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A new taxonomic backbone for the infrageneric classification of the species-rich genus *Silene* (Caryophyllaceae)

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Abstract The systematization of species in plant taxonomy based on the phylogenetic relationships among them are of utmost importance and also very challenging in large genera. In those, phylogenetic results often may suggest substantially different relationships than previous classifications, and call for large-scale taxonomic revisions. Delimitation of the genus *Silene* has been and is still somewhat controversial, and recent molecular phylogenetic studies have settled several monophyletic groups that differ substantially from previous taxonomies. The infrageneric taxonomy of *Silene* s.str. has not been updated as a whole taking the phylogenetic information into account. In this study, we review previous phylogenetic results based on multiple loci, and conducted comprehensive gene tree analyses based on the nrDNA ITS and cpDNA *rps16* regions for 1586 and 944 samples representing 415 and 397 species, respectively, including *Silene* and its allies, as well as a

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species tree analysis including 262 samples representing 243 species. We sampled representatives from all 44 sections recognized in the most recent global revision of the genus. The results support the recognition of three subgenera, i.e., *S. subg. Behenantha*, *S. subg. Lychnis* and *S. subg. Silene*, which is partly in agreement with previous molecular phylogenetic findings and contradicts all previous traditional classifications. *Silene* sect. *Atocion*, with a few annual species showing a narrow distribution range in the eastern Mediterranean, is treated as *incertae sedis* because of its uncertain phylogenetic position, possibly due to exceptionally high substitution rates. *Silene* subg. *Lychnis*, weakly supported as sister to the other subgenera, splits into three main clades and includes four sections. *Silene* subg. *Behenantha*, which forms a possible sister group in relation to *S. subg. Silene*, is poorly resolved basally and includes a large number of mostly small clades recognized as 18 sections. In *S. subg. Silene*, 11 sections are recognized, among which four are broadly circumscribed: *S. sect. Auriculatae*, *S. sect. Sclerocalycinae*, *S. sect. Silene* and *S. sect. Siphonomorpha*. *Silene* sect. *Acutifoliae* and *S. sect. Portenses* are described here as new taxa, whereas new status or new combinations are proposed for *S. sect. Anotites*, *S. sect. Muscipula*, *S. sect. Petrocoma*, *S. sect. Pulvinatae*, *S. sect. Sclerophyllae* and *S. sect. Uebelinia*. Five new combinations and two new names are proposed for taxa in *Silene* formerly assigned to *Lychnis* and *Uebelinia*. The correct infrageneric nomenclature compatible with the new infrageneric classification system is provided along with synonymy and type citations. Shortcomings of this study, such as the lack of a morphological diagnostic key and sparse sampling of some large sections, are listed and discussed.

Keywords infrageneric classification; nrDNA ITS; *rps16*; Sileneae; systematics; taxonomy

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

INTRODUCTION

Molecular phylogenetic approaches have blown a fresh wind into the concepts behind classification of “big” genera and the limits of their subsidiary categories such as subgenus, section and series warming up discussions about articulation (splitting) versus consolidation (lumping) approaches (Frodin, 2004). Although most botanists in the Linnaean era did not support recognition of genera with more than 100 species to maintain a universal view of the plant kingdom, the number of genera with more than 500 species grew rapidly (Stevens, 2002). This was due to increased exploration of morphological differences as well as intensive field studies. At the same time, the continuity of variation and lack of discrete borders among certain species groups cast controversy about species circumscriptions. In these big genera, subgeneric categories are essential to group the species into smaller, logical (natural) units as handling of such large groups becomes incomprehensible.

Silene L. (Caryophyllaceae) is one of these large genera, comprising around 850 species of annual, biennial and perennial plants, which are widely distributed in temperate regions of the Northern Hemisphere (www.sileneae.info; Hernández-Ledesma & al., 2015). The center of its diversity is in Western Asia and the Mediterranean area, but areas of Central Asia are also highly diverse. *Silene* plants can be hermaphroditic, gynomonoecious, or gynodioecious (Melzheimer, 1988; Desfeux & al., 1996; Taylor & al., 1999) or dioecious (e.g., Rautenberg & al., 2010; Slancarova & al., 2013). *Silene* spp. are primarily found in polar to subtropic climate regions, and they occur altitudinally from alpine zones to sea level, often in relatively dry habitats such as rocky or gravelly places, sandy soils in steppes, deserts, etc. (Fig. 1), with little competition from other plants. The flowers can be pollinated in various ways, for example by moths, bees and hummingbirds (Buide, 2006; Fenster & al., 2006; Reynolds & al., 2009), while autogamy is also common (Aydin & al., 2014a). Polyploidy has been observed in a number of Central Asian, arctic and subarctic taxa (Popp & al., 2005) and the majority of taxa endemic to North and South America (Kruckeberg, 1954, 1960; Bocquet, 1969; Popp & Oxelman, 2007;

Frajman & al., 2018), and a number of species from Western Asia (Sheidai & al., 2008, 2011; Gholipour & Sheidai, 2010a,b).

Linnaeus (1753) described 27 species of *Silene* when formally introducing the genus. According to him, *Silene* is one of the ten genera he characterized by 10 stamens (“Decandria”) and a tricarpellate ovary (“Trigynia”) (Linnaeus, 1754: 193). Since that time, the generic boundaries around *Silene* have been controversial (see, e.g., Greuter, 1995; Oxelman & Lidén, 1995). Oxelman & al. (2001) presented a classification based on phylogenetic hypotheses that recognized eight genera in tribe Sileneae DC., while Greuter (1995) had recognized only *Silene* and *Agrostemma* L., and Tzvelev (2001) counted 23 genera in eastern Europe alone within the tribe.

In Candolle’s monumental work *Prodromus systematis naturalis regni vegetabilis*, Otth (1824) classified 217 species of *Silene* into eight sections based on inflorescence type and calyx features. In *A Flora of North America*, Torrey & Gray (1838–1840) adopted six of Otth’s sections as subgenera in their treatment of *Silene* (for a detailed discussion, see the note under Taxonomic treatment). Endlicher (1840, 1842) treated *Silene* as one of the 12 genera he included in tribe Lychnideae Fenzl. Applying a system heavily influenced by Fenzl (see Greuter, 1995), Endlicher classified *Silene* into seven groups listed as “a–g”: *Behenantha* Otth, *Otites* Otth, *Conoimorpha* Otth, *Stachyomorpha* Otth, *Rupifraga* Otth, *Siphonomorpha* Otth and *Atocion* Otth. This subgeneric concept of *Silene* was expanded in *Supplementum secundum* (Endlicher, 1842) where Endlicher transferred three groups formerly assigned to *Saponaria* L. (Endlicher, 1840) into *Silene*. In Willkomm’s (1854) system, *Silene* was classified into three subgenera (*Physalocalyx* Willk., *Conocalyx* Willk., “*Eusilene*” (Godr.) Willk.) and four sections with several unranked groups. Boissier (1867) classified the oriental *Silene* spp. into two series (ser. *Annuae*, ser. *Perennes*) and 31 “grexes” preceded by the sign “§”, although he clearly noted “non sectiones proposui” (Boissier, 1867: 567). Rohrbach (1869) presented one of the most comprehensive monographs of the genus, with major groupings mainly based on petal aestivation. He divided the genus into two subgenera, *Silene* and *Behen* (Dumort.) Rohrb. with convolute and imbricate aestivations, respectively. *Silene* subg. *Silene* was divided into two unranked groups, *Conosilene* Rohrb. and “*Eusilene*” Rohrb. The latter was further divided into three sections based on inflorescence type, and each section included several series. Williams (1896) revised the genus, mostly following Rohrbach’s infrageneric system. Schischkin (1936) applied a narrow definition to subgroups of *Silene* and classified it into 4 subgenera, 17 sections and 32 series; some of these names validated Boissier’s names, while others were not validly published (Rabeler, 1993). Chowdhuri (1957) presented the most comprehensive and since then widely used infrageneric taxonomy of *Silene*, dividing the genus into 44 sections and 45 subsections, and assigned definite ranks to several unranked groups recognized by Boissier (stated as “§” – see Rabeler, 1993 for a discussion) as sections or subsections. Chowdhuri’s system was followed by most subsequent authors (e.g., Coode & Cullen, 1967; Melzheimer, 1988; Chater & al., 1993; Greuter, 1995; Townsend & al., 2016), but Tzvelev’s (2001) view was a distinct contradiction to this scheme, where eastern European species included by Chowdhuri (1957) in *Silene* were segregated into 14 genera. Greuter’s (1995) system implied some of the findings of the molecular phylogenetic investigations of Oxelman & Lidén (1995). He proposed a broad circumscription of *Silene* and related genera and divided *Silene* into four subgenera: *S.* subg. *Conoimorpha* (Otth) Fenzl ex Endl., *S.* subg. *Lychnis* (L.) Greuter, *S.* subg. *Silene* and *S.* subg. *Viscaria* (DC.) Greuter, assigning to each subgenus from 1 to 34 sections (*S.* subg. *Silene*), but rejected a subsectional division. Several additional sections have been described subsequent to Greuter’s (1995) work (e.g., Oxelman, 1995; Lazkov, 1999; Aydin & al., 2014b). Lazkov (2003) classified the Eurasian taxa into 43 sections and 86 series, although most of the series names were neither effectively (*ICN* Art. 30.9; Turland & al., 2018) nor validly published due to lack of both a Latin description (Art. 39.1) and type designation (Art. 40.1). Some important and widely used infrageneric classification systems of *Silene* and allied genera are summarized in Appendix 1.

One of the most challenging issues in the taxonomy of *Silene* is the complexity caused by a high level of homoplasy in morphological characters. Even at the generic level, the proposed effective characters in traditional keys often show a high degree of homoplasy (Oxelman & al., 2001). The same is true for the characters used in the discrimination of sections. For example, the numbers of styles (3 or 5) and capsule teeth have been widely used in the classification within and around the

genus, but they have turned out to be highly homoplasious (e.g., Oxelman & Lidén, 1995; Petri & Oxelman, 2011). Many transitions reported between annual and perennial habit in the genus reduce the diagnostic value of life time strategy in infrageneric classification. Compound dichasial inflorescences appear to be plesiomorphic in the genus, whereas monochasial and thyrsoid inflorescences have been suggested to represent synapomorphies supporting some of Rohrbach's main infrageneric groupings (Oxelmann & Lidén, 1995). Calyx characters (including the shape, degree of inflation, type of indumentum, and venation pattern) have also been considered as effective diagnostic features in *Silene*. Some proposed genera that exhibit a widely inflated calyx, including *Cucubalus* L., *Melandrium* Röhl. and *Schischkiniella* Steenis, are placed in different branches in reconstructed phylogenetic trees of *Silene*, indicating both their placement in *Silene* and the parallel evolution of a large bladderly calyx. Eggens (2006) showed that the superficial similarity between *S. cariensis* Boiss. and members of *S. sect. Rigidulae* (Boiss.) Schischk. is due to homoplasy, and does not reflect phylogenetic relationship. Furthermore, Rautenberg & al. (2012) showed that species with more than 10 calyx nerves, i.e., 15–60 parallel, prominent and unbranched nerves, do not form a clade, despite the strong similarity between the North American species *S. multinervia* S. Watson and members of the Eurasian *S. sect. Conoimorpha* Otth.

According to molecular phylogenetic studies on *Silene* and allied genera prior to this study: (1) *Lychnis* L. (excluding *Viscaria* Bernh., but including *Uebelinia* Hochst.) is monophyletic but its relationship to core *Silene* is not well resolved (Oxelmann & Lidén, 1995; Oxelman & al., 1997, 2001; Popp & Oxelman, 2004; Popp & al., 2008; Frajman & al., 2009a; Greenberg & Donoghue, 2011); (2) *Silene* s.str. forms a weakly supported clade based on nrDNA ITS and is not supported as monophyletic based on cpDNA sequences (Oxelmann & Lidén, 1995; Oxelman & al., 1997; Popp & Oxelman, 2004; Erixon & Oxelman, 2008a); (3) *Silene* s.str. can be split into two major clades: *S. subg. Behenantha* (Otth) Torr. & A. Gray and *S. subg. Silene* (Popp & Oxelman, 2004; Eggens & al., 2007; Rautenberg & al., 2010, 2012); (4) *S. subg. Behenantha* includes species previously classified in *Cucubalus*, *Gastrolychnis* (Fenzl) Rchb., *Melandrium* and *Pleconax* Raf. (= *S. sect. Conoimorpha*) along with a number of small branches with unresolved relationships (Popp & Oxelman, 2004, 2007; Rautenberg & al., 2010, 2012; Petri & Oxelman, 2011); (5) *S. subg. Silene* includes the following main sections/clades: *S. sect. Auriculatae* (Boiss.) Schischk. (including, e.g., *S. sect. Spergulifoliae* (Boiss.) Schischk., and the genus *Schischkiniella* (Boiss.) Steenis; Eggens & al., 2007), *S. sect. Rigidulae* (Eggens & al., 2007), *S. sect. Silene* (Oxelmann & Lidén, 1995), *S. sect. Sclerocalycinae* (Boiss.) Schischk. (Eggens & al., 2007), *S. sect. Siphonomorpha* Otth s.l. (Naciri & al., 2017), and several unassigned groups including the Hawaiian endemics (Eggens & al., 2007); (6) *S. sect. Atocion* Otth, which is restricted to the Eastern Mediterranean, represents an enigmatic group including species with high sequence substitution rates and unclear relationships at both subgeneric and generic levels (Erixon & Oxelman, 2008a; Toprak & al., 2016); (7) most of the traditionally proposed infrageneric taxa are not supported as monophyletic (Eggens, 2006; Popp & Oxelman, 2007; Rautenberg & al., 2010, 2012; Petri & Oxelman, 2011; Aydin & al., 2014b).

As implied above, there is considerable conflict between the results of phylogenetic studies and the available classification systems in the genus *Silene*. Most of the phylogenetic studies until now focused on small groups of species (either certain geographic regions or sections) and have not included a wide sampling covering all (morphological) lineages proposed in the genus. The objectives of the present study on *Silene* are to: (1) provide a comprehensive phylogenetic framework with adequate sampling of representative species of *Silene* and its relatives, primarily based on nrDNA ITS and cpDNA *rps16*, but also taking previous phylogenetic analyses based on other loci into account; (2) explore all main lineages within the genus; (3) provide a synthetic classification system linking phylogenetically well-supported clades with morphologically diagnosable, or otherwise biologically relevant, units; and (4) present infrageneric nomenclatural information under each section in order to trace the taxonomic background behind the applied names.

MATERIALS AND METHODS

Taxon sampling. — Our phylogenetic reconstruction is based on a comprehensive sampling of *Silene* and allied genera in the tribe Sileneae. With 1586 nrDNA ITS and 944 chloroplast DNA *rps16* sequences, representing all 44 sections recognized by Chowdhuri (1957) and covering the entire geographical range of the genus, we tried to discover all major lineages in the genus. *Agrostemma githago* L. was chosen as outgroup. The sampling covers 1 to 72 accessions of 387 species in the ITS dataset and 361 species in the *rps16* dataset for *Silene*. We also selected 262 representative individuals (243 species of Sileneae) for reconstructing a species tree (Appendix 2). A total of 474 (57 ITS sequences representing 53 species and 417 *rps16* sequences representing 256 species) new sequences were generated for the purpose of this study, and the remaining sequences were obtained from GenBank (www.ncbi.nlm.nih.gov). Voucher and GenBank information of the accessions are presented in Appendix 2 and suppl. Appendix S1.

DNA extraction and amplification. — Two DNA fragments, extensively used to trace the phylogeny of Caryophyllaceae (e.g., Oxelman & Lidén, 1995; Oxelman & al., 1997; Pirani & al., 2014; Sadeghian & al., 2015; Madhani & al., 2018), were selected for comparative sequencing, i.e., the internal transcribed spacer (ITS) region of the nuclear ribosomal cistron (consisting of ITS1, the intervening 5.8S gene, and ITS2) and the intron of the plastid gene *rps16*. DNA was extracted from fresh or herbarium materials using a NucleoSpin Plant DNA extraction kit (Macherey-Nagel, Düren, Germany) according to the manufacturer's protocol. Amplification of the ITS region was performed using one of the primer pairs ITS1 or ITS5 (White & al., 1990; Vargas & al., 1998) and ITS4 (White & al., 1990) or the pair P17/26S-82R (Popp & Oxelman, 2001). In the latter case, P16b (Popp & al., 2005) and ITS4 were used for sequencing. In some difficult cases, ITS2 and ITS3 were used as described by White & al. (1990). For the plastid region (covering the *rps16* intron), we used the primers rpsF and rpsR2R for amplification and rpsF2a and rpsR3R for sequencing (Oxelman & al., 1997; Petri & Oxelman, 2011). Cycle sequencing was done using the BigDye Terminator v.3.1, Cycle Sequencing Kit (Applied Biosystems, Carlsbad, California, U.S.A.). DNA samples were sequenced with a ABI3730 DNA Analyser 48-well capillary sequencer (Applied Biosystems), or performed by MacroGen (Seoul, South Korea).

Sequence alignment. — Sequences were edited using Geneious v.4.8.5 (Biomatters, <http://www.geneious.com>). Sequence alignment was performed in MAFFT v.7 (Katoh & Standley, 2013) at the web service (<http://mafft.cbrc.jp/alignment/server/>). The default setting was applied for all options. The preliminary alignments were then corrected manually.

Phylogenetic analyses. — Bayesian phylogenetic analyses of the alignments (suppl. Appendices S2, S3) were conducted in MrBayes v.3.2.6 (Ronquist & Huelsenbeck, 2003; Ronquist & al., 2012) with nucleotide models as proposed by the Akaike information criterion corrected for small sample sizes (AICc) using PAUP* v.4.0a 162 (Swofford, 2002, 2018). The Jukes Cantor (JC) substitution model was selected as the best substitution model for both the ITS and *rps16* regions. The Bayesian analyses were carried out with 240 million Markov chain Monte Carlo (MCMC) generations for ITS and 40 million generations for the *rps16* dataset. Four separate chains were run, with trees and parameter values saved every 5000th and 2000th generation in two parallel runs, respectively. The runs were stopped when the value of the average standard deviation for split frequencies reached below the critical value of 0.01. We considered these values to represent a good indication of convergence (Ronquist & al., 2011; Whidden & Matsen, 2015). After checking the effective sample size (ESS) sufficiency with Tracer v.1.7 (Rambaut & al., 2018), the first 20% of the sampled trees were discarded as burn-in. The remaining trees were then used to build a 50% majority-rule consensus tree with posterior probability (PP) values. Tree visualization was carried out using FigTree v.1.4.2 (Rambaut, 2014).

Species tree inference. — Species tree analyses were performed with STACEY (Species Tree And Classification Estimation, Yarely) v.1.2.4 (Jones, 2016) as implemented in BEAST v.2.5.0 (Bouckaert & al., 2014, 2018). The birth-death-collapse model (Jones & al., 2015) was used to estimate the Species or Minimal Clusters (SMC) tree representing the species tree for 262 individuals. The input xml files were prepared using the STACEY v.1.2.4 template in BEAUti v.2.5.0.

The input data was composed of two unlinked partitions containing the ITS and *rps16* alignments (suppl. Appendices S4, S5). Separate analyses with the HKY (Hasegawa-Kishino-Yano) and GTR (General time reversible) substitution models were performed, both with rate variation across sites according to a gamma distribution with four rate categories, and a relaxed lognormal clock for both partitions and fixed average clock rate for ITS set to 1. The ploidy level was set to 1 for both partitions. The prior growth rate was set to a lognormal distribution with mean 4.6 and standard deviation 2. The popPriorScale was set to a lognormal with mean -7 and standard deviation 2. The prior for uclMean was set to a log normal distribution with mean 0 and standard deviation 1, otherwise the default priors were applied. The input file was run for 250 million iterations by logging every 25,000th iteration, with four and six replicates for the GTR and HKY analyses, respectively. Convergence and ESS values were considered sufficient when each parameter had an ESS higher than 200 as verified in Tracer v.1.7 (Rambaut & al., 2018). LogCombiner v.2.5.0 (Bouckaert & al., 2014) was used to discard the 1000 first trees of each of the separate runs and then to combine the rest of the trees as an estimate of the posterior probabilities. The obtained trees were finally summarized in TreeAnnotator v.2.5.0 (Bouckaert & al., 2014).

All phylogenetic analyses were conducted using the facilities offered by the CIPRES science gateway (<http://www.phylo.org/>; Miller & al., 2010).

RESULTS

The number of variable sites, informative characters, some other characteristics of each dataset and the corresponding tree statistics for the nrDNA and cpDNA sequence matrices are presented in Table 1. The SMC trees reconstructed by STACEY based on the GTR (Fig. 2) and HKY (suppl. Fig. S1) models were similar to, and generally compatible with, the gene trees (Figs. 3, 4, suppl. Figs. S2, S3). The more robust groups recovered by these analyses are discussed below in detail (see under Discussion).

In the SMC tree (Fig. 2), the genera *Atocion* Adans., *Eudianthe* (Rchb.) Rchb., *Heliosperma* Rchb., *Petrocoptis* A.Braun. ex Endl., and *Viscaria* are all supported as monophyletic. *Atocion* and *Viscaria* are supported as sisters in all trees. The relationships among *Eudianthe*, *Petrocoptis*, *Heliosperma*, and *Viscaria-Atocion* are poorly resolved in the SMC tree, and these relationships differ among trees obtained by various methods and among the markers used (see Frajman & al., 2009a, for a discussion about the relationships among these genera based on several unlinked loci). *Silene* subg. *Lychnis* (L.) Greuter shows a well-supported sister relationship to the rest of *Silene* spp. in the ITS trees (Fig. 3, suppl. Fig. S2). Although the position of *S.* subg. *Lychnis* is unresolved among the Sileneae clades in the SMC tree, it is nested within *Silene* in the *rps16* tree (suppl. Fig. S3), but with poor support. The monophyly of *Silene* including *S.* subg. *Lychnis*, *S.* subg. *Behenantha*, *S.* subg. *Silene* and *S.* sect. *Atocion* is strongly supported by the ITS trees (Fig. 3, suppl. Fig. S2), but the position of *S.* sect. *Atocion* in the SMC and *rps16* trees makes the monophyly of *Silene* s.str. uncertain (Figs. 2, 4, suppl. Fig. S3). With a few exceptions (see next paragraph), most other species of *Silene* group into two major, well-supported clades, hereafter named *S.* subg. *Silene*, and *S.* subg. *Behenantha* in the SMC (Fig. 2) and ITS trees (Fig. 3, suppl. Fig. S2).

