Overall phylogenetic relationships of Scutellaria (Lamiaceae) shed light on the origin of the predominantly Caucasian and Irano-Turanian S. orientalis group

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Source: Willdenowia, 51(3) : 395-427

Published By: Botanic Garden and Botanical Museum Berlin (BGBM)

URL: https://doi.org/10.3372/wi.51.51307

Willdenowia
Annals of the Botanic Garden and Botanical Museum Berlin

Botanischer Garten Berlin

Overall phylogenetic relationships of *Scutellaria* (*Lamiaceae*) shed light on the origin of the predominantly Caucasian and Irano-Turanian *S. orientalis* group

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Abstract: *Scutellaria* is one of the largest genera in the *Lamiaceae* with an estimated 400–500 species with a nearly worldwide distribution. Most species occur in the N hemisphere, with the Caucasus and the wider Irano-Turanian region housing a large number of taxa, many of them considered endemic. We present an overall phylogeny of the monophyletic genus *Scutellaria* based on rapidly evolving plastid regions (*matK-trnK*, *rpl16*, *trnL-F*). Three well-supported clades are evident, which render the currently accepted *S.* subg. *Scutellaria* paraphyletic to *S.* subg. *Apeltanthus*, which appears nested in "clade A", in which the African *S. schweinfurthii* is sister to all remaining taxa, followed by other lineages of *S.* subg. *Scutellaria*. Ancestral states of 12 morphological characters frequently used as diagnostic from subgenus to species level were reconstructed with BayesTraits. The *S. orientalis* group appears as a major radiation in the Caucasus area and the Irano-Turanian region that may comprise up to a quarter of the species in the genus. This radiation corresponds to a monophyletically defined *S.* sect. *Lupulinaria*, characterized by decussate inflorescences and specialized (e.g. cucullate) bracts. Our phylogenetic data present significant resolution at the species level within the *S. orientalis* group, indicating complex geographically centred patterns of speciation in adaptation to steppe and high mountain habitats, including multiple evolution of pinnate and tomentose leaves. The detailed infrageneric classification of Juzepczuk (1951, 1954) mostly does not reflect natural groups.

Keywords: Caucasus ecoregion, character evolution, infrageneric classification, Irano-Turanian floristic region, *Labiatae*, *Lamiaceae*, molecular phylogeny, molecular species identification, *Scutellaria*, *Scutellaria* subg. *Apeltanthus*, *Scutellaria* sect. *Lupulinaria*, *Scutellarioideae*, species delimitation

Article history: Received 30 October 2021; peer-review completed 15 November 2021; received in revised form 25 November 2021; accepted for publication 26 November 2021.

Citation: Salimov R. A., Parolly G. & Borsch T. 2021: Overall phylogenetic relationships of *Scutellaria* (*Lamiaceae*) shed light on the origin of the predominantly Caucasian and Irano-Turanian *S. orientalis* group. – Willdenowia 51: 395–427. https://doi.org/10.3372/wi.51.51307

Introduction

Scutellaria L. is one of the largest genera of *Lamiaceae* with probably 400–500 species worldwide. These species numbers range from 360 species estimated by Paton (1990a, 1990b) and Harley & al. (2004) to 543 accepted names in World Flora Online (2019). *Scutellaria* is a subcosmopolitan genus centred mainly in temperate regions, with high species diversity in the E part of the Mediterranean region and the vast ranges of the Irano-Turanian region (see Manafzadeh & al. 2017 for current circumscription and history of the concept as a floristic region). For the area covered by the Euro+Med PlantBase (Europe, the Mediterranean, SW Asia and the Caucasus), 54 species are listed (Euro+Med 2006+). In the tropics most species occur in mountain regions of the Andes (e.g. 15 species reported from Peru; Zarucchi & Harley 1993), whereas tropical Africa has just two or three species (African Plant Database 2020–2021). Many species are highly variable morphologically, which has led to significantly deviating treatments of species in different Flora accounts (Juzepczuk 1954; Edmondson 1982; Rechinger 1982). According to such treatments, *Scutellaria* is represented by 15 species in Azerbaijan (Isayev 1957), 13 species in Georgia (Gagnidze & Ivanishvili 1987), three species and subspecies in Armenia (Menitsky 1987), eight species in Dagestan (Murtuzaliyev 2009), 27 species and 10 infraspecific taxa in Iran (Jamzad 2012, 2013) and 17 species and 22 infraspecific taxa in Turkey (Celep & Dirmenci 2017). The treatment by Ter-Chatschaturova (1967) in *Flora Kavkaza* recognizes 36 species for the Caucasus. Differences in taxon concepts at species level affect overall estimates of species diversity in *Scutellaria*. For example, *S. orientalis* L. alone encompasses currently 14 accepted subspecies in the Euro+Med area (Euro+Med 2006+) which eventually had been treated at different ranks. Also new species continue to be described, in particular from *S.* sect. *Lupulinaria* A. Ham., to which *S. orientalis* belongs, e.g. from Turkey [*S. anatolica* Çiçek & Ketenoğlu (2011) and *S. yildirimlii* Çiçek & Yaprak

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(2013)] and Iran [*S. bakhtiarica* Ranjbar & C. Mahmoudi (2018)], but also in other sections, e.g. from Mexico (González-Gallegos & Vázquez-García 2013).

The genus *Scutellaria* occurs in a wide range of habitats. Many species are chamaephytes and grow in rocky places, gravelly slopes, and steppes, to which they are well adapted as dwarf shrubs and subshrubs that sometimes even exhibit a cushion-plant-like branching pattern (Juzepczuk 1954; Paton 1990b; Guseva & Cheryomushkina 2015). Other species grow, mostly as hemicryptophytes, in forests, moist grassland habitats or marshes. Among neotropical species, only a few are from tropical forests (Zarucchi & Harley 1993).

When Linnaeus (1753) described the genus, he listed 12 species. The infrageneric classification of *Scutellaria* began with Hamilton (1832), who subdivided the genus into three sections (*S.* sect. *Lupulinaria*, *S.* sect. *Stachymacris* A. Ham. and *S.* sect. *Galericularia* A. Ham., see Appendix S1 in Supplemental content online), which were mainly based on the arrangement of flowers in the inflorescences and the morphology of bracts. *Scutellaria orientalis* was classified within *S.* sect. *Lupulinaria*. This classification was used by Ledebour (1949) in *Flora rossica*. Bentham (1834) added two new sections, *S.* sect. *Heteranthesia* Benth. (species with spirally arranged flowers) and *S.* sect. *Maschalostachys* Benth. (species with axillary inflorescences). He essentially maintained this sectional classification in his treatment for Candolle's *Prodromus* (Bentham 1848) while adding several subordinate groups. Later, Bentham (1876) merged *S.* sect. *Galericularia* and *S.* sect. *Stachymacris* into a new section that he superfluously and illegitimately named *S.* sect. *Vulgares* Benth. Boissier (1879) focused on species of the Old World and grouped them into the two sections, *S.* sect. *Lupulinaria* and *S.* sect. *Vulgares*, dividing the latter section into three unranked groups.

Briquet (1896) also recognized two sections, based mainly on the presence or absence of nutlet bands or wings rather than inflorescence characters. His first section, *Scutellaria* sect. "*Euscutellaria*" comprises plants with wingless nutlets (i.e. without a membranous margin) and includes Bentham's and Hamilton's *S.* sect. *Heteranthesia*, *S.* sect. *Lupulinaria* and *S.* sect. *Vulgares* as subordinate groups, also indicated as sections. In doing so, he subdivided *S.* sect. *Vulgares* into smaller taxonomic units – "Reihe" – for which he emphasized differences in floral, inflorescence and general habit as diagnostic characters. In addition to the three unranked groups already proposed by Boissier, he newly described *S.* [Reihe] *Coccineae* Briq., *S.* [Reihe] *Cuneatae* Briq. and adjusted the rank of *S.* [Reihe] *Angustifoliae* (Benth.) Briq. and *S.* [Reihe] *Lateriflorae* (Benth.) Briq. *Scutellaria* sect. "*Euscutellaria*" included almost all species of the genus, with the exception of the endemic North American species *S. nervosa* Pursh and the Japanese *S. guilielmi* A. Gray, which he distinguished in *S.* sect. *Scutellariopsis* Briq., characterized by conspicuously membranous banded nutlets. Moreover, he distinguished subgroups, but these were not given any formal rank.

Later regional treatments of *Scutellaria* in the 20th century, e.g. those by Epling (1942), Juzepczuk (1954), Wu & Li (1977), Edmondson (1982) and Rechinger (1982), were mainly based on Briquet's classification. However, these treatments differed from earlier infrageneric classifications because the complete global variation of the genus was not considered (Paton 1990a). Epling (1942) proposed 17 sections of the American species of *Scutellaria*, mainly based on floral, inflorescence, rhizome and general habit characteristics except for the genus *Salazaria* Torr., with one species in desert regions of SW North America, which he considered strongly deviating with its distinctly inflated calyx at maturity [*Salazaria mexicana* Torr., now *Scutellaria mexicana* (Torr.) A. J. Paton]. Three of Epling's sections contained species from the Old World. Juzepczuk (1951) accepted five sections, *S.* sect. *Anaspis* (Rech. f.) Juz., *S.* sect. *Apeltanthus* Nevski ex Juz., *S.* sect. *Cystaspis* Juz., *S.* sect. *Lupulinaria* and *S.* sect. *Vulgares*. In two cases, he derived the name from the former genera *Anaspis* Rech. f. and "*Apeltanthus* Nevski" (the latter never validly published). But later, in his treatment for *Flora URSS*, Juzepczuk (1954) raised the rank of these sections and subdivided the genus into four subgenera: *S.* subg. "*Euscutellaria*", *S.* subg. *Anaspis* (Rech. f.) Juz., *S.* subg. *Apeltanthus* (Nevski ex Juz.) Juz. and *S.* subg. *Cystaspis* (Juz.) Juz., which were mainly based upon the characteristics of upper lip of the calyx. In his classification, Juzepczuk (1954) placed *S.* sect. *Lupulinaria* (with *S.* subsect. *Alpinae* Juz., *S.* subsect. *Fruticosae* Juz., *S.* subsect. *Orientales* (Grossh.) Juz. and *S.* subsect. *Ramosissimae* Juz.) along with three other sections in a broadly defined *S.* subg. "*Euscutellaria*". Wu & Li (1977) accepted Briquet's classification for the most part but followed the earlier treatment of Bentham (1834) by including five sections in *S.* subg. "*Euscutellaria*". Rechinger (1982) adopted the classification of Juzepczuk (1954) for the taxa occurring in the Flora iranica area, whereas in *Flora of Turkey*, Edmondson (1982) followed Hamilton's circumscription of sections based on inflorescence characters and added *S.* sect. *Salviifoliae* (Boiss.) Edmondson. The most recent global taxonomic review and infrageneric classification of *Scutellaria* was proposed by Paton (1990b). He recognized the two subgenera, *S.* subg. *Scutellaria* and *S.* subg. *Apeltanthus*, with five and two sections, respectively, based on a phenetic analysis of a spectrum of morphological characters. The chronology of the infrageneric taxonomy of *Scutellaria* is shown in Appendix S1 in Supplemental content online.

The Caucasus ecoregion and the Irano-Turanian region are the areas with the highest species diversity of *Scutellaria* worldwide. The majority of the taxa occurring in these areas are considered to belong to the *S. orientalis* group This aggregate of taxa, which were supposed to be closely related to the Linnaean species *S. orientalis*, was mentioned by many authors from Popov (1916) to Paton (1990a, 1990b), who informally described it as the '*S. orientalis* species-group' next to the '*S. glechomoides* species-group', the '*S. linearis* species-group' and the '*S. colpodea* species-group' in *S.* subsect. *Lupulinaria* (A. Ham.) A. J. Paton. It is noteworthy that all infrageneric classification systems assigned *S. orientalis* and its allies to *S.* sect. *Lupulinaria*. However, the species-level taxonomy has long been a challenge, and species classification has not been satisfactorily solved due to high morphological polymorphism and often gradual variation. Characters used were the branching pattern of stems; the size, shape and degree of incision of leaf blades; the kind of the indumentum of leaves and bracts; and the size, shape, texture, and colour of bracts. Apart from its centre of diversity in the Caucasus area and the Irano-Turanian region, some species related to *S. orientalis* extend eastward to W China and westward with a few taxa to Spain and NW Africa.

Popov (1916) already stated that some scientists accepted *Scutellaria orientalis* as a "species aggregate" with some varieties. Using the observations made by Popov (1916), who had examined all the material available at his time from Crimea and the Caucasus, Juzepczuk (1939) came to the conclusion that a considerable number of taxa can be recognized based on morphology, which also deviates in their distribution and ecology. According to Juzepczuk (1939), the most useful differential characters were habit, indumentum, shape of cauline leaves and floral bracts as well as flower size. He placed the so-called "*S. orientalis* species cycle" in *S.* sect. *Lupulinaria* and further divided it into two series, *S.* ser. *Oxystegiae* Juz. and *S.* ser. *Platystegiae* Juz. Grossheim (1945) then described seven new species of *S.* sect. *Lupulinaria* from the Caucasus and also published a key for identification mostly based on the shape of cauline and floral leaves, as well as distribution maps of 19 species. Grossheim further noted that the "*S. orientalis* sensu lato" of earlier authors may not represent a natural group and suggested its division into two subsections, *S.* subsect. *Oxystegiae* (Juz.) Grossh. and *S.* subsect. *Platystegiae* (Juz.) Grossh., with *S.* ser. *Orientales* Grossh. placed under the latter subsection. Juzepczuk (1954) divided the species of *S.* sect. *Lupulinaria* into four subsections (Appendix S1 in Supplemental content online), one of which was *S.* subsect. *Orientales* with 56 species recognized in *Flora URSS*. Of these, 28 were originally described by him (Juzepczuk 1954), predominantly from Central Asia and Siberia. In his 1954 treatment, Juzepczuk further divided *S.* subsect. *Orientales* into two groups, the *Oxystegiae* group with five series and the *Platystegiae* group with two series. Later, Fedorov (1967) reduced most of the Crimean-Caucasian species within the *S. orientalis* group to subspecific rank. He argued that although these "species" possess more or less independent geographical areas, they would be connected by transitional forms. In his treatment for the *Flora of Turkey*, Edmondson (1982) followed Fedorov's concept and accepted subspecific ranks for the members of the group. In *Flora of Iran*, Jamzad (2012) essentially followed Rechinger (1982) and again recognized the members of the *S. orientalis* group at species level in *S.* sect. *Lupulinaria*. Paton (1990b) provided a global view on the genus *Scutellaria* based on a detailed analysis of morphological characters, including a phenetic tree and a revised infrageneric classification. Although the taxa from the Caucasus, SW and Central Asia were not fully represented, Paton (1990b) mentioned the '*S. orientalis* species-group' and its allies as an entity within *S.* subsect. *Lupulinaria* of *S.* sect. *Lupulinaria*.

Several morphological characters have been studied in detail in *Scutellaria*, such as mericarp micromorphology (Lane 1983) nand surface sculptures of the nutlets (Kim & Lee 1995; Billie & Delprete 1996). The first cladistic analysis based on 85 morphological and anatomical characters by Cantino & al. (1992) found *Scutellaria* in a clade together with *Salazaria*, *Perilomia* Kunth (= *S.* sect. *Perilomia* (Kunth) Epling), and *Harlanlewisia* Epling with a unique synapomorphy in the gynoecium (character 55, state 1, ovary lobes wholly free from each other but laterally attached to a more or less elongate upward extension to the disc that terminates between them), all of which are now regarded as synonyms of the genus *Scutellaria* (Paton 1990b; Harley & al. 2004). The African genera *Renschia* Vatke and *Tinnea* Kotschy ex Hook. f. were further resolved in a tritomy with *Scutellaria* (Cantino & al. 1992).

Molecular phylogenetic analyses of *Lamiaceae* (Wagstaff & Olmstead 1997; Bendiksby & al. 2011; Li & al. 2012; Li & al. 2016) resulted in the genera *Wenchengia* C. Y. Wu & S. Chow, *Holmskioldia* Retz. and *Tinnea* as successive sisters to *Scutellaria*. However, the sampling of *Scutellaria* in these studies was not representative enough to allow judging the monophyly of the genus and to contribute to understanding evolutionary relationships within *Scutellaria* based on molecular phylogenetic trees. Several studies generated sequence data of plastid genomic regions (*trnL-F*, *rpl16*) of a few *Scutellaria* species with the purpose of discriminating samples of these medicinal plants (Hosokawa & al. 2005); or studies looked at relationships within species complexes in specific geographical regions such as North America (Olmstead 1989), Taiwan (Chiang & al. 2012) and Iran (Safikhani & al. 2017). Datasets with a more comprehensive taxon sampling were generated by Zhao & al. (2017), who sequenced nuclear ribosomal (nr)ITS and ETS regions for 34 Chinese species, and Safikhani & al. (2018), who focused on resolving relationships of 42 Iranian species and subspecies using the nrITS and *trnL-F* regions as markers. Presenting the so-far taxonomically most representative sampling of *Scutellaria* in a phylogenetic analysis, the authors provided evidence for the monophyly of *S.* sect. *Lupuli-*

naria subsect. *Lupulinaria* in their ITS tree, whereas the *trnL-F* tree depicted a polytomy with *S. stocksii* Boiss. (*S.* sect. *Apeltanthus*). Salmaki & Müller (2019) used ITS sequences to place the Iranian endemic *S. xylorrhiza* Bornm. Son & Park (2015, only ENA/GenBank entry but no publication) generated a complete plastid genome from *S. insignis* Nakai, Zhang & al. (2016, only ENA/GenBank entry but no publication) from *S. lateriflora* L., Jiang & al. (2017) from *S. baicalensis* Georgi, and recently Zhao & al. (2020) published sequences of plastid genomes of eight further *Scutellaria* species from China as well as *Holmskioldia*, *Tinnea* and *Wenchengia*.

The present study aims at testing the monophyly of *Scutellaria* and at illuminating overall phylogenetic relationships in the genus based on a representative taxon sampling both at a species level in *Scutellaria* (see Paton 1990b) and for related lineages in *Lamiaceae* (Li & al. 2016). The specific objectives of this investigation were: (1) to clarify if the *Scutellaria orientalis* group represents a monophyletic lineage using a broad sampling of Eurasian, particularly Caucasian, SW Asian and Central Asian taxa; (2) to explore the phylogenetic utility of plastid markers to resolve relationships in this group at species level; (3) to reconstruct the evolution of morphological characters used as diagnostic for *S. orientalis* and relatives in previous classifications; (4) to test the hypothesis that decussate inflorescences with flowers subtended by cucullate bracts are a synapomorphy of a monophyletic *S.* subg. *Apeltanthus*; and (5) to evaluate the infrageneric classification of *Scutellaria* in light of phylogenetic relationships and morphology.

