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

Rashad A. Salimov1, Gerald Parolly2 & Thomas Borsch2

Version of record first published online on 23 December 2021 ahead of inclusion in December 2021 issue.

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. Apelanthus, 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. Apelanthus, 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 (Mentisky 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 & Ketenoglu (2011) and S. yildirimlii Çiçek & Yaprak

1 Institute of Botany, Azerbaijan National Academy of Sciences, Baku, Badamdar highway 40, AZ 1004, Azerbaijan.
2 Botanischer Garten und Botanisches Museum Berlin, Freie Universität Berlin, Königin-Luise-Str. 6–8, 14195 Berlin, Germany.
Author for correspondence: Rashad Salimov, resad_selimov@yahoo.com
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 hemicycrophytes, 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 infragenic classification of *Scutellaria* began with Hamilton (1832), who subdivided the genus into three sections (S. sect. *Lupulinaria*, S. sect. *Stachy- macris* 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 ros- sica*. Bentham (1834) added two new sections, S. sect. *Heteranthesia* Benth. (species with spirally arranged flowers) and S. sect. *Mischalostachys* Benth. (species with axillary inflorescences). He essentially maintained this sectional classification in his treatment for Candelole’s *Prodomus* (Bentham 1848) while adding several subordinate groups. Later, Bentham (1876) merged S. sect. *Galericularia* and S. sect. *Stachy- macris* 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 two sections, S. sect. *Lupulinaria* and S. sect. *Vulgares*, dividing the latter section into three unranked groups.

Briet (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. *Scutellariop- sis* 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 infrage- neric 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.) 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. *Apelanthus* Nevski ex Juz., S. sect. *Cystas- pis* Juz., S. sect. *Lupulinaria* and S. sect. *Vulgares*. In two cases, he derived the name from the former genera *Anaspis* Rech. f. and “*Apelanthus* 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. *Apelanthus* (Nevski ex Juz.) Juz. and S. subg. *Cystas- pis* (Juz.) Juz., which were mainly based upon the characteristics of upper lip of the calyx. In his classification, Juzepczuk (1954) placed S. sect. *Lupuli- naria* (with S. subsect. *Alpinae* Juz., S. subsect. *Fru- ticosae* 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 infragenic classification of *Scutellaria* was proposed by Paton (1990b). He rec- ognized the two subgenera, S. subg. *Scutellaria* and S. subg. *Apelanthus*, with five and two sections, respec- tively, based on a phenetic analysis of a spectrum of morphological characters. The chronology of the infragenic taxonomy of *Scutellaria* is shown in Appendix S1 in Supplemental content online.

The Caucasus ecoregion and the Irano-Turanian re- gion 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. colpolea* 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) and 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. ser. Perilomia* (Kunth) Epling), and *Harlanlevisia* Epling with a unique synapomorphy in the gynoeceum (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; Bendiksky & 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. 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. Lupulinaria*.
naria subsect. Lupulinaria in their ITS tree, whereas the trnL-F tree depicted a polytomy with S. stocksii Boiss. (S. sect. Apelantathus). 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. baicalesis Georgi, and recently Zhao & al. (2020) published sequences of plastid genomes of eight further Scutellaria species from China as well as Holmskioldia, Timnea 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. Apelantathus; 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 leaf 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 (Isaev 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. Apelantathus, including subsections and informal groups. We further included the remaining lineages of Scutellarioideae, the monotypic genera Holmskioldia and Wenchengia, and Timnea 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 Ajugaideae (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; Seydipour & 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 MgCl₂, and 23.7 µl ultrapure H₂O 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 + LAM-trnK724R (5′-AATTCGATTTGACTGTATCCG-3′) + ACmatK1400R (5′-CTTGGTTGTGACTGATC-3′) + ACmatK500F + LAMmatK1450R (5′-CTGTTGTATGAAATCTATCCC-3′) and LAMmatK1260F (5′-AAGAGTTTGATGCAATAGAAG-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 et 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′-GAAATT-GCAGTGTGTAATGCGG-3′) and LAMrpl16R (5′-TCGTTGATGAAATCTATCC-3′) designed in this study. For some in shorter fragments using primers LAMrps3F + LAMrpl16-290R (5′-CTGTTGATGAAATCTATCC-3′) and LAMrpl16-140F (5′-CTGTTGATGAAATCTATCC-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 100x 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 toENA/GenBank using the script of Gruenstäudl (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.2.063 (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) values were performed in PAUP by conducting a heuristic search within a total number of 10000 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 Akaie 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 GTR+GAMMA 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. Lapulinaria* 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 from 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 (–CCTCTTGCATTGCGAGCAGTATT). 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 (HS1), 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.