Silene cordifolia All. (representing *S.* sect. *Cordifoliae* Chowdhuri) is weakly supported as sister to the rest of *S.* subg. *Behenantha* in the SMC tree (Fig 2A). *Silene* sect. *Cordifoliae* is placed in an unresolved clade including *S.* subg. *Silene* and a group of *S.* subg. *Behenantha* in the *rps16* tree (suppl. Fig. S3), while it is supported as a member of *S.* subg. *Behenantha* in the ITS trees (Fig. 3, suppl. Fig. S2). *Silene hoefftiana* Fisch. ex C.A.Mey. (representing *S.* sect. *Petrocoma* comb. nov., see Taxonomic treatment) belongs to *S.* subg. *Silene* and is sister to *S.* sect. *Lasiocalycinae* (Boiss.) Chowdhuri and *S.* sect. *Auriculatae* in the SMC (Fig. 2B) and *rps16* (Fig. 4, suppl. Fig. S3) trees, while it forms a polytomy with the two main lineages of *Silene*, i.e., *S.* subg. *Behenantha* and *S.* subg. *Silene*, in the ITS trees (Fig. 3, suppl. Fig. S2).

In the SMC tree, *S.* subg. *Lychnis* (Fig. 2A) forms a well-supported clade including *S.* sect. *Agrostemma* (DC.) Greuter, *S.* sect. *Lychnis* and *S.* *lagrangei* (Coss.) Greuter & Burdet. Other representatives of the subgenus, i.e., *S.* sect. *Coccyganthe*

(Rchb.) Greuter and *S. sect. Uebelinia* comb. nov. included in the gene trees, are also nested in this subgenus. *Silene* subg. *Behenantha* (Fig. 2A) comprises the representatives of the following 16 sections (*S. sect. Cucubalus* and *S. sect. Sedoides* Oxelman & Greuter were not included in the SMC tree): *S. sect. Psammophilae* (Talavera) Greuter, *S. sect. Elisanthae* (Fenzl) Ledeb., *S. sect. Melandrium* (Röhl.) Rabeler, *S. sect. Conoimorpha*, *S. sect. Cryptoneurae* Aydin & Oxelman, *S. sect. Cucubaloides* Edgeworth & Hook.f., *S. sect. Cordifoliae*, *S. sect. Erectorefractae* Chowdhuri, *S. sect. Acutifoliae* sect. nov., *S. sect. Anotites* stat. nov., *S. sect. Odontopetalae* Chowdhuri, *S. sect. Fimbriatae* (Boiss.) Bornm., *S. sect. Dichotomae* (Rohrb.) Chowdhuri, *S. sect. Saponarioides* (Boiss.) Schischk., *S. sect. Behenantha* Otth, and *S. sect. Physolychnis* (Benth.) Bocquet s.l. (Popp & Oxelman, 2004), each forming a separate monophyletic group. *Silene akinfijewi* Schmalh., *S. auriculata* Sm., *S. elisabethae* Jan, *S. multinervia*, *S. nivea* (Nutt.) Muhl. ex DC., *S. samia* Melzh. & Christod., and *S. sordida* Hub.-Mor. & Reese are scattered as singletons among these clades. The composition of *S. subg. Behenantha* as depicted here is congruent with the ITS trees (Fig. 3, suppl. Fig. S2). In the *rps16* tree, the members of *S. sect. Cryptoneurae*, *S. sect. Odontopetalae* and *S. sordida* do not form a monophyletic clade with the rest of *S. subg. Behenantha*. *Silene* subg. *Silene* (Fig. 2A) is strongly supported in the ITS trees (Fig. 3, suppl. Fig. S2) excluding *S. hoefftiana*, but moderately supported in the *rps16* trees (Fig. 4, suppl. Fig. S3). This clade includes several well-supported subclades with the following species as placeholders: *S. gallica* L. plus *S. ciliata* Pourr. (representing *S. sect. Silene* s.l.), *S. hoefftiana* (representing *S. sect. Petrocoma*), *S. gallinyi* Heuff. ex Rchb. plus *S. crassipes* Fenzl (representing *S. sect. Lasiocalycinae*), *S. schafta* Hohen. plus *S. ampullata* Boiss. (representing *S. sect. Auriculatae* s.l.), *S. echinospermoides* Hub.-Mor. plus *S. cretica* L. (representing *S. sect. Rigidulae* s.str.), *S. cariensis* plus *S. bupleuroides* L. (representing *S. sect. Sclerocalycinae* (Boiss.) Schischk. s.l.), *S. saxatilis* Sims plus *S. nutans* L. (representing *S. sect. Siphonomorpha* s.l.), *S. oreades* Boiss. & Heldr. plus *S. linearifolia* Otth (representing *S. sect. Pulvinatae* stat. nov., *S. hawaiiensis* Sherff plus *S. antirrhina* L. (representing *S. sect. Sclerophyllae* stat. nov.), *S. cuatrecacasii* Pau & Font Quer plus *S. muscipula* L. (representing *S. sect. Muscipula* comb. nov.), *S. portensis* L. plus *S. mentagensis* Coss. (representing *S. sect. Portenses* sect. nov.), and *S. arenosa* K.Koch plus *S. microsperma* Fenzl (indicated here as the *S. arenosa* group; see Unplaced taxa in *S. subg. Silene*).

DISCUSSION

Our expanded molecular phylogenetic analyses of the genus *Silene* corroborate the previous molecular phylogenetic results and the generic classification system proposed by Oxelman & al. (2013) in tribe Sileneae, with *Silene* as the largest genus (~870 spp., now including *Lychnis* and *Uebelinia*, ca. 20 spp.) plus six smaller genera, i.e., *Agrostemma* (2–3 spp.), *Atocion* (6 spp.), *Eudianthe* (2 spp.), *Heliosperma* (3 spp. in the strict sense according to Reichenbach, 1841 or 18–20 spp. in the wide sense according to Ikonnikov, 1984 and Frajman, 2007), *Petrocoptis* (7 spp.), and *Viscaria* (3 spp.) supported as monophyletic.

Lychnis spp. form a monophyletic clade, but here we include it within *Silene* as a subgenus following Greuter (1995), since its placement could not be fully resolved, neither by our data nor by the previous phylogenies (see below for the references). Greuter's (1995) treatment of *S. subg. Lychnis* included only the two sections occurring in Europe; here we add both Asian and African species formerly assigned to *Lychnis* or *Uebelinia*. *Silene* subg. *Lychnis* is in a separate clade from the rest of *Silene*, i.e., the two main subgeneric lineages (*S. subg. Silene* and *S. subg. Behenantha*) and *S. sect. Atocion* (treated as incertae sedis, see below). Molecular phylogenetic studies based on chloroplast markers tend to show *Lychnis* as nested within *Silene* (Erixon & Oxelman, 2008a; Harbaugh & al., 2010; Greenberg & Donoghue, 2011). The analyses of low-copy nuclear genes (e.g., Popp & Oxelman, 2004; Frajman & al., 2009a) have also not been able to confidently resolve the *Silene/Lychnis* issue. An ongoing analysis of 1000 gene alignments from more than 30 transcriptomes of tribe Sileneae may shed more light to this problem (Bertrand & al., unpub. data), but it may also just reflect an ancient radiation where too

little evidence is available to resolve the apparently short branches.

For the large genus *Silene*, most of the subgeneric classification can be addressed sufficiently based on the sampling of ITS and *rps16* provided here, and it is in most cases also supported by results from other loci, published elsewhere. However, the positions of *S. cordifolia* and *S. hoefftiana* represent two unresolved issues. The SMC tree (Fig. 2A) puts *S. cordifolia* as a poorly supported (PP = 0.75) sister to the rest of *S. subg. Behenantha*. Sloan & al. (2009) used the plastid locus *matK* and obtained a similar result, and data from Oxelman & al. (unpub.) seem to confirm a position of *S. cordifolia*, *S. sordida*, *S. sect. Cryptoneurae*, and *S. sect. Odontopetalae* as separate from the core *S. subg. Behenantha* clade in the plastid phylogeny. The position of *S. hoefftiana* is weakly supported as sister to *S. sect. Auriculatae* in the SMC tree (Fig. 2B), a position, which is in accordance with earlier phylogenetic analyses (Frajman & al., 2009b). However, in both the ITS trees (Fig. 3, suppl. Fig. S2) and in an unpublished nuclear *RPB2* tree (Rautenberg & al., unpub. data), the two *S. hoefftiana* accessions hold an unresolved position relative to subgenera *Behenantha* and *Silene*. While further investigations based on more informative markers would likely clarify the phylogenetic ancestry of these species, based on available data, we tentatively assign *S. cordifolia* to *S. subg. Behenantha* sect. *Cordifoliae* and *S. hoefftiana* to *S. subg. Silene* sect. *Petrocoma*, and emphasize that their phylogenetic positions need further investigation.

A PHYLOGENETIC INFRAGENERIC TAXONOMY OF *SILENE*

The phylogenetic analyses performed here allow us to present a new infrageneric taxonomic system that can be correlated with some morphological features and geographic distributions. With the exception of two sections (*S. sect. Lasiocalycinae*, *S. sect. Auriculatae*), we included samples from the type in our analyses. When phylogenetic information from the type or from obviously closely related species is lacking, we indicate the tentative placement with a “?” preceding the heterotypic synonym. This strategy enables us to present a new infrageneric taxonomy for the genus *Silene* s.str. (including *Lychnis*), which we think will serve users better than the previous systems, and at the same time forms a basis for more detailed systems in the future.

In the taxonomic system presented here, the clade names are largely adopted from available generic, subgeneric and sectional names. The order of infrageneric taxa presented below follows the branching pattern of the SMC (Fig. 2A–C) and ITS trees (Fig. 3, suppl. Fig. S2). The oldest available name has been selected as the clade name, but only if the type of that name is nested in the corresponding clade. Most sections are, however, broadly circumscribed (*sensu lato*), because the morphological and phylogenetic data supporting smaller groups or narrower definitions are often either minor or lacking. The results of future studies will be continuously updated in the Sileneae classification page at the BoxTax database (Oxelman & al., 2013). In the following treatment, we focus on phylogenetic affinities, nomenclatural issues, geographical distribution and diagnostic morphological characters of the clades.

A list of all *Silene* spp. included in the current study is given in suppl. Appendix S6, but for a complete list of all recognized species the readers should check the BoxTax database (Oxelman & al., 2013). Ploidy levels are given in “Diagnosis” and are extracted from Goldblatt & Johnson (1979–), Chater & al. (1993), Popp & Oxelman (2007), Ghahremaninejad & al. (2013), Rice & al. (2015), and Frajman & al. (2018). The approximate number of species belonging to each section is extracted from the BoxTax database (Oxelman & al., 2013). For “Distribution”, we followed the definitions and the geographical system of the International Working Group on Taxonomic Databases for Plant Sciences (TDWG) (Brummitt & al., 2001).

A complete nomenclatural account of the infrageneric taxa compatible with the new system proposed here is presented under each section. In cases where there are already available names, we have retained monotypic sections; otherwise, we do not introduce new sectional names for those. We apply Greuter’s (1995) terminology for morphological characters.

We are correcting seven section names that end with “-oideae” under Art. 32.2 of the *ICN* (Turland & al., 2018) so they

agree in gender with *Silene* (Art. 21.2). We also correct here *Silene* and *Lychnis* typifications per *ICN* (Turland & al., 2018) Art. 10.5, 10.6, Ex. 6, and 10.7 and cited per format suggested by *ICN* Rec. 10A.2.

The seven groups of *Silene* listed as “a–g” in Endlicher (1840, 1842) are considered here as formal subgenera following arguments presented by Greuter (1995). We follow Brizicky (1969) and accept his argument that, based on the type style used for the taxonomic categories listed in the introduction (“Obs.”) of the index to volume 1 (p. 699), the subdivisions of genera in Torrey & Gray (1838–1840; *Silene* treatment in vol. 1, p. 189–194, published in 1838 – fide Stafleu & Cowan, 1986) should be considered as subgenera. Thus, the seven Otth names that appear in Torrey & Gray (1838–1840) have priority over the similar usage in Endlicher (1840, 1842).

We refrain here from providing an identification key to the assigned sections, since some sections in Chowdhuri’s (1957) system (e.g., *Dichotomae*, *Odontopetalae*) need to be investigated further, based on more species and samples that reflect the complete morphological variation reported earlier. The high homoplasy associated with some morphological characters at the sectional level would lead to an impractical key, and more detailed morphological studies are needed to provide accurate keys. In the current investigation, some species could not be assigned to any available section and are only be assigned to subgenera. For these unplaced taxa, which mostly belong to *S.* subg. *Behenantha*, information from additional loci is needed, but it is possible that the poor resolution reflects an ancient radiation that has not left enough information.

TAXONOMIC TREATMENT

Silene L., Sp. Pl.: 416. 1753, nom. cons. – Type (designated by Britton & Brown, Ill. Fl. N. U.S., ed. 2, 2: 62. 1913; affirmed by Green in Sprague, Nom. Prop. Brit. Bot.: 155. 1929): *Silene anglica* L., nom. rej. (= *S. gallica* L., nom. cons.).

Description. – Annual to perennial herbs, rarely subshrubs, often pubescent with various types of unbranched eglandular and glandular hairs, sometimes glabrous. Stems loosely to densely branched from the base, ending in cymose, few- to many-flowered inflorescences. Leaves opposite; stipules absent; petiole absent or short; blade linear to ovate. Bracts and bracteoles often similar in shape. Flowers mostly bisexual, rarely unisexual. Plants hermaphroditic, gynomonocious, gynodioecious or dioecious. Calyx tubular to conical, sometimes inflated, with 10, rarely 15–60, branched or unbranched primary veins; prominent, often thick and sometimes colored. Corolla variously colored; petals clawed, auriculate or exauriculate; limb broadly ovate or rounded to linear, usually bifid, sometimes entire, rarely quadrifid to fimbriate; usually with two coronal scales. Stamens normally 10; petals and stamens borne on an anthophore, anthophore glabrous to puberulent. Ovary with 3 or 5 carpels, borne on a carpophore surrounded by the anthophore. Fruit a capsule, dehiscent by teeth equal or twice the number of styles, rarely indehiscent. Seed reniform or orbicular, smooth or variously sculptured, dorsal surface often with a groove, sometimes winged. Chromosome base number x = usually 12, rarely 10 or 15, $2n = 2x$, $4x$, $6x$, $8x$, $10x$ (Heaslip, 1951; Bari, 1973; Ghazanfar, 1983; Gholipour & Sheidai, 2010a,b; Petri & Oxelman, 2011; Frajman & al., 2018).

Geographic distribution. – Native on all continents (Americas, Europe, Africa, Asia) except Australia and Antarctica.

Species number. – Ca. 870.

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

1.1 *Silene* sect. *Agrostemma* (DC.) Greuter in Taxon 44(4): 556. 1995 \equiv *Coronaria* Guett. in Hist. Acad. Roy. Sci. Mém. Math. Phys. (Paris, 4to) 1750: 229. 1754 \equiv *Lychnis* sect. *Agrostemma* DC. in Lamarck & Candolle, Fl. Franç., ed. 3, 4: 763. 1805 \equiv *L.* subg. *Muscipula* Riv. ex Rchb., Consp. Regn. Veg.: 207. 1828–1829 \equiv *Coronaria* sect.

Pseudagrostemma A.Braun in Flora 26: 368. 1843 ≡ *Lychnis* sect. *Pseudagrostemma* (A.Braun) Godron in Grenier & Godron, Fl. France 1: 224. 1847 ('*Pseudoagrostemma*') ≡ *Silene* sect. *Lychnidiformes* Melzh. in Rechinger, Fl. Iran. 163: 478. 1988, nom. illeg. – Type (designated by Greuter in Taxon 44(4): 556. 1995): *Lychnis coronaria* (L.) Desr. (*Agrostemma coronaria* L., *Coronaria tomentosa* L. ex A.Braun, *Silene coronaria* (L.) Clairv.).

- 1.2 *Silene* sect. *Lychnis* (L.) Greuter in Taxon 44(4): 556. 1995 ≡ *Lychnis* L., Sp. Pl.: 436. 1753, nom. rej. in favor of *Silene* L., ≡ *Lychnis* subg. *Lychnis* [per Reichenbach, Consp. Regn. Veg.: 207. 1828–1829] – Type (designated by Britton & Brown, Ill. Fl. N. U.S., ed. 2, 2: 62. 1913; affirmed by Green in Sprague, Nom. Prop. Brit. Bot.: 156. 1929): *Lychnis chalconica* L. (*Silene chalconica* (L.) E.H.L.Krause).
= *Hedona* Lour., Fl. Cochinch.: 259, 286. 1790 – Type: *Hedona sinensis* Lour. (*Lychnis coronata* Thunb., *Silene banksia* (Meerb.) Mabb., *S. sinensis* (Lour.) H. Ohashi & H. Nakai).
= *Exemix* Raf., Autik. Bot.: 27. 1840 – Type: *Exemix grandiflora* (Jacq.) Raf. (*Lychnis grandiflora* Jacq., *L. coronata* Thunb., *Silene grandiflora* (Jacq.) H. Ohashi & H. Nakai).
= *Lychnis* sect. *Fulgentes* Tzvelev in Novosti Sist. Vyssh. Rast. 33: 96. 2001 – Type: *Silene fulgens* (Fisch.) E.H.L.Krause (*Lychnis fulgens* Fisch.).

- 1.3 *Silene* sect. *Coccyganthe* (Rchb.) Greuter in Taxon 44(4): 556. 1995 ≡ *Lychnis* [unranked] *Coccyganthe* Rchb., Fl. Germ. Excurs.: 825. 1832 ≡ *Coccyganthe* (Rchb.) Rchb., Handb. Nat. Pfl.-Syst.: 298. 1837 ≡ *Lychnis* subg. *Coccyganthe* (Rchb.) A.Braun in Flora 22: 319. 1839 ≡ *Coronaria* sect. *Coccyganthe* (Rchb.) A.Braun in Flora 26: 368. 1843 ≡ *Lychnis* sect. *Coccyganthe* (Rchb.) Godr. in Grenier & Godron, Fl. France 1: 223. 1847 ≡ *Coronaria* subg. *Coccyganthe* (Rchb.) Devyatov & V.N.Tikhom. in Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 97: 122. 1992 – Type: *Lychnis flos-cuculi* L. (*Coccyganthe flos-cuculi* (L.) Fourr., *Silene flos-cuculi* (L.) Clairv.).

- 1.4 *Silene* sect. *Uebelinia* (Hochst.) F.Jafari, Oxelman & Rabeler, **comb. nov.** ≡ *Uebelinia* Hochst. in Flora 24: 664. 1841 ≡ *Lychnis* sect. *Uebelinia* (Hochst.) O.Kuntze in Post & Kuntze, Lex. Gen. Phan.: 341. 1903 – Type: *Uebelinia abyssinica* Hochst. (*Lychnis abyssinica* (Hochst.) Lidén, *Silene abyssinica* (Hochst.) Neumayer).
= *Uebelinia* sect. *Trigynuebelinia* T.C.E.Fr. in Repert. Spec. Nov. Regni Veg. 19: 85. 1923 – Type: *Uebelinia kiwuensis* T.C.E.Fr. (*Lychnis kiwuensis* (T.C.E.Fr.) M.Popp, *Silene kiwuensis*, **comb. nov.**, see under New combinations).

Unplaced taxa in *Silene* subg. *Lychnis*

The North African *Silene lagrangei* is a perennial plant with a dichasial inflorescence, glabrous calyx, tubular in flower and campanulate in fruit. It shows affinity with the Eurasian *S. flos-cuculi* (*S.* sect. *Coccyganthe*) and *S.* sect. *Uebelinia* in the ITS and *rps16* trees (Figs. 3, 4, suppl. Figs. S2, S3). Maire (1963) divided the North African *Lychnis* into two subgenera and three sections, but did not provide any Latin description for his new section, *L.* sect. “*Viscariopsis*”, including *S. lagrangei*, which therefore is not validly published.

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

For the list of synonymy see under 2.17.

- = *Charesia* E.A.Busch in Trudy Bot. Muz. 19: 182. 1926 – Type: *Charesia akinfjevi* (Schmalh.) E.A.Busch (*Silene akinfjevi* Schmalh.).

- 2.1 *Silene* sect. *Psammophilae* (Talavera) Greuter in Taxon 44(4): 571. 1995 ≡ *S.* subsect. *Psammophilae* Talavera in Lagasalia 8: 150. 1979 – Type: *Silene littorea* Brot.

