

Appendix S6. Notes on infrageneric divisions of *Silene* proposed in the current paper, including “Diagnosis”, “Distribution”, “Species phylogenetically analyzed”, and “Notes on phylogeny and circumscription”.

1. *Silene* subg. *Lychnis* (L.) Greuter in Taxon 44(4): 556. 1995.

Distribution. – About 20 species in Europe, Asia, N and E Africa.

Notes on phylogeny and circumscription. – *Silene* subg. *Lychnis* consists of three main clades in the gene trees (Figs. 3, 4, suppl. Figs. S2, S3); 1) *S. sect. Agrostemma* (DC.) Greuter, 2) *S. sect. Lychnis*, and 3) a clade which includes *S. sect. Coccyanthe* (Rchb.) Greuter, *S. lagrangei* (Coss.) Greuter & Burdet and *S. sect. Uebelinia* (T.C.E.Fr.) F.Jafari, Oxelman & Rabeler. *Silene sect. Uebelinia* has been recognized as the African genus *Uebelinia* Hochst., until recently synonymized with *Lychnis* L. by Oxelman & al. (2001) and Popp (2008). Neumayer (1923) included *Uebelinia* in his expanded concept of *Silene* L., a concept rejected by Fries (1923) and others until now. Gizaw & al. (2016) showed the divergence of the African *Lychnis* to occur in the late Miocene to early Pliocene.

1.1. *Silene sect. Agrostemma* (DC.) Greuter in Taxon 44(4): 556. 1995.

Diagnosis. – Short-lived perennials, tomentose, inflorescence dichasial or ± capitate, calyx villose and campanulate with prominent veins and petal limbs purple. Ploidy level: diploid.

Distribution. – Two species; SE Europe, W Asia (N Iran).

Species phylogenetically analyzed (2). – *S. coronaria* (L.) Clairv., *S. flos-jovis* (L.) Greuter & Burdet.

Notes on phylogeny and circumscription. – Popp & al. (2008) demonstrated that *S. coronaria* and *S. flos-jovis* form a monophyletic group based on a multi-loci analysis, which is corroborated by our trees (suppl. Figs. S2, S3). The ITS trees (Fig. 3, suppl. Fig. S2), which have better resolution than the *rps16* trees (Fig. 4, suppl. Fig. S3), shows that this section forms a sister group to the rest of *S. subg. Lychnis*.

1.2. *Silene sect. Lychnis* (L.) Greuter in Taxon 44(4): 556. 1995.

Diagnosis. – Perennials; inflorescence dichasial and dense to few-flowered or corymb-like, sometimes compact and capitate; calyx slightly pubescent, tomentose or hispid, narrowly campanulate, cylindrical or tubular in flower and campanulate or clavate in fruit; petal limbs bifid, often with basal appendages. Ploidy level: diploid, *Silene senno* (Siebold & Zucc.) S.Akiyama reported as triploid (Goldblatt & Johnson, 1979–).

Distribution. – About 10 species; E Asia, Russia, Mongolia, E Europe.

Species phylogenetically analyzed (10). – *S. banksia* (Meerb.) Mabb., *S. chalcedonica* (L.) E.H.L.Krause, *S. cognata* (Maxim.) H.Ohashi & H.Nakai, *S. fulgens* (Fisch.) E.H.L.Krause, *S. gracillima* Rohrb., *S. kiusiana* (Makino) H.Ohashi & H.Nakai, *S. miqueliana* (Rohrb.) H.Ohashi & H.Nakai, *S. senno* (Siebold & Zucc.) S.Akiyama, *S. sieboldii* (Van Houtte) H.Ohashi & H.Nakai, *S. wilfordii* (Regel) H.Ohashi & H.Nakai.

Notes on phylogeny and circumscription. – *Silene chalcedonica* shows a sister-group relationship with an E Asian clade (e.g., *S. cognata*, *S. sieboldii*, *S. wilfordii*, *S. fulgens* and *S. kiusiana*, form a clade with *S. banksia*; suppl. Figs. S2, S3). This phylogenetic relationship was revealed earlier by Ullbors (2008) based on the plastid loci *rps16*, *trnL-trnL-trnF*, and the *psbB-petG* spacer as well as the ITS region.

1.3. *Silene sect. Coccyanthe* (Rchb.) Greuter in Taxon 44(4): 556. 1995.

Diagnosis. – Perennials; inflorescence short corymbose thyrsoïd; calyx glabrous; petal limbs 4-fid. Ploidy level: diploid.

Distribution. – One or two species; Europe to C Asia.

Species phylogenetically analyzed (1). – *Silene flos-cuculi* (L.) Clairv.

Notes on phylogeny and circumscription. – Several phylogenies inferred from plastid, nuclear ribosomal and low-copy DNA regions have revealed (Oxelman & Lidén, 1995; Oxelman & al., 1997; Popp & Oxelman, 2004) the Eurasian *S. flos-cuculi* as unresolved in relation to the *Uebelinia* clade and *S. lagrangei* (Popp & al., 2008) (Fig. 4, suppl. Figs. S2, S3).

1.4. *Silene sect. Uebelinia* (Hochst.) F.Jafari, Oxelman & Rabeler

Diagnosis. – Perennials or annuals; calyx narrowly campanulate in flower and conical in fruit and sometimes hispid or hirsute on the nerves. Ploidy level: diploid (4 spp.) and tetraploid (2 spp., Ousted, 1985; Popp & al., 2008).

Distribution. – Six species; tropical Africa.

Species phylogenetically analyzed (5). – *S. abyssinica* (Hochst.) Neumayer, *S. afromontana* F.Jafari, Oxelman & Rabeler, *S. kenya* F.Jafari, Oxelman & Rabeler, *S. kigesiensis* (R.D.Good) F.Jafari, Oxelman & Rabeler, *S. kiwuensis* (T.C.E.Fr.) F.Jafari, Oxelman & Rabeler, *Silene scottii* (Turrill) F.Jafari, Oxelman & Rabeler.

Notes on phylogeny and circumscription. – Our phylogenetic trees (Fig. 3, suppl. Fig. S2) and a previous study (Popp & al., 2008) based on multiple loci support this section as monophyletic. The phylogenetic data (Popp & al., 2008) (Figs. 3, 4, suppl. Figs. S2, S3) support the two tetraploid species as monophyletic. They were assigned to *Uebelinia* sect. *Trigynuebelinia* T.C.E.Fr. by Ousted (1985).

Unplaced taxon in *Silene* subg. *Lychnis*. — *Silene lagrangei* (Coss.) Greuter & Burdet

2. *Silene* subg. *Behenantha* (Otth) Torr. & A.Gray, Fl. N. Amer. 1: 189. 1838.

Distribution. – Members of this subgenus exhibit a wide distribution in Eurasia, Central and E Asia, North and South America, the Arctic region and southern Africa.

Notes on phylogeny and circumscription. – A clade indicated as “Behenantha II” appears in the *rps16* tree (Fig. 4, suppl. Fig. S3), but it merges with “Behenantha I” in the SMC (Fig. 2A) and ITS trees (Fig. 3, suppl. Fig. S2). Previous studies, on subsets of these taxa and based more on plastome sequence information (Erixon & Oxelman, 2008a; Sloan & al., 2009; Aydin & al., 2014), have also failed to find support for the monophyly of the subgenus, while other nuclear (Petri & al., 2013; Oxelman & al., unpub. data) data strongly support the circumscription of *S.* subg. *Behenantha* we present here. The reason why the plastome sequences fail to give strong support for this group remains to be explored. As circumscribed here, this subgenus includes 18 sections: *Psammophilae* (Talavera) Greuter, *Elisanthe* (Fenzl) Ledeb., *Melandrium* (Röhl.) Rabeler, *Conoimorpha* Otth, *Cryptoneurae* Aydin & Oxelman, *Sedoides* Oxelman & Greuter, *Cucubalus* (L.) Greuter, *Cucubaloides* Edgeworth & Hook.f., *Cordifoliae* Chowdhuri, *Erectorefractae* Chowdhuri, *Acutifoliae* Oxelman & F.Jafari, *Anotites* (Greene) Oxelman, F.Jafari & Rabeler, *Odontopetalae* Chowdhuri, *Fimbriatae* (Boiss.) Bornm., *Dichotomae* (Rohrb.) Chowdhuri, *Saponarioides* (Boiss.) Schischk., *Behenantha* Otth and *Physolychnis* (Benth.) Bocquet, as well as few other species that form single, unresolved basal branches in this clade, which may indicate an ancient rapid radiation.

Greuter (1995) placed the Mediterranean members of these sections in *S.* subg. *Silene*; only *S.* sect. *Conoimorpha* (as defined here) was included in *S.* subg. *Conoimorpha* (Otth) Fenzl ex Endl. By contrast, results of phylogenetic analyses show that *S.* sect. *Conoimorpha* is nested within *S.* subg. *Behenantha*. This group has already been recognized as “*S.* subg. *Behenantha* (Otth) Endl.” in Rautenberg & al. (2010, 2012), Petri & Oxelman (2011), Oxelman & al. (2013), and Petri & al. (2013) following the rank concept in *Genera plantarum* and its supplement (Endlicher, 1840, 1842) suggested by Greuter (1995). The clade circumscribed here as *S.* subg. *Behenantha* consists mainly of taxa representing *S.* subg. *Behen* (Dumort.) Rohrb. in Rohrbach’s (1869) system as well as some taxa of *S.* [unranked] *Conosilene*, *S.* [unranked] “*Eusilene*” and *S.* sect. *Dichasiosilene* Rohrb.

2.1. *Silene* sect. *Psammophilae* (Talavera) Greuter in Taxon 44 (4): 571. 1995.

Diagnosis. – Annuals; inflorescence a few-flowered monochasial cyme; calyx cylindrical in flower and subclavate in fruit. Ploidy level: diploid.

Distribution. – Five species; SW Europe and the Balearic islands.

Species phylogenetically analyzed (5). – *S. adscendens* Lag., *S. cambessedesii* Boiss. & Reut., *S. littorea* Brot., *S. psammitis* Link ex Spreng., *S. stockenii* Chater.

Notes on phylogeny and circumscription. – The morphologically highly similar *S. littorea* and *S. stockenii* form a monophyletic group with strong support in the SMC tree (Fig. 2A) and the gene trees (Figs. 3, 4, suppl. Figs. S2, S3). Our study supports previous results (e.g., Rautenberg & al., 2012) indicating that *S. pendula* L. is distantly related to *S. littorea* in contrast to some previous classifications (Talavera, 1979; Greuter, 1995) but instead belongs to an expanded *S.* sect. *Behenantha* (see below). *Silene littorea* was classified in *S.* sect. *Succulentae* (Boiss.) Chowdhuri by Chowdhuri (1957) but the type of that section, *S. succulenta* Forssk., belongs to subg. *Silene* sect. *Silene* in our phylogenies. *Silene pendula* and *S. littorea* were classified in *S.* sect. *Erectorefractae* subsect. *Psammophilae* Talavera (Talavera, 1979), a treatment that was followed partly by Chater & al. (1993), whereas Greuter (1995) elevated this taxon to sectional rank (as followed here), adding testa cell shape (subisodiametric) and flowering rhythms (diurnal) to the diagnostic characters mentioned by Talavera (1979).