Material and methods

Field work and sampling

Plants were collected in the field as much as possible to obtain complete specimens and to document the life form and ecology. In these cases, corresponding fresh leave samples were dried in silica gel. Field trips were carried out between April and July in Azerbaijan from 2016–2018, with voucher specimens deposited in the herbarium BAK (Institute of Botany, Azerbaijan National Academy of Sciences), and also in Georgia and Russia between 2009 and 2017. Duplicates were deposited in B (Botanic Garden and Botanical Museum Berlin). Further material was obtained from the living collection of the Botanic Garden Berlin and the herbaria B, BAK and MO (Missouri Botanical Garden). The collected samples of the *Scutellaria orientalis* group were mostly determined according to treatments in *Flora of Azerbaijan* (Isayev 1957) and *Flora URSS* (Juzepczuk 1954). However, with respect to accepting ranks of the respective entities at species or subspecies level, we followed the treatment in Euro+Med (2006+). Additional samples from Germany were sequenced in the course of the German Barcode of Life (GBOL) Project (Geiger & al. 2016), appreciating that the GBOL markers for angiosperms correspond to the genomic regions used in this investigation.

Selection of taxa for phylogenetic analysis

Our dataset includes 76 taxa of *Scutellaria*, representing most infrageneric entities recognized by Paton (1990b). We sampled taxa from 15 of the 34 species groups of *S.* sect. *Scutellaria* as well as four of the five sections of *S.* subg. *Scutellaria*, and from all sections of *S.* subg. *Apeltanthus*, including subsections and informal groups. We further included the remaining lineages of *Scutellarioideae*, the monotypic genera *Holmskioldia* and *Wenchengia*, and *Tinnea* with two species. Furthermore, 17 outgroup species of 11 genera were added to represent other major lineages of *Lamiaceae* (Li & al. 2016) such as *Lamioideae* (*Galeopsis* L., *Lamium* L., *Leonurus* L., *Stachys* L.) and *Nepetoideae* (*Mentha* L., *Prunella* L., *Salvia* L.) and *Ajugoideae* (*Ajuga* L., *Teucrium* L.). *Ajuga* was used to root the trees. Detailed information about taxa and voucher specimens and the respective herbaria, the geographical origin of specimens and ENA/GenBank accession numbers of sequences obtained from these specimens are provided in Appendix 1.

DNA extraction, amplification and sequencing

Total genomic DNA was extracted from c. 20 mg of silica-dried leaf tissue with the Macherey-Nagel's NucleoSpin® Plant II kit and for older herbarium material using a modified CTAB method (Borsch & al. 2003). Dilutions of 1:10 in purified water were used for polymerase chain reactions (PCR).

Because two plastid genomic regions (*trnK-matK* and *trnL-F*) have been widely used to infer phylogenetic relationships in *Lamiaceae* (Schäferhoff & al. 2010; Li & al. 2016), as well as (*trnL-F*) in some studies of *Scutellaria* species (Safikhani & al. 2018; Seyedipour & al. 2020), we also employed these two markers in this investigation. We further added the group II intron in *rpl16* in combination with the *rps3-rpl16* spacer. All three regions have been shown to provide high levels of hierarchical phylogenetic signal across different taxonomic levels (see Borsch & Quandt 2009), and *trnK-matK* as well as *trnL-F* are increasingly used as a barcode for flowering plants (e.g. Geiger & al. 2016). Our goal was here to promote some standardization of markers to achieve additivity of datasets, which is crucial for surveying diversity in speciose genera such as *Scutellaria*. Yet, no comparable source of data exists for any nuclear DNA region for *Scutellaria*. Although data of nrITS were published (Safikhani & al. 2018; Salmaki & Müller 2019), we could not obtain single clear bands with PCR, and directly sequenced products usually showed overlying signal from multiple ribotypes, which can be due to a lack of ITS-concerted evolution (Nieto Feliner & Rossello 2007) as in several *Lamiales* as well as hybridization as reported from other *Lamiaceae* genera. In this investigation, we therefore focused on plastid data and morphology. More detailed analyses of nuclear loci of the *S. orientalis* group at the species level will be topics of follow-up work.

The PCR reactions for the three genomic regions of cpDNA were carried out in a total volume of 50 µl, containing 4 µl DNA template with a concentration of 10 ng/µl, 5 µl Taq buffer S (PeqLab, Erlangen), 2 µl of each forward and reverse primers (20 pm/µl), 10 µl dNTPs (each 1.25 mM), 5 units/µl of 0.3µl Hot Taq DNA polymerase (PeqLab), 3µl of 25 mM $MgCl_2$, and 23.7 µl ultrapure H_2O was added to obtain a total volume of 50 µl.

The *trnK* intron including the *matK* gene was amplified in two overlapping fragments using the primer pairs trnKF (Wicke & Quandt 2009) plus ACmatK1400R (Müller & Borsch 2005) and ACmatK500F (Müller & Borsch 2005) plus psbA5R (Shaw & al. 2005), therefore effectively also covering the *trnK-psbA* spacer. For some samples obtained from herbarium specimens this region had to be amplified in two shorter overlapping quarters using the primer pairs trnKF + LAMtrnK724R (5′-AATTCGATTTGAATCAAAGG-3′), LAMtrnK690F (5′-CTTGTTTTGACTGTATCGC-3′) + ACmatK1400R, ACmatK500F + LAMmatK1450R (5′-TCGTTGATAGAAATCATATCC-3′) and LAMmatK1260F (5′-AAGAGTTTGTATCGAATAAAG-3′) and psbA5R. The *Lamiaceae*-specific primers were newly designed in this study. The PCR programme was as follows: initial denaturation of 1 min 30 sec at 95°C, 1 min primer annealing at 50°C and 45 sec extension at 72°C, followed by 34 cycles each consisting of 30 sec denaturation at 95°C, 1 min annealing at 50°C and 45 sec extension at 72°C, with a further final extension of 10 min at 72°C.

Amplification and sequencing of the *trnL* intron and *trnL-trnF* intergenic spacer (the "*trnL-F* region") were performed with the primers trnTc, trnTf and trnTd (Taberlet & al. 1991) and trnL460F (Worberg & al. 2007), using an initial denaturation of 1 min 30 sec at 95°C, 1 min primer annealing at 52°C and 45 sec extension at 72°C, followed by 34 cycles each consisting of 30 sec denaturation at 95°C, 1 min annealing at 52°C and 45 sec extension at 72°C, with a further final extension of 10 min at 72°C.

The *rpl16* region was amplified as a whole with the *Lamiaceae* specific primers LAMrps3F (5′-GAAATTGCACGTGTCGAATGG-3′) and LAMrpl16R (5′-TCGTCCTCTATGTTGTTTACG-3′) designed in this study. For some in shorter fragments using primers LAMrps3F + LAMrpl16-290R (5′-ACTGTCTTTTATGAGATGAC-3′) and LAMrpl16-140F (5′-AGTCATATCTTTATAGCAAC-3′) + LAMrpl16R. The internal primers were designed based on an initial alignment of *rpl16* sequences of *Scutellaria* and other *Lamiaceae*. The temperature profile for the PCR amplification consisted of an initial denaturation of 1 min 30 sec at 95°C, 1 min primer annealing at 55°C and 1 min 30 sec extension at 72°C, followed by 34 cycles each consisting of 30 sec denaturation at 95°C, 1 min annealing at 55°C and 1 min 30 sec extension at 72°C, with a further final extension of 10 min at 72°C.

The DNA amplifications were performed in a peqSTAR 96X HPL thermocycler (Peqlab). All PCR products were stained with 100× SYBER-Gold nucleic acid stain (Life Technologies no. S11494, Carlsbad, California) and electrophoresed using a 1.5% agarose gels in TAE (Tris-Acetate-EDTA) buffer (pH 8.0) for 45 min. Bands were excised from the gel and purified using the Gel/PCR DNA Fragment Extraction Kit (Geneaid Biotech, New Taipei) following the manufacturer's protocols and sequenced via standard Sanger Sequencing at Macrogen Europe (Amsterdam).

Sequence alignment and phylogenetic reconstruction

PhyDE v.0.9971 (Müller & al. 2010) was used to check pherograms for errors in called bases and to generate the contigs for individual genomic regions. Sequences were then aligned following a motif-alignment approach and the rules described in Kelchner (2000) and Löhne & Borsch (2005). Mutational hotspots (including poly-A/T stretches) were excluded from analysis from the final matrix due to ambiguous homology assessment. Insertions and deletions (indels) were coded as binary characters according to the Simple Indel Coding method (Simmons & Ochoterena 2000) as implemented in SeqState v.1.4.1 (Müller 2005a). Sequences were submitted to ENA/GenBank using the script of Gruenstaeudl (2020).

Phylogenetic trees were reconstructed using maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI) methods. All trees were rooted with *Ajuga reptans* L. for the phylogenetic analyses including the whole dataset of 93 samples. In addition, we generated Bayesian trees using a matrix reduced to the *Scutellarioideae* and *Holmskioldia* as root for the analysis of morphological character evolution.

Analyses via MP were performed with heuristic searches in PAUP* v.4.0b10 (Swofford 2002) in conjunction with the parsimony ratchet (Nixon 1999) as implemented in PRAP v.2.0b3 (Müller 2004). Ratchet settings were 200 iterations with 25% of the positions randomly upweighted (weight = 2) during each replicate and 10 random addition cycles. Jackknife support (JK) calculations were performed in PAUP by conducting a heuristic search within a total number of 10 000 JK replicates using the tree bisection-reconnection (TBR) branch-swapping, saving one tree and deleting 36.79% of characters in each replicate (Müller 2005b). Homoplasy indices [consistency (CI), retention (RI), rescaled consistency (RC) and homoplasy indices (HI)] were calculated to assess homoplasy. The best model of nucleotide sequence evolution for each marker was selected using the Akaike information criterion (AIC) as implemented in jModelTest v.2.1.6 (Darriba & al. 2012). The plastid dataset was partitioned as follows: (1) *trnK*/*matK* with four partitions: *trnK* 5′ intron, *matK* gene, *trnK* 3′ intron and *trnK-psbA* spacer; (2) *rpl16* as one partition; and (3) *trnL-F* with two partitions: *trnL* and *trnL-F* spacer. The following models were found to best fit the sequence data: (1) TVM+G for *matK*, *rpl16* and the *trnK-psbA* and *trnL-F* spacers; (2) GTR+G for the *trnK* 5′ and *trnK* 3′ intron parts and the *trnL* intron. For the indel partition, a restriction site (binary model) was applied. Bayesian inference was carried out using MrBayes v.3.2.6 (Ronquist & al. 2012). For the combined plastid dataset, four parallel runs each with four Markov Chain Monte Carlo (MCMC) chains (one cold, three heated) were performed with a random starting tree for five million generations. The first 25% of generations of each run were discarded and only the trees after the burn-in sampled at a frequency of 1000. Analyses were stopped when the standard deviation of split frequencies was well below 0.01. ML tree inference and bootstrapping (BS) were conducted with RAxML v.8.2.8 (Stamatakis 2014). The model was set to GTRGAMMA and bootstrap analyses were carried out with 1000 replicates. The partition of microstructural mutations was not analysed in ML. Trees were visualized in TreeGraph2 v.2.10.1-641 beta (Stöver & Müller 2010).

Definition and assessment of morphological characters

The selection of morphological characters for ancestral state evolution is based on their previous usage to describe infrageneric taxa of *Scutellaria* in particular by Juzepczuk (1954) and Paton (1990a). We then also considered the work of further authors to define characters and states. The definitions of characters and states were evaluated in light of the state of knowledge on homology in the respective available literature. The assessment of character states was done from the herbarium specimens used to extract genomic DNA or the respective vouchers when samples were preserved in silica gel. This was of particular importance in *S.* sect. *Lupulinaria* where species limits are unclear, in order to make sure that the morphological data correspond to the same individual represented in the tree (see Kilian & al. 2015). For the other species, this procedure was applied as far as possible and complemented with information form the literature such as Flora treatments [*Flora of Bhutan* (Grierson & Long (1983–2002); *Flora zambesiaca* (Flora Zambesica Managing Committee 1950+)].

Ancestral character state reconstruction

Ancestral states were inferred with BayesTraits v. 2.0 (Pagel & al. 2004) and commands generated in TreeGraph2 (Stöver & Müller 2010). We used a population of 500 trees that were randomly selected with Mesquite v. 3.5 (Maddison & Maddison 2021) after the burn-in from the Bayesian analysis of the plastid dataset confined to *Scutellarioideae* (see above). Probabilities for ancestral states were visualized on the Maximum Clade Credibility tree from the Bayesian analysis with TreeGraph2. Since the diversity of the other *Lamiaceae* lineages outside the *Scutellarioideae* in the phylogenetic trees was only scarcely sampled, which would have resulted in an arbitrary representation of morphological variation, we confined the analysis of morphological character coding to the *Scutellarioideae*.

Results

Sequence and alignment characterization

The detailed sequence statistics of dataset A (105 taxa, three plastid genomic regions) can be found in Table 1. The complete matrix includes 5328 sequence positions and 290 coded indels. In all introns and spacers, we excluded mutational hotspots of unclear homology from the final matrix, most of which were poly A/T microsatellites. The *trnK-matK-psbA* region with a total alignment length of 3202 characters has hotspots in the *trnK* intron in alignment positions 402–406 (HS1), 511–518 (HS2), 552–661 (HS3), 2411–2432 (H4) and the *trnK-psbA* spacer in positions 178–186 (HS5) and 263–268 (HS6). The first 37 positions corresponding to the *trnK* 5′ exon were trimmed, and the 36 downstream positions belong to the *psbA* gene. The *matK* CDS lacks hotspots but has a frameshift mutation involving positions 1473–1498 of the CDS (-CCTCTTCGACTTTGCGAGCAGTATT). The *trnL-F* region with a total alignment length of 1133 positions (including the *trnL* 5′ exon and the *trnF* gene) has hotspots in the *trnL* intron in positions 198–207 (HS 1), 449–457 (HS2) and in the *trnL-F* spacer in positions 672–673 (HS3) and 718–736 (HS4). The alignment of the *rpl16* region has 1931 position in total, including 155 positions of the *rps3* gene (the first 58 were trimmed because of incomplete sequences) and 400 positions of the *rpl16* 3′ exon. The alignment was trimmed for 41 downstream positions of the intron due to incomplete sequences. Hotspots are in the *rps3-rpl16* spacer in positions 217–223 (HS1), 281–308 (HS2) and in the *rpl16* intron in positions 395–409 (HS3), 424–425 (HS4), 654–655 (HS5), 802–817 (HS6), 1125–1142 (HS7), 1302–1305 (HS8) and 1344–1357 (HS9). Dataset B (157 taxa, *trnL-F*) includes additional sequences of *Scutellaria* species available from ENA/GenBank added to the *trnL-F* partition from dataset A. It has the same alignment length and hotspots as dataset A. The highest number of informative substitution characters is provided by the *matK* gene, whereas it has only few indels (Table 1). The *trnK-matK-psbA* region overall contributes 54.6% of the informative characters. Annotated alignments are provided in the Supplemental content online.

Table 1. Sequence statistics and phylogenetic utility of chloroplast regions used.

	Characters	Length mean (S.D.)	Variable (%)	Informative (%)	Indels	Variable (%)	Informative (%)	GC%	Model
Dataset A (105 taxa)									
matK	1546	1495.7 (135.6)	519 (33.6)	335 (21.7)	16	16 (100)	6 (37.5)	33.9	TVM+G
trnL-F	949	773 (88.8)	262 (27.6)	165 (17.4)	69	69 (100)	38 (55.1)	36.1	GTR+I+G
trnK	1462	1153.8 (110.7)	356 (24.4)	226 (15.5)	111	111 (100)	51 (45.9)	33.0	GTR+G
rpl16	1371	1020.3 (24.3)	386 (28.1)	244 (17.8)	94	94 (100)	47 (50)	32.4	TVM+G
Dataset B (157 taxa)									
trnL-F	998	821.4 (42.9)	272 (27.3)	172 (17.2)	73	73 (100)	40 (54.8)	36.5	GTR+G

Phylogenetic analyses

All three inference methods of the combined plastid markers (dataset A) yielded well-resolved and largely congruent trees that deviated only in some inconsistently resolved nodes in shallow terminal clades (see supplement S1-S3). The Bayesian majority rule topology is presented in Fig. 1. The monophyletic genus *Scutellaria* received maximum support, as did three major clades (A–C) within it. *Tinnea* was found as sister, also with maximum statistical support. The members of the *S. orientalis* group are all depicted in clade A, and in a core clade corresponding to *S.* subg. *Apeltanthus* in the circumscription of Paton (1990b). Whereas *S.* subg. *Apeltanthus* is monophyletic, its *S.* sect. *Apeltanthus* is polyphyletic because *S. poecilantha* Nevski appears in a lineage different from *S. leptosiphon* Nevski and *S. stocksii* and nested within *S.* sect. *Lupulinaria* (Fig. 1). Furthermore, *S.* subsect. *Lupulinaria* shows members of *S.* subsect. *Cystaspis* (Juz.) A. J. Paton nested within it in different positions (*S. heydei* Hook. f., *S. physocalyx* Regel & Schmalh.). This means that the *S. orientalis* group also does not form a natural group, as currently understood. Most remarkably, there are two principal subclades with members of the *S. orientalis* group, one of which includes individuals currently identified as *S. orientalis* from the Lesser and Greater Caucasus along with *S. novorossica* Juz. and *S. poecilantha*. The other, more diverse subclade comprises the Central Asian taxa *S. altaica* Ledeb. ex A. Spreng, *S. glabrata* Vved. and *S. intermedia* Popov along with some individuals of *S. orientalis* from the Lesser Caucasus, along with *S. bornmuelleri* Hausskn. ex Bornm., *S. grossheimiana* Juz., *S. pinnatifida* A. Ham. and *S. prilipkoana* Grossh. and also the European *S. alpina* L. as nested among Caucasian taxa. *Scutellaria* subg. *Scutellaria* is broadly paraphyletic to *S.* subg. *Apeltanthus*. The first branches of clade A are constituted by a grade of different members of *S.* sect. *Scutellaria* and *S.* sect. *Salviifoliae* (*S. pontica* K. Koch). The African *S. schweinfurthii* Briq. (representing the '*S. violascens* species-group') is sister to the remainder of clade A.

