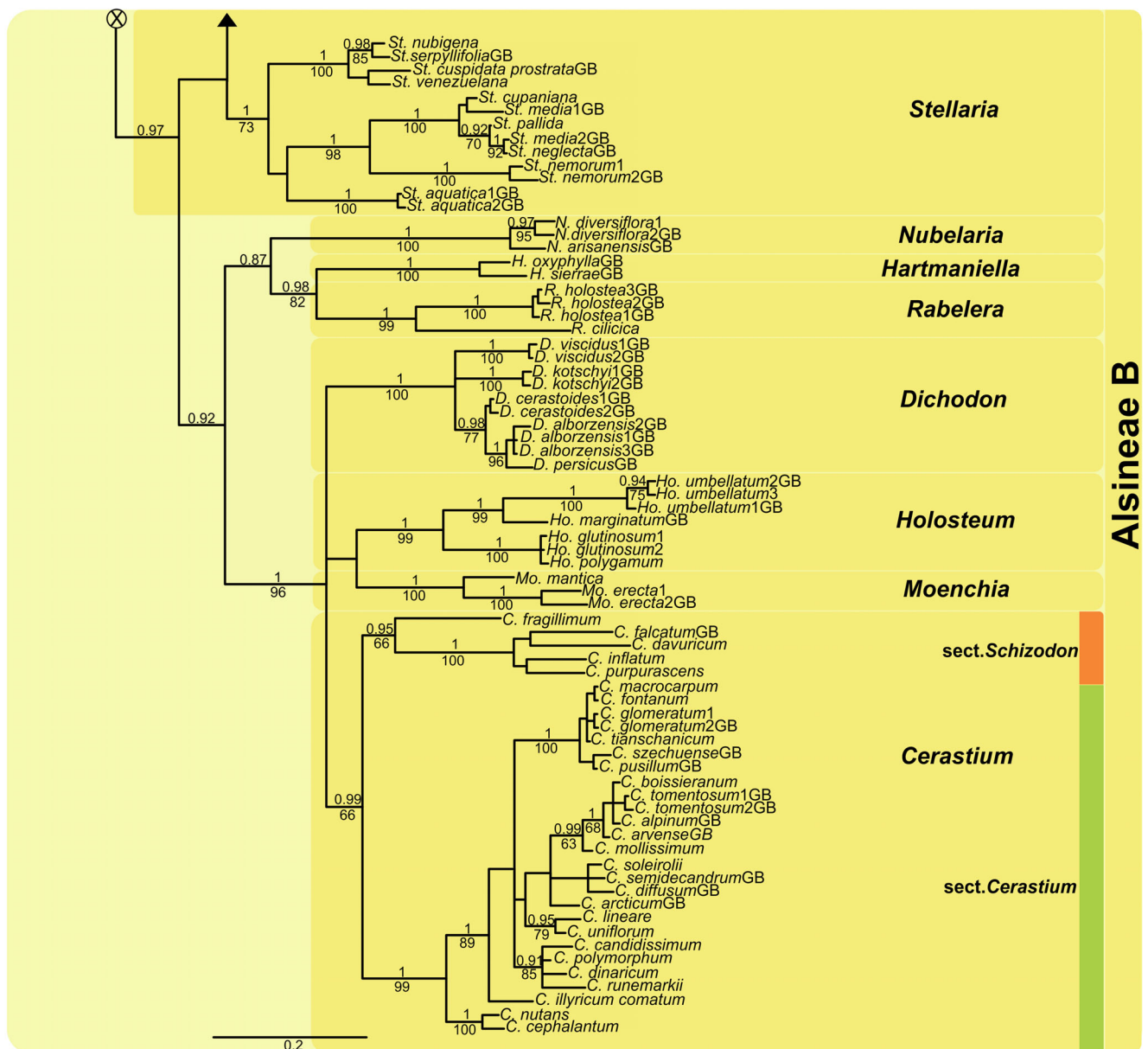


Fig. 2 (continued). Majority-rule consensus tree inferred from Bayesian analysis of ITS data in tribe Alsineae. Numbers above branches indicate posterior probability values; those below branches are MP bootstrap values. The generic names inside the boxes are those accepted in the present study. Species names are according to www.ipni.org and follow the taxonomic treatments suggested in the present study. Abbreviations in parentheses indicate generic names in traditional classification systems. Accessions marked by “GB” were downloaded from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>).

the nrITS tree (although with weak support, Fig. 2: PP 0.61, BS < 50% for the clade of both), while it shows a well-supported sister relationship to the remaining members of clade “Alsineae A” in the *rps16* tree (suppl. Fig. S1: PP 1.00, BS 77% for the monophylum, PP 1.00, BS 68% for the monophyly of the remaining members). The genus *Shivparvatia* is also supported in both ITS and *rps16* phylogenies (Fig. 2: PP 1.00, BS 72%; suppl. Fig. S1: PP 1.00, BS 79%). *Schizotechium* forms a monophylum with *St. americana* (Porter ex B.L. Rob.) Standl., *Pseudostellaria jamesiana* (Torr.) W.A.Weber & R.L.Hartm., *St. turkestanica* Schischk., and *Schizotechium monospermum* (Buch.-Ham. ex D.Don) Pusalkar & S.K.Srivast. as its components in the nrITS cladogram (Fig. 2: PP 1.00, BS 88%). Although the component taxa of this clade are the same in the *rps16* phylogeny, the relationships among them are not resolved (suppl. Fig. S1). *Pseudostellaria* spp. form a clade in both nrITS (Fig. 2: PP 1.00, BS 91%) and combined trees (Fig. 3: PP 1.00, BS 97%). The relationships among *Pseudostellaria*, *Shivparvatia*, and *Odontostemma* are not resolved in either nrITS (Fig. 2) or *rps16* topologies (suppl. Fig. S1).

The first diverging component of clade “Alsineae B” (suppl. Fig. S1: PP 0.99, BS 78%) is *Nubelaria diversiflora*

(Maxim.) M.T.Sharples & E.A.Tripp in the *rps16* tree (suppl. Fig. S1: PP 0.99, BS 69% for “Alsineae B” excluding *Nubelaria*), which shows a more internal position in the nrITS tree where it is retrieved in one clade with *Hartmaniella* and *St. cilicica* Boiss. & Balansa as well as *Rabelera holostea* (L.) M.T. Sharples & E.A.Tripp (Fig. 2). In both *rps16* (suppl. Fig. S1) and combined trees (Fig. 3), the clade including *Hartmaniella*, *St. cilicica*, and *R. holostea* is the sister to the remainder of clade “Alsineae B”. The core group of *Stellaria* is well supported in the nrITS cladogram (Fig. 2: PP 1.00, BS 76%), but weakly in the *rps16* tree (suppl. Fig. S1: PP 0.59, BS < 50%). The component clades within the *Stellaria* core group are almost similar among the obtained trees, although the relationships among these internal clades of *Stellaria* are more resolved in the nrITS cladogram (Fig. 2). In the second main clade of “Alsineae B”, *Dichodon* is the first diverging clade followed by the genera *Moenchia*, *Holosteum*, and *Cerastium* in the combined (Fig. 3) and the *rps16* (suppl. Fig. S1) phylogenies, while it is in a polytomy with the mentioned genera in the ITS tree (Fig. 2). All of the latter three genera are more or less highly supported in both trees, although the nrITS tree provides lower support for *Cerastium* (Fig. 2: PP 0.99, BS 66%).



Fig. 3. For caption, see p. 617.

■ DISCUSSION

Tribe Alsineae as currently circumscribed (Harbaugh & al., 2010; Greenberg & Donoghue, 2011) is confirmed as monophyletic. Some of the taxa traditionally assigned to this group (see below) are not associated with this clade or

with the genera they were originally assigned to. The number of genera within Alsineae has been increasing in recent years through the addition of several newly defined genera, e.g., *Hartmaniella* (Zhang & al., 2017) and *Shivparvatia* (Pusalkar & Singh, 2015; Sadeghian & al., 2015), and resurrection of others, e.g., *Dichodon* (Arabi & al., 2018) and

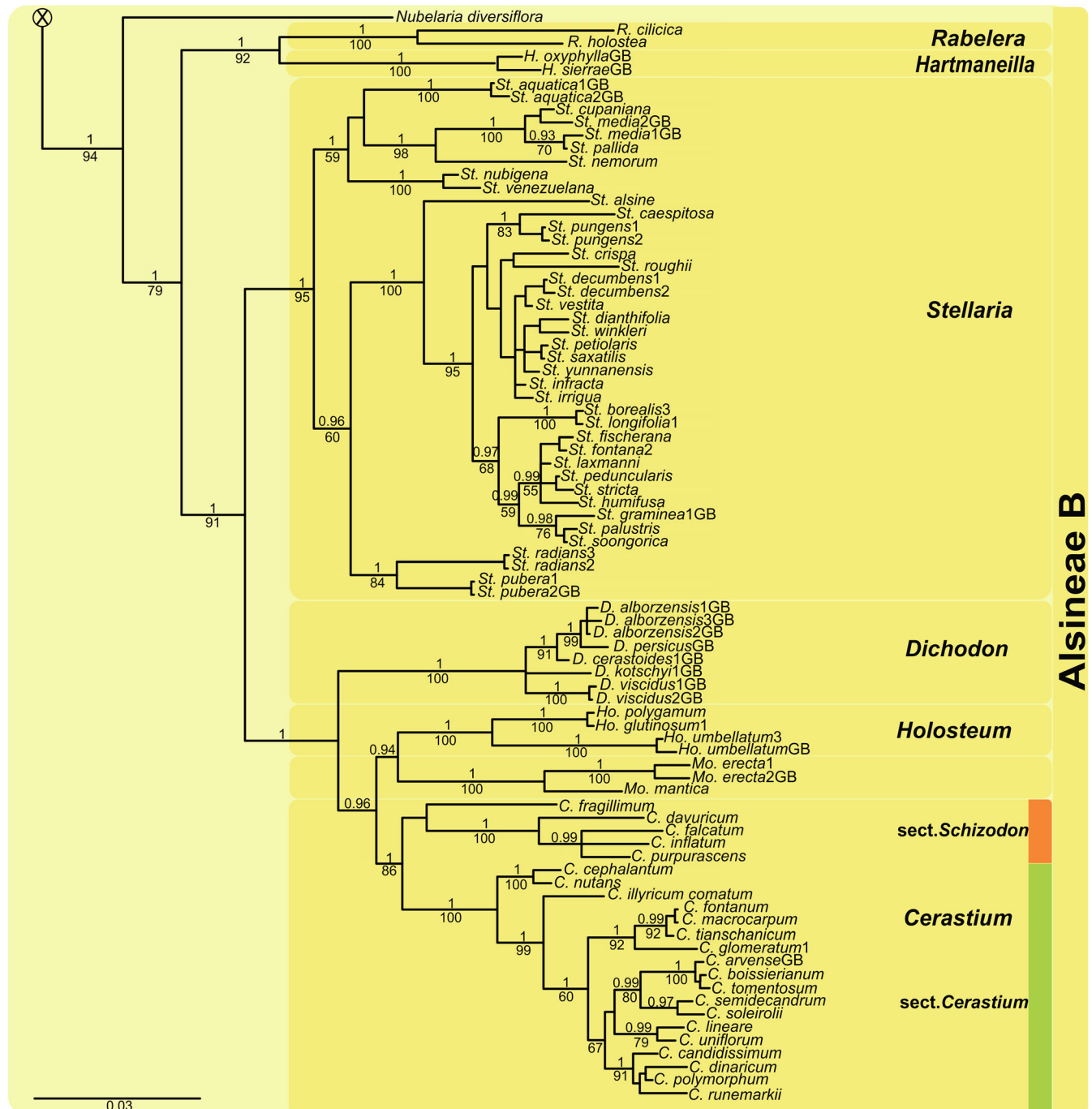


Fig. 3 (continued). Majority-rule consensus tree inferred from Bayesian analysis of combined data in tribe Alsineae. Numbers above the branches indicate posterior probability values; those below branches are MP bootstrap values. The generic names inside the boxes are those accepted in the present study. Species names are according to www.ipni.org and follow the taxonomic treatments suggested in the present study. Abbreviations in parentheses indicate generic names in traditional classification systems. Accessions marked by “GB” were downloaded from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>).

