

Untangling phylogenetic patterns and taxonomic confusion in tribe Caryophylleae (Caryophyllaceae) with special focus on generic boundaries

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Abstract Assigning correct names to taxa is a challenging goal in the taxonomy of many groups within the Caryophyllaceae. This challenge is most serious in tribe Caryophylleae since the supposed genera seem to be highly artificial, and the available morphological evidence cannot effectively be used for delimitation and exact determination of taxa. The main goal of the present study was to re-assess the monophyly of the genera currently recognized in this tribe using molecular phylogenetic data. We used the sequences of nuclear ribosomal internal transcribed spacer (ITS) and the chloroplast gene *rps16* for 135 and 94 accessions, respectively, representing all 16 genera currently recognized in the tribe Caryophylleae, with a rich sampling of *Gypsophila* as one of the most heterogeneous groups in the tribe. Phylogenetic trees were reconstructed using maximum parsimony and Bayesian inference methods. The results show that most of the large genera of Caryophylleae are not monophyletic. As a result, we propose a new classification system matching both molecular phylogenetic and morphological evidence. The main taxonomic conclusions include: (1) the description of three new genera, (2) treating five small genera as synonyms, (3) resurrecting the genus *Heterochroa* with six species, and (4) proposing 23 new combinations plus 2 replacement names at the specific level. As a result, we recognize 14 genera in Caryophylleae. A diagnostic key to all genera of Caryophylleae is provided.

Keywords carnation; *Dianthus*; *Gypsophila*; *Saponaria*; systematics; taxonomic revision

Supplementary Material DNA sequence alignments are available from <https://doi.org/10.12705/671.6.S>

■ INTRODUCTION

Assigning correct names to plant taxa as the basic elements of ecosystems is a critical first step for any biodiversity inventory or monitoring program. Such inventory programs are very important for resource management and conservation planning. In the flora of SW Asia, Caryophyllaceae are abundant in various natural ecosystems, but the delimitation of taxa in the family is problematic with issues such as clinal trends in morphological traits blurring the borders between taxa, frequent hybridization in some genera (such as *Dianthus* L., see Vítová & al., 2015), and seemingly artificial taxonomic borders appearing at various ranks.

The focal group of the present study is tribe Caryophylleae Lam. & DC., including about 630 species assigned currently to 16 genera (Hernández-Ledesma & al., 2015). It is, after tribe Sileneae DC., the second-largest tribe in family Caryophyllaceae (Bittrich, 1993; Harbaugh & al., 2010; Greenberg & Donoghue, 2011; Pirani & al., 2014; Hernández-Ledesma & al., 2015; R. Rabeler, personal data). The members

of the tribe are primarily Holarctic, with their diversity centered in Mediterranean and Irano-Turanian regions and few taxa extending to Africa. Like many other members of the large clade Plurcaryophyllaceae (sensu Greenberg & Donoghue, 2011), they are perennial or annual herbs, sometimes woody at base or even spiny cushions (e.g., *Acanthophyllum* C.A.Mey. spp.) characterized by five fused sepals, five more or less clawed petals, ten free stamens, and capsules opening with four, or rarely six, teeth (Bittrich, 1993). Some representative images of these plants are presented in Fig. 1. Contrary to the members of closely related tribe Sileneae, the commissural veins are absent or scarcely evident on the calyx tube in members of Caryophylleae. Many species are well-known ornamental plants (e.g., carnation: *Dianthus* spp., baby's-breath: *Gypsophila* L. spp.), used as source of triterpene saponins (e.g., *Acanthophyllum* spp.), or known as important weeds (e.g., *Gypsophila* spp.). Some species are important components of mountainous steppes (e.g., *Acanthophyllum* spp.) or saxicolous vegetation (e.g., *Dianthus* spp., *Gypsophila* spp.) in Europe, Central and Southwest (SW) Asia. The largest

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genera are *Dianthus* (ca. 300 spp.), *Gypsophila* (ca. 150 spp.), *Acanthophyllum* (ca. 90–100 spp.), *Petrorrhagia* (Ser.) Link (ca. 33 spp.), and *Saponaria* L. (ca. 30 spp.).

The monophyly of tribe Caryophylleae and some of its large genera such as *Dianthus* and *Acanthophyllum* are confirmed

by both morphological and molecular evidence (Fior & al., 2004; Harbaugh & al., 2010; Greenberg & Donoghue, 2011; Pirani & al., 2014), although some transfers and synonymy are still necessary to make these genera entirely monophyletic. *Dianthus* (including *Velezia* L.) as the largest genus of the tribe

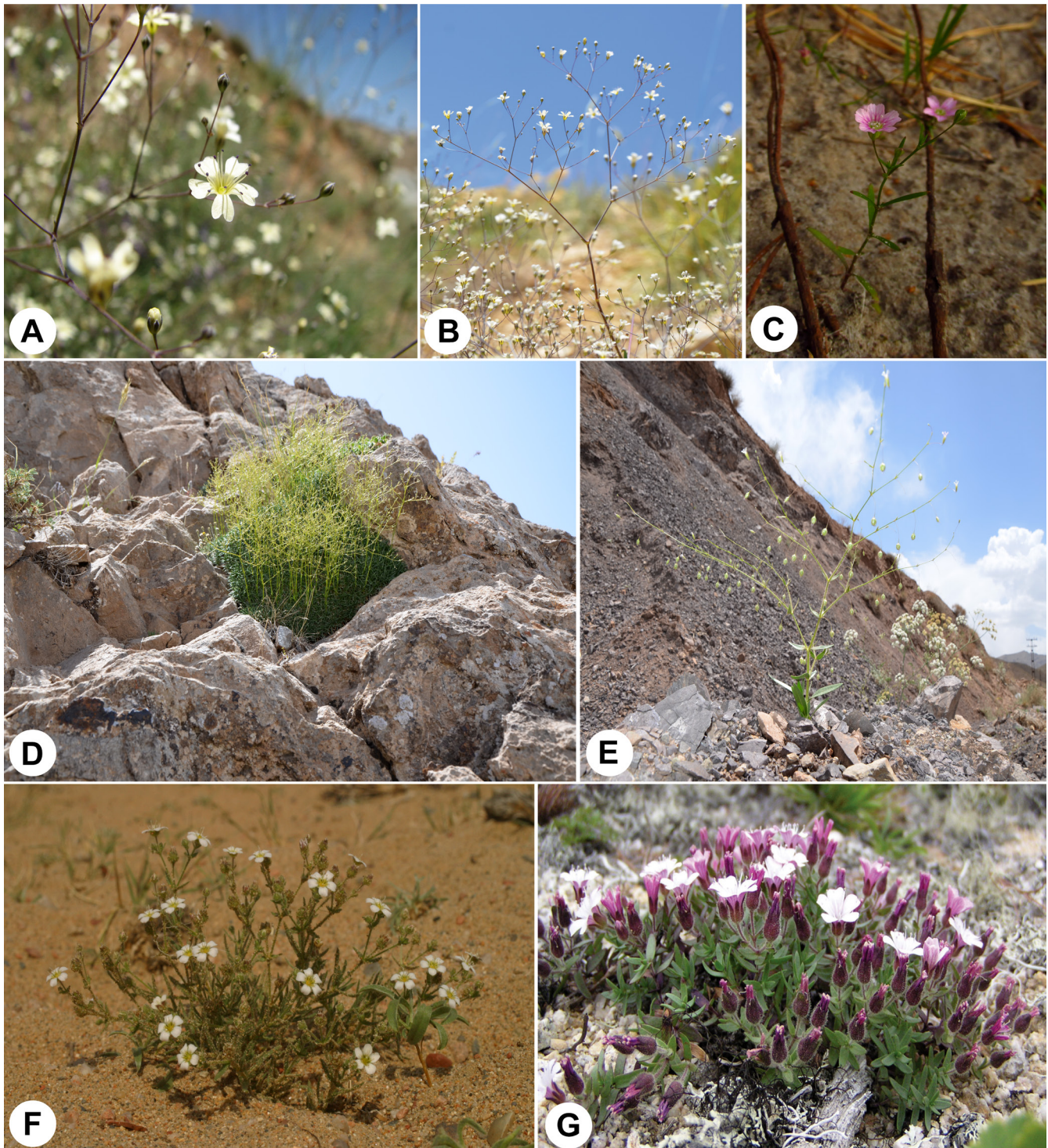


Fig. 1. (in two parts) Selected members of Caryophylleae in their natural habitat. **A & B**, *Gypsophila leioclada* (by H. Madhani); **C**, *Psammophiliella muralis* (by Natalia Gamow); **D**, *Gypsophila acantholimoides* (by H. Madhani); **E**, *G. pilosa* (by H. Madhani); **F**, *G. desertorum* (by Martin Schnittler in <http://floragreif.uni-greifswald.de>); **G**, *G. violacea* (by I. Khan in <http://www.plantarium.ru>); (continued on next page)

is monophyletic (Harbaugh & al., 2010; Valente & al. 2010; Greenberg & Donoghue, 2011) and is characterized by the presence of an epicalyx consisting of discrete bracteoles subtending the calyx (except *Velezia*), numerous fine veins on the calyx tube, and dentate or fimbriate petal apices in most species.

Acanthophyllum, with a predominantly cushion habit and spiny leaves, should include taxa formerly assigned to *Allochrusa* Bunge, *Ochotonophila* Gilli, *Scleranthopsis* Rech.f. and part of *Diaphanoptera* Rech.f (Pirani & al., 2014). However, the monophyly of other genera such as *Bolanthus* (Ser.) Rchb.,

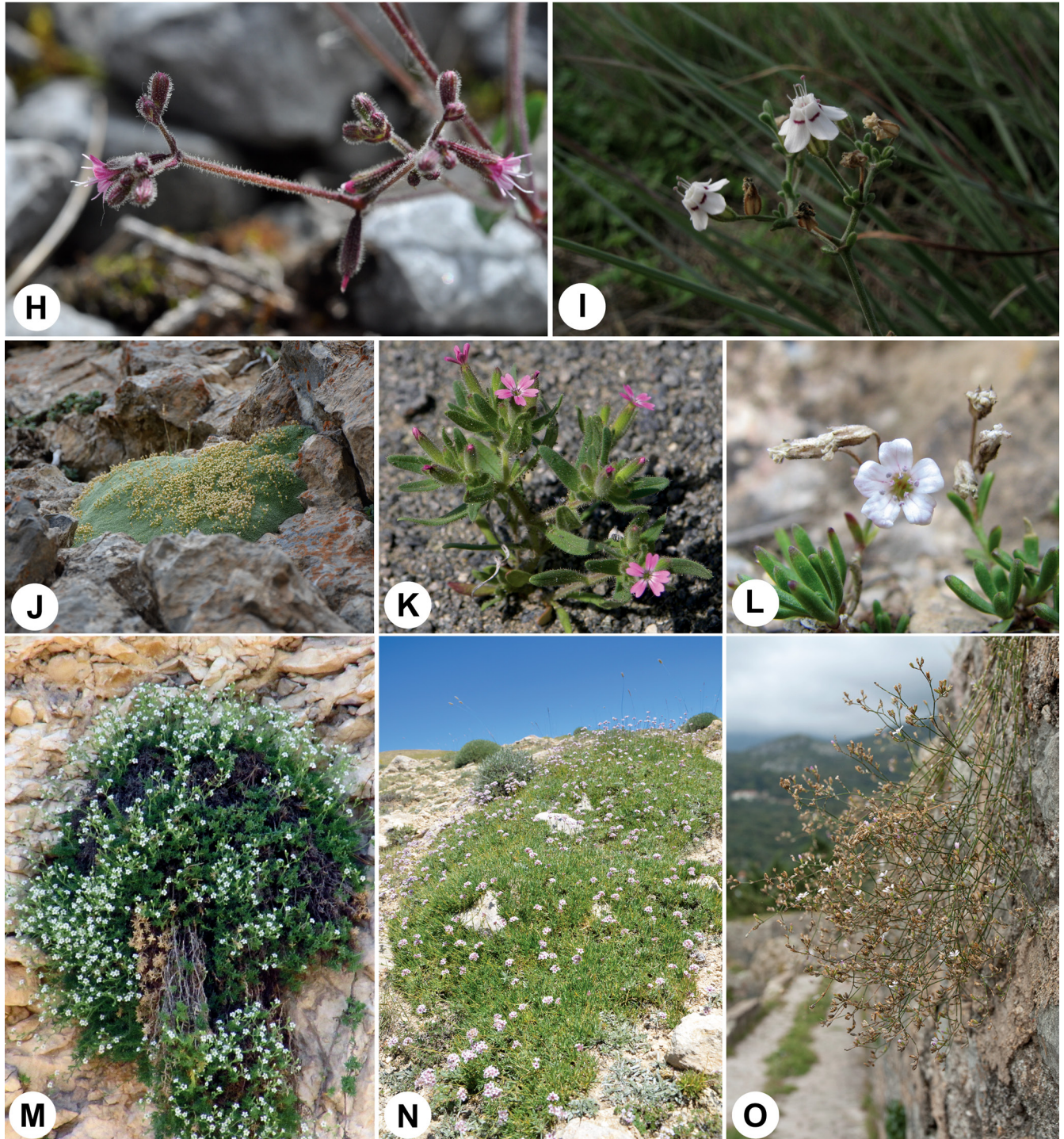


Fig. 1. (continued from previous page) **H**, *Psammosilene tunicoides* (by J.T. Johansson in <http://angio.bergianska.se>); **I**, *Bolanthus fruticosus* (by Armin Jagel); **J**, *G. aretioides* (by H. Madhani); **K**, *Saponaria viscosa* (by S. Banquet in <http://www.plantarium.ru>); **L**, *G. saponarioides* (by H. Madhani); **M**, *Gypsophila montserratii* (by A. Gutiérrez & S. Fajárnés); **N**, *Gypsophila bazorganica* (by Navid Madhani); **O**, *Petrorhagia saxifraga* (by D. Oreshkin in <http://www.plantarium.ru>).

Table 1. Classification history of Caryophylleae (tribes in bold, subtribes underlined) and its allied genera in Sileneae.

Candolle (1824)	Fenzl (1840)	Bentham & Hooker (1862)	Boissier (1867)	Pax & Hoffmann (1934)	Schischkin (1936)	Šourková (1978)	Bittrich (1993)	Harbaugh & al. (2010)
	Diantheae <i>Dianthus</i> subg. <i>Tunica</i> <i>Velezia</i>	Diantheae <i>Dianthus</i> <i>Tunica</i> <i>Velezia</i>	Diantheae <i>Dianthus</i> <i>Tunica</i> <i>Velezia</i>	Diantheae <i>Acanthophyllum</i> <i>Dianthus</i> <i>Gypsophila</i> subg. <i>Ankyropetalum</i> subg. <i>Bolanthus</i> <i>Phrynella</i> <i>Saponaria</i> <i>Tunica</i> sect. <i>Kohlrauschia</i> <i>Vaccaria</i> <i>Velezia</i>	Diantheae <i>Acanthophyllum</i> subg. <i>Allochrysa</i> <i>Dianthus</i> <i>Gypsophila</i> <i>Kohlrauschia</i> <i>Saponaria</i> <i>Tunica</i> <i>Vaccaria</i> <i>Velezia</i>	Diantheae <i>Dianthinae</i> <i>Dianthus</i> <i>Petrorhagia</i> <i>Velezia</i> <u><i>Gypsophilinae</i></u> <i>Gypsophila</i> <i>Phrynella</i> <i>Saponaria</i> <i>Vaccaria</i>	Caryophylleae <i>Acanthophyllum</i> <i>Allochrysa</i> <i>Ankyropetalum</i> <i>Bolanthus</i> <i>Cyathophylla</i> <i>Dianthus</i> <i>Diaphanoptera</i> <i>Gypsophila</i> <i>Kohlrauschia</i> <i>Ochotonophila</i> <i>Petrorhagia</i> <i>Phrynella</i> <i>Pleioneura</i> <i>Saponaria</i> <i>Scleranthopsis</i> <i>Vaccaria</i> <i>Velezia</i>	Caryophylleae <i>Acanthophyllum</i> <i>Allochrysa</i> <i>Dianthus</i> <i>Gypsophila</i> <i>Petrorhagia</i> <i>Saponaria</i> <i>Vaccaria</i> <i>Velezia</i>
Sileneae <i>Banffya</i> <i>Cucubalus</i> <i>Dianthus</i> <i>Drypis</i> <i>Gypsophila</i> sect. <i>Petrorhagia</i> <i>Lychnis</i> sect. <i>Viscaria</i> sect. <i>Agrostema</i> <i>Saponaria</i> sect. <i>Bolanthus</i> sect. <i>Vaccaria</i> <i>Silene</i> <i>Velezia</i>	Lychnideae <i>Cucubalus</i> <i>Gypsophila</i> sect. <i>Heterochroa</i> <i>Lychnis</i> <i>Saponaria</i> <i>Silene</i> <i>Vaccaria</i> <i>Viscaria</i>	Sileneae <i>Acanthophyllum</i> <i>Cucubalus</i> <i>Dianthus</i> <i>Drypis</i> <i>Gypsophila</i> sect. <i>Ankyropetalum</i> <i>Lychnis</i> sect. <i>Viscaria</i> <i>Saponaria</i> sect. <i>Vaccaria</i> sect. <i>Agrostema</i> <i>Silene</i> <i>Tunica</i> <i>Uebelimia</i> <i>Velezia</i>	Lychnideae <i>Acanthophyllum</i> <i>Allochrysa</i> <i>Ankyropetalum</i> <i>Cucubalus</i> <i>Drypis</i> <i>Githago</i> <i>Gypsophila</i> <i>Lychnis</i> <i>Melandrium</i> <i>Saponaria</i> <i>Silene</i> <i>Tunica</i>	Lychnideae <i>Cucubalinae</i> <i>Cucubalus</i> <u><i>Drypidinae</i></u> <i>Drypis</i> <i>Silennae</i> <i>Heliosperma</i> <i>Lychnis</i> <i>Melandrium</i> <i>Petrocoptis</i> <i>Silene</i> <i>Uebelimia</i> <i>Viscaria</i>	Lychnideae <i>Agrostemma</i> <i>Coronaria</i> <i>Cucubalus</i> <i>Lychnis</i> <i>Melandrium</i> <i>Petrocoma</i> <i>Silene</i> <i>Viscaria</i>	Lychnideae <i>Agrostemma</i> <i>Behenantha</i> <i>Coronaria</i> <i>Cucubalus</i> <i>Lychnis</i> <i>Melandrium</i> <i>Petrocoma</i> <i>Petrocoptis</i> <i>Pleconax</i> <i>Polyschemone</i> <i>Schischkiniella</i> <i>Steris</i> (<i>Viscaria</i>) <i>Silene</i> <i>Uebelimia</i>	Sileneae <i>Agrostemma</i> <i>Lychnis</i> <i>Petrocoptis</i> <i>Silene</i> <i>Uebelimia</i>	Sileneae <i>Agrostemma</i> <i>Lychnis</i> <i>Petrocoptis</i> <i>Silene</i>
	Drypideae <i>Drypis</i> <i>Acanthophyllum</i>					Drypideae <i>Acanthophyllinae</i> <i>Acanthophyllum</i> <u><i>Drypidinae</i></u> <i>Drypis</i>	Drypideae <i>Drypis</i>	Drypideae <i>Drypis</i>
							Insufficiently known genus <i>P-sammosilene</i>	

Gypsophila, *Petrorragia*, *Saponaria*, and *Vaccaria* Wolf has not been adequately addressed (Kadereit & al., 2016) in previous molecular phylogenetic studies (Fior & al., 2006; Harbaugh & al., 2010; Greenberg & Donoghue, 2011).

The taxonomy of this group has been subject of several treatments (for a review, see Table 1). The confusion began as Haller (1742) described *Tunica* with the names *Dianthus* and *Caryophyllus* below it (probably as synonyms or equivalents). Without naming any species of *Tunica*, Ludwig (1757) applied this name beside *Dianthus*, making the former a synonym of the latter. Using the generic name *Tunica*, replacing *Dianthus*, was followed by Scopoli (1771) when he replaced even the type of *Dianthus* with a *Tunica* (as *T. caryophyllus* (L.) Scop.). *Tunica* was later used by several authors (e.g., Boissier, 1867) as a genus distinct from *Dianthus*; the genus in this usage is now treated as a synonym of *Petrorragia* (for a detailed bibliography see Ball & Heywood, 1964). In addition, Linnaeus (1753) could not clearly delimit *Gypsophila*, *Saponaria*, and *Tunica*; some of the species that he described as members of *Gypsophila* are considered today as members of *Saponaria*, *Petrorragia*, and *Arenaria* L. There are only four genera of Caryophylleae (*Dianthus*, *Gypsophila*, *Saponaria*, *Velesia*) in its modern definition (sensu Harbaugh & al., 2010) that were first described by Linnaeus (1753). These genera plus a few more were assigned to tribe Sileneae by Candolle (1824). Among the genera currently assigned to Caryophylleae, six genera were recognized by Fenzl (1840) who classified them in three different tribes: Diantheae, Lychnideae Fenzl and Drypideae Fenzl. Bentham (1862) put all these genera in tribe Sileneae. In *Flora Orientalis*, Boissier (1867) adopted a system almost similar to Fenzl (1840) but added the genus *Tunica* (in this usage, a synonym of *Petrorragia*, see Ball & Heywood, 1964; Rabeler, 1984) to this list and divided these seven genera between two tribes: Diantheae and Lychnideae. Pax & Hoffmann (1934) also accepted the tribe name Diantheae and added the genus *Phrynella* Pax & K.Hoffm. to it in *Die natürlichen Pflanzenfamilien*. In *Flora U.R.S.S.* (Schischkin, 1936), the tribe Diantheae encompasses eight genera also including *Acanthophyllum* (divided into two subgenera: subg. *Acanthophyllum* and subg. *Allochrysa* (Bunge) Schischk.) and *Kohlrauschia* Kunth as well as *Tunica* in the sense of *Petrorragia*. In other floristic works such as *Flora Europaea* (Tutin & al., 1964), *Flora of Turkey* (Reeve & al., 1967) and *Flora Iranica* (Rechinger, 1988), the traditional subfamilial classification system (including three subfamilies: Illecebroideae Arn. [= Paronychioideae A.St.Hil ex Fenzl], Minuartioideae DC. [= Alsinoideae Beilschm.], Caryophylloideae Arn. [= Silenoideae Arn.]) has been applied to these genera, and Caryophylleae is assigned to subfamily Caryophylloideae.