| Dataset A (105 taxa) | Character | Length mean (S.D.) | Variable (%) | Informative (%) | Indels (%) | Variable (%) | Informative (%) | GC% | Model |
|----------------------|----------|--------------------|--------------|-----------------|------------|--------------|-----------------|-----|-------|
| 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) | Character | Length mean (S.D.) | Variable (%) | Informative (%) | Indels (%) | Variable (%) | Informative (%) | GC% | Model |
|----------------------|----------|--------------------|--------------|-----------------|------------|--------------|-----------------|-----|-------|
| 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. Timnea 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. heyderi Hook., 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 Bornn., S. grossheimiana Juz., S. pinnatifida A. Ham. and S. prilipoana 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. Salvijfoliae (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. scutellaroides (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. tsinymensis 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 (fruticosce 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) suffructicose 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. orientalis* 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, es- palier 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 hemicyryptophytes 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) cucul- late, 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 cuculate (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).
with its four subsections and the series in next to the name indicates taxa explicitly mentioned by Juzepczuk (1954) as members of S. orientalis group. An asterisk or, if not mentioned Orientales.

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. Scutellaria. 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. Orientalis 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: *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.
| Species | Collection Code |
|---------|----------------|
| S. grossheimiana | Scu029 AZE |
| S. prilipkoana | Scu030 AZE |
| S. grossheimiana | Scu046 AZE |
| S. prilipkoana | Scu047 AZE |
| S. alpina | Scu007 FRA |
| S. orientalis | Scu011 AZE |
| S. mesostegia | Scu016 ARM |
| S. orientalis | Scu018 ARM |
| S. bornmuelleri | Scu039 IRN |
| S. prilipkoana | Scu028 AZE |
| S. cf. orientalis | Scu025 RUS, Kar.-Cher. |
| S. orientalis | Scu022 RUS, Stavrop. |
| S. pinnatifida subsp. mucida | Scu009 IRN |
| S. orientalis | Scu019 ARM |
| S. orientalis | Scu017 ARM |
| S. physocalyx | Scu092 TJK |
| S. supina | Scu095 MNG |
| S. intermedia | Scu087 TJK |
| S. glabrata | Scu084 UZB |
| S. altaica | Scu080 KAZ |
| S. adenostegia | Scu079 TJK |
| S. grandiflora | Scu106 RUS |
| S. tuvensis | Scu040 RUS |
| S. luteocoerulea | Scu089 TKM |
| S. litwinowii | Scu088 TKM |
| S. heydei | Scu083 IND |
| S. linearis | Scu075 PAK |
| S. poecilantha | Scu091 TJK |
| S. cf. orientalis | Scu026 RUS, Krasn. |
| S. novorossica | Scu023 RUS, Krasn. |
| S. orientalis | Scu015 ARM |
| S. orientalis | Scu021 GEO |
| S. cf. orientalis | Scu020 GEO |
| S. peregrina | Scu093 YEM |
| S. pontica | Scu042 GEO |
| S. baicalensis | MF521632 CHN |
| S. stocksii | Scu076 AFG |
| S. leptosiphon | Scu074 AFG |
| S. cypria subsp. elatior | Scu034 CYP |
| S. cypria subsp. elatior | Scu008 CYP |
| S. schweinfurthii subsp. paucifolia | Scu098 ZMB |
| S. scutellarioides | Scu101 ECU |
| S. insignis | NC028533 KOR |
| S. discolor | Scu081 CHN |
| S. indica | Scu086 CHN |
| S. ovata | Scu036 USA |
| S. nummulariifolia | Scu102 ARG |
| S. resinosa | Scu105 USA |
| S. ovata | Scu038 USA |
| S. integrifolia | Scu103 USA |
| S. mexicana | Scu099 USA |
| S. ovata | Scu104 USA |
| S. volubilis | Scu100 ECU |
| S. incarnata | Scu101 ECU |
| S. costaricana | Scu100 C America |
| S. incarnata | Scu101 COL |
| S. scutellarioides | Scu101 ECU |