2.2. *Silene* sect. *Elisanthe* (Fenzl ex Endl.) Ledeb., Fl. Ross 1: 314. 1842.

Diagnosis. – Annuals to perennials; calyx glandular pubescent, cylindrical or tubular in flower, and clavate or conical in fruit. Ploidy level: diploid.

Distribution. – About nine species; Eurasia and southern Africa.

Species phylogenetically analyzed (3). – *S. noctiflora* L., *S. turkestanica* Regel, *S. undulata* Aiton.

Notes on phylogeny and circumscription. – The Eurasian *S. noctiflora*, the southern African *S. undulata* and the Central Asian *S. turkestanica* form a strongly supported group in all trees (Figs. 2A, 3, 4, suppl. Figs. S2, S3), properly called *S. sect. Elisanthe* (Rautenberg & al., 2010). The interrelationship among the species is unclear, but the highly similar sequences suggest a recent radiation, which is surprising given the wide and disjunct geographical distribution. The southern African members of the group were recently revised (Manning & Goldblatt, 2012) and are currently being investigated in more detail (Moilola & al., unpub. data).

This section was once widely circumscribed to include also the dioecious members of *S. sect. Melandrium* (Chowdhuri, 1957, as *S. sect. Melandriiformes* (Boiss.) Chowdhuri; Greuter, 1995, as *S. sect. Elisanthe*), but Rautenberg & al. (2010) confidently demonstrated polyphyly of this widely circumscribed section, rendering its splitting into two major groups treated as *S. sect. Elisanthe* and *S. sect. Melandrium* (Rabeler, 1993).

2.3. *Silene* sect. *Melandrium* (Röhl.) Rabeler in Contr. Univ. Michigan Herb. 19: 161. 1993.

Diagnosis. – Biennials or perennials, dioecious; the calyx of the male flower cylindrical in flower, and the calyx of the female flower campanulate in flower and fruit; and petal claws sometimes auriculate. Ploidy level: diploid.

Distribution. – About eight species; Europe and W Asia.

Species phylogenetically analyzed (5). – *S. diclinis* (Lag.) M.Lainz, *S. dioica* (L.) Clairv., *S. heuffelii* Soó, *S. latifolia* Poir., *S. marizii* Samp.

Notes on phylogeny and circumscription. – The dioecious species *S. diclinis*, *S. dioica*, *S. heuffelii*, *S. latifolia*, and *S. marizii* form a strongly supported monophyletic group in the SMC (Fig. 2A) and ITS trees (Fig. 3, suppl. Fig. S2), while a population of *S. latifolia* from Turkey is separated from other populations of this species and the remaining populations, which are nested in *S. sect. Melandrium* (Fig. 4, suppl. Fig. S3) possibly to be explained by absence of interspecies introgression (Rautenberg & al., 2010). In a species tree presented by Rautenberg & al. (2012) based on four unlinked loci, there is moderate support (PP = 0.86) favoring a sister-group relation between *S. sect. Behenantha* and *S. sect. Melandrium*. Other studies based on multiple nuclear genes have not been able to confidently resolve this issue (Marais & al., 2011; Havird & al., 2017).

2.4. *Silene* sect. *Conoimorpha* Otth in Candolle, Prodr. 1: 371. 1824.

Diagnosis. – Annuals, gynomonocious; calyx tubular to narrowly conical in flower and conical in fruit and glandular pubescent. Ploidy level: diploid with $x = 10$, and possibly $x = 11$.

Distribution. – About nine species; Eurasia, N Africa.

Species phylogenetically analyzed (7). – *S. ammophila* Boiss. & Heldr., *S. conica* L., *S. coniflora* Nees ex Otth, *S. conoidea* L., *S. lydia* Boiss., *S. macrodonta* Boiss., *S. subconica* Friv.

Notes on phylogeny and circumscription. – Rautenberg & al. (2012) demonstrated that despite sharing an unusual feature, i.e., having a multiveined calyx, the North American species *S. multinervia* S.Watson is unrelated to *S. sect. Conoimorpha*. There is low support for grouping this species with any other branch in *S. subg. Behenantha*. Previous ideas (Desfeux & Lejeune, 1996; Erixon & Oxelman, 2008a) on a possible sister-group relation between *S. sect. Conoimorpha* and *S. sect. Melandrium* have not been substantiated (e.g., Rautenberg & al., 2010, 2012; Marais & al., 2011). Havird & al. (2017) found weak support for a sister-group relation between *S. sect. Conoimorpha* and *S. sect. Elisanthe*. Interestingly, these two sections also share accelerated rates of organellar genome evolution (e.g., Erixon & Oxelman, 2008b; Sloan & al., 2009, 2014; Williams & al., 2018).

Greuter (1995) described the monotypic *S. sect. Lydiae* Greuter for *S. lydia*, based on a “negative anthophore” or broadly sessile anthophore, and a possible chromosome base number $x = 11$. Rautenberg & al. (2012) found *S. lydia* to be strongly supported as sister to the rest of *S. sect. Conoimorpha*, which is in accordance with the circumscription followed here.

2.5. *Silene* sect. *Cryptoneurae* Aydin & Oxelman in Phytotaxa 178(2): 101. 2014.

Diagnosis. – Annuals; calyx tubular in flower and subclavate in fruit; petal limbs entire or slightly emarginate; capsule thin-walled, transparent; and seeds subglobose. Ploidy level: diploid.

Distribution. – Four species; W Asia.

Species phylogenetically analyzed (4). – *S. cryptoneura* Stapf, *S. ertekinii* Aydin & Oxelman, *S. insularis* Barbey, *S. salamandra* Pamp.

Notes on phylogeny and circumscription. – The members of this section have traditionally been classified (Greuter, 1995) in *S. sect. Atocion* Otth, with which they share the unusual seed outline, but Aydin & al. (2014) showed that it is a monophyletic group separated from *S. sect. Atocion* (Figs. 2A, 3, 4, suppl. Figs. S2, S3).

2.6. *Silene* sect. *Sedoidea* Oxelman & Greuter in Willdenowia 25: 150. 1995 ('*Sedoideae*').

Diagnosis. – Annuals; leaves fleshy to succulent; calyx cylindrical in flower and narrowly obconical or clavate in fruit. Ploidy level: diploid and tetraploid.

Distribution. – Six species, northern Mediterranean area, from SW Europe to W Asia. All except one of the species are confined to Greece.

Species phylogenetically analyzed (6). – *S. aegaea* Oxelman, *S. haussknechtii* Heldr. ex Nyman, *S. integripetala* Bory & Chaub., *S. laconica* Boiss. & Orph., *S. pentelica* Boiss., *S. sedoidea* Poir.

Notes on phylogeny and circumscription. – *Silene haussknechtii* is sister to the rest of the species that belong to this section, and they form a well-supported clade in the gene trees (Figs. 3, 4, suppl. Figs. S2, S3). *Silene aegaea*, which is also assigned to this section, is a rare allotetraploid species from the Aegean islands. Popp & Oxelman (2001), using nuclear (*RPB2*, ITS) and plastid (*rps16*) markers, showed the ancestry of *S. aegaea* originated from *S. sedoidea* and *S. pentelica*, with the latter indicated as the maternal lineage. The assigned species here have previously been classified in *S. sect. Dichasiosilene* ser. *Rigidulae* (Boiss.) Rohrb. (Rohrbach, 1869) or *S. sect. Atocion* subsect. *Divaricatae* (Rohrb.) Gürke (Chowdhuri, 1957), but molecular phylogenetic studies (Oxelman, 1995, 1996; Oxelman & Lidén, 1995) revealed their isolated position.

2.7. *Silene* sect. *Cucubalus* (L.) Greuter in Taxon 44(4): 565. 1995.

Diagnosis. – Perennial; inflorescence thyrsoïdal; calyx campanulate in flower and fruit, deflexed at maturity and an indehiscent berry-like fruit. Ploidy level: diploid.

Distribution. – One species; Europe, from W Asia to E Asia.

Species phylogenetically analyzed (1). – *Silene baccifera* (L.) Roth.

Notes on phylogeny and circumscription. – Oxelman & Lidén (1995), Desfeux & Lejeune (1996) and Oxelman & al. (1997, 2001) demonstrated that the only member of this section (*S. baccifera*) belongs to the core *Silene* clade, in the *S. subg. Behenantha* subclade. Neither the RNA polymerase genes analyzed by Popp & Oxelman (2004), nor the extensive taxon sampling in the present study has been able to resolve the position of this section within the subgenus (Figs. 3, 4, suppl. Figs. S2, S3).

Linnaeus (1753) described *Cucubalus* L. based on the alleged (but erroneous) absence of corona and the berry-like fruits. Most of the species placed in *Cucubalus* by Linnaeus (1753) have been treated as *Silene* since then, but *C. baccifer* L. has been retained by most pre-phylogenetic taxonomists. Greuter (1995), following the molecular phylogenetic results, transferred it to *S. sect. Cucubalus*.

2.8. *Silene* sect. *Cucubaloides* Edgeworth & Hook.f. in Hooker, Fl. Brit. India 1: 221. 1875 ('*Cucubaloideae*').

Diagnosis. – Perennials with ± creeping habit and fleshy, fasciculate root tubers; inflorescence dichasial cyme or sometimes thyrsoïdal; calyx tubular to campanulate in flower and campanulate in fruit. Ploidy level: diploid.

Distribution. – About 27 species; E Asia.

Species phylogenetically analyzed (12). – *S. adenocalyx* F.N.Williams, *S. asclepiadea* Franch., *S. batangensis* H.Limpr., *S. cardiopetala* Franch., *S. grandiflora* Franch., *S. khasiana* Rohrb., *S. kumaonensis* F.N.Williams, *S. otodonta* Franch., *S. rosiflora* Kingdon-Ward ex W.W.Sm., *S. tatarinowii* Regel, *S. viscidula* Franch., *S. waltonii* F.N.Williams.

Notes on phylogeny and circumscription. – This group of mainly E Asian taxa has not been much explored previously in molecular phylogenetic studies. Frajman & al. (2009b) demonstrated that *S. tatarinowii* Regel is not related to the taxa

that Chowdhuri (1957) placed in *S.* sect. *Rupifraga* Otth. According to our phylogenies, *S. tatarinowii* also belongs here (Fig. 2A, suppl. Figs. S2, S3). Here, we show that *S. kumaonensis*, *S. waltonii*, *S. tatarinowii*, *S. cardiopetala* and *S. grandiflora* are supported as forming a monophyletic clade in the SMC tree (Fig. 2A). Thus, our extended sampling supports the circumscription and monophyly of this section as suggested earlier by Zhou & al. (2001). *Silene waltonii* was cited as a questionable synonym of *S. subcretacea* F.N. Williams by Zhou & al. (2001) but our results demonstrate that *S. waltonii* is closely related to *S. kumaonensis* and might even be considered as its synonym (Lidén & Oxelman, unpub. data).