- 2.2 *Silene* sect. *Elisanthe* (Fenzl ex Endl.) Ledeb., Fl. Ross. 1: 314. 1842 ≡ *Saponaria* sect. *Elisanthe* Fenzl ex Endl., Gen. Pl.: 972. 1840 ≡ *Elisanthe* (Fenzl ex Endl.) Rchb., Deut. Bot. Herb.-Buch: 206. 1841 ≡ *Silene* subg. *Elisanthe* (Fenzl ex Endl.) Fenzl in Endlicher, Gen. Pl., suppl. 2: 78. 1842 ≡ *Melandrium* sect. *Elisanthe* (Fenzl ex Endl.) A.Braun in Flora 26: 371. 1843 ≡ *Silene* [unranked] *Melandrifformes* Boiss., Fl. Orient. 1: 568. 1867 ≡ *Melandrium* subg. *Elisanthe* (Fenzl) Schischk. in Komarov, Fl. URSS 6: 704. 1936 ≡ *Silene* sect. *Melandrifformes* (Boiss.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 244. 1957 – Type (designated by Pfeiffer, Nomencl. Bot. 1(2): 1186. 1873): *Silene noctiflora* L. (*Elisanthe noctiflora* (L.) Rupr., *Melandrium noctiflorum* (L.) Fr.).
= *Elisanthe* subg. *Devjatovia* Tzvelev in Novosti Sist. Vyssh. Rast. 33: 99. 2001 ≡ *E.* sect. *Elatae* Devyatov & V.N.Tikhom. in Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 97(3): 123. 1992 – Type: *Elisanthe ovalifolia* (Regel & Schmalh.) Devyatov & V.N.Tikhom. (*Silene ovalifolia* (Regel & Schmalh.) Melzh.).
- 2.3 *Silene* sect. *Melandrium* (Röhl.) Rabeler in Contr. Univ. Michigan Herb. 19: 161. 1993 ≡ *Melandrium* Röhl., Deutschl. Fl., ed. 2, 2: 37, 274. 1812 ≡ *Lychnis* [unranked] *Melandrium* Rchb., Fl. Germ. Excurs.: 824. 1832 (*'Melandryum'*) ≡ *L.* subg. *Melandrium* (Röhl.) A.Braun in Flora 22: 319. 1839 (*'Melandryum'*) ≡ *Saponaria* subg. *Melandrium* (Röhl.) Fenzl ex Endl., Gen. Pl.: 972. 1840 ≡ *Melandrium* sect. *Melandrium* [per A.Braun, Flora 26: 371. 1843] – Type (designated by Pichi-Sermolli in Taxon 3(4): 114. 1954): *Melandrium pratense* Röhl. (*Silene latifolia* Poir.).
- 2.4 *Silene* sect. *Conoimorpha* Otth in Candolle, Prodr. 1: 371. 1824 ≡ *Pleconax* Raf., Autik. Bot.: 24. 1840 ≡ *Silene* subg. *Conoimorpha* (Otth) Fenzl ex Endl., Gen. Pl.: 973. 1840 ≡ *S.* subg. *Conocalyx* Willk., Icon. Descr. Pl. Nov. 1: 73. 1854, nom. illeg. ≡ *S.* [unranked] *Conosilene* Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 1. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 370. 1867 ≡ *Conosilene* (Rohrb.) Fourr. in Ann. Soc. Linn. Lyon, sér. 2, 16: 344. 1868 ≡ *Silene* subg. *Conosilene* (Rohrb.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(1b): 70. 1889 – Type (designated by Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 248. 1957): *Silene conica* L. (= *Conosilene conica* Fourr.).
= *Silene* [unranked] *Ammophilae* Boiss., Fl. Orient. 1: 568. 1867 ≡ *Pleconax* sect. *Ammophilae* (Boiss.) Ikonn. in Novosti Sist. Vyssh. Rast. 14: 77. 1977 – Type: *Silene ammophila* Boiss. & Heldr. (*Pleconax ammophila* (Boiss.) Šourková).
= *Pleconax* sect. *Coniflorae* Ikonn. in Novosti Sist. Vyssh. Rast. 14: 78. 1977 – Type: *Pleconax coniflora* (Nees) Šourková (*Silene coniflora* Nees ex Otth).
= *Pleconax* sect. *Macrodonatae* Ikonn. in Novosti Sist. Vyssh. Rast. 14: 77. 1977 – Type: *Pleconax macrodonta* (Boiss.) Šourková (*Silene macrodonta* Boiss.).
= *Silene* sect. *Lydiae* Greuter in Taxon 44(4): 578. 1995 – Type: *Silene lydia* Boiss.
- 2.5 *Silene* sect. *Cryptoneurae* Aydin & Oxelman in Phytotaxa 178(2): 101. 2014 – Type: *Silene cryptoneura* Stapf.
- 2.6 *Silene* sect. *Sedooides* Oxelman & Greuter in Willdenowia 25: 150. 1995 (*'Sedoideae'*) – Type: *Silene sedooides* Poir.
- 2.7 *Silene* sect. *Cucubalus* (L.) Greuter in Taxon 44(4): 565. 1995 ≡ *Cucubalus* L., Sp. Pl.: 414. 1753 ≡ *Lychnanthos* S.G.Gmel. in Novi Comment. Acad. Sci. Imp. Petrop. 14(1): 525. 1770 ≡ *Scribaea* Borkh. in Rhein. Mag. Erweit. Naturk. 1: 590. 1793 – Type (designated by Pfeiffer, Nomencl. Bot.: 937. 1873): *Cucubalus baccifera* L. (*Silene baccifera* (L.) Roth).
- 2.8 *Silene* sect. *Cucubalooides* Edgeworth & Hook.f. in Hooker, Fl. Brit. India 1: 221. 1875 (*'Cucubaloideae'*) ≡ *S.* subsect. *Sinenses* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 244. 1957 ≡ *Elisanthe* sect. *Cucubalooides* (Edgeworth & Hook.f.) Lazkov, Sem. Gvozd. (Caryophyllac.) Fl. Kyrgyzstana: 115. 2006 (*'Cucubaloideae'*) – Type (designated by

Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 244. 1957): *Silene khasiana* Rohrb.

- 2.9 *Silene* sect. *Cordifoliae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 240. 1957 ≡ *Elisanthe* sect. *Cordifoliae* (Chowdhuri) Lazkov in Bot. Zhurn. (Moscow & Leningrad) 95(10): 1485. 2010 – Type: *Silene cordifolia* All. (*Elisanthe cordifolia* (All.) Lazkov).
- 2.10 *Silene* sect. *Erectorefractae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 247. 1957 ≡ *S.* subsect. *Erectorefractae* (Chowdhuri) Talavera in Lagasalia 8: 145. 1979 [*S.* subsect. *Erectorefractae* (Chowdhuri) Fedor. in Ukrayins'k Bot. Zhurn 54: 179. 1997, isonym] – Type: *Silene boissieri* J.Gay ex Coss. (*S. germana* J.Gay ex Coss.).
- 2.11 *Silene* sect. *Acutifoliae* Oxelman & F.Jafari, **sect. nov.** – Type: *Silene acutifolia* Link ex Rohrb.
Diagnosis. – Perennials; inflorescence dichasial; calyx purplish, tubular or cylindrical in flower, inflated and ovoid in fruit; petal limbs pale to deep pink, emarginate to slightly bifid; capsule subconical or oblong. Ploidy level: diploid.
- 2.12 *Silene* sect. *Anotites* (Greene) Oxelman, F.Jafari & Rabeler, **comb. & stat. nov.** ≡ *Anotites* Greene in Leaf. Bot. Observ. Crit. 1: 97. 1905 – Type (designated by Tzvelev in Novosti Sist. Vyssh. Rast. 33: 97. 2001): *Anotites menziesii* (Hook.) Greene (*Silene menziesii* Hook.).
- 2.13 *Silene* sect. *Odontopetalae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 240. 1957 ≡ *S.* subsect. *Dentatae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 240. 1957 – Type: *Silene odontopetala* Fenzl.
?= *Silene* subsect. *Lychnideae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 240. 1957 – Type: *Silene lychnidea* C.A.Mey.
- 2.14 *Silene* sect. *Fimbriatae* (Boiss.) Bornm. in Bull. Herb. Boissier 7: 114. 1899 ≡ *S.* [unranked] *Fimbriatae* Boiss., Fl. Orient. 1: 574. 1867 ≡ *S.* ser. *Fimbriatae* (Boiss.) Schischk. in Komarov, Fl. URSS 6: 602. 1936 ≡ *Behenantha* sect. *Fimbriatae* (Boiss.) Ikonn. in Novosti Sist. Vyssh. Rast. 12: 199. 1975 ≡ *Oberna* sect. *Fimbriatae* (Boiss.) Ikonn. in Novosti Sist. Vyssh. Rast. 13: 120. 1976 – Type (designated by Ikonnikov in Novosti Sist. Vyssh. Rast. 13: 120. 1976): *Oberna multifida* (Adams) Ikonn. (*Silene simsii* F.Jafari, Rabeler & Oxelman, *Cucubalus multifidus* Adams, *Silene multifida* (Adams) Rohrb., nom. illeg. (non Edgew. 1846), *Silene fimbriata* Sims, nom. superfl. et illeg., *Behenantha multifida* (Adams) Ikonn.).
– “*Cucubalus fimbriatus* Gueldenst.”, Reis. Russland 2: 24. 1791, nom. nud. (Art. 38.1).
- 2.15 *Silene* sect. *Dichotomae* (Rohrb.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 247. 1957 ≡ *Alifiola* Raf., Autik. Bot.: 24. 1840 ≡ *S.* ser. *Dichotomae* Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 1. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 370. 1867 ≡ *S.* subsect. *Dichotomae* (Rohrb.) Gürke in Richter, Pl. Eur. 2: 290. 1899 [*S.* subsect. *Dichotomae* (Rohrb.) Fedor. in Ukrayins'k Bot. Zhurn. 54: 179. 1997, isonym] – Type: *Silene dichotoma* Ehrh.
- 2.16 *Silene* sect. *Saponarioides* (Boiss.) Schischk. in Komarov, Fl. URSS 6: 685. 1936 ('*Saponarioideae*') ≡ *S.* [unranked] *Saponarioides* Boiss., Fl. Orient. 1: 568. 1867 ('*Saponarioideae*') – Type (designated by Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 244. 1957): *Silene nana* Kar. & Kir.
- 2.17 *Silene* sect. *Behenantha* Otth in Candolle, Prodr. 1: 367. 1824 ≡ *S.* subg. *Behenantha* (Otth) Torr. & A.Gray, Fl. N. Amer. 1: 189. 1838 ≡ *S.* [unranked] *Leiocalycinae* Boiss., Fl. Orient. 1: 569. 1867 ≡ *S.* ser. *Leiocalycinae* (Boiss.)

- Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 3. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 369. 1867 ≡ *Behenantha* (Othth) Schur in Verh. Naturf. Vereins Brünn. 15(2): 130. 1877 ≡ *S.* subsect. *Leiocalycinae* (Boiss.) Gürke in Richter, Pl. Eur. 2: 307. 1899 ≡ *S.* subsect. *Muscipulae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 246. 1957, nom. illeg. ≡ *Ebraxis* sect. *Bechenantha* (Othth) Tzvelev in Novosti Sist. Vyssh. Rast. 33: 103. 2001 ('*Behenantha*') – Type (designated by Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 245. 1957): *Silene behen* L.
- = *Oberna* Adans., Fam. Pl. 2: 255. 1763 ≡ *Behen* Moench, Methodus: 709. 1794, nom. illeg. (non Hill 1762) ≡ *Silene* sect. *Behen* Dumort., Fl. Belg.: 107. 1827 ≡ *S.* subg. *Physalocalyx* Willk., Icon. Descr. Pl. Nov. 1: 73. 1854 ≡ *S.* subg. *Behen* (Dumort.) Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 1. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 369. 1867 ≡ *S.* [unranked] *Inflatae* Boiss., Fl. Orient. 1: 573. 1867 ≡ *S.* subg. *Gastrosilene* F.N.Williams in J. Bot. 32: 13. 1894, nom. illeg. ≡ *S.* sect. *Inflatae* (Boiss.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 241. 1957 ≡ *S.* subsect. *Latifoliae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 241. 1957 – Type (designated by Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 241. 1957): *Silene vulgaris* (Moench) Garcke (*Oberna behen* (L.) Ikonn., *Cucubalus behen* L., *Silene inflata* Sm., nom. illeg., *S. cucubalus* Wibel).
- 2.18 *Silene* sect. *Physolychnis* (Benth.) Bocquet in Candollea 22: 6. 1967 ≡ *Lychnis* sect. *Physolychnis* Benth. in Royle, Ill. Bot. Himal. Mts.: 80. 1834 ≡ *L.* subg. *Gastrolychnis* Fenzl ex Endl., Gen. Pl.: 974. 1840 ≡ *Gastrolychnis* (Fenzl ex Endl.) Rchb., Deut. Bot. Herb.-Buch: 206. 1841 ≡ *Wahlbergella* Fr. in Bot. Not. 1843: 143. 1843 ≡ *Melandrium* sect. *Wahlbergella* (Fr.) Boiss., Fl. Orient. 1: 661. 1867 ≡ *M.* sect. *Gastrolychnis* (Fenzl ex Endl.) Rohrb. in Linnaea 36: 197. 1869 ≡ *Physolychnis* (Benth.) Rupr. in Mém. Acad. Imp. Sci. Saint Pétersbourg, Sér. 7, 14(4): 41. 1869 ≡ *Melandrium* subg. *Gastrolychnis* (Fenzl ex Endl.) Schischk. in Komarov, Fl. URSS. 6: 714. 1936 ≡ *Silene* sect. *Gastrolychnis* (Fenzl ex Endl.) Chowdhuri in Notes. Roy. Bot. Gard. Edinburgh 22: 236. 1957, nom. illeg. – Type (designated by Bocquet, Revisio Physolychnidum, Phan. Monogr. 1: 7. 1969): *Silene uralensis* subsp. *apetala* (L.) Bocquet (*S. wahlbergella* Chowdhuri, *Lychnis apetala* L.).
- = *Evactoma* Raf., Autik. Bot.: 23. 1840 – Type: *Evactoma stellata* Raf. (*Silene stellata* (L.) W.T.Aiton).
- = *Silenanthe* (Fenzl ex Endl.) Griseb. & Schrenk in Arch. Naturgesch. 18(1): 300. 1852 ≡ *Saponaria* subg. *Silenanthe* Fenzl ex Endl., Gen. Pl.: 972. 1840 ≡ *Elisanthe* sect. *Silenanthe* (Fenzl ex Endl.) Fedor. in Didukh, Ecofl. Ukraine 3: 31. 2002 – Type: *Silenanthe zawadzki* (Herbich) Griseb. & Schenk (*Silene zawadzki* Herbich).
- ?= *Carpophora* Klotzsch in Klotzsch & Garcke, Bot. Ergebn. Reise Waldemar: 139. 1862 ≡ *Elisanthe* sect. *Carpophora* (Klotzsch) Devyatov & V.N.Trikhom. in Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 97(3): 124. 1992 – Type: *Carpophora hoffmeisteri* Klotzsch (*Silene suaveolens* Kar. & Kir.).
- = *Silene* [unranked] *Viscosae* Boiss., Fl. Orient. 1: 568. 1867 ≡ *S.* sect. *Viscosae* (Boiss.) C.L.Tang in Wu, Fl. Reip. Pop. Sin. 26: 338. 1996 – Type: *Silene viscosa* (L.) Pers.
- = *Silene* sect. *Occidentales* Chowdhuri in Notes. Roy. Bot. Gard. Edinburgh 22: 234. 1957 – Type: *Silene montana* S.Watson, nom. illeg. (non Arrond. 1863) (*S. bernardina* subsp. *maguirei* Bocquet).
- = *Silene* sect. *Quadrilobatae* Chowdhuri in Notes. Roy. Bot. Gard. Edinburgh 22: 243. 1957 – Type: *Silene grayi* S.Watson.
- = *Silene* subsect. *Songaricae* Bocquet in Candollea 22: 2. 1967 ≡ *Gastrolychnis* sect. *Songaricae* (Bocquet) Lazkov, Sem. Gvozd. (Caryophyllac.) Fl. Kyrgyzstana: 120. 2006 – Type: *Silene songarica* (Fisch., C.A.Mey. & Avé-Lall.) Bocquet.
- = *Silene* subsect. *Echinatae* C.L.Tang in Acta Bot. Yunnan. 9: 32: 1987 – Type: *Silene salicifolia* C.L.Tang.
- = *Elisanthe* sect. *Apricae* Devyatov & V.N.Tikhom. in Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 97(3): 124. 1992 ≡ *Ussuria* Tzvelev in Novosti Sist. Vyssh. Rast. 33: 100. 2001, nom. illeg. (non Nevolina 1984) ≡ *Neoussuria* Tzvelev in Novosti Sist. Vyssh. Rast. 34: 299. 2002 – Type: *Elisanthe aprica* (Turcz. ex Fisch. & C.A.Mey.) Peschkova (*Silene aprica* Turcz. ex Fisch. & C.A.Mey., *Neoussuria aprica* (Turcz. ex Fisch. & C.A.Mey.) Tzvelev, *Ussuria aprica* (Turcz. ex Fisch. & C.A.Mey.) Tzvelev).

- = *Lychnis* sect. *Sibiricae* Devyatov & V.N.Tikhom. in Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 97(3): 122. 1992 = *Sofianthe* Tzvelev in Novosti Sist. Vyssh. Rast. 33: 97. 2001 = *Silene* sect. *Sibiricae* (Devyatov & V.N.Tikhom.) Lazkov & Sennikov in Ann. Bot. Fenn. 53: 438. 2016 – Type: *Lychnis sibirica* L. (*Silene linnaeana* V.N.Voroschilov, *S. orientalmongolica* Kozhev., *Sofianthe sibirica* (L.) Tzvelev).
- = *Silene* sect. *Morrisonmontanae* C.L.Tang in Acta Bot. Yunnan. 16(2): 119. 1994 – Type: *Silene morrisonmontana* (Hayata) Ohwi & Ohashi.
- = *Gastrolychnis* subsect. *Pauciflorae* Tzvelev in Bot. Zhurn. (Moscow & Leningrad) 85(11): 100. 2000 – Type: *Gastrolychnis pauciflora* (Ledeb.) Tzvelev (*Silene involucrata* (Cham. & Schltldl.) Bocquet).
- = *Gastrolychnis* subg. *Peschkovia* Tzvelev in Novosti Sist. Vyssh. Rast. 33: 99. 2001 = *Peschkovia* (Tzvelev) Tzvelev in Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 111(6): 37. 2006 – Type: *Peschkovia saxatilis* (Turcz. ex Fisch. & C.A.Mey.) Tzvelev (*Silene tolmachevii* Bocquet, *S. saxatilis* Turcz. ex Fisch. & C.A.Mey., nom.illeg. [non Sims 1803]).
- = *Gastrolychnis* sect. *Kozhanczikovia* Tzvelev in Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 111(6): 38. 2006 – Type: *Gastrolychnis sachalinensis* (F.Schmidt) Tzvelev (*Silene sachalinensis* F.Schmidt).
- = *Sofianthe* sect. *Ajanenses* Tzvelev in Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 111(6): 38. 2006 – Type: *Sofianthe ajanensis* (Regel & Tiling) Tzvelev (*Silene ajanensis* (Regel & Tiling) Vorosch.).
- = *Sofianthe* sect. *Submelandrium* Tzvelev in Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 111(6): 39. 2006 – Type: *Sofianthe brachypetala* (Hornem.) Tzvelev. (*Silene songarica*).

Unplaced taxa in *Silene* subg. *Behenantha*. — *Silene akinfijewi*, *S. auriculata*, *S. elisabethae*, *S. multinervia*, *S. nivea*, *S. remotiflora* Vis., *S. samia*, and *S. sordida* do not group confidently with any of our recognized sections in *S.* subg. *Behenantha* and are left here as incertae sedis, as there are no available section names for them.

Silene samia was placed by Coode & Cullen (1967) in *S.* sect. *Atocion*, but it is nested within *S.* subg. *Behenantha* in all published trees (Oxelman & Lidén, 1995; Oxelman & al., 1997; Erixon & Oxelman, 2008b; Sloan & al., 2009; Rautenberg & al., 2012) as well as those presented here (Figs. 2–4, suppl. Figs. S2, S3). It does not form a supported clade with any other member of the subgenus. Greuter (1995) considered it as incertae sedis within the genus due to aberrant floral characters and lack of any morphological connection to other species of *Silene*. This rare annual species is characterized by basal spatulate leaves and a glandular-pubescent calyx and is distributed in the east Aegean Islands and South-West Anatolia.

Silene sordida was thought to represent a potential homoploid hybrid in an earlier study (Erixon & Oxelman, 2008a). Although its position varies among our gene trees, this hypothesis remains to be tested thoroughly.

The New World tetraploid *S. nivea* does not belong to any section and shows a close relationship to *S.* sect. *Cucubalus* according to our ITS tree (Fig. 3, suppl. Fig. S2). Popp & Oxelman (2007) also found strong support for this relationship from the nuclear *RPA2* and *RPB2* genes. Although there is no support for this relationship in the cpDNA data, *S. nivea* should perhaps be placed in *S.* sect. *Cucubalus*. However, *S. nivea* is easily recognized by its long willow-like leaves and leafy inflorescence, which has some similarities with that of *S. baccifera* (L.) Roth). Awaiting a more detailed study, we keep it as incertae sedis.

Rautenberg & al. (2012) noted a close and well-supported relationship between *S. akinfijewi* and *S. elisabethae* based on a species tree inferred from four unlinked loci. However, most of the information appears to come from the *RPA2* locus. Although the two species have some superficial characteristics in common, we refrain from classifying them together until a more detailed study is conducted.

3. *Silene* subg. *Silene*

- 3.1 *Silene* sect. *Silene* ≡ *Viscago* Zinn, Cat. Pl. Hort. Gott.: 188. 1757, nom. illeg. ≡ *Kaleria* Adans., Fam. Pl. 2: 506. 1763 ≡ *Silene* sect. *Stachyomorpha* Otth in Candolle, Prodr. 1: 371. 1824, nom. illeg. ≡ *S.* subg. *Viscago* (Zinn) Rchb., Consp. Regn. Veg.: 207. 1828–1829 ≡ *S.* [unranked] *Corone* Hoffmanns. ex Rchb., Fl. Germ. Excurs.: 812. 1832 ≡ *S.* sect. *Viscago* (Zinn) W.D.J.Koch, Syn. Fl. Germ. Helv.: 100. 1835 ≡ *S.* subg. *Stachyomorpha* (Otth) Torr. & A.Gray, Fl. N. Amer. 1: 191. 1838 ≡ *Silene* sect. *Racemosae* Willk., Icon. Descr. Pl. Nov. 1: 73. 1854 ≡ *S.* [unranked] *Coelospermae* Willk., Icon. Descr. Pl. Nov. 1: 73. 1854 ≡ *Silene* sect. *Cincinnosilene* Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 1. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 370. 1867 ≡ *S.* [unranked] *Gallicae* Batt. in Battandier & Trabut, Fl. Algérie, Dicot.: 131. 1888 ≡ *S.* subsect. *Cincinnosilene* (Rohrb.) Rouy & Foucaud, Fl. France 3: 111. 1896 – Type (designated by Britton & Brown, Ill. fl. n. US., ed. 2, 2: 62. 1913; affirmed by Green, Nom. Prop. Brit. Bot.: 155. 1929): *S. anglica* L. (*S. gallica* L., nom. cons.).
- = *Corone* (Hoffmanns. ex Rchb.) Hoffmanns. ex Steud., Nomencl. Bot., ed. 2. 1: 422. 1840 – **Type (designated here):** *Corone gallica* (L.) Hoffmanns. ex Rchb. (*S. gallica* L.).
- = *Silene* [unranked] *Fasiculatae* Willk., Icon. Descr. Pl. Nov. 1: 74. 1854 ≡ *S.* ser. *Nicaeenses* Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 3. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 375. 1867 ≡ *S.* subsect. *Nicaeenses* (Rohrb.) Gürke in Richter, Pl. Eur. 2: 304. 1899 ≡ *S.* sect. *Nicaeenses* (Rohrb.) Talavera in Anales Jard. Bot. Madrid 45: 361. 1988 – Type (designated by Talavera in Anales Jard. Bot. Madrid 45: 304. 1988): *Silene nicaeensis* All.
- = *Silene* [unranked] *Fruticulosae* Willk., Icon. Descr. Pl. Nov. 1: 73. 1854 ≡ *S.* ser. *Fruticulosae* (Willk.) Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 2. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 370. 1867 ≡ *S.* subsect. *Fruticulosae* (Willk.) Gürke in Richter, Pl. Eur. 2: 298. 1899 ≡ *S.* sect. *Fruticulosae* (Willk.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 246. 1957 – Type (designated by Greuter in Taxon 44(4): 573. 1995): *Silene ciliata* Pourr.
- = *Silene* [unranked] *Pterospermae* Willk., Icon. Descr. Pl. Nov. 1: 74. 1854 ≡ *S.* [unranked] *Bipartitae* Boiss., Fl. Orient. 1: 591. 1867 ≡ *S.* ser. *Bipartitae* (Boiss.) Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 1. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 370. 1867 – Type: *Silene bipartita* Desf. (*S. colorata* Poir.).
- = *Oncerum* Dulac, Fl. Hautes-Pyrénées: 225. 1867 – **Type (designated here):** *Oncerum gallicum* (L.) Dulac (*S. gallica* L.).
- = *Silene* [unranked] *Unilaterales* Boiss., Fl. Orient. 1: 574. 1867 – Type (designated by Greuter in Taxon 44(4): 573. 1995): *Silene graefferi* Guss. (*S. ciliata* subsp. *graefferi* (Guss.) Nyman).
- = *Silene* [unranked] *Succulentae* Boiss., Fl. Orient. 1: 576. 1867 ≡ *S.* sect. *Succulentae* (Boiss.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 244. 1957 – Type: *Silene succulenta* Forssk.
- = *Silene* [unranked] *Dipterospermae* Rohrb., Monogr. Silene: 69. 1869 ≡ *S.* subsect. *Dipterospermae* (Rohrb.) Gürke in Richter, Pl. Eur. 2: 296. 1899 ≡ *S.* sect. *Dipterospermae* (Rohrb.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 248. 1957 – Type (designated by Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 248. 1957): *Silene colorata* Poir.
- ?= *Silene* ser. *Scorpioides* Rohrb., Monogr. Silene: 67. 1869 (*‘Scorpioideae’*) ≡ *S.* subsect. *Scorpioides* (Rohrb.) Gürke in Richter, Pl. Eur. 2: 291. 1899 ≡ *S.* sect. *Scorpioides* (Rohrb.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 247. 1957 (*‘Scorpioideae’*) ≡ *S.* subsect. *Pubicalycinae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 247. 1957, nom. illeg. – Type (designated by Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 248. 1957): *Silene hirsuta* Lag., nom. illeg. (non Poir. 1789) (*S. scabriflora* Brot.).
- = *Silene* [unranked] *Divaricatae* Batt. in Battandier & Trabut, Fl. Algérie, Dicot.: 138. 1888 ≡ *S.* subsect. *Divaricatae* (Batt.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 245. 1957 – Type: *Silene divaricata* Clemente ex Lag., nom. illeg. (non Sm. 1809) (*S. aellenii* Sennen).
- = *Silene* [unranked] *Nocturnae* Batt. in Battandier & Trabut, Fl. Algérie, Dicot.: 132. 1888 ≡ *S.* subsect. *Nocturnae* (Batt.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 247. 1957 – Type: *Silene nocturna* L.
- = *Silene* [unranked] *Rubellae* Batt. in Battandier & Trabut, Fl. Algérie, Dicot.: 137. 1888 ≡ *S.* subsect. *Rubellae* (Batt.)

Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 245. 1957 ≡ *S.* sect. *Rubellae* (Batt.) Oxelman & Greuter in Taxon 44(4): 575. 1995 – Type: *Silene rubella* L., nom. utique rej. (*S. bergiana* Lindm.).

- 3.2 *Silene* sect. ***Petrocoma*** (Rupr.) F.Jafari, Oxelman & Rabeler, **comb. nov.** ≡ *Petrocoma* Rupr. in Mém. Acad. Imp. Sci. Saint Pétersbourg, Ser. 7, 15(2) [Fl. Caucasi]: 200. 1869 ≡ *Elisanthe* sect. *Petrocoma* (Rupr.) Lazkov in Bot. Zhurn. (Moscow & Leningrad) 95(10): 1485. 2010 – Type: *Silene hoefftiana* Fisch. & C.A.Mey. (*Elisanthe hoefftiana* (Fisch. ex C.A.Mey.) Lazkov, *Petrocoma hoefftiana* (Fisch. ex C.A.Mey.) Rupr.).
- 3.3 *Silene* sect. ***Lasiocalycinae*** (Boiss.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 246. 1957 ≡ *S.* [unranked] *Lasiocalycinae* Boiss., Fl. Orient. 1: 569. 1867 ≡ *S.* ser. *Lasiocalycinae* (Boiss.) Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 4. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 377. 1867 ≡ *S.* subsect. *Lasiocalycinae* (Boiss.) Gürke in Richter, Pl. Eur. 2: 309. 1899 ≡ *S.* subsect. *Squamatae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 246. 1957, nom. illeg. – Type (designated by Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 246. 1957): *Silene squamigera* Boiss.
= *Silene* subsect. *Papillosae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 246. 1957. – Type: *S. papillosa* Boiss.
- 3.4 *Silene* sect. ***Auriculatae*** (Boiss.) Schischk. in Komarov, Fl. URSS 6: 656. 1936 ≡ *S.* [unranked] *Auriculatae* Boiss., Fl. Orient. 1: 572. 1867 ≡ *S.* ser. *Auriculatae* (Boiss.) Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 2. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 373. 1867 ≡ *S.* subsect. *Auriculatae* (Boiss.) Gürke in Richter, Pl. Eur. 2: 298. 1899 ≡ *S.* subsect. *Brevicaules* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 242. 1957, nom. illeg. – Type (designated by Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 242. 1957): *Silene brevicaulis* Boiss.
= *Silene* [unranked] *Ampullatae* Boiss., Fl. Orient. 1: 571. 1867 ≡ *Gastrocalyx* Schischk. in Izv. Kavkazsk. Muz. 12: 200. 1919, nom. illeg. (non Gardner 1838) ≡ *Silene* sect. *Ampullatae* (Boiss.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 238. 1957 ≡ *Schischkiniella* Steenis in Blumea 15: 145. 1967 – Type: *Silene ampullata* Boiss.
= *Silene* [unranked] *Schaftae* Boiss., Fl. Orient. 1: 577. 1867 ≡ *S.* subsect. *Schaftae* (Boiss.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 244. 1957 ≡ *S.* sect. *Schaftae* (Boiss.) Melzh. in Rechinger, Fl. Iran. 163: 466. 1988 – Type: *Silene schafta* Hohen.
= *Silene* [unranked] *Spergulifoliae* Boiss., Fl. Orient. 1: 572. 1867 ≡ *S.* ser. *Spergulifoliae* (Boiss.) Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 5. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 380. 1867 ≡ *S.* subsect. *Spergulifoliae* (Boiss.) Gürke in Richter, Pl. Eur. 2: 314. 1899 ≡ *S.* sect. *Spergulifoliae* (Boiss.) Schischk. in Komarov, Fl. URSS 6: 652. 1936 ≡ *S.* subsect. *Polyphyllae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 238. 1957, nom. illeg. – Type (designated by Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 237. 1957): *Silene spergulifolia* (Willd.) M.Bieb.
=? *Silene* subsect. *Fruticosae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 242. 1957 – Type: *Silene goniocaula* Boiss.
=? *Silene* sect. *Pinifoliae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 241. 1957 – Type: *Silene echinus* Boiss. & Heldr.
= *Silene* subsect. *Pungentes* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 242. 1957 – Type: *Silene pungens* Boiss.
= *Silene* subsect. *Repentes* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 238. 1957 ≡ *S.* sect. *Repentes* (Chowdhuri) Tzvelev in Novosti Sist. Vyssh. Rast. 33: 106. 2001 – Type: *Silene repens* Patr. ex Pers. (*S. amoena* L.).
= *Silene* subsect. *Scapiformes* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 242. 1957 – Type: *Silene rhynhocarpa* Boiss.
= *Silene* subsect. *Supinae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 239. 1957 – Type: *Silene supina* M.Bieb.

- = *Silene* subsect. *Pachyneurae* Devyatov & V.N.Tikhom. in Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 97(3): 123. 1992 – Type: *Silene sisianica* Boiss. & Buhse (*S. pachyneura* Schischk.).
- 3.5 *Silene* sect. ***Rigidulae*** (Boiss.) Schischk. in Komarov, Fl. URSS 6: 681. 1936 ≡ *S.* [unranked] *Rigidulae* Boiss., Fl. Orient. 1: 571. 1867 ≡ *S.* ser. *Rigidulae* (Boiss.) Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 3. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 376. 1867 ≡ *S.* subsect. *Rigidulae* (Boiss.) Gürke in Richter, Pl. Eur. 2: 306. 1899 – Type: *Silene rigidula* Sm., nom. illeg. (non L. 1756) (*S. corinthiaca* Boiss. & Heldr.).
- = *Silene* [unranked] *Sparsiflorae* Willk., Icon. Descr. Pl. Nov. 1: 74. 1854 ≡ *S.* subsect. *Creticae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 245. 1957 – Type (designated by Greuter in Taxon 44(4): 571. 1995): *Silene cretica* L.
- 3.6 *Silene* sect. ***Sclerocalycinae*** (Boiss.) Schischk. in Komarov, Fl. URSS 6: 636. 1936 ≡ *S.* [unranked] *Sclerocalycinae* Boiss., Fl. Orient. 1: 575. 1867 ≡ *S.* ser. *Sclerocalycinae* (Boiss.) Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 4. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 378. 1867 ≡ *S.* subsect. *Sclerocalycinae* (Boiss.) Gürke in Richter, Pl. Eur. 2: 310. 1899 ≡ *S.* subsect. *Longiflorae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 235. 1957, nom. illeg. – Type (designated by Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 235. 1957): *Silene bupleuroides* L.
- = *Silene* [unranked] *Lasiostemones* Boiss., Fl. Orient. 1: 574. 1867 ≡ *S.* ser. *Lasiostemones* (Boiss.) Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 5. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 381. 1867 ≡ *S.* subsect. *Lasiostemones* (Boiss.) Gürke in Richter, Pl. Eur. 2: 315. 1899 ≡ *S.* sect. *Lasiostemones* (Boiss.) Schischk. in Komarov, Fl. URSS 6: 631. 1936 – Type (designated by Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 234. 1957): *Silene longipetala* Vent.
- ?= *Silene* [unranked] *Stenophyllae* Boiss., Fl. Orient. 1: 577. 1867 ≡ *S.* sect. *Caespitosae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 238. 1957 ≡ *S.* subsect. *Stenophyllae* (Boiss.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 239. 1957 – Type: *Silene tenella* C.A.Mey.
- = *Silene* [unranked] *Tunicoides* Boiss., Fl. Orient. 1: 577. 1867 (*'Tunicoideae'*) ≡ *S.* sect. *Tunicoides* (Boiss.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 235. 1957 (*'Tunicoideae'*) – Type: *Silene tunicoides* Boiss.
- = *Silene* subsect. *Chlorifoliae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 235. 1957 – Type: *Silene chlorifolia* Sm.
- = *Silene* subsect. *Dianthifoliae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 243. 1957 – Type: *Silene dianthifolia* J.Gay (*S. armena* Boiss.).
- = *Silene* subsect. *Dianthoides* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 239. 1957 (*'Dianthoidea'*) ≡ *S.* sect. *Dianthoides* (Chowdhuri) Lazkov in Bot. Zhurn (Moscow & Leningrad) 81(8): 103. 1996 (*'Dianthoidea'*) – Type: *Silene dianthoides* Pers.
- ?= *Silene* subsect. *Asiaticae* Devyatov & V.N.Tikhom. in Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 97(3): 122. 1992 – Type: *Silene plurifolia* Schischk.
- ?= *Silene* subsect. *Bucharicae* Devyatov & V.N.Tikhom. in Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 97(3): 123. 1992 – Type: *Silene bucharica* M.Pop.
- 3.7 *Silene* sect. ***Siphonomorpha*** Otth in Candolle, Prodr. 1: 377. 1824 ≡ *S.* subg. *Siphonomorpha* (Otth) Torr. & A. Gray, Fl. N. Amer. 1: 192. 1838 ≡ *S.* sect. *Cymosae* Willk., Icon. Descr. Pl. Nov. 1: 74. 1854, nom. illeg. ≡ *S.* ser. *Nutantes* Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 5. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 381. 1867 ≡ *S.* subsect. *Nutantes* (Rohrb.) Gürke in Richter, Pl. Eur. 2: 315. 1899 – Type (designated by Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 234. 1957): *Silene nutans* L.
- = *Otites* Adans., Fam. Pl. 2: 255. 1763 ≡ *Silene* sect. *Otites* (Adans.) Otth in Candolle, Prodr. 1: 369. 1824 ≡ *S.* subg. *Otites* (Adans.) Rchb., Consp. Regn. Veg.: 207. 1828 ≡ *S.* [unranked] *Verticillatae* Willk., Icon. Descr. Pl. Nov. 1: 74. 1854 ≡

- S. sect. Botryosilene* Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 4. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 377. 1867, nom. illeg. ≡ *S. ser. Otites* (Adans.) Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 4. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 379. 1867 ≡ *S. subsect. Botryosilene* (Rohrb.) Rouy & Foucaud, Fl. France 3: 139. 1896, nom. illeg. ≡ *S. subsect. Otites* (Adans.) Gürke in Richter, Pl. Eur. 2: 312. 1899 – Type (designated by Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 237. 1957): *Silene otites* (L.) Wibel.
- = *Silene sect. Nanosilene* Otth in Candolle, Prodr. 1: 367. 1824 ≡ *S. subg. Nanosilene* (Otth) Torr. & A.Gray, Fl. N. Amer. 1: 189. 1838 ≡ *Xamilenis* Raf., Autik. Bot.: 24. 1840 ≡ *Nanosilene* (Otth) Rchb., Deut. Bot. Herb.-Buch: 206. 1841 ≡ *Silene ser. Nanosilene* (Otth) Rohrb. in App. Alt. Ind. Sem. Hort. Bot. Berol. 1867: 3. 1867; et in Ann. Sci. Nat., Bot., ser. 5, 8: 377. 1867 – Type (designated by Chowdhuri, Notes Roy. Bot. Gard. Edinburgh 22: 243. 1957): *S. acaulis* (L.) Jacq.
- = *Polyschemone* Schott, Nyman & Kotschy, Analect. Bot.: 55. 1854 ≡ *Silene ser. Polyschemone* (Schott, Nyman & Kotschy) Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 3. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 377. 1867 ≡ *S. subsect. Polyschemone* (Schott, Nyman & Kotschy) Gürke in Richter, Pl. Eur. 2: 301. 1899 ≡ *Steris sect. Polyschemone* (Schott, Nyman & Kotschy) Ikonn. in Novosti Sist. Vyssh. Rast. 24: 82. 1987 ≡ *Lychnis subg. Polyschemone* (Schott, Nyman & Kotschy) Rabeler in Contr. Univ. Michigan Herb. 19: 154. 1993 – Type: *Polyschemone nivalis* (Kit.) Schott, Nyman & Kotschy (*Silene nivalis* (Kit.) Rohrb.).
- = *Silene* [unranked] *Paniculatae* Willk., Icon. Descr. Pl. Nov. 1: 74. 1854 ≡ *S. ser. Italicae* Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 5. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 377. 1867 ≡ *S. subsect. Italicae* (Rohrb.) Gürke in Richter, Pl. Eur. 2: 317. 1899 ≡ *S. sect. Italicae* (Rohrb.) Schischk. in Komarov, Fl. URSS 6: 675. 1936 ≡ *S. sect. Paniculatae* (Willk.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 233. 1957 ≡ *S. subsect. Patulae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 233. 1957, nom. illeg. ≡ *S. subsect. Paniculatae* (Willk.) Fedor., Ukrayins'k Bot. Zhurn 54: 180. 1997, nom. illeg. – Type (designated by Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 233. 1957): *Silene italica* (L.) Pers.
- = *Silene sect. Saxifragoides* Willk., Icon. Descr. Pl. Nov. 1: 73. 1854 ('*Saxifragoideae*') ≡ *S. ser. Macranthae* Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 2. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 377. 1867 ≡ *S. subsect. Macranthae* (Rohrb.) Gürke in Richter, Pl. Eur. 2: 299. 1899 ≡ *S. sect. Macranthae* (Rohrb.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 243. 1957 ≡ *S. subsect. Saxifragae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 243. 1957, nom. illeg. – Type (designated by Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 243. 1957): *Silene saxifraga* L.
- = *Silene* [unranked] *Brachypodae* Boiss., Fl. Orient. 1: 575. 1867 ≡ *S. ser. Brachypodae* (Boiss.) Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 3. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 377. 1867 ≡ *S. subsect. Brachypodae* (Boiss.) Gürke in Richter, Pl. Eur. 2: 303. 1899 ≡ *S. sect. Brachypodae* (Boiss.) Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 241. 1957 ≡ *S. subsect. Nutantes* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 241. 1957, nom. illeg. (non *S. ser. Nutantes* Rohrb. 1867) – Type (designated by Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 241. 1957): *Silene grisea* Boiss. (*S. leptoclada* Boiss.).
- ?= *Silene ser. Capitellatae* Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 4. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 377. 1867 ≡ *S. subsect. Capitellatae* (Rohrb.) Gürke in Richter, Pl. Eur. 2: 312. 1899 ≡ *S. sect. Capitellatae* (Rohrb.) Schischk. in Komarov, Fl. URSS 6: 681. 1936 – Type: *Silene capitellata* Boiss.
- = *Silene ser. Chloranthae* Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 4. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 377. 1867 ≡ *S. subsect. Chloranthae* (Rohrb.) Gürke, Pl. Eur. 2: 310. 1899 ≡ *S. sect. Chloranthae* (Rohrb.) Schischk. in Komarov, Fl. URSS 6: 616. 1936 ≡ *S. subsect. Ecoronatae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 235. 1957, nom. illeg. – Type: *Silene chlorantha* (Willd.) Ehrh.

- = *Silene* [unranked] *Viridiflorae* Boiss., Fl. Orient. 1: 574. 1867 ≡ *S.* sect. *Viridiflorae* (Boiss.) Schischk. in Komarov, Fl. URSS. 6: 675. 1936 ≡ *S.* subsect. *Viridiflorae* (Boiss.) Fedor. in Ukrayins'k Bot. Zhurn 54: 180. 1997 – Type: *Silene viridiflora* L.
- ?= *Silene* subsect. *Coronatae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 235. 1957 ≡ *S.* sect. *Coronatae* (Chowdhuri) Greuter in Taxon 44(4): 561. 1995 – Type: *Silene reichenbachii* Vis.
- = *Silene* subsect. *Erectae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 241. 1957 – Type: *Silene flavescens* Waldst. & Kit.
- = *Silene* sect. *Graminifoliae* Chowdhuri in Notes. Roy. Bot. Gard. Edinburgh 22: 236. 1957 ≡ *S.* ser. *Graminifoliae* (Chowdhuri) Rabeler in Contr. Univ. Michigan Herb. 19: 162. 1993 – Type: *Silene tenuis* Willd. (= *S. saxatilis* Sims).
- = *Silene* sect. *Holopetalae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 237. 1957 ≡ *S.* subsect. *Sibiricae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 237. 1957 ≡ *Otites* sect. *Holopetali* (Chowdhuri) Tzevelev in Novosti Sist. Vyssh. Rast. 33: 109. 2001 (*'Holopetalae'*) – Type: *Silene holopetala* Bunge (*Otites holopetalus* (Bunge) Tzvelev).
- = *Silene* sect. *Tataricae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 236. 1957 ≡ *S.* subsect. *Tataricae* (Chowdhuri) Devyatov & V.N.Tikhom. in Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 97: 122. 1992 – Type: *Silene tatarica* (L.) Pers.
- = *Silene* sect. *Albopetalae* Panov in Dokl. Bulg. Akad. Nauk 27: 1571. 1974 ≡ *S.* sect. *Balcanosilene* Šourková in Preslia 49: 10. 1977, nom. illeg. ≡ *Otites* sect. *Albopetali* (Panov) Holub in Preslia 70(2): 108. 1998 (*'Albopetalae'*) – Type: *Silene roemeri* Friv.
- = *Otites* sect. *Ciliati* Klokov in Novosti Sist. Vyssh. Nizsh. Rast. 1974: 59. 1974 (*'Ciliatae'*) ≡ *Silene* ser. *Borysthenicae* Šourková in Preslia 49(1): 11. 1977 ≡ *Otites* ser. *Borysthenici* (Šourková) Devyatov in Novosti Sist. Vyssh. Rast. 24: 93. 1987 (*'Borysthenicae'*) ≡ *O.* subsect. *Parviflori* Fedor. in Didukh, Ecofl. Ukraine 3: 31. 2002 (*'Parviflorae'*) ≡ *O.* subsect. *Borysthenici* (Šourková) Fedor. in Ukrayins'k. Bot. Zhurn. 73(1): 38. 2016 (*'Borysthenicae'*) – Type: *Otites borysthenicus* (Gruner) Klokov. (*Silene borysthenica* (Gruner) Walters).
- = *Silene* ser. *Effusae* Šourková in Preslia 49(1): 11. 1977 ≡ *Otites* ser. *Effusi* (Šourková) Devyatov in Novosti Sist. Vyssh. Rast. 24: 92. 1987 (*'Effusae'*) ≡ *O.* subsect. *Effusi* (Šourková) Fedor. in Ukrayins'k. Bot. Zhurn. 73(1): 39. 2016 (*'Effusae'*) – Type: *Silene wolgensis* (Hornem.) Oth (*Otites wolgensis* (Hornem.) Grossh.).
- ?= *Silene* ser. *Macrocarpae* Šourková in Preslia 49: 10. 1977 ≡ *Otites* ser. *Macrocarpi* (Šourková) Devyatov in Novosti Sist. Vyssh. Rast. 24: 88. 1987 (*'Macrocarpae'*) ≡ *O.* subsect. *Macrocarpi* (Šourková) Fedor. in Didukh, Ecofl. Ukraine 3: 31. 2002 (*'Macrocarpae'*) – Type: *Otites hellmannii* (Claus) Klokov (*Silene hellmannii* Claus).
- = *Silene* sect. *Longitubulosae* C.L.Tang in Acta Bot. Yunnan. 16(2): 117. 1994 – Type: *Silene fortunei* Vis. (*'fortunei'*) (*S. fissipetala* Turcz.).
- = *Silene* sect. *Barbeyanae* Greuter in Taxon 44(4): 568. 1995 – Type: *Silene barbeyana* Boiss.
- = *Silene* sect. *Paradoxae* Greuter in Taxon 44(4): 559. 1995 – Type: *Silene paradoxa* L.
- = *Silene* sect. *Graminiformes* Lazkov in Bot. Zhurn. (Moscow & Leningrad) 82(1): 109. 1997 – Type: *Silene chamarensis* Turcz.
- = *Silene* sect. *Koreanae* Lazkov in Bot. Zhurn. (Moscow & Leningrad) 83(10): 117. 1998 – Type: *Silene koreana* Kom.
- 3.8 *Silene* sect. *Pulvinatae* (Chowdhuri) F.Jafari, Oxelman & Gholipour, **stat. nov.** ≡ *S.* subsect. *Pulvinatae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 243. 1957 – Type: *Silene oreades* Boiss. & Heldr.
- 3.9 *Silene* sect. *Sclerophyllae* (Chowdhuri) F.Jafari, Oxelman & Rabeler, **stat. nov.** ≡ *S.* subsect. *Sclerophyllae* Chowdhuri in Notes Roy. Bot. Gard. 22: 234. 1957 – Type: *Silene alexandri* Hillebr.
- = *Ebraxis* Raf., Autik. Bot.: 29. 1840 – Type: *Ebraxis virgata* Raf., nom. illeg. (citing *S. antirrhina* in synonymy) (= *Silene antirrhina* L.).