Schizotechium (Pusalkar & Srivastava, 2016), that were described earlier and then synonymized. The phylogenetic analyses performed here provide better resolution of the relationships and delimitation of genera in Alsineae. Information on morphological characters, distribution, and types of the genera assessed are presented in Table 2.

Outgroup relationships. — The placement of a few species of *Stellaria*, i.e., *St. ovata* (Mexico to S America), *St. minutifolia*, and *St. howardii* (Dominican Republic), among the outgroups is in agreement with previous molecular phylogenies (Harbaugh & al., 2010; Greenberg & Donoghue, 2011; Dillenberger & Kadereit, 2014). Morphological and geographic evidence (growth habit, 4-merous flowers, relatively shallowly cleft petals, seed with prominent dorsal tubercles, and distribution in Antillean islands) suggests *St. antillana* Urb. is closely allied to *St. ovata* (Maguire, 1958) and belongs to this group, which was also confirmed by a recent phylogenetic analysis (Sharples & Tripp, 2019a). Greenberg & Donoghue (2011) were the first to demonstrate that these species belong to tribe Scleranthae Link ex DC., a conclusion that was confirmed later by Dillenberger & Kadereit (2014). These species are superficially similar to *Stellaria*, but upon closer examination differ in possessing clawed petals, a shallowly cleft petal apex, dehiscent capsules with as many teeth as styles, lentil-shaped seeds with specific testa sculpturing (as reported for *St. ovata*: see Arabi & al., 2017). Our analyses, however, do not confirm the placement of *St. obtusa* Engelm. as sister to the genera *Honckenya* Erh., *Wilhelmsia* Rehb., and *Schiedea* Cham. & Schtdl. as suggested by Greenberg & Donoghue (2011), which might be explained by different taxon sampling and alignments in the two studies. The affinity of *St. obtusa* to *St. nitens* as recovered here (Fig. 2) is corroborated by the patterns of geographic distribution (western U.S.A.) and morphological similarities. Even the increased sampling of *Stellaria* and adding a new plastid marker to the dataset as conducted in our analyses confirmed these taxa should be excluded from *Stellaria*. Although the former studies also seriously doubted the monophyly of *Stellaria*, no formal taxonomic change can be made in this group due to lack of sufficient sampling from the members of tribe Scleranthae. Therefore, a formal transfer of these species will have to wait for a phylogenetic analysis with a much-expanded sampling of Scleranthae to identify their affinities.

Circumscription of genera within clade “Alsineae A”. — As noted earlier, several attempts have been made to resolve the systematics of tribe Alsineae (e.g., Pax & Hoffmann, 1934; McNeill, 1962; Harbaugh & al., 2010; Greenberg & Donoghue, 2011). “Alsineae A” is congruent with the *Odontostemma* clade in Sadeghian & al. (2015). Many of the problems in the classification of Alsineae are centered around the problematic genus *Stellaria* (for a detailed discussion, see below under Circumscription of genera within clade “Alsineae B”). Here, based on a broader sampling, we are able to present a more precise picture of generic delimitation of taxa in this clade.

Lepyrodiclis, with a distribution centered in SW to C Asia, is recovered as an early-diverging genus of “Alsineae

A” in the combined tree (Fig. 3), followed by *St. tibetica* and *Odontostemma glandulosum*, corroborating the previous findings (Harbaugh & al., 2010; Greenberg & Donoghue, 2011) based on a smaller sampling (fewer species of *Pseudostellaria*, no representatives of *Mesostemma*, *Schizotechium*, and *Shivparvatia*). *Lepyrodiclis* was considered as an early-branching member of *Minuartia* stock by McNeill (1962), but this was not confirmed by previous phylogenetic results (Harbaugh & al., 2010; Greenberg & Donoghue, 2011) nor by our data, retrieving this genus as an early branch of “Alsineae A”. *Lepyrodiclis* is an annual plant with bicarpellate ovaries and a base chromosome number of $x = 17$ (Table 2).

Mesostemma comprises phylogenetically poorly understood taxa, which have also been included in *Stellaria* in the past. This xerophytic segregate of *Stellaria* is distinguished by perennial habit, two styles, terete stems, sessile leaves, emarginate petals that are not as deeply lobed as in most members of *Stellaria*, and 4-valved capsules containing only 1(–2) large seed(s). *Mesostemma* species are considered typical Iranian-Turkestan mountain plants (Rechinger, 1988). *Mesostemma* is here (Figs. 2, 3, suppl. Fig. S1) retrieved as a monophylum in “Alsineae A” (remote from *Stellaria* retrieved in “Alsineae B”). *Stellaria dichotoma*, another perennial species of the clade “Alsineae A”, shares some morphological characters and geographical distribution with members of *Mesostemma*. It has a cylindrical taproot, numerous dichotomous stems forming a spherical bushy habit, and 2–5-seeded capsules, and is thus overall very similar to *Mesostemma*. The main difference used for separation of this species from *Mesostemma* is the 3-styled ovary versus the 2-styled one recognized in most species of *Mesostemma*. Our results suggest a high degree of homoplasy for this character, reducing its value in the delimitation of the genus in tribe Alsineae. Although the position of *St. dichotoma* is weakly supported as sister to *Mesostemma* in the nrITS phylogeny (Fig. 2, PP 0.61), we believe it is best placed in this genus.

Odontostemma, previously treated as *Arenaria* subg. *Odontostemma* (McNeill, 1962), was recognized as a distinct genus by Sadeghian & al. (2015). *Odontostemma* spp. are diffuse annual, biennial or perennial herbs showing an essentially Sino-Himalayan distribution. They are characterized by sepals truncate at apex, \pm saccate at base and recurved, usually 2 styles, and 4-valved capsules. The position of *Odontostemma* as a separate genus is confirmed by our nuclear data (Fig. 2, PP 1.00, BS 51%). Based on a smaller sampling of Alsineae, placement of *Odontostemma* in this tribe has been previously suggested (Harbaugh & al., 2010; Greenberg & Donoghue, 2011; Sadeghian & al., 2015).

Our phylogenetic results, together with known morphological characters, confirm an isolated placement of Sino-Himalayan *Arenaria* subg. *Solitaria* from *Arenaria* s.str. (Sadeghian & al., 2015). Accordingly, this taxon was elevated to generic rank as *Solitaria* (McNeill) Sadeghian & Zarre (Sadeghian & al., 2015); unfortunately, the authors were not aware that a new genus, i.e., *Shivparvatia*, had already been described for this species group three months earlier (Pusalkar & Singh, 2015). The three specific combinations in

Table 2 (left). Genera of tribe Alsineae recognized in this paper, their morphological characteristics, chromosome number, distribution and type. (Continues to the right)

Character	<i>Adenonema</i>	<i>Cerastium</i>	<i>Dichodon</i>	<i>Hartmaniella</i>	<i>Holosteum</i>	<i>Leppyrodiclis</i>	<i>Mesostemma</i>	<i>Moenchia</i>
Habit	Perennial	Annual, perennial	Annual, biennial, perennial	Perennial	Annual	Annual	Perennial	Annual
Inflorescence	(3–)12-flowered terminal cymes or sometimes solitary	Terminal, open or congested cymes, flowers solitary, axillary	Terminal or axillary cymes	Terminal, solitary or paired flowers	Umbel-like cymes	Compound to few-flowered cymes	Paniculate-dichasial	Solitary or few-flowered lax cymes
Sepal number	5	(4–)5	5	5	5	5	5	4–5, with broad membranous margin
Petals	5, minute or sometimes absent	(4–)5 or sometimes absent, or 5	5	5, with apical notch	5, entire, toothed, jagged	5, entire, emarginate or deeply toothed	5, emarginate or lobed	4 or 5, entire or retuse
Stamen number	10	(5 or 8) 10	8–10	5	3–5/8–10	7–10	10	4(–)5–8(10)
Style number	3	5	3	3	3	2(3)	2	4–5
Capsule	Subglobose-obovoid	Oblong-cylindrical	Oblong-cylindrical	Globose-ovoid	Ovoid-cylindrical	Globose	Ovoid	Cylindrical
Number of c. teeth	6	10	6	6	6	2(3)	4	8 or 10
Ovule number	Many-ovuled	Numerous	Numerous	Numerous	Numerous	2(–5)	2(–5)	Numerous
Seed number	1–2	15–150	Many	1–2	Many	1–2	1(–2)	Many
Seed surface	Tuberculate	Tuberculate-colliculate	Verrucate	Tuberculate	Tuberculate	Tuberculate	Corrugate	Tuberculate/papillate
Chromosome number	–	2n = 30–144	2n = 36, 38	–	2n = 20	2n = 34, 68	–	2n = 38
Special feature/s	Few-seeded, woody at the base and underground	Long cylindrical capsules exerted from calyx	Verrucate seeds	Stamens 5, shallowly lobed petals	Shield-shaped seeds	Globose seeds	Styles 2 (3 for <i>M. dichotomum</i>) and capsule teeth 4 (6 for <i>M. dichotomum</i>), corrugate ornamentation of seeds	Sepals sharply acute, all with wide scarious margins
Number of species	2	150–200	7	2	3–4	3	10	3
Distribution	Restricted to greater Siberia	Cosmopolitan	Arctic, C Europe to Iran and Taiwan	W North America	Temperate Eurasia, one species in Ethiopia	Turkey, C Asia to W Tibet and W Himalayas	Turkey, Iraq, Iran, C Asia	W and C Europe, Mediterranean
Type	<i>A. petraeum</i> (Bunge) Bunge	<i>C. arvense</i> L.	<i>D. dubius</i> (Bastard) Ikonn.	<i>H. sierrae</i> (Rabaler & R.L. Hartm.) M.L. Zhang	<i>H. umbellatum</i> L.	<i>L. holosteoides</i> (C.A. Mey.) Fisch. & C.A. Mey.	<i>M. koitschyannum</i> (Fenzl ex Boiss.) Vved.	<i>M. erecta</i> (L.) G. Gaertn., B. Mey. & Scherb.

Abbreviations: ch, chasmogamous flowers; cl, cleistogamous flowers; number of c. teeth, number of capsule teeth.

Table 2 (right). Continued from the left part.

Character	<i>Nubelaria</i>	<i>Odontostemma</i>	<i>Rabelera</i>	<i>Pseudocerastium</i>	<i>Pseudostellaria</i>	<i>Schizotechium</i>	<i>Shivparvati</i>	<i>Stellaria</i>
Habit	Annual or perennial	Annual, biennial or perennial	Annual or perennial	Perennial	Perennial	Perennial	Perennial	Annual/perennial
Inflorescence	Solitary, axillary	Various	Terminal, 3–30-flowered cymes	A leafy dichasium	Terminal cymes or solitary	Many-flowered compound cymes	Solitary	Lax dichasial cymes, rarely solitary
Sepal number	5	5	5	5	ch.: 5(4); cl.: 4	5	5	5
Petals	5	5, retuse, emarginate or fimbriate	5, deeply incised	5, deeply bifid	ch.: 5(4), bifid; cl.: none	5, 2-lobed for more than 1/3	5, with apex obtuse, rounded to acute	(0)4–5, deeply bifid
Stamen number	10	10	10	10	ch.: 10(8); cl.: 2	5 or 10	10	(3)5–10(11)
Style number	3	2	3	5	ch.: (1)2–3(–4); cl.: 2	(2)–3	3	(2)3(4–5)
Capsule	Globose	Ovoid	Subglobose	Shortly cylindrical	Ovoid	Oblong-ovoid to globose	Ovoid	Globose/conical
Number of c. teeth	–	4	6	10	4–6	6	6	6, rarely 4, 8, 10
Ovule number	–	–	–	–	8–16	–	–	–
Seed number	Numerous	1–2	3–5	Numerous	2–10	1–6	Less than 10	Numerous
Seed surface	–	Rugose	Tuberculate	Tuberculate	Echinata	Corrugate	Rugose	Rugose-tuberculate
Chromosome number	2n = 20	–	2n = 26	–	2n = 12, 14, 32	2n = 96 (<i>S. jamesianum</i>)	–	2n = 20–188
Special features	Inflorescence, leaves petiolate, with numerous warty projections on surfaces	Sepal saccate at the base; winged seeds	4-angled stems; creeping rhizomes	Capsule shortly cylindrical and 5 deeply bifid petals	Tuberous root, dimorphous flowers	Tuberous root, without dimorphous flowers	Sepals non-saccate at base and petals entire, sepals hardened at the apex and margin	Petals deeply cleft, fruits capsule or utricle
Number of species	3	65	2	Monotypic	19	5	10	150–200
Distribution	Maritime E Asia	Himalayas and adjacent S China	Mediterranean and Euro-Siberian	China	C Asia, east to Japan, Europe, W North America	Himalayan area to SE and E Asia	Sino-Himalaya	Cosmopolitan, mainly in Eurasia
Type	<i>N. arisanensis</i> (Hayata) M.T. Sharples & E.A. Tripp	<i>O. glandulosum</i> Benth. ex G. Don	<i>R. holostea</i> (L.) M.T. Sharples & E.A. Tripp	<i>P. stellariooides</i> X.H. Guo & X.P. Zhang	<i>P. rupestris</i> (Turcz.) Pax	<i>S. monospermum</i> (Buch.-Ham. ex D. Don) Pusalkar & S.K. Srivast.	<i>S. glanduligera</i> (Edgew.) Pusalkar & D.K. Singh	<i>S. graminea</i> L.