Chowdhuri (1957) divided this section into two groups: *S.* subsect. *Schaftae* (Boiss.) Chowdhuri and *S.* subsect. *Sinenses* Chowdhuri. The circumscription of the latter subsection matches well with our circumscription of the section based on the species analyzed here. The type of *S.* subsect. *Schaftae*, *S. schafta*, clearly belongs to *S.* subg. *Silene* sect. *Auriculatae* (Boiss.) Schischk. (see below).

2.9. *Silene* sect. *Cordifoliae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 240. 1957.

Diagnosis. – Perennial, caespitose; inflorescence dichasial; calyx with glandulose-pubescent hairs or rarely hirsute, cylindrical in flower and campanulate in fruit; petal limbs white, emarginate, claws exauriculate. Ploidy level: diploid.

Distribution. – One species; SW Europe and Caucasus.

Species phylogenetically analyzed (1). – *S. cordifolia* All.

Notes on phylogeny and circumscription. – Chowdhuri (1957) introduced this section with three taxa distributed in S Europe, Turkey and Caucasus. Our analyses, however, suggest transferring the W Iberian *S. acutifolia* Link ex Rohrb. and *S. foetida* Link ex Spreng. to a new section (see below under *S.* sect. *Acutifoliae*). Morphological characters such as cordate-ovate cauline leaves, bifid petal limbs and a claw not auriculate separate *S. cordifolia* from *S. acutifolia* and *S. foetida*.

2.10. *Silene* sect. *Erectorefractae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 247. 1957.

Diagnosis. – Annuals; calyx cylindrical to fusiform in flower, ovoid in fruit and prominently hairy and with parallel veins. Ploidy level: diploid.

Distribution. – Two species; SW Europe.

Species phylogenetically analyzed (2). – *S. almolae* J.Gay ex Coss., *S. germana* J.Gay ex Coss.

Notes on phylogeny and circumscription. – The monophyly of *S.* sect. *Erectorefractae* as defined by Talavera (1979) is not supported by our results, since the members of *S.* subsect. *Psammophilae* appeared in a separate clade (see above under *S.* sect. *Psammophilae*). We circumscribe this section much narrower than Chowdhuri (1957) and Talavera (1979) and assign only two species to it.

2.11. *Silene* sect. *Acutifoliae* Oxelman & F.Jafari

Description. – Plants perennial; stoloniferous, procumbent and branched; basal leaves oblanceolate, cauline leaves ovate to ovate-oblanceolate, acute, loosely to densely glandular; inflorescence dichasial, sometimes reduced to one flower; calyx purplish with glandular hairs, tubular or cylindrical in flower and inflated and ovoid in fruit with glandular hairs; petal limbs pale to deep pink, emarginate to slightly bifid; coronal scales present; anthophore glabrous; capsule subconical or oblong; seeds reniform, reticulate or tuberculate.

Distribution. – Three species; SW Europe.

Species phylogenetically analyzed (2). – *S. acutifolia* Link ex Rohrb., *S. foetida* Link ex Spreng.

Notes on phylogeny and circumscription. – *Silene acutifolia* and *S. foetida* (Figs. 3, 4, suppl. Figs. S2, S3) are supported as members of *S.* subg. *Behenantha* in the gene trees, but their affinities differ among these trees. In the ITS tree, *S.* sect. *Acutifoliae* is weakly supported as sister group to *S.* sect. *Anotites* (Fig. 3, suppl. Fig. S2), while it forms a strongly supported clade together with *S.* sect. *Erectorefractae* (Fig. 4).

Silene acutifolia and *S. foetida* belong to *S.* sect. *Dichasiosilene* ser. *Macranthae* Rohrb. in Rohrbach's (1869) system, while Talavera (1990) followed Chowdhuri (1957) and placed them in *S.* sect. *Cordifoliae* (see above). *Silene herminii* Welw. ex Rouy, placed in *S.* sect. *Cordifoliae* by Chater & al. (1993), is likely to be another member of this section.

2.12. *Silene* sect. *Anotites* (Greene) Oxelman, F. Jafari & Rabeler

Diagnosis. – Perennials; calyx pubescent or glandular, campanulate in flower and fruit; capsule ellipsoid, ovoid to tubular; seeds not winged. Ploidy level: diploid, tetraploid and hexaploid (Popp & Oxelman, 2007; Petri & Oxelman, 2011).

Distribution. – Three species; North America.

Species phylogenetically analyzed (3). – *S. menziesii* Hook., *S. seelyi* C.V.Morton & J.W.Thomps., *S. williamsii* Britton.

Notes on phylogeny and circumscription. – The included species here were identified as a strongly supported clade based on six unlinked DNA regions by Popp & Oxelman (2007), which is also recovered in our ITS tree (suppl. Fig. S2). They also showed that the hexaploid *S. hookeri* Nutt. of *S. sect. Physolychnis* harbors parental genomes from both *S. sect. Anotites* and sect. *Physolychnis*.

Chowdhuri (1957) classified the North American *S. menziesii* and its allies in *S. sect. Rupifraga*, with *S. rupestris* L. as its type. However, the latter species clearly falls outside *Silene* as indicated in the classification presented by Oxelman & al. (2001) as *Atocion rupestre* (L.) Oxelman. Therefore, a new combination and status were established within *Silene* for this North American clade with *Anotites* Greene as basionym. Although *S. menziesii* has usually been placed in *Silene*, it has five carpels rather than three. As this character used to be a diagnostic feature at the genus level in pre-phylogenetic classifications, Greene (1905) assigned this group to a separate genus as *Anotites*.

2.13. *Silene* sect. *Odontopetalae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 240. 1957.

Diagnosis. – Perennials; inflorescence solitary or few-flowered dichasium; calyx vesicular-campanulate in flower and fruit; petals bifid and auriculate. Ploidy level: diploid.

Distribution. – Three species (as circumscribed here); W Asia.

Species phylogenetically analyzed (2). – *S. joerstadii* Wendelbo, *S. odontopetala* Fenzl.

Notes on phylogeny and circumscription. – We include two species in our narrow circumscription. Chowdhuri (1957) proposed a wide circumscription for this section and divided its 19 species into two subsections (*S. subsect. Dentatae* Chowdhuri, subsect. *Lychnideae* Chowdhuri). We did not find phylogenetic support for these subdivisions. *Silene zawadzki* Herbich, which was assigned to *S. sect. Odontopetalae* subsect. *Dentatae*, belongs to *S. sect. Physolychnis* according to the phylogenetic results (see below). At a different phylogenetic position within *S. sect. Physolychnis*, the Himalayan representatives of Chowdhuri's (1957) subsect. *Dentatae* (such as *S. oblanceolata* W.W.Sm., the "*Odontopetalae*" group in Zhou & al., 2001) are found. Chowdhuri (1957) also included *S. elisabethae* Jan in this section, but it forms a separate branch in the molecular phylogenetic studies (Oxelman & Lidén, 1995; Rautenberg & al., 2010, 2012) (Fig. 2A).

In the SMC tree (Fig. 2A), *S. auriculata* Sm., *S. sordida* Hub.-Mor. & Reese, *S. joerstadii*, and *S. odontopetala* form a weakly supported clade. Greuter's (1995) suggestion and Boissier's (1867) decision to include *S. auriculata* in *S. sect. Odontopetalae* receives low support (PP < 0.75) in our analyses.

The type of *S. sect. Odontopetalae* is *S. odontopetala* (Chowdhuri, 1957; Greuter, 1995). However, Melzheimer (1988) placed *S. joerstadii* and *S. odontopetala* in *S. sect. Inflatae* (Boiss.) Chowdhuri (synonymized here with *S. sect. Behenantha*, see below). This treatment is not supported by the molecular data.

Silene lychnidea C.A.Mey., the type of *S. subsect. Lychnideae*, is tentatively included here despite no available phylogenetic information. The few-flowered inflorescence, vesicular calyx, and leaf morphology make it fit well morphologically with our definition of this section. To make a robust circumscription of this section, detailed taxonomic studies and DNA sequence data from multiple loci are needed.

2.14. *Silene* sect. *Fimbriatae* (Boiss.) Bornm. in Bull. Herb. Boissier 7: 114. 1899.

Diagnosis. – Perennials; calyx glandular pubescent, vesiculate-inflated in flower and fruit; petal limbs multifid. Ploidy level: diploid.

Distribution. – About four species; W Asia and Caucasus.

Species phylogenetically analyzed (1). – *S. simsii* F.Jafari, Oxelman & Rabeler.

Notes on phylogeny and circumscription. – Our ITS sequence of *S. simsii* (*S. fimbriata* Sims, nom. superfl. et illeg.) is identical to the GenBank accession JX274535, named *S. zawadzki*. The sequence was also included in a phylogenetic study by Volodin & Volodina (2015). We interpret this as an identification error, because the four other accessions of *S. zawadzki* included in our analyses are very similar to each other and related to members of *S. sect. Physolychnis* (see below). In the SMC tree, there is modest support for a relationship to *S. dichotoma* Ehrh. (Fig. 2A). The circumscription of the section by

Chowdhuri (1957) also included *S. lacera* (Steven) Sims, which was included in a phylogenetic study by Sloan & al. (2009) using the plastid *matK* gene, which revealed an unresolved position of this species in the *S.* subg. *Behenantha* clade while no *S. simsii* sequence was included. However, the close morphological and geographical proximity of the two species lead us to hypothesize that they are closely related. Chowdhuri (1957) also included *S. physalodes* Boiss. in *S.* sect. *Fimbriatae*, which remains to be studied phylogenetically. The North American *Silene greenei* (S. Watson ex B.L. Rob.) Howell, another proposed member of this section (Chowdhuri, 1957), is nested within *S.* sect. *Physolychnis* (e.g., Popp & Oxelman, 2007).

The type of *S. simsii* could not be retrieved in Jafari & al. (2019), but a lectotype for *S. multifida* (Adams) Rohrb., nom. illeg., was formally designated by Lazkov (1996).

2.15. *Silene* sect. *Dichotomae* (Rohrb.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 247. 1957.

Diagnosis. – Annuals, biennials, or short-living perennials; inflorescences dichasial at the base and monochasial in axillary branches; calyx nerves with crisp or papillose hairs. Ploidy level: diploid, rarely tetraploid (reported by Nazarova, 2004 in Goldblatt & Johnson (1979–)).

Distribution. – One to four species; SE Europe and W Asia.

Species phylogenetically analyzed (2). – *S. dichotoma* Ehrh., *S. heldreichii* Boiss.

Notes on phylogeny and circumscription. – Despite having been included in many molecular phylogenetic studies (e.g., Oxelman & Lidén, 1995; Desfeux & Lejeune, 1996; Sloan & al., 2009; Mikhaylova & al., 2016; Martyniuk & al., 2018), no close relative clade of *S. dichotoma* s.l. has been found, indicating that it appears to be another example of the many species-poor branches from an ancient radiation.

In our present analyses, we only included accessions of *S. dichotoma*, but Moilola & al. (unpub. data) recently showed that *S. heldreichii* also belongs here. Our results support that *S. remotiflora* Vis., another representative of this section according to Chowdhuri's system (1957), is not closely related to *S. heldreichii*, with which it has been synonymized (see Authier, 1992, for an excellent account) and is excluded from this section.