There are relatively few monographs of genera of Caryophylleae. Bittrich (1993) provides the most recent comprehensive synopsis of the Caryophylleae, dividing the tribe into 17 genera. The monographic work on *Gypsophila* and its related genera (Barkoudah, 1962) has provided the primary source for determination of species in *Gypsophila* and *Bolanthus*. The genus *Petrorragia* was revised by Ball &

Heywood (1964), with Rabeler (1984) providing additional nomenclatural clarification. No recent monograph exists for *Dianthus*, with the most recent infrageneric classification appearing in Pax & Hoffman (1934), or for *Saponaria*, with the only monograph published by Simmler (1910) and Shults (1989) providing additional information for taxa occurring in Russia.

Recent molecular phylogenetic studies on Caryophyllaceae have indicated the necessity for major changes in the classification of the family and rejected the subfamilial system, which has commonly been in use (Fior & al., 2006; Harbaugh & al., 2010; Greenberg & Donoghue, 2011). Today, the family is divided into 11 tribes including Caryophylleae with *Dianthus caryophyllus* L. as type (Harbaugh & al., 2010). Until now, 12 of the Caryophylleae genera accepted by Hernández-Ledesma & al. (2015) have been included in molecular analyses, but genera such as *Gypsophila*, *Petrorragia* and *Saponaria* are poorly represented.

Gypsophila is one of the most heterogeneous and largest groups. The genus comprises approximately 150 species of annual or perennial herbaceous, creeping or cushion-forming plants, inhabiting primarily the mountainous steppes in the north temperate part of the Old World with a diversification hotspot in the Irano-Turanian region (Barkoudah, 1962; Amini & al., 2011). These species also show major variation in inflorescence type ranging from many-flowered lax thyrses or panicles (e.g., *G. elegans* M.Bieb., *G. paniculata* L., *G. pilosa* Huds.) to compact head-like cymes (*G. capitata* M.Bieb., *G. capituliflora* Rupr., *G. caricifolia* Boiss.), and few-(uni)-flowered raceme-like monochasia (e.g., *G. bazor-ganica* Rech.f., *G. saponarioides* Bornm. & Gauba). The morphological differences between *Ankyropetalum* Fenzl, *Bolanthus*, *Gypsophila* and *Phrynella* are minor (Table 2) and their delimitations appear artificial.

The main focus of the present study is to clarify the generic delimitation in Caryophylleae. The detailed aims of the study are: (1) to elucidate phylogenetic relationships and natural groupings in Caryophylleae, (2) to clarify the limits of the genera in the tribe, (3) to test the monophyly of *Gypsophila* and its closely related genera, and (4) to assess evolutionary progressions for morphological traits applied in former generic classifications of the tribe Caryophylleae.

■ MATERIALS AND METHODS

Taxon sampling. — This investigation is based primarily upon specimens deposited in the herbaria: B, G, LE, M, MSB and TUH. Over 2000 herbarium sheets of the representatives of Caryophylleae have been determined/revised and studied.

The present study is the largest phylogenetic study on the tribe in terms of both numbers of genera and species. Since the tribe itself was proven to be monophyletic in previous analyses with tribe Eremogoneae Rabeler & W.L.Wagner or Sileneae as outgroup (Harbaugh & al., 2010; Greenberg & Donoghue, 2011), we included 12 representatives of the most

Table 2. Characteristics of genera of Caryophylleae according to Bittrich (1993) and revisions proposed by Pirani & al. (2014).

	<i>Gypsophila</i>	<i>Saponaria</i>	<i>Ankyropetalum</i>	<i>Pleioneura</i>	<i>Vaccaria</i>	<i>Acanthophyllum</i>	<i>Phrynella</i>
Type	<i>G. repens</i> L.	<i>S. officinalis</i> L.	<i>A. gypsophilooides</i> Fenzl	<i>Pl. griffithiana</i> (Boiss.) Rech.f.	<i>V. pyramidata</i> Medik.	<i>A. mucronatum</i> C.A.Mey.	<i>Ph. ortegioides</i> Pax & K.Hoffm.
Chromosome number	2n = 24, 26, 28, 30, 34, 36, 48, 51, 60, 68	2n = 28, 56	2n = 26	–	2n = 24, 30	2n = 26, 30, 60, 90	–
No. of species	ca. 150	ca. 30	4	1	1	ca. 90–100	1
Habit	Annual and perennial, sometimes densely caespitose	Perennial, rarely annual herbs	Perennial, densely caespitose to densely pulvinate	Perennial herbs with thick rhizome (geophyte)	Annual glabrous herbs	Small, shrubby, cushion-forming perennials with spiny leaves, or rarely perennial herbs	Perennial herb with woody caudex, rigid stem,
Seed shape	Reniform	Reniform to almost globular	Reniform-globose, with marginal hilum, with granular wrinkles	Globular-reniform, compressed	Reniform or globose	Obovoid-reniform	Oblong, comma-shaped, with a marginal hilum
Inflorescence type/position	Paniculate or head-like cyme	Lax or dense paniculate or capitate cymes, rarely solitary	Lax cymes	Panicle cymes	Inflorescence terminal, regularly dichasial, lax, richly branched	Dichasial cymes arranged in terminal heads and/or axillary verticillasters, sometimes paniculate or corymbose	Dichasial inflorescence very often reduced to solitary sessile flowers
Calyx	Hemispherical, campanulate, turbinate, or rarely tubular, 5-nerved with broad scarious commissures, 5-toothed	Cylindrical, obscurely 15–25-veined	Campanulate-tubular, 5-nerved with 5 small teeth	Tubular, 15-nerved, 5-toothed	Ovoid with 5 prominent angles	Tubular-turbinate, 5–15-nerved, 5-toothed	Long-campanulate, up to about 1/3 divided in teeth, 5-costate, the ribs alternating with hyaline intervals
Embryo	(Circular) peripheral, central endosperm, with prominent radicle	(Curved) peripheral, central endosperm	Peripheral; endosperm central	Curved	Curved	Unciform or strongly curved	Hook-shaped, with a straight prominent radicle
Petals	Entire or slightly emarginate	Mostly distinctly clawed, coronal scales usually present	Clawed, limb 3(–5)-partite	Pink, with narrowly winged claw, limb entire, coronal scales present	5, pink or purple, clawed, limb entire, dentate or notched, coronal scales absent	Limb entire, sometimes bifid, gradually tapering into claw	Cuneate, with a bare claw and without corona
Capsule	Always exceeding the calyx, dehiscence	Opening by 4(6) teeth	Dehiscing from base by irregular longitudinal slits	Capsule opening by 4 teeth	With papery exocarp opening by 4 teeth, endocarp dehiscing irregularly	1- or 2-seeded, mode of dehiscence various	Long-ovoid, opening with 4 fissures extending to the middle, with 1–3 seeds
Ovules number	4–36	2–14	8–10	12	Numerous	4(–21)	8
Special features	–	Seeds usually smooth and shiny	Gynophore absent, ovary more or less sessile	Coronal scales present	Seeds shiny	Bracts and leaves mostly spiny	Calyx with one to four pairs of bracteoles at base (epicalyx)
Distribution	Temperate Eurasia, E Mediterranean, and Irano-Turanian region, Egypt, Arabia, Somalia, Australia	Temperate Eurasia, chiefly in Mediterranean and Irano-Turanian region	Turkey, Iran, Iraq, Lebanon, Syria, Palestine	From C Asia to W Himalaya; Afghanistan	C, E & S Europe; Asia	C, W & SW Asia, Siberia	S & C Turkey

Table 2. Continued.

	<i>Bolanthus</i>	<i>Petrorhagia</i>	<i>Velezia</i>	<i>Dianthus</i>	<i>Cyathophylla</i>	<i>Psammosilene</i>	<i>Diaphanoptera</i>
Type	<i>B. hirsutus</i> (Labill.) Barkoudah	<i>P. saxifraga</i> (L.) Link	<i>V. rigida</i> L.	<i>D. caryophyllus</i> L.	<i>C. chlorifolia</i> (Poir.) Bocquet & Strid	<i>P. tunicoides</i> W.C. Wu & C.Y. Wu	<i>D. khorasanica</i> Rech.f.
Chromosome number	2n = 20, 30	2n = 26, 28, 30, 60	2n = 28	2n = 30, 60, 90	2n = 30	2n = 28	–
No. of species	ca. 18	ca. 33	2	ca. 300	1	1	6
Habit	Perennial, puberulent to hirsute, grey-green to velvety herbs, with thin short stems and small leaves	Annual and perennial herbs	Annual, rigid, dichotomously branching herbs	Annual or perennial herbs, rarely subshrubs	Annual herbs	Perennial puberulent herbs	Perennial and tufted herbs, woody at base
Seed shape	Comma-shaped, compressed on both sides, with flat or channelled back; testa with small tubercles; hilum marginal	Peltate with facial hilum	Peltate with facial hilum	Peltate with facial hilum	Roundish, reddish brown to blackish,	Peltate	Reniform
Inflorescence type/position	Contracted dichasial cymes	Panicles or capitate cymes	Solitary or monochasial cymes	Solitary or capitate terminal cymes often subtended by bracts	Terminal heads subtended by bowl-shaped, entire involucre	Terminal cymes	Lax few-flowered cymes
Calyx	Tubiform, pentagonal, turbinate at base, with small teeth and with 5 projecting ribs alternating with comparatively broad hyaline bands	Cylindrical or campanulate, 5-toothed, 5–15-nerved, with scarious commissures	Tubular, usually (5–)15-nerved, without scarious commissures, 1–3 bracts in form of epicalyx present	Tubular with many parallel veins, without membranous commissures, 5-toothed	Cylindrical with 5 short teeth, without scarious commissures and commissural veins	Tubular, 15-nerved, 5-toothed	Turbinate or vase-shaped
Embryo	Hook-shaped, with long prominent radicle, peripheral	Straight	Straight	Straight	Curved	Straight	Curved
Petal	Entire, cuneate, with small limb and winged claw	5, entire or bifid, clawed or not, coronal scales absent	5(10), long-clawed with small 2–4-toothed or emarginated limb, coronal scales absent	White, pink or red, rarely yellow, limb entire, toothed or fimbriate, without coronal scales, claw long, with two longitudinal ridges	Linear oblong, inconspicuous	5, purple-violet, inconspicuously clawed, entire	5, rose or violet, entire or emarginate
Capsule	Longer than sepals, with 4 teeth	Opening by 4 teeth	4 teeth splitting into 2 valves	Opening by 4 teeth	Opening by 4 teeth	Membranous, probably indehiscent, 1-seeded	4-valved
Ovules number	8–20	Numerous	Few	Numerous	Unknown	2	(6–)8–19
Special features	Seeds smooth and shiny	Leaves narrow, grass-like	Sepal hardened at the apex and margin	Epicalyx scales two to many	Bowl-shaped involucre subtending inflorescence	Nearly non-splitting, 1-seeded and membranous in texture	Inflated calyx, winged at ribs, caespitose woody cushions
Distribution	Greece, S Turkey, Syria, Lebanon, Palestine	Europe, from Mediterranean to Kashmir, and on Canary Islands	Sino-Himalaya, and from the Mediterranean east to Afghanistan	Europe, Asia, especially Mediterranean, Africa	Mountains of Greece and Turkey	China, prov. Yunnan	High altitude of NE Iran, Turkmenistan, and Afghanistan

closely related tribes to Caryophylleae (i.e., Alsineae Lam. & DC., Arenarieae Kitt., Eremogoneae and Sileneae) in our analyses in order to keep the effect of sequence homoplasy on tree reconstruction at minimum. In general, six species of different clades known in *Silene* L. (Sileneae), one species each of *Cerastium* L. and *Stellaria* L. (Alsineae), two species of *Eremogone* Fenzl (Eremogoneae), one species each of *Arenaria* and *Moehringia* L. (Arenarieae) were selected as outgroups according to the results of previous molecular phylogenetic studies (Harbaugh & al., 2010; Greenberg & Donoghue, 2011). Within the tribe, we tried to perform a balanced sampling representing almost all major morphological lineages known to us based on personal experience and examining pertinent literature. Therefore, the present study allows us to define the genera in Caryophylleae more appropriately, matching morphological, geographical and molecular phylogenetic evidence.

We produced a dataset of nrDNA ITS with 136 (59 new sequences and 77 obtained from GenBank) accessions representing 112 species, and a dataset of cpDNA *rps16* with 94 (58 new sequences and 36 obtained from GenBank) accessions representing 85 species. Dissatisfied with the poor sampling of *Gypsophila* in previous molecular phylogenetic studies, we focused more intensively on this genus, and generated sequences for 44 and 34 species of this genus for nrDNA ITS and cpDNA *rps16*, respectively. For this purpose we attempted to sample all subgenera and sections recognized in Barkoudah (1962). Representatives of four formerly recognized genera of Caryophylleae, i.e., *Ankyropetalum*, *Bolanthus*, *Cyathophylla* Bocquet & Strid, and *Phrynella* as well as the new genera described in this paper, i.e. *Balkana* gen. nov., *Graecobolanthus* gen. nov., were sequenced in this study for the first time. The voucher specimens for the sequences generated in this study (Appendix 1) are deposited in B, M, MSB and/or TUH.

DNA extraction, amplification and sequencing. — The present study was performed based on two molecular markers, one nuclear: the internal transcribed spacer (ITS) region of the ribosomal cistron (consisting of ITS1, the intervening 5.8S gene, and ITS2) and one plastid intron: *rps16*. DNA was extracted from dried leaf material using a NucleoSpin Plant DNA extraction kit (Macherey-Nagel, Düren, Germany) according to the manufacturers' protocol. Amplification of the ITS region was performed using the primer pair Leul (Vargas & al., 1998) and ITS4 (White & al., 1990). In some difficult cases ITS2 and ITS3 were used, as described by White & al. (1990). For the plastid region (complete intron *rps16*), we used the primers rpsF and rpsR2R or rpsF and rpsR3R (Oxelman & al., 1997; Petri & Oxelman, 2011; Kool & al., 2012). All PCR amplifications were performed in a Thermocycler T-Personal 48 (Biometra, Göttingen, Germany), Primus 96 plus (MWG: Biotech, Ebersberg, Germany), or 2720 (Applied Biosystems, Carlsbad, California, U.S.A.).

Cycle sequencing was done using BigDye Terminator v.3.1, Cycle Sequencing Kit (Applied Biosystems). DNA samples were sequenced with ABI3730 DNA Analyser 48-well capillary sequencer (Applied Biosystems).

Alignment and tree reconstruction. — We edited the sequences with Geneious v.8.0.5 (Kearse & al., 2012), and conducted the multiple alignment using MAFFT v.7 with default parameters (Kato & Standley, 2013). The alignments were manually corrected using Mesquite v.3.02 (Maddison & Maddison, 2011).

Alignments of the present phylogenetic datasets are available as supplementary material (<https://doi.org/10.12705/671.6.S>). The beginning and end of the alignments, where the sequences of many individuals lack sharp electropherogram peaks, were trimmed prior to analysis. The ITS and *rps16* datasets were analyzed separately as their taxon composition differed. Two kinds of analyses were run on each dataset separately: Bayesian inference (BI) and maximum parsimony (MP). Before running BI, the optimal substitution models were estimated using the Akaike information criterion (AIC) in jModelTest v.0.1.1 (Posada, 2008). General time reversible model with gamma-shaped rate variation and a proportion of invariable sites (GTR+I+ Γ) was estimated as the best-fit model for both ITS and *rps16* markers. For BI we used MrBayes v.3.2.6 (Ronquist & Huelsenbeck, 2003) under CIPRES server (Miller & al., 2010) with the number of MCMC generations for ITS and *rps16* datasets set to 40 million. Trees were sampled every 1000 generations with the default of three “heated” and one “cold” chain, and pre-stationarity MCMC samples were discarded as burn-in (2500 samples as calculated by Tracer v.1.6 software, Rambaut & al., 2014). The remaining trees were summarized in a 50% majority-rule consensus tree for each dataset. MP analyses were performed using PAUP* v.4.0b10 (Swofford, 2003) with the following parameters: all characters unordered and equally weighted, heuristic search with random sequence addition, tree-bisection-reconnection branch swapping, 50 random-addition-sequence replicates, and MAXTREES option set to 10,000. The obtained trees were summarized in a strict consensus tree. Bootstrapping was done using maximum likelihood method as implemented in RAxML-HPC2 on XSEDE v.8 (Stamatakis, 2014) the following settings: model = GTRCAT, bootstrap nreps = 1000 (summarized in a 50% majority-rule consensus tree as a cladogram).

Morphological character mapping. — A data matrix of four morphological characters for all taxa included in the phylogenetic analysis of ITS was prepared. The selected characters were: (1) membranous commissures of calyx (present/absent), (2) bracteoles (present/absent), (3) seed shape (reniform or pyriform/reniform-oblong/peltate/comma shaped), and (4) embryo shape (curved/straight/hook-shaped). The evolutionary pathways were reconstructed using Mesquite v.3.02 (Maddison & Maddison, 2011). We employed the Markov *k*-state 1 (Mk1) parameter model of evolution for the ML reconstructions, with equal probability for any particular character change.

Typification information. — Details about type specimens of the basionyms of the new combinations and resurrected names that we have included are based on examining protologues and searching major indices (Tropicos, <http://www.tropicos.org/>; JSTOR Global Plants, <https://plants.jstor.org/>), as well as websites of several individual herbaria (BM, BR, E,

G, GH, K, KEW, L, LINN, OS, P, US, WU) for extant specimens. We have examined a digital image from one (or more) of these sources for any specimen where we cite a barcode in the type citations.

■ RESULTS

The alignment of the ITS dataset needed introduction of ten large indels (≥ 5 bp). The final ITS matrix for 135 terminals comprised a total of 700 characters, whereas the *rps16* dataset with 94 terminals was finally 1034 bp long and included 29 large indels. A list of alignment characteristics and parsimony statistics is presented in Table 3. The results of MP and BI for both datasets were congruent. Therefore, we present and discuss only the 50% majority-rule trees obtained from BI of the ITS (Fig. 2) and *rps16* (Fig. 3). For a better comparison of the obtained trees and checking for congruency between the two datasets, the mirror image of obtained trees is shown in Fig. 4.

All trees are congruent in showing tribe Caryophylleae as monophyletic with *Silene* (in *rps16* trees) or *Eremogone* (in ITS trees) as sister group. We recognize three main clades in both trees which are called Gypsophilinae, *Saponaria* s.str. and Caryophyllinae. In the ITS tree (Fig. 2), *Psammophilinae* W.C.Wu & C.Y.Wu, missing in the *rps16* tree, is sister to these three. The largest clade in the tribe in terms of species number is Caryophyllinae and can be subdivided into four clades: (1) *Acanthophyllum* s.l. (incl. *Allochrusa*, *Diaphanoptera*); (2) *Cyathophylla* (including *Cyathophylla* spp., *Saponaria viscosa* C.A.Mey. and a few species placed in *Gypsophila* by Barkoudah, 1962); (3) *Dianthus* s.l. (including *Bolanthus* spp., *Phrynella ortegioides* (Fisch. & C.A.Mey.) Pax & K.Hoffm., *Gypsophila confertifolia*, *Petrorhagia* spp., *Psammophiliella* spp., *G. spergulifolia* Griseb., *Dianthus* spp., and *Velezia rigida*); and (4) *Petroana* (including *Gypsophila montana* and *G. montserratii*). Gypsophilinae and *Saponaria* s.str. show a sister relationship in the *rps16* tree, and their clade is in turn sister to Caryophyllinae, while *Saponaria* s.str. forms the sister to the Caryophyllinae in the ITS topology (Fig. 2). The Gypsophilinae clade embraces most species of *Gypsophila* including the type of the genus (*G. repens* L.) along with the representatives of the genera *Vaccaria*, *Ankyropetalum*, and *Bolbosaponaria* Bondarenko as well as one species of *Diaphanoptera* (*D. afghanica* Podlech).

■ DISCUSSION

Despite many molecular phylogenetic studies in Caryophyllaceae during recent years (Fior & al., 2006; Harbaugh & al., 2010; Greenberg & Donoghue, 2011; Pirani & al., 2014; Dillenberger & Kadereit, 2014; Sadeghian & al., 2015) the generic boundaries in the tribe Caryophylleae are still blurred (Pirani & al., 2014; Hernández-Ledesma & al., 2015). The scanty sampling of some large genera in the tribe, such as *Gypsophila* and *Saponaria*, as well as missing sequences of

some smaller genera and little knowledge of the morphology of many crucial taxa are the main reasons for this uncertainty. Since many ornamental and medicinal plants are representatives of this tribe, and due to frequent occurrence of the members of this tribe in natural ecosystems in SW Asia, providing the correct taxonomic name to these taxa is very important, though challenging.

The general topology of the trees obtained here supports the presence of three major clades in Caryophylleae, fitting partly with the subtribal system proposed by Šourková (1978). Our phylogenies suggest adding two subtribes to subtribes Dianthinae Šourková (homotypic synonym of Caryophyllinae (Juss.) Rabeler & Bittrich, see Rabeler & Bittrich, 1993) and Gypsophilinae Šourková, namely subtribes Saponariinae and Psammosileninae. However, as three of the four subtribes would each include only one genus, this system seems unnecessary. Therefore, we prefer to name not all clades formally as shown on the trees (Figs. 2–4). According to the results we obtained, we provide below a detailed survey on the delimitation of genera in tribe Caryophylleae.