Abbreviations: ch., chasmogamous flowers; cl., cleistogamous flowers; number of c. teeth, number of capsule teeth.

Solitaria published by Sadeghian & Zarre (in Sadeghian & al., 2015) were superfluous as they had previously been published under *Shivparvatia* by Pusalkar & Singh (2015). The present study, consistent with Sadeghian & al. (2015) and with a broader sampling of tribe Alsineae, supports the recognition of *Shivparvatia* (syn. *Solitaria*, compare Rabeler, 2017) as a distinct genus (see under “Taxonomic treatment”). The genus is morphologically distinguished by caespitose habit; flowers solitary; sepals acute, acuminate, or obtuse at apex, non-saccate at base; petals obovate, entire at apex; 3-styled ovary and 6-toothed capsule.

Pseudostellaria is different from nearly all other genera of clade “Alsineae A” by having tubers, cleistogamous flowers (Ohwi, 1937; Mizushima, 1965) and echinate seeds (Arabi & al., 2017). It is distributed in Central Asia and Afghanistan with outliers in Japan and one species in Europe, viz. *Ps. europaea* Schaeffl. Three species had been reported for the flora of North America (Hartman & Rabeler, 2005), but the morphological evidence was inconclusive. A recent phylogenetic study (Zhang & al., 2017) resolved the relationships between most of the American and Asian species of *Pseudostellaria*, indicating an isolated position for the American species *Ps. oxyphylla* (B.L. Rob.) R.L. Hartm. & Rabeler and *Ps. sierrae* Rabeler & R.L. Hartm., and led to their segregation into the new genus *Hartmaniella*. Although relationships of *Pseudostellaria* are not resolved in the plastid *rps16* phylogeny (suppl. Fig. S1), they form a well-supported clade in both nrITS (Fig. 2, PP 1.00, BS 91%) and combined trees (Fig. 3, PP 1.00, BS 97%); this result is consistent with the findings of Zhang & al. (2017). The lack of resolution of the *Pseudostellaria* clade in the plastid *rps16* tree might be due to a low number of informative characters generated by this marker and a large number of representatives of Alsineae included in our dataset, increasing the potential source of homoplasy.

The position of *Schizotechium* is not resolved with respect to other taxa of “Alsineae A” according to our phylogenetic analyses. Although *Schizotechium* was published as a genus in the mid-19th century (Reichenbach, 1841), all three species currently included in this genus are new combinations and were transferred from the genus *Stellaria* (Pusalkar & Srivastava, 2016); all earlier usages of *Schizotechium* were as a subgenus or section of *Stellaria*. Our phylogenetic data (Figs. 2, 3, suppl. Fig. S1) show that three additional species initially classified in *Stellaria*, i.e., *St. americana*, *St. jamesiana* Torr. (\equiv *Pseudostellaria jamesiana*) and *St. turkestanica* are closely related to *Schizotechium* (Fig. 2, PP 1.00, BS 88%; Fig. 3, PP 1.00, BS 100%; suppl. Fig. S1, PP 1.00, BS 96%) and should be included in that genus. A close relationship between *Pseudostellaria jamesiana* and *Stellaria americana* and their distant placement from the *Stellaria* core group was suggested by Zhang & al. (2017) and is confirmed in our study. Based on a study involving four loci, Zhang & al. (2017) showed that *P. jamesiana* and *St. americana* segregated between *Odontostemma* and *Shivparvatia* in their combined analysis, clearly away from the remainder of

Pseudostellaria. The species of *Schizotechium* as defined here are perennial tuberous or stoloniferous herbs, characterized by 4-angled stems, 3-styled ovary, 1–6-seeded capsules as well as seeds which are 2.5–3.5 mm in diam. and slightly beaked inwards at the apex. The six members of the *Schizotechium* clade sampled show a transpacific distribution pattern with four species of *Schizotechium* are recognized in East Asia (Bhutan, China, India, Japan, Myanmar, Nepal, Pakistan, Thailand, and Vietnam) to Central Asia (Afghanistan to Tibet), while two species are known from western North America.

Stellaria tibetica was included in a phylogenetic study for the first time, but its position could not be resolved in either the ITS (Fig. 2) or the *rps16* phylogenies (suppl. Fig. S1). This species is morphologically characterized by physospermous seeds (i.e., the testa surrounding them is loosely attached and easily removable leaving a cavity) and membranous sepal margins. It is another orphan Tibetan representative of Alsineae, indicating the high phyletic diversity of Alsineae in this region. A new genus should probably be described for this species, but we refrain from presenting any formal treatment here, due to little knowledge about morphological variability in this species and insufficient molecular resolution.

Circumscription of genera within clade “Alsineae B”. —

One of the early-branching groups in “Alsineae B” is represented by members of *Nubelaria*, namely *N. diversiflora* (from maritime eastern Asia) and *N. arisanensis* (Hayata) M.T. Sharples & E.A. Tripp (from Taiwan), which form a well-supported clade in the ITS dataset (Fig. 2). The same position for this clade was recovered by previous phylogenetic analyses (Greenberg & Donoghue, 2011; Sharples & Tripp, 2019a), which allowed the segregation of these taxa from *Stellaria* and their recognition as *Nubelaria*. Morphologically, *Nubelaria* differs from *Stellaria* in its petiolate leaves, which have a warty surface and mucronate tips. In addition, inflorescences are always solitary, and petals merely notched rather than deeply bilobed in *Stellaria* (Sharples & Tripp, 2019a).

Another early-branching clade includes only two species: *Rabelera holostea* (\equiv *Stellaria holostea*), the former type of *Stellaria*, and *St. cilicica*. The *Rabelera* clade in our analyses contains annual and perennial species that superficially resemble the majority of *Stellaria* spp., especially in their habit and some other morphological characters, for example: 3-styled ovary, petal incision, and quadrangular stems, but they differ from them by lower seed number and larger seed size (Cullen, 1967; Arabi & al., 2017). Since these species form the sister clade to *Hartmaniella*, their inclusion in the latter would be possible. However, Sharples & Tripp (2019a) treated *St. holostea* as a distinct genus named *Rabelera* based on the morphological differences in stem, leaves and petals as well as molecular phylogenetic findings. We follow this treatment here, but add *St. cilicica* to that genus and provide a new combination for this taxon (see under Taxonomic Treatment).

Hartmaniella includes two North American species, which differ from their sister genus, *Rabelera*, in the presence of 5 (vs. 10) stamens and shallowly notched petals. The relationships between the members of *Hartmaniella* to Asian species of *Pseudostellaria* had been ambiguous due to the similarity of *Hartmaniella* spp. with some species of *Pseudostellaria* in the mentioned morphological characters, but the molecular data provided robust evidence on the segregation of these genera.

Moenchia as a member of “Alsineae B” and sister to *Holosteum* in the ITS phylogeny (though with low support, Fig. 2), is a genus with three species. They occur in W and C Europe and the Mediterranean region. All species of this genus are glabrous, glaucous annual herbs that are distinguished from each other by details of the floral morphology. A close relationship between *Moenchia* and *Cerastium* has been suggested based on chromosome number ($n = 19$, $2n = 38$, Celebioglu & Favarger, 1993). The placement of *Moenchia* as sister to *Holosteum* was shown first by Harbaugh & al. (2010), but its position changed to sister of *Cerastium* in Greenberg & Donoghue (2011). Although our results did not fully resolve the uncertainty associated with the phylogenetic placement of *Moenchia* (as sister to *Holosteum* or *Cerastium*), morphological and chromosome number evidence suggests a closer relationship to *Cerastium*. However, it is distinct morphologically from both mentioned genera and is here kept separate as a distinct genus.

Dichodon, which was previously treated as a subgenus of *Cerastium* (Möschl, 1988), is another member of clade “Alsineae B”. It includes seven species, ranging from the Arctic over central Europe to Iran (Arabi & al., 2018). According to our phylogenetic data, *Dichodon* shares a common clade with *Holosteum*, *Moenchia* and *Cerastium* recovered in all trees (Figs. 2, 3, suppl. Fig. S1). Morphological characters such as number of styles and capsule valves (3 styles and 6 capsule teeth in *Dichodon* vs. 5 styles and 10 capsule teeth in *Cerastium*) along with seed characteristics, e.g., color and ornamentation of seed coat (greyish yellow and verrucate in *Dichodon* vs. reddish or dark brown and tuberculate-colliculate in *Cerastium*; Arabi & al., 2017), provide reliable synapomorphies for *Dichodon* spp., supporting their recognition as distinct from *Cerastium* (Arabi & al., 2018).

Holosteum is another small group within clade “Alsineae B”, consisting of small annual herbs, which differs from other genera of this clade in having the flowers arranged in simple umbels, and shield-shaped seeds (Sadeghian & al., 2014). They have a chromosome number of $2n = 20$ and are distributed predominantly in temperate Eurasia.

Stellaria as traditionally circumscribed (e.g., Bittrich, 1993) is a polyphyletic genus with the majority of species forming a large clade within “Alsineae B”, here called *Stellaria* s.str. In its classical definition (*Stellaria* s.l.), it is a large genus showing considerable variability in morphological and karyological features. Chromosome numbers of $2n = 20$ –188 have been reported for *Stellaria* s.l. (Bittrich, 1993). Since the initially designated type of the generic name (*St. holostea*) was not nested

within *Stellaria* s.str. in Greenberg & Donoghue’s (2011) analysis, Tikhomirov (2016) proposed to conserve the name *Stellaria* with *St. graminea* as its type, which would allow the retention of this genus name for the vast majority of species, i.e., members of *Stellaria* s.str., and this has been accepted (Applequist, 2017; Wilson, 2017; <https://naturalhistory2.si.edu/botany/codes-proposals/>). According to the phylogenetic results presented here (Figs. 2, 3) and previously (Harbaugh & al., 2010; Greenberg & Donoghue, 2011; Sharples, 2019; Sharples & Tripp, 2019a), members representing the genera *Alsine* L., *Fimbripetalum* (Turcz.) Ikonn., and *Myosoton*, as well as the three subgenera recognized in *Stellaria* (Tzvelev, 2000b; Vlassova, 2011), are included in *Stellaria* s.str. According to the nrITS phylogeny obtained here (Fig. 2), *Stellaria* s.str. falls into three subclades, which more or less correspond to two of the three genera proposed by Tzvelev (2000a) for the eastern European species of the genus, i.e., *Alsine* (incl. *Hylebia* (W.D.J.Koch) Fourr.) and *Stellaria*. Since the type of *Hylebia* (*H. nemorum* (L.) Fourr.) shares the same clade with the type of *Alsine* (*A. media* L.) in both nuclear and plastid phylogenies (Fig. 2, suppl. Fig. S1), the generic name *Hylebia* should be considered as a synonym of the latter. Furthermore, Tzvelev (2000b), as well as Vlassova (2011), preferred to treat *Hylebia* and *Alsine* as subgenera. In order to keep the consistency of nomenclature in *Stellaria* and to maximize taxonomic stability, we prefer to retain all species formerly assigned to *Alsine* and *Hylebia* under *Stellaria*.