**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 Salazararia (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. Apelanthus 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. Apelanthus. 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. Apelanthus 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. Salvijoflæae as possible closest ancestors of S. subg. Apelanthus, which appear as one of the branches of our clade A and therefore among the closest relatives of S. subg. Apelanthus 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. Apelanthus (incl. S. orientalis, S. pinatifida, S. stocksi) 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. Apelanthus, due to the lack of sampling the African ’S. violascens species-group’ and other early-branching lineages in this clade such as S. baikalensis 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. Apelanthus) sister to a lineage composed of S. amoena, S. baikalensis 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. Apelanthus in line with our results.

**Evolution of selected morphological characters**

Inflorescences with decussately arranged flowers evolved in the core of clade A, in the common ancestor of Scutellaria sect. Lupulinaria and S. sect. Apelanthus (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. tsinyanensis*, 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. poeciliantha* (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. luteocoeurea* Borrn. & Sint., whereas the subclade with *S. heydei*, *S. kotakaiensis* Rech. f. and *S. linearis* Benth. evolved scutellate-inflated lips (in fruit), and testudinate lips evolved in parallel in *S. poeciliantha* 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 charts, 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 suffrutescent 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. schwefinfurthii*, 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
**Diels, sect.**

412 Salimov & al.: Phylogenetic relationships of clade A, followed by a lineage of Central to E Asian _paucifolia_, here represented by _Scutellaria_ group’ sensu Paton (1990b) of 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_. _rederiana_ Diels, _S_. _viscidula_ Bunge; Fig. 2) and _S_. sect. _Anaspis_ ( _S_. _kingiana_) and the Caucasian _S_. _pontica_ ( _S_. _Scutellariae_) in a tritomy. _Scutellaria_ sect. _Salviifoliae_ was considered as morphologically intermediate between _S_. _Apeltanthus_ and _S_. _Apeltanthus_ ( _S_. _Apeltanthus_ 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; _S_. 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_. _rederiana_. A detailed comparative study of nutlet morphology and anatomy will be relevant to test if 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. _Cystaspid_ ( _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_. _kotaiensis_ 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_. _luteocoele_ 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. _Lupulinaria_ subsect. _Fruticosae_, according to _Juzepczuk_ (1954) characterized as being subsburb 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_ 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 _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 com-
posed 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 Platystegea 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. Ramosisissimae. 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 un-interrupted 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. poceliana and the members of S. subsect. Cystasais appearing nested in S. subsect. Lupulinaria.

The Oxystegiae and Platystegea 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. Platystegea appear in all three lineages, and the only member of the Adenostegiae series (the second series of the Platystegea group) currently sampled (S. adenosetoga) is in the same lineage as the Mesostegiae and Pulchellae series. It is noteworthy that the members of Scutellaria subsection. 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. adenosetoga 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 several 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. mutilicaulis, 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. Taureac 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. alitissima and S. tournefortii (S. subg. Scutellaria sect. Scutellaria) and a core of species from S. subg. Scutellaria sect. Anaspis (S. ariana, S. fragilissima 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. alitissima 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 (Em 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. Sutellaria 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 Sutellaria, 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 (Jupezpaczuk 1954; Fig. 2), which represents one of the three sublineages of clade B.