Gypsophila. — As circumscribed currently, this is a heterogeneous group morphologically (Bittrich, 1993). Our study shows that a major revision is necessary to make this genus monophyletic. All analyses conducted here show clearly that the generic names *Ankyropetalum*, *Bolbosaponaria* (already included in the genus, see Bittrich, 1993), *Dichoglottis* Fisch. & C.A.Mey. (already included in the genus, see Barkoudah, 1962), *Vaccaria* and one species of *Diaphanoptera* (*D. afghanica*) are nested within *Gypsophila*. In each of these cases, the morphological diagnostic features are shared by certain species assigned to *Gypsophila*. In the case of *Ankyropetalum* the deeply incised petals as well as exerted stamens (in addition to other features mentioned by Barkoudah, 1962) might represent autapomorphies. The membranous commissures and the winged veins of the calyx as well as its inflated form in *Vaccaria* are also evident in *Diaphanoptera khorasanica* Rech.f. and partly in *D. afghanica* as well as *Bolbosaponaria bucharica* (B.Fedtsch.) Bondarenko (also nested within *Gypsophila* in our analyses). The possible inclusion of *Vaccaria* in *Gypsophila* has been suggested before (Kadereit & al., 2016). The genus *Diaphanoptera* is clearly polyphyletic with three species

Table 3. Alignment characteristics and statistics of phylogenetic analyses of *rps16* and ITS datasets in Caryophylleae.

	<i>rps16</i>	ITS
Number of terminals	94	135
Sequence length [bp]	414–810	242–648
Aligned length [bp]	1034	700
Constant characters [bp]	541	261
Parsimony-uninformative characters [bp]	158	82
Parsimony-informative characters [bp]	335	357
Parsimony-informative characters [%]	32.4	51

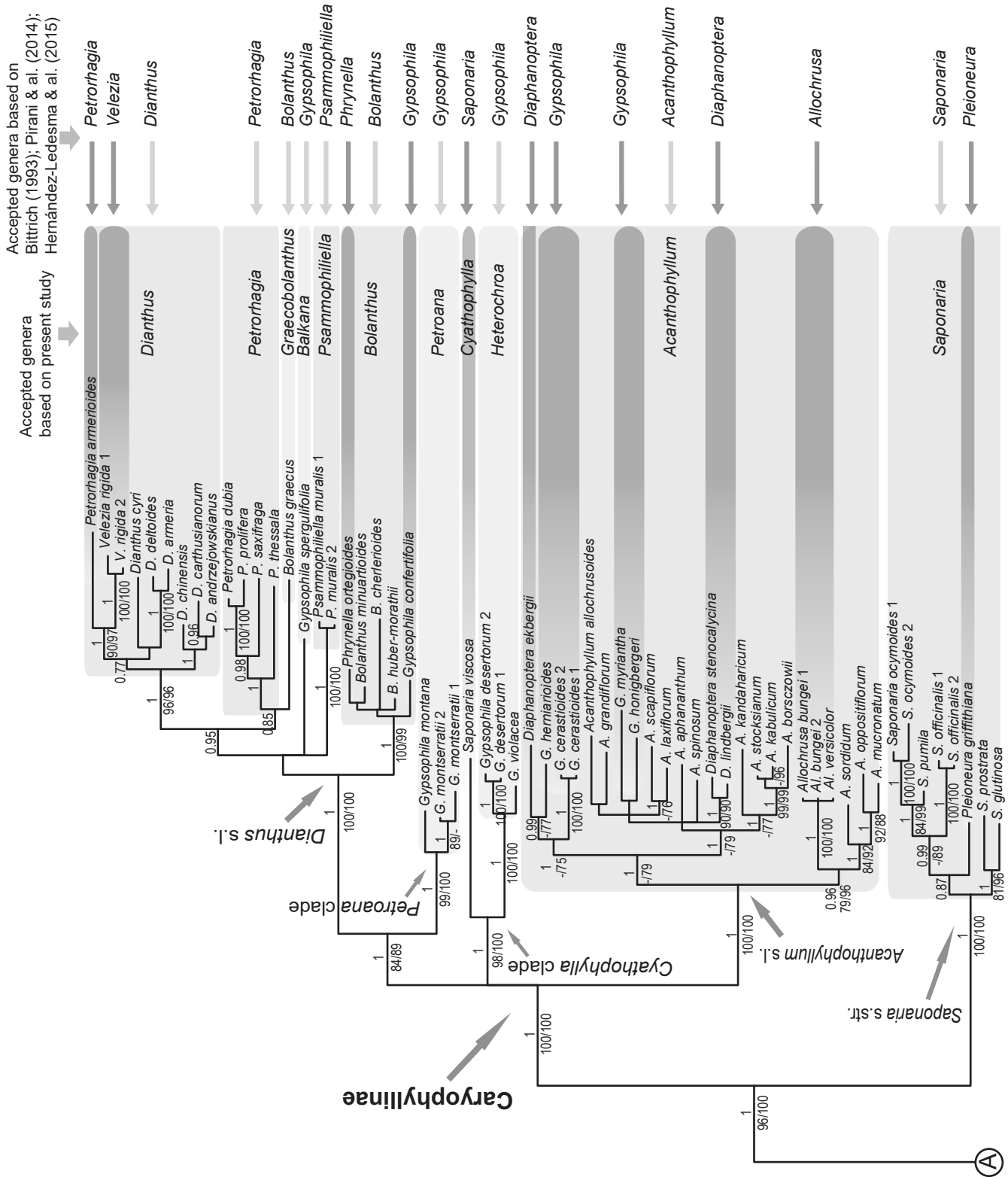


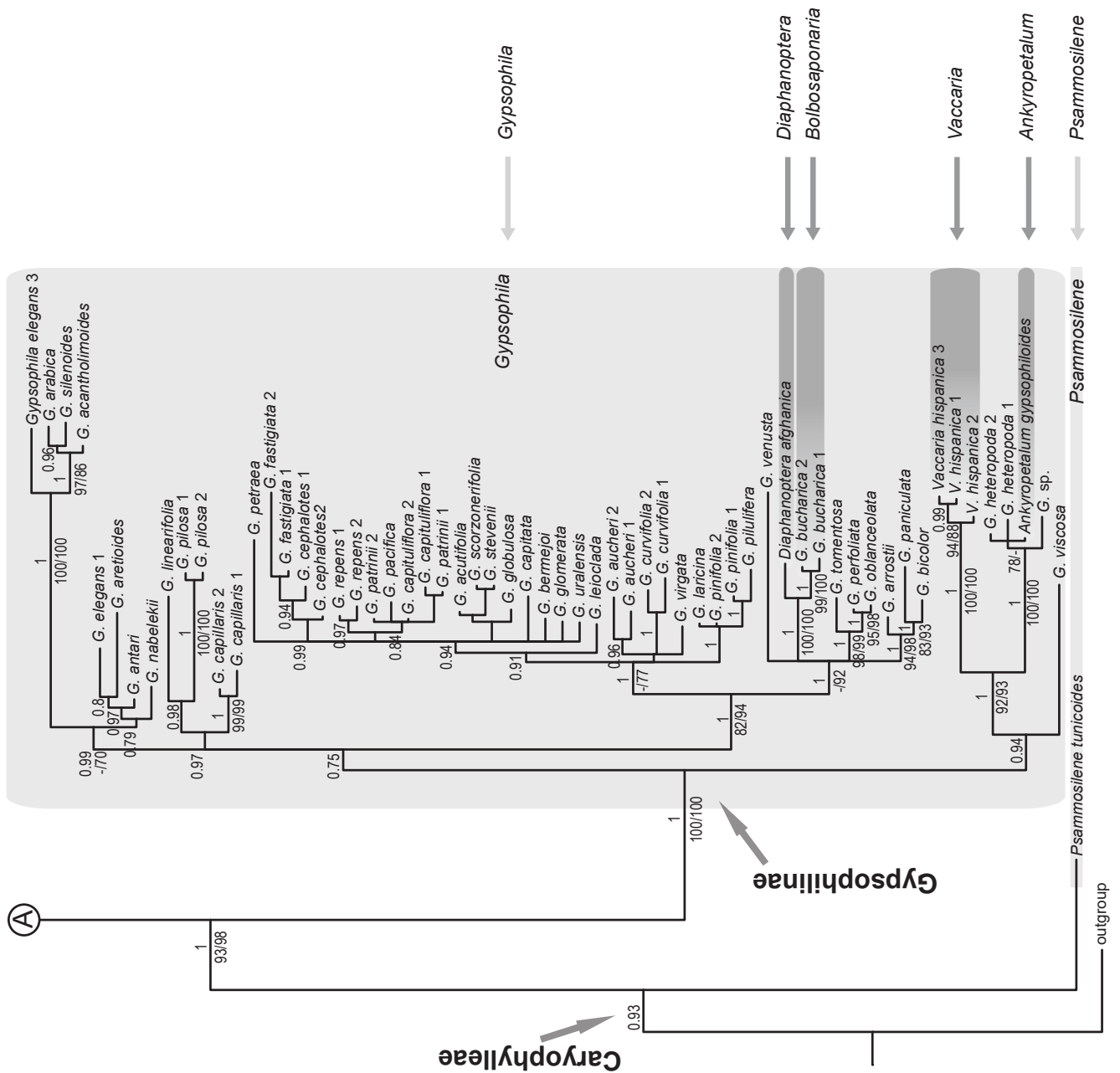
Fig. 2. Majority-rule consensus tree inferred from Bayesian analysis of ITS data in tribe Caryophylleae. Numbers above the branches indicate posterior probability values; those below branches are MP/ML bootstrap values. The generic names inside the grey boxes are those accepted in the present study. Species names are according to www.ipni.org and do not follow the taxonomic treatments suggested in the present study. The generic names in the column right to the grey area are those accepted by Bittrich (1993), Pirani & al. (2014), and Hernández-Ledesma & al. (2015). Values below 0.5 for posterior probability and below 50% for ML/MP bootstrap are not shown.

that are woody at base nested within *Acanthophyllum* (see also Pirani & al., 2014) and one species in *Gypsophila*. In line with previous analyses, the genus *Diaphanoptera* cannot be maintained and should be reduced to a synonym under *Acanthophyllum* (Pirani & al., unpub. data). It seems that the unique tuberous roots and long tubular calyces with membranous commissures between the calyx veins in *Bolbosaponaria* are not applicable at generic rank, but may be useful for separating lower ranks such as sections. However, the subgeneric classification of *Gypsophila* needs a richer sampling and is not addressed here, but it is included in the scope of our future investigations.

Another important finding of our study relating to *Gypsophila* is the necessity to exclude some morphologically

aberrant taxa. Such a treatment has already been applied to *G. muralis* L. and three related taxa now considered as *Psammophiliella* Ikonn. (Hernández-Ledesma & al., 2015: based on results obtained by Greenberg & Donoghue, 2011, and Pirani & al., 2014). Our results show that *Gypsophila violacea* (Ledeb.) Fenzl, *G. desertorum* (Bunge) Fenzl, *G. mонтserratii* Fern.Casas, *G. montana* Balf.f., *G. spergulifolia*, *G. confertifolia* Hub.-Mor., *G. cerastioides* D.Don, *G. herniarioides* Boiss., *G. honigbergeri* (Fenzl) Boiss. and *G. myriantha* Rech.f. should also be transferred to other genera.

The last four species listed above are placed in the *Acanthophyllum* s.l. clade. *Gypsophila cerastioides* is neither spiny nor shows the typical many-flowered rich axillary inflorescences known in most species of *Acanthophyllum*.



The broad leaves, many-ovulate capsules and large petals in this species indicate rather its unique position that led some earlier taxonomists to assign it to the genus *Acosmia* Benth. (or *Timaeosia* Klotzsch). In the ITS tree presented here, this species is closely related to *Diaphanoptera ekbergii* Hedge & Wendelbo, and *G. hernarioides*.

In line with our molecular phylogenetic results, the woody cushion-forming habit, the well-developed short lateral branches in *G. hernarioides* resulting in a false verticillate phyllotaxy as well as dense and many-flowered corymbose inflorescences, and 4- to 12-ovulate ovary fit well with *Acanthophyllum*, but are absent or rarely observed in *Gypsophila*. However, the *Acanthophyllum* s.l. clade includes some other unarmed plants such as members of *Allochrusa*, and therefore, recognition of neither *G. hernarioides* nor *Allochrusa* spp. under separate genera are supported by molecular data (see also Pirani & al., 2014). Our extended taxon sampling (especially regarding the number of genera sampled) for both markers, does not allow *Allochrusa* to be separated from *Acanthophyllum*. The species of the genus *Allochrusa* were considered once as members of *Acanthophyllum* subg. *Allochrusa* (Schischkin, 1936) and our molecular phylogenetic studies corroborate the taxonomic treatment performed by Pirani & al. (2014) and contradict the treatment by Hernández-Ledesma & al. (2015) where it was recognized provisionally at the generic level. According to this concept, it is necessary to resurrect the generic name *Acanthophyllum* for some taxa treated as *Allochrusa* in recent taxonomic surveys (see under Taxonomic implications).

Gypsophila honigbergeri is spiny (at least at leaf apex) and shows characteristic capsules of *Acanthophyllum* (low ovule number, one-seeded), and was suggested previously to be a member of this genus (Barkoudah, 1962). Aggregation of some characters, i.e., cylindrical calyx, shortly exserted petals and long stamens, which are unusual characters in *Gypsophila*, associated with a cushion-forming habit resembling *Acanthophyllum* drove Rechinger (1988) to describe the distinct subgenus *Kabulianthe* under *Gypsophila*. Ikonnikov (2004) even elevated this taxon to generic rank and introduced the combination *Kabulianthe honigbergeri* (Fenzl) Ikonn.

Gypsophila myriantha is also spiny and similar to *Acanthophyllum* in general habit except for the open paniculate inflorescence that is similar to many species of *Gypsophila*. The capsules in this species have not been seen, but the number of ovules is lower than 12, associating it again with *Acanthophyllum*. Our molecular phylogenetic investigations clearly place this species in *Acanthophyllum*.

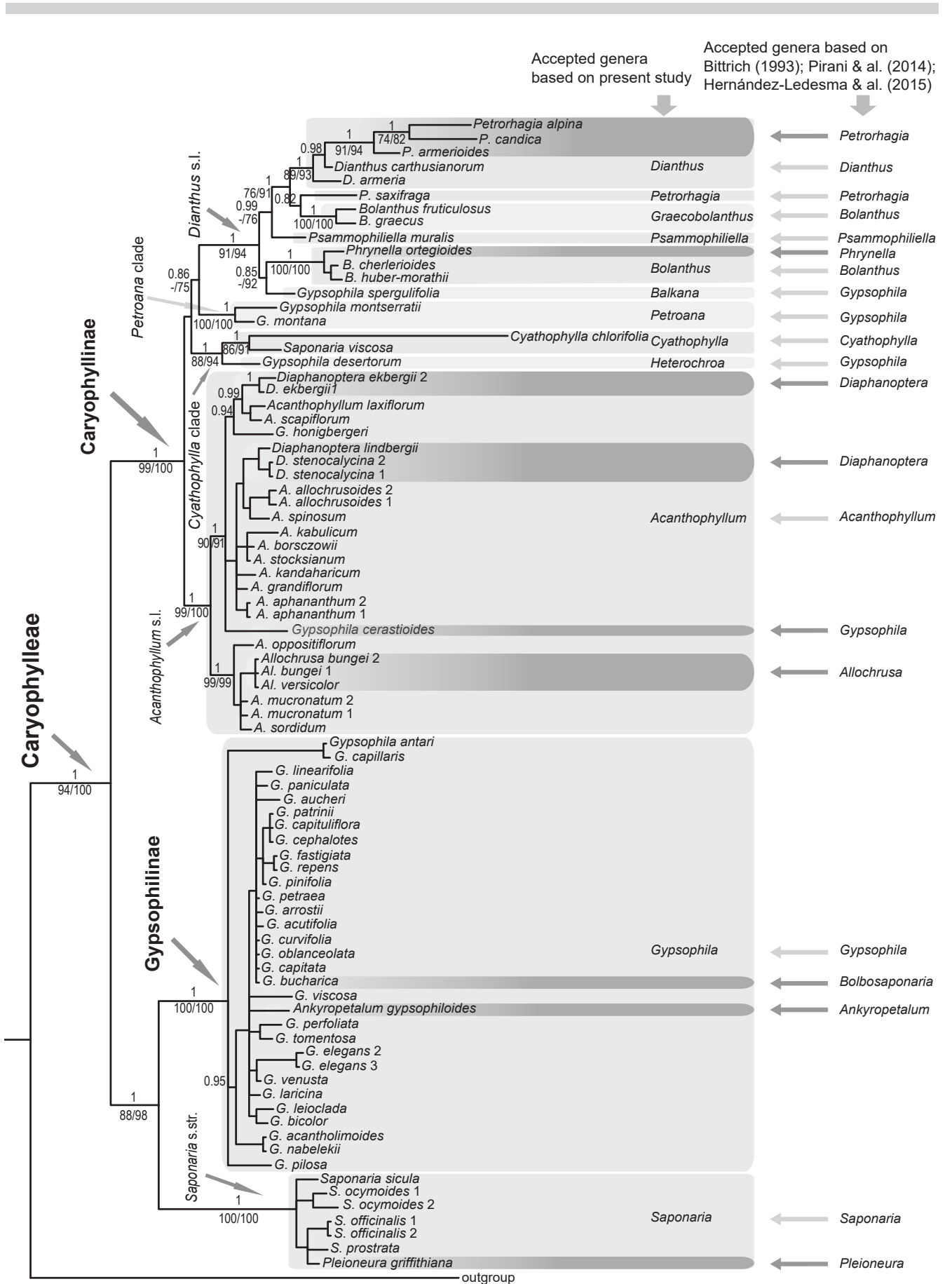
Gypsophila desertorum and *G. violacea* form a distinct clade sister to *Acanthophyllum* s.l. + *Dianthus* s.l. clades. Both species are representatives of *Gypsophila* sect. *Heterochroa*

(Bunge) A. Braun (for notes on correct name and typification of this taxon see Rabeler, 1993) and show a south to east Siberian distribution. Among the species Barkoudah originally assigned to *G.* sect. *Heterochroa*, *G. cerastioides* and *G. hernarioides*, should be transferred to *Acanthophyllum* and are restricted to Afghanistan and Pakistan (see above), while other species show a more northern distribution reaching Far East and Central Asia. This latter group including *G. antoninae* Schischk., *G. desertorum*, *G. microphylla* (Schrenk) Fenzl, *G. sericea* (Ser.) Krylov (\equiv *Heterochroa petrea* Bunge: type of the genus *Heterochroa*), *G. turkestanica* Schischk. and *G. violacea* are low herbaceous plants with short internodes, small leaves, short pedicels and short campanulate calyces with calyx teeth mostly scarious at margins, and lack calcium oxalate crystals (which are present in most species of *Gypsophila*: Barkoudah, 1962). Our phylogenetic results, in accordance with geographical distribution patterns and morphology, suggest resurrection of the genus *Heterochroa* Bunge similar to *Gypsophila* sect. *Heterochroa* as defined by Barkoudah (1962) but excluding *G. cerastioides*, *G. hernarioides* and *G. honigbergeri* that should be transferred to *Acanthophyllum*. No material of *G. glandulosa* (Boiss.) Walp. was available to us; a species distributed in Turkey showing intermediate morphological characters between *Heterochroa*, *Gypsophila* and *Acanthophyllum*.

Gypsophila montserratii and *G. montana* (\equiv *Saponaria montana* (Balf.f.) Barkoudah) are characterized by a very small calyx and petals. The haploid base chromosome number is known only for the former ($x = 13$: Löve, 1973), which is neither congruent with *Gypsophila* (mostly $x = 17$) nor with *Dianthus* ($x = 15$). They form a highly supported clade sister to the *Dianthus* s.l. clade in the ITS and *rps16* trees (Figs. 2, 3). Like Miller & Cope (1996), who treated *G. montana* within *Gypsophila*, we were not able to trace any important morphological character that supported Barkoudah (1962) transferring *G. montana* to *Saponaria*, but the morphological resemblance of this taxon to *G. montserratii* is strong enough to correlate it with the latter. These two species are geographically remote from each other: *G. montserratii* is known from the Iberian Peninsula, and *G. montana* is distributed in mountains and wadi-beds of Socotra (an archipelago in Arabian Sea, territory of Yemen) (Miller & Cope, 1996). In line with our molecular phylogenetic analyses and morphological evidence, we suggest describing a new genus, *Petroana*, for this group (see below under Taxonomic implications).

Saponaria. — Seven species of *Saponaria* are included in our analyses, most of which form a clade in both analyses that includes *Pleioneura griffithiana* (Boiss.) Rech.f. Although the *Saponaria* clade is fully supported in the analyses of both markers, its placement varies between the markers used (see under

Fig. 3. Majority-rule consensus tree inferred from Bayesian analysis of *rps16* data in tribe Caryophylleae. Numbers above the branches indicate posterior probability values; those below branches are MP/ML bootstrap values. Species names are according to www.ipni.org and do not follow the taxonomic treatments suggested in the present study. The generic names inside the grey boxes are those accepted in the present study. The generic names in the column right to the grey area are those accepted by Bittrich (1993), Pirani & al. (2014), and Hernández-Ledesma & al. (2015). Values below 0.5 for posterior probability and below 50 for ML/MP bootstrap are not shown.



Results). Our results show clearly that *Pleioneura* is nested within *Saponaria* in spite of the unique stigma (positioned just at the end of the style) and the membranous commissures between the calyx veins. In contrast to Bittrich (1993) and Hernández-Ledesma & al. (2015), who recognized *Pleioneura*, we suggest its synonymy within *Saponaria*.

Among the species currently assigned to *Saponaria*, *S. viscosa* is nested within the *Cyathophylla* clade (Fig. 3). Unfortunately, the ITS sequence for *Cyathophylla chlorifolia* Bocquet & Strid could not be generated, but the *rps16* sequences put *C. chlorifolia* and *S. viscosa* together clearly with full support. The perfoliate leaves and congested inflorescence in *Cyathophylla* are the most important morphological features separating it from *Saponaria*. However, the pedicels in *S. viscosa* are relatively short, so that the young inflorescences do show a congested form. In general, only the ovate to rounded leaves in *C. chlorifolia*, which look perfoliate at the base, can be considered as important characters separating these taxa. Furthermore, *C. chlorifolia* is found in Greece and Turkey, whereas *S. viscosa* is distributed in eastern Turkey, Azerbaijan, Iraq, Iran and Turkmenistan. The distribution of these species overlaps somewhat in Ankara Province in Turkey.