3.10 *Silene* sect. **Muscipula** (Tzvelev) Oxelman, F.Jafari & Gholipour, **comb. nov.** ≡ *Ebraxis* sect. *Muscipula* Tzvelev in Novosti Sist. Vyssh. Rast. 33: 103. 2001 – Type: *Ebraxis muscipula* (L.) Tzvelev (*Silene muscipula* L.).
= *Silene* [unranked] *Viscosissimae* Batt. in Battandier & Trabut, Fl. Algérie, Dicot.: 136. 1888 – Type (designated by Greuter in Taxon 44(4): 571. 1995): *Silene muscipula* L.

3.11 *Silene* sect. **Portenses** F.Jafari & Oxelman, **sect. nov.** – Type: *Silene portensis* L.

Diagnosis. – Annuals or perennials; inflorescence an asymmetric dichasium; calyx glabrous, cylindrical in flower, clavate in fruit, anthophore pubescent; capsule spherical.

Unplaced taxa in *Silene* subg. *Silene*. — Clearly distinct from *S.* sect. *Rigidulae* s.str., there is a clade (Figs. 2B, 3, 4, suppl. Fig. S2, S3) of about nine species recognized here as the *S. arenosa* group occurring in the eastern parts of the Mediterranean region and Western Asia to Pakistan. This clade will be further explored by Eggens, Jafari & al. (in prep.) and probably deserves to be considered as a distinct section.

Silene subcretacea F.N.Williams from the Eastern Himalayas is of uncertain affinity within *S.* subg. *Silene*. It is the closest relative to *S.* sect. *Sclerocalycinae* s.l. in the ITS tree (Fig. 3, suppl. Fig. S2) and forms a weakly supported clade including *S. linearifolia*, *S. oreades* (*S.* sect. *Pulvinatae*) and *S. falcata* in the *rps16* tree (suppl. Fig. S3). This species seems to be intermediate between *S.* sect. *Pulvinatae* and *S.* sect. *Sclerocalycinae*. Future studies using low-copy loci might provide more resolution and reliable hypotheses on placement of this taxon.

Two accessions of *S. falcata* generated by Đurović & al. (2017) are nested within, and almost identical to, sequences of *S.* sect. *Pulvinatae* in the chloroplast tree (suppl. Fig. S3), whereas the ITS sequences confidently put this species with *S. caryophylloides* Otth in *S.* sect. *Auriculatae* (Fig. 3, suppl. Fig. S2). This may be an indication that *S. falcata*, which is easily recognized by its falcate leaves and naked capsule, might be of hybrid origin, and further studies to test this hypothesis are needed. Therefore, we leave *S. falcata* as unclassified at this point.

Incertae sedis

Silene sect. **Atocion** Otth in Candolle, Prodr. 1: 383. 1824 ≡ *S.* subg. *Ocymastrum* Riv. ex Rchb., Consp. Regn. Veg.: 207. 1828–1829 ≡ *S.* subg. *Atocion* (Otth) Torr. & A.Gray, Fl. N. Amer. 1: 194. 1838 ≡ *S.* sect. *Dichasiosilene* Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 2. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 373. 1867, nom. illeg. ≡ *S.* ser. *Atocion* Rohrb. in Braun, Index Semin. Hort. Bot. Berol. 1867, Append. Altera [= Consp. Syst. Silenes]: 3. 1867 & in Ann. Sci. Nat., Bot., ser. 5, 8: 376. 1867 ('*Atocia*') ≡ *S.* subsect. *Dichasiosilene* (Rohrb.) Rouy & Foucaud, Fl. France 3: 121. 1896 ≡ *S.* subsect. *Atocion* (Otth) Gürke in Richter, P1. Eur. 2: 304. 1899 ('*Atocia*'), nom. illeg. – Type: *Silene atocion* Jacq. (= *S. aegyptiaca* (L.) L.f.).
= *S.* subsect. *Delicatulae* Chowdhuri in Notes Roy. Bot. Gard. Edinburgh 22: 245. 1957, nom. illeg. – Type: *Silene aegyptiaca* (L.) L.f. (*Cucubalus aegyptiacus* L.)

New names and combinations

Due to inclusion of the genus *Lychnis* in *Silene*, it is necessary to propose the following new names and combinations under *Silene*.

Silene afromontana F.Jafari, Oxelman & Rabeler, **nom. nov.** ≡ *Uebelinia rotundifolia* Oliv. in J. Linn. Soc., Bot. 21: 397. 1885 ≡ *Lychnis rotundifolia* (Oliv.) M.Popp in Novon 18(1): 99. 2008, non *Silene rotundifolia* Nutt., Gen. N. Amer. Pl. 1: 288. 1818 – Holotype: Tanzania, Northern Province, Moshi Rural District, Mt. Kilimanjaro, 9–10,000 ft., Sep 1884, J. Thomson s.n. (K barcode K000313078!).

Silene kenyana F.Jafari, Oxelman & Rabeler, **nom. nov.** ≡ *Uebelinia crassifolia* T.C.E.Fr. in Repert. Spec. Nov. Regni Veg. 19: 91. 1923 ≡ *Lychnis crassifolia* (T.C.E.Fr.) M.Popp in Novon 18(1): 99. 2008, non *Silene crassifolia* L., Sp. Pl., ed. 2, 1: 597. 1762 – Holotype: Kenya, Rift Valley/Central Province, Aberdare Mtns., 13 Mar 1922, R.E. & T.C.E. Fries 2266 (UPS barcode V-060329!; isotypes: B barcode B 10 0154682!, K barcode K000313073!, S No. S14-47145!).

Silene kigesiensis (R.D.Good) F.Jafari, Oxelman & Rabeler, **comb. nov.** ≡ *Uebelinia kigesiensis* R.D.Good in J. Bot. 62: 332. 1924 ≡ *Lychnis kigesiensis* (R.D.Good) M.Popp in Novon 18(1): 99. 2008 – Holotype: Uganda, Western Province, Kigezi District, Behungi, E. & C. Godman 237 (BM barcode BM000582975!).

Silene kigesiensis subsp. *ragazziana* (Ousted) F.Jafari, Oxelman & Rabeler, **comb. nov.** ≡ *Uebelinia kigesiensis* subsp. *ragazziana* Ousted in Bull. Jard. Bot. Belg. 55: 446. 1985 ≡ *Lychnis kigesiensis* subsp. *ragazziana* (Ousted) M.Popp in Novon 18(1): 99. 2008 – Holotype: Ethiopia, Shoa Province, Entotto, 2 Oct 1886, V. Ragazzi s.n. (FT barcode FT001069!; isotype: FT barcode FT001070!).

Silene kiwuensis (T.C.E.Fr.) F.Jafari, Oxelman & Rabeler, **comb. nov.** ≡ *Uebelinia kiwuensis* T.C.E.Fr. in Repert. Spec. Nov. Regni Veg. 19: 90. 1923 ≡ *Lychnis kiwuensis* (T.C.E.Fr.) M.Popp in Novon 18(1): 99. 2008 – Holotype: Rwanda, J. Mildbraed 1749 (B, destroyed). Neotype (designated by Ousted in Bull. Jard. Bot. Belg. 55: 452. 1985): Rwanda, Pass between Sabinyo & Kahinga, 2200–2600 m, H. Humbert 8647 (B barcode B 10 0212783; isotypes: BR barcode BR0000005538997!, G barcode G00426843!, P barcode P05012470!).

Silene kiwuensis subsp. *erlangeriana* (Engl.) F.Jafari, Oxelman & Rabeler, **comb. nov.** ≡ *Uebelinia rotundifolia* var. *erlangeriana* Engl. in Bot. Jahrb. Syst. 48: 381. 1912 ≡ *U. erlangeriana* (Engl.) T.C.E.Fr. in Repert. Spec. Nov. Regni Veg. 19: 89. 1923 ≡ *U. kiwuensis* subsp. *erlangeriana* (Engl.) Ousted in Bull. Jard. Bot. Belg. 55: 457. 1985 ≡ *Lychnis kiwuensis* subsp. *erlangeriana* (Engl.) M.Popp in Novon 18(1): 99. 2008 – Holotype: Ethiopia, Arussi-Gala, Busaftu, Ellenbeck 1876 (B, destroyed). Neotype (designated by S. Ousted in Bull. Jard. Bot. Belg. 55: 457.1985): Ethiopia, NE of Agere Selam, 1 Nov 1972, I. Friis, M.G. Gilbert, F. Rasmussen & K. Vollesen 757 (BR barcode BR0000005539604!; isoneotypes: C barcode C10000457!, ETH barcode ETH000000010!).

Silene scottii (Turrill) F.Jafari, Oxelman & Rabeler, **comb. nov.** ≡ *Uebelinia scottii* Turrill in Kew Bull. 9(2): 260. 1954 ≡ *Lychnis scottii* (Turrill) M.Popp in Novon 18(1): 99. 2008 – Holotype: Ethiopia, Gamo-Gofa Province, Gughé Highlands, Mt. Tola, c. 3000 m, 17 Dec 1948, H. Scott 156 (K on 2 sheets, barcodes K000313086! and K000313089!).

Shortcomings

Although the present study is the most inclusive phylogenetic investigation on *Silene* to date, there are still several points needing to be investigated in more detail. The most critical deficiency is our inability to present a diagnostic morphological key to all sections recognized here, which can be explained by the high morphological variation in many species (especially the weedy and ornamental ones) of certain sections and high number of species in some sections; we

were unable to investigate all species completely from a morphological point of view. On the other hand, the morphological features diagnosing subgroups overlap significantly, and they may be characterized only by a set of combined characters.

Despite the large taxon sampling of many groups in *Silene*, some sections are covered here by less than half the number of the recognized species. *Silene* sect. *Auriculatae*, *S. sect. Physolychnis*, *S. sect. Sclerocalycinae*, and *S. sect. Siphonomorpha* are some examples of such sections, though the general picture of the phylogeny and the position of the sections will probably remain unaltered.

The markers and phylogenetic approaches used in this study are not sufficiently appropriate for depicting the phylogenetic relationships in polyploid species complexes that are frequent in some sections such as *S. sect. Auriculatae* and *S. sect. Physolychnis*. Modern approaches from next-generation sequencing will probably shed light on relationships in such groups in the future.

We were unable to assign several species to any appropriate section, due to their isolated position in the corresponding subgenus, their unresolved phylogenetic placement or our hesitation to describe additional monotypic sections. Such unique placement is most evident in *S. subg. Behenantha* with eight unassigned species. We believe that future investigations will clarify the relationships in such groups by adding more data to the analyses.

CONCLUSION

We present a novel taxonomic framework for the infrageneric classification of *Silene*, based on numerous previous phylogenetic analyses with more restricted taxon sampling, but often based on more than two loci. We added taxa by sequencing the ITS and *rps16* regions as informative and efficient markers in an attempt to resolve the phylogenetic relationships in *Silene*, simply because taxon sampling is by far most extensive for these, and they are often straight-forward to generate and interpret. However, they are not without problems. It is widely known that gene trees and species trees are expected to differ. Therefore, we chose to analyse them in a species tree under the multispecies coalescent framework, which efficiently handles the problem of incomplete lineage sorting (Jones & al., 2015; Jones, 2016). There may be other reasons for the discrepancies between the gene trees, e.g., stochasticity, hybridization and paralogy (Popp & Oxelman, 2001; Petri & Oxelman, 2011; Jones & al., 2013; Petri & al., 2013; Pfeil & al., 2017). Careful interpretation of support may reduce the impact of stochasticity, but support can be quantified in many different ways. We believe the posterior probabilities derived from species tree analyses are those best suited for the impact of stochasticity because all the parameterization makes the assumptions very clear. However, those may be violated, as in the case of homoploid hybridization, which may be a possibility to explore for the origins of *S. falcata* and *S. hoefftiana* (current study) and *S. waldsteinii* Griseb. (Naciri & al., 2017). Paralogy may, in a certain way, be problematic for the ITS region because in fact it is a multi-copy gene present in very many tandemly repeated copies that are kept similar by the process of concerted evolution (Baldwin & al., 1995), and the sequence used for phylogenetic interpretation is usually a consensus of the copies that have been amplified by PCR. For example, Naciri & al. (2017) noted that the same accession of *S. acaulis* (L.) Jacq. gave different sequences depending on which PCR primers had been used for amplification. For cpDNA, paralogy is usually not a problem, but paralogous nuclear copies are sometimes found (Bailey & al., 2003). In the era of next-generation sequencing, systematists have access to the nuclear genome in a unprecedented way, but caution should be given to the high rates of gene duplication, that may render orthology determination very difficult (Godden & al., 2012; Bravo & al., 2019).

Nevertheless, we believe that our new taxonomic framework provides a great improvement over previous attempts, and that it will provide a baseline for further studies on the many open questions remaining. Comparing the current infrageneric classification to Greuter's (1995) system at the subgeneric level, we leave *S. subg. Viscaria* (DC.) Greuter as a small segregate genus, while *S. subg. Conoimorpha* is transferred to the sectional level and included in *S. subg. Behenantha* in our system. We treat *S. subg. Silene* in a narrower sense compared with Greuter's view, with *S. sect. Rupifraga*, *S. sect.*

Compactae (Boiss.) Schischk. and *S. sect. Heliosperma* (Rchb.) Ledeb. excluded and accepted as the independent genera *Atocion* and *Heliosperma*, following previous molecular phylogenetic concepts (e.g., Oxelman & Lidén, 1995; Oxelman & al., 2001; Frajman & al., 2009a,b; Frajman & al., 2013). In agreement with Greuter's (1995) system, we acknowledge the poor support for *Silene*, as circumscribed by Oxelman & al. (2001) and merge *Lychnis* with *Silene* and treat it as a subgenus. Even if *Lychnis* would turn out to be sister to the rest of *Silene*, the short branch length associated with *Lychnis* reflects its low divergence from the rest of *Silene* warranting rather its inclusion in the strongly supported and widely circumscribed genus *Silene*. The current infrageneric classification includes three subgenera, and a total of 34 sections. *Silene sect. Atocion* is not assigned to any subgenus and considered as incertae sedis due to discrepancies in its placement from different genes and also because of what seem to be genome-wide highly accelerated DNA substitution rates (Toprak & al., 2016). *Silene sect. Physolychnis* s.l. with about 162 species is the largest section in the genus followed by *S. sect. Siphonomorpha* and *sect. Auriculatae* as the next most species rich sections as circumscribed here. Some other sections (e.g., *S. sect. Behenantha*, *sect. Sclerocalycinae* and *sect. Silene*) are also expanded and include more species than formerly circumscribed, while in some cases (e.g., *S. sect. Atocion* and *sect. Rigidulae*), the sections are circumscribed more narrowly. Two new sections (*S. sect. Acutifoliae*, *sect. Portenses*) and the status or combination of six groups is changed, viz. *S. sect. sect. Anotites*, *sect. Muscipula*, *sect. Petrocoma*, *sect. Pulvinatae*, *sect. Sclerophyllae* and *sect. Uebelina*. There are still some unplaced taxa that do not belong to existing sections and need additional study. We propose five new combinations and two new names in the genus *Silene* for those species assigned formerly to *Lychnis* and *Uebelina*. Future investigations will include more taxa, ideally with genome-scale sequence data to perform robust and reliable hypotheses of monophyly and species delimitations. In particular, a well-resolved phylogeny could potentially bring information about different morphological traits and their correlation with diversification in this diverse group of plants showing extensive homoplasy in morphological characters.

AUTHOR CONTRIBUTIONS

FJ: specimen study, plant collection, generating some DNA sequences, phylogenetic analyses, manuscript preparation and nomenclatural issues. SZ: supervising the study, manuscript revision and nomenclatural issues. AG: plant collection, determination and confirmation of some specimens and commenting on the manuscript. FE: generating some DNA sequences. RKR: commenting on the manuscript and nomenclatural issues. BO: supervising the study, specimen study, providing laboratory and technical facilities, providing some previously unpublished DNA sequences, phylogenetic analyses, nomenclatural issues and manuscript revision. — FJ, <https://orcid.org/0000-0003-1890-7789>, jafari_far1435@ut.ac.ir; SZ, <https://orcid.org/0000-0001-9159-1800>; AG, <https://orcid.org/0000-0003-1737-3607>, a.gholipour@pnu.ac.ir; FE, frida.eggens@gmail.com; RR, <https://orcid.org/0000-0002-6765-0353>, rabeler@umich.edu; BO, <https://orcid.org/0000-0002-6104-4264>

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[format Appendix 1 as table, font size 8 pt, leading 9 pt, keep shading as is]

Appendix 1. Comparison of three selected frequently used infrageneric classifications of *Silene* s.str. (including *Lychnis*) with the system presented in the current study (Jafari & al., this study).

Jafari & al. (this study)	Type/s included	Rohrbach (1869)	Chowdhuri (1957)	Greuter (1995)
1-subg. <i>Lychnis</i> (L.) Greuter		<i>Lychnis</i> L.	<i>Lychnis</i> L.	subg. <i>Lychnis</i>
1-1-sect. <i>Agrostemma</i> (DC.) Greuter	<i>S. coronaria</i> (L.) Clairv.			sect. <i>Agrostemma</i>
1-2-sect. <i>Lychnis</i>	<i>S. chalconica</i> (L.) E.H.L.Krause			
1-3-sect. <i>Coccyganthe</i> (Rchb.) Greuter	<i>S. flos-cuculi</i> (L.) Clairv.			sect. <i>Coccyganthe</i>
1-4-sect. <i>Uebelinia</i> (Hochst.) F.Jafari, Oxelman & Rabeler	<i>S. abyssinica</i> (Hochst.) F.Jafari, Oxelman & Rabeler			
Incertae sedis	<i>S. lagrangei</i> (Coss.) Greuter & Burdet			
2-subg. <i>Behenantha</i> (Oth) Torr. & A.Gray				
2-1-sect. <i>Psammophilae</i> (Talavera) Greuter	<i>S. littorea</i> Brot.	ser. <i>Scorpioides</i> Rohrb.	sect. <i>Succulentae</i> (Boiss.) Chowdhuri	sect. <i>Psammophilae</i>
2-2-sect. <i>Elisanthe</i> (Fenzl ex Endl.) Ledeb.	<i>S. noctiflora</i> L.	<i>Melandrium</i> Röhl	sect. <i>Melandriiformes</i> (Boiss.) Chowdhuri	sect. <i>Elisanthe</i>
2-3-sect. <i>Melandrium</i> (Röhl.) Rabeler	<i>S. latifolia</i> Poir.	<i>Melandrium</i>		sect. <i>Elisanthe</i>
2-4-sect. <i>Conoimorpha</i> Oth	<i>S. conica</i> L.	§ <i>Conosilene</i> Rohrb.	sect. <i>Conoimorpha</i>	subg. <i>Conoimorpha</i> (Oth) Fenzl ex Endl. sect. <i>Conoimorpha</i>
	<i>S. lydia</i> Boiss.	§ <i>Conosilene</i>	sect. <i>Conoimorpha</i>	sect. <i>Lydiae</i> Greuter
2-5-sect. <i>Cryptoneurae</i> Aydin & Oxelman	<i>S. cryptoneura</i> Stapf			
2-6-sect. <i>Sedoides</i> Oxelman & Greuter	<i>S. sedoides</i> Poir.	ser. <i>Rigidulae</i> (Boiss.) Rohrb.	subsect. <i>Divaricatae</i> (Batt.) Chowdhuri	sect. <i>Sedoides</i>
2-7-sect. <i>Cucubalus</i> (L.) Greuter	<i>S. baccifera</i> (L.) Roth	<i>Cucubalus</i> L.	<i>Cucubalus</i>	sect. <i>Cucubalus</i>
2-8-sect. <i>Cucubaloides</i> Edgeworth & Hook.f.	<i>S. khasiana</i> Rohrb.	incertis sedis	subsect. <i>Sinenses</i> Chowdhuri	
2-9-sect. <i>Cordifoliae</i> Chowdhuri	<i>S. cordifolia</i> All	ser. <i>Macranthae</i> Rohrb.	sect. <i>Cordifoliae</i>	

2-10-sect. <i>Erectorefractae</i> Chowdhuri	<i>S. boissieri</i> J.Gay ex Coss. (= <i>S. germana</i> J.Gay ex Coss.)	ser. <i>Leiocalycinae</i> (Boiss.) Rohrb	sect. <i>Erectorefractae</i>	
2-11-sect. <i>Acutifoliae</i> Oxelman & F.Jafari	<i>S. foetida</i> Link ex Spreng.	ser. <i>Macranthae</i>	sect. <i>Cordifoliae</i>	
2-12-sect. <i>Anotites</i> (Greene) Oxelman, F.Jafari & Rabeler	<i>S. menziesii</i> Hook.	ser. <i>Brachyanthae</i> Rohrb.	sect. <i>Rupifraga</i> Otth	
2-13-sect. <i>Odontopetalae</i> Chowdhuri	<i>S. odontopetala</i> Fenzl	subg. <i>Behen</i> (Dumort.) Rohrb.	sect. <i>Odontopetalae</i> subsect. <i>Dentatae</i> Chowdhuri	sect. <i>Odontopetalae</i>
2-14-sect. <i>Fimbriatae</i> (Boiss.) Bornm.	<i>S. simsii</i> F.Jafari, Rabeler & Oxelman	subg. <i>Behen</i>	sect. <i>Fimbriatae</i>	
2-15-sect. <i>Dichotomae</i> (Rohrb.) Chowdhuri	<i>S. dichotoma</i> Ehrh.	ser. <i>Dichotomae</i> Rohrb.	sect. <i>Dichotomae</i>	sect. <i>Dichotomae</i>
2-16-sect. <i>Saponarioides</i> (Boiss.) Schischk.	<i>S. nana</i> Kar. & Kir.	ser. <i>Rigidulae</i> (Boiss.) Rohrb.	sect. <i>Saponarioides</i>	
2-17-sect. <i>Behenantha</i> Otth	<i>S. behen</i> L.	ser. <i>Leiocalycinae</i> (Boiss.) Rohrb.	sect. <i>Behenantha</i> subsect. <i>Muscipulae</i> Chowdhuri	sect. <i>Behenantha</i>
	<i>S. vulgaris</i> (Moench) Gracke	subg. <i>Behen</i>	sect. <i>Inflatae</i> (Boiss.) Chowdhuri subsect. <i>Latifoliae</i> Chowdhuri	sect. <i>Behen</i> Dumort
2-18-sect. <i>Physolychnis</i> (Benth.) Bocquet	<i>S. uralensis</i> subsp. <i>apetala</i> (L.) Bocquet	<i>Melandrium</i>	sect. <i>Gastrolychnis</i> (Fenzl ex Endl.) Chowdhuri	
	<i>S. viscosa</i> (L.) Pers.	ser. <i>Otites</i> (Adans.) Rohrb.	sect. <i>Chloranthae</i> (Rohrb.) Schischk.	
	<i>S. morrisonmontana</i> (Hayata) Ohwi & Ohashi		sect. <i>Gastrolychnis</i> ?	
	<i>S. grayi</i> S.Watson		sect. <i>Quadrilobatae</i> Chowdhuri	
	<i>S. montana</i> S.Watson (<i>S. bernardina</i> subsp. <i>maguirei</i> Bocquet		sect. <i>Occidentales</i> Chowdhuri	
3-subg. <i>Silene</i>	<i>S. subg. Silene</i>			<i>S. subg. Silene</i>
3-1-sect. <i>Silene</i>	<i>S. anglica</i> L.	sect. <i>Cininosilene</i> Rohrb.	sect. <i>Silene</i>	sect. <i>Silene</i>
	<i>S. colorata</i> Poir.	§ <i>Dipterospermae</i> Rohrb. ser. <i>Bipartitae</i> (Boiss.) Rohrb.	sect. <i>Dipterospermae</i> (Rohrb.) Chowdhuri	sect. <i>Dipterospermae</i>
	<i>S. nicaeensis</i> All.	ser. <i>Nicaeenses</i> Rohrb.	subsect. <i>Pubicalycinae</i> Chowdhuri	sect. <i>Nicaeenses</i> (Rohrb.) Talavera
	<i>S. ciliata</i> Pourr.	ser. <i>Fruticulosae</i> (Willk.) Rohrb.	sect. <i>Fruticulosae</i> (Willk.) Chowdhuri	sect. <i>Fruticulosae</i>
	<i>S. succulenta</i> Forssk.	ser. <i>Macranthae</i>	sect. <i>Succulentae</i> (Boiss.) Chowdhuri	sect. <i>Succulentae</i>