Five major clades have been recognized in *Stellaria* according to previous molecular phylogenetic studies (Sharples & Tripp, 2019a), i.e., Insignes, Larbreae, Nitentes, Petiolares and Plettkeae (not analyzed here). Members of the Larbreae clade, which is the largest in the genus, are mostly perennial plants with sessile leaves and obovate seeds. The species delimitation in this clade is a challenging task, especially since some species are widely distributed. A long-distance dispersal of *St. irrigua* Bunge, one of the problematic complexes in this clade, between Asia and North America has recently been rejected (Sharples & Tripp, 2019b). The Petiolares clade contains both annual and perennial species with petiolate leaves and orbicular seeds. The formerly recognized monotypic genus *Myosoton*, characterized by 5 styles and a capsule dividing into 5 bluntly bidentate teeth, is also nested within this clade, corroborating its synonymy under *Stellaria* (Harbaugh & al., 2010; Greenberg & Donoghue, 2011; Li & al., 2016; Wang & al., 2017; Sharples, 2019; Sharples & Tripp, 2019a). In a further study, based on phylogenetic analyses and field investigations, Sharples & al. (2021) suggested that petal loss in *Stellaria* is repeated several times across the clades and is associated mostly with self-pollination.

Greenberg & Donoghue (2011) showed *Plettkea cryptantha* Mattf. (= *Pycnophyllopsis cryptantha* (Mattf.) Molinari) to be nested within core *Stellaria*. Sharples & Tripp (2019a) included another species of *Pycnophyllopsis*, *P. tetra-sticha* (Mattf.) Timaná, confirmed its placement between the Petiolares and Nitentes clades and reduced *Pycnophyllopsis* (= *Plettkea*) to synonymy within *Stellaria*. This treatment

contradicts recent taxonomic revisions of *Pycnophyllopsis* that considered it a segregate genus (Molinari-Novoa, 2016; Timaná, 2017). However, following the latter treatment would necessitate a different generic name for the members of the Petiolares clade and several new combinations.

Cerastium is another large clade in “Alsineae B”. Although the monophyly of *Cerastium* is supported by molecular phylogenetic results presented previously (Scheen & al., 2004; Harbaugh & al., 2010; Greenberg & Donoghue, 2011) and morphological characters (Bittrich, 1993), there are still many unresolved issues regarding the infrageneric classification of the genus, which are briefly addressed below. While our study comprises a relatively small portion of *Cerastium*, we did represent all of the sections currently known in the genus, including those recently described (Sokolova, 1996; Lazkov, 2006).

Some classical systems (e.g., Fenzl, 1838–1840) recognized five sections in *Cerastium*, viz. *C. sect. Cerastium* (formerly known as *C. sect. Orthodon* Ser.), *C. sect. Dichodon* (Bartl. ex Rchb.) Griseb. (\equiv *Dichodon* (Bartl. ex Rchb.) Rchb., see Arabi & al., 2018), *C. sect. Moenchia* (Ehrh.) Fenzl (\equiv *Moenchia* Ehrh.), *C. sect. Schizodon* (Fenzl) F.N. Williams, and *C. sect. Strepshodon* Ser.; removing those now treated as distinct genera (*C. sect. Dichodon* and *sect. Moenchia*), members of three sections are still included in *Cerastium*. In agreement with previous studies (Scheen & al., 2004; Greenberg & Donoghue, 2011), we retrieved two major clades (Figs. 2, 3, suppl. Fig. S1): the smaller one comprising the members of *C. sect. Schizodon* and *C. sect. Strepshodon*, and a larger one including representatives of *C. sect. Cerastium* (= *C. sect. Orthodon*). In a contribution to the flora of the Caucasus, Sokolova (1996) divided the genus into two subgenera, viz. *C. subg. Cerastium*, divided into three sections, and *C. subg. Schizodon* Fenzl ex Rchb., divided into two sections. Members of *C. subg. Cerastium* as circumscribed by Sokolova (1996) are characterized by cylindrical capsules and erect to divergent involute teeth and show variations in both testa ornamentations and seed size, reflecting a high morphological variability among the species of this subgenus (Arabi & al., 2017). Members of this subgenus are predominant in Eurasia. The representatives of the second clade, i.e., *C. subg. Schizodon* (including *C. sect. Strepshodon*), are mostly glandular-pubescent annuals or perennials with cylindrical-conical capsules distinctly longer than the calyx and possessing revolute or flat teeth, large dark brown seeds with a colliculate surface (Arabi & al., 2017), and are distributed throughout C and SW Asia and the Caucasian region. Although our analyses provide support for the subgenera recognized by Sokolova (1996), the sectional classification in the above-mentioned study is only partly supported and will require a broader sampling in order to be sufficiently addressed.

Adenonema Bunge, another segregate of *Stellaria*, was resurrected recently by Sharples & Tripp (2019a) and more narrowly defined than in past treatments. The morphological characteristics supporting its separation from *Stellaria* are glandular trichomes on stamens and the presence of few seeds

in a capsule. The two recognized species of this genus, i.e., *A. cherleriae* (Fisch. ex Ser.) M.T. Sharples & E.A. Tripp and *A. petraeum* Bunge, are geographically restricted to greater Siberia. It was not sampled here.

Pseudocerastium C.Y. Wu is a less-known Chinese monotypic genus that is morphologically similar to members of *Stellaria* (Lu & al., 2001). Although a short capsule included in sepals and episealous styles were listed as diagnostic characters for recognizing this genus from *Stellaria* (or *Myosoton*), it has been regarded as a misinterpretation by Yao & al. (2021: 307, and their fig. 5E). These authors used an accession assigned to *P. stellarioides* collected in field with long capsules similar to *Cerastium* spp. that is definitely different from those described and depicted in the protologue (Zhang & Guo, 1998: fig. 1.6) and those of the isotype (KUN, barcode KUN0603914!). Therefore, we doubt correct identification of the voucher specimen used as *P. stellarioides* in molecular phylogenetic analyses presented by Yao & al. (2021). In conclusion, the isolated position of *Pseudocerastium* from *Cerastium* or *Stellaria* remains still to be investigated. It is treated here as a distinct genus, though was not sampled in our analyses.

■ TAXONOMY

Key to genera of Alsineae

1. Fruits capsules; seeds few (up to 10)2
1. Fruits capsules; seeds many (more than 10); if fruit a utricle, then 1-seeded10
2. Capsule opening with as many teeth as styles*Lepyrodiclis*
2. Capsule opening with twice as many teeth as styles3
3. Roots tuberous4
3. Taproot, or rhizomatous plants with fibrous roots, never tuberous or woody at the base and underground5
4. Cleistogamous flowers present; seed testa echinate*Pseudostellaria*
4. Cleistogamous flowers absent; seed testa corrugate*Schizotechium*
5. Stamens 5*Hartmaniella*
5. Stamens 106
6. Sepals saccate; seeds winged*Odontostemma*
6. Sepals non-saccate; seeds wingless7
7. Petals entire at apex*Shivparvatia*
7. Petals emarginate to lobed to ½ or more of petal length or absent8
8. Capsules mostly with 2 styles and 4 valves (except *M. dichotomum* with 3 styles and 6 valves); stems terete; petals emarginate or lobed at the apex*Mesostemma*
8. Capsules with 3 styles and 6 valves; stems terete or not; petals lobed nearly to the base or minute/absent9
9. Stems 4-angled, slender; rhizomes creeping; petals lobed to ½ or more of petal length*Rabelera*
9. Stems \pm circular in cross-section; woody at the base and underground; petals minute or absent*Adenonema*

10. Capsule globose or conic, or fruit indehiscent (in the former *Plettkea* spp.).....11
10. Capsule cylindrical12
11. Petals deeply notched, rarely absent*Stellaria*
11. Petals not deeply notched*Nubelaria*
12. Cymes umbellate; seeds shield-shaped.....*Holosteum*
12. Cymes not umbellate or weakly so; seeds not shield-shaped13
13. Seed testa verrucate; styles 3 *Dichodon*
13. Seed testa not verrucate, mostly tuberculate or colliculate; styles 4–514
14. Glaucous annuals; sepals sharply acute, all with wide scarious margins; petals entire or scarcely retuse.....*Moenchia*
14. Mostly glandular-hairy annuals or perennials; sepals acute, outer ones mostly without or with narrow scarious margins; petals emarginate or bifid, rarely absent.....15
15. Petals deeply bifid; capsules shortly cylindric, included in sepals.....*Pseudocerastium*
15. Petals shallowly bifid, mostly emarginate, rarely entire or absent; capsules cylindric, exceeding sepals ...*Cerastium*

Typification information. — Details about type specimens of the basionyms of the new combinations and resurrected names are based on examining protologues and searching major indices (Tropicos, <http://www.tropicos.org/>; JSTOR Global Plants, <https://plants.jstor.org/>; GBIF, <http://gbif.org>), as well as websites of several individual herbaria (BM, BR, E, G, K, L, P, US, WU) for extant specimens. We have examined a digital image from one (or more) of these sources for any specimen.

New combinations

- Mesostemma dichotomum*** (L.) Arabi, Rabeler & Zarre, **comb. nov.** ≡ *Stellaria dichotoma* L., Sp. Pl. 1: 421. 1753 – Lectotype (designated by Lazkov in Taxon 53: 1053. 2004): [Russia] [*J. Amman*] s.n., Herb. Linnaeus No. 584.2 (LINN!),
- = *Stellaria pallasiana* Ser. in Candolle, Prodr. 1: 399. 1824 – Type [from the protologue]: “*St. dichotoma* Willd. in herb. ex Schlecht. berl. mag. 1816. p. 194, non L.” (B?).
- = *Stellaria schlechtendalians* Ser. in Candolle, Prodr. 1: 399. 1824 ≡ *St. villosa* Willd. ex D.F.K.Schltld. in Mag. Neuesten Entdeck. Gesamnten Naturk. Ges. Naturf. Freunde Berlin 7(3): 194. 1816, nom. illeg., non Poir. (1806) – Holotype: Russia, Siberia, 1768, *P.S. Pallas* s.n. (B, destroyed?; isotype: HAL barcode HAL0118099!).
- = *Stellaria filipes* Kom. in Repert. Spec. Nov. Regni Veg. 13: 235. 1914 – **Lectotype (designated here)**: [China, Inner Mongolia] [Eastern slope of Khingan, Talyr River, above Uldzetu, under rock in shadow of shrubs, 20 Jul 1899, *Potanin & Soldatov* s.n.] (LE barcode LE 01053094!; isotype: LE barcode LE 01053093!).

Mesostemma dichotomum* var. *lanceolatum (Bunge) Arabi, Rabeler & Zarre, **comb. nov.** ≡ *Stellaria dichotoma* var.

lanceolata Bunge in Mém. Acad. Imp. Sci. St.-Petersbourg Divers Savans 2(6): 547. 1835 ≡ *Stellaria dichotoma* f. *lanceolata* (Bunge) Kitag. in J. Jap. Bot. 40: 183. 1965 ≡ *Stellaria lanceolata* (Bunge) Y.S.Lian, Fl. Gansu 2: 391. 2005, nom. illeg., non Poir. (1806) – Protologue: “*St. pallasiana* Turcz. mss.: in Sibiria ulteriore, nec non in Mongholiae desertis” – **Lectotype (designated here)**: [Russia], *St. pallasiana*, Fl. Baicalensi-Dahurica, *Turczaninow* s.n., Herb. Al. de Bunge (P barcode P05006583!; isotypes: LE barcodes LE 01056916!, LE 01056917!, LE 01056918! & LE 01056919!).