***Dianthus* s.l.** — *Bolanthus*, *Dianthus*, *Petrorhagia*, *Phrynella*, *Psammophiliella*, and *Velesia* are the main representatives of the clade *Dianthus* s.l.; our study is the first molecular investigation including genera *Bolanthus* and *Phrynella*. Furthermore, we extended the sampling of *Petrorhagia*, supporting its paraphyly as previously indicated but based on a different grouping of sampled taxa (Greenberg & Donoghue, 2011). The relatively rich sampling of *Dianthus* in previous analyses (Valente & al., 2010; Greenberg & Donoghue, 2011) indicated that *Dianthus* was monophyletic with *Velesia* nested within (Harbaugh & al., 2010; Kemler & al., 2013). Despite low sampling here, our analyses also suggest inclusion of *Velesia* as well as a few species of *Petrorhagia* (excluding its type: *P. saxifraga* (L.) Link) in *Dianthus*.

***Petrorhagia*.** — Morphologically, species of *Petrorhagia* either have conspicuous bracts encircling the calyx (including the type) or such bracts are missing. Our analyses clearly suggest including this latter group in *Dianthus*; most of these species have in the past been placed within *Gypsophila* (Grisebach, 1843).

In both trees (Figs. 2, 3) the *Dianthus* s.l. clade is divided into five main lineages with unresolved or moderately to low-supported relationships: (1) *Bolanthus* core group including some species of this genus as well as *Gypsophila confertifolia* and *Phrynella*; (2) *Psammophiliella muralis*; (3) *G. spergulifolia*; (4) the core group of *Petrorhagia* (including its type) along with the second group of *Bolanthus* (*B. graecus*, *B. fruticosus*); and (5) *Dianthus*, *Velesia* and the second

group of *Petrorhagia* (including *P. armerioides*, *P. alpina* and *P. candida*).

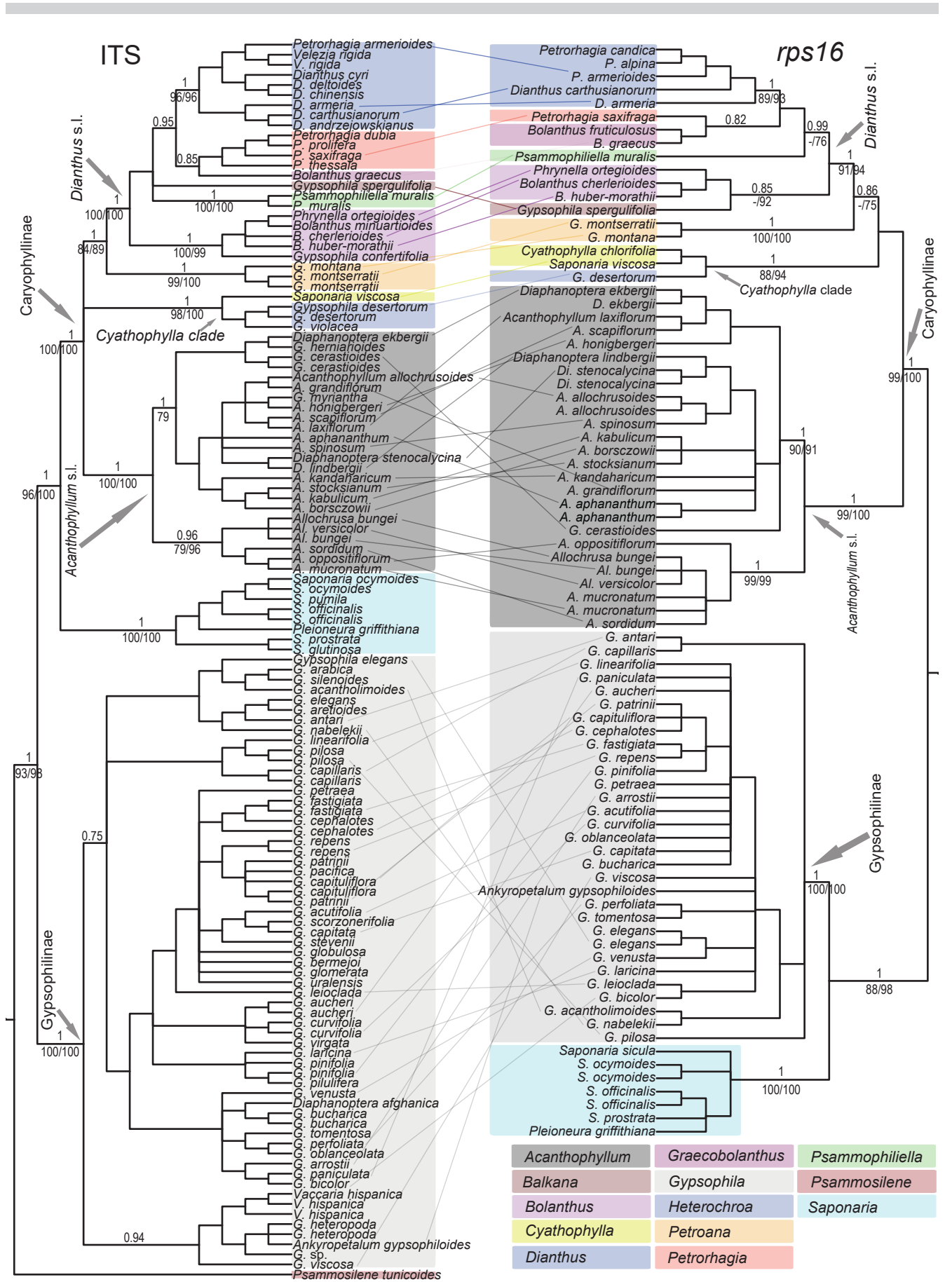
The findings of our analyses indicate that a group of species currently assigned to *Petrorhagia* sect. *Pseudotunica* (Fenzl) Post & Kuntze and sect. *Pseudogypsophila* (A. Braun) P. Ball & Heywood, which are characterized by the absence of conspicuous epicalyx bracts, are also associated with *Dianthus* and form a common clade with *Velesia*. Since *Dianthus* sect. *Armeriastrum* Ser. forms the most basally branching clade of the genus (as currently circumscribed, see Valente & al., 2010) and the clade composed of *Velesia rigida* and part of *P.* sect. *Pseudotunica* are sister to the *Dianthus* crown group, it seems that it is inevitable to extend the formerly suggested lumping approach to place *P.* sect. *Pseudotunica* in *Dianthus*. However, as the type of this section was not available to us, the formal synonymy of this section should wait for further investigations, but the few species of this section analyzed here are transferred to *Dianthus* (see under Taxonomic implications).

***Bolanthus*.** — *Bolanthus fruticosus* and *B. graecus* are both distributed in Greece (Strid, 1986) slightly disjunct from most species of the genus, which is known from Turkey and Middle East. The representatives of the genus from both areas are mostly saxicolous plants with showy petals rounded at the apex as well as conspicuous calyx veins and narrow commissural membranes. However, the petals in the Greek species turn abruptly downwards and become clearly deflexed shortly after anthesis, while in species from Turkey and the Middle East the petals might be recurved, but not abruptly deflexed. Our results agree with this morphological characteristic and geographical data, suggesting a new genus for the Greek representatives formerly assigned to *Bolanthus* is needed (see *Graecobolanthus* under Taxonomic implications).

Gypsophila confertifolia, which shows an overlapping distribution pattern with the main group of *Bolanthus* centered in the East-Mediterranean phytogeographic subregion (sensu Eig, 1931), is characterized by a tubular calyx and short pedicels, which give rise to capitate inflorescences, resembling some species of *Bolanthus* such as *B. minuartioides* (Jaub. & Spach) Hub.-Mor. The main difference between this species and members of *Bolanthus* is its annual habit. Our ITS trees (Fig. 2) suggest that this species is more closely related to *Bolanthus* rather than *Gypsophila* or, as suggested by Ikonnikov (1976), *Psammophiliella*. This assumption is also supported by geographical and morphological data. Based on available data, *G. confertifolia* should be transferred to *Bolanthus*.

A similar situation involves the obligate serpentinophyte taxon (Marin & Tatić, 2001; Jakovljević & al., 2011) *G. spergulifolia*. Morphologically this species is characterized by a basal aggregate of linear leaves, which are triangular in cross-section,

Fig. 4. Tanglegram of Dendroscope program package (Huson & Scornavacca, 2012) comparing the phylogenies of ITS (left side) and *rps16* datasets (right side) based on the 50% majority-rule consensus trees obtained from Bayesian phylogenetic analyses. Numbers above the branches indicate posterior probability values; those below branches are MP/ML bootstrap values. Values below 0.5 for posterior probability and below 50% for ML/MP bootstrap are not shown. Grey boxes represent same genera of Caryophylleae as mentioned in the key at the bottom right of the figure.



relatively long pedicels and a short campanulate-turbinate calyx. Furthermore, the petals are uniquely bicolored, red on the outer surface, but with a white or pink inner surface. It shows also an isolated geographic distribution, endemic to the Balkan region (in Albania and Serbia). Our results suggest recognizing this taxon as distinct from both *Bolanthus* and *Gypsophila* (see *Balkana* under Taxonomic implications), although the commissural membranes of the calyx known in both genera occur also

in this taxon. In our phylogenetic trees this species is placed more closely to *Bolanthus* rather than to *Gypsophila*.

Phylogenetic analyses of both markers clearly place *Phrynella* within *Bolanthus*. Morphological and geographical data also support this relationship. The monotypic genus *Phrynella* is known only from Turkey, where several species of *Bolanthus* are also found, sometimes in similar regions (Reeve & al., 1967). Short internodes, 1- to 3-flowered

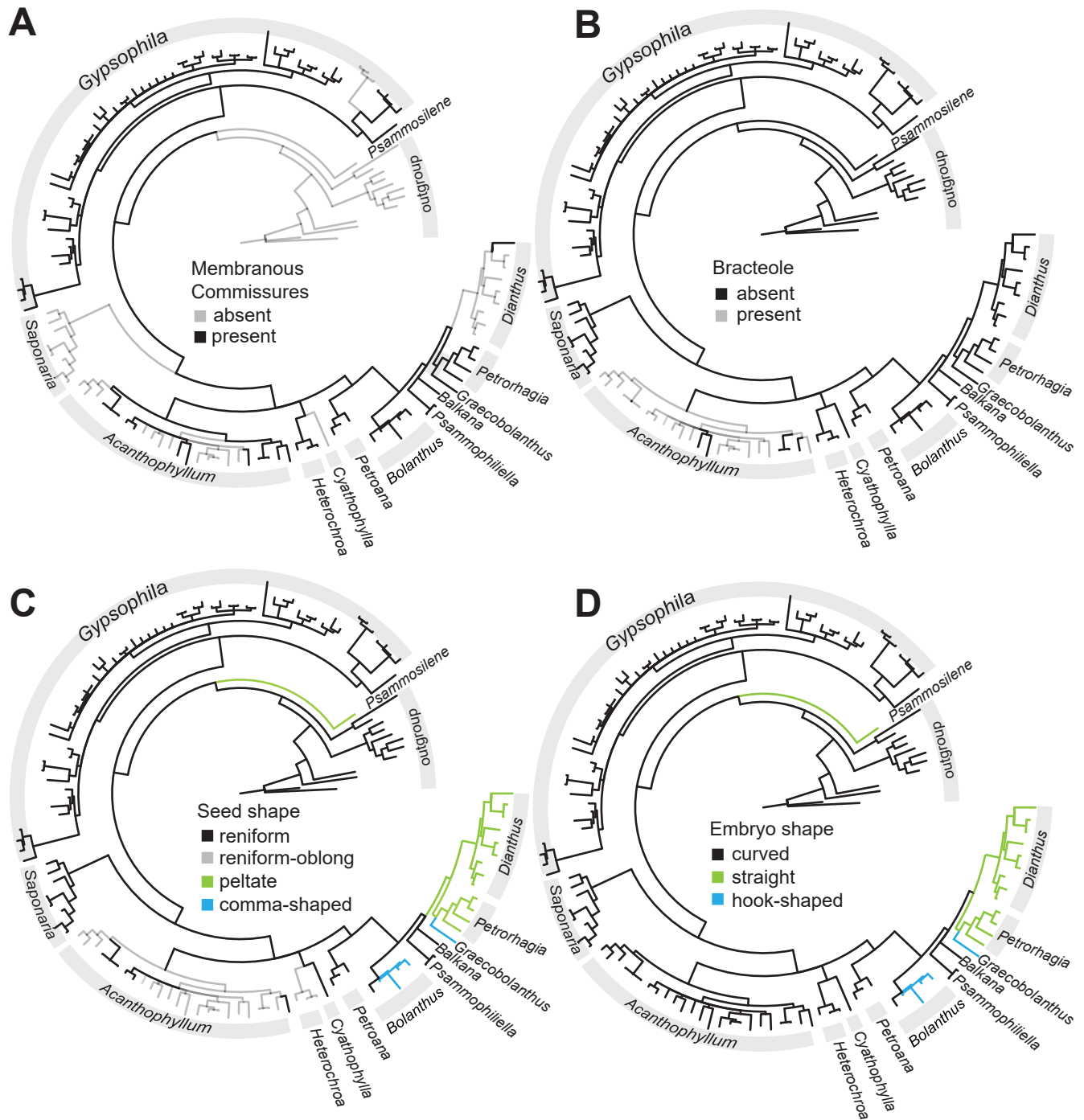


Fig. 5A–D. Evolutionary histories of four selected morphological characters mapped on Bayesian semi-strict consensus tree of nrITS sequences in Caryophylleae. The characters and their states are mentioned in the center of each circular tree.

axillary inflorescences, sessile flowers, and petals slightly overtopping the calyx are shared by *Phrynella ortegioides* and several species of *Bolanthus*. Our results are partly in accordance with Barkoudah's (1962) morphological concept, associating *Phrynella* with *B. minuartioides*. However, he transferred the latter to *Acanthophyllum* mainly due to its rigid habit, linear parallel-nerved leaves, sessile axillary and terminal flowers and unequal stamens (Barkoudah, 1962). The analyses presented here, despite showing a close relationship between *Ph. ortegioides* and *B. minuartioides*, rejects their affinity with *Acanthophyllum*.

Evolution of selected morphological characters. — Mapping of morphological characters on the consensus ITS tree shows that most of the diagnostic traits used formerly in tribe Caryophylleae are homoplasious and not useful for defining the boundaries between the genera (Fig. 5A–D). Therefore, from a taxonomic point of view, it is inevitable that we apply a combination of characters for defining the genera in this group, noting that only a few genera might show no overlap in these characters. It appears as if membranous commissures between the sepals evolved in basal branches of the ITS tree (Fig. 5A), suggesting a reversal of this character in some species or species groups in *Acanthophyllum* and *Dianthus*. However, in *Psammosilene*, which occupies a basal position in Caryophylleae, commissural membranes are absent, and the membranous parts of the calyx are confined to tooth margins. Seed shape (Fig. 5C) in the members of Caryophylleae is quite variable and, therefore, we determined four states for this character. Peltate, dorsiventrally compressed seeds, which have been considered as a major synapomorphy for *Dianthus*, are shared by *Petrorhagia*, *Psammosilene* and *Velesia*, among which *Psammosilene* is not closely related to *Dianthus*. Within the *Dianthus* s.l. clade the peltate shape is the most common state, but the reniform type (as in *Gypsophila spergulifolia* = *Balkana spergulifolia* (Griseb.) Madhani & Zarre: see below under Taxonomic implications) and the comma-shaped type (as in *Bolanthus* spp.) represent some cases of homoplasy regarding this character state. Ball & Heywood (1964) considered the peltate seeds as a feature separating the genera *Dianthus*, *Petrorhagia* and *Velesia* from all other members of Silenoideae, but recent studies reported this seed type also in *Psammosilene* (Bittrich, 1993). In *Acanthophyllum* s.l. and *Heterochroa*, the common seed shape is the reniform-oblong, which can be considered as intermediate between reniform and peltate types. A detailed seed micromorphological investigation in the *Dianthus* s.l. clade, like those already conducted on *Gypsophila* (Amini & al., 2011), *Velesia* (Poyraz & Ataşlar, 2010) and *Acanthophyllum* (Pirani & al., in prep.), will shed light on the evolutionary pathways of this character.

The curved embryo is the most common type in the basally branching clades of Caryophylleae except *Psammosilene*, which has a straight embryo, but the straight and hook-shaped ones are most common in members of the *Dianthus* s.l. clade suggesting a derived position for this state (Fig. 5D). Embryo shape is otherwise correlated with seed shape, so that reniform/reniform-oblong, peltate, and comma-shaped seeds show curved, straight, and hook-shaped embryos, respectively.

Another important morphological character addressed in the present study is the presence/absence of bracteoles (Fig. 5B). Presence of bracteoles in *Allochrusa*, *Diaphanoptera*, *Ochotonophila* and *Scleranthopsis*, reflects their phylogenetic position nested within *Acanthophyllum*. However, absence of bracteoles in other taxa of *Acanthophyllum* s.l. clade (*Gypsophila cerastioides*, *G. hernarioides*, *G. honigbergeri*, *G. myriantha*), suggests at least two reversals for this character in this clade.

■ TAXONOMIC IMPLICATIONS

The molecular phylogenetic analyses performed here, together with morphological and geographic evidence, suggest a new generic concept in tribe Caryophylleae. It is necessary to transfer some species to other genera or describe new genera in order to make them natural and monophyletic. Based on this new concept, we provide a diagnostic key to all genera we currently recognize in the tribe and then brief descriptions of each genus (most based on Bittrich, 1993 and modified as necessary). New combinations are made only when material of the taxa was available to us for analysis. Therefore, for many taxa we did not propose any taxonomic change due to lack of specimens for detailed herbarium or molecular examination.

Diagnostic key to genera of Caryophylleae. — In many genera there are a few species showing some deviation from the typical variation exhibited within the genus. In most cases, it is necessary to use a combination of characters in order to determine the genus with certainty.

1. Seeds peltate, with central (facial) hilum; embryo straight 2
1. Seeds reniform, reniform-oblong or comma-shaped, with lateral hilum; embryo curved or hook-shaped 5
2. Leaves with short petiole, ovate; stamens 5; capsules membranous, nearly indehiscent *Psammosilene*
2. Leaves sessile, linear, subulate, grass-like; stamens (5)10; capsules papery, dehiscent 3
3. Calyx without membranous commissures, with 35 or more veins, rarely 5- to 15-nerved (cf. *Velesia*); calyx tube long tubular, teeth straight *Dianthus* (incl. *Velesia*)
3. Calyx with membranous commissures, with 5–15 veins; calyx tube variously shaped, if tubular the teeth recurved to deflexed 4
4. Seeds >1.5 mm, with thin margin, smooth on surface *Dianthus* (incl. *Petrorhagia* p.p.)
4. Seeds <1.5 mm, with thickened margin, reticulate on surface *Petrorhagia*
5. Seeds comma-shaped (or oblong), with hook-shaped embryo 6
5. Seeds reniform to reniform-oblong, embryo curved .. 7
6. Petals turning abruptly downward and becoming clearly deflexed (Greece) *Graecobolanthus*
6. Petals recurved gradually (Turkey to the coastal mountains of Syria, Lebanon and Palestine) *Bolanthus* (incl. *Phrynella*)

7. Calyx bladderly inflated, or turbinate, constricted at teeth, commissural regions membranous hyaline, sometimes wing-like *Diaphanoptera*
7. Calyx campanulate to tubular, if inflated, commissural regions papery or leafy and main veins with leafy wings 8
8. Bracteoles present, leafy, papery or rarely membranous; calyx papery in texture or only membranous at intervals *Acanthophyllum* (incl. *Allochrusa*, *Ochotonophila*, *Scleranthopsis*)
8. Bracteoles absent 9
9. Calyx bladderly inflated, nerves prominent and thick, costate, or winged, midveins 5; bracteoles membranous hyaline *Gypsophila* (cf. *Vaccaria*)
9. Calyx tubular, campanulate, or obconical, not much inflated, lateral nerves obscure, not prominent and thick, midveins 5 or more; bracteoles absent 10
10. Calyx obscurely nerved or with 15–25 nerves, commissures absent or present; petals inconspicuous, or clawed, mostly with appendages 11
10. Calyx 5-nerved, with membranous commissures; petals not or only indistinctly clawed, without appendages .. 12
11. Plants annual; inflorescences congested; capsule slightly longer than the calyx; coronal scales absent *Cyathophylla*
11. Plants annual, biennial or perennial; inflorescences usually lax; capsule mostly shorter than the calyx; coronal scales mostly present *Saponaria*
12. Leaves fleshy, spatulate; flowers very small: calyx <4mm, corolla <5 mm; seed testa with swollen cells tuberculate on periclinal wall, testa cells polygonal-oblong, moderately elongated (Iberian Peninsula, Socotra) .. *Petroana*
12. Leaves not fleshy or subfleshy, linear to ovate; flowers small or large; seed testa variously shaped, with or without tubercles 13
13. Petals bicolored, red on the outer surface, white or pink on the inner surface; leaves triquetrous, mostly 3 or 4 at each node (Albania, Serbia, Bosnia) *Balkana*
13. Petals always concolored, variously colored; leaves slender, in few species triquetrous, then the plants mostly caespitose, paired at nodes 14
14. The stigmatic surface terminal; ovules less than 24 .. 15
14. The stigmatic surface extending along the inner side of styles; ovules 24–36 20
15. Stem nodes with small lateral shoots in leaf axils giving a verticillate appearance; leaves acerose, spiny, or terminating to a spine *Acanthophyllum*
15. Lateral shoots in leaf axils absent; leaves not spiny except in *Gypsophila acantholimoides* and *G. pinifolia* 16
16. Capsules shorter than the calyx 17
16. Capsules exceeding the calyx 18
17. Plants annual, shorter than 10 cm, covered by long glandular hairs *Bolanthus confertifolius*
17. Plants perennial, if annual then taller than 10 cm and glandular hairs absent or short *Gypsophila*
18. Plants perennial; capsules ± indehiscent *Acanthophyllum* (cf. *A. cerastioides*)