Clade C

The phylogenetic position of Scutellaria sect. Perilonia, represented here by S. scutellarioides (type species of S. sect. Perilonia; 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. Perilonia by Paton (1990a) to include S. sect. Perilonia, 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. nummularifolia Hook. f. from Argentina (the only species of the ‘S. nummularifolia species-group’ sensu Panton (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 Hudon, and the 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. tsiyunnensis; 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), Mentitsky (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 oreoypes, indicating that specialisation 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; Seydipour & 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), Ranjarb & 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 (SAF105466, TARI image!), this plant appears with deeply pinnatifid, tomentose cauleine 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*. Although *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 second 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. Esmina 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 Asadi (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.

**References**

African Plant Database 2020–2021: African Plant Database, version 3.4.0. – Geneva: Conservatoire et Jardin botaniques de la Ville de Genève; Pretoria: South African National Biodiversity Institute. – Published at [https://www.ville-ge.ch/musinfo/bd/cjb/africa/index.php](https://www.ville-ge.ch/musinfo/bd/cjb/africa/index.php) [accessed 4 Oct 2020 and 12 Aug 2021].

Barniske A., Borsch T., Müller K., Krug M., Neinhuis C. & Quandt D. 2012: Phylogenetics of early branching...
Borsch, T., Berendsohn W. G., Dalcin E., Delmas M., Engelmann.

Borsch, T., Hilu K. W., Quandt D., Wilde V., Neinhuis C.

Borghese, V. 1848:

Bentham G. 1834: Scutellaria and Perilomia. – Pp. 419–446 in Labiatarum genera et species. – London: Ridgeway.

Bentham G. 1848: Labiatae. – Pp. 412–431 in: Candolle A. P. de (ed.), Prodrumus systematis naturalis regni vegetabilis 12. – Paris: Treuttel et Wurtz.

Bentham G. 1876: Scutellaria, Salazaria and Perilomia. – Pp. 1201–1203 in: Bentham G. & Hooker J. D., Genera plantarum 2. – London: Lovell Reeve & Co.

Billie L. T. & Delprete P. G. 1996: Nutlet sculpturing in Scutellaria sect. Resinosa (Lamiaceae) and its taxonomic utility. – Pl. Syst. Evol. 199: 109–120.

Boissier P. E. 1879: Scutellaria. – Pp. 681–691 in: Flora orientalis 4. – Genevae et Basileae: H. Georg.

Borsch, T., Berendsohn W. G., Dalcin E., Delmas M., Demissew S., Elliott A., Fritsch P., Fuchs A., Geltman D., Güner A., Haevermans T., Knapp S., le Roux M. M., Loizeau P.-A., Miller C., Miller J., Miller J. T., Palese R., Paton A., Parnell J., Pendry E., Qin H.-N., Sosa V., Sosef M., von Raab-Straube E., Ranwashe Çiçek M., Yaprak A. E. 2013: Scutellaria yildirimlii (Lamiaceae), a new species from Turkey. – Phytotaxa 132: 53–58.

Cieslack T., Polepalli J. S., White A., Müller K., Borsch T., Barthlott W., Steiger J., Marchant A. & Legendre L. 2005: Phylogenetic analysis of Pinguicula (Lentibulariaceae): chloroplast DNA sequences and morphology support several geographically distinct radiations. – Amer. J. Bot. 92: 1723–1736.

Darriba D., Taboada G. L., Doallo R. & Posada D. 2012: jModelTest2: more models, new heuristics and parallel computing. – Nature, Meth. 9: 772–772.

Edmondson J. 1982: Scutellaria. – Pp. 78–100 in: Davis P. H. (ed.), Flora of Turkey and the East Aegean Islands 7. – Edinburgh: Edinburgh University Press.

Ellenberg H. & Mueller-Dombois D. 1967: A key to Raunkiara plant life forms with revised subdivisions. – Ber. Geobot. Inst. E.T.H. Stiftung Rübel. 37: 56–73.

Epling C. 1942: American species of Scutellaria. – Univ. Calif. Publ. Bot. 20: 1–146. – Berkeley & Los Angeles: University of California Press.

Escobar B., Borsch T., Quedensley T. S. & Gruenstaeudl M. 2021: Plastid phylogenomics of the Gynoxoid group (Senecioneae, Asteraceae) highlights the importance of motif-based sequence alignment amid low genetic distances. – Amer. J. Bot. 108: 2235–2256.