Clade B contains E Mediterranean species of *Scutellaria* subg. *Scutellaria* but also *S. scandens* D. Don from the Himalaya, representing the '*S. repens* species-group' and a *S. altissima* L.–*S. tournefortii* Benth. clade. Clade C depicts a grade of New World lineages: the South American lineage (*S. costaricana* H. Wendl., *S. scutellarioides* (Kunth) R. Harley, etc.), a North American lineage (*S. incana* Spreng. etc.) followed by *S. mexicana* (*S.* sect. *Salazaria* (Torr.) A. J. Paton). Two terminal sublineages comprise *S. galericulata* L. and relatives and *S. indica* L. and the other a number of species from China (e.g. *S. tsinyunensis* C. Y. Wu & S. Chow), respectively (terminal part of clade C in Fig. 1).

The extended *trnL-F* tree (Fig. 2) also shows the same major clades A and B, but all relevant nodes are less well supported. Clade C is not fully resolved, with the South American clade appearing in a tritomy. Within clade A, the additional samples from ENA/GenBank, which are mostly from Iran, appear mostly in two subclades: the *Scutellaria przewalskii* Juz. lineage that consists of only one sample in the combined tree (Fig. 1) is depicted in the wider-sampled *trnL-F* tree (Fig. 2) as a subclade including *S. araxensis* Grossh., *S. bornmuelleri*, several subspecies of *S. pinnatifida* and *S. platystegia* Juz. In addition, *S. glechomoides* Boiss., *S. nepetifolia* Benth. and others are resolved together with *S. physocalyx*.

Morphological characters

We developed a list of twelve characters with their respective states, which are presented in the following.

1. Life form — (1) Dwarf shrubs (fruticose chamaephyte) s.l., here defined as erect plants strongly branched from base, woody throughout and taller than 25–50 cm (nevertheless terminal branches can develop into herbaceous climbing branches); (2) suffruticose chamaephytes, with branches woody at base and for at least 10 cm in height and an erect stem; (3) caespitose creeping and cushion-forming chamaephytes, with woodiness restricted to very base, mostly comprising rhizome only, herbaceous branches and a creeping or cushion-like habit; (4) erect herbs; (5) herbaceous stems sprouting from a woody xylopodium with buds hiding under soil surface.

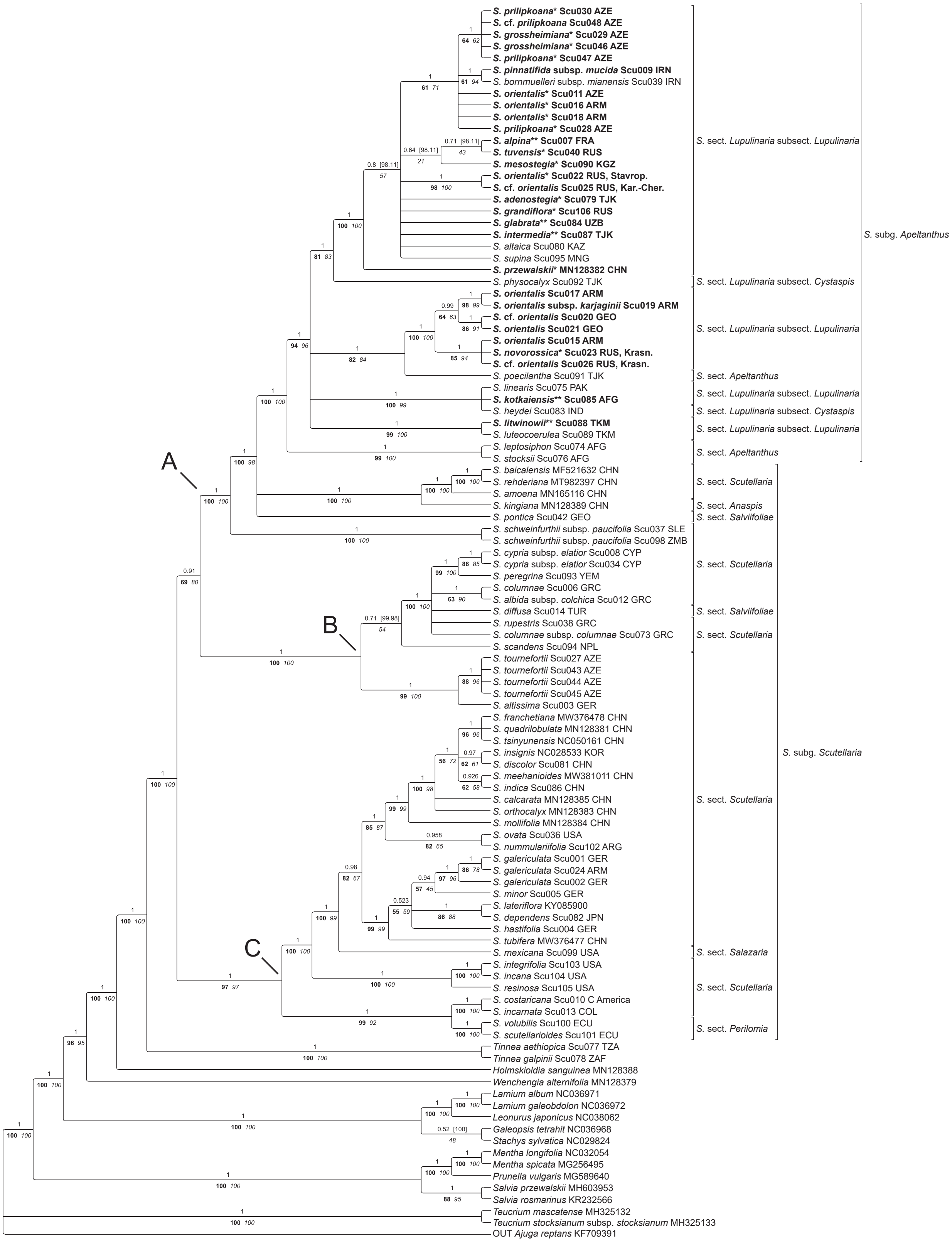


Fig. 1. Phylogeny of *Scutellaria* based on a combined matrix of *matK-trnK, rpl16* and *trnL-F* sequence data. Node support values are presented on the Bayesian majority rule consensus tree with Bayesian posterior probabilities shown above branches and Maximum Likelihood BS values (right, italics) and Maximum Parsimony JK values (left, bold) shown below branches. Infrageneric entities annotated on the tree show the classification of Paton (1990b). Taxa in bold are members of the *S. orientalis* group. An asterisk next to the name indicates taxa explicitly mentioned by Juzepczuk (1954) as members of *S.* subsect. *Orientales* or, if not mentioned there, listed as members of the '*S. orientalis* species-group' by Paton (1990b; two asterisks). Country codes are ISO 3166-1 alpha-3. For voucher information, see Appendix 1.

These definitions follow Ellenberg & Mueller-Dombois (1967), but combine all life forms into one category which can form transitions and are therefore sometimes hard to distinguish.

Character state 1 combines dwarf shrubs in a strict sense (fruticose chamaephytes; by far prevailing in *Scutellaria*) and low-growing shrubs (caespitose nanophanerophytes) only to be distinguished by the overall height of the woody vegetation body along an artificial 50(–100) cm limit (Raunkiaer 1934; Ellenberg & Mueller-Dombois 1967). Very few woody *Scutellaria* species grow taller than 50(–100) cm and hence do not fully fit into the conventional definition of a chamaephyte proper. Shoots rapidly thinning out at the tip and which may die back to the woody branch during untoward conditions occur only within chamaephytes s. str.

Character state 2 corresponds to what is commonly understood as a subshrub.

Plants exhibiting character state 3 are often described as being largely herbaceous plants with creeping stems or at least non-erect stems. The length of the creeping branches distinguishes creeping (reptant) chamaephytes, rooting at the nodes or not (so-called carpet shrubs, espalier shrubs or mat-forming subshrubs) from pulvinate, i.e. cushion-forming, sometimes almost herbaceous chamaephytes (Ellenberg & Mueller-Dombois 1967). Due to the many transitional stages, we accept only one wide character state.

Character state 4 unites all types of non-creeping hemicryptophytes without any subtypes. The term “scandent”, which is used by Paton (1990b) for the life form of *Scutellaria scandens*, is not considered as its own state here. Sometimes erect herbs develop into straggling shoots, and these are still accepted under the state erect herbs, as for example *S. scandens* in *Flora of China* (Li & Hedge 1994).

2. Leaf shape — (1) oblong-lanceolate to oblanceolate; (2) elliptic-ovate to deltoid; (3) broadly ovate to orbicular.

Leaf shape refers to the outline of the lamina.

3. Leaf margin — (1) entire; (2) toothed (to repand), all kinds of crenation to dentations less than 30%; (3) pinnatifid, incised or more than 50%.

4. Leaf base — (1) sagittate or hastate; (2) leaf lamina abruptly narrowing into petiole, including cordate, rounded and truncate at base; (3) leaf lamina gradually merging into petiole, including cuneate and attenuate at base.

5. Leaf indumentum of upper leaf surface — (1) glabrous (to subglabrous); (2) hairy.

6. Leaf texture — (1) leathery (xeromorphic); (2) thin-textured (mesomorphic).

7. Inflorescence architecture — Flowers in *Scutellarioideae* are basically arranged in indeterminate thyrses, but individual cymes are mostly reduced to a single flower. Therefore, inflorescences appear raceme-like. Our character “inflorescence architecture” is understood as a complex character describing the general appearance of inflorescences: (1) flowers opposite and decussate, in a conspicuous inflorescence; (2) flowers opposite and secund, therefore appearing raceme-like, in a more or less conspicuous inflorescence; (3) flowers helically arranged, in a more or less conspicuous inflorescence; (4) flowers in axils of opposite cauline leaves, through curved peduncles also more or less oriented to one side; (5) cymes with branches of first order present, so that several flowers appear from axil of one leaf or bract (“cymose” in Li & al. 2016).

The terminology of inflorescences is according to Weberling (1989), and the presence of inflorescence types in different genera follows Harley & al. (2004). Character state 4 is exemplified by *Scutellaria galericulata* as also described in Paton (1990b: fig. 2). It encompasses the same arrangement of flowers as state 2 but differs by unreduced cauline leaves supporting flowers instead of reduced cauline leaves or bracts. As a consequence, there is no appearance of a morphologically well-defined inflorescence in relation to the vegetative branching system.

8. Shape of flower-supporting organs — (1) cucullate, bract-like and smaller than cauline leaves; (2) flat, bract-like and smaller than cauline leaves; (3) similar to cauline leaves in size, texture and indumentum, i.e. specific bracts absent.

The character state cucullate (Paton 1990b) is called navicular in Juzepczuk (1954). Character state 3 occurs e.g. in *Scutellaria galericulata*, and some E Asian species such as *S. amoena* C. H. Wright (Fig. 3J), in which flowers sit directly in the axils of cauline leaves. Alternatively, character 8 could have been defined for bracts only, which would have resulted in coding it as “not applicable” in species possessing states 4 and 5 of character 7.

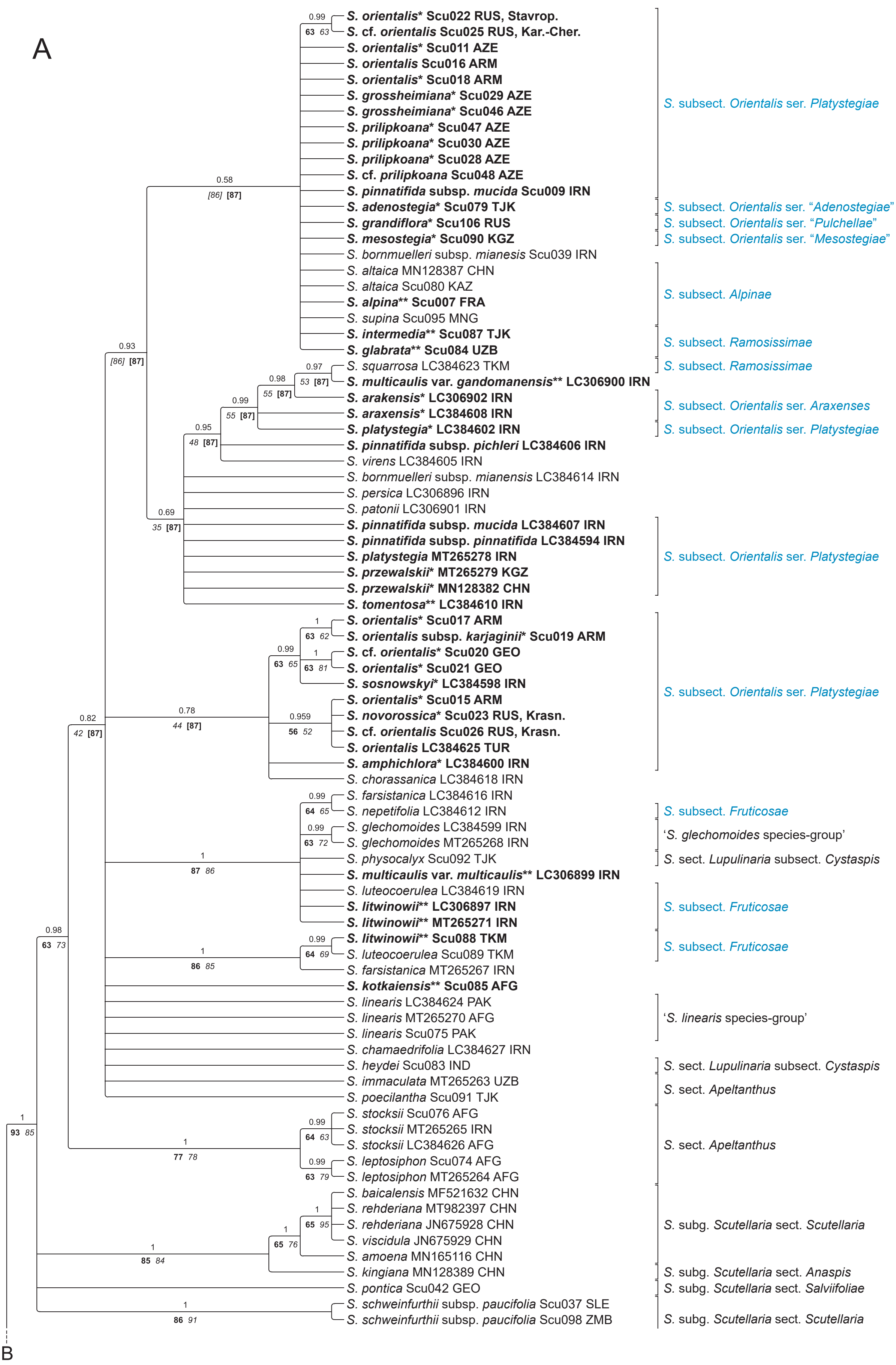
9. Texture of flower-supporting organs at fruiting stage — (1) membranous to scarious; (2) herbaceous.

10. Shape of upper lip of calyx — (1) testudinate, slight ridge midway along at anthesis, becoming testudinate in fruit; (2) scutellate, the upper lip is folded midway along its length forming a rigid, erect sail-like structure usually less than 6 mm tall and wide; (3) scutellate-inflated, similar to character state 2, expanding in fruit becoming membranous inflated, usually more than 6 mm tall and wide; (4) bladder-like, upper and lower lips identical, inflated and papery in fruit, forming a bladder; (5) patelliform, disk-shaped with a narrow rim, saucer-shaped (in *Holmskioldia*); (6) funnelform.

Definitions for character states 1–4 are in line with Paton (1990b), character state 5 is based on Harley & al. (2004) and character state 6 corresponds to the description in Li & al. (2012: fig. 2G). In the reconstruction with BayesTraits, states 5 and 6 are put together because of limited degrees of freedom in the program.

11. Upper lip of corolla — (1) not galeate; (2) galeate.

12. Flower colour — (1) bright red; (2) mainly yellow; (3) several colours (various combinations).


A
0.99
63 63
S. orientalis* Scu022 RUS, Stavrop.
S. cf. orientalis Scu025 RUS, Kar.-Cher.
S. orientalis* Scu011 AZE
S. orientalis Scu016 ARM
S. orientalis* Scu018 ARM
S. grossheimiana* Scu029 AZE
S. grossheimiana* Scu046 AZE
S. prilipkoana* Scu047 AZE
S. prilipkoana* Scu030 AZE
S. prilipkoana* Scu028 AZE
S. cf. prilipkoana Scu048 AZE
0.58
[86] [87]
S. pinnatifida subsp. mucida Scu009 IRN
S. adenostegia* Scu079 TJK
S. grandiflora* Scu106 RUS
S. mesostegia* Scu090 KGZ
S. bornmuelleri subsp. mianesis Scu039 IRN
S. altaica MN128387 CHN
S. altaica Scu080 KAZ
S. alpina** Scu007 FRA
S. supina Scu095 MNG
S. intermedia** Scu087 TJK
S. glabrata** Scu084 UZB
0.93
[86] [87]
0.97
53 [87]
S. squarrosa LC384623 TKM
0.98
55 [87]
S. multicaulis var. gandomanensis** LC306900 IRN
0.99
55 [87]
S. arakensis* LC306902 IRN
S. araxensis* LC384608 IRN
0.95
48 [87]
S. platystegia* LC384602 IRN
S. pinnatifida subsp. pichleri LC384606 IRN
S. virens LC384605 IRN
S. bornmuelleri subsp. mianensis LC384614 IRN
S. persica LC306896 IRN
0.69
35 [87]
S. patonii LC306901 IRN
S. pinnatifida subsp. mucida LC384607 IRN
S. pinnatifida subsp. pinnatifida LC384594 IRN
S. platystegia MT265278 IRN
S. przewalskii* MT265279 KGZ
S. przewalskii* MN128382 CHN
S. tomentosa** LC384610 IRN
1
63 62
S. orientalis* Scu017 ARM
S. orientalis subsp. karjaginii* Scu019 ARM
0.99
63 65
1
63 81
S. cf. orientalis* Scu020 GEO
S. orientalis* Scu021 GEO
S. sosnowskyi* LC384598 IRN
S. orientalis* Scu015 ARM
0.82
42 [87]
0.78
44 [87]
0.959
56 52
S. novorossica* Scu023 RUS, Krasn.
S. cf. orientalis Scu026 RUS, Krasn.
S. orientalis LC384625 TUR
S. amphichlora* LC384600 IRN
S. chorassanica LC384618 IRN
0.99
64 65
S. farsistanica LC384616 IRN
S. nepetifolia LC384612 IRN
0.99
63 72
S. glechomoides LC384599 IRN
S. glechomoides MT265268 IRN
1
87 86
S. physocalyx Scu092 TJK
S. multicaulis var. multicaulis** LC306899 IRN
S. luteocoerulea LC384619 IRN
S. litwinowii** LC306897 IRN
S. litwinowii** MT265271 IRN
0.98
63 73
1
86 85
0.99
64 69
S. litwinowii** Scu088 TKM
S. luteocoerulea Scu089 TKM
S. farsistanica MT265267 IRN
S. kotkaiensis** Scu085 AFG
S. linearis LC384624 PAK
S. linearis MT265270 AFG
S. linearis Scu075 PAK
S. chamaedrifolia LC384627 IRN
S. heydei Scu083 IND
S. immaculata MT265263 UZB
S. poecilantha Scu091 TJK
1
93 85
0.99
64 63
S. stocksii Scu076 AFG
S. stocksii MT265265 IRN
1
77 78
S. stocksii LC384626 AFG
0.99
63 79
S. leptosiphon Scu074 AFG
S. leptosiphon MT265264 AFG
S. baicalensis MF521632 CHN
1
65 95
S. rehderiana MT982397 CHN
1
65 76
S. rehderiana JN675928 CHN
1
85 84
S. viscidula JN675929 CHN
S. amoena MN165116 CHN
S. kingiana MN128389 CHN
S. pontica Scu042 GEO
1
86 91
S. schweinfurthii subsp. paucifolia Scu037 SLE
S. schweinfurthii subsp. paucifolia Scu098 ZMB
B
S. subsect. Orientalis ser. Platystegiae
S. subsect. Orientalis ser. "Adenostegiae"
S. subsect. Orientalis ser. "Pulchellae"
S. subsect. Orientalis ser. "Mesostegiae"
S. subsect. Alpinae
S. subsect. Ramosissimae
S. subsect. Ramosissimae
S. subsect. Orientalis ser. Araxenses
S. subsect. Orientalis ser. Platystegiae
S. subsect. Orientalis ser. Platystegiae
S. subsect. Orientalis ser. Platystegiae
S. subsect. Fruticosae
'S. glechomoides species-group'
S. sect. Lupulinaria subsect. Cystaspis
S. subsect. Fruticosae
S. subsect. Fruticosae
'S. linearis species-group'
S. sect. Lupulinaria subsect. Cystaspis
S. sect. Apeltanthus
S. sect. Apeltanthus
S. subg. Scutellaria sect. Scutellaria
S. subg. Scutellaria sect. Anaspis
S. subg. Scutellaria sect. Salviifoliae
S. subg. Scutellaria sect. Scutellaria