18. Plants annual or perennial; capsules dehiscent 19
19. Calyx without membranous commissural intervals or with very narrow ones, calcium oxalate crystals absent; stamens shorter than the petals *Heterochroa*
19. Calyx with membranous commissural intervals encompassing calcium oxalate crystals; stamens longer (or sometimes shorter) than petals 20
20. Annual plants with fibrous roots, puberulent below and glabrous in inflorescence (subcosmopolitan, absent in Australia and New Zealand) *Psammophiliella*
20. Annual or perennial plants with tap root, variously hairy *Gypsophila*

Accepted genera and taxonomic changes

1. *Acanthophyllum* C.A.Mey., Verz. Pfl. Casp. Meer.: 210. 1831 – Type (designated by Schiman-Czeika in Rechinger, Fl. Iranica 163: 274. 1988): *Acanthophyllum mucronatum* C.A.Mey.
= *Timaeosia* Klotzsch in Klotzsch & Garcke, Bot. Ergebn. Reise Waldemar: 138, t. 33. 1862 – Type: *T. cerastioides* (D. Don) Klotzsch (= *Acanthophyllum cerastioides* (D. Don) Madhani & Zarre).
= *Allochrusa* Bunge ex Boiss., Fl. Orient. 1: 559. 1867 = *Acanthophyllum* subg. *Allochrusa* (Bunge) Schischk., Fl. URSS 6: 608. 1936 = *Acanthophyllum* sect. *Allochrusa* (Bunge ex Boiss.) Pirani & Rabeler in Phytotaxa 303(2): 198. 2017 – Type (designated by J.J. Swart, ING Card 13030, 1 Apr 1961): *Allochrusa versicolor* (Fisch. & C.A.Mey.) Boiss. (= *Acanthophyllum versicolor* Fisch. & C.A.Mey.).
= *Ochotonophila* Gilli in Feddes Repert. Spec. Nov. Regni Veg. 59: 169. 1956 = *Acanthophyllum* sect. *Ochotonophila* (Gilli) Pirani in Taxon 63(3): 604. 2014 – Type: *O. allochrusoides* Gilli (= *Acanthophyllum allochrusoides* (Gilli) Pirani).
= *Kuhitangia* Ovcz. in Dokl. Akad. Nauk Tadzhiksk. S.S.R. 10: 50. 1967 – Type: *K. popovii* (Preobr.) Ovcz. (= *Acanthophyllum popovii* (Preobr.) Barkoudah).
= *Scleranthopsis* Rech.f. in Ann. Naturhist. Mus. Wien 70: 37. 1967 – Type: *S. aphanantha* (Rech.f.) Rech.f. (= *Acanthophyllum aphananthum* Rech.f.).
= *Kabulianthe* (Rech.f.) Ikonn. in Bot. Zhurn. (Moscow & Leningrad) 89(1): 114. 2004 = *Gypsophila* subg. *Kabulianthe* Rech.f., Fl. Iranica 163: 244. 1988 – Type: *K. honigbergeri* (Fenzl) Ikonn. (= *Acanthophyllum honigbergeri* (Fenzl) Barkoudah).
Diagnosis. – Most of the species are spinose and cushion-like, often bracteate and bracteolate, and oblong-reniform seeds.
Description. – Small shrubby, tufted perennial plants, rarely perennial herbs (e.g., *Acanthophyllum cerastioides*, see below); leaves subulate, acerose, spiny, spring leaves herbaceous, or rarely thinly herbaceous with mostly spinulose apex; flowers often in fragile, ± dense, globose heads, or lax panicles (sect. *Allochrusa*) and rarely solitary; calyx tubular-turbinate, or rarely campanulate to campanulate-tubular, 5- to 15-nerved, 5-toothed, sometimes with narrow membranous commissures; petals 5, white, pink, rose or lilac, limbs entire, rarely bifid;

stamens 10; styles 2; ovary with 4–12(–20) ovules, on a short gynophore; capsule often with 1–2 seeds and opening in various ways; seeds oblong-reniform, or rarely reniform; embryo curved ($2n = 26, 30, 60, 90$; species: ca. 90–100).

Distribution. – SW and Central Asia, one species in China.

Habitat. – *Acanthophyllum* grows in subalpine steppes, on gravelly, sandy or stony hills and rocky slopes.

Resurrected names

Acanthophyllum bungei (Boiss.) Trautv. in Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 511. 1873 \equiv *Allochrusa bungei* Boiss., Fl. Orient. 1: 560. 1867 – Holotype: Iran, East Azerbaijan, inter Marand to Jolfa, 1859, *A. Bunge s.n.* (G barcode G00150411!; isotypes: K barcode K000725639!, W No. W 1988-0009970!).

Acanthophyllum gypsophiloides Regel, Descr. Pl. Nov. Rar. Fedtsch.: 15. 1882 \equiv *Allochrusa gypsophiloides* (Regel) Schischk. in Trudy Bot. Inst. Akad. Nauk S.S.S.R., Ser. 1, Fl. Sist. Vyssh. Rast. 4: 306. 1937 – Type: [Central Asia, Kazakhstan], Kara-Tau, *A. Fedtschenko s.n.* (LE).

Acanthophyllum honigbergeri (Fenzl) Barkoudah in Wentia 9: 182. 1962 \equiv *Silene honigbergeri* Fenzl in Endlicher & Fenzl, Sert. Cabul.: 3. 1836 \equiv *Gypsophila honigbergeri* (Fenzl) Boiss., Fl. Orient. 1: 558. 1867 \equiv *Kabulianthe honigbergeri* (Fenzl) Ikonn. in Bot. Zhurn. (Moscow & Leningrad) 89(1): 114. 2004 – Holotype: [Afghanistan] E montibus prope Kabul, *J.M. Honigberger s.n.* (W No. W 0048192!; possible isotypes: W No. W 0048249 [not imaged], W No. W 1914-0006602 [not imaged]).

= *Gypsophila galiifolia* Gilli in Feddes Repert. Spec. Nov. Regni Veg. 59: 165. 1956 – Lectotype (designated by Rechinger, Fl. Iranica 163: 245. 1988): [Afghanistan] near Kabul, *A. Gilli 1264* (W No. W 1969-0001338!).

Acanthophyllum paniculatum Regel & Herder in Bull. Soc. Imp. Naturalistes Moscou 39(1): 539. 1866 \equiv *Allochrusa paniculata* (Regel & Herder) Ovcz. & Czukav. in Ovcz. & Czukav., Fl. Tadzhiksk. S.S.R. 3: 611. 1968 – Holotype: Central Asia, [Kazakhstan, Dzhungarian Alatau] die Hügel in der Nähe des Piquet Sary-bulka am Füsse des Alatau der sieben Flüsse, 2500 ft., ?1857, *C.L. Semenov s.n.* (LE).

Acanthophyllum tadshikistanicum (Schischk.) Schischk., Fl. URSS 6: 801. 1936 \equiv *Allochrusa tadshikistanica* Schischk. in Trudy Bot. Muz. 24: 40. 1932 – Type: Tadzhikistan, (Buchara olim), in itinere Kizil-su et Sarai, in declivitatibus montanis ad ripam dextram flum. Kizil-su, *D. Divnogorskaja s.n.* (LE).

Acanthophyllum transhyrcanum Preobr. in Bot. Mater. Gerb. Glavn. Bot. Sada R.S.F.S.R. 1(3): 1. 1920 \equiv *Allochrusa transhyrcana* (Preobr.) Czerep., Sosud. Rast. S.S.S.R.: 154. 1981 \equiv *Diaphanoptera transhyrcana* (Preobr.) Rech.f. & Schiman-Czeika in Rechinger, Fl. Iranica 163: 335. 1988

– Holotype: Turkmenistan: Mulla-Kara, in deserto prope Balchan, 1889, *A. Antonow s.n.* (LE; isotype: W No. W 1986-0005948!).

Acanthophyllum versicolor Fisch. & C.A.Mey. in Index Seminum (St. Petersburg [Petropolitanus]) 4: 31. 1838 \equiv *Allochrusa versicolor* (Fisch. & C.A.Mey.) Boiss., Fl. Orient. 1: 559. 1867 – Holotype: [Azerbaijan, Armenia], in locis lapidosis aridissimis desertisque salsis provinciae Nakitschiwan, *J.N. Szovits s.n.* (LE; possible isotype: US barcode 00289322!).

New combinations

Acanthophyllum cerastioides (D.Don) Madhani & Zarre, **comb. nov.** \equiv *Gypsophila cerastioides* D.Don, Prodr. Fl. Nepal.: 213. 1825 \equiv *Timaeosia cerastioides* (D.Don) Klotzsch in Klotzsch & Garcke, Bot. Ergebn. Reise Waldemar: 138. 1862 – Holotype: [Nepal], Gosaingsthan, 1980–3900 m, 1829, *M. Wallich Cat. 644* (K barcode K000725774!; isotypes: E barcode E00301689, G barcode G00226904!).

Acanthophyllum herniarioides (Boiss.) Madhani & Zarre, **comb. nov.** \equiv *Gypsophila herniarioides* Boiss., Fl. Orient., Suppl.: 84. 1888 – Holotype: Afghanistan, Kurrum valley, Sikaram, 7 Aug 1879, *J.E. Aitchison 961* (G; isotype: K barcode K000725698!).

Acanthophyllum myrianthum (Rech.f.) Madhani & A.Pirani, **comb. nov.** \equiv *Gypsophila myriantha* Rech.f. in Anz. Österr. Akad. Wiss., Math.-Naturwiss. Kl. 105: 11. 1969 – Holotype: Afghanistan, Deh Kundi, in declivibus saxosis aridis (Tonschiefer) 10 km W Shahrestan, 33°40'N, 66°35'E, versus Deh Kundi, 34°10'N, 66°07'E, 2200 m, 2 Jul 1967, *K.H. Rechinger 36812* (W No. W 1969-0013845!; isotypes: B barcode B 10 0365629!, E barcode E00301855!, G barcode G00226867!, K barcode K000725739!, LE barcode LE 00012091!, MO barcode MO-176943!, S No. S-G-8666!, US barcode 00103460!).

Acanthophyllum persicum (Boiss.) A.Pirani & Rabeler, **comb. nov.** \equiv *Saponaria persica* Boiss., Diagn. Pl. Orient., ser. 1, 1: 18. 1843 \equiv *Allochrusa persica* (Boiss.) Boiss., Fl. Orient. 1: 560. 1867 – **Lectotype (designated here)** [following annotation on herbarium sheet by Schiman-Czeika, 1982]: [Iran] in lapidosis circa Tabriz, *P.M.R. Aucher-Eloy 4242* (G [herb. Boissier] barcode G00226480!; isolectotypes: G barcode G00226470!, K barcode K000725640!).

Acanthophyllum sedifolium (Kurz) Madhani & Zarre, **comb. nov.** \equiv *Gypsophila sedifolia* Kurz in Flora 55: 285. 1872 – Holotype: [India] Kashmir; Zanskar, 12–13,000 ft., 2 Jul 1848, *T. Thomson s.n.* (B, destroyed) – **Lectotype (designated here)**: (K barcode K000725777!).

Acanthophyllum takhtajanii (Gabrieljan & Dittrich) A.Pirani & Rabeler, **comb. nov.** \equiv *Allochrusa takhtajanii* Gabrieljan &

Dittrich in Biol. Žhurn. Armenii 43: 184. 1990 – Holotype: Armenia, Ararat Distr., lower part of Uztz mountains near Surenavan, 800 m, 20 Jun 1986, *E.T. Gabrieljan & K.G. Tamanian s.n.* (ERE barcode ERE0000046!; isotype: G barcode G00226486!).

2. ***Balkana*** Madhani & Zarre, **gen. nov.** – Type: *Balkana spergulifolia* (Griseb.) Madhani & Zarre.

Diagnosis. – This monotypic genus differs from all other genera of Caryophylleae by its verticillate phyllotaxy at least at some nodes, as well as leaves distinctly swollen and connate at base.

Description. – Perennial herbs; leaves linear, triquetrous, (2–)3–4 at each node; flowers in terminal panicles composed of dichasial partial inflorescences; pedicel longer than the calyx; calyx campanulate-turbinate with 5 veins and membranous commissures; petals 5, bicolored, outer surface red, inner surface white or pink; stamens 10; styles 2; ovules ca. 16; capsule opening by 4 teeth; seeds reniform with small flat tubercles; embryo curved; monotypic.

Etymology. – *Balkana* is named after the general distribution of the plants which is centered in Balkan Peninsula.

Distribution. – The genus is a Mediterranean element distributed in the inner and western part of the Balkan Peninsula: Albania, Serbia, Bosnia-Herzegovina.

Habitat. – These plants are thermophilous, growing on limestone or serpentine soils.

Included species

Balkana spergulifolia (Griseb.) Madhani & Zarre, **comb. nov.** ≡ *Gypsophila spergulifolia* Griseb., Spic. Fl. Rumel. 1: 183. 1843, non *G. spergulifolia* (Jaub. & Spach) Boiss., Fl. Orient. 1: 559. 1867 – Holotype: W Albania, Mt. Puka near Alessia, *A.H.R. Griesbach s.n.* (GOET barcode GOET005978!; isotype: K; possible isotype: M barcode M-0242533!).

3. ***Bolanthus*** (Ser.) Rechb., Deut. Bot. Herb.-Buch: 205. 1841 ≡ *Saponaria* sect. *Bolanthus* Ser. in Candolle, Prodr. 1: 366. 1824 ≡ *Gypsophila* sect. *Bolanthus* (Ser.) Boiss., Fl. Orient. 1: 537. 1867 – Type (designated by Barkoudah in Wentia 9: 168. 1962): *B. hirsutus* (Labill.) Barkoudah.

= *Phrynella* Pax & K.Hoffm. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 16c: 364. 1934 ≡ *Phryna* (Boiss.) Pax & K.Hoffm. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 16c: 351. 1934, non *Phryna* Bubani 1901, **syn. nov.** – Type: *P. ortegioides* (Fisch. & C.A.Mey.) Pax & K.Hoffm. (≡ *Bolanthus ortegioides* (Fisch. & C.A.Mey.) Madhani & Rabeler).

Diagnosis. – Seeds in the members of this genus (except *B. confertifolius*) are comma-shaped and the embryo is hook-shaped. The projecting veins on the tubular calyx give a pentagonal shape to the calyx in these plants. Unlike its related genus *Graecobolanthus*, the petals in members of *Bolanthus* are recurved gradually, not abruptly deflexed.

Description. – Perennials, low prostrate or cushion-forming, or rarely annual (*B. confertifolius*), plants hairy; leaves

small and linear; flowers small, in paniculate to subcapitate dichasia or solitary; calyx tubular-turbinate with 5 projecting veins and membranous commissures; petals 5, recurved gradually, white or pink with purple veins; stamens 10; styles 2; ovary on a short gynophore; capsule opening by 4 teeth; seeds comma-shaped with prominent radicle; embryo hook-shaped; species ca. 10.

Etymology. – From the Greek *bolosi*: lump+nugget+*anthos*: flower.

Distribution. – The genus includes East Mediterranean elements, reaching higher elevations in western parts of the Mediterranean from Turkey to Syria, Lebanon and Palestine.

Habitat. – These plants mostly grow in crevices of calcareous rock and on stony slopes.

New combinations

Bolanthus confertifolius (Hub.-Mor.) Madhani & Heubl, **comb. nov.** ≡ *Gypsophila confertifolia* Hub.-Mor. in Feddes Repert. Spec. Nov. Regni Veg. 52: 42. 1943 – Holotype: [Turkey, C2] Muğla: Muğla-Fethiye, 141 km SE of Muğla, 7 Jun 1938, *J. Reese s.n.* (G barcode G00006010! [ex Hb. Huber-Morath]; isotype: BASBG).

Bolanthus ortegioides (Fisch. & C.A.Mey.) Madhani & Rabeler, **comb. nov.** ≡ *Tunica ortegioides* Fisch. & C.A. Mey. in Ann. Sci. Nat., Bot., sér. 4, 1: 36. 1854 (“*artegioides*”) ≡ *Saponaria ortegioides* (Fisch. & C.A.Mey.) Boiss. & Balansa in Boissier, Diagn. Pl. Orient., ser. 2, 6: 25. 1859 ≡ *Gypsophila ortegioides* (Fisch. & C.A.Mey.) Boiss., Fl. Orient. 1: 552. 1867 ≡ *Phryna ortegioides* (Fisch. & C.A.Mey.) Pax & K.Hoffm. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 16c: 351. 1934 ≡ *Phrynella ortegioides* (Fisch. & C.A.Mey.) Pax & K.Hoffm. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 16c: 364. 1934 – Holotype: [Turkey, B5], Ali Dag, near Kayseri, *M. de Tchihatcheff 601* (P barcode P01903203!).

= *Tunica xylorrhiza* Boiss. in Ann. Sci. Nat., Bot., sér. 4, 2: 246. 1854 – Type: [Turkey, Tokat] In locis montosis sylvaticis Ponti meridionalis inter pagum Almus et urbem Niksar, *M. de Tchihatcheff s.n.* (G [herb. Boissier]).

Note. – The type specimen of *Tunica ortegioides* is probably also the type of *T. xylorrhiza*; further study is required to clarify whether these names are based on same collection/plant.

4. ***Cyathophylla*** Bocquet & Strid in Strid, Mount. Fl. Greece 1: 175. 1986 – Type: *C. chlorifolia* (Poir.) Bocquet & Strid (≡ *Cucubalus chlorifolius* Poir.).

Diagnosis. – Capsules exceeding the calyx, congested inflorescences in both species of this genus, perfoliate leaves in the type (*C. chlorifolia*), and dense glandular indumentum covering the entire plant in *C. viscosa* (C.A.Mey.) Madhani & Rabeler, are the characteristics separating *Cyathophylla* from *Saponaria*.

Description. – Annual herbs, glabrous or with glandular hairs covering entire plant; leaves linear-lanceolate or ovate to rounded, perfoliate or shortly petiolate; flowers in a capitate

inflorescence; calyx tubular-cylindric or tubular-ovoid, 5–15 veins lacking membranous commissures; petals 5, rose or pink, linear to linear-oblong; stamens 10; styles 2; capsule oblong-ovate, opening by 4 teeth; seeds reniform with flat tubercles; embryo hookshaped; 2 species.

Etymology. – From the Greek *cyath*: a cup + *phylla*: leaves.

Distribution. – Greece, Turkey, Iraq, Azerbaijan, Iran, and Turkmenistan.

Habitat. – In rocky slopes, mostly on limestone.

New combination

Cyathophylla viscosa (C.A.Mey.) Madhani & Rabeler, **comb. nov.** ≡ *Saponaria viscosa* C.A.Mey., Verz. Pfl. Casp. Meer.: 212. 1831 – Holotype: [Azerbaijan], Talysh, Swant, *C.A. von Meyer 145* (LE; isotype: E).

5. ***Dianthus*** L., Sp. Pl.: 409. 1753 – Type (designated by Hitchcock & Green, in Sprague, Nom. Prop. Brit. Bot.: 155. 1929): *D. caryophyllus* L.

= *Velesia* L., Sp. Pl.: 332. 1753 – Type: *V. rigida* L.

Diagnosis. – Peltate seeds and straight embryos are characteristic features of the members of this genus. An epicalyx is often present and membranous commissures are usually absent (except: *Dianthus candidus* (P.W.Ball & Heywood) Madhani & Heubl, *D. recticaulis* Ledeb., *D. nudiflorus* Griff. and *D. tunicooides* (Ser. ex DC.) Madhani & Heubl, see below).

Description. – Annual or perennial herbs, rarely subshrubs; leaves grass-like, often linear to oblong (ovate); flowers mostly hermaphrodite or rarely unisexual, solitary or in capitate (rarely paniculate or monochasial) cymes, often subtended by bracts, and calyx mostly subtended by two or many epicalyx scales; calyx tubular with 20–60 parallel veins, without membranous commissures or rarely 5- to 15-veined (former *Petrorhagia* spp. and *Velesia rigida*) and sometimes with membranous commissures (former *Petrorhagia* spp.), 5-toothed; petals white, pink or red, rarely yellow, limb entire, toothed or fimbriate, without coronal scales; stamens 10; styles 2; ovary on a short gynophore; capsule opening by 4 teeth; seeds many, peltate; embryo straight; $2n = 26$ (*Dianthus tunicooides*), 28, 30, 60, 90; species more than 300.

Etymology. – *Dianthus* is the contracted form of *Diosanthos*; from Greek *Dios*:- of Zeus + *anthos*: flower.

Distribution. – Europe, Asia, and Africa, especially in Mediterranean regions; introduced in North and South America, Hawaii, and Australia.

Habitat. – Mostly in hillsides, mountain slopes, dry meadows, and rocky hills.

Resurrected name

Dianthus nudiflorus Griff., Not. Pl. Asiat. 4: 466. 1854 – Holotype: Afghanistan, barren rocky mountains around Otipore, 7 Apr 1839, *W. Griffith 132* (K).

= *Velesia rigida* L., Sp. Pl.: 332. 1753 – Lectotype (designated by Strid in Taxon 53: 1053. 2004): *Loefling 307*, Herb. Linn. No. 326.1 (LINN).

Note. – Since the name *Dianthus rigidus* had already been used by Marschall von Bieberstein (Fl. Taur.-Caucas. 1: 325. 1808), this name was not available for a new combination. Therefore, one of the oldest synonyms of this species under *Dianthus* (i.e., *D. nudiflorus* Griff. 1854) is resurrected here.

New combinations

Dianthus candidus (P.W.Ball & Heywood) Madhani & Heubl, **comb. nov.** ≡ *Petrorhagia candida* P.W.Ball & Heywood, Bull. Brit. Mus. (Nat. Hist.), Bot. 3: 141. 1964 ≡ *Fiedleria candida* (P.W.Ball & Heywood) Ovcz., Fl. Tadzhikskoi S.S.R. 3: 608. 1968 – Holotype: [Greece], Crete, Sitia, May 1846, *T.H.H. Heldreich s.n.* (BM; isotypes: CGE, K barcodes K000725564! & K000725566!).