Euro+Med 2006+ [continuously updated]: Euro+Med PlantBase – the information resource for Euro-Mediterranean plant diversity. – Published at http://www.euro-med.plantbase.org [accessed 4 Oct 2020].

Ezer N. & Renda G. 2012: Comparative morphological studies on Scutellaria salviifolia Benth. and Scutellaria diffusa Benth. (Lamiaceae) growing in Turkey. – FABAD J. Pharm. Sci. 37: 197–203.

Fedorov A. 1967: 4838. Scutellaria orientalis L. subsp. platystegia (Juz.) Fed. comb. nova. – Pp. 73–74 in: Schedae ad herbarium floriae URSS 17. – Leningrad: Nauka.

Flora Zambesiaca Managing Committee 1950+: Flora zambesiaca 1–45. – Richmond: Royal Botanic Gardens, Kew.
Gagnidze R. I. & Ivanishvili M. A. 1987: *Scutellaria* L. – Pp. 35–51 in: Gagnidze R. I. (ed.), Flora Georgia, ed. 2, 11. – Tbilisi: Metsniereba.

Geiger M. F., Astrin J. J., Borsch T., Burkhardt U., Grobe P., Hand R., Hausmann A., Hohberg K., Krogsman L., Lutz M., Monje C., Misof B., Morinière J., Müller K., Pietsch S., Quandt D., Rulik B., Scholler M., Traunspurger W., Haszprunar G. & Wägele W. 2016: How to tackle the molecular species inventory for an industrialized nation—lessons from the first phase of the German Barcode of Life initiative GBOL (2012–2015). – Genome 59: 1–10. [Crossref]

González-Gallegos J. G. & Vázquez-García J. A. 2013: *Scutellaria cuevasiana* and *Scutellaria sublitoralis* (*Lamiaceae*), two new species from Jalisco and Nayarit, Mexico. – Revista Mex. Biodivers. 84: 20–29. [Crossref]

Grierson A. J. C. & Long D. G. (ed.) 1983–2002: Flora of

Jamzad Z. 2013: A survey of

Jamzad Z. 2012:...
cally endangered genus. – Taxon 61: 392–401.

Li X. W. & Hedge I. 1994: Labiatae. – Pp. 50–299 in: Wu Z. Y. & Raven P. H. (ed.), Flora of China 17 (Verbenaceae through Solanaceae). – Beijing: Science Press; St. Louis: Missouri Botanical Garden Press.

Linnaeus C. 1753: Species plantarum. – Holmiae: Laurentii Salvii.

Löhne C. & Borsch T. 2005: Molecular evolution and phylogenetic utility of the petD group II Intron: a case study in basal angiosperms. – Molec. Biol. Evol. 22: 317–332.

Maddison W. P. & Maddison D. R. 2021: Mesquite: a modular system for evolutionary analysis. Version 3.70. – Published at http://www.mesquiteproject.org/

Manafzadeh S., Staedler Y. M. & Conti E. 2017: Visions of the past and dreams of the future in the Orient: the Irano-Turanian region from classical botany to evolutionary studies. – Biol. Rev. 92: 1365–1388.

Menitsky Y. L. 1987: Scutellaria. – Pp. 23–30 in: Tahtadzjan A. (ed.), Flora of Armenia 8. – Yerevan: Akademiia nauk Armianskoi SSR.

Menitsky Y. L. 1992: Synopsis of species of the family Lamiaceae (Labiatae) from the Caucasus. – Bot. Zhurn. (Moscow & Leningrad) 77(6): 63–78.

Müller K. F. 2004: PRAP—computation of Bremer support for large data sets. – Molec. Phylogen. Evol. 31: 780–782.

Müller K. F. 2005a: SeqState. Primer design and sequence statistics for phylogenetic DNA datasets. – Appl. Bioinf. 4: 65–69.

Müller K. F. 2005b: The efficiency of different search strategies in estimating parsimony jackknife, bootstrap, and Bremer support. – B.M.C. Evol. Biol. 5: 58.