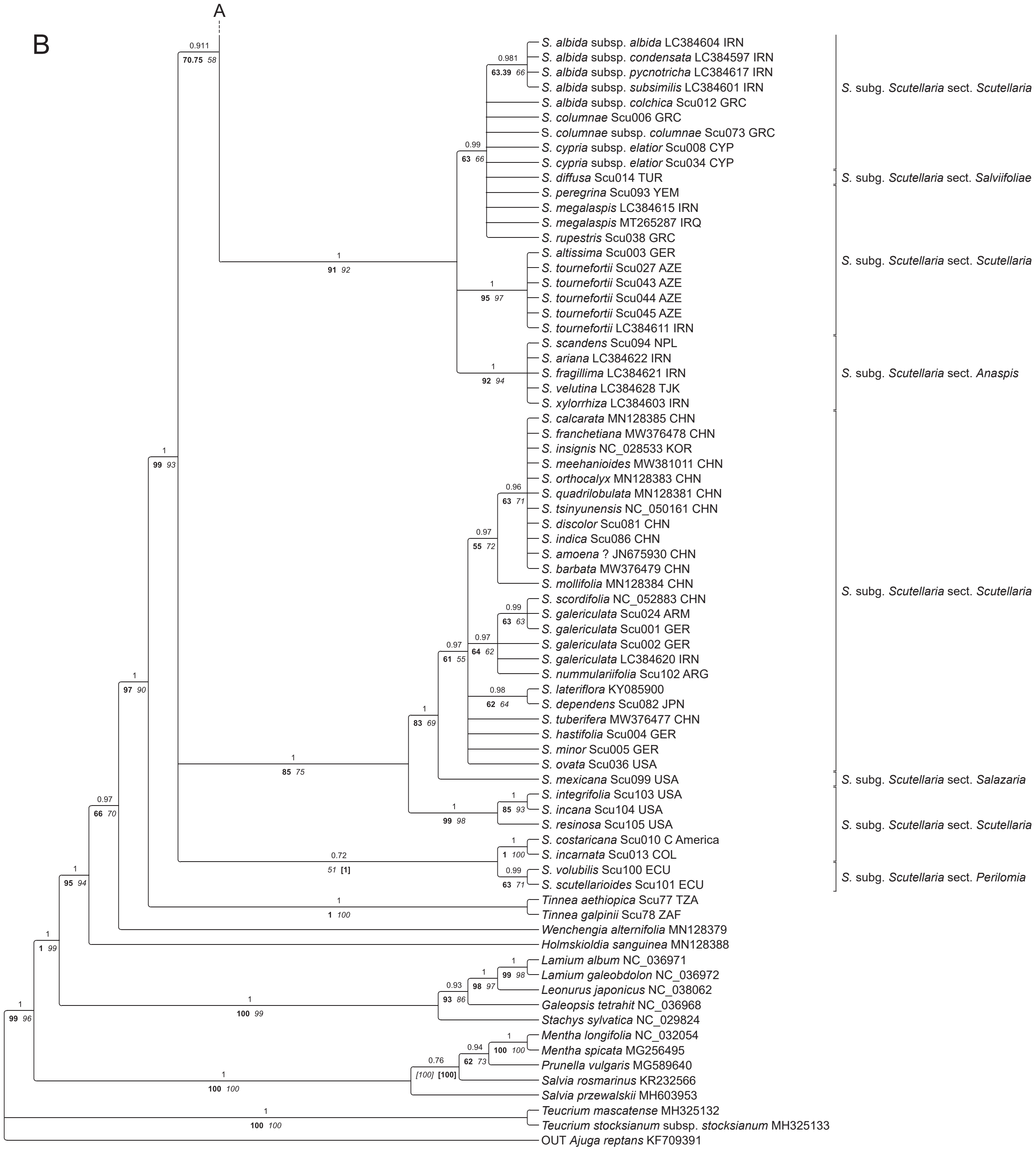


Fig. 2 (A, B). Extended phylogeny of *Scutellaria* based on *trnL-F* sequence data including sequences from published sources. Node support values are presented on the Bayesian majority rule consensus tree with Bayesian posterior probabilities shown above branches and Maximum Likelihood BS values (right, italics) and Maximum Parsimony JK values (left, bold) shown below branches. Infrageneric entities annotated on the tree in clade A show the classification of Juzepczuk (1954) for *S.* sect. *Lupulinaria* with its four subsections and the series in *S.* subsect. *Orientales.* Taxa in bold are members of the *S. orientalis* group. An asterisk next to the name indicates taxa explicitly mentioned by Juzepczuk (1954) as members of *S.* subsect. *Orientales* or, if not mentioned there, listed as members of the '*S. orientalis* species-group' by Paton (1990b; two asterisks). Blue text indicates the infrageneric classification of *S.* sect. *Lupulinaria* sensu Juzepczuk (1954); for species outside of this section, black text indicates the infrageneric classification of Paton (1990b). For sequences downloaded from ENA/GenBank, the corresponding accession number is indicated with the taxon name instead of the Scu DNA-isolation code. Country codes are ISO 3166-1 alpha-3.

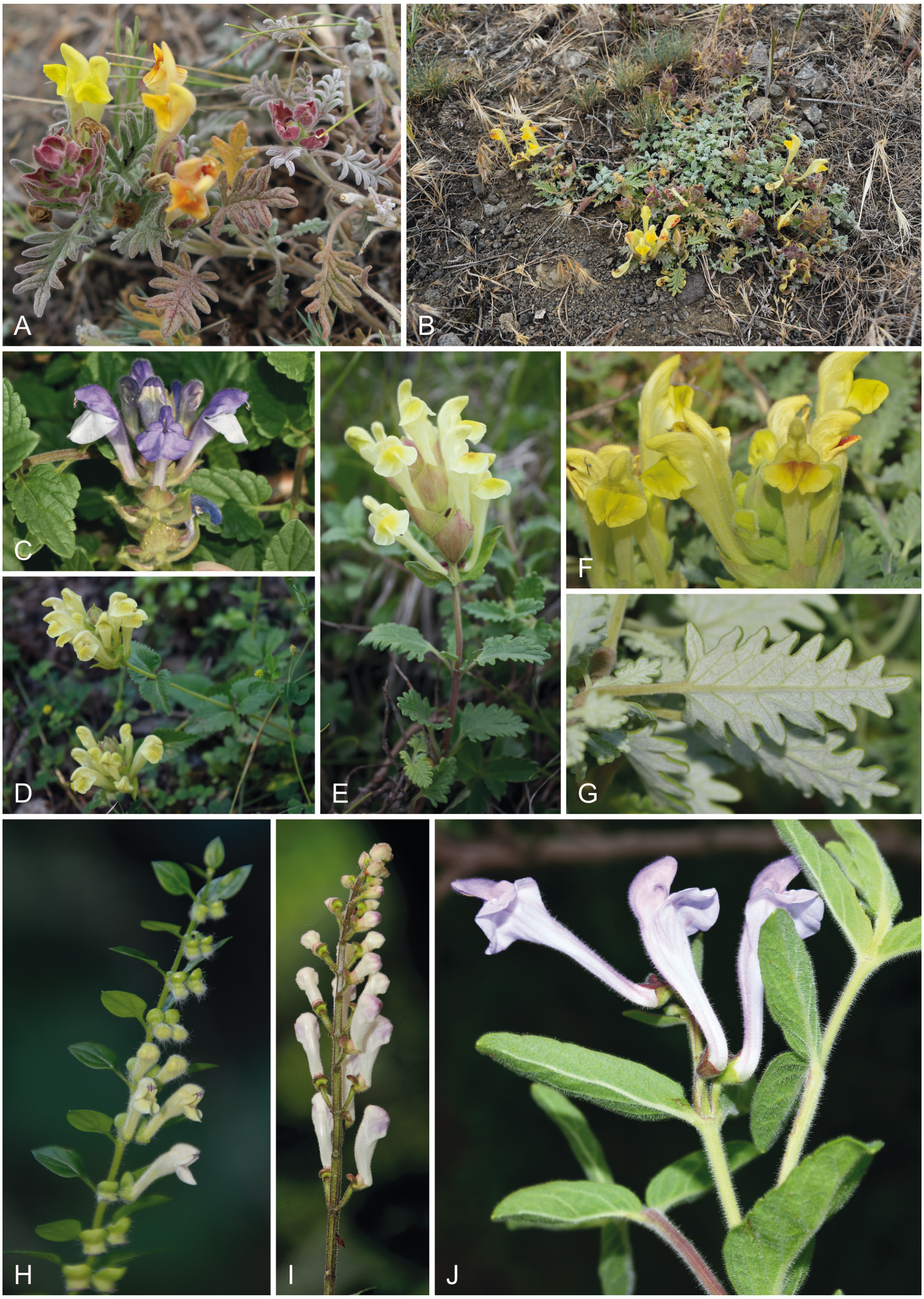


Fig. 3. Morphological diversity of *Scutellaria*. A–G correspond to the *S. orientalis* group and clade A; H and I represent clade B; J represents clade C. – A, B: *S. prilipkoana*, *Salimov & Safarov RSA0417*, Scu030, from Lerik, Talysh; plants with deeply pinnatifid leaves that have a dense indumentum; C: *S. alpina*, living collection in Botanic Garden Berlin; D: *S. orientalis* from Quba, Azerbaijan; note almost glabrous and only slightly dentate cauline leaves; E: *S. orientalis*, *Borsch & al. 5804*, Scu025, from Stavropol, N Caucasus, Russia; inflorescence with cucullate bracts and leaves slightly pinnatifid and sparsely pubescent; F, G: *S. orientalis*, *Parolly & al. 15096*, Scu021, from Georgia close to Tbilisi; leaves slightly pinnatifid and densely tomentose abaxially; H: *S. albida* from Artvin, Turkey; raceme leafy, with leaves but distinctly smaller than cauline leaves; I: *S. tsinyunensis* possessing a distinct raceme-like inflorescence with flower-supporting organs strongly reduced to small, membranous bracts; J: *S. amoena* with solitary flowers arising from axils of regular-sized cauline leaves. – Photographs: R. Salimov (A, B, D), G. Parolly (C, F, G, H), T. Borsch (E), C.-L. Xiang (I, J).

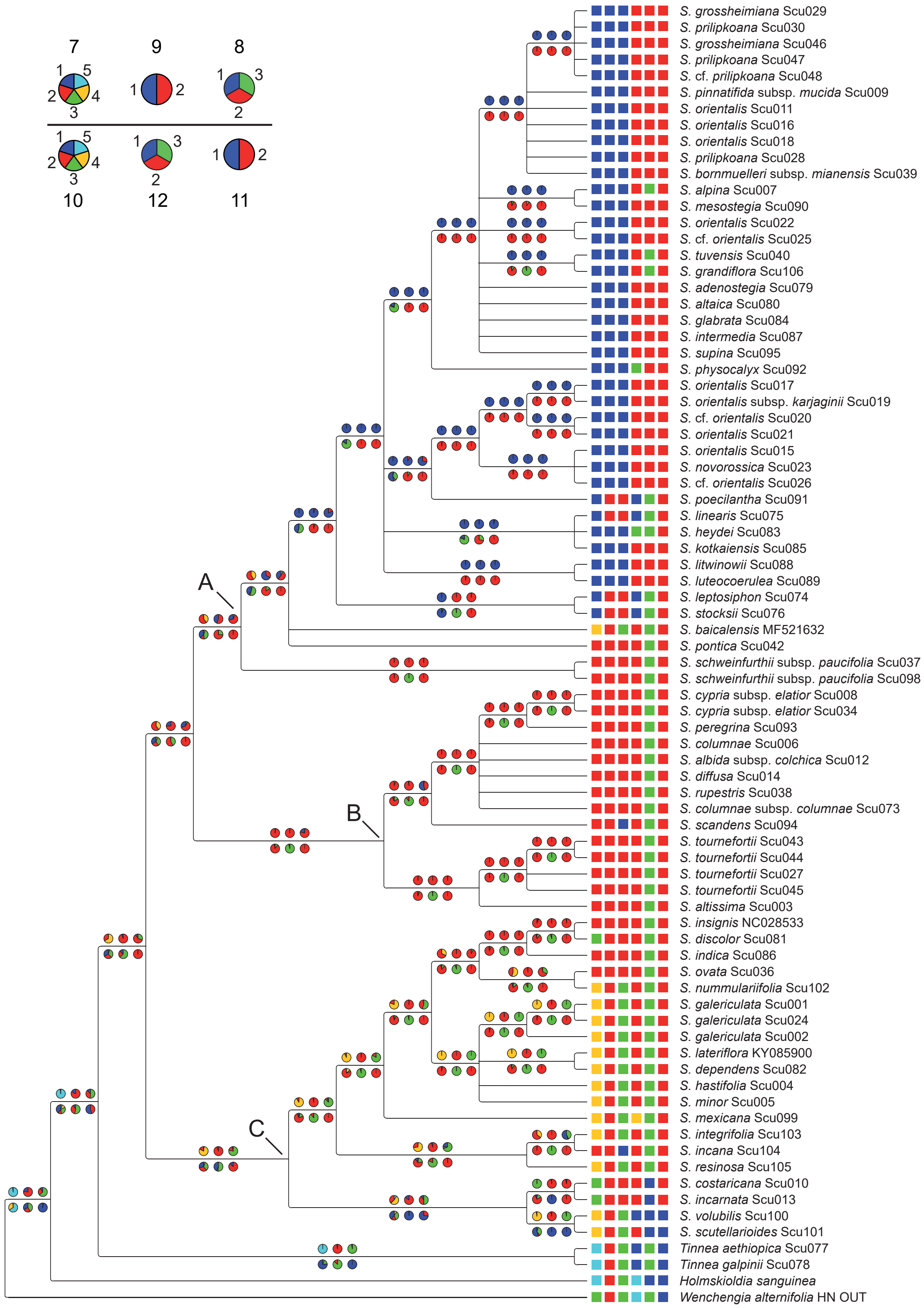


Fig. 4. Evolution of inflorescence architecture and flower morphology shown on the Bayesian majority rule consensus tree of the combined plastid dataset. Pie charts illustrate the probabilities for ancestral character states reconstructed for inflorescence type (character 7), texture of bracts in fruit (character 9), shape of bracts (character 8), shape of upper calyx (character 10), flower colour (character 12) and shape of upper lip of corolla (character 11). A specific colour is assigned to each state (character and state definitions are found in the Results), and the position of the pie chart for each character is indicated at the top left of the figure. Boxes next to terminal branches indicate the respective state present in the specimen included in the tree.

Fig. 5. Evolution of leaf morphology shown on the Bayesian majority rule consensus tree of the combined plastid dataset. Pie charts illustrate the probabilities for ancestral character states reconstructed for leaf indumentum (character 5), leaf texture (character 6), leaf shape (character 2), leaf base (character 4) and leaf margin (character 3). A specific colour is assigned to each state (character and state definitions are found in the Results), and the position of the pie chart for each character is indicated at the top left of the figure. Boxes next to terminal branches indicate the respective state present in the specimen included in the tree.