Chowdhuri (1957) validated and elevated *S.* ser. *Dichotomae* Rohrb. to section rank and designated *S. dichotoma* as its type, a treatment followed also by Greuter (1995). Melzheimer (1988) placed *S. dichotoma* with the annual species *S. apetala* Willd. and *S. gallica* L. in *S.* sect. *Lasiocalycinae* (Boiss.) Chowdhuri, which belong to *S.* sect. *Silene* in our classification system. Whether *S. oxyodonta* Barb.-Boiss. & Barbey, included in this section by Chowdhuri (1957), belongs to *S.* sect. *Dichotomae*, remains to be investigated.

2.16. *Silene* sect. *Saponarioides* (Boiss.) Schischk. in Komarov, Fl. URSS 6: 685. 1936 ('*Saponarioideae*').

Diagnosis. – Annual; calyx glabrous, inflated and not striate, ovoid in flower and fruit, umbilicate at base; seeds winged. Ploidy level: diploid.

Distribution. – One species; E, W and Central Asia.

Species phylogenetically analyzed (1). – *S. nana* Kar. & Kir.

Notes on phylogeny and circumscription. – *Silene nana* Kar. & Kir. was included in a previous phylogenetic study by Eggens & al. (2007), where an analysis of a concatenated dataset of nuclear ITS and *RPB2*, and plastid *rps16* sequences showed weak support for affinity with *S. uniflora* Roth (*S.* sect. *Behenantha* as circumscribed here) and *S. conica* (*S.* sect. *Conoimorpha*). Our analyses show a strong support for a sister-group relation to *S. pendula* and *S.* sect. *Dichotomae* in the ITS tree (Fig. 3), but only to *S.* sect. *Behenantha* in the *rps16* trees (Fig. 4, suppl. Fig. S3).

2.17. *Silene* sect. *Behenantha* Otth in Candolle, Prodr. 1: 367. 1824.

Diagnosis. – Annuals or perennials; inflorescence a dichasial cyme, sometimes turning into monochasia after the first branching; calyx ovoid-cylindrical or ovoid-campanulate in flower and ovoid-campanulate in fruit. Ploidy level: diploid and/or rarely tetraploid.

Distribution. – About 21 species; Eurasia, N Africa, and introduced in North America and southern Africa.

Species phylogenetically analyzed (13). – *S. behen* L., *S. caesia* Sm., *S. fabaria* (L.) Sm., *S. fabarioides* Hausskn., *S. graeca* Boiss. & Spruner, *S. holzmannii* Heldr. ex Boiss., *S. nutabunda* Greuter, *S. pendula* L., *S. pseudobehen* Boiss., *S. reinholdii* Heldr., *S. uniflora* Roth, *S. variegata* (Desf.) Boiss. & Heldr., *S. vulgaris* (Moench) Garcke.

Notes on phylogeny and circumscription. – Greuter (1995) suggested the possibility of a close relationship between the annuals of *S.* sect. *Behenantha* s.str. (i.e., the *S. behen* species group) and the perennial *S. fabaria* group (represented in our

SMC tree by *S. caesia*, *S. fabaria* and *S. variegata*), which he classified together with the *S. vulgaris* group in *S. sect. Behen* Dumort. (a synonym of *S. sect. Behenantha* as circumscribed here). The phylogenetic data support this suggestion. The SMC tree shows moderate support (Fig. 2A) for the clade including these two groups but excluding *S. vulgaris*, thus corroborating previous results from ITS-only analysis (Oxelman & Lidén, 1995). In addition, the Balkan species *S. graeca* and *S. nutabunda* also belong here. Most members of the *S. behen* group (*S. behen*, *S. holzmannii*, and *S. pseudobehen*) form a well supported clade in our SMC tree (Fig. 2A). The Greek endemic *S. reinholdii* is only weakly supported as sister to this clade, but is morphologically very similar.

We also tentatively include the *S. vulgaris* species group and *S. pendula* in *S. sect. Behenantha*. Greuter (1995) discussed the possibility that the *S. vulgaris* group might end up being separate from the *S. behen* and *S. fabaria* groups. Although the phylogenetic data does not strongly support the groups forming a monophylum, it doesn't reject it either. Rautenberg & al. (2010) found strong cpDNA support based on five loci for monophyly of *S. pendula*, *S. reinholdii*, and the *S. vulgaris* species group. Petri & Oxelman (2011) found ambiguous support for monophyly of *S. uniflora* and *S. pendula* in nuclear *NRPD2* paralogues. Greenberg & Donoghue (2011), based on concatenated plastome and nuclear sequences, found strong support for monophyly of a clade consisting of *S. caesia*, *S. fabaria*, *S. pendula*, *S. reinholdii*, *S. uniflora*, and *S. vulgaris*. Furthermore, *S. nana* was found to be sister to this clade also with moderate support (Greenberg & Donoghue, 2011). However, such conclusions might be flawed, since concatenation of data from unlinked regions under some circumstances can produce inflated support values. Rautenberg & al. (2012) made a species tree based on four unlinked loci, but only included *S. pendula*, *S. uniflora*, and *S. vulgaris* in their datasets and found some support for the clade including these species.

Our increased taxon sampling seems to complicate the picture even more. *Silene remotiflora* is unresolved within *S. subg. Behenantha* in the ITS tree (Fig. 3), but is nested within *S. sect. Behenantha*, as circumscribed here, in the *rps16* tree (Figs. 4, S3), and moderately supported as sister to *S. sect. Behenantha* in the SMC tree (Fig. 2A). The incongruence between the ITS and *rps16* datasets might be too large to be explained by incomplete lineage sorting (as assumed in the STACEY analysis). Moreover, there is only a poor morphological link between *S. remotiflora* and *S. sect. Behenantha* expressed by the rather similar inflorescences found in some of the annual members of the section.

This section could potentially be expanded to include *S. dichotoma*, *S. simsii*, and *S. nana* (see above under *S. sect. Dichotomae*), which are weakly supported as early successive branches in SMC tree (Fig. 2A) to the core group of this section. However, among these species, we assign only the *S. behen*, *S. fabaria*, *S. graeca* and *S. vulgaris* groups to this section at this stage. These are often glabrous, glaucous plants, and have similar inflorescences and seed morphology to some extent. *Silene pendula* deviates from these characteristics, but the phylogenetic data is rather strong to support it ultimately as a member of *S. sect. Behenantha*.

The other species that were placed in *S. sect. Behenantha* by Greuter (1995) with some hesitation were the members of *S. cretica* L. and *S. muscipula* L. groups (not to be confused with *S. subsect. Muscipulae* Chowdhuri, which is a synonym of *S. sect. Behenantha*). These latter species, however, clearly belong to *S. sect. Rigidulae* (Boiss.) Schischk. s.str. and *S. sect. Muscipula* (Tzvelev) Oxelman, F.Jafari & Gholipour, respectively (see below under *S. subg. Silene*).

2.18. *Silene* sect. *Physolychnis* (Benth.) Bocquet in Candollea 22: 6. 1967.

Diagnosis. – Perennials or rarely biennials; inflorescence single-flowered, compound dichasia or irregular thyrses; calyx tubular or campanulate in flower, ovoid to globose in fruit. Ploidy level: diploid to decaploid.

Distribution. – 162 species; E and Central Asia, Siberia, the Arctic region and the American continents.

Species phylogenetically analyzed (80). – *S. ajanensis* (Regel & Tiling) Vorosch., *S. andicola* Gillies, *S. antarctica* (Kuntze) Pedersen, *S. aprica* Turcz. ex Fisch. & C.A.Mey., *S. argentina* (Pax) Bocquet, *S. bernardina* S.Watson, *S. bungei* Bocquet, *S. caespitella* F.N.Williams, *S. caroliniana* Walter, *S. chilensis* (Naudin) Bocquet, *S. chubutensis* (Speg.) Bocquet, *S. chungtienensis* W.W.Sm., *S. cuspidata* Pedersen, *S. davidii* (Franch.) Oxelman & Lidén, *S. delavayi* Franch., *S. densifolia* (Dusén) Bocquet, *S. douglasii* Hook., *S. drummondii* Hook., *S. echegarayi* (Hieron.) Bocquet, *S. falconeri* (Rohrb.) Bocquet, *S. fedtschenkoana* Preobr., *S. firma* Siebold & Zucc., *S. gonosperma* (Rupr.) Bocquet, *S. greenii* (S.Watson ex B.L.Rob.) Howell, *S. herbilegorum* (Bocquet) Lidén & Oxelman, *S. himalayensis* (Edgew.) Majumdar, *S. hookeri* Nutt., *S. hupehensis* C.L.Tang, *S. indica* Roxb. ex Otth, *S. invisca* C.L.Hitchc. & Maguire, *S. involucrata* (Cham. & Schldl.) Bocquet, *S. keiskei* Miq., *S. kialensis* (F.N.Williams) Lidén & Oxelman, *S. laciniata* Cav., *S. lemmonii* S.Watson, *S. linnaeana* Vorosch., *S. madens* Majumdar, *S. magellanica* (Desr.) Bocquet, *S. mandonii* (Rohrb.) Bocquet, *S. melanantha*

Franch., *S. nangqenensis* C.L.Tang, *S. nepalensis* Majumdar, *S. nigrescens* (Edgew.) Majumdar, *S. nuda* (S.Watson) C.L.Hitchc. & Maguire, *S. oblanceolata* W.W.Sm., *S. occidentalis* S.Watson, *S. oregana* S.Watson, *S. ostenfeldii* (A.E.Porsild) J.K.Morton, *S. ovata* Pursh, *S. parryi* (S.Watson) C.L.Hitchc. & Maguire, *S. patagonica* (Speg.) Bocquet, *S. petersonii* Maguire, *S. polypetala* (Walter) Fernald & B.G.Schub., *S. quadriloba* Turcz. ex Kar. & Kir., *S. regia* Sims, *S. rotundifolia* Nutt., *S. sachalinensis* F.Schmidt, *S. salicifolia* C.L.Tang, *S. samojedorum* (Sambuk) Oxelman, *S. scaposa* B.L.Rob., *S. scopulorum* Franch., *S. scouleri* Hook., *S. seoulensis* Nakai, *S. soczaviana* (Schischk.) Bocquet, *S. songarica* (Fisch., C.A.Mey. & Avé-Lall.) Bocquet, *S. sorensenis* (B.Boivin) Bocquet, *S. stellata* (L.) W.T.Aiton, *S. subciliata* B.L.Rob., *S. suksdorfii* B.L.Rob., *S. thysanodes* Fenzl, *S. tolmachevii* Bocquet, *S. uralensis* (Rupr.) Bocquet, *S. verecunda* S.Watson, *S. villosula* (Trautv.) V.V.Petrovsky & Elven, *S. violascens* (Tolm.) V.V.Petrovsky & Elven, *S. virginica* L., *S. viscosa* (L.) Pers., *S. wardii* (C.Marquand) Bocquet, *S. yetii* Bocquet, *S. zawadzki* Herbich.