- = *Stellaria stephaniana* Willd. ex D.F.K.Schltld. in Mag. Neuesten Entdeck. Gesamnten Naturk. Ges. Naturf. Freunde Berlin 7: 194. 1816 ≡ *Stellaria dichotoma* var. *stephaniana* (Willd. ex D.F.K.Schltld.) Regel in Bull. Soc. Imp. Naturalistes Moscou 35: 237. 1862 ≡ *Arenaria stephaniana* (Willd. ex D.F.K.Schltld.) Shinnars in Sida 1: 50. 1962 – Holotype: [Russia], in Sibiria, *W. Stephan* s.n. (B barcode B-W 08697-010!).
- = *Stellaria dichotoma* var. *heterophylla* Fenzl in Ledebour, Fl. Ross. 1: 379. 1842 – Isosyntypes: “*St. alsinaefolia*. Lessing msc. in herb. gen. berol. in montibus Ssojuticis (Lessing)” [the Lessing specimen in B now is likely destroyed] (LE barcodes LE 01053543! & LE 01053544!).
- = *Stellaria dichotoma* var. *linearis* Fenzl in Ledebour, Fl. Ross. 1: 380. 1842 – Type: [Russia], in Sibiriae altaicae mont. Ssabinensibus, *Lessing* s.n. (B, destroyed?).

Rabelera cilicica (Boiss. & Balansa) Arabi, Rabeler & Zarre, **comb. nov.** ≡ *Stellaria cilicica* Boiss. & Balansa in Boissier, Diagn. Pl. Orient., ser. 2, 5: 59. 1856 – **Lectotype (designated here)**: [Turkey], in herbidis faucis Guzeldéré suprâ Sedichig in regione littorali Ciliciae [à 4 lieuse au NO. de Mersina (Cilicie)], Floret Aprili [24 Apr 1855], *B. Balansa* 609 (G-BOIS barcode G00546111!; isotypes: FI barcode FI0059560!, G barcodes G00390407!, G00390408! & G00390409!, GH barcodes 00038009!, 00038010! & 00339424!, GOET barcode GOET000709!, JE barcode JE00011365!, K barcodes K000723444! & K000723445!, MPU barcode MPU021832!, P barcodes P05006533! & P05006537!, US barcode 00289455!; WAG barcode WAG0000419!).

Schizotechium americanum (Porter ex B.L.Rob.) Arabi, Rabeler & Zarre, **comb. nov.** ≡ *Stellaria dichotoma* var. *americana* Porter ex B.L.Rob. in Proc. Amer. Acad. Arts 29: 289. 1894 ≡ *Alsine americana* (Porter ex B.L.Rob.) Rydb. in Mem. New York Bot. Gard. 1: 144. 1900 ≡ *Stellaria americana* (Porter ex B.L.Rob.) Standl. in Contr. U.S. Natl. Herb. 22: 336. 1921 ≡ *Arenaria stephaniana* var. *americana* (Porter ex B.L.Rob.) Shinnars in Sida 1: 50. 1962 – Holotype: U.S.A., Montana, near Virginia City, 1871, *W.B. Platt (Hayden Survey)* s.n. (GH barcode 00037985!; isotypes: NY barcode 00353059!, PH barcode 00027794!).

Although the GH specimen has an incorrect date, it should be considered the holotype since the specimen was

sent by Porter to B.L. Robinson at GH for his study and Robinson eventually published the name.

Schizoteichium jamesianum (Torr.) Arabi, Rabeler & Zarre, **comb. nov.** ≡ *Stellaria jamesiana* Torr. in Ann. Lyceum Nat. Hist. New York 2(6): 169. 1827 ≡ *Arenaria jamesiana* (Torr.) Shinnery in Sida 1: 50. 1962 ≡ *Pseudostellaria jamesiana* (Torr.) W.A.Weber & R.L.Hartm. in Phytologia 44(4): 314. 1979 – Holotype: U.S.A., within the Rocky Mountains, *E. James s.n.* (NY barcode 00353063!).

= *Alsine glutinosa* A.Heller in Bull. S. Calif. Acad. Sci. 2: 67. 1903 – Holotype: U.S.A., California, Lake County, about summit lake, near the summit of Mt. Sanhedrin, 15 Jul 1902, *A.A. Heller 5880* (NY barcode 00342328!; isotypes: AC barcode 00319666!, CAS barcodes 0008461! & 0008462!, GH barcode 00037986, ILL barcode ILL00007360!, K barcode K000723560, L 2D-code L.1688821!, MICH barcode 1210635!, MIN barcode 1000109!, MO No. 1715896 [barcode MO-216545]!, MSC barcode MSC0129873, NY barcode 00342327!, P barcode P01902934!, PH barcode 00001956!, RENO barcode 9344!, RM barcode RM0002116!, RSA barcode RSA0002305!, US barcodes 00103218!, 00103219! & 01049884!).

Schizoteichium turkestanicum (Schischk.) Arabi, Rabeler & Zarre, **comb. nov.** ≡ *Stellaria turkestanica* Schischk. in Trudy Bot. Muz. 24: 31. 1932 – Lectotype (designated by Lazkov, Semeystvo Gvozdichnye vo Flore Kyrgyzstana: 25. 2006): Tajikistan, “Flora Seravschanica, Mura pass, alt. 9000 pd., 28.06.1892”, *V.L. Komarov s.n.* (LE barcode LE 01053542!).

■ CONCLUSION

The molecular phylogenetic study presented here is based on a rich sampling of almost all genera and subgenera in the tribe Alsineae. The large genera *Cerastium* and *Stellaria*, which were represented poorly in former studies, are well represented here and permit a clearer perspective on the relationships among the species of Alsineae. Several long-standing questions in the classification of this clade could be resolved, and genera such as *Stellaria* can now be more clearly delimited, and some segregates could be better defined. Based on current knowledge, the recognition of a total of 16 genera is proposed. The lack of molecular data for the Chinese *Pseudocerastium* precludes its firm placement in the tribe. An expansion of the sampling, particularly from the New World and there especially from South America to place taxa associated with *Pycnophyllopsis*, and the addition of another set of markers to increase statistical support are clearly desirable for the future. This will then also permit a comprehensive classification for this clade. Infrageneric classification of the large genera

Cerastium and *Stellaria* will require both a broad sampling and the use of rapidly evolving markers.

■ AUTHOR CONTRIBUTIONS

ZA: Specimen study, plant collection, laboratory procedures, molecular analyses, manuscript preparation. FG: Supervising the study, nomenclatural research, manuscript revision. RKR: Nomenclatural research, manuscript revision, providing some references, comments on consensus trees, some taxonomic novelties in the study group. IS: Specimen study, providing some references, typification of taxon names in LE. MW: Providing some material and laboratory facilities, manuscript revision. SZ: Supervising the study, nomenclatural research, manuscript revision. — ZA, <https://orcid.org/0000-0003-2877-9397>, z.arabi@yahoo.com; FG, <https://orcid.org/0000-0001-5860-9976>, fgh@khu.ac.ir; RKR, <https://orcid.org/0000-0002-6765-0353>, rabeler@umich.edu; IS, <https://orcid.org/0000-0001-5277-6669>, ISokolova@binran.ru; MW; <https://orcid.org/0000-0003-0813-6650>, mweigend@uni-bonn.de; SZ, <https://orcid.org/0000-0001-9159-1800>, zarre@khayam.ut.ac.ir.

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■ LITERATURE CITED

- Applequist, W.L. 2017. Report of the Nomenclature Committee for Vascular Plants: 69. *Taxon* 66: 500–513. <https://doi.org/10.12705/662.17>
- Arabi, Z., Ghahremaninejad, F., Rabeler, R.K., Heubl, G. & Zarre, S. 2017. Seed micromorphology and its systematic significance in tribe Alsineae (Caryophyllaceae). *Flora* 234: 41–59. <https://doi.org/10.1016/j.flora.2017.07.004>
- Arabi, Z., Ghahremaninejad, F., Rabeler, R.K., Sokolova, I., Heubl, G. & Zarre, S. 2018. On the taxonomic status of the genus *Dichodon* (Caryophyllaceae: Tribe Alsineae): Morphological and molecular evidence reassessed. *Phytotaxa* 360: 220–236. <https://doi.org/10.11646/phytotaxa.360.3.3>
- Benthham, G. & Hooker, W.J. 1862. *Genera plantarum*, vol. 1(1). Londini [London]: venit apud A. Black; etc. <https://doi.org/10.5962/bhl.title.747>
- Bittrich, V. 1993. Caryophyllaceae. Pp. 206–236 in: Kubitzki, J., Rohwer, J.G. & Bittrich, V. (eds.), *The families and genera of vascular plants*, vol. 2. Berlin: Springer. https://doi.org/10.1007/978-3-662-02899-5_21
- Boissier, E. 1867. *Flora orientalis*, vol. 1. Basileae [Basel]: apud H. Georg. <https://doi.org/10.5962/bhl.title.20323>
- Celebioglu, T. & Favarger, C. 1993. Rapports (125–166). Pp. 323–333 in: Kamari, G., Felber, F. & Garbari, F. (eds.), *Mediterranean chromosome number reports – 3. Fl. Medit.* 3: 323–373.
- Cullen, J. 1967. *Cerastium* L. Pp. 73–85 in: Davis, P.H. (ed.), *Flora of Turkey and the East Aegean Islands*, vol. 2. Edinburgh: Edinburgh University Press.