Müller K. & Borsch T. 2005: Phylogenetics of Amaranthaceae based on matK/irnK sequence data—evidence from parsimony, likelihood, and Bayesian analyses. – Ann. Missouri Bot. Gard. 92: 66–102.

Müller K., Quandt D., Müller J. & Neinhuis C. 2010: Phylogenetics of Scutellaria (Lamiales). – Kew Bull. 65: 399–450.

Pagel M., Meade A. & Barker D. 2004: Bayesian estimation of ancestral character states on phylogenies. – Syst. Biol. 53: 673–684.

Paton A. 1990a: The phytogeography of Scutellaria L. – Notes Roy. Bot. Gard. Edinburgh 46: 345–359.

Popov N. P. 1916: Labiatae [Ajuga — Marrubium]. – In: Kuznetsov N., Busch N. & Fomin A. (ed.), Flora caucasica critica. Materialy dlya floy Kavkaz. Kriticheskoe sistematicheskoe-geograficheskoe izsledovanie 4(3) (No. 43, 45). – Yur’ev: Tipografiya K. Mattisen.

Raunkiaer C. 1934: The life forms of plants and statistical plant geography: being the collected papers of C. Raunkiaer. – Oxford: The Clarendon Press.

Rechinger K. H. 1982: Scutellaria L. – Pp. 48–84 in: Rechinger K. H. (ed.), Flora iranica 150. – Graz: Akademische Druck- und Verlagsanstalt.

Ronquist F., Teslenko M., Mark P. van der, Ayres D. L., Darling A., Höhna S., Larteg B., Liu L., Suchard M. A. & Huelsenbeck J. P. 2012: MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. – Syst. Biol. 61: 539–542.

Safikhani K., Jamzad Z. & Saeidi H. 2018: A taxonomic revision of Scutellaria sect. Lupulinaria (Lamiaceae) based on nuclear ribosomal ITS and chloroplast trnL-F DNA data. – Pl. Syst. Evol. 304: 1077–1089.

Salmi Y. & Müller J. 2019: Rediscovery of the enigmatic Scutellaria xylorrhiza (Scutellariaeae; Lamiaeae)—a rare endemic species from Iran. – Phytotaxa 394: 267–275.

Schäferhoff B., Fleischmann A., Fischer E., Albach D. C., Borsch T., Heubö G. & Müller K. F. 2010: Towards resolving Lamiales relationships: insights from rapidly evolving chloroplast sequences. – B.M.C. Evol. Biol. 10: 352.

Seyedipour S., Salmi Y. & Xiang C.-L. 2020: Molecular phylogeny of Scutellaria (Lamiaceae; Scutellarioidae) in Iranian highlands inferred from nrITS and trnL-F sequences. – Progr. Biol. Sci. 7: 169–181.