Notes on phylogeny and circumscription. – This is a diverse and taxonomically very challenging group with a broad geographic distribution. In the recently updated checklist of *Silene* (Oxelman & al., 2013), 162 species were listed as members of this section. Our sampling for the SMC tree is very limited due to the many polyploid taxa in this section (Popp & al., 2005; Popp & Oxelman, 2007; Petri & Oxelman, 2011; Frajman & al., 2018) that would limit the application of the SMC approach to our dataset (Jones, 2016). Although models for allopolyploid phylogenetic inference exist (e.g., Jones & al., 2013; Oxelman & al., 2017), they are not suitable for the two loci utilized here, with cpDNA being uniparentally inherited. In addition, in direct sequencing, the ITS PCR products are either expected to be polymorphic, or concerted in an unpredictable way to one of their parental lineages (Popp & Oxelman, 2004).

Bocquet (1969) defined *S. sect. Physolychnis* based on a gynoecium having five carpels. Previous studies have revealed that the presence of five carpels is not a reliable synapomorphy within *Silene*, nor even within *S. sect. Physolychnis* (e.g., Oxelman & Lidén, 1995; Oxelman & al., 2001; Popp & Oxelman, 2007; Petri & Oxelman, 2011). Our circumscription of this section follows and agrees with several previous studies, which provided novel informal circumscription of *sect. Physolychnis* s.l. (Oxelman & Lidén, 1995; Oxelman & al., 1997, 2001; Popp & Oxelman, 2004, 2007; Popp & al., 2005; Petri & Oxelman, 2011; Rautenberg & al., 2012; Frajman & al., 2018). This section has strong support in our SMC tree (Fig. 2A), and the placement of *S. zawadzki* as sister to the rest of the section also received strong support in a species tree analysis by Rautenberg & al. (2012) based on four unlinked loci.

Silene viscosa, which has been placed in *S. sect. Chloranthae* (Rorhb.) Schischk. (Chowdhuri, 1957; Coode & Cullen, 1967; Melzheimer, 1988) or in *S. sect. Viscosae* (Boiss.) C.L.Tang (Tang, 1996), is recovered as a member of this section in all trees obtained here.

Unplaced taxa in *Silene* subg. *Behenantha*. — *Silene akinfijewi* Schmalh., *S. auriculata* Sm., *S. elisabethae* Jan, *S. multinervia* S.Watson, *S. nivea* (Nutt.) Muhl. ex DC., *S. remotiflora* Vis., *S. samia* Melzh. & Christod., and *S. sordida* Hub.-Mor. & Reese.

3. *Silene* subg. *Silene*

Distribution. – Eurasia, N Africa, southern Africa, North and South America and the Hawaiian islands.

Notes on phylogeny and circumscription. – This subgenus is strongly supported as a monophyletic group in the SMC tree (Fig. 2B,C) and in several previously published phylogenies based on multiple unlinked loci (e.g., Popp & Oxelman, 2004; Eggens & al., 2007; Rautenberg & al., 2012; Naciri & al., 2017; Eggens & al., in prep.). In contrast to *S. subg. Behenantha*, this subgenus is phylogenetically well-resolved basally and shows an extensive recent radiation, especially in *S. sect. Siphonomorpha* s.l. (Đurović & al., 2017; Naciri & al., 2017).

Some taxa (e.g., *S. ampullata* Boiss., *S. pungens* Boiss., *S. pygmaea* Adams) that were classified in *S. subg. Behenantha* by Rohrbach (1869) belong to *S. subg. Silene* according to our phylogenetic results. In our proposed classification, the subgenus comprises 11, mostly widely circumscribed sections, and *S. subcretacea* and *S. falcata* Sm. are left unplaced as to section membership.

3.1. *Silene* sect. *Silene*

Diagnosis. – Annuals or perennials; inflorescence monochasial, sometimes dichasial; petal claws often not or rarely (*S. sect. Fruticosae* (Willk.) Chowdhuri sensu Greuter) auriculate; seeds often excavate or flat with testa cells usually long and narrow. Ploidy level: diploid.

Distribution. – About 93 species (as circumscribed here); Europe, Asia and Africa from the Mediterranean to Pakistan, and some species extending to southern Africa.

Species phylogenetically analyzed (28). – *S. aellenii* Sennen, *S. aethiopica* Burm.f., *S. apetala* Willd., *S. arabica* Boiss., *S. arenarioides* Desf., *S. argillosa* Munby, *S. atlantica* Coss. & Durieu, *S. ayachica* Humbert, *S. bellidifolia* Jacq., *S. bergiana* Lindm., *S. burchellii* Otth, *S. ciliata* Pourr., *S. cisplatensis* Cambess., *S. colorata* Poir., *S. corrugata* Ball, *S. damascena* Boiss. & Gaill., *S. disticha* Willd., *S. diversifolia* Otth, *S. fuscata* Link ex Brot., *S. gallica* L., *S. ghiarensis* Batt., *S. imbricata* Desf., *S. niceensis* All., *S. pseudoatocion* Desf., *S. succulenta* Forssk., *S. turbinata* Guss., *S. villosa* Forssk., *S. volubilitana* Braun-Blanq. & Maire.

Notes on phylogeny and circumscription. – The inclusiveness of this species-rich clade is strongly supported by our analyses. The circumscription of this section is extended here to encompass species previously included in the following eight sections: *S. sect. Atocion*, *S. sect. Dipterospermae* (Rohrb.) Chowdhuri, *S. sect. Fruticosae*, *S. sect. Nicaeenses* (Rohrb.) Talavera, *S. sect. Rubellae* (Batt.) Oxelman & Greuter, *S. sect. Scorpioides* (Rohrb.) Chowdhuri, *S. sect. Silene*, and *S. sect. Succulentae*, among which *S. sect. Fruticosae* and *S. sect. Succulentae* consist of perennial species (Chowdhuri, 1957; Greuter, 1995), whereas the others include annual species. *Silene ciliata*, classified in *S. sect. Fruticosae* by Chowdhuri (1957) and designated as its type by Greuter (1995), is sister to the rest of the clade with strong support in all trees, in accordance with previous molecular phylogenetic studies (e.g., Oxelman & Lidén, 1995; Greenberg & Donoghue, 2011) (see Fig. 2B). Most likely it is closely related to two morphologically very similar perennial species from the Iberian peninsula, *S. borderei* Jord. and *S. legionensis* Lag. (Talavera, 1990). However, other perennial species previously assigned to *S. sect. Fruticosae* are nested in the sister clade to *S. ciliata* (including, for example, *S. ayachica*, *S. atlantica* and *S. burchellii* in Fig 2B; Mesbah & al., in prep.).

Silene cisplatensis (accession JX560218), a South American taxon very similar to the western Mediterranean *S. micropetala* Lag. (Rohrbach, 1869), is sister to *S. ciliata* in our phylogeny (suppl. Fig. S2). The often cited synonymy with *S. pendula* (e.g., Zuloaga & Morrone, 1997) is certainly erroneous. The position away from other similar annual Mediterranean species is unexpected and needs further study.

Silene gallica, which is the correct name for the type of the genus *Silene* (*S. anglica* L., nom. rej.), is nested in the clade including all members of *S. sect. Silene*. The relationships among the taxa of the clade are fairly unresolved in the SMC tree (Fig. 2B). It seems also that some of the previously recognized sections of this clade (e.g., *S. sect. Rubellae* and *S. sect. Scorpioides*) are not monophyletic. The SE Mediterranean species *S. succulenta* is the closest relative of the N African endemic *S. arenarioides* in both of the gene trees (suppl. Figs. S2, S3) and SMC tree (Fig. 2B), but not to *S. sect. Spergulifoliae* (Boiss.) Schischk. as suggested by Greuter (1995).

Silene villosa is also placed in this section, contrary to Greuter (1995), who tentatively classified this species in *S. sect. Psammophilae*.

3.2. *Silene sect. Petrocoma* (Rupr.) F.Jafari, Oxelman & Rabeler

Diagnosis. – Perennial, procumbent plant; inflorescence solitary or few-flowered cyme; calyx pubescent, tubular in flower; petal limbs white and bifid. Ploidy level: diploid.

Distribution. – One species; Caucasus (Dagestan).

Species phylogenetically analyzed (1). – *S. hoefftiana* Fisch. ex C.A.Mey.

Notes on phylogeny and circumscription. – The uncertain phylogenetic position of this monotypic section was discussed above. The Caucasian *S. hoefftiana* was placed in *S. sect. Rupifraga* by Rohrbach (1869), Williams (1896), as well as Pax & Hoffmann (1934), or was treated as a separate genus, *Petrocoma* Rupr. (Ruprecht, 1869; Schischkin, 1936); neither placement has been supported by previous molecular phylogenetic studies (Frajman & al., 2009b). It is weakly supported as sister to *S. sect. Lasiocalycinae* and the rest of *S. sect. Auriculatae* in its broad sense (Fig. 2B; see also under “Discussion”). Unilocular capsules and seed characteristics (surface shining and ridged near the hilum) led Ruprecht (1869) to regard this taxon as a separate genus.

3.3. *Silene sect. Lasiocalycinae* (Boiss.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 246. 1957.

Diagnosis. – Annuals; calyx covered by coarse, thick-based (bulbous) hairs on prominent veins, narrowly cylindrical or fusiform in flower, clavate in fruit; petal limbs pink or white, entire to ± bifid. Ploidy level: diploid.

Distribution. – About 10 species; SE Europe and W Asia.

Species phylogenetically analyzed (4). – *S. crassipes* Fenzl, *S. gallinyi* Heuff. ex Rehb., *S. linicola* C.C.Gmel., *S. papillosa* Boiss.

Notes on phylogeny and circumscription. – Although Greuter (1995) included *S. crassipes* (and also *S. remotiflora*) in *S. sect. Lasiocalycinae*, he discussed its possible affinity to *S. sect. Silene* due to the excavate seeds. The phylogenetic analyses presented here reveal that the annual species assigned to *S. sect. Lasiocalycinae* (sensu Greuter, 1995, excluding *S. remotiflora*) form a sister clade to *S. sect. Auriculatae* s.l., and are distantly related to *S. sect. Silene* based on the SMC tree (Fig. 2B) and ITS phylogeny (Fig. 3, suppl. Fig. S2) and previous studies (Oxelmann & al., 1995; Sloan & al., 2009; Greenberg & Donoghue, 2011).

Silene sect. Lasiocalycinae is represented by *S. crassipes* and *S. gallinyi* in the SMC tree (Fig. 2B) and also includes *S. linicola* and *S. papillosa* in the ITS tree (suppl. Fig. S2). The strong support (Figs. 2B, 3, suppl. Fig. S2) for this group of annuals as sister to the perennials assigned previously to several different sections (see under *S. sect. Auriculatae* s.l.) by previous authors (e.g., Chowdhuri, 1957; Coode & Cullen, 1967; Melzheimer, 1988; Chater & al., 1993) substantiate recognizing these annuals as a monophyletic group.