- Darriba, D., Taboada, G.L., Doallo, R. & Posada, D.** 2012. jModel-Test 2: More models, new heuristics and parallel computing. *Nature, Meth.* 9: 772. <https://doi.org/10.1038/nmeth.2109>
- Davis, J.I., Stevenson, D.W., Petersen, G., Seberg, O., Campbell, L.M., Freudenstein, J.V., Goldman, D.H., Hardy, C.R., Michelangeli, F.A. & Simmons, M.P.** 2004. A phylogeny of the monocots, as inferred from *rbcL* and *atpA* sequence variation, and a comparison of methods for calculating jackknife and bootstrap values. *Syst. Bot.* 29: 467–510. <https://doi.org/10.1600/0363644041744365>
- Dillenberger, M.S. & Kadereit, J.W.** 2014. Maximum polyphyly: Multiple origins and delimitation with plesiomorphic characters require a new circumscription of *Minuartia* (Caryophyllaceae). *Taxon* 63: 64–88. <https://doi.org/10.12705/631.5>
- Fateryga, A.V., Fateryga, V.V., Sokolova, I., Svirin, V.S.A., Yena, A.V. & Yevseyenkov, P.E.** 2020. Is *Holosteum glutinosum* (M.Bieb.) Fisch. et C.A.Mey. (Caryophyllaceae: Alsinoideae) just a subtaxon of *H. umbellatum* L. or a distinct species? *Turczaninowia* 23: 50–64. <https://doi.org/10.14258/turczaninowia.23.4.5>
- Fenzl, E.** 1839–1840. Ordo CCVII. Caryophylleae. Pp. 955–974 in: Endlicher, S. (ed.), *Genera plantarum secundum ordines naturales disposita*. Vindobonae [Vienna]: apud Fr. Beck. <https://doi.org/10.5962/bhl.title.728>
- Fior, S., Karis, P.O., Casazza, G., Minuto, L. & Sala, F.** 2006. Molecular phylogeny of the Caryophyllaceae (Caryophyllales) inferred from chloroplast *matK* and nuclear rDNA ITS sequences. *Amer. J. Bot.* 93: 399–411. <https://doi.org/10.3732/ajb.93.3.399>
- Greenberg, A.K. & Donoghue, M.J.** 2011. Molecular systematics and character evolution in Caryophyllaceae. *Taxon* 60: 1637–1652. <https://doi.org/10.1002/tax.606009>
- Harbaugh, D.T., Nepokroeff, M., Rabeler, R.K., McNeill, J., Zimmer, E.A. & Wagner, W.L.** 2010. A new lineage-based tribal classification of the family Caryophyllaceae. *Int. J. Pl. Sci.* 171: 185–198. <https://doi.org/10.1086/648993>
- Hartman R.L. & Rabeler, R.K.** 2005. Caryophyllaceae Jussieu: Pink family. In: Flora of North America Editorial Committee (eds.), *Flora of North America north of Mexico*, vol. 5. http://www.efloras.org/florataxon.aspx?flora_id=2&taxon_id=10166
- Hernández-Ledesma, P., Berendsohn, W.G., Borsch, T., Mering, S.V., Akhani, H., Arias, S., Castañeda-Noa, I., Eggli, U., Eriksson, R., Flores-Olvera, H., Fuentes-Bazán, S., Kadereit, G., Klak, C., Korotkova, N., Nyffeler, R., Ocampo, G., Ochoterena, H., Oxelman, B., Rabeler, R.K., Sanchez, A., Schlumpberger, B.O. & Uotila, P.** 2015. A taxonomic backbone for the global synthesis of species diversity in the angiosperm order Caryophyllales. *Willdenowia* 45: 281–383. <https://doi.org/10.3372/wi.45.45301>
- Katoh, K. & Standley, D.M.** 2013. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molec. Biol. Evol.* 30: 772–780. <https://doi.org/10.1093/molbev/mst010>
- Kool, A., Perrigo, A. & Thulin, M.** 2012. Bristly versus juicy: Phylogenetic position and taxonomy of *Sphaerocoma* (Caryophyllaceae). *Taxon* 61: 67–75. <https://doi.org/10.1002/tax.611005>
- Lamarck, J.D. & Candolle, A.D. de** 1806. *Synopsis plantarum in Flora Gallica descriptorum*. Parisiis [Paris]: apud H. Agasse. <https://doi.org/10.5962/bhl.title.6624>
- Lazkov, G.A.** 2006. *Semeystvo vyvozdichnye vo flore Kyrgyzstana [Pink family in the flora of Kyrgyzstan]*. Moscow: Tovarischestvo Nauchnykh Izdaniy KMK.
- Li, Z., Liao, H., Bai, L., Zhou, X. & Wu, L.** 2016. Comparative anatomy of *Myosoton aquaticum* and *Stellaria media* and its systematic significance. *Pakistan J. Bot.* 48: 1527–1535.
- Lu, D., Wu, Z., Zhou, L., Chen, S., Gilbert, M.G., Lidén, M., McNeill, J., Morton, J.K., Oxelman, B., Rabeler, R.K., Thulin, M., Turland, N.J. & Wagner, W.L.** 2001. Caryophyllaceae. Pp. 1–113 in: Wu, Z.Y., Raven, P.H. & Hong, D.Y. (eds.), *Flora of China*, vol. 6. Beijing: Science Press; St. Louis: Missouri Botanical Garden Press.
- Maddison, W. & Maddison, D.** 2010. Mesquite: A modular system for evolutionary analysis, version 2.75. mesquiteproject.org/mesquite/download/download.html
- Madhani, H., Rabeler, R., Pirani, A., Oxelman, B., Heubl, G. & Zarre, S.** 2018. Untangling phylogenetic patterns and taxonomic confusion in tribe Caryophylleae (Caryophyllaceae) with special focus on generic boundaries. *Taxon* 67: 83–112. <https://doi.org/10.12705/671.6>
- Maguire, B.** 1958. Two dominican stellarias. *Brittonia* 10: 32. <https://doi.org/10.2307/2804691>
- McNeill, J.** 1962. Taxonomic studies in the Alsinoideae: I. Generic and infra-generic groups. *Notes Roy. Bot. Gard. Edinburgh* 24: 79–155.
- Miller, M.A., Pfeiffer, W. & Schwartz, T.** 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Pp. 45–52 in: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, New Orleans, Louisiana, 14 Nov 2010. Piscataway: IEEE. <https://doi.org/10.1109/GCE.2010.5676129>
- Mizushima, M.** 1965. Critical studies on Japanese plants, 11: The genus *Pseudostellaria* Pax in Japan. *Nelumbo* 7: 62–72. <https://doi.org/10.20324/nelumbo/v7/1965/76289>
- Molinari-Novoa, E.A.** 2016. Further nomenclatural changes regarding Peruvian endemics. *Polish Bot. J.* 61: 275–277. <https://doi.org/10.1515/pbj-2016-0021>
- Morton, J.K.** 2005. *Stellaria* L. Pp. 96–114 in: Flora of North America Editorial Committee (eds.), *Flora of North America north of Mexico*, vol. 5. Oxford: Oxford University Press.
- Möschl, W.** 1988. *Cerastium* L. Pp. 85–108 in: Rechinger, K.H. (ed.), *Flora Iranica*, vol. 163. Akademische Druck- u. Verlagsanstalt, Graz.
- Ohwi, J.** 1937. The revision of the genus *Pseudostellaria*. *Jap. J. Bot.* 9: 95–105.
- Oxelman, B., Lidén, M. & Berglund, D.** 1997. Chloroplast *rps16* intron phylogeny of the tribe Sileneae (Caryophyllaceae). *Pl. Syst. Evol.* 206: 393–410. <https://doi.org/10.1007/BF00987959>
- Pax, F. & Hoffmann, K.** 1934. Caryophyllaceae. Pp. 275–364 in: Engler, A. & Harms, H. (eds.), *Die natürlichen Pflanzenfamilien*, 2nd ed., vol. 16c. Leipzig: Engelmann.
- Petri, A. & Oxelman, B.** 2011. Phylogenetic relationships within *Silene* (Caryophyllaceae) section *Physolychnis*. *Taxon* 60: 953–968. <https://doi.org/10.1002/tax.604002>
- Pirani, A., Zarre, S., Pfeil, B.E., Bertrand, Y.J.K., Assadi, M. & Oxelman, B.** 2014. Molecular phylogeny of *Acanthophyllum* (Caryophyllaceae: Caryophylleae), with emphasis on infrageneric classification. *Taxon* 63: 592–607. <https://doi.org/10.12705/633.39>
- Pirie, M.D.** 2015. Phylogenies from concatenated data: Is the end night? *Taxon* 64: 421–423. <https://doi.org/10.12705/643.1>
- Pusalkar, P.K. & Singh, D.K.** 2015. Taxonomic rearrangement of *Arenaria* (Caryophyllaceae) in Indian Western Himalaya. *J. Jap. Bot.* 90: 77–91.
- Pusalkar, P.K. & Srivastava, S.** 2016. The genus *Schizotechium* (Caryophyllaceae) resurrected. *Phytotaxa* 252: 81–84. <https://doi.org/10.11646/phytotaxa.252.1.10>
- Rabeler, R.K.** 2017. New combinations and typification in *Shivparvati* (Alsineae, Caryophyllaceae). *Phytotaxa* 303(3): 293–296. <https://doi.org/10.11646/phytotaxa.303.3.11>
- Rambaut, A.** 2012. FigTree, version 1.4.0. University of Oxford. Oxford, U.K. <http://tree.bio.ed.ac.uk/software/figtree>
- Rechinger, K.** 1988. *Mesostemma* Vved. Pp. 76–84 in: Rechinger, K. (ed.), *Flora Iranica*, vol. 163. Graz: Akademische Druck- u. Verlagsanstalt.
- Reichenbach, H.G.L.** 1841. *Das Herbarienbuch*. Dresden & Leipzig: in der Arnoldischen Buchhandlung. <https://doi.org/10.5962/bhl.title.7694>
- Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A.**

- & Huelsenbeck, J.P. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 61: 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Sadeghian, S., Zarre, S. & Heubl, G. 2014. Systematic implication of seed micromorphology in *Arenaria* (Caryophyllaceae) and allied genera. *Flora* 209: 513–529. <https://doi.org/10.1016/j.flora.2014.07.004>
- Sadeghian, S., Zarre, S., Rabeler, R.K. & Heubl, G. 2015. Molecular phylogenetic analysis of *Arenaria* (Caryophyllaceae: tribe Arenarieae) and its allies inferred from nuclear DNA internal transcribed spacer and plastid DNA *rps16* sequences. *Bot. J. Linn. Soc.* 178: 648–669. <https://doi.org/10.1111/boj.12293>
- Salmaki, Y., Zarre, S., Ryding, O., Lindqvist, C., Scheunert, A., Bräuchler, C. & Heubl, G. 2012. Phylogeny of the tribe Phlomiodeae (Lamiaceae) with special focus on *Eremostachys* and *Phlomoides*: New insights from nuclear and chloroplast sequences. *Taxon* 61: 161–179. <https://doi.org/10.1002/tax.611012>
- Scheen, A.-C., Brochmann, C., Brysting, A.K., Elven, R., Morris, A., Soltis, D.E., Soltis, P.S. & Albert, V.A. 2004. Northern Hemisphere biogeography of *Cerastium* (Caryophyllaceae): Insights from phylogenetic analysis of noncoding plastid nucleotide sequences. *Amer. J. Bot.* 91: 943–952. <https://doi.org/10.3732/ajb.91.6.943>
- Schischkin, B.K. 1936. *Cerastium* L. Pp. 430–466 in: Komarov, V.L. (ed.), *Flora of the U.S.S.R.*, vol. 6. Moscow & Leningrad: Izdatel'stvo Akademii Nauk SSSR. [in Russian, English translation, 1970 by Scientific Translation, Jerusalem. Pp. 330–359].
- Sharples, M.T. 2019. Taxonomic observations within *Stellaria* (Caryophyllaceae): Insights from ecology, geography, morphology, and phylogeny suggest widespread parallelism in starworts and erode previous infrageneric classifications. *Syst. Bot.* 44: 877–886. <https://doi.org/10.1600/036364419X15710776741459>
- Sharples, M.T. & Tripp, E.A. 2019a. Phylogenetic relationships within and delimitation of the cosmopolitan flowering plant genus *Stellaria* L. (Caryophyllaceae): Core stars and fallen stars. *Syst. Bot.* 44: 857–876. <https://doi.org/10.1600/036364419X15710776741440>
- Sharples, M.T. & Tripp, E.A. 2019b. RAD sequencing rejects a long-distance disjunction in *Stellaria* (Caryophyllaceae) and yields support for a new southern Rocky Mountains endemic. *Taxon* 68: 280–296. <https://doi.org/10.1002/tax.12059>
- Sharples, M.T., Bentz, P.C. & Tripp, E.A. 2021. Evolution of apetaly in the cosmopolitan genus *Stellaria*. *Amer. J. Bot.* 108: 869–882. <https://doi.org/10.1002/ajb2.1650>
- Smitsen, R.D., Clement, J.C., Garnock-Jones, P.J. & Chambers, G.K. 2002. Subfamilial relationships within Caryophyllaceae as inferred from 5' *ndhF* sequences. *Amer. J. Bot.* 89: 1336–1341. <https://doi.org/10.3732/ajb.89.8.1336>
- Sokolova, I.V. 1996. Conspectus generis *Cerastium* L. (Caryophyllaceae) florum Caucasi. *Novosti Sist. Vyssh. Rast.* 30: 33–47. [in Russian]
- Swofford, D.L. 2002. PAUP*: Phylogenetic analysis using parsimony, version 4.0 b10. Sunderland, MA: Sinauer.
- Takhtajan, A. 2009. *Flowering plants*, 2nd ed. Dordrecht: Springer. <https://doi.org/10.1007/978-1-4020-9609-9>
- Tikhomirov, V.N. 2016. (2427) Proposal to conserve the name *Stellaria* (Caryophyllaceae) with a conserved type. *Taxon* 65: 389–390. <https://doi.org/10.12705/652.21>
- Timaná, M.E. 2017. Nomenclatural notes on the Andean genera *Pycnophyllopsis* and *Pycnophyllum* (Caryophyllaceae). *Lundellia* 20: 4–24. <https://doi.org/10.25224/1097-993X-20.1.4>
- Turland, N.J., Wiersema, J.H., Barrie, F.R., Greuter W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T.W., McNeill, J., Monro, A.M., Prado, J., Price, M.J. & Smith, G.F. (eds.) 2018. *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017*. Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books. <https://doi.org/10.12705/Code.2018>
- Tzvelev, N.N. 2000a. On the genus *Stellaria* L. (Caryophyllaceae) in Eastern Europe. *Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol.* 105: 69–72.
- Tzvelev, N.N. 2000b. *Opredelitel' sosudystrykh rasteniy Severo-Zapadnoy Rossii*. St. Petersburg: Izdatel'stvo Sankt-Peterburgskoy Gosudarstvennoy Khimiko-Farmatsevticheskoy Akademii.
- Vlassova, N.V. 2011. The genus *Stellaria* (Caryophyllaceae) of the flora of the Sakha Republic (Yakutia). *Rastitel'n. Mir Aziatsk. Rossii* 1: 23–30.
- Wang, L., Zhao, Y.-Y. & Liu, J.-X. 2017. Embryology of *Myosoton* and *Stellaria* and its taxonomic significance (Caryophyllaceae). *Phytotaxa* 306: 124–134. <https://doi.org/10.11646/phytotaxa.306.2.2>
- White, T.J., Bruns, T., Lee, S. & Taylor, J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 in: Innis, M.A., Gelfand, D.H., Sninsky, J.J. & White, T.J. (eds.), *PCR protocols: A guide to methods and applications*. San Diego: Academic Press. <https://doi.org/10.1016/B978-0-12-372180-8.50042-1>
- Wilson, K.L. 2017. Report of the General Committee: 18. *Taxon* 66: 742–744. <https://doi.org/10.12705/664.15>
- Yao, G., Xue, B., Liu, K., Li, Y., Huang, J. & Zhai, J. 2021. Phylogenetic estimation and morphological evolution of Alsineae (Caryophyllaceae) shed new insight into the taxonomic status of the genus *Pseudocerastium*. *Pl. Diversity* 43: 299–307. <https://doi.org/10.1016/j.pld.2020.11.001>
- Zhang, M.-L., Zeng, X.-Q., Li, C., Sanderson, S.C., Byalt, V.V. & Lei, Y. 2017. Molecular phylogenetic analysis and character evolution in *Pseudostellaria* (Caryophyllaceae) and description of a new genus, *Hartmaniella*, in North America. *Bot. J. Linn. Soc.* 184: 444–456. <https://doi.org/10.1093/botlinnean/box036>
- Zhang, X.-P. & Guo, X.-H. 1998. A new genus of Caryophyllaceae from China. *Acta Bot. Yunnan.* 20: 395–398.