Dianthus strictiformis Madhani & Zarre, **nom. nov.**, non *Dianthus strictus* Banks ex Sol. in Russel, Nat. Hist. Aleppo, ed. 2, 2: 252. 1794 ≡ *Gypsophila stricta* Bunge in Ledeb., Fl. Altaic. 2: 129. 1830 ≡ *Tunica stricta* (Bunge) Fisch. & C.A.Mey. in Index Seminum (St.Petersburg [Petropolitanus]) 4: 50. 1837 ≡ *Dianthus recticaulis* Ledeb., Fl. Ross. 1(2): 287. 1842, nom. superfl. [citing *G. stricta* and *Tunica stricta* in synonymy] – Holotype: Russia, in siccis prope Buchtorminsk et Alexandrowsk, in rupestribus prope pagum Krasnojarsk ad fl. Irtysch, *C.F. Ledebour s.n.* (LE). = *Petrorhagia alpina* (Hablitz) P.W.Ball & Heywood in Bull. Brit. Mus. (Nat. Hist.), Bot. 3: 145. 1964 ≡ *Gypsophila alpina* Hablitz in Neueste Nord. Beytr. Phys. Geogr. Erd-Völkerbeschreib. 4: 57. 1783 ≡ *Tunica alpina* (Hablitz) Bobrov in Bot. Zhourn. S.S.S.R. 43: 1546. 1958 ≡ *Fiedleria alpina* (Hablitz) Ovcz. in Dokl. Akad. Nauk Tadzhiksk. S.S.R. 7: 52. 1967 – Holotype: [Russia] Siberia, Irtysch River, gravelly banks, 2000–3000 m, *C.L. von Hablitz s.n.* (LE).

Dianthus tunicooides Madhani & Heubl, **nom. nov.**, non *D. armerioides* Raf. in J. Bot. (Paris) 4: 269. 1814 ≡ *Gypsophila armerioides* Ser. ex DC., Prodr. 1: 353. 1824 ≡ *Tunica sibthorpii* Boiss. in Diagn. Pl. Orient., ser. 1, 8: 61. 1849, nom. illeg., ≡ *Tunica armerioides* (Ser. ex DC.) Halácsy, Consp. Fl. Graec. 1: 194. 1900 ≡ *Petrorhagia armerioides* (Ser. ex DC.) P.W.Ball & Heywood in Bull. Brit. Mus. (Nat. Hist.), Bot. 3: 139. 1964 ≡ *Fiedleria armerioides* (Ser. ex DC.) Ovcz., Fl. Tadzhikskoi S.S.R. 3: 608. 1968 – Holotype: Turquie [Turkey], Troade, *G.A. Olivier s.n.* (G-DC barcode G00214254!; isotype: MW).

6. ***Diaphanoptera*** Rech.f. in Repert. Spec. Nov. Regni Veg. 48: 41. 1940 – Type: *D. khorasanica* Rech.f.

Diagnosis. – The members of this genus are characterized by their membranous winged-vein calyces.

Description. – Perennial tufted plants, woody at base and sometimes glandular pubescent; leaves slightly succulent; flowers in lax few-flowered cymes; bracts and bracteoles often present; calyx turbinate, membranous, with 5 prominent or winged veins, 5-toothed; petals 5, rose or violet, entire or emarginate; stamens 10; styles 2; ovary obovate, on a gynophore, ovules

(6–)8–19; capsule opening by 4 teeth; seeds reniform; embryo curved; species 6.

Etymology. – From Ancient Greek *diaphanês*: transparent + *ptron*: wing.

Distribution. – Mountainous areas up to 3800 m in NE Iran, Turkmenistan, and Afghanistan.

Habitat. – High altitudes of mountain peaks, on serpentine, calcareous or rocky substrates.

7. *Graecobolanthus* Madhani & Rabeler, **gen. nov.** – Type: *G. graecus* (Schreb.) Madhani & Rabeler (≡ *Saponaria graeca* Schreb.).

Diagnosis. – This new genus differs from *Bolanthus* mainly by its abruptly deflexed petals.

Description. – Perennial herbs; caudex woody and thick, leaves paired at nodes, small, linear, linear-lanceolate, lanceolate or spathulate; flowers in lax dichasial or capitate inflorescences; calyx tubular-turbinate with 5 winged veins and membranous commissures; petals 5, abruptly deflexed, white or purple; stamens 10; styles 2, stigmatic surface all along the inner side; ovary on a short gynophore; ovules 8–28; capsule opening by 4 teeth; seeds comma-shaped with small tubercles on testa and with a prominent radicle; embryo hook-shaped; $2n = 20$; species 8.

Etymology. – From Latin *Graeco*: Greek + *Bolanthus*.

Distribution. – The members of this genus are Mediterranean elements restricted to Greece, in particular to Peloponnese Peninsula.

Habitat. – The members of this genus are found in mountainous areas and mainly inhabit rocky and stony slopes.

Included species

Graecobolanthus chelmicus (Phitos) Rabeler & Madhani, **comb. nov.** ≡ *Bolanthus chelmicus* Phitos in Bot. Chron. (Patras) 1(1): 40. 1981 – Holotype: Greece, prov. Achaia: mons Chelmos, supra pagum Peristera, in declivibus orientalibus, 1100–1200 m, *Georgiadis 1783* (UPA).

Graecobolanthus creutzburgii (Greuter) Rabeler & Madhani, **comb. nov.** ≡ *Bolanthus creutzburgii* Greuter in Candollea 20: 210. 1965 – Holotype: Greece, Creta, prov. Piriotisi, NW-Hang des Berges Mavri, ob. der Quelle Skaronero, Tripolitaa-Kalk, 1800–1900m, 30 Jun 1961, *W. Greuter 3733* (PAL [herb. Greuter]; isotypes: G barcode G00226560!, W No. W 1966-0016564!, Z).

Graecobolanthus fruticosus (Bory & Chaub.) Madhani & Zarre, **comb. nov.** ≡ *Saponaria fruticulosa* Bory & Chaub. in Bory & al., Exp. Sci. Morée, Bot.: 118. 1832 ≡ *Gypsophila fruticulosa* (Bory & Chaub.) Boiss., Fl. Orient. 1: 556. 1867 ≡ *Bolanthus fruticosus* (Bory & Chaub.) Barkoudah in Wentia 9: 164. 1962 – Holotype: [Greece, Peloponnese] Coteaux de Laconie, 1829, *J.B.G.M. Bory s.n.* (P barcode P04982600!).

Note. – Phitos (1981) designated a lectotype (P04982599) that he notes was collected in 1833. Since this specimen was

collected after the species protologue, this lectotypification cannot be considered as effective (McNeill & al., 2012: Art. 9.3).

Graecobolanthus graecus (Schreb.) Madhani & Rabeler, **comb. nov.** ≡ *Saponaria graeca* Schreb. in Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 4: 138. 1770 ≡ *Gypsophila graeca* Britten in J. Bot. 44: 345. 1906 ≡ *Bolanthus graecus* (Schreb.) Barkoudah in Wentia 9: 164. 1962 – Lectotype (designated by Phitos in Strid & Tan, Fl. Hellenica 1: 327. 1997): “*Lychnis pumila*, umbellifera, Polygoni folio, flore albo, cum circulo atro-purpureo”, *Tournefort 3032* (P-TRF).

= *Cucubalus polygonoides* Willd., Sp. Pl. 2: 690. 1799 ≡ *Silene polygonoides* (Willd.) Pers., Syn. Pl. 1: 500. 1805 ≡ *Saponaria polygonoides* (Willd.) Jaub. & Spach, Ill. Pl. Orient. 5: 2, t. 402. 1853 ≡ *Gypsophila polygonoides* (Willd.) Halácsy in Denkschr. Akad. Wiss. Wien, Math.-Naturwiss. Kl. 61: 473. 1894 – Holotype: Greece, Nákos, [*Gundelsheimer ex*] *W. Wierweg 1* (B-W barcode B-W 08601 -01 0!).

= *Gypsophila ocellata* Sm. in Sibthorp & Smith, Fl. Graec. Prodr. 1: 281. 1809 ≡ *Gypsophila hirsuta* var. *ocellata* (Sm.) Boiss., Fl. Orient. 1: 556. 1867 ≡ *Gypsophila polygonoides* subsp. *ocellata* (Sm.) Hayek in Repert. Spec. Nov. Regni Veg. Beih. 30(1): 220. 1924 – Lectotype (designated by Phitos in Strid & Tan, Fl. Hellenica 1: 327. 1997): [Greece, Evonia] in Delphi monte Euboeae, *Sibthorp s.n.* (OXF [IDC photo 43: A4]).

Graecobolanthus intermedius (Phitos) Rabeler & Madhani, **comb. nov.** ≡ *Bolanthus intermedius* Phitos in Bot. Chron. (Patras) 1(1): 39. 1981 – Holotype: Greece, Ins. Euboea, in saxosis serpentinicis et magesiticis litorcis ad pagu Mantudi [rocky shore, Mantudi], *Georgiadis 1657* (UPA).

Graecobolanthus laconicus (Boiss. & Heldr. ex Boiss.) Madhani & Zarre, **comb. nov.** ≡ *Gypsophila fasciculata* var. *laconica* Boiss. & Heldr. ex Boiss., Fl. Orient. 1: 556. 1867 ≡ *Gypsophila laconica* Boiss. & Heldr. ex Boiss., Fl. Orient., Suppl.: 88. 1888 ≡ *Bolanthus laconicus* (Boiss. & Heldr. ex Boiss.) Barkoudah in Wentia 9: 163. 1962 – Lectotype (designated by Phitos in Bot. Chron. (Patras) 1: 36. 1981): Greece, Peloponnese, in regione media montis Malevo (Napvov) prope Vromopigadon, 2000 ft, 7–19 Jul 1850, *G.H. Orphanides*, *Fl. Graeca Exs. 1* (ATHU; isolecotypes: BR barcode 000006970062!, FI, G [herb. Boissier], JE barcodes JE00015406! & JE00015407!, K barcodes K000725783! & K000725784!, L, LD barcode 1006486!, US barcode 00589410!, WU No. 0073639!).

Graecobolanthus thessalus (Jaub. & Spach) Madhani & Zarre, **comb. nov.** ≡ *Saponaria thessala* Jaub. & Spach, Ill. Pl. Orient. 5: 2. 1853 ≡ *Gypsophila thessala* (Jaub. & Spach) Halácsy in Consp. Fl. Graec. 1: 191. 1900 ≡ *Gypsophila polygonoides* subsp. *thessala* (Jaub. & Spach) Hayek in Repert. Spec. Nov. Regni Veg. Beih. 30(1): 221. 1924 – Holotype: Greece, Thessaliae, prope Vólos, 1837, *P.M.R.*

Aucher-Eloy 566 (P barcode P05075275!, isotypes: BM barcodes BM000572757! & BM000810718!, FI, K barcodes K000725780! & K000725781!, P).

Graecobolanthus thymifolius (Sm.) Rabeler & Madhani, **comb. nov.** ≡ *Gypsophila thymifolia* Sm. in Sibthorp & Smith, Fl. Graec. Prodr. 1: 282. 1809 ≡ *Saponaria thymifolia* Boiss., Diagn. Pl. Orient, ser. 1, 1: 17. 1843 ≡ *Gypsophila hirsuta* var. *thymifolia* Boiss., Fl. Orient. 1: 556. 1867 ≡ *Bolanthus thymifolius* (Sm.) Phitos in Bot. Chron. (Patras) 1: 39. 1981 – Lectotype (designated by Phitos in Strid & Tan, Fl. Hellenica 1: 328. 1997): [Greece, Sterea Ellas] in monte Parnasso, *Sibthorp s.n.* (OXF [IDC photo 43: A5]).

8. ***Gypsophila*** L., Sp. Pl.: 406. 1753 – Type (designated by Hitchcock & Green in Sprague, Nom. Prop. Brit. Bot. 154. 1929): *G. repens* L.
 = *Rokejeka* Forssk., Fl. Aegypt.-Arab.: 90. 1775 – Type: *R. capillaris* Forssk. (≡ *Gypsophila capillaris* (Forssk.) C.Chr.).
 = *Vaccaria* Wolf, Gen. Pl.: III. 1776. – Lectotype (designated by Phillips, Gen. S. African Fl. Pl., ed. 2: 330. 1951): *V. pyramidata* Medik. (≡ *Gypsophila hispanica* Mill.).
 = *Hagenia* Moench, Methodus: 61. 1794, non J.F.Gmel. 1791 – Type: *H. filiformis* Moench (= *Gypsophila pilosa* Huds.).
 = *Arrostia* Raf., Caratt. Nouv. Gen.: 75. 1810 – Type: *A. dichotoma* Raf. (≡ *Gypsophila arrostii* (Raf.) Guss.).
 = *Dichoglottis* Fisch. & C.A.Mey. in Index Seminum (St. Petersburg [Petropolitanus]) 1: 25. 1835 – Type: *D. linearifolia* Fisch. & C.A.Mey. (≡ *Gypsophila linearifolia* (Fisch. & C.A.Mey.) Boiss.).
 = *Ankyropetalum* Fenzl in Bot. Zeitung (Berlin) 1: 393. 1843 – Type: *A. gypsophiloides* Fenzl (≡ *Gypsophila gypsophiloides* (Fenzl) Blakelock).
 = *Bolbosaponaria* Bondarenko in Kovalevskaja, Opred. Rast. Sred. Azii 2: 327. 1971 – Type: *B. sewerzowii* (Regel & Schmalh.) Bondarenko (“*severtzowii*”) (≡ *Saponaria sewerzowii* Regel & Schmalh (“*sewerzowi*”).
 = *Pseudosaponaria* (F.N.Williams) Ikonn. in Novosti Sist. Vyssh. Rast. 15: 144. 1979 – Type: *P. pilosa* (Huds.) Ikonn. (≡ *Gypsophila pilosa* Huds.).

Diagnosis. – The members of this genus are separated from *Acanthophyllum*, *Heterochroa* and *Saponaria* by the presence of distinct membranous commissures and calcium oxalate druses in the mesophyll of the calyx. They differ from *Acanthophyllum*, *Bolanthus* and *Petrorhagia* by reniform or reniform-globular seeds. The concolored petals and opposite phyllotaxy can discriminate these species from *Balkana* (see above).

Description. – Annual or perennial herbs to tufted caespitose or pulvinate subshrubs; leaves linear or even spiny to lanceolate and ovate, often somewhat fleshy; flowers hermaphrodite or sometimes unisexual, in many-flowered lax thyrses or panicles, or compact head-like or few-(uni-)flowered raceme-like monochasia; bracts present; pedicel longer than the calyx; calyx campanulate-turbinate or tubular, mostly with calcium oxalate druses, with 5 veins and membranous commissures, or inflated with 5 winged veins and lacking membranous commissures; petals 5, white, pink, or purple, often concolorous

(upper and lower side) with purple veins; stamens 10, rarely 5; styles 2(–3), stigmatic surface extending all along the style; ovules 4–36; capsule opening by 4 valves; seeds reniform; embryo curved; $2n = 12, 24, 26, 28, 30, 34, 36, 48, 51, 60, 68$; species ca. 150.

Etymology. – From Greek *gypsos*: chalk, gypsum + *philos*: loving.

Distribution. – Temperate regions of Eurasia, Africa, Pacific Islands, with one species extending to Australia; introduced in North and South America.

Habitat. – Mostly in steppes on calcareous hills, dry or rocky slopes, and sandy soils, sometimes weeds on farms, some species ruderals growing along roadsides.

Resurrected names

Gypsophila arsiusiana (Kotschy ex Boiss.) F.N.Williams in J. Bot. 27: 322. 1889 ≡ *Ankyropetalum arsiusianum* Kotschy ex Boiss., Fl. Orient. 1: 533. 1867 – Syntypes: [Turkey C5 Hatay], Mount Amanus, supra Arsus, 2 Jul 1862, *Th. Kotschy 117* (G [herb. Boissier]; isosyntypes: JE barcodes JE00015413! & JE00015412!, K barcode K000725802!, L barcode L 0038665!, P barcodes P01903163!, P01903164! & P01903165!); Mount Akkerdagh prope Marasch, *Hausknecht s.n.* (G [herb. Boissier], JE).

Gypsophila bucharica B.Fedtsch. in Trudy Imp. S.-Peterburgsk. Bot. Sada 32: 7. 1911 ≡ *Saponaria bucharica* (B.Fedtsch.) Preobr. ex Popov in Trudy Turkestansk. Gosud. Univ. 4: 24. 1922 ≡ *Bolbosaponaria bucharica* (B.Fedtsch.) Bondarenko in Opred. Rast. Sred. Azii 2: 292. 1971 – Holotype: [Tajikistan], Viloyati Khatlon (Qurghontepa), Chanatus Buchara, Prov. Balduchuan, in montibus ad pagum Tutkaul in valle fluvii Wachs, 8 May 1906, *G.G. Morren s.n.*, *Anonymous*, *Ed. Horti Bot. Imp. 10* (LE; isotype: FR barcode FR-0030878!).

Gypsophila gypsophiloides (Fenzl) Blakelock in Kew Bull. 12(2): 193. 1957 ≡ *Ankyropetalum gypsophiloides* Fenzl in Bot. Zeitung (Berlin) 1: 393. 1843 – Syntypes: [Turkey C8 Mardin], zwischen Mardin, Assuauer und Tichalaga, *Th. Kotschy 356* (W, destroyed; isosyntypes: E barcode E00301841!, K barcodes K000725796! & K000725797!); [Iraq, Kurdistan:] prope Gara, Jul 1841, *Th. Kotschy, Pl. Alepp. Kurd. Moss. 406* (W, destroyed; isosyntypes: BM barcode BM000572761!, K barcode K000725795!, HAL barcode HAL0117954!, P barcodes P04982620!, P04982621!, P04982623! & P04982624!).

Gypsophila reuteri (Boiss. & Hausskn.) F.N.Williams in J. Bot. 27: 322. 1889 ≡ *Ankyropetalum reuteri* Boiss. & Hausskn. in Boissier, Fl. Orient. 1: 533. 1867 – Holotype: [Turkey], Maras, Akkerdagh, 15 Jul 1861, *H.C. Hausknecht s.n.* (G [herb. Boissier]; isotype: JE barcode JE00015414!).

Gypsophila vaccaria (L.) Sm. in Sibthorp & Smith, Fl. Graec. Prodr. 1: 279. 1809 ≡ *Saponaria vaccaria* L., Sp. Pl.: 409.