3.4. *Silene sect. Auriculatae* (Boiss.) Schischk. in Komarov, Fl. URSS 6: 656. 1936.

Diagnosis. – Perennials, often gynomonoecious or gynodioecious; inflorescence cymose; leaves sometimes fasciculate in sterile shoots, linear and oblong, sometimes rigid; calyx pubescent or glandular pubescent, cylindrical or campanulate in flower; petals white, yellow, to pink, claws auriculate or non-auriculate; seeds reniform. Ploidy level: diploid, tetraploid or hexaploid.

Distribution. – As circumscribed here, 130 species; W Asia, sometimes in SE and SW Europe and rarely in N Africa.

Species phylogenetically analyzed (47). – *S. albescens* Boiss., *S. amoena* L., *S. ampullata* Boiss., *S. araratica* Schischk., *S. aucheriana* Boiss., *S. boryi* Boiss., *S. brahuica* Boiss., *S. breviauriculata* Ghaz., *S. brevistaminea* Gilli, *S. cappadocica* Boiss. & Heldr., *S. caryophylloides* Oth., *S. cephalantha* Boiss., *S. commelinifolia* Boiss., *S. crispans* Litv., *S. daenensis* Melzh., *S. demawendica* Bornm., *S. elymaitica* Bornm., *S. eremicana* Stapf, *S. eriocalycina* Boiss., *S. erysimifolia* Stapf, *S. ferdowsii* Joharchi, Nejati & F.Ghahrem., *S. gertraudiae* Melzh., *S. gynodioica* Ghaz., *S. indepressa* Schischk., *S. kuhistanica* Ovcz., *S. lucida* Chowdhuri, *S. meyeri* Fenzl ex Boiss. & Buhse, *S. microphylla* Boiss., *S. moorcroftiana* Benth., *S. oligophylla* Melzh., *S. oxelmanii* Gholipour, *S. palinotricha* Fenzl ex Boiss., *S. parjumanensis* Podlech, *S. persepolitana* Melzh., *S. pruinosa* Boiss., *S. pungens* Boiss., *S. pygmaea* Adams., *S. rhynchocarpa* Boiss., *S. schafta* Hohen., *S. sisanica* Boiss. & Buhse, *S. sojakii* Melzh., *S. spergulifolia* (Willd.) M.Bieb., *S. stenobotrys* Boiss. & Hausskn., *S. supina* M.Bieb., *S. syreistschikowii* P.A.Smirn., *S. vallesia* L., *S. virgata* Stapf.

Notes on phylogeny and circumscription. – As circumscribed here, this section is much more inclusive than in previous classifications. Most of the species in this clade have previously been placed in *S. sect. Auriculatae*, characterized by few-flowered dichasia and an auriculate petal claw, or in *S. sect. Spergulifoliae*, which has non-auriculate petal claws, and usually many yellowish nocturnal flowers (Chowdhuri, 1957; Melzheimer, 1988). The phylogenetic resolution within *S. sect. Auriculatae* s.l. is poor, even if there are morphological tendencies that support the recognition of *S. sect. Auriculatae* and *sect. Spergulifoliae* sensu Chowdhuri (1957) and Melzheimer (1988). The picture is complicated by several other taxa, so we refrain from distinguishing subgroups until a more detailed study is performed. This clade has been identified in previous phylogenetic studies (e.g., Oxelman & Lidén, 1995; Eggens & al., 2007; Rautenberg & al., 2012; Petri & al., 2013; Naciri & al., 2017), but here we increase the taxon sampling significantly. The species in this clade are predominantly distributed in W Asia (from Turkey, Caucasus, Iraq, and Iran to Afghanistan), but are also found in SW Europe and W Himalaya.

Silene schafta, widely cultivated as a garden plant, is characterized by perennial habit, cylindrical calyx and non-auriculate petal claws. Chowdhuri (1957) put this species in *S. sect. Cucubaloides* subsect. *Schaftae*, but Melzheimer (1988) elevated its rank to section, thus raising doubt about the affinity to *S. sect. Cucubaloides* (see above). Schischkin (1936) placed this species in *S. sect. Auriculatae*, which is supported by our (Fig. 2B, suppl. Figs. S2, S3) and previous molecular phylogenetic studies (Oxelmann & Lidén, 1995; Eggens & al., 2007).

Silene caryophylloides and *S. pungens* are distributed in Anatolia and identified by perennial habit, rigid to spiny leaves, and an often one-flowered or reduced dichasial inflorescence. Chowdhuri (1957), followed by Coode & Cullen (1967), classified these species in *S. sect. Pinifoliae* Chowdhuri, but Melzheimer (1988) recognized *S. pungens* as a member of *S. sect. Inflatae* (which in our classification is synonymous to *S. sect. Behenantha*). Our phylogenetic trees (Fig. 2B, suppl.

Figs. S2, S3) show that *S. caryophylloides* and *S. pungens* should be transferred to *S. sect. Auriculatae* s.l. as circumscribed here. *Silene ampullata*, previously assigned to *S. sect. Ampullatae* (Boiss.) Chowdhuri or treated as the distinct genus *Schischkiniella* Steenis, characterized by unisexual flowers, filiform leaves and 1–2-seeded capsules, is also included in this widely circumscribed section.

Some species, such as the Ukrainian endemic *S. cretacea* Fisch. ex Spreng. (Martyniuk & al., 2018), with suffruticose and subshrubby habit, previously placed in *S. sect. Spergulifoliae* sensu Chater & al. (1993) (including *S. sect. Suffruticosae* (Rohrb.) Schischk. and *S. sect. Macranthae* (Rohrb.) Chowdhuri), might be part of *S. sect. Siphonomorpha* s.l. (see below) as our ITS phylogeny (suppl. Fig. S2) and previous investigations (Martyniuk & al., 2018) indicate that. *Silene nizvana* Melzh. was originally described as a member of *S. sect. Auriculatae* (Melzheimer, 1988), but the phylogenetic studies presented here place it within *S. sect. Siphonomorpha* s.l. (see below).

Chowdhuri (1957) designated *S. brevicaulis* Boiss. as the type of *S. sect. Auriculatae*. We do not have any sequence data of the species, but its close morphological resemblance to *S. araratica* (Coode & Cullen, 1967) makes us confident in its position here.

Silene sect. Suffruticosae may be a synonym under *S. sect. Spergulifoliae* according to some previous treatments (Chater & al., 1993; Grueter, 1995), but due to unavailability of type material (*S. suffrutescens* M.Bieb.), we cannot confirm this placement.

3.5. *Silene sect. Rigidulae* (Boiss.) Schischk. in Komarov, Fl. URSS 6: 681. 1936.

Diagnosis. – Annuals; basal leaves spatulate; cauline leaves linear to linear-lanceolate, stem internodes viscous; peduncles long, and flowers nocturnal, or rarely, diurnal; calyx glabrous, cylindrical in flower, clavate in fruit. Ploidy level: diploid.

Distribution. – About 10 species; mainly SE Europe.

Species phylogenetically analyzed (7). – *S. corinthiaca* Boiss. & Heldr., *S. cretica* L., *S. echinosperma* Boiss. & Heldr., *S. echinospermoides* Hub.-Mor., *S. pinetorum* Boiss. & Heldr., *S. reinwardtii* Roth, *S. ungeri* Fenzl.

Notes on phylogeny and circumscription. – This section consists of a group of mainly Greek and E Mediterranean species, viz. *S. corinthiaca* (= *S. rigidula* Sm.), *S. echinosperma* and *S. pinetorum* (suppl. Fig. S3). The NE Mediterranean species *S. echinospermoides* and *S. reinwardtii* (suppl. Figs. S2, S3) form a sister clade to the Greek group, which also includes *S. cretica* and *S. ungeri*, previously (Grueter, 1995) placed in *S. sect. Behenantha* (Fig. 2C, suppl. Fig. S3). The SMC tree (Fig. 2C) recovers these species as monophyletic, which was also shown in a previous study based on ITS, *rps16* and the nuclear *RPB2* gene (Eggen & al., 2007).

Silene sect. Rigidulae is circumscribed narrowly here, compared to previous accounts (Chowdhuri, 1957; Maire, 1963; Coode & Cullen, 1967; Chater & al., 1993), which included many other, superficially similar, annual species from the Mediterranean and the Middle East characterized by narrow cauline leaves, more or less viscous glabrous internodes, dichasial inflorescences, a glabrous calyx, and usually nocturnal flowers with white, deeply dissected petal limbs (Maire, 1963; Coode & Cullen, 1967; Chater & al., 1993). Our results agree with Eggen (2006) indicating non-monophyly and splitting of this group of species into five distinct robust clades, which are named here as representing four different sections, i.e., *Muscipula*, *Portenses*, *Rigidulae* s.str., *Sclerocalycinae* (Boiss.) Schischk. and one informal group (*S. arenosa* group). Grueter (1995) was correct in expressing some hesitation about classification of *S. cretica* and *S. ungeri* in *S. sect. Behenantha*, and it is clear that these two species belong here, despite their entire to emarginate, deep pink, and diurnal petal limbs.

The selection of *S. picta* Pers., nom. illeg. (non Desf.), as type of the section by Chowdhuri (1957: 245) has no standing per ICN Art. 10.8 (Turland & al., 2018).

3.6. *Silene sect. Sclerocalycinae* (Boiss.) Schischk. in Komarov, Fl. URSS 6: 636. 1936.

Diagnosis. – Annuals or perennials; calyx coriaceous and glabrous, cylindrical, tubular or slightly campanulate in flower and clavate or campanulate in fruit, umbilicate at the base. Ploidy level: diploid or tetraploid.

Distribution. – About 71 species; mainly W Asia to SE Europe.

Species phylogenetically analyzed (26). – *S. armena* Boiss., *S. baldshuanica* B.Fedtsch., *S. brevicalyx* Hartvig & Strid, *S. bupleuroides* L., *S. cariensis* Boiss., *S. chlorifolia* Sm., *S. claviformis* Litv., *S. danaensis* Danin, *S. dianthoides* Pers., *S. idaea* Hausskn., *S. laxa* Boiss. & Kotschy, *S. longipetala* Vent., *S. lycanica* Chowdhuri, *S. marschallii* C.A.Mey.,

S. morganae Freyn, *S. olympica* Boiss., *S. peduncularis* Boiss., *S. pharnaceifolia* Fenzl, *S. phrygia* Boiss., *S. propinqua* Schischk., *S. sclerophylla* Chowdhuri, *S. shanbashakensis* Rech.f., *S. swertifolia* Boiss., *S. tunicoides* Boiss., *S. urvillei* Schott ex d'Urv., *S. vittata* Stapf.

Notes on phylogeny and circumscription. – The petals often have a thick and “creamy” appearance. *Silene* sect. *Sclerocalycinae* s.l. as circumscribed here includes most species traditionally (Chowdhuri, 1957; Greuter, 1995) assigned to *S. sect. Lasiostemones* (Boiss.) Schischk. and *S. sect. Sclerocalycinae*, together with the annuals *S. cariensis* and *S. vittata*, which formed the sister clade to other members of *S. sect. Sclerocalycinae* in previous analyses (Eggens, 2006; Eggens & al., 2007; Sloan & al., 2009) and all trees presented here (Fig. 2C, suppl. Figs. S2, S3). Coode & Cullen (1967) placed *S. cariensis* and *S. vittata* (erroneously under synonymy of *S. rigidula*, see Eggens, 2006) in two different sections, *S. sect. Behenantha* and *S. sect. Rigidulae*, a classification that is not supported by our phylogenetic results.