Appendix 1. Voucher information.

Species name, geographical origin, collector(s), voucher (herbarium), GenBank accession numbers for ITS and *rps16*, respectively (* indicates sequences new for this study; – indicates missing sequences). Species names follow the taxonomic treatment suggested in the present study. Geographical origin, collector(s), voucher (herbarium) are given only for the newly generated sequences. GB stands for sequences downloaded from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>).

Agrostemma githago L., GB, JN589107.1, Z83154.1; *Arenaria gracilis* Waldst. & Kit., GB, KP148869.1, KP148967.1; *Arenaria serpyllifolia* L., GB, KP148896.1, KP148996.1; *Bufoia tenuifolia* L., Spain, P. Montserrat, 185077 (M), *MT624555, *MT624637; *Cerastium alpinum* L., GB, KX166754.1, –; *Cerastium arcticum* Lange, GB, KX167686.1, –; *Cerastium arvense* L., GB, MH219805, MH243535; *Cerastium boissierianum* Greuter & Burdet, France (Corsica), J. Lambinon & al., s.n. (MSB), *MT624556, *MT624638; *Cerastium candidissimum* Correns, Greece, Meierott, 02/Gr62 (M), *MT624557, *MT624639; *Cerastium cephalanthum* S.F.Blake, Venezuela, B. & F. Oberwinkler, 13493 (M), *MT624558, *MT624640; *Cerastium davuricum* Fisch ex Spreng., Armenia, E. Vitek, 03-0329 (MSB), *MT624559, *MT624641; *Cerastium diffusum* Pers., KX167022.1, –; *Cerastium dinaricum* Beck

Appendix 1. Continued.

& Szyzyl, Yugoslavia, *J. Schimmitat*, s.n. (M), *MT624560, *MT624642; *Cerastium falcatum* (Ser.) Bunge, GB, MH219807; MH243537; *Cerastium fontanum* Baumg. subsp. *fontanum*, Germany, O. Angerer, s.n. (M), *MT624561, *MT624643; *Cerastium fragillimum* Boiss., Lebanon, H. Roessler, 5352 (M), *MT624562, *MT624644; *Cerastium glomeratum* Thuill. 1, Germany, F. Schuhwerk 12/16 (M), *MT624563, *MT624645; *Cerastium glomeratum* 2, GB, AY857977.1, –; *Cerastium illyricum* subsp. *comatum* (Desv.) P.D.Sell & Whitehead, France (Corsica), G. Bosc, 12995 (MSB), *MT624564, *MT624646; *Cerastium inflatum* Link ex Gren., Iran, L. Gilani, 8149 (T), *MT624565, *MT624647; *Cerastium lineare* All., Italy, H. Merxmüller & W. Wiedmann, 157/64 (M), *MT624566, *MT624648; *Cerastium macrocarpum* Schur, Austria, T. Barta, 2002-361 (M), *MT624567, *MT624649; *Cerastium mollissimum* Poir, Ecuador, M. Acosta-Solis, 1389 (MSB), *MT624568, –; *Cerastium nutans* Raf., U.S.A., H.E. Ahles, 82549 (M), *MT624569, *MT624650; *Cerastium polymorphum* Rupr., Georgia, Meierott & al., 07/33 (MSB), *MT624570, *MT624651; *Cerastium purpurascens* Adams, Turkey, Meierott & Gregor, 2010/442 (MSB), *MT624571, *MT624652; *Cerastium pusillum* Ser. ex Fisch., GB, JN589112.1, –; *Cerastium runemarkii* Möschl & Rech.f., Greece, K.H. Rechinger, 17130 (MSB), *MT624572, *MT624653; *Cerastium semidecandrum* L. 1, Germany, R. Urban, 7833/1 (MSB), –; *MT624654; *Cerastium semidecandrum* 2, GB, KX167026.1, –; *Cerastium soleirolii* Ser. ex Duby, France (Corsica), D. Herbel, s.n. (MSB), *MT624573, *MT624655; *Cerastium szechuense* F.N. Williams, GB, JN589116.1, –; *Cerastium tianschanicum* Schischk., Afghanistan, D. Podlech, 7865 (MSB), *MT624574, *MT624656; *Cerastium tomentosum* L. 1, GB, MH219808, MH243538; *Cerastium tomentosum* 2, GB, JN589031.1, –; *Cerastium uniflorum* Clairv., Germany, F. Eberlein, s.n. (M), *MT624575, *MT624657; *Dianthus armeria* L., GB, JN589087, FJ404903; *Dichranthus plocamoides* Webb, GB, AJ310976.1, FJ404904.1; *Dichodon alborzensis* Arabi & Zarre 1, GB, MH219809, MH243539; *Dichodon alborzensis* 2, GB, MH219810; MH243540; *Dichodon alborzensis* 3, GB, MH219811, MH243541; *Dichodon cerastioides* Rechb. 1, GB, MH219812, MH243542; *Dichodon cerastioides* 2, GB, MH243513, –; *Dichodon kotschyi* (Boiss.) Ikonn. 1, GB, MH219816, MH243545; *Dichodon kotschyi* 2, GB, MH219817, –; *Dichodon persicus* Boiss., GB, MH219818, MH243546; *Dichodon viscidus* (M.Bieb.) Holub 1, GB, MH219814, MH243543; *Dichodon viscidus* 2, GB, MH219815, MH243544; *Eremogone congesta* (Nutt.) Ikonn., GB, KP148911.1, KP149013.1; *Eremogone polaris* (Schischk.) Ikonn., GB, KP148934.1, KP149036.1; *Facchinia rupestris* (Scop.) Dillenb. & Kadereit, GB, AY936237.1, FJ404923.1; *Gypsophila repens* L., GB, MF401101.1, MF401153.1; *Hartmaniella oxyphylla* (B.L. Rob.) M.L. Zhang, GB, KX158311.1, KX158422.1; *Hartmaniella sierrae* (Rabeler & R.L. Hartm.) M.L. Zhang, GB, KX158314.1, KX158425.1; *Holosteum glutinosum*¹ (M.Bieb.) Fisch. & C.A. Mey. 1, Afghanistan, A. Dieterle, 56 (MSB), *MT624576, *MT624658; *Holosteum glutinosum* 2, Kazakhstan, I. Rusanovitsch & N. Alianskaja, 13994 (MSB), *MT624577, –; *Holosteum marginatum* Fisch. & C.A. Mey., GB, JN589093.1, –; *Holosteum polygamum* K.Koch., Turkmenistan, V.V. Nikitin & al., s.n. (M), *MT624578, *MT624659; *Holosteum umbellatum* L. 1, GB, JN589051.1, FJ404909.1; *Holosteum umbellatum* 2, GB, AY936242.1, –; *Holosteum umbellatum* 3, Germany, J. Sellmair, 7536/2 (M), *MT624579, *MT624660; *Lepyrodiclis holosteoides* (C.A. Mey.) Fenzl ex Fisch. & C.A. Mey. 1, GB, –; FJ404911.1; *Lepyrodiclis holosteoides* 2, GB, –; KP148941.1; *Lepyrodiclis stellaroides* Schrenk ex Fisch. & C.A. Mey., GB, KP148941.1, KP149044.1; *Mesostemma dichotomum* (L.) Arabi, Rabeler & Zarre 1, Russia, A.K. Skvortsov, s.n. (M), *MT624580, –; *Mesostemma dichotomum* 2, Russia, L. Martins, 2421 (B), –; *MT624661; *Mesostemma dichotomum* 3, China, D.E. Boufford & al., 25951 (MSB), *MT624581, *MT624662; *Mesostemma kotschyianum* (Fenzl ex Boiss.) Vved. 1, Afghanistan, D. Podlech, 31932 (MSB), –; *MT624663; *Mesostemma kotschyianum* 2, Iran, Z. Arabi, 47160 (TUH), *MT624582, *MT624664; *Mesostemma perfoliatum* (Rech.f.) Rech.f., Afghanistan, K.H. Rechinger, 36690 (M), *MT624583, *MT624665; *Mesostemma platyphyllum* Rech.f., Afghanistan, O. Anders, 9058 (MSB), *MT624584, *MT624666; *Moenchia erecta* (L.) G. Gaertn., B. Mey. & Scherb. 1, Greece, R. Eisenblätter & E. Willing, 45.253 (B), *MT624585, *MT624667; *Moenchia erecta* 2, GB, JN589103.1, FJ404926.1; *Moenchia mantica* Bartl. ex W.D.J. Koch, Bulgaria, C. Gangale & D. Uzunov, 10-2-14 (B), *MT624586, *MT624668; *Myosoton aquaticum* Moench 1, GB, MH219819, MH243547; *Myosoton aquaticum* 2, GB, AY594303.1, FJ404928.1; *Nubelaria arisanensis* (Hayata) M.T. Sharples & E.A. Tripp, GB, JN589058.1, –; *Nubelaria diversiflora* Maxim. 1, Japan, K. Seto, 38087 (M), *MT624587, *MT624669; *Nubelaria diversiflora* 2, GB, JN589119.1, –; *Odontostemma glandulosum* Benth., GB, KP148863.1, KP148961.1; *Odontostemma ionandrum* (Diels) Sadeghian & Zarre, GB, KP148877.1, KP148976.1; *Odontostemma roseiflorum* (Sprague) Sadeghian & Zarre, GB, AY936244.1, FJ404895.1; *Paronychia argyrocoma* (Michx.) Nutt., GB, JN589120.1, FJ404929.1; *Pseudostellaria davidii* (Franch.) Pax 1, GB, KX158302.1, KX158413.1; *Pseudostellaria davidii* 2, GB, KX158301.1, KX158412.1; *Pseudostellaria davidii* 3, GB, JN589085.1, –; *Pseudostellaria ebracteata*, GB, KX158303.1, KX158414.1; *Pseudostellaria europaea* Schaeftl. 1, Slovenia, O. Angerer, s.n. (M), *MT624588, –; *Pseudostellaria europaea* 2, GB, KX158319.1, KX158430.1; *Pseudostellaria heterantha* (Maxim.) Pax 1, China, D. Podlech, 55469 (MSB), *MT624589, *MT624670; *Pseudostellaria heterantha* 2, China, D. Podlech, 55469 (MSB), *MT624590, *MT624671; *Pseudostellaria heterantha* 3, GB, KX158304.1, KX158415.1; *Pseudostellaria heterophylla* (Miq.) Pax 1, GB, EF121855.1, –; *Pseudostellaria heterophylla* 2, GB, KX158305.1, KX158416.1; *Pseudostellaria himalaica* (Franch.) Pax, Afghanistan, H. Freitag, 6009 (MSB), *MT624591, *MT624672; *Pseudostellaria japonica* (Korsh.) Pax, GB, KX158307.1, KX158418.1; *Pseudostellaria maximowicziana* (Franch. & Sav.) Pax 1, GB, KX158309.1, KX158420.1; *Pseudostellaria maximowicziana* 2, GB, KX158308.1, KX158419.1; *Pseudostellaria palibiniana* (Takeda) Ohwi, GB, KX158333.1, KX158444.1; *Pseudostellaria rigida* (Komarov) Pax, GB, KX158312.1, KX158423.1; *Pseudostellaria rupestris* (Turcz.) Pax, GB, KX158313.1, KX158424.1; *Pseudostellaria sylvatica*, GB, KX158316.1, KX158427.1; *Pseudostellaria tianmushanensis* G.H. Xia & G.Y. Li, GB, KX158318.1, KX158429.1; *Pseudostellaria tibetica* Ohwi 1, GB, KX158317.1, KX158428.1; *Pseudostellaria tibetica* 2, GB, KX158310.1, KX158421.1; *Rabelera cilicica* (Boiss. & Balansa) Arabi, Rabeler & Zarre, Cyprus, Meierott, 95/Cyp-189 (M), *MT624592, *MT624673; *Rabelera holostea* (L.) M.T. Sharples & E. Tripp 1, GB, MH219821, MH243549; *Rabelera holostea* 2, GB, JX274531.1, –; *Rabelera holostea* 3, GB, JN589079.1, –; *Sagina saginoides* (L.) H. Karst, Iran, H. Madhani, s.n. (TUH), *MT624593, *MT624674; *Schiedea membranacea* H. St. John, GB, AY517662.1, FJ404939.1; *Schizotechium americanum* (Standl.) Arabi, Rabeler & Zarre, GB, JN589090.1, KX158446; *Schizotechium jamesianum* (Torr.) Arabi, Rabeler & Zarre 1, GB, JN589138.1, FJ404933.1; *Schizotechium jamesianum* 2, GB, JN589048.1, KX158417.1; *Schizotechium jamesianum* 3, U.S.A., F.W. Hoffmann, 1684 (B), *MT624594, –; *Schizotechium monospermum* (Buch.-Ham. ex Don) P. Usalkar & S.K. Srivast. 1, Pakistan, H. Ern & P. Praelz, 7565 (B), *MT624595, *MT624675; *Schizotechium monospermum* 2, Pakistan, F. Lobbichler, 406 (M), *MT624596, *MT624676; *Schizotechium turkestanicum* (Schischk.) Arabi, Rabeler & Zarre, Pakistan, E. Eberhardt, 3749 (MSB), *MT624597, *MT624677; *Scleranthus annuus* L., GB, JX274538.1, FJ404943.1; *Shivparvatia ciliolata* (Edgew. & Hook.f.) Pusalkar & D.K. Singh, GB, KP148859.1, KP148956.1; *Shivparvatia glandulifera* (Edgew.) Pusalkar & D.K. Singh, GB, KP148867.1, KP148965.1; *Shivparvatia stracheyi* (Edgew.) Pusalkar & D.K. Singh, GB, KP148898.1, KP148999.1; *Silene gallica* L., GB, LC424050, LC424035; *Spergularia media* (L.) C. Presl, GB, EU812820.1, FJ404950.1; *Stellaria alsinea* Grimm, Morocco, D. Podlech, 48119 (MSB), *MT624598, *MT624678; *Stellaria arenarioides* Shi L. Chen, Rabeler & Turland, GB, JN589096.1, –; *Stellaria borealis* Bigelow 1, GB (as *St. calycantha* (Ledeb.) Bong.), JN589064.1, –; *Stellaria borealis* 2, GB (as *St. calycantha* (Ledeb.) Bong.), JN589094.1, –; *Stellaria borealis* 3, Finland, A. Komulainen, s.n. (M), *MT624599, *MT624679; *Stellaria borealis* × *longifolia* Mühl. ex Willd., Finland, M. Ohehoja, s.n. (M), –; *MT624680; *Stellaria caespitosa* Hook.f., Australia, H. Eichler, 17754 (M), *MT624600, *MT624681; *Stellaria chinensis* Regel 1, China, B. Dickoré, 8024 (MSB), *MT624601, –; *Stellaria chinensis* Regel 2, GB, JN589133.1, –; *Stellaria congestiflora* H. Hara, GB, JN589035.1, –; *Stellaria corei* Shinnars, GB, JN589046.1, –; *Stellaria crassifolia* Ehrh. 1, Poland, O. Angerer, s.n. (M), *MT624602, –; *Stellaria crassifolia* 2, GB, JN589071.1, –; *Stellaria crassipes* Hultén, GB, –; FJ404951.1; *Stellaria crispa* Cham. & Schltdl. 1, Canada, J.A. Calder & al., 20957 (M), *MT624603, *MT624682; *Stellaria crispa* 2, GB, JN589149.1, –; *Stellaria cupaniana* Nyman, Greece, J. Tillich, 5339 (MSB), *MT624604, *MT624683; *Stellaria cuspidata* D.F.K. Schltdl., GB, –; FJ404952.1; *Stellaria cuspidata* subsp. *prostrata* (Baldwin) J.K. Morton 1, Costa Rica, P. Döbbeler, 4/169 (M), –; *MT624684; *Stellaria cuspidata* subsp. *prostrata*, GB, JN589121.1, –; *Stellaria decumbens* Edgew. 1, China, B. Dickoré, 10043 (MSB), *MT624605, *MT624685; *Stellaria decumbens* Edgew. 2, China, B. Dickoré, 9703 (MSB), *MT624606, *MT624686; *Stellaria decumbens* Edgew. 3, GB, JN589101.1, –; *Stellaria dianthifolia* F.N. Williams, China, B. Dickoré, 9441 (MSB), *MT624607, *MT624687; *Stellaria edwardsii* R.Br., JN589040.1, –; *Stellaria fischeriana* Ser., Russia, V. Petrovsky & E. Norkina, 6017 (M), *MT624608, *MT624688; *Stellaria flaccida* Hook., Australia, W. Greuter 21321 (B), *MT624609, –; *Stellaria fontana* Popov 1, Pakistan, A. Bosshard & al., 053.01 (MSB), *MT624610, –; *Stellaria fontana* Popov 2, Pakistan, E. Eberhardt, 4397 (MSB), *MT624611, *MT624689; *Stellaria graminea* L. 1, GB, MH219820, MH243548; *Stellaria graminea* 2, GB,