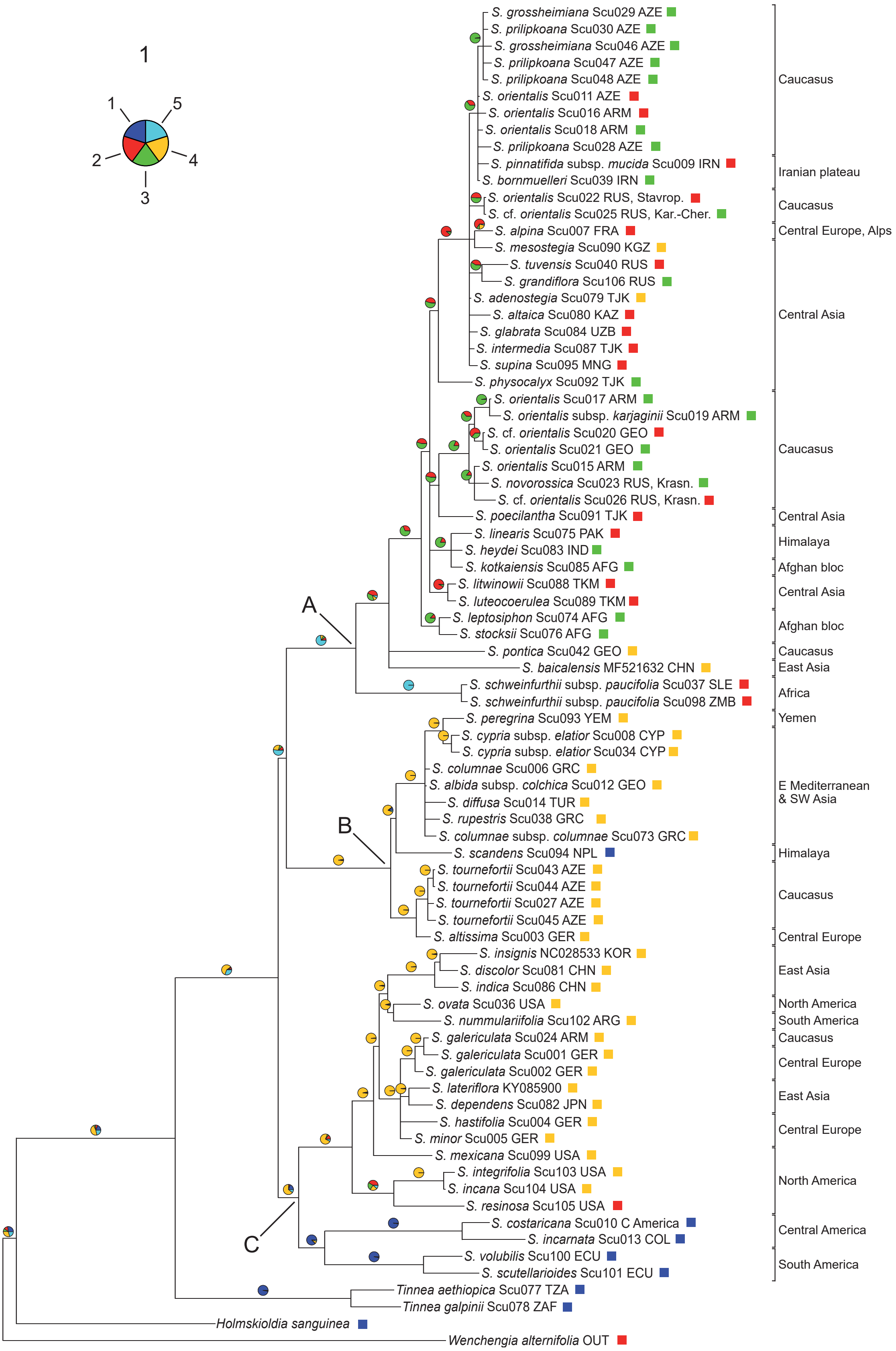


Fig. 6. Evolution of life forms shown on the Bayesian majority rule consensus tree depicted as a phylogram of the combined plastid dataset. Pie charts illustrate the probabilities for ancestral character states (definitions are found in the Results). Boxes next to terminal branches indicate the respective state present in the specimen included in the tree. Countries in which the specimens were collected as well as major geographic areas are annotated on the tree. Country codes are ISO 3166-1 alpha-3.

Ancestral character state reconstruction

The results from the analysis with BayesTraits are presented in Fig. 4–6 as pie charts showing the respective probabilities for the ancestral states on the respective nodes. Fig. 4 summarizes inflorescence and flower characters, whereas Fig. 5 presents leaf characters. Fig. 6 presents the evolution of the life form and also shows an annotation of geographical areas for the respective samples.

Discussion

Monophyly of *Scutellaria* and overall relationships within the genus

This study comprises the so-far most complete sampling of species, many of which are included in a molecular phylogenetic analysis for the first time. It represents most sections recognized by Paton (1990b) on morphological grounds and also a broad geographical coverage, therefore entailing putative hitherto unrecognized lineages. The genus *Scutellaria* as circumscribed by Paton (1990b) is found as a clade with maximum support in all three tree inference methods in the combined tree (Fig. 1) and also with *trnL-F* sequence data alone (Fig. 2, 1.0 PP, 99% ML-BS, 93% MP-JK). The formerly accepted genus *Salazaria* (type and only species is *S. mexicana*), which was merged with *Scutellaria* by Paton (1990b) on the basis of morphology, is found deeply nested in clade C of our phylogeny (Fig. 1), and so is *S. scutellarioides*, representing the former genus *Perilomia*. The latter was already included in *Scutellaria* by Epling (1942) with its two Andean species and is resolved in a South American lineage of clade C (Fig. 2).

Our analyses further show *Tinnea* as the sister group of *Scutellaria* and depict *Holmskioldia* and *Wenchengia* as successive branches also receiving maximum statistical support in the combined *matK-trnK+rpl16+trnL-F* trees (Fig. 1) and high support with *trnL-F* alone (Fig. 2). Our results therefore confirm the monophyly of *Scutellarioideae* and the generic relationships presented by Li & al. (2012) and more recently Zhao & al. (2020) based on complete plastome sequences.

Our phylogeny resolves three well-supported major clades within the monophyletic genus *Scutellaria* (Fig. 1). Clade A comprises *S.* subg. *Apeltanthus* sensu Paton (1990b), which also includes all members of the *S. orientalis* group and an assemblage of lineages from *S.* subg. *Scutellaria* with *S. schweinfurthii* depicted with maximum support as sister to all other species in clade A (Fig. 1).

Clades B and C are exclusively composed of members of *Scutellaria* subg. *Scutellaria*, which is therefore paraphyletic to *S.* subg. *Apeltanthus*. Paton (1990b), considering the results from his broad set of phenotypic characters (vegetative, inflorescence and floral morphology, nutlet morphology, embryo shape) analysed by UPGMA, and further considerations on the polarity of some character state transitions, assumed that *S.* subg. *Apeltanthus* could be monophyletic and derived. However, Paton (1990b) did not implement a consistent phylogenetic analysis due to the difficulty of establishing outgroups at a time when there was no phylogenetic hypothesis for the overall relationships of the *Lamiaceae*. Interestingly, Paton considered members of *S.* sect. *Salviifoliae* as possible closest ancestors of *S.* subg. *Apeltanthus*, which appear as one of the branches of our clade A and therefore among the closest relatives of *S.* subg. *Apeltanthus* in our molecular phylogeny.

Safikhani & al. (2018) provided a tree of mostly Iranian species based on *trnL-F* sequence data that shows *Scutellaria galericulata* (*S.* subg. *Scutellaria*) as sister to all remaining species, and further depicts two major clades of *S.* subg. *Apeltanthus* (incl. *S. orientalis*, *S. pinnatifida*, *S. stocksii*) and members of *S.* subg. *Scutellaria* (*S. albida* L., *S. tournefortii* and *S. xylorrhiza*), respectively. These clades correspond to our three clades, although Safikhani & al. (2018) depicted their “Clade II” as composed only of *S.* subg. *Apeltanthus*, due to the lack of sampling the African ‘*S. violascens* species-group’ and other early-branching lineages in this clade such as *S. baicalensis* or *S. pauciflora* Baker (Fig. 1, 2). The topology inferred by Zhao & al. (2020) includes 11 species of *Scutellaria*, which are resolved in two clades. The “subclade I” as annotated by the authors corresponds to clade A of our investigation (Fig. 1) and is further subdivided into a *S. altaica–S. przewalskii* lineage (*S.* subg. *Apeltanthus*) sister to a lineage composed of *S. amoena*, *S. baicalensis* and *S. kingiana* Prain (*S.* subg. *Scutellaria*). The “subclade II” of Zhao & al. (2020) corresponds to a terminal core of our clade C, whereas clade B is not represented in their study. Albeit their much more restricted taxon sampling, these two studies also provide some evidence for the paraphyly of *S.* subg. *Scutellaria* to *S.* subg. *Apeltanthus* in line with our results.

Evolution of selected morphological characters

Inflorescences with decussately arranged flowers evolved once in the core of clade A, in the common ancestor of *Scutellaria* sect. *Lupulinaria* and *S.* sect. *Apeltanthus* (*S. leptosiphon–S. stocksii* subclade; Fig. 4; blue colour in pie charts). As an ancestral state in the genus *Scutellaria*, unspecialized inflorescences are inferred (character 7, state 4) where flowers arise from the axils of cauline leaves so that the inflorescence is not conspicuously separated from the vegetative branching system of the plants. This state is present in many species of clade C, such as in *S. galericulata* (Fig. 4) or *S. amoena* (Fig. 2, 3). Our ancestral character state reconstruction reveals that inflorescences with opposite flowers arranged to one side in a more or less well-defined raceme-like structure (state 2, red colour in the pie charts in Fig. 4) evolved several times in all three major clades. These inflorescences have flower-supporting organs that are flat and herbaceous in texture but differ considerably from cauline leaves by their much smaller size (e.g. *S. albida*; Fig. 3) to become further reduced and membranous to scarious (e.g. in *S. tsinyunensis*, Fig. 3). Inflorescence with helically arranged flowers are derived in *S. costaricana* and *S. incarnata* Vent. (Fig. 1–3), whereas cymes with more than one flower are found in *Tinnea* as the sister group of *Scutellaria* and appear to be also plesiomorphic in *Scutellarioideae*.

The evolution of the shape and texture of bracts (characters 8 and 9; Fig. 4) seems to be closely linked to the evolution of the inflorescence architecture. Cucullate bracts (character 8, state 1, blue colour in pie charts) as well as their membranous to scarious nature were present in the common ancestor of *Scutellaria* sect. *Lupulinaria* and *S.* sect. *Apeltanthus*, but appear to have already been present earlier, before the divergence of *S. pontica* and *S. baicalensis* in clade A. However, the precise reconstruction of this character state transformation requires a clarification of the phylogenetic position of *S. pontica*, because the topological uncertainty with respect to the second and third branch of clade A certainly has influenced our calculated state probabilities for the second node of clade A. In case further phylogenetic research leads to resolving an earlier-diverging position of *S. poecilantha* (see below, discussion of relationships within clade A), cucullate bracts may be revealed to mark a core of clade A as a synapomorphy.

The evolution of the shape of the upper lip of the calyx (character 10) is difficult to assess with equal probabilities for states 1 (testudinate), 2 (scutellate) and 3 (scutellate-inflated) at the deep nodes of *Scutellaria* (Fig. 4, colours blue, red and green, respectively). There seems to be a trend toward scutellate upper calyx lips in most of the '*S. orientalis* species-group' members, including *S. litwinowii* Bornm. & Sint. and *S. luteocoerulea* Bornm. & Sint., whereas the subclade with *S. heydei*, *S. kotkaiensis* Rech. f. and *S. linearis* Benth. evolved scutellate-inflated lips (in fruit), and testudinate lips evolved in parallel in *S. poecilantha* and the *S. leptosiphon*–*S. stocksii* subclades (Fig. 4). The bladder-like inflated upper and lower calyx lips in fruit in *S. mexicana* are derived from a scutellate calyx, and also the patelliform and funnelform ones in *Holmskioldia* and *Wenchengia* mark developments specific to these two genera. Homoplasy is present in the evolution of flower colours, although the bright red corollas are a synapomorphy for *S.* sect. *Perilomia* as currently defined (character 12, state 1, blue colour in pie chart, Fig. 4).

The evolution of leaf characters 2 to 6 as summarized in Fig. 5 shows significant homoplasy, and this is evident for example for the prominent, deeply pinnatifid leaf margins present in e.g. *Scutellaria pinnatifida* subsp. *mucida* (Stapf) Rech. f. and *S. prilipkoana* (Fig. 3, character 3, state 3, green colour in pie charts in Fig. 5), which appear as further derived from already toothed leaves in *S. grossheimiana* (character 3, state 2, red colour in pie charts). Most of the states are a simplification of the actual gradual variation in the extension of the incision of the leaf margin or the density of trichomes, which was illustrated by e.g. Edmondson (1982). Using a more densely sampled tree of *S.* sect. *Lupulinaria* in the future, a direct illustration of the actual morphological variation in the specific samples as well as numerical approaches will be useful in species delimitation. However, leaf characters do not support major clades as synapomorphies, which is also expected due to their highly adaptive nature (e.g. a dense indumentum and pinnatifid lamina in dry and sunny habitats).

Most of the species of *Scutellaria* are erect perennial herbs (character 1, state 4, yellow colour in pie charts in Fig. 6). Clade A evolved different life forms, being chamaephytes with a woody base. One of these is a caespitose life form with decumbent stems and branches and woodiness restricted to the very base (character 1, state 3, green colour in pie charts; e.g. in *S. grossheimiana* and *S. orientalis*), whereas in a similar life form stems are suffruticose and upright (state 3, green colour in pie charts, e.g. in *S. litwinowii*). Both states resemble adaptations to open habitats with a longer dry season, where the plants form part of open grassland, steppe or savanna communities. These chamaephytic life forms may therefore have contributed to the diversification of clade A. In the African *S. schweinfurthii*, herbaceous stems sprout from a woody xylopodium following the rains (A. Paton, pers. comm.). Such vegetative structures are common in plants adapted to fire in savannah ecosystems. On the other hand, dwarf shrubs with numerous erect, woody stems characterize a clade of Central and South American species (e.g. *S. costaricana*, *S. scutellarioides*; character 1, state 1, blue colour in pie charts in Fig. 6).

There are further morphological characters, such as surface sculpture, indumentum and colour of nutlets, which will be informative at the level of infrageneric lineages as well as species. Ripe nutlets are missing in most herbarium specimens or even field gatherings, so that nutlet characters cannot be linked to individual specimens. Since a direct link of molecular and morphological data, derived from the same individual or specimen is crucial for testing species limits in the *Scutellaria orientalis* group, we have not included nutlet characters in this investigation. Nevertheless, they should be a subject in future research, and fruiting stages should be collected during field work. This also underscores the importance of documented living collections, where the same individual plant can be sampled in various stages.

Clade A and the *Scutellaria orientalis* group

Clade A comprises all members of *Scutellaria* subg. *Apeltanthus* in the wider circumscription (Paton 1990b), which is found monophyletic with maximum support in the combined dataset (Fig. 1) and is also recovered with *trnL-F* alone (Fig. 2, 0.98 PP, 73 ML-BS, 63 MP-JK). *Scutellaria* subg. *Apeltanthus* therefore forms a core of clade A. One of the noteworthy new findings in this investigation is that the African '*S. violascens* species-group' sensu Paton (1990b) of *S.* subg. *Scutellaria* sect. *Scutellaria*, here represented by *S. schweinfurthii* subsp. *paucifolia* (Baker) A. J. Paton, is sister to the remainder of clade A, followed by a lineage of Central to E Asian species of *S.* sect. *Scutellaria* (*S. amoena*, *S. baicalensis*, *S. rehderiana* Diels, *S. viscidula* Bunge; Fig. 2) and *S.* sect. *Anaspis* (*S. kingiana*) and the Caucasian *S. pontica* (*S.* sect. *Salviifoliae*) in a tritomy. *Scutellaria* sect. *Salviifoliae* was considered as morphologically intermediate between *S.* subg. *Apeltanthus* and *S.* subg. *Scutellaria* (Paton 1990a), which is in line with the now inferred phylogenetic position. However, further taxon sampling will be needed to test if the other species of the section form a lineage with *S. pontica*. Also, a phylogenomic approach will be required to resolve the phylogenetic position of *S. pontica* and test if it is sister to *S.* subg. *Apeltanthus* sensu Paton (1990b; Fig. 1). Whereas *S. kingiana* appears in clade A, the more extensive *trnL-F* tree (Fig. 2) depicts other species currently included in *S.* sect. *Anaspis* (e.g. *S. ariana* Hedge; Paton 1990b; Safikhani & al. 2018) in clade B, related to *S. albida*. It is possible that *S. kingiana* does not belong to *S.* sect. *Anaspis* as supported by Paton (1990b) and Zhao & al. (2020), but rather in an E Asian lineage that may correspond to the '*S. strigillosa* species-group' (Paton 1990b) together with *S. baicalensis* and *S. rehderiana*. A detailed comparative study of nutlet morphology and anatomy will be relevant to test if the nutlets with a grey-black colour and their surface only partly covered with hairs that are considered diagnostic for *S.* sect. *Apeltanthus* (see Paton 1990b) are homoplastic or could be confined to the lineage corresponding to *S.* sect. *Apeltanthus* (Fig. 1). Salmaki & Müller (2019) also depicted *S. baicalensis*, *S. kingiana* and *S. rehderiana* in a clade with their ITS data, which is in line with our plastid tree.

Further, the molecular data provide a strong signal for an early branch in the core of clade A that corresponds to a core of *Scutellaria* sect. *Apeltanthus* (sensu Paton 1990b). The remainder of the core clade A then corresponds to *S.* sect. *Lupulinaria*, which at the rank of section appears largely monophyletic as circumscribed by Paton (1990b). *Scutellaria* sect. *Apeltanthus* is here represented by *S. leptosiphon* and *S. stocksii*. Although there is currently no sequence for the type species, *S. orbicularis* Bunge, the suite of morphological characters shared by all species currently included in the section in concert with a relatively limited range (from the Afghan and Pamir mountains to Central Asia) may indicate its monophyly. From the species included by Juzepczuk (1954) in his more narrowly defined fourth subgenus, *S.* subg. *Apeltanthus* (corresponding to *S.* sect. *Apeltanthus* sensu Paton 1990a), *S. poecilantha* is inferred in our molecular trees among the taxa of the *S. orientalis* group (Fig. 2) and therefore would have to be excluded from a monophyletic *S.* sect. *Apeltanthus*. However, the respective node is supported by 1.0 PP in the Bayesian tree but receives only 82JK and 84 BS support in the parsimony and likelihood analyses, respectively (Fig. 1). Future analyses should therefore test the signal for this node with more completely sampled plastid genomes and if *S.* sect. *Apeltanthus* is paraphyletic to *S.* sect. *Lupulinaria* (incl. *S.* sect. *Cystaspis*). Also, further species placed here by Juzepczuk (1954) and Rechinger (1982) require inclusion in molecular datasets in the future (e.g. *S. andrachnoides* Vved., *S. baldshuanica* Nevski, *S. guttata* Nevski, *S. macrodonta* Nevski and *S. rubromaculata* Juz. & Vved.). *Scutellaria immaculata* Nevski also belongs to these species and is included in the *trnL-F* tree (Fig. 2), but this marker alone does not yield the necessary resolution to judge on the circumscription of *S.* sect. *Apeltanthus.*

Looking at the classification system of Paton (1990b), *Scutellaria* subsect. *Lupulinaria* is paraphyletic to *S.* subsect. *Cystaspis* (Fig. 2), with *S. physocalyx* appearing in an isolated position between two main subclades comprising samples of *S. orientalis* and allies, whereas *S. heydei* is resolved in a terminal shallow tritomy together with *S. kotkaiensis* and *S. linearis*. As a consequence, a membranous-inflated scutellum, which was used as diagnostic character for the entity at differing ranks (section, Juzepczuk 1951; subgenus, Juzepczuk 1954; or subsection, Paton 1990b), evolved convergently. On the other hand, all three species share a similar geographical distribution in the Afghan and Pamir mountains to the Himalaya, which would be in line with relatively recent speciation from a common ancestor. The close relationship of *S. litwinowii* and *S. luteocoerulea* found in the combined tree (Fig. 2) was also indicated by Safikhani & al. (2018). Whereas Paton (1990b) listed *S. litwinowii* for the '*S. orientalis* species-group', Juzepczuk (1954) grouped both species in *S.* subsect. *Fruticosae* (Fig. 2) and not in *S.* subsect. *Orientales*. *Scutellaria* subsect. *Fruticosae*, according to Juzepczuk (1954) characterized as being subshrubs with numerous, usually virgate stems, may represent a sublineage within the Irano-Turanian radiation of *S.* subsect. *Lupulinaria* also including *S. glechomoides* [in its own species group sensu Paton (1990b)], *S. multicaulis* Boiss. and *S. nepetifolia* based on our *trnL-F* tree (Fig. 2). A similar lineage was depicted by Safikhani & al. (2018), who also analysed *trnL-F* sequences. However, resolution of this genomic region alone is not enough to make any conclusions about further relationships in *S.* subsect. *Lupulinaria*.