	<i>S. hirsuta</i> Lag.	ser. <i>Scorpioides</i> Rohrb.	sect. <i>Scorpioides</i> (Rohrb.) Chowdhuri subsect. <i>Pubicalycinae</i> Chowdhuri	sect. <i>Silene</i>
	<i>S. nocturna</i> L.	ser. <i>Scorpioides</i>	subsect. <i>Nocturnae</i> (Batt.) Chowdhuri	sect. <i>Silene</i>
	<i>S. bergiana</i> Lindm.	ser. <i>Atocion</i> Rohrb.	subsect. <i>Rubellae</i> (Batt.) Chowdhuri	sect. <i>Rubellae</i> (Batt.) Oxelman & Greuter
	<i>S. divaricata</i> Clemente ex Lag.	ser. <i>Atocion</i>	subsect. <i>Divaricatae</i>	sect. <i>Rubellae</i>
3-2-sect. <i>Petrocoma</i> (Rupr.) F.Jafari, Oxelman & Rabeler	<i>S. hoefftiana</i> Fisch. & C.A.Mey.	ser. <i>Brachyanthae</i>		
3-3-sect. <i>Auriculatae</i> (Boiss.) Schischk.	<i>S. brevicaulis</i> Boiss.	ser. <i>Auriculatae</i> (Boiss.) Rohrb.	subsect. <i>Brevicaules</i> Chowdhuri	
	<i>S. suffrutescens</i> M.Bieb.	ser. <i>Suffruticosae</i> Rohrb.	subsect. <i>Aucherianae</i> Chowdhuri	sect. <i>Spergulifoliae</i> (Boiss.) Schischk.
	<i>S. ampullata</i> Boiss.	subg. <i>Behen</i>	sect. <i>Ampullatae</i> (Boiss.) Chowdhuri	
	<i>S. schafta</i> Hohen.	ser. <i>Macranthae</i>	subsect. <i>Schaftae</i> (Boiss.) Chowdhuri	
	<i>S. spergulifolia</i> (Willd.) M.Bieb.	ser. <i>Spergulifoliae</i> (Boiss.) Rohrb.	subsect. <i>Polyphyllae</i> Chowdhuri	sect. <i>Spergulifoliae</i>
	<i>S. odoratissima</i> Bunge	ser. <i>Suffruticosae</i> Rohrb.	subsect. <i>Laciniatae</i> (Boiss.) Chowdhuri	
	<i>S. repens</i> Patrin ex Pers. (= <i>S. amoena</i> L.)	ser. <i>Spergulifoliae</i>	subsect. <i>Repentes</i> Chowdhuri	
	<i>S. supina</i> M.Bieb.	ser. <i>Spergulifoliae</i>	subsect. <i>Supinae</i> Chowdhuri	sect. <i>Spergulifoliae</i>
	<i>S. goniocaula</i> Boiss.	ser. <i>Suffruticosae</i> Rohrb.	subsect. <i>Fruticosae</i> Chowdhuri	
	<i>S. pungens</i> Boiss.	subg. <i>Behen</i>	subsect. <i>Pungentes</i> Chowdhuri	
3-4-sect. <i>Lasiocalycinae</i> (Boiss.) Chowdhuri	<i>S. squamigera</i> Boiss.	ser. <i>Lasiocalycinae</i> (Boiss.) Rohrb.	subsect. <i>Squamatae</i> Chowdhuri	sect. <i>Lasiocalycinae</i>
	<i>S. papillosa</i> Boiss.	ser. <i>Lasiocalycinae</i>	subsect. <i>Papillosae</i> Chowdhuri	sect. <i>Lasiocalycinae</i>
3-5-sect. <i>Rigidulae</i> (Boiss.) Schischk.	<i>S. rigidula</i> Sm.	ser. <i>Rigidulae</i> (Boiss.) Rohrb.	sect. <i>Rigidulae</i>	sect. <i>Rigidulae</i>
	<i>S. cretica</i> L.	ser. <i>Leiocalycinae</i> (Boiss.) Rohrb.	subsect. <i>Creticae</i> Chowdhuri	sect. <i>Behenantha</i> Oth
3-6-sect. <i>Sclerocalycinae</i> (Boiss.) Schischk.	<i>S. bupleuroides</i> L.	ser. <i>Sclerocalycinae</i> (Boiss.) Rohrb.	subsect. <i>Longiflorae</i> Chowdhuri	sect. <i>Sclerocalycinae</i>
	<i>S. longipetala</i> Vent.	ser. <i>Lasiostemones</i> (Boiss.) Rohrb.	sect. <i>Lasiostemones</i> (Boiss.) Schischk.	sect. <i>Lasiostemones</i>
	<i>S. tunicoides</i> Boiss.	ser. <i>Sclerocalycinae</i>	sect. <i>Tunicoides</i> (Boiss.) Chowdhuri	sect. <i>Tunicoides</i>

	<i>S. chlorifolia</i> Sm.	ser. <i>Sclerocalycinae</i>	subsect. <i>Chlorifoliae</i> Chowdhuri	sect. <i>Sclerocalycinae</i>
	<i>S. dianthoides</i> Pers.	ser. <i>Capitellatae</i> Rohrb.	subsect. <i>Dianthoides</i> Chowdhuri	
	<i>S. tenella</i> C.A.Mey.	ser. <i>Suffruticosae</i> Rohrb.	sect. <i>Caespitosae</i> Chowdhuri subsect. <i>Stenophyllae</i> (Boiss.) Chowdhuri	
	<i>S. dianthifolia</i> J.Gay	ser. <i>Auriculatae</i> (Boiss.) Rohrb.	subsect. <i>Dianthifoliae</i> Chowdhuri	
3-7-sect. <i>Siphonomorpha</i> Otth	<i>S. nutans</i> L.	ser. <i>Nutantes</i> Rohrb.	sect. <i>Siphonomorpha</i>	sect. <i>Brachypodae</i> (Boiss.) Chowdhuri
	<i>S. otites</i> (L.) Wibel	ser. <i>Otites</i> (Adans.) Rohrb.	sect. <i>Otites</i> (Adans.) Otth	sect. <i>Otites</i>
	<i>S. acaulis</i> (L.) Jacq.	ser. <i>Nanosilene</i> (Otth) Rohrb.	sect. <i>Nanosilene</i> Otth	
	<i>S. italica</i> (L.) Pers.	ser. <i>Italicae</i> Rohrb.	sect. <i>Paniculatae</i> (Willk.) Chowdhuri subsect. <i>Patulae</i> Chowdhuri	sect. <i>Italicae</i> (Rohrb.) Schischk.
	<i>S. chlorantha</i> (Willd.) Ehrh.	ser. <i>Chloranthae</i> Rohrb.	subsect. <i>Ecoronatae</i> Chowdhuri	sect. <i>Chloranthae</i> (Rohrb.) Schischk.
	<i>S. viridiflora</i> L.	ser. <i>Nutantes</i> Rohrb.	sect. <i>Siphonomorpha</i>	sect. <i>Siphonomorpha</i>
	<i>S. saxifraga</i> L.	ser. <i>Macranthae</i> .	sect. <i>Macranthae</i> (Rohrb.) Chowdhuri	sect. <i>Saxifragoides</i> Willk.
	<i>S. grisea</i> Boiss.	ser. <i>Brachypodae</i> (Boiss.) Rohrb.	sect. <i>Brachypodae</i> subsect. <i>Nutantes</i> Chowdhuri	sect. <i>Brachypodae</i>
	<i>S. nivalis</i> (Kit.) Rohrb.	ser. <i>Polyschemone</i> Rohrb.	<i>Lychnis</i> L.	
	<i>S. capitellata</i> Boiss.	ser. <i>Capitellatae</i> Rohrb.	sect. <i>Otites</i>	
	<i>S. flavescens</i> Waldst. & Kit.	ser. <i>Brachypodae</i> (Boiss.) Rohrb.	subsect. <i>Erectae</i> Chowdhuri	sect. <i>Brachypodae</i>
	<i>S. tenuis</i> Willd.	ser. <i>Chloranthae</i> Rohrb.	sect. <i>Gramininifoliae</i> Chowdhuri	
	<i>S. tatarica</i> (L.) Pers.	ser. <i>Chloranthae</i>	sect. <i>Tataricae</i> Chowdhuri	sect. <i>Tataricae</i>
	<i>S. holopetala</i> Bunge	ser. <i>Otites</i>	sect. <i>Holopetalae</i> Schischk. ex Chowdhuri subsect. <i>Sibiricae</i> Chowdhuri	
	<i>S. roemerii</i> Friv.	ser. <i>Capitellatae</i> Rohrb.	sect. <i>Otites</i>	sect. <i>Otites</i>
	<i>S. chamarensis</i> Turcz.		sect. <i>Gramininifoliae</i>	
	<i>S. fortunei</i> Vis.	ser. <i>Italicae</i> Rohrb.	subsect. <i>Laciniatae</i> (Boiss.) Chowdhuri	
	<i>S. barbeyana</i> Boiss.		subsect. <i>Pulvinatae</i> Chowdhuri	sect. <i>Barbeyanae</i> Greuter
	<i>S. reichenbachii</i> Vis.		subsect. <i>Coronatae</i> Chowdhuri	sect. <i>Coronatae</i> (Chowdhuri) Greuter

	<i>S. paradoxa</i> L.	ser. <i>Italicae</i> Rohrb.	subsect. <i>Patulae</i> Chowdhuri	sect. <i>Paradoxae</i> Greuter
3-8-sect. <i>Pulvinatae</i> (Chowdhuri) F.Jafari, Oxelman & Gholipour	<i>S. oreades</i> Boiss. & Heldr.	ser. <i>Macranthae</i>	subsect. <i>Pulvinatae</i>	
3-9-sect. <i>Sclerophyllae</i> (Chowdhuri) F.Jafari, Oxelman & Rabeler	<i>S. alexandri</i> Hillebr.		subsect. <i>Sclerophyllae</i> Chowdhuri	
3-10-sect. <i>Muscipula</i> Oxelman, F.Jafari & Gholipour	<i>S. muscipula</i> L.	ser. <i>Leiocalycinae</i> (Boiss.) Rohrb.	subsect. <i>Muscipulae</i> Chowdhuri	sect. <i>Behenantha</i>
3-11-sect. <i>Portenses</i> F.Jafari & Oxelman	<i>S. portensis</i> L.	ser. <i>Rigidulae</i> (Boiss.) Rohrb.	sect. <i>Rigidulae</i> (Boiss.) Schischk.	
Incertae sedis				
sect. <i>Atocion</i> Otth	<i>S. atocion</i> L. (= <i>S. aegyptiaca</i> (L.) L.f.)	sect. <i>Dichasiosilene</i> Rohrb. ser. <i>Atocion</i> Rohrb.	sect. <i>Atocion</i> subsect. <i>Delicatulae</i> Chowdhuri	sect. <i>Atocion</i>

Appendix 2. Voucher information of specimens used in species and minimal clusters trees from nrDNA ITS and cpDNA *rps16* datasets.

Species, country, collector name and collection number, herbarium and GenBank accessions for ITS and *rps16*. New sequences are indicated with an * after the GenBank accession number. Missing GenBank accessions are indicated by –; *s.n.* refers to missing collection number and unknown herbaria are replaced by a question mark.

Agrostemma githago L., Cult. Sweden, *Oxelman 2274* (GB), X86895, –; Cult. Sweden, *Oxelman ITS-AGR 30616* (GB), –, Z83154; *Atocion armeria* (L.) Raf., Slovenia, *B. Frajman & M. Turjak 136972* (LJU), FJ384027, FJ383986; *Atocion compactum* (Fisch. ex Hornem.) Tzvelev, Iran, *S. Zarre, Y. Salmaki & H. Moazzeni 39629* (TUH), LC424092*, LC423983*; *Atocion rupestre* (L.) Oxelman, Italy, *P. Schönswetter & B. Frajman 11396* (LJU), FJ384039, FJ383998; *Eudianthe laeta* Rchb. ex Willk., Algeria, *Oxelman 1876* (GB), KX757661, Z83155; *Heliosperma alpestre* (Jacq.) Griseb., Slovenia, *B. Surina 136562* (LJU), EF118055, EF118116; *Heliosperma pusillum* (Waldst. & Kit.) Rchb., Slovakia, *M. Ronikier 137745* (LJU), EF118069, EF118155; *Petrocoptis pyrenaica* (Bergeret) A. Braun ex Walp., Spain, *Schneeweiß & al. 6549* (WU), FJ384018, HQ334964; *Silene acaulis* (L.) Jacq., Italy, *Schneeweiß & al. 5315* (WU), FJ384019, FJ376822; *Silene ajanensis* (Regel & Tiling) Vorosch., Russia, *Rautenberg 68* (UPS), KX757376, JF970809; *Silene akinfijewi* Schmalh., Russia, *Portenier 3814* (LE), FN821096, FN821267; *Silene albescens* Boiss., Iran, *Parishani 14587* (M), KX757430, LC423625*; *Silene almolae* J. Gay ex Coss., Spain, *Merxmüller & Lippert 25372* (M), KX757424, LC423626*; *Silene ammophila* Boiss. & Heldr., Greece, *Raus 7631* (GB), FN821099, FN821268; *Silene amoena* L., Unknown, *Egger 431* (WTU), KX757436, DQ908842; *Silene ampullata* Boiss., Iran, *Ghahreman 39249* (TUH), LC424066*, LC423994*; *Silene andryalifolia* Pomel, Spain, *DSBG 4285* (GB), KX757481, LC423627*; *Silene antirrhina* L., Unknown, *Wincent & Lammers 3137* (GB), KX757575, Z83193; *Silene apetala* Willd., Iran, *Kyasat 6218* (TUH), LC424052*, LC424034*; *Silene aprica* Turcz., Cult. Sweden, *C.Y. Wu & H. Chuang s.n.* (GB), FN821097, Z83181; *Silene arabica* Boiss., Iran, *Ghahreman & Mozaffarian 14096* (TUH), LC424053*, LC424032*; *Silene araratica* Schischkin, Turkey, *Gregor & Meierott 6800* (M), KX757453, LC423628*; *Silene arenarioides* Desf., Tunisia, *Lambinon & Margot 99* (M), KX757256, LC423629*; *Silene arenosa* K. Koch, Armenia, *Tachgabzjan & al. 26/V 1960* (W), KX757588, LC423630*; *Silene argillosa* Munby, Algeria, *Oxelman 1836* (GB), X86839, LC423631*; *Silene aristidis* Pomel, Algeria, *Podlech 39424* (M), KX757466, LC423632*; *Silene armena* Boiss., Turkey, *Görk & al. 24112* (Strid private Hb.), KX757620, LC423633*; *Silene atlantica* Coss. & Durieu, Algeria, *Dubuis 15980* (M), KX757258, LC423634*; *Silene aucheriana* Boiss., Iran, *Gholipour 4* (GB), KX757447, LC423635*; Iran, *Attar & Zamani 36196* (TUH), LC424065*, LC424001*; *Silene auriculata* Sm., Greece, *Baden & Franzén 795* (Strid private Hb.), KX757292, LC423636*; *Silene austroiranica* Rech.f., Aellen & Esfand., Iran, *Rechinger & al. 3261* (B), KX757590, EF061364; Iran, *Veiskarami 23960* (TUH), LC424094*, LC423985*; *Silene ayachica* Humbert, Morocco, *Podlech 47202* (M), KX757267, LC423637*; *Silene baldshuanica* B. Fedtsch., Afghanistan, *Podlech & Jarmal 30172* (M), KX757615, LC423638*; *Silene behen* L., Turkey, *Oxelman 2591* (GB), KX757301, LC423639*; *Silene bellidifolia* Jacq., Greece, *Strid & al. 35179* (Strid private Hb.), KX757261, LC423640*; *Silene bergiana* Lindm., Spain, *Holmdahl 1182* (GB), X86835, Z83191; *Silene berthelotiana* Webb ex Christ, Canary Islands, *Santos Guerra s.n.* (ORT), KX757495, LC423641*; *Silene bourgaei* Webb ex Christ, Canary Islands, *Santos Guerra s.n.* (ORT), KX757496, LC423642*; *Silene brahuica* Boiss., Kyrgyzstan, *Čuba s.n.* (M), KX757455, LC423643*; Iran, *Ghahreman & Mozaffarian 5795* (TUH), LC424091*, LC424016*; Iran, *Joharchi 45011* (FUMH), LC424071*, LC424009*; *Silene breviauriculata* Ghaz., Afghanistan, *Podlech 11852* (M), KX757456, LC423644*; *Silene brevicalyx* Hartvig & Strid, Turkey, *Hartvig & al. 23274* (Strid private Hb.), KX757624, LC423645*; *Silene brevistaminea* Gilli, Afghanistan, *Anders 6457* (M), KX757434, LC423646*; *Silene* cf. *brevistaminea* Gilli, Afghanistan, *Schloeder & Jacobs 1656* (M), KX757431, LC423675*; *Silene bupleuroides* L., Cult. Sweden, *Oxelman 2266* (GB) Garden, X86864, LC423647*; Iran, *A. Talebi 43213* (TUH), LC424085*, LC424026*; Iran, *Faghihnia & Zangoeei 27442* (FUMH), LC424086*, LC424019*; *Silene burchellii* Otth, South Africa, *Hull 63* (M), KX757263, LC423649*; *Silene caesia* Sm., Greece, *Baden 1114* (Strid private Hb.), KX757304, LC423650*; *Silene cardiopetala* Franch., China,