Shan Y.-Y., Pei X.-Y., Yong S.-Y., Li J.-L., Qin Q.-L., Zeng S.-Y. & Yu J. 2021: Analysis of the complete chloroplast genomes of Scutellaria tsinyunensis and
Scutellaria tubifera (Lamiaceae). – Mitochondrial DNA Part B 6: 2672–2680. Crossref.
Shaw J., Lickey E. B., Beck J. T., Farmer S. B., Liu W.-S., Miller J., Siripun K. C., Winder C. T., Schilling E. E. & Small R. L. 2005: The tortoise and the hare II: relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. – Amer. J. Bot. 92: 142–166. Crossref.
Silakadze N., Kilian N., Korotkova N., Mosulishvili M. & Borsch T. 2019: Multiple evolutionary origins of high mountain bellflowers with solitary flowers and calyx scales render a core Caucasian clade of the Scapiflorae group (Campanulaceae). – Syst. Biodivers. 17: 690–711. Crossref.
Simmons M. P. & Ochoterena H. 2000: Gaps as characters in sequence-based phylogenetic analyses. – Syst. Biol. 49: 369–381. Crossref.
Stamatakis A. 2014: RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. – Bioinformatics 30: 1312–1313. Crossref.
Stöver B. C. & Müller K. F. 2010: TreeGraph 2: combining and visualizing evidence from different phylogenetic analyses. – B.M.C. Bioinf. 11: 7. Crossref.
Stamatakis A. 2014: RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. – Bioinformatics 30: 1312–1313. Crossref.
Stöver B. C. & Müller K. F. 2010: TreeGraph 2: combining and visualizing evidence from different phylogenetic analyses. – B.M.C. Bioinf. 11: 7. Crossref.
Stamatakis A. 2014: RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. – Bioinformatics 30: 1312–1313. Crossref.
Stöver B. C. & Müller K. F. 2010: TreeGraph 2: combining and visualizing evidence from different phylogenetic analyses. – B.M.C. Bioinf. 11: 7. Crossref.
Stamatakis A. 2014: RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. – Bioinformatics 30: 1312–1313. Crossref.
Stöver B. C. & Müller K. F. 2010: TreeGraph 2: combining and visualizing evidence from different phylogenetic analyses. – B.M.C. Bioinf. 11: 7. Crossref.
Taberlet P., Gielly L., Pautou G. & Bouvet J. 1991: Universal primers for amplification of three non-coding chloroplast DNA regions of land plants. – Pl. Molec. Biol. 17: 1105–1109. Crossref.
Ter-Chatschaturova S. Ya. 1967: Scutellaria L. – Pp. 308–322 in: Grossheim A. A., Flora Kavkaza, ed. 2, 7, – Leningrad: Nauka.
Volókova P., Laczkó L., Demina O., Schanzer I. & Sennikov A. N., Lazkov G. A., Litvinskaya S. A., Gabrielian E., Borsch T. & Raab-Straube E. von 2019: Phylogeny of the Eurasian genus Jurinea (Asteraceae: Cardueae): support for a monophyletic genus concept and a first hypothesis on overall species relationships. – Taxon 68: 112–131. Crossref.
Wagstaff S. J. & Olmstead R. G. 1997: Phylogeny of Labiatae and Verbenaceae inferred from rbcL sequences. – Syst. Bot. 22: 165–179. Crossref.
Wang X.-G., Hai M.-R. & Liu T. 2012: Analysis of trnL-F sequences of the medicinal plants Scutellaria baicalensis and its adulterants. – Chin. Agric. Sci. Bull. 28: 173–177.
Weberling F. 1989: Morphology of flowers and inflorescences. – Cambridge: Cambridge University Press.
Wickel S. & Quandt D. 2009: Universal primers for the amplification of the plastid trnK(matK) region in land plants. – Anales Jard. Bot. Madrid 66: 285–288. Crossref.
Worberg A., Quandt D., Barniske A.-M., Löhne C., Hilu K. W. & Borsch T. 2007: Phylogeny of basal eudicots: insights from non-coding and rapidly evolving DNA. – Org. Divers. Evol. 7: 55–77. Crossref.
World Flora Online 2019: World Flora Online. – Published at http://www.worldfloraonline.org/ [accessed 10 Nov 2019].
Wu C. Y. & Li H. W. 1977: Scutellaria. – Pp. 124–248 in: Flora Reipublicae Popularis Sinicae 65(2). – Beijing: Science Press.
Zarucchi J. L. & Harley R. M. 1993: Lamiaceae. – Pp. 579–590 in: Zarucchi J. L. & Brako L. (ed.), Catalogue of the flowering plants and gymnosperms of Peru. – Monogr. Syst. Bot. Missouri Bot. Gard. 45. – St. Louis: Missouri Botanical Garden Press.
Zhao F., Li B., Drew B. T., Chen Y.-P., Wang Q., Yu W.-B., Liu E.-D., Salmaki Y., Peng H. & Xiang C.-L. 2020: Leveraging plastomes for comparative analysis and phylogenomic inference within Scutellarioideae (Lamiaceae). – PLoS ONE 15(5): e0232602. Crossref.
Zhao F., Liu E.-D., Peng H. & Xiang C.-L. 2017: A new species of Scutellaria (Scutellarioideae, Lamiaceae) from Sichuan Province in southwest China. – Peer J. 5: e3624. Crossref.