The narrowest circumscription of a taxon relating to the *Scutellaria orientalis* group was made by Juzepczuk (1939) with his "cycle *Orientales*". As is evident from our phylogenetic trees [samples with taxon names in bold and marked with an asterisk in Fig. 1 and 2, indicating taxa that were explicitly mentioned by by Juzepczuk (1954) as members of *S.* subsect. *Orientales*], these species are concentrated in *S.* sect. *Lupulinaria* (two subclades in Fig. 1 and three subclades in the more extensively sampled *trnL-F* tree), but these subclades are not exclusively composed of members of this subsection. Grossheim (1945) also argued that ”cycle *Orientales*” as circumscribed by Juzepczuk (1939) is not a natural group, in particular as he assumed that the *Oxystegiae* and *Platystegiae* groups have different origins. Juzepczuk (1954) defined *S.* subsect. *Orientales* as plants with decussate, 4-angled, spike-like, elongated inflorescences, in contrast to interrupted inflorescences in *S.* subsect. *Fruticosae* and short, subcapitate inflorescences in *S.* subsect. *Ramosissimae*. These three subsections were further described as possessing leaves with a silvery, tomentose indumentum beneath, whereas leaves in *S.* subsect. *Alpinae* are green or mostly greyish green, and plants have also spike-like, elongated and uninterrupted inflorescences (see tree in Fig. 2 for annotation of subsections). It needs to be considered that not all species sharing the respective characters occur in the area covered by the *Flora URSS* and are therefore not annotated (e.g. *S. tomentosa* Bertol.). On the other hand, the characters used by Juzepczuk to delimit his subsections are prone to rapid change in the course of speciation and adaptation to habitats differing in elevation and humidity. We have therefore also indicated in bold, with two asterisks, those species that were mentioned by (Paton 1990b) in the ‘*S. orientalis* species-group’. Paton (1990b) circumscribed his ‘*S. orientalis* species-group’ to contain all species with cucullate bracts clasping the calyx at anthesis, a thick, woody rhizome (therefore excluding *S. glechomoides*) and ovate to narrowly ovate, entire, dentate or pinnatifid leaves (therefore excluding *S. linearis*). Most of the taxa resolved as part of *S.* subsect. *Lupulinaria* are therefore included in this broader *S. orientalis* group, except *S. glechomoides* (Paton’s ‘*S. glechomoides* species-group’), *S. linearis* (Paton’s ‘*S. linearis* species-group’), *S. poecilantha* and the members of *S.* subsect. *Cystaspis* appearing nested in *S.* subsect. *Lupulinaria*.

The *Oxystegiae* and *Platystegiae* groups as defined by Juzepczuk (1954) are not monophyletic (see especially Fig. 2). Within the *Oxystegiae* group, *S.* ser. *Araxenses* Grossh. on one hand and the *Mesostegiae* and *Pulchellae* series on the other are resolved in two different lineages. Members of *S.* ser. *Platystegiae* appear in all three lineages, and the only member of the *Adenostegiae* series (the second series of the *Platystegiae* group) currently sampled (*S. adenostegia*) is in the same lineage as the *Mesostegiae* and *Pulchellae* series. It is noteworthy that the members of *Scutellaria* subsect. *Orientales* in the strict sense of Juzepczuk (1954) are resolved in two different, well-supported, major subclades. One subclade contains most samples from the Greater Caucasus (including N Caucasus, Scu22 and Scu25; see also Fig. 3), the Talysh mountains (SW of the Caspian Sea and part of the Iranian plateau, e.g. *S. grossheimiana* Scu29, Scu46, Scu47 and *S. prilipkoana* Scu28, Scu30 from Lerik) and Central Asia (*S. adenostegia* Briq., *S. tuvensis* Juz.; Fig. 1). *Scutellaria alpina*, although with a different distribution (the sample sequenced here is from the W Alps), is also found here, along with further species of Juzepczuk’s *S.* subsect. *Alpinae* (Fig. 2). The position of *S. alpina* within the *S. orientalis* group is also supported by morphology of the inflorescence and the cucullate bracteoles, although this species differs by its blue flowers (Fig. 3).

The other subclade incudes samples from the Lesser and Greater Caucasus and adjacent steppe areas, westward to the Krasnodar area in Russia (*Scutellaria novorossica*, Scu23; Fig. 1). Most of the Iranian samples are found in a third, albeit weakly supported lineage of the *trnL-F* tree (Fig. 2), including *S. bornmuelleri*, *S. multicaulis*, *S. platystegia* and several subspecies of *S. pinnatifida*. Moreover, Pichugin (2015) suggested that the Crimean endemic *S. taurica* Juz. has affinities with *S. stevenii* Juz. (both from *S.* ser. *Tauricae* Grossh. of the *Oxystegiae* group), being distant from *S. orientalis*. Because their sampling was scarce and *trnL-F* sequences are not available, it remains unclear if there are further lineages in addition to those presented in Fig. 2. Future analyses of the species-level relationships and species limits within the *S. orientalis* group also need to extend the sampling to further geographical areas (especially the Balkan peninsula, W Mediterranean subregion and Anatolian highlands) and improve the sampling in Central Asia and Siberia.

Clade B

This major clade is constituted by the ‘*Scutellaria albida* species-group’ as defined by Paton (1990b) including *S. altissima* and *S. tournefortii* (*S.* subg. *Scutellaria* sect. *Scutellaria*) and a core of species from *S.* subg. *Scutellaria* sect. *Anaspis* (*S. ariana*, *S. fragillima* Rech. f., *S. velutina* Juz. & Vved., *S. xylorrhiza*; Paton 1990b; Safikhani & al. 2018). *Scutellaria scandens*, which was informally assigned to the ‘*S. repens* species-group’ in *S.* sect. *Scutellaria* by Paton (1990a), appears in the same clade as the other members of *S.* sect. *Anaspis* in clade B (Fig. 2). *Scutellaria* sect. *Anaspis* therefore appears nested among the lineages of clade B (Fig. 2). However, further increased taxon sampling has to test if *S. altissima* and *S. tournefortii* mark a specific lineage that is sister to the remainder of clade B. Also Safikhani & al. (2018) presented an ITS tree in which their “Clade I” depicts members of *S.* sect. *Anaspis* as sister to *S. albida* and *S. megalaspis* Rech. f., and *S. tournefortii* as sister to both. These nodes have gained statistical support, whereas their inferred position of *S. galericulata* as sister to the aforementioned taxa has no statistical confidence. Earlier authors (Paton 1990b) indicated the similarity in nutlet morphology of the ‘*S. albida* species-group’ with *S.* sect. *Anaspis*. The current results of our molecular phylogenetic analysis therefore appear to be consistent with morphology. *Scutellaria diffusa* Benth., which is a member of *S.* sect. *Salviifoliae* according to Edmondson (1982), is inferred as a sole species within the clade representing the ‘*S. albida* species-group’ (Fig. 2). This was recently also observed by Seyedipour & al. (2020), who presented *trnL-F* and ITS trees of *Scutellaria* species mostly from Iran and sequenced the same material as in our investigation (*Ern 6923*), and it is confirmed here with increased node support as inferred from our larger molecular character set. Considering the type species of the section, *S. salviifolia* Benth. (Paton 1990a), and the morphological similarity of this species to *S. diffusa* (Edmondson 1982; Ezer & Renda 2012), it is very possible that *S. pontica* just exhibits a convergent evolution of a prostrate habit [in *S. diffusa* and *S. pontica*, whereas *S. salviifolia* has upright stems; Ezer & Renda (2012)], with small and entire leaves, otherwise also characteristic of the core of *S.* sect. *Salviifoliae*. *Scutellaria diffusa* differs from *S. salviifolia* by a purple, versus yellow, flower colour, while purple flowers are also present in *S. pontica*. However, shifts in flower colour are homoplastic in *Scutellaria*, as is also evident in *S. alpina* with purple flowers but yellow-flowered ancestors (Fig. 4).

Rechinger (1982) accepted *Scutellaria* sect. *Stachymacris* including *S. fragillima*, *S. megalaspis* and *S. tournefortii*, all of which are resolved in clade B (Fig. 1, 2). As such, *S.* sect. *Stachymacris* could be a taxon concept to formally classify clade B, although it is currently at sectional rank (see below). *Scutellaria fragillima* was alternatively classified in *S.* sect. *Anaspis* (Juzepczuk 1954; Fig. 2), which represents one of the three sublineages of clade B.

Clade C

The phylogenetic position of *Scutellaria* sect. *Perilomia*, represented here by *S. scutellarioides* (type species of *S.* sect. *Perilomia*; Paton 1990a) and *S. volubilis* Kunth, is resolved among other neotropical members of *Scutellaria* representing the '*S. costaricana* species-group' (*S. costaricana*) and the '*S. speciosa* species-group' (*S. incarnata*), all of which are well supported with an early divergence in clade C as sister to all its other species. This lineage is also morphologically characterized by red or scarlet flowers, distally bent corolla tube and other characters that had resulted in a very distinct grouping in the UPGMA analysis of Paton (1990b). Our molecular tree suggests that the emended circumscription of *S.* sect. *Perilomia* by Paton (1990a) to include *S.* sect. *Perilomia*, *S.* sect. *Perilomioideae* (Benth.) Epling and *S.* sect. *Theresa* (Clos) Epling (Epling 1942) should be further extended to include other neotropical species. However, this has to await a more complete inclusion of those taxa in the molecular phylogeny, considering that there are several species groups of *S.* sect. *Scutellaria* present in Central and South America, with potential relatives. Most interestingly, there are several lineages within clade C that extend into the Neotropics, such as *S. mexicana* (*S.* sect. *Salazaria*) as the third branch (Fig. 1) and a lineage comprising *S. ovata* Hill (representing the '*S. ovata* species-group' occurring in the U.S.A. and Mexico) sister to *S. nummulariifolia* Hook. f. from Argentina [the only species of the '*S. nummulariifolia* species-group' sensu Paton (1990b)]. Our molecular phylogenetic results indicate that at least two lineages of *Scutellaria* may have migrated southward from North to South America (see below), underscoring the need of a very dense taxon sampling to better understand relationships among New World *Scutellaria* in future studies. Morphological similarities of the '*S. ovata* species-group' to species in clade B as indicated by Paton (1990b), such as a pericarp (also present in *S. schweinfurthii*), and overall similarity to *S. altissima* of the '*S. albida* species-group' must therefore be explained by convergence. Further, this investigation provides some evidence for the monophyly of the '*S. galericulata* species-group' as circumscribed by Paton (1990b) including *S. galericulata*, *S. minor* Huds. and the E Asian *S. dependens* Maxim. as a core, but also including *S. lateriflora* and *S. hastifolia* L. (Fig. 2), albeit node support is yet weak. The morphological similarity of *S. galericulata* to *S. lateriflora* was pointed out by Paton (1990b), although he assigned the latter to its own species group ('*S. lateriflora* species-group'). Another well-supported terminal subclade comprises species from China (e.g. *S. franchetiana* H. Lév., *S. tsinyunensis*; for the latter see also Fig. 3) and appears to correspond to a more species-rich radiation in subtropical parts of China identified by Zhao & al. (2017) based on ITS sequence data.

Species limits, species identification and species diversity in the *Scutellaria orientalis* group

The employed molecular markers (*matK-trnK*, *rpl16*, *trnL-F*) exhibit substantial phylogenetic signal within the *Scutellaria orientalis* group and indicate complex speciation patterns, which happened and appear to be ongoing more or less isolated from each other in different parts of the Caucasus and the Irano-Turanian region. Molecular phylogenetic results (Fig. 1, 2) contradict a treatment of *S. orientalis* as a single species with many subspecies as implemented by various authors such as Fedorov (1967), Edmondson (1982), Menitsky (1992), Celep & Dirmenci (2017) and reflected by the World Checklist of Selected Plant Families that is largely implemented also in the Euro+Med PlantBase (Euro+Med 2006+). Several of the entities treated at subspecific rank (but identified in our investigation at the level of species) appear in different subclades of the molecular trees. Assuming a concept of vicariance as a result of ongoing allopatric speciation, all subspecies of a species would have to be found in the same terminal clade as the nominate subspecies. The lectotype of *S. orientalis* (Herb. Linnaeus no. 751.1, LINN [image at http://linnean-online.org/6677/]; Edmondson 1982) has long and slender stems that must have been procumbent with many short side branches, leaves with a pinnate margin and a short inflorescence with few flowers, the lower of which have just opened. Plants similar to this morphotype were included in this investigation under the name *S. orientalis*, but appear in two also geographically different subclades of *S.* sect. *Lupulinaria* (Fig. 2).

The lectotype does not convey any locality information, whereas other historical material of *S. orientalis* in LINN comes from "Caucasus Mt." or "Taurus" and apparently comes from morphologically deviant populations. Using morphology alone, a clarification of the proper identity of the type specimen may therefore be limited.

On the other hand, the phylogeny depicts several individuals of the morphotype and current species identification in the same terminal lineage, such as *Scutellaria grossheimiana*, which was described from Lerik (Juzepczuk 1951), and *S. prilipkoana* (see also Fig. 3), which was also described from Talysh (Grossheim 1945). Both taxa have very close affinities morphologically, phylogenetically and also geographically, and stand for the other species that may be range restricted or much narrower endemics that can be resolved by their genotypes found in a certain geographical area. Also Charadze (1961) argued that *S.* sect. *Lupulinaria* in the Caucasus contains several range-restricted oreophytes, indicating that speciation by adaptation to high mountain environments and probably geographic isolation plays a significant role. A much denser taxon sampling and a more representative geographical coverage will be needed throughout the *S. orientalis* group for species delimitation that samples type localities if possible and at best also type specimens directly. Our experience with herbarium material was quite good (Scu083 from 1933, Scu76 from 1962 and Scu075 from 1965), so this perspective exists for at least a significant number of type specimens.

We have also implemented an extended analysis by adding the available *trnL-F* sequences from other published studies to cover additional species and to ideally provide some insights into infraspecific variability and species limits through sequences from individuals from further geographic localities. The *trnL-F* region appeared as the most widely used marker, and in several cases the only plastid region employed (Safikhani & al. 2018; Seyedipour & al. 2020). The *trnL-F* tree in Fig. 2 therefore gives the currently most representative approximation on relationships within *Scutellaria* in terms of taxonomic coverage. As expected, the resolution by *trnL-F* alone is considerably less than through the combined plastid data set, so individuals of several closely related species appear in polytomies (e.g. *S. altissima* and *S. tournefortii*; compare Fig. 1 and 2). Nevertheless, the placement of some of the currently accepted species is in line with similarities in morphology in our trees, e.g. *S. farsistanica* Rech. f. and *S. nepetifolia* as sisters; see also Rechinger (1982), Ranjbar & Mahmoudi (2018), albeit the *trnL-F* topology presented by Safikhani & al. (2018: fig. 2) differs significantly. A possible explanation is differences in the matrix subjected to tree inference, by not excluding mutational hotspots of uncertain homology. Correct alignment matters greatly in plastid data sets, and in particular when genetic distances are low, as among closely related species (Escobari & al. 2021). Noteworthy is also the placement of all individuals of *S. albida* from Iran in a clade to which the individual from Greece appears close, but unresolved (Fig. 2), which points to phylogeographic patterns within this species. On the other hand, our Fig. 2 reveals several taxa in significantly different parts of the tree, such as *S. litwinowii* or *S. platystegia*. In the latter case, *S. platystegia* (LC384602) is from a specimen collected in the Kiamaghi Dagh mountains in N Iran. Considering the specimen (*Safikhani 105466*, TARI image!), this plant appears with deeply pinnatifid, tomentose cauline leaves and very densely arranged, shortly tomentose, cucullate bracts, whereas the type specimen (LE 01010199 image!) is a mesophytic plant with moderately pinnatifid leaves from a different geographic area in the Caucasus. As a consequence, the sequence LC384602 could also be misidentified. This example shows that a direct comparison with the respective type specimens is essential in a situation with so-far prevailing regional treatments and identification keys as well as species diagnoses based largely on gradually varying leaf, inflorescence and flower characters.

The employed combined plastid regions (*matK-trnK-psbA+rpl16+trnL-F*) form a good basis for an overall species-level phylogeny within *Scutellaria* sect. *Lupulinaria*, which confirms the high levels of hierarchical phylogenetic signal observed in these genomic regions in other angiosperm lineages (Barniske & al. 2012; Korotkova & al. 2011). Compared to recent radiations within angiosperm genera such as *Dianthus* L. (*Caryophyllaceae*; G. Fassou pers. comm. 2021), *Gynoxys* Cass. (*Asteraceae*; Escobari & al. 2021) or *Pyrus* L. in the Caucasus (*Rosaceae*; Korotkova & al. 2018), the genetic distances of the same plastid regions found here in *S. orientalis* and relatives (Table 1) are much greater. This not only suggests that the *S. orientalis* group is composed of many phylogenetically defined entities, but also holds promise in further improving the resolution of phylogenetic trees in this group by complementing with additional highly variable spacer regions (Zhao & al. 2020) and the application of numerous loci through a phylogenomic approach. Nuclear loci will be required to identify possible reticulate evolution and incomplete lineage sorting.