Lidén 4-17 (GB), KX757284, LC423652*; *Silene cariensis* Boiss., Turkey, *Oxelman 1681* (GB), KX757642, EF061365; *Silene caryophylloides* Otth, Turkey, *Görk & al. 2436* (Strid private Hb.), KX757438, LC423653*; *Silene cephalantha* Boiss., Turkey, *Nydegger 44428* (M), KX757433, LC423654*; Iran, A. *Gholipour 3601* (SPNH), LC424075*, LC424006*; *Silene cephalenia* Heldr., Greece, *Strid & al. 28150* (Strid private Hb.), KX757513, LC423655*; *Silene chaetodonta* Boiss., Iraq, *Rechinger 10060* (W), KX757596, LC423656*; *Silene chalcedonica* (L.) E.H.L.Krause, Cult. Sweden, *Oxelman 2277* (GB), X86894, Z83164; *Silene chamarensis* Turcz., Mongolia, *Rautenberg 115* (UPS), KX757544, LC423657*; *Silene chlorantha* (Willd.) Ehrh., Germany, *Angerer s.n.* (M), KX757527, LC423658*; *Silene ciliata* Pourr., Greece, *Franzén & al. 822* (Strid private Hb.), KX757268, LC423659*; *Silene claviformis* Litv., Afghanistan, *Jacobs & Schloeder 1233* (M), KX757632, LC423660*; *Silene commelinifolia* Boiss., Iran, *Oxelman 2611* (GB), KX757449, LC423661*; *Silene congesta* Sm., Greece, *Strid & al. 27446* (Strid private Hb.), KX757515, LC423662*; *Silene conglomeratica* Melzh., Greece, *Strid 44044* (Strid private Hb.), KX757492, LC423663*; *Silene conica* L., Unknown, *Erixon 70* (UPS), FN821100, FN821269; Iran, A.R. *Naqinezhad 27208* (TUH), LC424059*, LC424031*; *Silene coniflora* L., Syria, *Samuelsson 3783* (S), HQ334908, HQ334967; *Silene conoidea* L., Cult. Sweden, *Anja Rautenberg 290* (UPS), FN821101, FN821270; *Silene cordifolia* All., Italy, *Lippert & Merxmüller 17265* (Strid private Hb.), KX757314, LC423664*; *Silene corinthiaca* Boiss. & Heldr., Greece, *Oxelman 1934* (GB), KX757633, EF061366; *Silene coronaria* (L.) Clairv., Iran, *Joharchi 35095* (FUMH), LC424093*, LC424014*; *Silene corrugata* Ball, Morocco, *Podlech 41597* (M), KX757259, LC423665*; *Silene crassipes* Fenzl, Lebanon, *Doppelbaur 491* (M), KX757462, LC423666*; *Silene cretica* L., Greece, *Oxelman & Tollsten 1324* (GB), KX757640, Z83195; *Silene crispans* Litv., Iran, *Zarre & al. s.n.* (M), KX757452, LC423667*; *Silene cryptoneura* Stapf, Turkey, *Deniz s.n.* (GB), KX757322, LC423668*; *Silene cuatrecasasii* Pau & Font Quer, Morocco, *Optima Iter V 1553* (RNG), KX757581, EF061367; *Silene cyri* Schischk., Iran, A. *Gholipour 4726* (SPNH), LC424083*, LC423988*; *Silene cythnia* (Halácsy) Walters, Greece, *Rautenberg 74* (UPS), KX757488, LC423669*; *Silene daenensis* Melzh., Iran, A. *Gholipour 8779* (TUH), LC424060*, LC424005*; *Silene damascena* Boiss. & Gaill., Lebanon, *Roessler 5381* (M), KX757265, LC423670*; *Silene damboldtiana* Greuter & Melzh., Greece, *Stamatiadou 22142* (Strid private Hb.), KX757482, LC423671*; *Silene danaensis* Danin, Jordan, *Frey & al. 80-879* (BSB), KX757625, LC423672*; *Silene davidii* (Franch.) Oxelman & Lidén, China, *Eggens 86* (UPS), KX757367, JF970816; *Silene demawendica* Bornm., Iran, A. *Talebi 43217* (TUH), LC424062*, LC423995*; *Silene dianthoides* Pers., Armenia, *Fayvush & al. 0090* (M), KX757626, LC423673*; *Silene dichotoma* Ehrh., Unknown, *Till s.n.* (WU), KX757313, LC423674*; Iran, *Rezvanian 23094* (TUH), LC424058*, LC424038*; *Silene diclinis* (Lag.) M.Lainz, Spain, *H.C. Prentice DIC-7* (?), FN821103, FN821273; *Silene dinarica* Spreng., Romania, *Csergö s.n.* (?), KX757564, LC423676*; *Silene dioica* (L.) Clairv., Finland, *H.C. Prentice D169:9* (?), FN821110, FN821279; *Silene disticha* Willd., Algeria, *Podlech 39246* (M), KX757260, LC423677*; *Silene echinospermoides* Hub.-Mor., Greece, *Oxelman 2202* (GB), KX757636, EF061368; *Silene elisabethae* Jan, Cult. Sweden, *Oxelman 2261* (GB), X86828, Z83184; *Silene elymaitica* Bornm., Iran, A. *Gholipour 8666* (TUH), LC424074*, LC423997*; *Silene eremicana* Stapf., Iran, S. *Zarre, Y. Salmaki & H. Moazzeni 39486* (TUH), LC424070*, LC424008*; *Silene eriocalycina* Boiss., Iran, *Bertrand s.n.* (GB), KX757432, LC423678*; *Silene ertekinii* Aydin & Oxelman, Turkey, *Aydin 31* (GB), KX757328, LC423679*; *Silene esquamata* W.W.Sm., China, *Podlech 54568* (M), KX757528, LC423680*; *Silene exsudans* Boiss. & Heldr., Turkey, *Oxelman 1660* (GB), KX757607, EF061369; *Silene fabaria* (L.) Sm., Greece, *Oxelman 2211* (GB), X86851, LC423681*; *Silene fissipetala* Turcz., China, *Zheng-Yu Li 20954* (PE), KX757531, LC423682*; *Silene flavescens* Waldst. & Kit., Greece, *Strid & Papanicolaou 15820* (Strid private Hb.), KX757516, LC423683*; *Silene foetida* Link ex Spreng., Cult. Sweden, *Oxelman 2311* (GB), X86827, Z83178; *Silene fraudatrix* Meikle, Cyprus, *Davis 2846K* (E), KX757413, LC423684*; *Silene fruticosa* L., Greece, *Oxelman & Tollsten 934* (GB), X86865, LC423685*; *Silene fuscata* Link, Algeria, *Oxelman 1887* (GB), X86837, LC423686*; *Silene gallica* L., Iran, A.R. *Naqinezhad 27286* (TUH), LC424050*, LC424035*; *Silene gallinyi* Heuff. ex Rchb., Greece, *Strid & Hansen 9283* (Strid private Hb.), KX757464, LC423687*; *Silene georgievskiyi* Lazkov, Syria, *Rechinger 13136* (G), KX757609, LC423688*; *Silene gertraudiae* Melzh., Iran, *Gholipour 8* (GB), KX757454,

LC423689*; *Silene gigantea* (L.) L., Greece, *Oxelman 2209* (GB), KX757558, LC423690*; *Silene graeca* Boiss. & Spruner, Greece, *Oxelman & Tollsten 1040* (GB), KX757308, LC423691*; *Silene graminifolia* Otth, Russia, *Rautenberg 241* (UPS), KX757545, LC423692*; *Silene grandiflora* Franch., Unknown, *KGB 275* (GB), KX757286, LC423693*; *Silene hawaiiensis* Sherff, U.S.A., *Degener & al. 19828* (GB), KX757573, EF061378; *Silene heuffelii* Soo, Greece, *Strid & al. 44643* (GB), FN821114, FN821287; *Silene hifacensis* Rouy, Cult. Sweden, *Rautenberg 102* (UPS), KX757483, LC423694*; *Silene hoefftiana* Fisch. ex C.A.Mey., Russia, *Popova s.n.*, 9 Aug. 1976 (LE), FJ384021, FJ383981; *Silene holzmannii* Heldr. ex Boiss., Cult., *Rautenberg 2* (GB), KX757303, LC423695*; *Silene iche-bogdo* Grubov, Mongolia, *Iwarsson & al. 305* (GB), KX757540, LC423696*; *Silene idaea* Hausskn., Turkey, *Hartvig & al. 23241* (Strid private Hb.), KX757618, LC423697*; *Silene imbricata* Desf., Algeria, *Oxelman 1881* (GB), KX757266, LC423700*; *Silene inaperta* L., Portugal, *Silva 1688* (LD), KX757584, LC423698*; *Silene indepressa* Schischk., Iran, *S. Zarre, Y. Salmaki & A. Ebrahimi 38158* (TUH), LC424069*, LC424003*; *Silene insularis* Barbey, Greece, *Raus 9700* (UPS), KX757324, LC423699*; *Silene intramongolica* Lazkov, Mongolia, *Undiakh s.n.* (UPS), KX757541, LC423701*; *Silene italica* (L.) Pers., Turkey, *Oxelman 2619* (GB), KX757559, LC423702*; Iran, *Eslami 29564* (TUH), LC424095*, LC424015*; *Silene jennisseensis* Willd., Russia, *Solstad & Elven 04/1573* (O), KX757542, LC423703*; *Silene joerstadii* Wendelbo, Afghanistan, *Hedge & Wendelbo W 8992* (GB), KX757293, LC423704*; *Silene koreana* Kom., Korea, *Hong & Han 13480001* (UPS), KX757538, LC423705*; *Silene kumaonensis* F.N.Williams, Nepal, *Miehe & Miehe 01-109-08* (GB), KX757273, LC423706*; *Silene lagrangei* (Coss.) Greuter & Burdet, Morocco, *Huber-Morath 3408* (LD), KX757656, Z83162; *Silene lagunensis* H.Christ, Canary Islands, *Santos Guerra s.n.* (ORT), KX757499, LC423707*; *Silene lanceolata* A.Gray, U.S.A., *Perlman 14329* (BISH), KX757576, LC423708*; *Silene latifolia* Poir., Spain, *H.C. Prentice L200-2* (?), FN821134, FN821302; *Silene leptoclada* Boiss., Turkey, *Oxelman 2475* (GB), KX757520, LC423709*; *Silene leyseroides* Boiss., Kuwait, *Boulos 15500* (S), KX757614, LC423710*; *Silene linearifolia* Otth, Georgia, *Hörandl & al. C88-31* (WU), KX757580, LC423711*; *Silene linearis* Decne., Palestine, *Bierkamp & Zinth 177* (BSB), KX757592, EF061372; *Silene linnaeana* Vorosch., Russia, *Arnell s.n.* (S), KX757378, JF970812; *Silene linoides* Otth, Greece, *Laulund 919* (Strid private Hb.), KX757490, LC423712*; *Silene littorea* Brot., Spain, *Oxelman 2589* (GB), KX757658, LC423713*; *Silene longicilia* (Brot.) Otth, Cult. Sweden, *Rautenberg 75* (UPS), KX757484, LC423714*; *Silene longipetala* Vent., Iran, *American-Iranian Botanical Delegation 34636* (TUH), LC424088*, LC424023*; *Silene lucida* Chowdhuri, Iran, *A. Gholipour & M. Amini Rad 2497* (SPNH), LC424072*, LC424000*; *Silene lycaonica* Chowdhuri, Turkey, *Görk & al. 24112* (Strid private Hb.), KX757621, LC423715*; *Silene lydia* Boiss., Sweden, *Ljungstrand, Erik 2008-09-20* (GB), HQ334910, HQ334971; *Silene macrodonta* Boiss., Turkey, *Bengt Oxelman 2441* (GB), FN821135, FN821303; *Silene macrostyla* Maxim., Russia, *Oxelman 2603* (GB), KX757537, LC423716*; *Silene marizii* Sampaio, Portugal, *H.C. Prentice M4-7* (?), FN821137, FN821305; *Silene marschallii* C.A.Mey., Iran, *Wendelbo & Assadi 27674* (GB), KX757622, EF061387; Iran, *A. Talebi 43212* (TUH), LC424087*, LC424017*; *Silene martyi* Emb. & Maire, Morocco, *Jacquemoud & Jeanmonod MAR 1168* (G), KX757582, EF061373; *Silene melzheimeri* Greuter, Greece, *Rautenberg 355* (UPS), KX757467, LC423717*; *Silene mentagensis* Coss., Morocco, *Jahandiez 329* (LD), KX757644, EF061396; *Silene menziesii* Hook., U.S.A., *Holmgren & al. 2356* (UPS), AJ409059, AJ409062; *Silene meyeri* Fenzl ex Boiss. & Buhse, Iran, *A. Gholipour 8629* (TUH), LC424063*, LC423991*; *Silene microphylla* Boiss., Iran, *Gholipour 2* (GB), KX757446, LC423718*; *Silene microsperma* Fenzl, Palestine, *Samuelsson 777* (S), KX757604, LC423719*; *Silene moorcroftiana* Benth., Tajikistan, *Dickoré 17783* (MSB), KX757442, EF061388; *Silene multicaulis* Guss., Italy, *Eriksen & Schøler 1741* (GB), KX757469, LC423720*; *Silene multinervia* S.Watson, U.S.A., *A.C. Sanders 24130* (CAS), FN821140, FN821308; *Silene muscipula* L., Morocco, *Bengt Oxelman 1780* (GB), EF060201, Z83197; *Silene nana* Kar. & Kir., Turkmenistan, *Kereverzova & Mekeda 1976.V.5* (LECB), KX757312, EF061377; Iran, *Ghahreman, Attar, Mehdigholi & Okhovvat 28488* (TUH), LC424057*, LC424030*; *Silene nemoralis* Waldst. & Kit., Austria, *Oxelman 2259* (GB), KX757485, EF061389; *Silene nivalis* (Kit.) Rohrb., Cult. Sweden, *Oxelman 2255* (GB), KX757557, LC423721*; *Silene nivea* (Nutt.) Muhl. ex DC., U.S.A., *Scofield 1892* (WTU), KX757291, DQ908831; *Silene nizvana* Melzh., Iran, *A. Gholipour 8621* (TUH),

LC424082*, LC423986*; *Silene nocteolens* Webb & Berthel., Canary Islands, Santos Guerra s.n. (ORT), KX757498, LC423722*; *Silene noctiflora* L., Sweden, H.C. Prentice N2-2 (?) FN821141, FN821309; *Silene nocturna* L., Greece, Oxelman & Tollsten 654 (GB), X86841, Z83192; Iran, Mozaffarian 6771 (TUH), LC424051*, LC424033*; *Silene nodulosa* Viv., Corsica, Emanuelsson 1890 (S), KX757486, LC423723*; *Silene nutabunda* Greuter, Greece, Oxelman & Tollsten 1079 (GB), KX757309, LC423724*; *Silene nutans* L., Cult. Sweden, Rautenberg 347 (UPS), KX757472, LC423725*; *Silene odontopetala* Fenzl, Turkey, Görk & al. 23817 (Strid private Hb.), KX757294, LC423726*; Iran, A. Gholipour 4693 (SPNH), LC424055*, LC423984*; *Silene oligantha* Boiss. & Heldr., Greece, Strid & al. 12445 (Strid private Hb.), KX757494, LC423727*; *Silene oreades* Boiss. & Heldr., Turkey, Rautenberg 167 (UPS), KX757579, LC423728*; *Silene orphanidis* Boiss., Greece, Strid & Papanicolaou 15930 (Strid private Hb.), KX757556, KX852490; *Silene otites* (L.) Wibel, Hungary, Rautenberg 83 (UPS), KX757567, EF061393; *Silene oxelmanii* Gholipour, Iran, A. Gholipour 3487 (SPNH), LC424061*, LC424012*; *Silene palinotricha* Fenzl ex Boiss., Iran, A. Gholipour 8681 (TUH), LC424067*, LC424004*; *Silene paradoxa* L., Italy, Till & Till s.n. (WU), KX757509, LC423729*; *Silene paucifolia* Ledeb., Russia, Solstad & Elven 04/1336 (O), KX757543, LC423730*; *Silene pendula* L., Cult. Sweden, Anja Rautenberg 289 (UPS), FN821142, FN821310; *Silene perlmanii* W.L. Wagner, D.R. Herbst & Sohmer, U.S.A., Perlman & Obata 5401 (BISH), KX757571, EF061380; *Silene persepolitana* Melzh., Iran, Attar, Khatamsaz & Sheikholeslami 20359 (TUH), LC424073*, LC423992*; *Silene pharnaceifolia* Fenzl, Turkey, Oxelman 2602 (GB), KX757630, LC423731*; *Silene pinetorum* Boiss. & Heldr., Greece, Greuter 4408 (B), KX757635, EF061374; *Silene pogonocalyx* (Svent.) Bramwell, Canary Islands, Santos Guerra s.n. (ORT), KX757497, LC423732*; *Silene portensis* L., Spain, Sanchez Garcia 1974.VI.17 (C), KX757646, EF061397; *Silene propinqua* Schischk., Afghanistan, Grey-Wilson & Hewer 899 (GB), KX757616, EF061392; *Silene pruinosa* Boiss., Iran, Veiskarami 23964 (TUH), LC424076*, LC424013*; *Silene pseudobehen* Boiss., Turkey, Oxelman 2630 (GB), KX757302, LC423733*; *Silene pungens* Boiss., Iran, Ghahreman & Mozaffarian 9673 (TUH), LC424080*, LC423998*; *Silene pygmaea* Adams, Russia, Amirkhanov 22.VI-1977 (MW), FN821143, FN821311; *Silene quadrifida* L., Russia, V. Khanmintchun & N. Idt 100099 (MW), FN821144, FN821312; *Silene reinholdii* Heldr., Greece, Oxelman & Tollsten 847 (GB), KX757307, LC423734*; *Silene remotiflora* Vis., Greece, Strid & Kjellsson 11016a (Strid private Hb.), KX757300, LC423736*; *Silene reticulata* Desf., Algeria, Davis 53457 (BM), KX757585, KX757480; *Silene rhynchocarpa* Boiss., Turkey, Görk & al. 23737 (Strid private Hb.), KX757439, LC423737*; *Silene ruprechtii* Schischk., Iran, A. Gholipour 3554 (SPNH), LC424084*, LC423987*; *Silene sabinosae* Pit., Spain, Mesa & al. 28-II2002 (ORT), KX757503, LC423738*; *Silene samia* Melzh. & Christod., Greece, Rautenberg 112 (UPS), KX757316, LC423739*; *Silene samojedorum* (Sambuk) Oxelman, Russia, Schönswetter & Tribsch T601 (GB), KX757380, JF970808; *Silene saxatilis* Sims, Turkey, Gregor & Meierott 7054 (M), KX757525, LC423740*; *Silene saxifraga* L., Spain, Rautenberg 213 (UPS), KX757493, EF061394; *Silene schafta* Hohen., Cult. Sweden, Oxelman 2264 (GB), X86852, Z83194; Iran, A. Gholipour 4706 (SPNH), LC424078*, LC424002*; *Silene schwarzenbergeri* Halácsy, Greece, Hartvig & Christiansen 8167 (Strid private Hb.), FN821095, FN821313; *Silene sclerophylla* Chowdhuri, Iran, Zarre & al. 39600 (M), KX757627, LC423648*; Iran, S. Zarre, Y. Salmaki & H. Moazzeni 39600 (TUH), LC424089*, LC424021*; *Silene seoulensis* Nakai, Korea, Hong & Han 13420001 (UPS), KX757373, JF970806; *Silene sibirica* (L.) Pers., Russia, Coll. unknown (?), JX274521, -; *Silene simsii* F. Jafari, Rabeler & Oxelman, Iran, Y. Salmaki, H. Moradi & S. Siadati 39821 (TUH), LC424056*, LC424028*; *Silene sisianica* Boiss. & Buhse, Armenia, Fayvush & al. s.n. (M), KX757461, LC423741*; *Silene* cf. *sojakii* Melzh., Iran, Gholipour 9 (GB), KX757450, LC423742*; Iran, A. Gholipour 8625 (TUH), LC424081*, LC423993*; *Silene sordida* Hub.-Mor. & Reese, Turkey, Oxelman 2206 (GB), X86824, Z83186; *Silene stenobotrys* Boiss. & Hausskn., Iran, S. Zarre, Y. Salmaki & H. Moazzeni 39632 (TUH), LC424079*, LC423990*; *Silene stenophylla* Ledeb., Russia, Molau & Raszhivin 4092 (GB), KX757536, LC423743*; *Silene stockenii* Chater, Spain, Holmdahl 1595 (GB), KX757657, LC423744*; *Silene striata* Ehrenb. ex Rohrb., Syria, Samuelsson 1522 (S), KX757610, LC423745*; *Silene struthioloides* A. Gray, U.S.A., Henrickson 3854 (US), KX757574, EF061379; *Silene subconica* Friv., Greece, Bengt Oxelman & Lars Tollsten 159 (GB), HQ334913, HQ334973; *Silene subcretacea* F.N. Williams, China, Hu &

Chuang 7355 (GB), KX757628, EF061390; *Silene succulenta* Forssk., Greece, *Strid & Tan* 55028 (Strid private Hb.), KX757257, LC423746*; *Silene supine* M.Bieb., Unknown, *Hörandl & al.* 4776 (WU), KX757459, LC423747*; *Silene swertiifolia* Boiss., Iran, *Joharchi & Zangoeei* 40037 (FUMH), LC424090*, LC424022*; *Silene tamaranae* Bramwell, Canary Islands, *Santos Guerra s.n.* (ORT), KX757500, LC423748*; *Silene tatarinowii* Regel, *Harry Smith* 6735 (UPS), FJ384025, FJ383984; *Silene thessalonica* Boiss. & Heldr., Greece, *Rautenberg* 81 (UPS), KX757518, LC423750*; *Silene tunicoides* Boiss., Greece, *Runemark* 5970 (Strid private Hb.), KX757629, LC423751*; *Silene turbinata* Guss., Algeria, *Oxelman* 1886 (GB), X86836, LC423752*; *Silene turkestanica* Regel, Tajikistan, *K. Kiseleva s.n.*, 20 Jun 1970 (MW), FN821147, FN821315; *Silene undulata* Aiton, South Africa, *Bayliss & Abbot* BS7700 (M), KX757332, LC423753*; *Silene ungeri* Fenzl, Greece, *Oxelman & Tollsten* 1431 (GB), KX757641, EF061362; *Silene uralensis* (Rupr.) Bocquet, U.S.A., *Elven & al.* SUP 02-1002-02 (UPS), AJ831781, AJ831765; *Silene variegata* (Desf.) Boiss. & Heldr., Greece, *Strid & al.* 55066 (Strid private Hb.), KX757305, LC423756*; *Silene villosula* (Trautv.) V.V.Petrovsky & Elven, Russia, *Yurtsev s.n.* (LE), KX757381, JF970814; *Silene virgata* Stapf, Turkey, *Podlech s.n.* (M), KX757457, LC423828*; Iran, *Attar* 14212 (TUH), LC424077*, LC423996*; *Silene viridiflora* L., Greece, *Rautenberg* 78 (UPS), KX757504, LC423757*; *Silene viscariopsis* Bornm., Macedonia, *Mayer & al.* 78672 (Strid private Hb.), KX757487, LC423758*; *Silene viscosa* (L.) Pers., Sweden, *Anja Rautenberg* 104 (UPS), FN821148, FN821316; *Silene vittata* Stapf, Turkey, *Oxelman* 2390 (UPS), KX757643, LC423749*; *Silene vulgaris* (Moench) Garcke, Spain, *Mats Thulin* 5717 (UPS), FN821149, FN821317; Iran, *A. Talebi* 43221 (TUH), LC424096*, LC424029*; *Silene waldsteinii* Griseb., Greece, *Rautenberg* 168 (UPS), KX757471, LC423754*; LC424049*, LC423804*; *Silene waltonii* F.N.Williams, China, *Miehe & Miehe* 0343-13 (GB), KX757274, LC423755*; *Silene yemensis* Deflers, Yemen, *Hepper* 5792 (WU), KX757519, LC423759*; *Silene zawadzkii* Herbich, Romania, *Černoch* 47354 (M), KX757363, LC423760*; *Viscaria alpina* (L.) G.Don, Canada, *M. Garneau & al. s.n.*, 4 Aug 1988 (O), FJ384048, FJ384007; *Viscaria asterias* (Griseb.) Frajman, Macedonia, *B. Frajman s.n.*, 11 Jul 2005 (LJU), FJ384051, FJ384010; *Viscaria vulgaris* Bernh., Sweden, *Oxelman* 2199 (GB), FJ384056, FJ376823.

FIGURE LEGENDS

[figures have been prepared to final size, minor adjustments, i.e., to make a caption fit, are ok. Fig. 1: 17.6 cm wide, caption below; Fig. 2A-C: all three parts 17.6 cm wide, main caption below part A, NO body text on pages with Figs. 2B and 2C!; Fig. 3: 17 cm wide, caption below; Fig. 4: 15 cm wide, caption below.]

Fig. 1. Habitats and morphological characters of *Silene* spp. representing different subgenera and sections. **A**, *S. aegyptiaca* (*S. sect. Atocion*); **B–H**, *S. subg. Behenantha*: **B**, *S. ertekinii* (*S. sect. Cryptoneurae*); **C**, *S. latifolia* (*S. sect. Melandrium*); **D**, *S. viscosa* (*S. sect. Physolychnis*); **E**, *S. vulgaris* (*S. sect. Behenantha*); **F**, *S. coniflora* (*S. sect. Conoimorpha*); **G**, *S. noctiflora* (*S. sect. Elisanthe*); **H**, *S. odontopetala* (*S. sect. Odontopetalae*); **I–O**, *S. subg. Silene*: **I**, *S. arabica* (*S. sect. Silene*); **J**, *S. retinervis* (*S. sect. Auriculatae*); **K**, *S. meyeri* (*S. sect. Auriculatae*); **L**, *S. gynodioica* (*S. sect. Auriculatae*); **M**, *S. swertiifolia* (*S. sect. Sclerocalycinae*); **N**, *S. bupleuroides* (*S. sect. Sclerocalycinae*); **O**, *S. italica* (*S. sect. Siphonomorpha*). — Photos: A & B by Z. Toprak; C–H, J–N by F. Jafari; I & O by A. Talebi.