Silene baldshuanica, *S. claviformis* and *S. propinqua*, all previously placed in *S. sect. Lasiostemones* (Melzheimer, 1988), form a monophyletic group in the SMC and gene trees (Figs. 2C, suppl. Figs. S2, S3). However, *S. longipetala*, the type of the section (Chowdhuri, 1957), forms a separate group with *S. dianthoides* and *S. marschallii* in the SMC tree, thus indicating no support for monophyly of *S. sect. Lasiostemones*. As the section name *Sclerocalycinae* (with *S. bupleuroides* as type) is of equal priority with *S. sect. Lasiostemones*, we have accepted the former as the sectional name for the whole clade, since *S. sect. Lasiostemones* as traditionally circumscribed is polyphyletic, albeit with weak support, according to our phylogenetic results.

The accessions of *S. bupleuroides* are divided into two subclades, one eastern (Iran) associated with *S. peduncularis* (suppl. Fig. S3) and one western (Turkey, Greece, Bulgaria) with *S. idaea* in the plastid phylogeny (suppl. Fig. S3), while these accessions are scattered in a subclade including *S. armena* and *S. idaea* in the ITS tree (suppl. Fig. S2), reflecting the taxonomic complexity of this group of species and possibly the presence of some cryptic species among them, which need to be investigated both morphologically and genetically.

Our trees confirm Greuter’s (1995) view on assigning *S. lycaonica* to *S. sect. Sclerocalycinae* rather than *S. sect. Coronatae* (included in *S. sect. Siphonomorpha* s.l., see below) as suggested by Chowdhuri (1957). *Silene brevicalyx* and *S. tunicoides* of *S. sect. Tunicoides* (Boiss.) Chowdhuri (Coode & Cullen, 1967; Greuter, 1995) also belong here (Fig. 2B).

Silene urvillei was placed in *S. sect. Macranthae* or *S. sect. Saxifragoides* Willk. by Chowdhuri (1957) and Greuter (1995), respectively. A recent molecular phylogenetic study places this species in a clade matching with our definition of *S. sect. Sclerocalycinae* s.l. (Đurović & al., 2017).

As earlier shown by Naciri & al. (2017), the accessions of *S. phrygia* (*S. sect. Paniculatae* (Willk.) Chowdhuri) and *S. pharnaceifolia* (*S. sect. Caespitosae* Chowdhuri) are also nested within *S. sect. Sclerocalycinae* s.l. (suppl. Fig. S2).

Silene odoratissima Bunge, the type of *S. sect. Laciniatae* (Boiss.) C.L.Tang, has been included either in *S. sect. Sclerocalycinae* (Schischkin, 1936) or *S. sect. Paniculatae* (Chowdhuri, 1957; see under synonymy of *S. sect. Siphonomorpha* s.l.). We do not place this section because of unavailability of type material.

3.7. *Silene* sect. *Siphonomorpha* Otth in Candolle, Prodr. 1: 377. 1824.

Diagnosis. – Perennials; inflorescence often thyrsoïdal or 1-2 flowers; calyx tubular or campanulate in flower, clavate or campanulate in fruit; corolla with or without coronal scales, petal limbs entire to deeply bifid, and petal claws auriculate or not. Ploidy level: diploid.

Distribution. – About 150 species (as circumscribed here); Europe, W Asia, Central Asia, and N Africa

Species phylogenetically analyzed (101). – *S. acaulis* (L.) Jacq., *S. andryalifolia* Pomel, *S. antri-jovis* Greuter & Burdet, *S. aristidis* Pomel, *S. auriculifolia* Pomel, *S. barbeyana* Boiss., *S. baschkirorum* Janisch., *S. berthelotiana* Webb ex Christ, *S. borysthenica* (Gruner) Walters, *S. bourgaei* Webb ex Christ, *S. campanula* Pers., *S. cephalenia* Heldr., *S. chamarensis* Turcz., *S. chlorantha* (Willd.) Ehrh., *S. colpophylla* Wrigley, *S. confertiflora* Chowdhuri, *S. congesta* Sm., *S. conglomeratica* Melzh., *S. cretacea* Fisch. ex Spreng., *S. cythnia* (Halácsy) Walters, *S. cyri* Schischk., *S. damboldtiana* Greuter & Melzh., *S. dinarica* Spreng., *S. dirphyia* Greuter & Burdet, *S. esquamata* W.W.Sm., *S. fernandezii* Jeanm., *S. fissipetala* Turcz., *S. flavescens* Waldst. & Kit., *S. frivaldskyana* Hampe, *S. fruticosa* L., *S. galataea* Boiss., *S. gazulensis* A.Galán, J.E.Cortés, Vicente Orell. & Mor.Alonso, *S. gigantea* L., *S. goulimyi* Turrill, *S. gracilicaulis* C.L.Tang, *S. graminifolia* Otth, *S. hayekiana* Hand.-Mazz. & Janch., *S. hicesiae* Brullo & Signor., *S. hifacensis* Rouy, *S. iche-bogdo* Grubov, *S. intramongolica* Lazkov, *S. italica* (L.) Pers., *S. jennisseensis* Willd., *S. koreana* Kom., *S. lagunensis* C.Sm. ex Link, *S. leptoclada* Boiss., *S. linoides* Otth, *S. longicilia* (Brot.) Otth, *S. macrostyla* Maxim., *S. mellifera* Boiss. & Reut.,

S. melzheimeri Greuter, *S. mollissima* (L.) Pers., *S. multicaulis* Guss., *S. multiflora* Pers., *S. nemoralis* Waldst. & Kit., *S. niederi* Heldr., *S. nivalis* (Kit.) Rohrb., *S. nizvana* Melzh., *S. nocteolens* Webb & Berthel., *S. nodulosa* Viv., *S. notarisii* Ces., *S. nutans* L., *S. oenotriae* Brullo, *S. oligantha* Boiss. & Heldr., *S. orphanidis* Boiss., *S. otites* (L.) Wibel, *S. paeoniensis* Bornm., *S. paradoxa* L., *S. parnassica* Boiss. & Spruner, *S. patula* Desf., *S. paucifolia* Ledeb., *S. pogonocalyx* (Svent.) Bramwell, *S. pseudoatocion* Desf., *S. radicata* Boiss. & Heldr., *S. roemerii* Friv., *S. rosulata* Soy.-Will. & Godr., *S. rothmaleri* P.Silva, *S. ruprechtii* Schischk., *S. sabinosae* Pit., *S. saxatilis* Sims, *S. saxifraga* L., *S. schmuckeri* Wettst., *S. schwarzenbergeri* Halácsy, *S. sibirica* (L.) Pers., *S. sieberi* Fenzl, *S. spinescens* Sm., *S. stenophylla* Ledeb., *S. sytnikii* Krytzka, Novosad & Protop., *S. tamaranae* Bramwell, *S. tanakae* Maxim., *S. tatarica* Pers., *S. taygetea* Halácsy ex Vierh., *S. thessalonica* Boiss. & Heldr., *S. tomentosa* Otth, *S. velcevii* Jordanov & Panov, *S. velutina* Pourr. ex Loisel., *S. viridiflora* L., *S. viscariopsis* Bornm., *S. waldsteinii* Griseb., *S. wolgensis* Otth, *S. yemensis* Defflers.

Notes on phylogeny and circumscription. – We refer to Naciri & al. (2017) for a comprehensive account on the circumscription of *S.* sect. *Siphonomorpha* s.l. However, the inclusion of *S.* sect. *Dianthoides* (Chowdhuri) Lazkov suggested by Naciri & al. (2017), which was probably based on a misidentified sample (GenBank accession KJ918493), determined as *S. dianthoides* by Mikhaylova & al. (2016), is not confirmed according to our analyses. In the previous published phylogenetic tree (Mikhaylova & al., 2016) as well as in ours (suppl. Fig. S2), this accession, which is labelled as *S. dianthoides*, groups with *S. cyri* Schischk. (a member of *S.* sect. *Siphonomorpha* s.l. as circumscribed here), whereas another *S. dianthoides* accession, which matches our own accession of *S. dianthoides* (KJ918494), groups with *S. bupleuroides* in Mikhaylova & al. (2016). Also in the study of Đurović & al. (2017), *S. bupleuroides* and *S. dianthoides* were resolved as sister species. Thus, we conclude that *S.* sect. *Dianthoides* should be included in *S.* sect. *Sclerocalycinae* s.l. (see also above).

Despite the absence of DNA sequence information, we also add *S.* sect. *Capitellatae* (Rohrb.) Schischk. to *S.* sect. *Siphonomorpha* s.l. due to its considerable morphological resemblance to *S. roemerii* Friv. We also include *S. nizvana*, originally placed in *S.* sect. *Auriculatae* by Melzheimer (1988), since it is nested in the *S.* sect. *Siphonomorpha* clade with strong support and shows a close relationship (Fig. 2C) to members of the *S.* sect. *Otites* (Adans.) Otth p.p. (sensu Chowdhuri, 1957) and some E Asian taxa previously classified in the sections *Longitubulosae* C.L.Tang, *Graminifoliae* Chowdhuri, and *Koreanae* Lazkov. Morphologically, *S. nizvana* seems to be isolated. *Silene cretacea* was found in a corresponding position in an ITS tree published by Martyniuk & al. (2018). Both species are calcicolous semishrubs or suffruticose plants, with few-flowered inflorescences, and a calyx cylindrical in flower and clavate in fruit.

Silene ruprechtii and *S. saxatilis*, previously classified in *S.* sect. *Lasiostemones* (Chowdhuri, 1957), also belong here (Fig. 2C, suppl. Figs. S2, S3) (Slancarova & al., 2013; Naciri & al., 2017). Although these two species are placed in a separate clade from other members of *S.* sect. *Graminifoliae* sensu Chowdhuri (Fig. 2C, suppl. Figs. S2, S3), which have been transferred to *S.* sect. *Graminiformes* by Lazkov (1997), our wide definition of *S.* sect. *Siphonomorpha* includes both sections, thus both sections are treated as synonyms here.

Silene sibirica, the only member of *S.* sect. *Holopetalae* Chowdhuri sensu Chowdhuri (1957), for which there was already sequence information (Volodin & Volodina, 2015) shows affinities to the *Otites* group in SMC and ITS trees (Fig. 2C, suppl. Fig. S2). Lazkov (1999) and Lazkov & Sennikov (2016) appear to agree on this based on morphological data.

3.8. *Silene* sect. *Pulvinatae* (Chowdhuri) F.Jafari, Oxelman & Gholipour

Diagnosis. – Perennials; leaves narrowly linear to linear-oblongate; inflorescence few-flowered cymes; calyx widely cylindrical in flower, short conical to clavate in fruit; and petal limbs whitish above and pink or greenish below. Ploidy level: diploid.