Despite the resolution obtained with markers also used in other DNA barcoding projects (e.g. the German Barcode of Life, GBOL; Geiger & al. 2016), the still largely unclear species limits, with the need to link samples represented in molecular datasets to formally described taxa (including type specimens), hamper attempts of molecular species identification in the *Scutellaria orientalis* group at the moment. What is needed is an integrative taxonomic approach, using structured character data, both molecular and morphological (Kilian & al. 2015), and also testing geographical and ecological scenarios relevant for speciation. In the example of *S. galericulata*, which is a morphologically well-characterized species, the *matK-trnK* and *rpl16* plastid genomic regions reveal several substitutions that resolve the species as monophyletic but show the individual from the

German state of Bavaria (Scu001) to possess a haplotype closer related to that in the individual from the Caucasus (Scu024) than to the sampled individual from the German state of Saxony-Anhalt (Fig. 1). This underscores the complexity in the evolution of the flora of the N hemisphere and the need to implement range-wide sampling in the study of widespread taxa.

As a consequence, none of the currently available Flora treatments or checklists at continental to global level will describe the species diversity of the *Scutellaria orientalis* group in a way reflecting only biologically meaningful entities as taxa at species level. An interim strategy for a species-level checklist will therefore be to accept species, rather than infraspecific taxa with doubtful assignments, and to evaluate the species to be accepted on the basis of all existing data, even if this results in a mosaic-like pattern of different stages of knowledge for different taxa. The level of taxonomic evaluation should be indicated and the authority of the accepted respective taxon concept cited to facilitate the stepwise improvement of the taxonomic backbone. Such an approach has been taken by the Taxonomic Expert Networks (TENs) of the World Flora Online consortium (Borsch & al. 2020), and would ideally also be followed up in the case of *Scutellaria*.

Implications for biogeography

The core of clade A entails the members of *Scutellaria* subg. *Apeltanthus* sensu Paton, which are mainly distributed from the Anatolian plateau, the Caucasus, to the Altay, Tien Shan and Pamir Mountains in the east to the Iranian plateau in the south. The majority of taxa is therefore concentrated in the W Irano-Turanian region (see Manafzadeh & al. 2017 for review and circumscription), which corresponds to the earlier idea that the Irano-Turanian region is a major centre of diversification of *S.* subg. *Apeltanthus* (Paton 1990b). The phylogenetic position of *S. alpina* within the subclade of the *S. orientalis* group, which is mostly composed of samples from the Greater Caucasus and Central Asia, suggests a migration from this area westward to the Alps and Pyrenees. Considering that the species ranges from the W coast of the Black Sea (Bulgaria, Romania) over the Balkan peninsula and Carpathians to the Alps (Euro+Med 2006+), it would be interesting to test if the western genotypes are more derived. Plant migrations out of the Caucasus to Central Europe have also been documented in *Campanula* L. (*Campanulaceae*; Jones & al. 2017) and *Primula* L. (*Primulaceae*; Volkova & al. 2020).

The subdivision of the *Scutellaria orientalis* group into two major (Fig. 1) or even a third (Fig. 2) subclade, each of which corresponds to more restricted geographical areas, contradicts the subdivision of the *S. orientalis* group by Juzepczuk (1954) into the *Platystegiae* group, which was considered to contain predominantly mesophytic species, versus xerophilic species in the *Oxystegiae* group. It is very possible that the *S.* sect. *Lupulinaria* radiation encompasses several subclades that diversified predominantly in particular mountain ranges such as the Greater or Lesser Caucasus but also the Iranian plateau. Silakadze & al. (2019) found similar patterns in the diversification of the Caucasian high-mountain bellflowers (*Campanula* sect. *Scapiflorae* (Boiss.) Kharadze), which evolved from a common ancestor. On the other hand, Szukala & al. (2019) showed for the genus *Jurinea* Cass. (*Asteraceae*), which has a largely similar distribution to *S.* sect. *Lupulinaria*, that the Caucasus was colonized several times during the evolutionary history of the genus, followed by subsequent speciation, especially in the N Caucasus. Also, different subclades were found including species in Central Asia and SW Asia, suggesting several independent species radiations in the wider Irano-Turanian region. So far, our phylogenetic trees of the *S. orientalis* group are not yet sufficiently conclusive with respect to species-level relationships of the Central Asian taxa such as *S. altaica* and *S. supina* L. (Fig. 2, 6), but this is likely to be resolved with a more extensive molecular character set.

The genus *Scutellaria* appears to be a N hemisphere group, from which several lineages migrated south, once to Africa (*S. schweinfurthii* and relatives) and at least two times to South America (Fig. 6) within clade C (*S.* subg. *Scutellaria* as defined in this study). The patterns are very similar to other temperate genera (e.g. *Pinguicula* L., *Lentibulariaceae*; Cieslack & al. 2005), where a southward migration also occurred from ancestors in Central America and SE North America. On the other hand, there are E Asian as well as North American species groups that appear rather unrelated to the lineages that gave rise to the Central and South American taxa, and these may be explained by recent migration in the N hemisphere via Beringia. A dense taxon sampling of *S.* subg. *Scutellaria* is needed to reveal the biogeographic history and test if there are other hitherto unrecognized migration events to South America. *Scutellaria* subg. *Anaspis* as defined here represents a Eurasian lineage that is centred in the E Mediterranean, SW Asia and the Caucasus and may have diversified to Central Europe in the west and the Himalaya in the east.

Implications for a phylogeny-based infrageneric classification

Based on phylogenetic evidence and the evolution of morphological characters, an infrageneric classification system of the genus *Scutellaria* with more than two subgenera will be necessary in order to make these monophyletic. The current taxon sampling entails three major clades, A, B and C, with *S.* subg. *Scutellaria* largely paraphyletic to *S.* subg. *Apeltanthus* (Fig. 1). The core of clade A is formed by *S.* subg. *Apeltanthus*, and one option could be to extend the circumscription of this subgenus to clade A. *Scutellaria orbicularis* was designated as the type species of *S.* sect. (and subg.) *Apeltanthus* by Paton (1990a), but its position in the molecular phylogenetic tree is yet to be determined. The disadvantage of such a treatment based on the current phylogenetic results would be that there would be no synapomorphic morphological character state. The situation is not only complicated by the hitherto unresolved phylogenetic position of *S. pontica* but also by the position of a lineage of *S. baicalensis* and relatives (*S.* subg. *Scutellaria* sect. *Scutellaria*) among the earliest branches of clade A, which contains species that are more similar to the E Asian taxa in clade C in terms of the morphological characters investigated here (Fig. 4–6). Any formal infrageneric treatment therefore needs to await a much more comprehensive phylogenetic analysis that can test which other species potentially belong to this E Asian lineage within clade A and examine the evolution of further morphological characters (e.g. of nutlets). Based on the current results, the African *S. schweinfurthii* lineage, which deviates morphologically from the core of clade A, could also be classified at subgeneric rank. However, the specific life form (Fig. 6) may not suffice as a synapomorphy, because there seems to be some variability in potential close allies of the '*S. violascens* species-group' not yet sampled here.

The core of *Scutellaria* sect. *Anaspis* falls within clade B, so that there is a name at subgeneric rank for this clade. *Scutellaria* subg. *Anaspis* was accepted by Wu & Li (1977) and Rechinger (1982), and the type species is *S. fedtschenkoi* Bornm. (see Paton 1990a). Although previous authors argued for the consistency of the section based on morphology, and several taxa are included at least in our *trnL-F* tree (Fig. 2), there are yet no sequence data available for *S. fedtschenkoi*. Additional sequencing needs to confirm that this species falls within clade B to support eventual acceptance of the name *S.* subg. *Anaspis* in a wider circumscription of this clade. Paton (1990b) also mentioned that nutlet anatomy links the '*S. albida* species-group' to *S.* sect. *Anaspis*. Altough *S.* sect. *Stachymacris*. would match clade B, there is no validation of this name at subgeneric rank. Therefore, the name *S.* subg. *Anaspis* will have priority when formally classifying clade B at subgeneric level in the future.

Scutellaria subg. *Scutellaria* would have to be limited to clade C through a narrower circumscription, and *S. galericulata* as the type species is included in our phylogeny. A majority of species in this clade seems to possess unspecialized inflorescences (character 7 state 4), which are therefore clearly resolved as an ancestral state of clade C (Fig. 4). However, because raceme-like inflorescences with opposite and secund flowers, which are consistently present in clade B, are reconstructed to have also evolved in parallel in a terminal lineage within clade A (e.g. *S. indica*, *S. ovata*), there is no actual synapomorphy among the currently investigated morphological characters.

Author contributions

The study was designed by R.S. and T.B. Field and herbarium work as well as the identification of plant material and the assessment of morphological character states was mostly done by R.S. with smaller contributions by G.P. and T.B. The molecular dataset was generated and analysed by R.S. with help from T.B. and with technical support in the lab. T.B. processed the GBOL data. All authors contributed to the text and approved the final version of the manuscript.

Acknowledgements

We gratefully acknowledge Dr. James C. Solomon and Dr. James S. Miller, Missouri Botanical Garden, for providing samples from many relevant specimens and for their help during a visit by R.S. Dr. Chun-Lei Xiang, Kunming Institute of Botany, Chinese Academy of Sciences, sent us plastid sequences of *Holmskioldia* and *Wenchengia* even before they were published as well as photos of Chinese *Scutellaria* species. We thank Prof. Dr. Valida Alizade and Dr. Esmira Alirzayeva for support as focal and local coordinators of the project "Developing tools for conserving the plant diversity of the South Caucasus" funded by the VolkswagenStiftung (AZ85021 and AZ89950). The sequence data for the *Scutellaria* samples from Germany were generated at the Botanic Garden and Botanical Museum Berlin (BGBM) in the context of the German Barcode of Life GBOL5 Project (Botany) funded by the German Federal Ministry of Education and Research (BMBF) under FKZ01LI1101E and FKZ01LI1501E. R.S. appreciates the many years of support and mentoring from Prof. Dr. Alizade, which was very important for the successful implementation of this project. Thanks are due to the herbarium and lab staff at the BGBM, in particular Bettina Giesicke, Kim Govers and Peter Hein, and to Nicholas Turland for insightful discussions regarding various aspects of nomenclature, classification and historical literature. We acknowledge various kinds of help and scientific discussion during the implementation of this project by Dr. Ramazan Murtazaliyev (Makhachkala), Prof. Dr. Ahmed Ouhammou (Marrakech), Prof. Dr. Mostafa Assadi (Tehran), Prof. Dr. Komiljon Tojibaev (Tashkent) and Dr. Valery Tikhomirov (Minsk). The insightful comments by Dr. Dmitry Geltman (Saint Petersburg) and Dr. Alan Paton (Kew), who reviewed an earlier version of this paper, are greatly appreciated.

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Supplemental content online

See https://doi.org/10.3372/wi.51.51307

Appendix S1. Chronology and comparison of infrageneric taxonomy of *Scutellaria* proposed by different authors. Subgenera are bold and underlined, sections are bold and italic, lower ranks are only italic.

Appendix S2. Matrix of morphological characters.

Annotated alignments in Nexus format for *matK-trnK-psbA* (dataset A), *rpl16* (dataset A), *trnL-F* (dataset A) and *trnL-F* (dataset B).

Willdenowia
Open-access online edition bioone.org/journals/willdenowia
Online ISSN 1868-6397 · Print ISSN 0511-9618 · 2020 Journal Impact Factor 0.985
Published by the Botanic Garden and Botanical Museum Berlin, Freie Universität Berlin

Appendix 1. Voucher information for phylogenetic analyses and ENA/GenBank accession numbers. The first bloc lists specimens from which sequences were newly generated in this investigation and incudes the respective DNA bank (DB) numbers as well as the DNA lab code (Scu). The second bloc includes sequences of *Scutellaria* that were downloaded from ENA/GenBank. In most cases a voucher specimen could be found in the respective publication and is indicated in the voucher column. The corresponding publications are [1]Wang & al. (2012), [2]Jiang & al. (2017), [3]Safikhani & al. (2017), [4]Safikhani & al. (2018), [5]Chen & Zhang (2019), [6]Seyedipour & al. (2020), [7]Zhao & al. (2020) and [8]Shan & al. (2021). In some cases, mostly of complete plastid genomes, only an entry in ENA/GenBank could be found without actual publication and voucher citation. These were [a]Song & Park (2015), [b]Zhang & Handy (2016), [c]Cai (2020), [d]Huang (2020), [e]Li & al. (2020) and [f]Zhang (2020).

Code	DB No.	Taxon name	Field / garden origin	Voucher	*rpl16*	*trnL-F*	*matK-trnK-psbA*
Scu079	DB 45045	*Scutellaria adenostegia* Briq.	Tajikistan, Region of Republican Subordination	*Kudratov & Halimov TJP 0098* (MO 6269857)	OV140701	OV139433	OV140631
Scu012	DB 45003	*S. albida* subsp. *colchica* (Rech. f.) J. R. Edm.	BG Berlin 010-11-15-40 [Georgia, Ratcha-Letkhumi, *Gröger & al. 231-8*]	*Gartenherbarbeleg 50260* (B 10 0627137)	OV140663	OV139396	OV140593
Scu007	DB 44998	*S. alpina* L.	France, Hautes-Alpes	*Dürbye 1834* (B 10 0080357)	OV140659	OV139392	OV140589
Scu080	DB 45046	*S. altaica* Ledeb. ex A. Spreng	Kazakhstan, Markakolskyi Rayon	*Solomon 20530* (MO 6704111)	OV140702	OV139434	OV140632
Scu003	DB 11295	*S. altissima* L.	Germany, Sachsen-Anhalt	*Hand 8028* (B 10 0705125)	OU991554	OU991559	OU991605
Scu039	DB 45030	*S. bornmuelleri* subsp. *mianensis* Rech. f.	Iran, East Azerbaijan	*Rechinger 42258* (B)	OV140686	OV139419	OV140616
Scu006	DB 44997	*S. columnae* All.	Greece, Thessalia	*Willing 229771* (B 100502145)	OV140658	OV139391	OV140588
Scu073	DB 45039	*S. columnae* All. subsp. *columnae*	Greece, Karditsa	*Willing 142024* (B)	OV140695	OV139427	OV140625
Scu010	DB 45001	*S. costaricana* H. Wendl.	BG Berlin 136-15 74-83 [Central America]	*Gartenherbarbeleg 14968* (B)	OV142134	OV142135	OV142809 *trnK/matK* OV146697 *psbA-trnK*
Scu008	DB 44999	*S. cypria* subsp. *elatior* (Meikle) Hand	Cyprus, Limassol	*Hand 4680* (B 10 0270416)	OV140660	OV139393	OV140590
Scu034	DB 45025	*S. cypria* subsp. *elatior* (Meikle) Hand	Cyprus, Paphos	*Alziar & al. 1072* (B)	OV140682	OV139415	OV140612
Scu082	DB 45048	*S. dependens* Maxim.	Japan, Tohoku	*Kurosawa (4121)* (MO 4365808)	OV140704	OV139436	OV140634
Scu014	DB 45005	*S. diffusa* Benth.	BG Berlin 246-23-81-10 [Turkey, Hatay]	*Ern & Krone 6923* (B)	OV140665	OV139398	OV140595
Scu081	DB 45047	*S. discolor* Wall. ex Benth.	China, Yunnan	*Xiang 438* (MO 6422059)	OV140703	OV139435	OV140633
Scu001	DB 11293	*S. galericulata* L.	Germany, Bayern	*Hand 7750* (B 10 0628676)	OU991552	OU991557	OU991603
Scu002	DB 11294	*S. galericulata* L.	Germany, Sachsen-Anhalt	*Hand 8025* (B 10 0705468)	OU991553	OU991558	OU991604
Scu024	DB 45015	*S. galericulata* L.	Armenia	*Böcker 121* (B 10 0846889)	OV140675	OV139408	OV140605
Scu084	DB 45050	*S. glabrata* Vved.	Uzbekistan, Djirzak	*Haydarov 00357* (MO 6716106)	OV140706	OV139438	OV140636
Scu106	DB 45072	*S. grandiflora* Sims	Russia, Altay	*Skvortsov* (MO 4254449)	OV140726	OV139458	OV140656
Scu029	DB 45020	*S. grossheimiana* Juz.	Azerbaijan, Lerik, on road to Zuvand	*Salimov & Safarov RSA 0417* (BAK)	OV140680	OV139413	OV140610
Scu046	DB 45036	*S. grossheimiana* Juz.	Azerbaijan, around Lerik dist. on road to Zuvand	*Salimov RSA 1717* (BAK)	OV140692	OV139424	OV140622