- 1753 ≡ *Lychnis vaccaria* (L.) Scop., Fl. Carniol., ed. 2, 1: 303. 1771 ≡ *Vaccaria vulgaris* Host, Fl. Austriac. 1: 518. 1827 ≡ *Silene vaccaria* (L.) E.H.L.Krause, Deutschl. Fl., ed. 2, 5: 120. 1901 – Lectotype (designated by Sell, 1980, on the sheet): Cultivated material from the garden of *George Clifford III*: Hartekamp Garden, Holland, *Hort. Cliff. 166* (BM barcode BM000628472!).
- = *Saponaria hispanica* Mill., Gard. Dict., ed. 8, in Errata. 1768 ≡ *Vaccaria hispanica* (Mill.) Rauschert in Wiss. Z. Martin-Luther-Univ. Halle-Wittenberg, Math.-Naturwiss. Reihe 14: 496. 1965 – Type: not specified (indicated as “... grows naturally in Spain”).
- = *Saponaria segetalis* Neck., Delic. Gallo-Belg. 1: 194. 1768 ≡ *Vaccaria segetalis* (Neck.) Garcke ex Asch., Fl. Brandenburg 1: 84. 1860, nom. illeg. (cited *S. vaccaria* L. in synonymy).
- = *Saponaria rubra* Lam., Fl. Franç. 2: 541. 1779, nom. illeg. (cited *S. vaccaria* L. in synonymy).
- = *Vaccaria pyramidata* Medik. in Philos. Bot. 1: 96. 1789 – Syntypes(?): East India, *W. Roxburgh s.n.* (K barcodes K000725844! & K000725845!).
- = *Vaccaria parviflora* Moench, Methodus: 63. 1794, nom. illeg. (cited *Saponaria vaccaria* L. in synonymy).
- = *Saponaria perfoliata* Roxb. ex Willd., Enum. Hort. Berol.: 464. 1809 ≡ *Vaccaria perfoliata* (Roxb. ex Willd.) Sweet, Hort. Brit., ed. 2: 51. 1830 – Holotype(?): India?, *W. Roxburgh s.n.* (B barcode B-W 08501-01 0!; isotype: BR barcode 00006981341!).
- = *Saponaria vaccaria* var. *grandiflora* Fisch. ex DC., Prodr. 1: 365. 1824 ≡ *Vaccaria grandiflora* (Fisch. & DC.) Jaub. & Spach, Ill. Pl. Orient. 3: 40, t. 231. 1847 ≡ *Vaccaria perfoliata* var. *grandiflora* (Fisch. ex Seringe) Halaesy, Consp. Fl. Graec. 1: 190. 1900 ≡ *Vaccaria hispanica* subsp. *grandiflora* (Fisch. ex DC.) Holub in Folia Geobot. Phytotax. 11: 83. 1976 ≡ *Vaccaria hispanica* var. *grandiflora* (Fisch. ex DC.) J.Léonard in Bull. Jard. Bot. Natl. Belg. 55: 298. 1985 – Holotype: [Georgia] Iberia, Tiflis, 1819, *F.E.L. Fischer s.n.* (G-DC barcode G00211736!).
- = *Vaccaria arvensis* Link, Handbuch 2: 240. 1829, nom. illeg. (cited *V. pyramidata* Medik. in synonymy).
- = *Vaccaria sessilifolia* Sweet, Hort. Brit., ed. 2: 51. 1830, nom. illeg. (cited *V. pyramidata* Medik. in synonymy).
- = *Vaccaria oxyodonta* Boiss., Diagn. Pl. Orient., ser. 2, 1: 68. 1854 ≡ *Saponaria oxyodonta* (Boiss.) Boiss., Fl. Orient. 1: 525. 1867 ≡ *Vaccaria pyramidata* var. *oxyodonta* (Boiss.) Zohary, Fl. Palaestina 1: 104. 1966 ≡ *Vaccaria hispanica* subsp. *oxyodonta* (Boiss.) Greuter & Burdet in Willdenowia 12: 191. 1982 – Lectotype (designated by Rechinger, F. Iranica 163: 339. 1988): Afghanistan, *W. Griffith* Herb. Late East Ind. Comp. 309 (G; isotype: C).
- = *Saponaria liniflora* Boiss. & Hausskn. in Boissier, Fl. Orient. 1: 525. 1867 ≡ *Vaccaria liniflora* (Boiss. & Hausskn.) Bornm. in Notizbl. Bot. Gart. Berlin-Dahlem 7: 142. 1917 ≡ *Vaccaria pyramidata* var. *liniflora* (Boiss. & Hausskn.) Cullen in Notes Roy. Bot. Gard. Edinburgh 27: 214. 1967 ≡ *Vaccaria hispanica* subsp. *liniflora* (Boiss. & Hausskn.) Greuter & Burdet in Willdenowia 12: 191. 1982 ≡ *Vaccaria hispanica* var. *liniflora* (Boiss. & Hausskn.) J.Léonard in Bull. Jard. Bot. Natl. Belg. 55: 298. 1985 – Syntypes: [Turkey, C7] Inter segetes, inter Orfa et Karan, 1865, *H.K. Haussknecht, Iter syriaco-armeniaceum s.n.* (or 542) (JE barcodes JE00015333!, JE00015334!, JE00015335! & JE00015336!; isosytype: K barcode K000725843!).
- = *Vaccaria perfoliata* Halacsy, Consp. Fl. Graec. 1: 189. 1900, nom. illeg., non (Roxb. ex Willd.) Sweet 1830.
- = *Vaccaria brachycalyx* Pau in Trab. Mus. Ci. Nat., Ser. Bot. 14: 10. 1918 – Type: [Iran, Prov. Khuzestan] Gotevend y Valle de Bazouft, bajo Karum, 400 m, *Martinez de la Escalera s.n.* (MA).
9. ***Heterochroa*** Bunge in Ledeb., Fl. Altaic. 2: 131. 1830 ≡ *Gypsophila* sect. *Heterochroa* (Bunge) A. Braun in Flora 26: 383. 1843. – Type: *H. petraea* Bunge.
- Diagnosis.* – Reniform-oblong seeds and narrow membranous commissures are the main characteristic features of this genus.
- Description.* – Perennial low herbs, or dense caespitose plants, mostly with thick roots, often glandular hairy; leaves very small, linear, linear-subulate, linear-lanceolate, lanceolate, or ovate; inflorescence dichasial, lax-dichasial, or solitary; calyx campanulate or widely campanulate, either with narrow or without membranous commissures and without calcium oxalate druses; petals 5, white to purple; stamens 10, often shorter than petals; styles 2; ovules 8–24; capsule opening by 4 valves; seeds reniform, slightly oblong; embryo curved; *2n* = 34, 36; species 6.
- Etymology.* – From Greek *hetero*: different + *chroa*: skin, color of skin.
- Distribution.* – Kazakhstan (Turkestan), Russia (West Siberia; Altai; Far East, Kamchatka peninsula), Mongolia and N China.
- Habitat.* – On stony or rubble hills and alpine zones, or on stony semi-desert soils.
- Resurrected names*
- Heterochroa desertorum*** Bunge in Mém. Acad. Imp. Sci. St.-Petersbourg Divers Savans 2: 543. 1835 ≡ *Gypsophila desertorum* (Bunge) Fenzl in Ledebour, Fl. Ross. 1: 292. 1842 – Holotype: [Russia, West Siberia], Altai, along the river Tshuya, 1832, *A. Bunge s.n.* (LE; isotype: P barcode P04980638!; possible isotypes: CAS barcode 00123503!, E barcode E00301730!, K barcode K000725758!, L barcode L 0038678!).
- Heterochroa microphylla*** Schrenk in Fischer & Meyer, Enum. Pl. Nov. 1: 92. 1841 – Holotype: [Kazakhstan] Alatau, Tarbagatai Mts., 1840, *A.G. Schrenk s.n.* (LE; isotypes: BR, P barcode P04980989!).
- Heterochroa petraea*** Bunge in Ledebour, Fl. Altaic. 2: 131. 1830 ≡ *Gypsophila petraea* (Bunge) Fenzl in Ledebour, Fl. Ross. 1: 291. 1842, nom. illeg., non (Baumg.) Rchb. 1830 – Syntypes: [Russia: West Siberia], Altai, Baschkau,

A. Bunge s.n. (LE; possible isosyntypes: BR, E barcode E00301729!, G barcode G00226863!, HAL barcode HAL0117888!, K barcodes K000725762!, K000725763! & K000725764!, M, P barcodes P04981532! & P04981533!); prope Riddersk, collector? (LE).

Heterochroa violacea (Ledeb.) Walp., Repert. Bot. Syst. 5: 81. 1845 ≡ *Gypsophila violacea* (Ledeb.) Fenzl in Ledebour, Fl. Ross. 1: 291. 1842 ≡ *Arenaria violacea* Ledeb. in Mém. Acad. Imp. Sci. St. Pétersbourg Hist. Acad. 5: 533–534. 1815 – Holotype: [Russia, Far East], Okhotsk, Yablonov Mts, near the city Okhotsk, *D. Redowsky s.n.* (LE).

New combinations

Heterochroa antoninae (Schischk.) Madhani & Zarre, **comb. nov.** ≡ *Gypsophila antoninae* Schischk., Fl. URSS 6: 744. 1936; and in Trudy Bot. Inst. Akad. Nauk S.S.S.R., Ser. 1, Fl. Sist. Vyssh. Rast. 3: 180. 1937 – Holotype: Turkmenistan, Kopet Dag, Kyzyl Chasar, 27 Jun 1934, *A. Borissova s.n.* (LE).

= *Gypsophila porphyrantha* Rech.f. & Aellen in Bot. Jahrb. Syst. 75: 356. 1951 – Holotype: [Iran], Khorasan, Montes Hezar Masjed, inter Gash et Talqur, 1600–1800 m, 7–10 Jun 1948, *K.H. Rechinger & F. Rechinger*, Iter Iranicum II, 5173 (W No. W 1960-0001226!; isotypes: G barcodes G00006044! & G00006045!).

Heterochroa turkestanica (Schischk.) Madhani & Zarre, **comb. nov.** ≡ *Gypsophila turkestanica* Schischk. in Trudy Bot. Muz. 24: 38. 1932 – Holotype: [Russia], Middle Asia, Tien Shan, Alexandrov Mts., between the rivers Tshatshke and Terek, 20 Jul 1930, *M. Iljin s.n.* (LE).

10. ***Petroana*** Madhani & Zarre, **gen. nov.** – Type: *P. montserratii* (Fern. Casas.) Madhani & Zarre (≡ *Gypsophila montserratii* Fern.Casas.).

Diagnosis. – It is similar to *Gypsophila* but differs in having spatulate and fleshy leaves as well as seeds with testa cells moderately polygonal (not elongated as in *Gypsophila*), swollen and tuberculate on periclinal walls.

Description. – Perennial herbs; leaves spatulate and fleshy, paired at each node, and sometimes condensed; flowers small, arranged in dichasial lax inflorescences; pedicel 4–6 mm long; calyx campanulate with membranous commissures; petals 5, concolorous, white to pinkish; stamens 10; ovary on a very short gynophore; ovules ca. 16; styles 2, stigma terminal; capsule opening by 4 valves; seeds subreniform, testa cells polygonal, swollen and tuberculate; embryo curved; $2n = 26$; species 2.

Etymology. – *Petro*: rock+*ana*: pertaining.

Distribution. – The two members of this genus show a disjunct distribution pattern; *P. montserratii* is a mountainous element in the Iberian peninsula and *P. montana* is found in Yemen (N & S), Socotra, Oman and Somalia.

Habitat. – Open rocky slopes and gravelly wadi-bed (for *P. montana*) and cracks in limestone, overhangs, and vertical walls (for *P. montserratii*).

Included species

Petroana montana (Balf.f.) Madhani & Zarre, **comb. nov.** ≡ *Gypsophila montana* Balf.f. in Proc. Roy. Soc. Edinburgh 11: 501. 1882 ≡ *Saponaria montana* (Balf.f.) Barkoudah in Wentia 9: 183. 1962 – **Lectotype (designated here):** Socotra, Feb–Mar 1880, *Balfour, Cockburn & Scott 442* (E barcode E00239367!; isolectotype: P barcode P05018082!).

Petroana montserratii (Fern.Casas) Madhani & Zarre, **comb. nov.** ≡ *Gypsophila montserratii* Fern.Casas in Publ. Inst. Biol. Aplicada 52: 121. 1972 – Holotype: Spain, Fuensanta nomen auclit, inter oppidula El-che de la Sierra et Yeste (Albacete), ubi legel'Unt, 14 Jul 1971, *J. Molero & J. Fernandez Casas s.n.* (GDA; isotypes: BC, BCC, BCF, JACA, MA barcode MA 327148!, SEV barcode SEV 9303!).

11. ***Petrorhagia*** (Ser.) Link, Handbuch 2: 235. 1831 ≡ *Gypsophila* sect. *Petrorhagia* Ser. in DC., Prodr. 1: 354. 1824 – Type (designated by Britton & Brown, Ill. Fl. N.U.S., ed. 2, 2: 72. 1913): *P. saxifraga* (L.) Link.

= *Imperatia* Moench, Methodus: 60. 1794 – Type: *I. filiformis* Moench (≡ *Petrorhagia saxifraga* (L.) Link).

= *Tunica* Ludw., Inst. Regn. Veg., ed. 2: 129. 1757 – Type: *T. saxifraga* Scop. (≡ *Petrorhagia saxifraga* (L.) Link).

= *Kohlrauschia* Kunth, Fl. Berol. 1: 108. 1838 ≡ *Dianthus* sect. *Kohlrauschia* (Kunth) Fenzl in Endlicher, Gen. Pl.: 971. 1840 ≡ *Petrorhagia* sect. *Kohlrauschia* (Kunth) Ball & Heywood in Bull. Brit. Mus. (Nat. Hist.), Bot. 3. 1964 – Type: *K. prolifera* (L.) Kunth (≡ *Petrorhagia prolifera* (L.) P.W.Ball & Heywood).

= *Fiedleria* Rchb., Deut. Bot. Herb.-Buch: 206. 1841 ≡ *Tunica* sect. *Fiedleria* (Rchb.) Graebn. in Ascherson & Graebner, Syn. Mitteleur. Fl. 5(2): 272. 1921 – Type: *F. illyrica* (Sm.) Rchb. (≡ *Petrorhagia illyrica* (Ard.) P.W.Ball & Heywood). **Diagnosis.** – Peltate seeds and a straight embryo along with membranous calyx commissures as well as the presence of an epicalyx in most members of *Petrorhagia*, separate it from *Bolanthus*, *Dianthus*, *Gypsophila* and *Saponaria*.

Description. – Annual, biennial, or perennial herbs, sometimes woody at base; leaves often narrow and grass-like, linear, subulate to oblong; flowers hermaphrodite or sometimes unisexual in panicles, capitate or fasciculate cymes, or solitary; bracts and bracteoles absent or present, when present often surrounding the calyx as an epicalyx; calyx campanulate, cylindrical or tubular, 5- to 15-veined, 5-toothed with broad membranous commissures; petals 5, white to pink or reddish-lilac; stamens 10; styles 2; capsule opening by 4 teeth; seeds numerous, peltate, dorsiventrally compressed, with facial hilum; embryo straight; $2n = 26, 28, 30,$ or 60 ; species ca. 30.

Etymology. – From the Greek *petra*: rock+*rhagas*: a chink or break.

Distribution. – Europe (Mediterranean region), C and SW Asia, Africa (Mediterranean region); introduced in North (with only four species being native) and South America, Africa (Republic of South Africa), Hawaii, Australia.

Habitat. – These plants mostly grow in rocky cliffs of mountainous areas, calcareous or rocky substrates.

12. ***Psammophiliella*** Ikonn. in *Novosti Sist. Vyssh. Rast.* 11: 116. 1976 ≡ *Psammophila* Fourr. ex Ikonn., *Novosti Sist. Vyssh. Rast.* 8: 273. 1971, nom. illeg., non Schult. 1822 – Type: *P. muralis* (L.) Ikonn. (≡ *Gypsophila muralis* L.). – “*Psammophila*” Fourr. in *Ann. Soc. Linn. Lyon*, sér. 2, 16: 345. 1868, nom. nud., not validly published.

Diagnosis. – Roots more or less fibrillary (*P. muralis*), and the stigmatic surface extending along the inner side of the style are the diagnostic features of these species.

Description. – Annual herbs; leaves linear to lanceolate; flowers in lax dichasial cymes; bracts present; calyx campanulate or turbinate-tubular, with membranous or inconspicuously membranous commissures; petals 5, white or pink; stamens 10, the stigmatic surface extending all along the style; styles 2; capsule opening by 4 teeth, oblong; seeds reniform, with flat tubercles; embryo curved; $2n = (30), 34$; species 4.

Etymology. – From Greek *psammos*: sand + *philia*: loving.

Distribution. – Central Asia; *P. muralis* is native to Europe and introduced to North America.

Habitat. – Sandy and calcareous hills, and sometimes ruderal environments (*P. muralis*).

13. ***Psammosilene*** W.C.Wu & C.Y.Wu in King & al., *Icon. Pl. Medic. Libro Tien-Nan-Pen-Tsao Lanmaoano* 1: [s.n.], t. 1. 1945 – Type: *P. tunicooides* W.C.Wu & C.Y.Wu.

Diagnosis. – The membranous capsules in this genus are unique among the members of tribe Caryophylleae.

Description. – Perennial herbs, puberulous; leaves ovate, subsessile; flowers in terminal cymes; bracts leafy; calyx tubular, 15-veined and 5-toothed, densely glandular pubescent, veins green; petals 5 purple-violet, inconspicuously clawed; stamens 5; styles 2; ovary sessile, membranous, narrowly ob-ovoid; ovules 2; capsule membranous, probably indehiscent, 1-seeded, enclosed by the persistent sepals; seeds peltate, embryo straight; species 1.

Etymology. – From Greek *psammos*: sand + *Silene*.

Distribution. – China (prov. Yunnan).

Habitat. – Rocky mountain slopes, dry pastures, calcareous rock crevices, forests.

14. ***Saponaria*** L., *Sp. Pl.*: 408. 1753 – Type (designated by Hitchcock & Green in Sprague, *Nom. Prop. Brit. Bot.* 155. 1929): *S. officinalis* L.

= *Bootia* Neck., *Delic. Gallo-Belg.*: 193. 1768, nom. illeg., non Adans. 1763 ≡ *Saponaria* sect. *Bootia* (Neck.) DC., *Prodr.* 1: 365. 1824 – Type: *B. vulgaris* Neck. (≡ *Saponaria officinalis* L.).

= *Saponaria* sect. *Proteinia* Ser. ex DC., *Prodr.* 1: 366. 1824 ≡ *Proteinia* (Ser. ex DC.) Rchb., *Deut. Bot. Herb.-Buch*: 205. 1841 – Type (designated by Schulz in *Bot. Zhurn. (Moscow & Leningrad)* 69: 1479. 1984): *Saponaria orientalis* L.

= *Spanizium* Griseb., *Spic. Fl. Rumel.* 1: 180. 1843 – Type: *S. ocyroides* (L.) Griseb. (≡ *Saponaria ocyroides* L.).

= *Pleioneura* Rech.f. in *Bot. Jahrb. Syst.* 75(3): 357. 1951 – Type: *P. griffithiana* (Boiss.) Rech.f. (≡ *Saponaria griffithiana* Boiss.).

Diagnosis. – Distinctly clawed petals with coronal appendages separate the members of this genus from other related genera, i.e., *Gypsophila*.

Description. – Perennial or rarely annual herbs; leaves lanceolate to ovate or linear; inflorescence formed of lax or densely paniculate or capitate cymes, rarely solitary; bracts herbaceous, bracteoles absent; calyx tubular, obscurely 15- to 25-veined, without membranous commissures or with very narrow ones; petals 5, mostly distinctly clawed, coronal scales usually present; stamens 10; styles 2, rarely 3; ovary on a very short gynophore; ovules ca. 16; capsules opening by 4, rarely 6, teeth; seeds reniform-globular with a distinct hilum; embryo curved; $2n = 28, 56$; species ca. 30.

Etymology. – From the Latin *sapo*: soap.

Distribution. – Temperate Eurasia, mainly in the Mediterranean and Irano-Turanian regions, Mediterranean Africa; introduced to North and South America, India, and Australia.

Habitat. – Various habitats, sometimes on serpentine and calcareous soils.

Resurrected name

Saponaria griffithiana Boiss., *Diagn. Pl. Orient.*, ser. 2, 1: 70. 1854 ≡ *Pleioneura griffithiana* (Boiss.) Rech.f. in *Bot. Jahrb. Syst.* 75: 357. 1951 – Holotype: [Afghanistan], Afghanistan, 2100–3800 m, *W. Griffith 1642* (G [herb. Boissier]; isotypes: K barcodes K000725812! & K000725813!; possible isotypes [*Griffith s.n.* in *Herb East India Co. 308*]: C barcode C10009153!, GH barcode 00096746!, K barcode K000725815!, P barcode P05017981!, S No. S08-18!, W No. W 0047801!).

■ AUTHOR CONTRIBUTIONS

HM: Specimen study, plant collection, laboratory procedures, molecular analyses, manuscript preparation. RR: Nomenclatural research, manuscript revision, providing some references, comments on consensus trees, some taxonomic novelties in the study group. AP: Providing some sequences, commenting the manuscript. BO: Manuscript revision, providing some sequences. GH: Providing laboratory and technical facilities, providing some plant materials, manuscript revision. SZ: Supervising the study, manuscript revision. — HM, <https://orcid.org/0000-0003-0360-9527>, hossein.madhani@ut.ac.ir; RR, <https://orcid.org/0000-0002-6765-0353>, rabeler@umich.edu; AP, <https://orcid.org/0000-0003-4937-5711>, atefeh.pirani@gmail.com; BO, <https://orcid.org/0000-0002-6104-4264>, bengt.oxelman@bioenv.gu.se; GH, <https://orcid.org/0000-0001-9159-1800>, zarre@khayam.ut.ac.ir

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Appendix 1. Voucher information: species name, geographical origin, collector(s), voucher (herbarium), GenBank accession numbers for ITS and *rps16*, respectively (* indicates sequences new for this study). Species names follow the taxonomic treatment suggested in the present study. Voucher data are given only for accessions used in generating new sequences or those generated previously by our team (Pirani et al., 2014).

Acanthophyllum aphananthum Rech.f. 1, Afghanistan, Kabul, *Rechinger 31265* (M), KF924626, KF924681; *Acanthophyllum aphananthum* 2, Afghanistan, Prov. Kabul, Kabul, Band-I Kharghak, 34°32'N 69°06'E, 2050 m, 24.6.1965, *Rechinger 31265* (MSB), –, *MF401175; *Acanthophyllum allochrousoides* (Gilli) A.Pirani 1, Afghanistan, Bamian, *Wendelbo & Ekberg W9801* (GB), KF924627, KF924682; *Acanthophyllum allochrousoides* 2, Afghanistan, Prov. Baghlan, Andarab-Tal, Fuß des Koh-e Shindadara bei Shashan (NE von Deh Salah), 1900–2000 m, 35°47'N 69°21'E, 28.5.1972, *O. Anders 9367* (MSB), –, *MF401172; *Acanthophyllum borsezowii* Litv., Iran, Khorassan, *Zarre & al. 41034* (TUH), KF924675, KF924727; *Acanthophyllum bungei* (Boiss.) Trautv. 1, Iran, E Azarbaijan, *Rechinger 43834* (M), KF924634, KF924688; *Acanthophyllum bungei* 2, Turkey, A9 Kars, Kağızman-Tuzluca, 13 km W Tuzluca, 1060 m, 30.7.1984, *Nydegger 19519* (MSB), *MF401121, *MF401169; *Acanthophyllum cerastioides* (D.Don) Madhani & Zarre 1, Pakistan, Hazar, *Ewald & Zetterlund 6227* (GB), KF924628, –, *Acanthophyllum cerastioides* 2, NW Pakistan, Swat, in valle Jabba E Kolalai, substr. Granit, 1600–2200 m, 4.6.1965, *Rechinger 30724* (M), *MF401122, *MF401168; *Acanthophyllum grandiflorum* Stocks, Afghanistan, Bamian, *Podlech 1340* (MSB), KF924666, KF924718; *Acanthophyllum herniarioides* (Boiss.) Madhani & Zarre, Tajikistan, N von Dushanbe Anzob-Pass im Gissar-Massiv, ca. 3400 m, 14.7.1975, *Mueller-Doblies 75083* (B), *MF401123, –, *Acanthophyllum honigbergeri* (Fenzl) Barkoudah, E Afghanistan, Gardes, in altoplanitie lapidosa vallis Logar 50 km N Gardez, 33°37'N, 69°09'E, 2000 m, *Rechinger 35371* (B), *MF401125, *MF401176; *Acanthophyllum kabulicum* Schiman-Czeika, Afghanistan, Ghazni, *Frey s.n.* (GB), KF924663, KF924715; *Acanthophyllum kandaharicum* Gilli, Iran, Khorassan, *Joharchi & Zangouei 36245* (FUMH), KF924662, KF924714; *Acanthophyllum laxiflorum* Boiss., Afghanistan, Lugar, *Ekberg W9184* (GB), *KF924659, *KF924711; *Acanthophyllum mucronatum* C.A.Mey. 1, Iran,

Appendix 1. Continued.