Fig. 2. Species or minimal clusters (SMC) tree of the combined nrDNA ITS and cpDNA *rps16* datasets of *Silene* based on GTR model. Posterior probability values ≥ 0.75 are indicated above branches. *Silene* subg. *Lychnis*, *S. subg. Behenantha* and *S. subg. Silene*, are placed in boxes. The scale bar is proportional to substitution rate per site. Taxon names are followed by specimen identifiers according to suppl. Appendix S1.

Fig. 3. 50% majority-rule consensus tree obtained from the Bayesian inference analysis of the nrDNA ITS sequences of *Silene* and its close relatives including 1586 accessions. Posterior probabilities ≥ 0.75 are shown above branches. The GenBank accession of *S. zawadzkii* is misidentified and indicated here as *S. Not zawadzkii* (see the text). Taxon names are followed by specimen identifiers according to suppl. Appendix S1.

Fig. 4. 50% majority-rule consensus tree obtained from the Bayesian inference analysis of the cpDNA *rps16* sequences of *Silene* and its close relatives including 944 accessions. Posterior probabilities ≥ 0.75 are shown above branches. Taxon names are followed by specimen identifiers according to suppl. Appendix S1.

Fig. S1. Species or minimal clusters (SMC) tree from the nrDNA ITS and cpDNA *rps16* datasets based on GTR model. Posterior probability values of the analysis based on the HKY model are indicated above branches.

Fig. S2A–P. Phylogenetic tree of the nrDNA ITS region reconstructed with FastTreeMP v.2.1.0. Support values of nodes ≥ 0.75 (Shimodaira-Hasegawa test) and ≥ 0.75 (posterior probability) are shown above branches separated by a slash.

Fig. S3A–K. Phylogenetic tree of the cpDNA *rps16* region reconstructed with FastTreeMP v.2.1.0. Support values of nodes ≥ 0.75 (Shimodaira-Hasegawa test) and ≥ 0.75 (posterior probability) are shown above branches separated by a slash.

SUPPL. APPENDICES CAPTIONS

Appendix S1. Voucher information and GenBank accession numbers used for reconstructing the gene trees of nrDNA ITS (Fig. S2A–P) and cpDNA *rps16* sequences (Fig. S3A–K). Dashes represent data downloaded from GenBank. The table is prepared according to the template format extracted from www.sileneae.info

Appendix S2. The nrDNA ITS alignment with 1586 accessions used for reconstructing the gene trees represented in Fig. 3 and suppl. Fig. S2

Appendix S3. The cpDNA *rps16* alignment with 944 accessions used for reconstructing the gene trees represented in Fig. 4 and suppl. Fig. S3

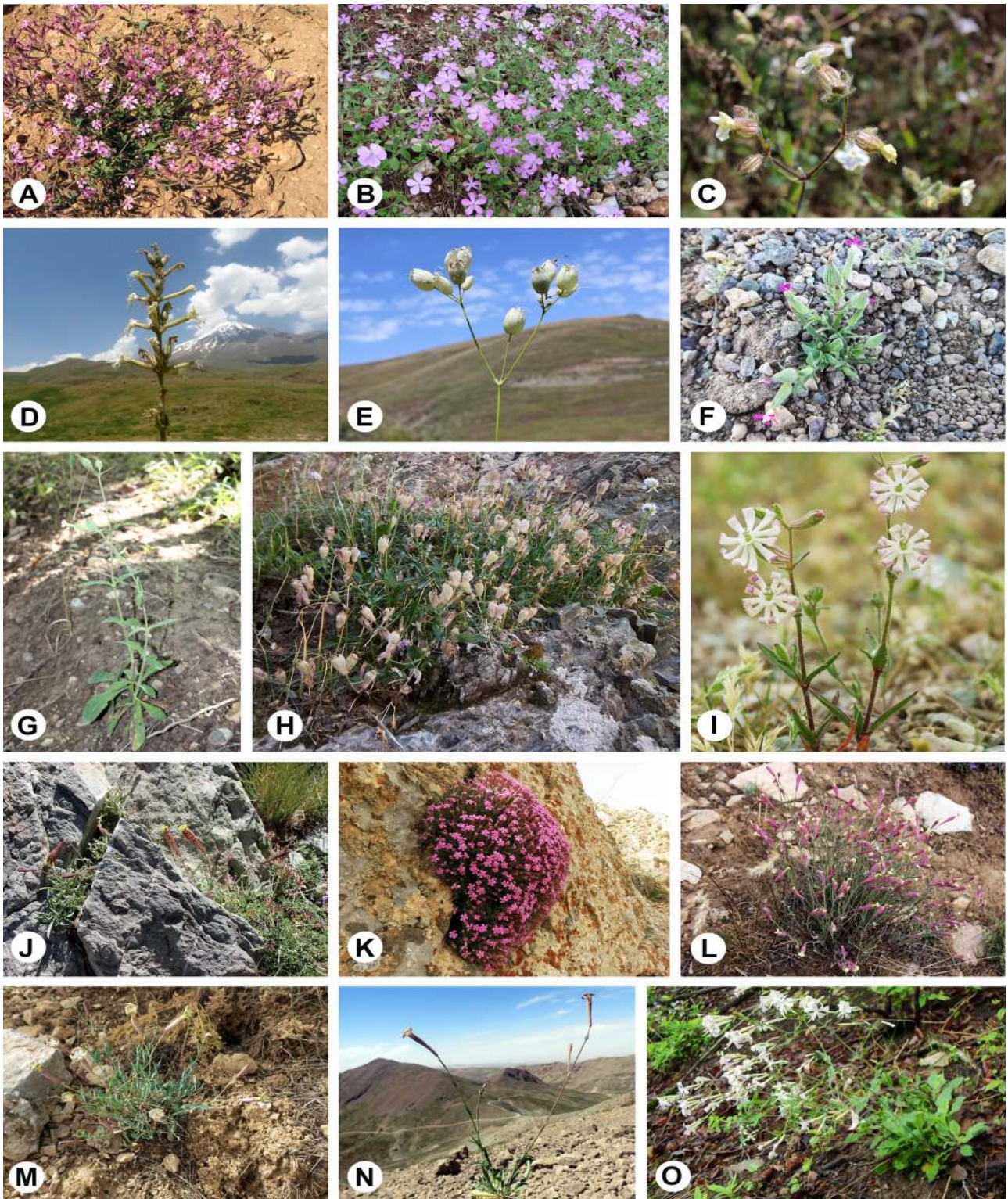
Appendix S4. The nrDNA ITS alignment with 262 accessions used for reconstructing SMC tree in Fig. 2

Appendix S5. The nrDNA *rps16* dataset alignment with 262 accessions used for reconstructing SMC tree in Fig. 2

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.

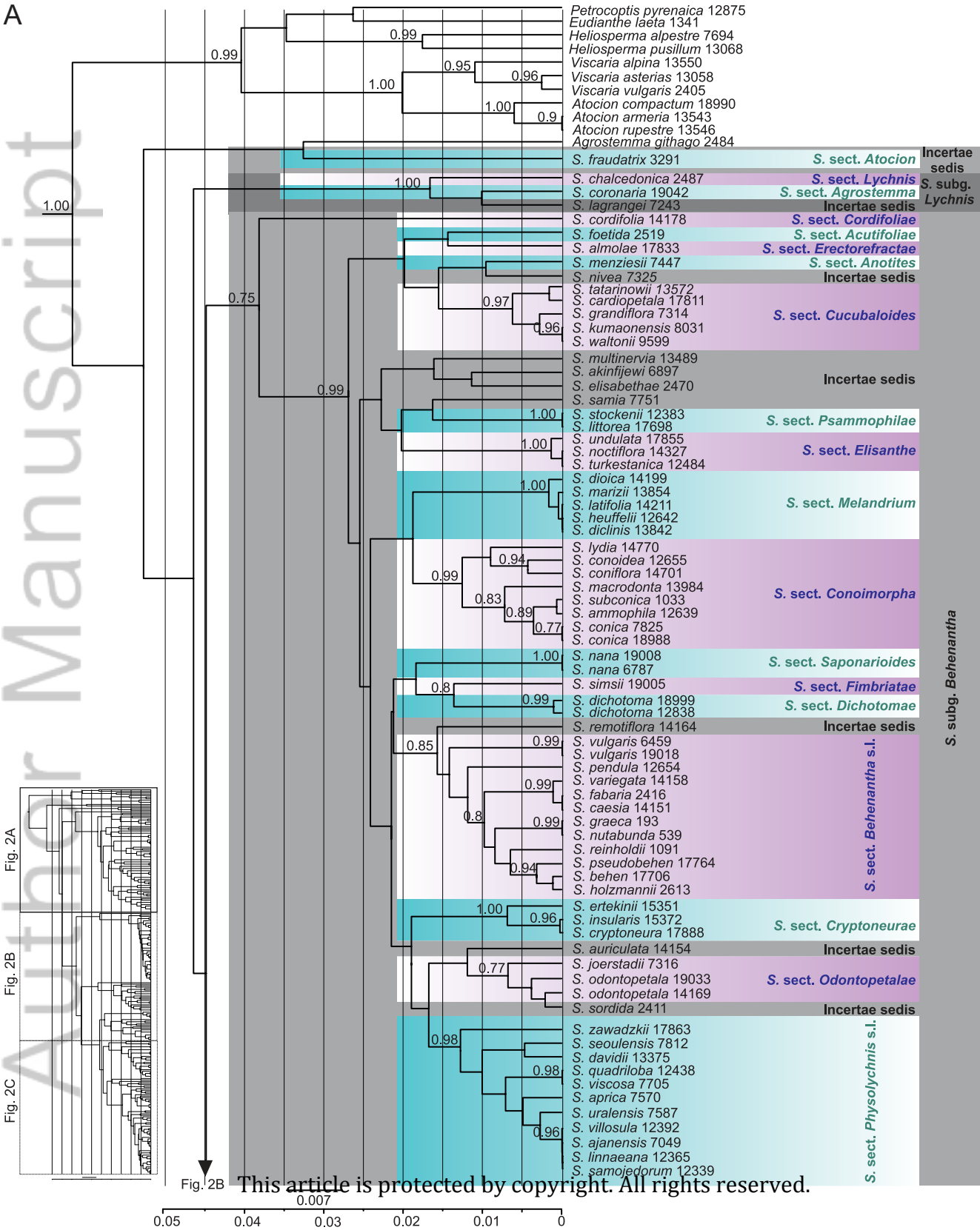
Table 1. Statistics of parsimony analysis for the included datasets.

	nrDNA ITS	cpDNA <i>rps16</i>
Number of samples	1586	944
Aligned matrix length [bp]	891	1719
Constant characters [bp]	327	1024
Variable characters [bp]	160	195
Parsimony-informative characters [bp]	404	500
Consistency index (CI)	0.2308	0.5111
Retention index (RI)	0.9188	0.9396
Homoplasy index (HI)	0.7692	0.4889
Rescaled consistency index (RC)	0.2121	0.4802
Tree length	4306	1937



TAX_12230_Figure_1_RGB_LZW.tif

A



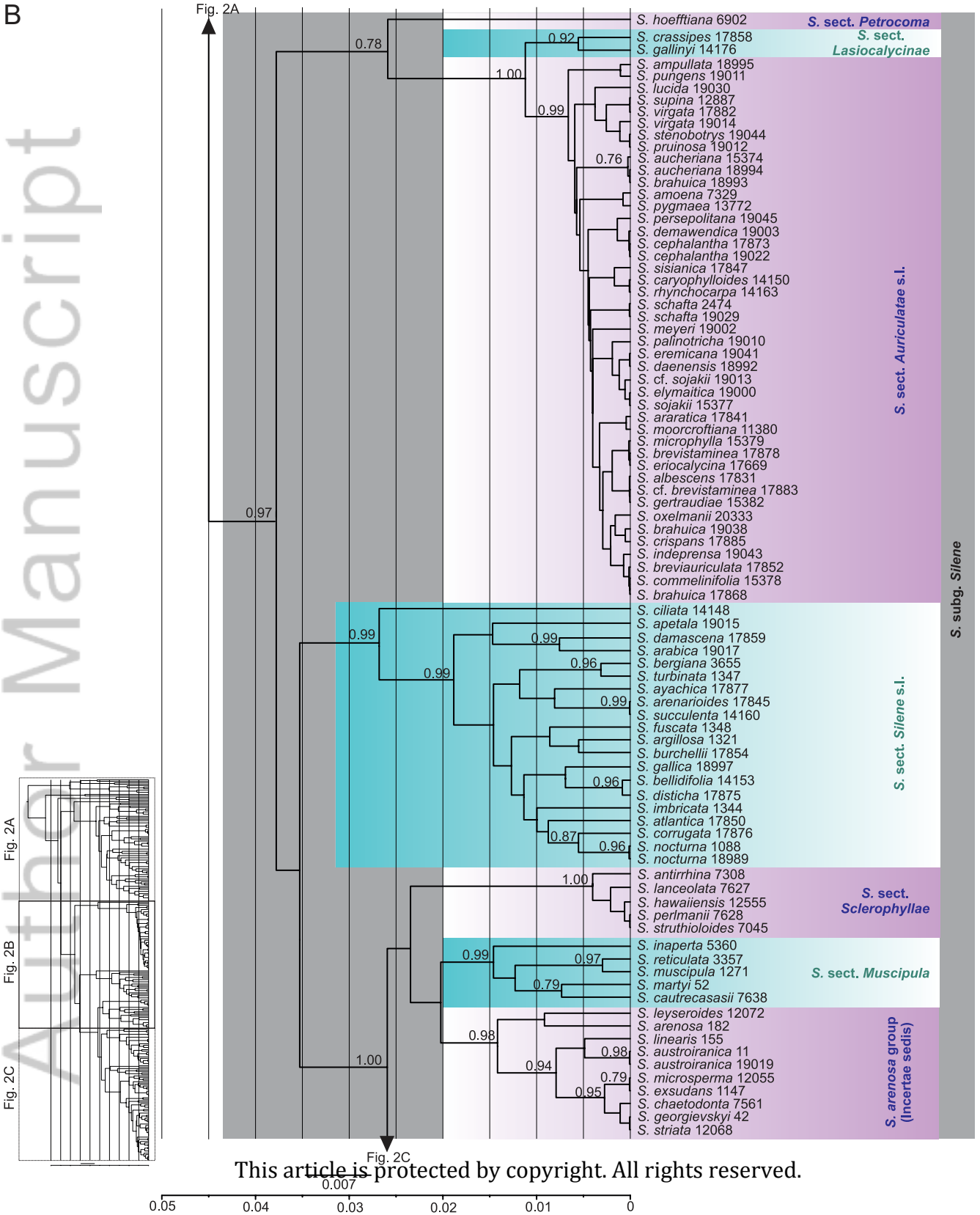
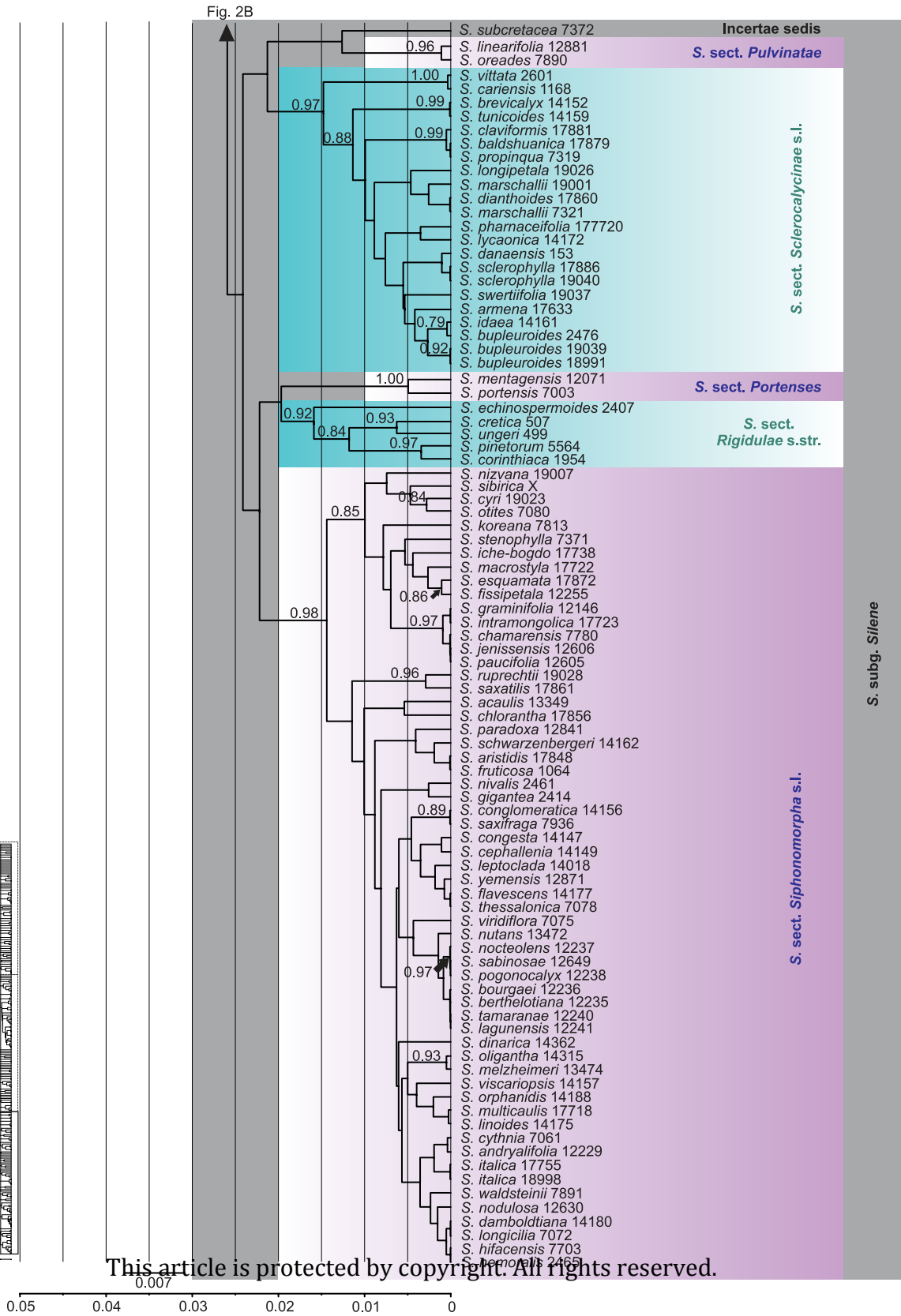


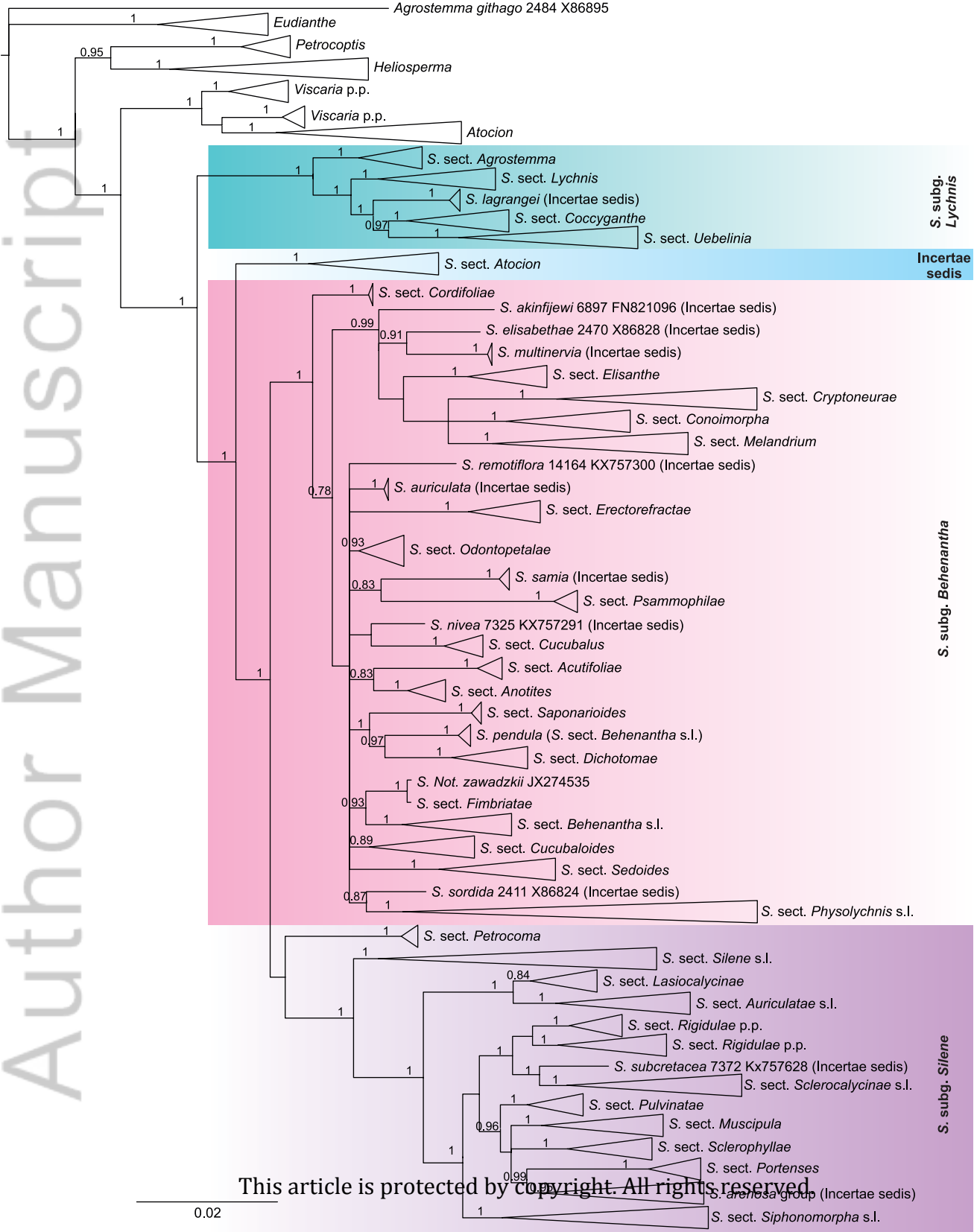
Fig. 2A

Fig. 2B

Fig. 2C



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