Appendix 1. Continued.

AY594304.1, –; *Stellaria howardii* Maguire, GB, JN589135.1, –; *Stellaria humifusa* Rottb. 1, Canada, J.A. Calder & R.L. Taylor, 23784 (M), *MT624612, *MT624690; *Stellaria humifusa* 2, GB, JN589067.1, –; *Stellaria infracta* Maxim., China, D.E. Boufford & al., 38879 (MSB), *MT624613, *MT624691; *Stellaria irrigua* Bunge 1, GB, JN589088.1, –; *Stellaria irrigua* 2, GB (as *St. umbellata* Turcz. in Greenberg & Donoghue, 2011), JN589109.1, –; *Stellaria irrigua* 3, China, B. Dickoré, 6565 (MSB), *MT624614, *MT624692; *Stellaria koelzii* Rech.f., Afghanistan, H. Freitag, 5717 (MSB), –, *MT624693; *Stellaria lanata* Hook.f., GB, JN589015.1, –; *Stellaria laxmannii* Fisch., Russia, V. Petrovsky, s.n. (M), *MT624615, *MT624694; *Stellaria longifolia* Mühl. ex Willd. 1, Finland, R. Lampinen, 19746 (MSB), *MT624616, *MT624695; *Stellaria longifolia* 2, GB, JN589146.1, –; *Stellaria longipes* Goldie, GB, JN589086.1, –; *Stellaria media* (L.) Vill. 1, GB, JN589063.1, FJ404953.1; *Stellaria media* 2, GB, KR082779.1, Z83152.1; *Stellaria minutifolia* Maguire, GB, JN589038.1, –; *Stellaria neglecta* (Lej.) Weihe, GB, JN589089.1, –; *Stellaria nemorum* L. 1, Germany, F. Schuhwerk, 08/38 (M), *MT624617, *MT624696; *Stellaria nemorum* 2, GB, AY936246.1, –; *Stellaria nitens* Nutt., GB, JN589137.1, –; *Stellaria nubigena* Standl., Costa Rica, P. Döbbeler & J. Poelt, 3224 (M), *MT624618, *MT624697; *Stellaria obtusa* Engelm., GB, JN589083.1, –; *Stellaria ovata* Willd. ex D.F.K. Schldt., Panama, S. Mori & J. Kallunki, 5655 (B), *MT624619, *MT624698; *Stellaria pallida* (Dumort.) Crép., Germany, R. Muhr, s.n. (M), *MT624620, *MT624699; *Stellaria palustris* Retz. 1, Finland, K. Alho, s.n. (MSB), *MT624621, *MT624700; *Stellaria palustris* 2, GB, JN589080.1, –; *Stellaria patens* D. Don, Nepal, U. Wündisch, UW 51 (M), –, *MT624701; *Stellaria peduncularis* Bunge 1, Lebanon, A.K. Skvortsov & V.R. Filin, 10911 (M), –, *MT624702; *Stellaria peduncularis* 2, GB, JN589131.1, –; *Stellaria petiolaris* Hand.-Mazz., China, D.E. Boufford & al., 35171 (MSB), *MT624622, *MT624703; *Stellaria pterosperma* Ohwi, GB, JN589074.1, –; *Stellaria pubera* Michx. 1, U.S.A., A. Bresinsky, s.n. (M), *MT624623, *MT624704; *Stellaria pubera* 2, GB, JN589127.1, FJ404954.1; *Stellaria pungens* Brongn. 1, Australia, A. Strid, 22039 (B), *MT624624, *MT624705; *Stellaria pungens* 2, isovoucher (M), *MT624625, *MT624706; *Stellaria radians* L. 1, Russia, K. Skvortsov, s.n. (M), –, *MT624707; *Stellaria radians* 2, Russia, G. Krebs, 2587 (B), *MT624626, *MT624708; *Stellaria radians* 3, Russia, Siberia, L. Rybalov, s.n. (MSB), *MT624627, *MT624709; *Stellaria roughii* Hook.f., New Zealand, H. Hertel, 32181 (M), *MT624628, *MT624710; *Stellaria saxatilis* Buch.-Ham. ex D. Don, China, D. Podlech, 54248 (MSB), *MT624629, *MT624711; *Stellaria serpyllifolia* (L.) Scop., GB, JN589062.1, –; *Stellaria sessiliflora* Y. Yabe, GB, JN589129.1, –; *Stellaria soongorica* Roshev. ex Schischk., Kyrgyzstan, V. Vašák, s.n. (M), *MT624630, *MT624712; *Stellaria stricta* Richardson, Canada, H. & H. Doppelbaur, s.n. (M), *MT624631, *MT624713; *Stellaria subvestita* Greene, Canada, W.J. Cody, 15189 (MSB), –, *MT624714; *Stellaria tibetica* Kurz, China, Tibet, H. Hartmann, 2681 (MSB), *MT624632, *MT624715; *Stellaria venezuelana* Steyerem., Venezuela, B.F. Oberwinkler, 13380 (M), *MT624633, *MT624716; *Stellaria vestita* Kurz, China, B. Dickoré, 8123 (MSB), *MT624634, *MT624717; *Stellaria winkleri* (Briq.) Schischk., Tajikistan, B. Dickoré, 18269 (MSB), *MT624635, *MT624718; *Stellaria yunnanensis* Franch., China, B. Dickoré, 14181 (MSB), *MT624636, *MT624719.

¹ According to the recent treatment of *Holosteum glutinosum* (Fateryga & al., 2020), both specimens used in the analyses here should represent *H. glutinosum* subsp. *glutinosum*, but we do not follow splitting this species in two subspecies, since the morphological characters used for discrimination of the subspecies are minor or too variable.