W Azarbaijan, *Assadi & Olfat 68668* (TARI), KF924652, KF924705; *Acanthophyllum mucronatum* 2, Armenia, Vayotsdzor Prov., Yeghegnadzor, vicinity of Agarakadzor village, Azar gorge, 1320 m, 26.6.2002, *Optima Iter XI/2050* (M), –, *MF401170; *Acanthophyllum myrianthum* (Rech.f.) Madhani & A.Pirani, C Afghanistan, Deh Kundi: in saxosis 10 km w Shahrestan, 33°40'N, 66°35'E, versus Deh Kundi, 34°10'N 66°07'E, 2200 m, 1967, *Rechinger 36812* (B), *MF401124, –, *Acanthophyllum oppositiflorum* Aytaç, Turkey, Sivas, *Aytaç 7476* (GAZI), KF924651, KF924704; *Acanthophyllum scapiflorum* (Akhtar) Schiman-Czeika, Afghanistan, Kabul, *Podlech 31232* (MSB), KF924646, KF924699; *Acanthophyllum sordidum* Bunge ex Boiss., Iran, Isfahan, *Pirani & Moazzeni 2147* (TMRC), KF924644, KF924697; *Acanthophyllum spinosum* C.A.Mey., Iran, Isfahan, *Pirani & Moazzeni 2150* (TMRC), KF924642, KF924696; *Acanthophyllum stocksianum* Boiss., Afghanistan, Kandahar, *Toncev s.n.* (MSB), KF924639, KF924693; *Acanthophyllum versicolor* Fisch. & C.A.Mey., Turkey, Kars, *Nydegger 43597b* (MSB), KF924633, KF924687; *Arenaria serpyllifolia* Gay, KP148897, KP148997; *Balkana spergylifolia* (Griseb.) Madhani & Zarre, Serbia, Altserbien, Zlatibor, südlich von Kremna, Umgebung von Gaj, Cigota Höhen, 1020–1475 m, 15.9.2004, *Kalheber 04-1558* (M), *MF401126, *MF401185; *Bolanthus cherlerioides* (Bornm.) Bark., Turkey, B3 Isparta, Akşehir-Şarkikaraağaç, 5.1 km NE Örkenez an der Paßauffahrt, Schutt, 1480 m, 12.8.1975, *K.P. & E. Buttler 19986* (M), *MF401128, *MF401183; *Bolanthus confertifolius* (Hub.-Mor.) Madhani & Heubl, Turkey, Antalya, between Fethiye and Kalkan, *Pinus brutia* forest, ca. 200 m, 5.2002, *Özkan Eren 4362* (B), *KX834007, –, *Bolanthus huber-morathii* Simon, Turkey, A2 Bursa, Soğukpinar-Keles, 4 km nach Soğukpinar, 860 m, 5.7.1980, *Nydegger 15138* (MSB), *KX834006, *MF401184; *Bolanthus minu-artioides* (Jaub. & Spach) Hub.-Mor., Turkey, Denizli, Muğla, 6.6.1955, *Walter 201* (B), *KX834005, –, *Bolanthus ortegioides* (Fisch. & C.A.Mey.) Madhani & Rabeler, Turkey, B5 Kayseri, above Talas, Ağda mt., 1700 m, 8.8.1997, *Zarre 42* (MSB), *KX834008, *MF401182; *Cerastium fontanum* Baumg., AY936241, FJ404899; *Cyathophylla chlorifolia* (Poir.) Bocquet & A.Strid, Turkey, C3 Antalya, SW Anatolien, offener Steinschutt über Salikent, 2050 m, Exp. N, 2.9.1995, *Ulrich s.n.* (M), –, *MF401186; *Cyathophylla viscosa* (C.A.Mey.) Madhani & Rabeler, Armenia, Vayotsdzor Prov., Vajk Distr, road Vajk–Kochbek, ca. 8 km ENE Vajk, gorge of Darab river, 1380 m, sandy area, 1380 m, 26.6.2002, *Optima Iter XI/1846* (M), *MF401117, *MF401165; *Dianthus andrzejowskianus* Kulcz., JN589032, –, *Dianthus armeria* L., JN589087, FJ404903; *Dianthus candicus* (Ball & Heywood) Madhani & Heubl, Greece, Ep. Sfakia, in declivibus australibus montis Akones ad orientem pagi Imvros, 1100–1150 m, 8.10.1966, *Greuter 7679* (M), –, *MF401178; *Dianthus carthusianorum* L., EF407941, EF674194; *Dianthus chinensis* L., JN589157, –, *Dianthus cyri* Fisch. & C.A.Mey., GU440808, –, *Dianthus deltoides* L., JN589027, –, *Dianthus recticaulis* Ledeb., Armenia, Vayotsdzor Prov., Yeghegnadzor Distr., ca. 12 km N Yeghegnadzor, around village Eghegis, 1540 m, 45°22'E, 39°52'N, humid meadows along river, forest with *Quercus macranthera*, dry slopes and rocks, 27.6.2002, *Fayyush & al., OPTIMA Iter XI/2199* (M), –, *MF401177; *Dianthus tunicoides* (Ser.) Madhani & Heubl., Greece, Chios, ca. 2 km nordöstlich Volissos am Rand der Straße nach Potamia, Grauwacke, 200 m, 16.6.1966, *Lüdtke 581* (M), *MF401129, *MF401179; *Diaphanoptera afghanica* Podlech, Afghanistan, Baghlan, *Podlech 21075* (MSB), KF924632, –, *Diaphanoptera ekbergii* Hedge & Wendelbo 1, Afghanistan, Takhar, *Podlech 11848* (MSB) & *11760* (MSB), KF924631, KF924686; *Diaphanoptera ekbergii* 2, Afghanistan, Prov. Takhar, Khost-o-Fereng, oberes Khaush-Tal, Granitfelsen, 3800 m, 11.7.1965, *Podlech 11760* (MSB), –, *MF401173; *Diaphanoptera lindbergii* Hedge & Wendelbo, Afghanistan, Fariab, *Hedge & al. W8336* (GB), KF924630, KF924685; *Diaphanoptera stenocalycina* 2, Iran, Prov. Golestan, Golestan National Park, Almelh, 1600 m, 19.5.1975, *Firuznia 1174* (M), –, *MF401174; *Eremogone aculeata* (S.Watson) Ikonn., JN589018, FJ404882; *Eremogone picta* (Sm.) Dillenb. & Kadereit, KP148933, KP149035; *Graecobolanthus fruticosus* (Bory & Chaub.) Madhani & Zarre, Greece, Inula Euboea septentrionalis, in saxosis serpentinicis et maneticis ad litus a pago Mantudii orientem versus, 30.6.1958, *Rechinger 19439* (M), –, *MF401180; *Graecobolanthus graecus* (Schreb.) Madhani & Rabeler, Greece, Epirus, Tal des Venetikos nördlich Eleftherokhori, an der Straße Kalambaka-Grevena, 500 m, 11.10.1975, *Merxmüller & Podlech 31173* (MSB), *KX834004, *MF401181; *Gypsophila acantholimoides* Bornm., Iran, Kuh-i Karkas (Kuh-i Kargiz), in declivibus supra Tar, 2300–2500 m, 27.5.1974, *Rechinger 46581* (MSB), *MF401083, *MF401141; *Gypsophila acutifolia* Fisch., Russia, Podkumok-Tal bei Kislovodsk, 21.7.1967, *Quasdorf 67* (B), *MF401100, *MF401156; *Gypsophila antari* Post, Iraq, Distr. Basra, Desertum meridionale (Southern Desert) Jabal Sanam, ca. 30°10'N, 47°30'E, 18.3.1967, *Rechinger 8568* (M), *MF401089, *MF401134; *Gypsophila arabica* Barkoudah, Israel, Negev Highlands: Makhtesh Hazera (Makhtesh Katan), sandy alluvium, pebbly wadis and limestone outcrops, Altim. 10 m, 10.3.1989, *Danin & al. 35.036* (B), *MF401082, –, *Gypsophila aretioides* Boiss., Iran, Gachsar, Hezar Band mountain, alt. 3200 m, 30.7.2015, 36°03'N 51°17'E, *Madhani 47116* (TUH), *MF401090, –, *Gypsophila arrostii* Guss., JN589043, –, *Gypsophila arrostii* var. *nebulosa* (Boiss. & Heldr.) Greuter & Burdet, Turkey, C3 Afyon, Isparta-Denizli, 21 km SE Dinar, 990 m, 5.8.1978, *Nydegger 13410* (MSB), –, *MF401155; *Gypsophila aucheri* Boiss. 1, JN589077, –, *Gypsophila aucheri* 2, Turkey, B8 Erzincan, Erzerum und Tercan, 18 km östlich Tercan, 1860 m, Steilbord, 2.8.1983, *Nydegger 18633* (MSB), *MF401098, *MF401147; *Gypsophila bermejoi* G.Lopez, Spain, Prov. Segovia, Valledado, UTM 30t Ul 78, alt. 750 m, 26.8.1983, *Ladero & Casaseca 12107* (B), *MF401106, –, *Gypsophila bicolor* Grossh., JN589151, –, *Gypsophila bicolor*, Iran, Prov. Ghazvin, Abgarm to Avaj, 12 km to Avaj, 1 km to tunnel, beside the road, 1420–1500 m, 10.5.2004, *Zarre, Mashayekhi, Taeb, Pirani & Moazzeni 35136* (MSB), –, *MF401149; *Gypsophila bucharica* B.Fedtsch. 1, JN589057, –, *Gypsophila bucharica* 2, Tadzchikistania, jugum Chodzha-Kazian, declivibus australis montis Koipioztau, 1000 m, 8.5.1976, *Kinzikaeva & Koczkareva 6663* (M), *MF401102, *MF401162; *Gypsophila capillaris* (Forssk.) C.Chr. 1, KJ021878, –, *Gypsophila capillaris* 2, Egypt, Sinai Peninsula, Jebel Maghara, 8 km N of Bir el Hamma, 270 m, siliceous rocks and flats, 33°30'E, 30°40'N, 3.5.1991, *Podlech 50067* (MSB), *MF401092, *MF401135; *Gypsophila capitata* M.Bieb., Russia: Caucasus, Dagestan, Distr. Chunzach, inter pag, Golotl et Kachib, vallis fl. Avarskiy Koissu, 17.7.1961, *Tzvelev, Czerepanov, Bobrov & Dogadova 7559* (B), *MF401103, *MF401161; *Gypsophila capituliflora* Rupr. 1, JN589143, –, *Gypsophila capituliflora* 2, Tadzchikistan: Pamir orientalis, Czeckety, prope Stationem Biologicam, fundus siccus valliculae, 3850 m, 21.8.1959, *Ikonnikov 4365* (M), *MF401111, *MF401157; *Gypsophila cephalotes* (Schrenk) F.N.Williams 1, JN589105, –, *Gypsophila cephalotes* 2, Afghanistan, Prov. Badakhshan, Wakhan, untes Weghijr Tal bis Zemestan-e Tikili, 37°06'E, 74°05'N, 3950–400 m, 21.7.1971, *Anders 7613* (MSB), *MF401105, *MF401158; *Gypsophila curvifolia* Fenzl 1, JN589159, –, *Gypsophila curvifolia* 2, Turkey, C4 Antalya, Orta Toroslar, zwischen Anamur und Kazanci, Friedhof bei Akpinar, Hügel aus (Kreide-)Kalk, offene Ruderalflur, 1630 m, 36°20'N, 32°50'E, 22.7.1992, *P. Hein 52-2* (B), *MF401099, *MF401159; *Gypsophila elegans* M.Bieb. 1, JN589130, –, *Gypsophila elegans* 2, Iran, Prov. Azarbaijan Sharqi, 19 km SE of Asheegli (Ashglo) in the Aras valley at road to Kaleibar, Arasbaran Protected Area, 1850 m, 46°48'55"E, 38°53'54"N, 1850 m, 20.6.2001, *Podlech & Zarre 55293* (MSB), –, *MF401143; *Gypsophila elegans* 3, Germany, Bayern, Oberpfalz, Weiden, Mülldeponie/Bauschuttdeponie, offene Erde, 410–420 m, MTB 6338/2, 28.8.1991, *Weigend 1895* (M), *MF401081, *MF401144; *Gypsophila fastigiata* L. 1, JN589144, –, *Gypsophila fastigiata* 2, Germany, Rheinland-Pfalz, Rheinhessen, Mainz, Autobahnböschung am NSG Großer Sand, 17.7.1988, *Kalheber 88-2892* (M), *MF401097, *MF401152; *Gypsophila globulosa* Stev. Russia, Caucasicca, Pjatiorsk, Felshügel über den Mineralquellen, ca. 4–500 m 11.7.64, *Köhler (61) Bm 4306210* (B), *MF401108, –, *Gypsophila glomerata* Pall. ex M.Bieb., Bulgaria, Bezirk Kolarovgrad, Kalkfelsen bei Madara, 17.8.1968, *Merxmüller & Zollitsch 24599* (M), *MF401109, –, *Gypsophila gypsophilioides* (Fenzl) Blakelock, Iran, Prov. Luristan, Dow Rud, in declivibus aridis ad intorium faucium fluvii Dez, substr. Calc., 1500–1600 m, 17.6.1974, *Rechinger 48149* (M), *MF401086, *MF401138; *Gypsophila heteropoda* Freyn 1, JN589110, –, *Gypsophila heteropoda* 2, Georgia, Caucasus, peripharia urbis Tbilisi, haud procul a lacu Lisi, Alt. 600 m s. m., 17.5.1985, *Vasák s.n.* (B), *MF401085, –, *Gypsophila larinica* Schreb., Turkey, C5 Adana, Aladagliari, Kayacik Deresi, entrance to Narpiz Bogazi gorge, northern slope, alt. 2450 m, 7.8.1999, *Doring, Parolly & Tolimir 1231* (B), *MF401112, *MF401145; *Gypsophila leioclada* Rech.f., Iran, Prov. Azarbaijan Sharqi, near At Darrehisi, ca. 70 km SE Bostanabad toward Mianeh, 1434 m, 47°23'23"E, 37°30'54"N, 18.6.2001, *Podlech & Zarre 55219* (MSB), *MF401104, *MF401148; *Gypsophila linearifolia* (Fisch. & C.A.Mey.) Boiss., Iran, Prov. Ilam, 36 km from Delhoran towards Mehran, gypsum hills, *Pteropyrum* community, 320 m, 4.5.1992, *Akhani 8509* (MSB), *MF401091, *MF401136; *Gypsophila nabelekii* Schischk., Iran, Azerbaijan occidentalis, in monte Chalil Kuh prope Razhan, 2600–3200 m, 1974, *Rechinger 48847* (B), *MF401088, *MF401142; *Gypsophila oblancoolata* Bark., Turkey, Provinz Nigde, bei Eregli nordlich von Ulukila, 1150 m ü. m., Steppe, Bodenoberfläche mit Trockenrissen und Salzabscheidungen, 27.9.1984, *Hagemann, Binder & Schwarz 2144* (B), *MF401115, *MF401160; *Gypsophila sp.* (Fisch. & C.A.Mey.) Boiss., Turkey, Akdagh bei Amasya, *Manissadjian 1165* (B), *MF401087, –, *Gypsophila pacifica* Komarov, JX274528, –, *Gypsophila paniculata* L., JN589150, FJ404908; *Gypsophila patrinii*

Appendix 1. Continued.

Ser. 1, JN589076, –; *Gypsophila patrinii* 2, Russia, Altay Republic, Ongudayskiy Rayon, N side of Chuya valley near Belyy Bom 31 km SSE of Inya, Dry shrubland with *Artemisia*, S-exposed, limestone, 980 m, 50°21'N, 87°03'E, 15.7.2002, *Raab-Straube 020105* (B), *MF401110, *MF401150; *Gypsophila perfoliata* L., Turkey, B4 Ankara, Yassihuyuk (ancient site of Gordion), ancient of Gordion proper, 39°36'N 32°02'E, alt. ca. 1100 m, 30.9.1999, *Doring, Parolly & Tolimir 7438* (B), *MF401114, *MF401139; *Gypsophila petraea* (Baumg.) Rchb., Romania, Reg. Ploiesti Bucegi, vale Jepilor zwischen Busteni cab. Caraman, Felsen, 1600–2000 m, 30.7.1965, *Butler & Dietrich 8953* (B), *MF401095 (ITS1), *MF401151; *Gypsophila pilosa* Huds. 1, Spain, Murcia, Provincia de Albacete, Abzweigung von der Straße Hellin–Cieza in Richtung Agramón kurz vor Minateda, Felsen aus miozänen Kalken und Gipsflächen, ca. 520 m, 19.5.1983, *Bayer & Grau 34* (M), *MF401093, *MF401140; *Gypsophila pilosa* 2, Iran, Prov. Isfahan, at the entrance of Ghamsar to Ghohroud, ruderal vegetation of main Boulevard 5 km after Ghamsar, alt. 1667 m, 33°45'33.09"N, 51°28'31.50"E, 27.05.2015, *Zarre & Madhani 34287* (TUH) *MF401094, –; *Gypsophila pilulifera* Boiss. & Heldr., JN589132, –; *Gypsophila pinifolia* Boiss. & Hausskn. ex Boiss. 1, JN589050, –; *Gypsophila pinifolia* 2, Turkey, B6 Malataya, (Straße O, Malataya–36,5–Gürün, 140) ca. 4 km E Sarıhacı köyü an der Straße nach Malataya Felshang, 1480 m, 29.8.1971, *Butler 5774* (M), *MF401116, *MF401163; *Gypsophila repens* L. 1, KF737521, –; *Gypsophila repens* 2, Austria, Tirol, Stubai Alpen, E-Hänge der Serlesscharte SW Maria Waldrast bei Matrie a. Brenner, 2100 m, 1.8.1983, *Podlech 38401* (MSB), *MF401101, *MF401153; *Gypsophila scorzonerifolia* Ser., JN589100, –; *Gypsophila silenoides* Rupr., JN589049, –; *Gypsophila stevenii* Fisch. ex Schrank, JN589022, –; *Gypsophila tomentosa* L., Spain, Alicante, El Salobrar, 12.6.1986, *Molero 30SWJ90* (33) (M), *MF401113, *MF401146; *Gypsophila uralensis* Less., KF317641, –; *Gypsophila venusta* Fenzl, Turkey, Anatolia, B6, Sivas, Zwischen Zara und Sivas, 15 km E Sivas, alt. 1250 m, Steppe auf Marmor, 22.7.1981, *Nydegger 16995* (B), *MF401096, *MF401154; *Gypsophila virgata* Boiss., Iran, Prov. Azerbaijan orient., in saxosis faucium 38 km NNW Marand versus Jolfa, 1100 m, *Rechinger 43614* (B), *MF401107, –; *Gypsophila viscosa* Murray, Turkey, B5 Nevşehir, Goreme Tarihi Milli Parkim Goreme Valley, slopes SE of the Open Air Museum, ca. 1050–1100 m, tuff, secondary steppe and ruderal vegetation, 25.5.2006, *Bircan & Parolly 110* (B), *MF401084, *MF401137; *Heterochroa desertorum* (Bunge) Fenzl 1, JN589021, –; *Heterochroa desertorum* 2, Russia, Tuviskaja ACCP, Tuva, Distr., Ovjur, prope pagum Ak-Czyra Cleistogeneto-Nanphyteta Stepposa, 3.8.1973, *Timokhina & Daniljuk 6371* (M), *MF401118, *MF401171; *Heterochroa violacea* Fenzl, JN589068, –; *Moehringia lateriflora* (L.) Fenzl, JX274536, FJ404924; *Petroana montana* (Balf.f.) Madhani & Zarre, Aden peninsula, Upper Crater, plateau SE of the Tower of Silence, ca. 120–170 m, 12°47'N, 45°02'E, on fine-gravelly Pozzolane, 22.3.1997, *Kilian, Hein & Smalla NK 4487* (B), *MF401119, *MF401167; *Petroana montserratii* (Fern.Casas) Madhani & Zarre 1, JN589155, –; *Petroana montserratii* 2, Spain, Albacete: pr. Perez, 800 m, in rupi bus calcareis verticalibus, 19.8.1972, *Casas s.n.* (B), *MF401120, *MF401166; *Petrorhagia prolifera* (L.) P.W.Ball & Heywood, GU440883, –; *Petrorhagia saxifraga* (L.) Link, JQ307895, FJ404930; *Petrorhagia thessala* (Boiss.) P.W. Ball & Heywood, GU440885, –; *Petrorhagia dubia* (Raf.) G.López & Romo, AY857974, –; *Psammophiliella muralis* (L.) Ikonn. 1, JN589037, –; *Psammophiliella muralis* 2, Germany, Bayern, MTB 6831/1: Acker nahe Mohrhof bei Poppenried/Höchstädt, 25.8.1987, *E. Dörr s.n.* (M), *MF401127, *MF401186; *Psammosilene tunicoides* W.C.Wu & C.Y.Wu, JN589122, –; *Saponaria glutinosa* M.Bieb., HE602400, –; *Saponaria griffithiana* Boiss., Afghanistan, Prov. Badakhshan, Shewa valley, 37°16'N 70°38'E, 2640 m, 29.5.2008, *Schloeder & Jacobs 1757* (M), *MF401080, *MF401133; *Saponaria ocymoides* L. 1, AY936271, FJ404936; *Saponaria ocymoides* 2, Spain, Prov. Teruel, Monte Sierra de Javambre, 1650–1700 m, 9.7.2002, *Šida & Vagnerová 3658* (M), *MF401077, *MF401130; *Saponaria officinalis* L. 1, AY594313, FJ404937; *Saponaria officinalis* 2, Japan, Kamite, Toyoshina-machi, Minami-azumi-gun, Nagano Pref., 550 m, 9.9.2002, dry bed river, *Sugawara 2080906* (M), *MF401078, *MF401131; *Saponaria prostrata* Willd., Turkey, B6 Kahramanmaraş, 30 km to Göksun from Sariy, Bin Boğa Dağı, above Yalak village, 2100–2400 m, 11.8.1997, *Zarre 122* (MSB), *MF401079, *MF401132; *Saponaria pumila* Hayek, AY594311, –; *Saponaria sicula* Raf., –, Z83153; *Silene alexandri* Hillebr., EF060222, EF061382; *Silene gallica* L., U30959 (ITS1), U30985 (ITS), JX560214; *Silene italica* (L.) Pers., AY936258, KF305909; *Silene repens* Patrin, JX274527, DQ908842; *Silene viscosa* (L.) Pers., FN821148, FN821316; *Silene vulgaris* (Moench) Garcke, AY857967, EF674192; *Stellaria media* (L.) Vill., KF737498, FJ404953; *Vaccaria hispanica* (Mill.) Rauschert 1, X86896.1; *Vaccaria hispanica* 2, JF421553.1 (ITS2); *Vaccaria hispanica* 3, X83847.1 (ITS2); *Velezia rigida* L. 1, AY936269, –; *Velezia rigida* 2, GU440888, –.