Distribution. – Two species; Caucasus (Georgia, Dagestan), Turkey.

Species phylogenetically analyzed (2). – *S. linearifolia* Otth, *S. oreades* Boiss. & Heldr.

Notes on phylogeny and circumscription. – *Silene linearifolia* and *S. oreades*, the two Caucasian and Anatolian endemics, form a strongly supported clade in the SMC and ITS trees (Figs. 2C, 3, suppl. Fig. S2). The study on the *S. saxifraga* alliance (Đurović & al., 2017) included *S. linearifolia* and *S. oreades* in their ITS and *rps16* datasets, but these taxa did not form a clade. Most likely the poor taxon sampling or the lack of informative sites in the chloroplast phylogeny lead to non-monophyly of *S.* sect. *Pulvinatae* (Chowdhuri) F.Jafari, Oxelman & Gholipour as circumscribed here. Among different accessions of *S. oreades*, only KX852487 is placed within *S.* sect. *Auriculatae* in both our *rps16* tree (suppl. Fig. S3) and that presented by Đurović & al. (2017), caused probably due to an error. Unpublished nuclear *RPA2* and *RPB2*

sequences (Oxelman & al., unpub.) also support the relationships found in this study. The specimen of *S. linearifolia* included in our analyses was misidentified as *S. raddeana* Trautv. in Petri & al. (2013) and Slancarova & al. (2013), which, albeit being superficially very similar, probably is better placed in *S. sect. Odontopetalae*. The tree derived from the analyses of a combined dataset of five markers (ITS, *rps16-matK* region and *rps16*, *RPB2*, calcium dependent protein kinase and spermidine synthase genes) (Slancarova & al., 2013) supported *S. oreades* as sister to *S. linearifolia*. *Silene linearifolia* was placed in *S. sect. Auriculatae* by Schischkin (1936), whereas *S. oreades* has been assigned to *S. sect. Macranthae* subsect. *Pulvinatae* Chowdhuri (Chowdhuri, 1957). Coode & Cullen (1967) placed *S. oreades* in the heterogeneous *S. sect. Caespitosae* (see under synonymy of *S. sect. Sclerocalycinae* s.l.). Phytogeographically, these species are disjunct, with *S. linearifolia* being distributed in the Greater Caucasus and *S. oreades* in W Asia. Future studies on unsampled Anatolian and Caucasian species will contribute to understanding of the relationships in this group and will probably add to the number of species belonging to this section.

3.9. *Silene sect. Sclerophyllae* (Chowdhuri) F.Jafari, Oxelman & Rabeler

Diagnosis. – Mostly perennial shrubs and subshrubs or rarely annuals; calyx glabrous to hairy, campanulate to cylindrical in fruit. Ploidy level: diploid.

Distribution. – About eight species; Hawaiian islands and the North and South American continents.

Species phylogenetically analyzed (6). – *S. alexandri* Hillebr., *S. antirrhina* L., *S. hawaiiensis* Sherff, *S. lanceolata* A.Gray, *S. perlmanii* W.L.Wagner, D.R.Herbst & Sohmer, *S. struthioloides* A.Gray.

Notes on phylogeny and circumscription. – Eggens & al. (2007), based on ITS, cpDNA and nuclear *RPB2* sequences, showed that *S. antirrhina*, a weedy annual species widely distributed on the North and South American continents is sister to the perennial *Silene* species endemic to the Hawaiian islands. This is also supported by our SMC tree (Fig. 2B).

Eggens & al. (2007) recognized a more inclusive clade consisting of *S. sect. Sclerophyllae*, and several members of *S. sect. Muscipula* and sect. *Portenses* (as circumscribed here, see below) from the Mediterranean and W Asia. This clade received strong parsimony support based on analyses of concatenated dataset of ITS, *rps16*, and the nuclear low-copy gene *RPB2* (Eggens & al., 2007). Our SMC tree fails to support this clade, thus cautioning the inflated support that sometimes can result from concatenation of alignments with different underlying gene trees (Liu & al., 2009).

The Hawaiian endemics along with two E Asian species were included in *S. sect. Paniculatae* subsect. *Sclerophyllae* Chowdhuri by Chowdhuri (1957). We elevate this subsection to the rank of section, exclude the E Asian species (now in *S. sect. Siphonomorpha* s.l., see Eggens & al., 2007), and add *S. antirrhina* here, which formerly was classified in *S. sect. Behenantha* (Chowdhuri, 1957).

3.10. *Silene sect. Muscipula* (Tzvelev) Oxelman, F.Jafari & Gholipour

Diagnosis. – Annuals or perennials; inflorescence ±dichasial or reduced to 1 or 2 flowers; calyx glabrous, conical or clavate in fruit; petal limbs emarginate to bi- or multifid, coronal scales sometimes united or divided into several lobes (*S. martyi* Emb. & Maire). Ploidy level: diploid.

Distribution. – Seven species; N Africa, SW Europe.

Species phylogenetically analyzed (6). — *S. cuatrecasii* Pau & Font Quer, *S. filipetala* Litard. & Maire, *S. inaperta* L., *S. martyi* Emb. & Maire, *S. muscipula* L., *S. reticulata* Desf.

Notes on phylogeny and circumscription. – Two Moroccan endemics, *S. cuatrecasii* and *S. martyi*, together with *S. inaperta*, *S. muscipula* and the Algerian endemic *S. reticulata*, form a monophyletic group in all trees (Fig. 2B, suppl. Figs. S2, S3).

Members of this section have never been placed in the same section. *Silene cuatrecasii*, *S. inaperta*, *S. martyi* and *S. reticulata* have been classified in *S. sect. Rigidulae* or *S. subsect. Rigidulae* (Boiss.) Gürke (Chowdhuri, 1957; Maire, 1963), *S. muscipula* in *S. sect. Behenantha* (Chowdhuri, 1957; Greuter, 1995) or in *S. sect. Dichasiosilene* subsect. *Leiocalycinae* Boiss. (Maire, 1963).

3.11. *Silene sect. Portenses* F.Jafari & Oxelman

Description. – Plants annual or perennial; stem erect, internodes sometimes viscid, with rosette or fasciculate leaves; inflorescence an asymmetric dichasium with long internodes, pedicellate; cauline leaves linear to lanceolate, glabrous, scabrid at margin; calyx glabrous, cylindrical in flower, clavate in fruit; petal limbs white above, brownish-red below, bifid,

nocturnal; anthophore pubescent; capsule spherical, globose-conical; seeds reniform with or without mamillae on surface. Ploidy level: diploid (Baltisberger & al., 2006).

Distribution. – Two species; N Africa, SW Europe.

Species phylogenetically analyzed (2). – *S. mentagensis* Coss., *S. portensis* L.

Notes on phylogeny and circumscription. – This W Mediterranean clade consists of the annual *S. portensis* and the perennial *S. mentagensis*, a Moroccan endemic (Fig. 2C, suppl. Figs. S2, S3) previously placed in *S. sect. Rigidulae* by Chowdhuri (1957) and in *S. sect. Dichasiosilene* subsect. *Auriculatae* (Boiss.) Gürke by Maire (1963). Except for the life duration, these two taxa are very similar morphologically, which provides another example of plasticity associated with this trait. The position of this section is ambiguous, being sister to the *S. arenosa* group (see below) in the ITS trees (Fig. 3, suppl. Fig. S2) or close to *S. sect. Siphonomorpha* s.l. in the *rps16* tree (Fig. S3).

Silene inaperta and *S. portensis* were treated as the same species by Linnaeus (1753), but are distantly related to each other according to previous and our results (Eggens & al., 2007) (Fig. 2, suppl. Figs. S2, S3).

Unplaced taxa in *Silene* subg. *Silene*. — The *S. arenosa* group, *S. falcata* Sm. and *S. subcretacea* F.N. Williams.

Incertae sedis

Silene* sect. *Atocion Otth in Candolle, Prodr. 1: 383. 1824.

Diagnosis. – Annuals; inflorescence a compound dichasium; calyx clavate or conical in fruit, glandular pilose or puberulent; usually with emarginate petals, which usually have basal appendages; seeds subglobose to reniform. Ploidy level: diploid.

Distribution. – Nine or 10 species (Toprak & al., 2016); E Mediterranean and W Asia.

Species phylogenetically analyzed (5). — *S. aegyptiaca* L.f., *S. assyriaca* Hausskn. & Bornm. ex Lazkov, *S. atocioides* Boiss., *S. delicatula* Boiss., *S. fraudatrix* Meikle.

Notes on phylogeny and circumscription. – This group, which should not be mistaken with the genus *Atocion*, forms a monophyletic and distinct clade in all trees (e.g., Aydin & al., 2014; Toprak & al., 2016) (Figs. 2A, 3, 4, suppl. Figs. S2, S3), although its position with respect to the other subgenera is poorly resolved in the SMC (Fig. 2A) and *rps16* trees (Fig. 4, suppl. Fig. S3). Erixon & Oxelman (2008a) analyzed ca. 25 kb of the plastome and found good support for the group being sister to the rest of *Silene* and *Lychnis*. However, ongoing analyses of about 1000 transcriptomic alignments of unlinked single-copy nuclear genes (Bertrand & al., unpub. data) reveal highly elevated substitution rates across the genomes in this group of *Silene*. Our results, along with other studies (e.g., Sloan & al., 2009), put *S. sect. Atocion* as distinct from the other main lineages recognized here as subgenera. At this point, recognition of the *S. sect. Atocion* clade as a distinct subgenus (the available name is *S. subg. Ocymastrum* Riv. ex Rchb.) may seem warranted, but the very high substitution rates in this group of plants may compromise the phylogenetic results found so far.

The circumscription of, and possible cryptic speciation in, *S. sect. Atocion* have been explored recently (Toprak & al., 2016). The considerable morphological similarity despite the distant phylogenetic relationship between the *S. cryptoneura* group (*S. sect. Cryptoneurae*, see above) and members of *S. sect. Atocion* has been extensively addressed (Erixon & Oxelman, 2008a; Aydin & al., 2014). Our circumscription of this section is identical to the one by Aydin & al. (2014), and Toprak & al. (2016). Chowdhuri (1957) defined this section as including plants with annual habit, mono- or dichasial cyme inflorescence, petal limb entire or emarginate and pink in color, and concave or convex seed. He divided the section into three subsections, and applied the name *Delicatulae* to the subsection including the type (*S. atocion* L. [= *S. aegyptiaca* L.f.]), ignoring the previously described *S. subsect. Atocion* (Adans.) Gürke for this group (Gürke in Richter, 1897–1903). According to previous works (Oxelman & al., 2001; Eggens & al., 2007; Erixon & Oxelman 2008a; Aydin & al., 2014) and our results, *S. sect. Atocion* as circumscribed by Chowdhuri (1957) and Greuter (1995) is polyphyletic, with members of its other two subsections nested in *S. sect. Cryptoneurae*, *S. sect. Sedoides*, and *S. sect. Silene* (Figs. 2A, 3, 4, suppl. Figs. S2, S3).

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