Scu004	DB 11296	*S. hastifolia* L.	Germany, Hessen	*Buttler 31510* (B 10 0628240)	OU991555	OU991560	OU991606
Scu083	DB 45049	*S. heydei* Hook. f.	Kashmir India	*Koelz 5840* (MO 1213523)	OV140705	OV139437	OV140635
Scu104	DB 45070	*S. incana* Spreng.	U.S.A., Missouri	*Smith & Leary 4309* (MO 04860322)	OV140724	OV139456	OV140654
Scu013	DB 45004	*S. incarnata* Vent.	BG Berlin 136-31-74-83 [Colombia]	*Gartenherbarbeleg 3983* (B)	OV140664	OV139397	OV140594
Scu086	DB 45052	*S. indica* L.	Hong Kong	*Hu & But 21983* (MO 5330876)	OV140708	OV139440	OV140638
Scu103	DB 45069	*S. integrifolia* L.	U.S.A., Maryland	*Longbottom 25274* (MO 6855778)	OV140723	OV139455	OV140653
Scu087	DB 45053	*S. intermedia* Popov	Tajikistan	*Yunusov & Karimova 9984* (MO 5201896)	OV140709	OV139441	OV140639
Scu085	DB 45051	*S. kotkaiensis* Rech. f.	Afghanistan, Khost	*Rechinger 35615* (MO 3486755)	OV140707	OV139439	OV140637
Scu074	DB 45040	*S. leptosiphon* Nevski	Afghanistan, Mazari-Sharif	*Rechinger 34114* (B)	OV140696	OV139428	OV140626
Scu075	DB 45041	*S. linearis* Benth.	Pakistan, Kohat	*Rechinger 30260* (B)	OV140697	OV139429	OV140627
Scu088	DB 45054	*S. litwinowii* Bornm. & Sint.	Turkmenistan	*Kurbanov 73* (MO 5346660)	OV140710	OV139442	OV140640
Scu089	DB 45055	*S. luteocoerulea* Bornm. & Sint.	Turkmenistan	*Kurbanov 303* (MO 5576701)	OV140711	OV139443	OV140641
Scu090	DB 45056	*S. mesostegia* Juz.	Kyrgyzstan, Jalal-Abad oblast	*Osborne 481* (MO 6140318)	OV140712	OV139444	OV140642
Scu099	DB 45065	*S. mexicana* (Torr.) A. J. Paton	U.S.A., Nevada	*Gust & al. 3308* (MO 6860275)	OV140719	OV139451	OV140649
Scu005	DB 11297	*S. minor* Huds.	Germany, Hessen	*Borsch 5828* (B 10 1154557)	OU991556	OU991561	OU991607
Scu023	DB 45014	*S. novorossica* Juz.	Russia, Krasnodarskiy Kray	*Raab-Straube & al. 6724* (B 10 0520163)	OV140674	OV139407	OV140604
Scu102	DB 45068	*S. nummulariifolia* Hook. f.	Argentina, Tierra del Fuego	*Torres & al. 1061* (MO 6600353)	OV140722	OV139454	OV140652
Scu011	DB 45002	*S. orientalis* L.	Azerbaijan, Ganja	*Parolly & al. 13009a* (B)	OV140662	OV139395	OV140592
Scu015	DB 45006	*S. orientalis* L.	Armenia, Gegharkunik	*Fayvush & al. 62* (B 10 0483729)	OV140666	OV139399	OV140596
Scu016	DB 45007	*S. orientalis* L.	Armenia, Gegharkunik	*Gröger & Schuhwerk 612* (B 10 0483211)	OV140667	OV139400	OV140597
Scu017	DB 45008	*S. orientalis* L.	Armenia, Vayotsdzor	*Fayvush & al. 2170* (B 10 0040838)	OV140668	OV139401	OV140598
Scu018	DB 45009	*S. orientalis* L.	Armenia, Ararat	*Gröger & Schuhwerk 1331* (B 10 0476736)	OV140669	OV139402	OV140599
Scu020	DB 45011	*S. orientalis* L.	Georgia, Tsagveri-Borjomi	*Agababyan & Parolly s.n.* (B 10 0479729)	OV140671	OV139404	OV140601
Scu021	DB 45012	*S. orientalis* L.	Georgia	*Parolly 15096* (B 10 0518047)	OV140672	OV139405	OV140602
Scu022	DB 45013	*S. orientalis* L.	Russia, Stavropolskiy Kray	*Borsch & al. 5786* (B 10 0719129)	OV140673	OV139406	OV140603
Scu025	DB 45016	*S. orientalis* L.	Russia, Karachay-Cherkessia	*Borsch & al. 5804* (B 10 0719164)	OV140676	OV139409	OV140606
Scu026	DB 45017	*S. orientalis* L.	Russia, Krasnodarskiy Kray	*Raab-Straube & al. 6844* (B 10 0520155)	OV140677	OV139410	OV140607

Code	**DB No.**	**Taxon name**	**Field / garden origin**	**Voucher**	***rpl16***	***trnL-F***	***matK-trnK-psbA***
Scu019	DB 45010	*S. orientalis* subsp. *karjaginii* Grossh.	Armenia, Vayotsdzor	*Gröger & Schuhwerk 1638* (B 10 0476439)	OV140670	OV139403	OV140600
Scu036	DB 45027	*S. ovata* Hill	U.S.A., Georgia, Walker County	*Smith 248* (B)	OV140683	OV139416	OV140613
Scu093	DB 45059	*S. peregrina* L.	Yemen, Ibb Governate	*Spellenberg 7235* (MO 05017038)	OV140715	OV139447	OV140645
Scu092	DB 45058	*S. physocalyx* Regel & Schmalh.	Tajikistan	*Strizhova 6501* (MO 5201894)	OV140714	OV139446	OV140644
Scu009	DB 45000	*S. pinnatifida* subsp. *mucida* (Stapf) Rech. f.	Iran, East Azerbaijan, Maraghah	*Taeb 35326* (B 10 0270085)	OV140661	OV139394	OV140591
Scu091	DB 45057	*S. poecilantha* Nevski ex Juz.	Tajikistan	*Strizhova 3550* (MO 5201893)	OV140713	OV139445	OV140643
Scu042	DB 45032	*S. pontica* K. Koch	BG Berlin 150-24-14-10 [Georgia, Gomismta]	*Parolly & al. 14200* (B photos)	OV140688	OV139420	OV140618
Scu028	DB 45019	*S. prilipkoana* Grossh.	Azerbaijan, Lerik, Zuvand, on road to Kalvaz village	*Salimov & Safarov RSA 0317* (BAK)	OV140679	OV139412	OV140609
Scu030	DB 45021	*S. prilipkoana* Grossh.	Azerbaijan, Lerik, on road to Mistan village from Hiveri	*Salimov & Safarov RSA 0517* (BAK)	OV140681	OV139414	OV140611
Scu047	DB 45037	*S. prilipkoana* Grossh.	Azerbaijan, Lerik, the road crossing of Diviagac and Pirasora villages	*Salimov RSA 1817* (BAK)	OV140693	OV139425	OV140623
Scu048	DB 45038	*S. prilipkoana* Grossh.	Azerbaijan, Lerik, around Gosmalian village	*Salimov RSA1917* (BAK)	OV140694	OV139426	OV140624
Scu105	DB 45071	*S. resinosa* Torr.	U.S.A., Oklahoma	*Freeman & Loing 16947* (MO 6377762)	OV140725	OV139457	OV140655
Scu038	DB 45029	*S. rupestris* Boiss. & Heldr.	Greece, Arkadia	*Willing 118505* (B)	OV140685	OV139418	OV140615
Scu094	DB 45060	*S. scandens* D. Don	Nepal, Gandaki zone	*Suzuki & al. 9470244* (MO 6192463)	OV140716	OV139448	OV140646
Scu037	DB 45028	*S. schweinfurthii* subsp. *paucifolia* (Baker) A. J. Paton	Sierra Leone, Loma	*Jaeger 8823* (B)	OV140684	OV139417	OV140614
Scu098	DB 45064	*S. schweinfurthii* subsp. *paucifolia* (Baker) A. J. Paton	Zambia	*Harder & al. 1945* (MO 05054043)	OV140718	OV139450	OV140648
Scu101	DB 45067	*S. scutellarioides* (Kunth) Harley	Ecuador, Loja	*Lewis & al. 2269* (MO 5723138)	OV140721	OV139453	OV140651
Scu076	DB 45042	*S. stocksii* Boiss.	Afghanistan, Kabul	*Rechinger 16997* (B)	OV140698	OV139430	OV140628
Scu095	DB 45061	*S. supina* L.	Mongolia, Altay	*Kamelin 1581* (MO 5824432)	OV140717	OV139449	OV140647
Scu027	DB 45018	*S. tournefortii* Benth.	Azerbaijan, Lankaran, Khanbulan	*Salimov & Safarov RSA 1117* (BAK)	OV140678	OV139411	OV140608
Scu043	DB 45033	*S. tournefortii* Benth.	Azerbaijan, Lankaran, Parakand village	*Salimov RSA0117* (BAK)	OV140689	OV139421	OV140619
Scu044	DB 45034	*S. tournefortii* Benth.	Azerbaijan, on 25 km of road Lankaran-Lerik	*Salimov RSA0217* (BAK)	OV140690	OV139422	OV140620
Scu045	DB 45035	*S. tournefortii* Benth.	Azerbaijan, Lankaran	*Mehdiyeva* (BAK)	OV140691	OV139423	OV140621

Scu040	DB 45031	*S. tuvensis* Juz.	Russia, Tuva	*Timokhina & Sakowicz 6593* (B)	OV140687	–	OV140617
Scu100	DB 45066	*S. volubilis* Kunth	Ecuador, Loja	*Lewis 2256* (MO 5723133)	OV140720	OV139452	OV140650
Scu077	DB 45043	*Tinnea aethiopica* Kotschy ex Hook. f.	Tanzania, Kilimanjaro	*Kindeketa & al. 2935* (MO 5993071)	OV140699	OV139431	OV140629
Scu078	DB 45044	*Tinnea galpinii* Briq.	South Africa, Mpumalanga	*Bester 8769* (MO 6342308)	OV140700	OV139432	OV140630
		Scutellaria albida L. subsp. *albida*	Iran, Kurdistan	*Safikhani 20038* (TARI)		[4]LC384604	
		S. albida subsp. *condensata* (Rech. f.) J. R. Edm.	Iran, Kurdistan	*Safikhani 105477* (TARI)		[4]LC384597	
		S. albida subsp. *pycnotricha* (Rech. f.) Jamzad & Safikhani	Iran, Kurdistan	*Safikhani 105480* (TARI)		[4]LC384617	
		S. albida subsp. *subsimilis* (Rech. f.) Jamzad & Safikhani	Iran, Kermanshah	*Safikhani 105476* (TARI)		[4]LC384601	
		S. altaica Ledeb. ex A. Spreng	China, Xinjiang, Xinyuan	*Zhang & al. 17CS16318* (KUN)		[7]MN128387	
		S. amoena C. H. Wright	China, Yunnan	*ZDQ17067* (Herbarium Dali University)	[5]MN165116	[5]MN165116	[5]MN165116
		S. amoena C. H. Wright	China	–		[1]JN675930	
		S. amphichlora Juz.	Iran, West Azerbaijan	*Assadi & al. 68834* (TARI)		[4]LC384600	
		S. arakensis Jamzad & Safikhani	Iran, Markazi	*Safikhani 105204* (TARI)		[3]LC306902	
		S. araxensis Grossh.	Iran, West Azerbaijan	*Safikhani 105467* (TARI)		[4]LC384608	
		S. ariana Hedge	Iran, Hormozgan	*Mozaffarian 58730* (TARI)		[4]LC384622	
		S. baicalensis Georgi	China, Heilongjiang	*BOP028265* (CMMI)	[2]MF521632	[2]MF521632	[2]MF521632
		S. barbata D. Don	China	–		[e]MW376479	
		S. bornmuelleri subsp. *mianensis* Rech. f.	Iran, East Azerbaijan	*Safikhani 105470* (TARI)		[4]LC384614	
		S. calcarata C. Y. Wu & H. W. Li	China, Yunnan, Gongshan	*Li & al. NJ023* (KUN)	[7]MN128385	[7]MN128385	[7]MN128385
		S. chamaedrifolia Hedge & A. J. Paton	Pakistan, Khyber Pakhtunkhwa (Swat)	*Lamond 30629* (TARI)		[4]LC384627	
		S. chorassanica Bunge	Iran, Khorasan	*Assadi & al. 84839* (TARI)		[4]LC384619	
		S. farsistanica Rech. f.	Iran, Isfahan	*Safikhani 105474* (TARI)		[4]LC384616	
		S. farsistanica Rech. f.	Iran, W-Qashqai, Kuhruyeh,	*Rechinger 47342* (B)		[6]MT265267	
		S. fragillima Rech. f.	Iran, Fars	*Mozaffarian 83613* (TARI)		[4]LC384621	
		S. franchetiana H. Lév.	China	–	[e]MW376478	[e]MW376478	[e]MW376478
		S. galericulata L.	Iran, Kurdistan	*Maroufi & al. 3611* (TARI)		[4]LC384620	
		S. glechomoides Boiss. ex Benth.	Iran, N Elbruz	*Bornmüller 8048* (B)		[6]MT265268	
		S. glechomoides Boiss. ex Benth.	Iran, Tehran	*Mozaffarian 78291* (TARI)		[4]LC384599	
		S. immaculata Nevski ex Juz.	Uzbekistan, Tianschan	*Vatolkina 6757* (B)		[6]MT265263	

Code	DB No.	Taxon name	Field / garden origin	Voucher	***rpl16***	***trnL-F***	***matK-trnK-psbA***
		S. insignis Nakai	Korea	–	[a]NC028533	[a]NC028533	[a]NC028533
		S. kingiana Prain	China, Xizang, Cuona	*Yang & al. ZJW-3890* (KUN)	[7]MN128389	[7]MN128389	[7]MN128389
		S. lateriflora L.	?	–	[b]KY085900	[b]KY085900	[b]KY085900
		S. leptosiphon Nevski	Afghanistan, Mazar-e Sharif	*Rechinger, 16220* (B)		[6]MT265264	
		S. linearis Benth.	Pakistan, Khyber Pakhtunkhwa (Kohat)	*Rechinger 30260* (TARI)		[4]LC384624	
		S. linearis Benth.	Afghanistan, Khost	*Rechinger 35513* (B)		[6]MT265270	
		S. litwinowii Bornm. & Sint.	Iran, Khorasan	*Rechinger 51098* (B)		[6]MT265271	
		S. litwinowii Bornm. & Sint.	Iran, Khorasan	*Assadi & al. 35409* (TARI)		[4]LC306897	
		S. luteocaerulea Bornm. & Sint.	Iran, Khorasan	*Assadi & al. 50809* (TARI)		[4]LC384619	
		S. meehanioides C. Y. Wu	China	–	[f]MW381011	[f]MW381011	[f]MW381011
		S. megalaspis Rech. f.	Iran, Kurdistan	*Safikhani 105478* (TARI)		[4]LC384615	
		S. megalaspis Rech. f.	Iraq	*Rechinger 10866* (B)		[6]MT265287	
		S. mollifolia C. Y. Wu & H. W. Li	China, Sichuan, Emei	*Chen & al. EM201* (KUN)	[7]MN128384	[7]MN128384	[7]MN128384
		S. multicaulis Boiss. subsp. *multicaulis* var. *multicaulis*	Iran, Chaharmahal-o-Bakhtiari	*Mohebbi 91626* (TARI)		[4]LC306899	
		S. multicaulis var. *gandomanensis* Jamzad & Safikhani	Iran, Chaharmahal-o-Bakhtiari	*Assadi 72391* (TARI)		[3]LC306900	
		S. nepetifolia Benth.	Iran, Hamedan	*Safikhani 105464* (TARI)		[4]LC384612	
		S. orientalis L.	Turkey, A8, Murgul-Damar Koyu	*Duzenli 756* (TARI)		[4]LC384625	
		S. orthocalyx Hand.-Mazz.	China, Yunnan	*Zhao & al. ZF035* (KUN)	[7]MN128383	[7]MN128383	[7]MN128383
		S. patonii Jamzad & Safikhani	Iran, Chaharmahal-o-Bakhtiari	*Mohebbi 91621* (TARI)		[4]LC306901	
		S. persica Bornm.	Iran, Markazi	*Safikhani K 105472* (TARI)		[4]LC306896	
		S. pinnatifida subsp. *mucida* (Stapf) Rech. f.	Iran, Zanjan	*Foroughi 1500* (TARI)		[4]LC384607	
		S. pinnatifida subsp. *pichleri* (Stapf) Rech. f.	Iran, Hamedan	*Mozaffarian 64562* (TARI)		[4]LC384606	
		S. pinnatifida A. Ham. subsp. *pinnatifida*	Iran, Kermanshah	*Safikhani 105473* (TARI)		[4]LC384594	
		S. platystegia Juz.	Iran, West Azerbaijan	*Safikhani 105466* (TARI)		[4]LC384602	
		S. platystegia Juz.	Iran, Azerbaijan	*Ghahraman 7697* (TUH)		[6]MT265278	
		S. przewalskii Juz.	China, Xinjiang, Aletai	*Chen & al. YC_ZX027* (KUN)	[7]MN128382	[7]MN128382	[7]MN128382
		S. przewalskii Juz.	Kyrgyzstan, Tianschan	*Durbay 1755* (B)		[6]MT265279	
		S. quadrilobulata Y. Z. Sun	China, Yunnan, Xinping	*Li & al. XP965* (KUN)	[7]MN128381	[7]MN128381	[7]MN128381

S. rehderiana Diels	China	–	[c]MT982397	[c]MT982397	[c]MT982397
S. rehderiana Diels	China	–		[1]JN675928	
S. scordifolia Fisch. ex Schrank	?	–		[d]NC052883	
S. sosnowskyi Takht.	Iran, West Azerbaijan	*Assadi & al. 30187* (TARI)		[4]LC384598	
S. squarrosa Nevski	Turkmenistan	*Proskuryakova s.n.* (TARI)		[4]LC384623	
S. stocksii Boiss.	Iran	*Anonymous 30348* (TUH)		[6]MT265265	
S. stocksii Boiss.	Afghanistan, Kabul	*Rechinger 16997* (TARI)		[4]LC384626	
S. tomentosa Bertol.	Iran, Isfahan	*Safikhani 105471* (TARI)		[4]LC384610	
S. tournefortii Benth.	Iran, Gilan	*Safikhani 105479* (TARI)		[4]LC384611	
S. tsinyunensis C. Y. Wu & S. Chow	China, Chongqing	*20200320-CQ1* (SW Univ. Chongqing)	[8]NC_050161	[8]NC_050161	[8]NC_050161
S. tuberifera C. Y. Wu & C. Chen	China	*20200320-CQ1* (SW Univ. Chongqing)		[8]MW376477	
S. velutina Juz. & Vved.	Tajikistan	*Tsvetkova s.n.* (TARI)		[4]LC384628	
S. virens Boiss. & Kotschy	Iran, East Azerbaijan	*Safikhani 105468* (TARI)		[4]LC384605	
S. viscidula Bunge	China	–		[1]JN675929	
S. xylorrhiza Bornm.	Iran, Isfahan	*Safikhani 105475* (TARI)		[4]LC384603	
Ajuga reptans L.			KF709391	KF709391	KF709391
Galeopsis tetrahit L.			NC_036968	NC_036968	NC_036968
Holmskioldia sanguinea Retz.			HQ911720	HQ911720	HQ911720
Lamium album L.			NC_036971	NC_036971	NC_036971
Lamium galeobdolon (L.) L.			NC_036972	NC_036972	NC_036972
Leonurus japonicus Miq.			NC_038062	NC_038062	NC_038062
Mentha longifolia (L.) L.			NC_032054	NC_032054	NC_032054
Mentha spicata L.			NC_037247	NC_037247	NC_037247
Prunella vulgaris L.			NC_039654	NC_039654	NC_039654
Salvia przewalskii Maxim.			NC_041091	NC_041091	NC_041091
Salvia rosmarinus Spenn.			KR232566	KR232566	KR232566
Stachys sylvatica L.			NC_029824	NC_029824	NC_029824
Teucrium mascatense Boiss.			MH325132	MH325132	MH325132
Teucrium stocksianum Boiss. subsp. *stocksianum*			MH325133	MH325133	MH325133
Wenchengia alternifolia C. Y. Wu & S. Chow			JX893339	JX893339	JX893339