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).

Wildenowia
Open-access online edition bioone.org/journals/wildenowia
Online ISSN 1866-6397 · Print ISSN 0511-9618 · 2020 Journal Impact Factor 0.985
Published by the Botanic Garden and Botanical Museum Berlin, Freie Universität Berlin
© 2021 The Authors · This open-access article is distributed under the CC BY 4.0 licence
### 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 includes 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 Chen & Zhang (2019), 5 Seyedinpop & al. (2020), 6 Zhao & al. (2020) and 7 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                        | rp16     | trnL-F | matK-trnK-psbA |
|----------|--------|-----------------------------------------|--------------------------------------------|--------------------------------|----------|--------|----------------|
| Scu079   | DB 45045 | *Scutellaria adenostegia* Briq.          | Tajikistan, Region of Republican Subordination | Kudratov & Hallinov TJP 0098 (MO 6269857) | OV140701 | OV139433 | OV140631 |
| Scu012   | DB 45003 | *S. albida* subsp. colchica (Reich. f.) J. R. Edm. | BG Berlin 010-11-15-40 [Georgia, Ratcha-Letikhumi, Gröger & al. 231-8] | Gartenherbarbeleg 50260 (B 10 0627137) | OV140663 | OV139396 | OV140593 |
| Scu007   | DB 44998 | *S. alpina* L.                          | France, Hautes-Alpes                       | Dürrye 1834 (B 10 0080357) | OV140659 | OV139392 | OV140589 |
| Scu080   | DB 45046 | *S. altaica* Ledeb. ex A. Spreng        | Kazakhstan, Markakolskyi Rayon            | Solomon 20530 (MO 6704411) | OV140702 | OV139434 | OV140632 |
| Scu003   | DB 11295 | *S. altissima* L.                       | Germany, Sachsen-Anhalt                   | Hand 8028 (B 10 0705125) | U0991554 | U0991559 | U0991605 |
| Scu039   | DB 45030 | *S. boranuelleri* 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 136-1574-83 [Central America]   | Gartenherbarbeleg 14968 (B) | OV142134 | OV142135 | OV142809 |
| Scu008   | DB 44999 | *S. cypria* subsp. elatior (Meikle) Hand | Cyprus, Limassol                          | Hand 6408 (B 10 0270416) | OV140660 | OV139393 | OV140590 |
| Scu034   | DB 45025 | *S. cypria* subsp. elatior (Meikle) Hand | Cyprus, Paphos                            | Alistar & 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]    | Erm & 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) | U0991552 | U0991557 | U0991603 |
| Scu002   | DB 11294 | *S. galericulata* L.                    | Germany, Sachsen-Anhalt                   | Hand 8025 (B 10 0705468) | U0991553 | U0991558 | U0991604 |
| Scu024   | DB 45015 | *S. galericulata* L.                    | Armenia                                   | Böcker 121 (B 10 0846889) | OV140675 | OV139408 | OV140605 |
| Scu084   | DB 45050 | *S. glabrata* Vved.                     | Uzbekistan, Dzirzak                       | Haydanov 00357 (MO 6716106) | OV140706 | OV139438 | OV140636 |
| Scu106   | DB 45072 | *S. grandiflora* Sims                   | Russia, Altai                             | 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 |
| 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 16.88 (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 72.35 (MO 05017038) | OV140715 | OV139447 | OV140645     |
| Scu092 | DB 45058 | *S. physocalyx* Regel & Schmalh.    | Tajikistan                                     | Strizhova 6501 (MO 5201894)   | OV140714 | OV139446 | OV140644     |
| Scu099 | DB 45000 | *S. pinnatifida* subsp. *mucida* (Stapf) Rech. f. | Iran, East Azerbaijan, Maragha | Taub 33526 (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, Gomisnta]    | Parolly & al. 14200 (B photos) | OV140688 | OV139420 | OV140618     |
| Scu028 | DB 45019 | *S. prilipkova* Grossh.             | Azerbaijan, Lerik, Zavand, on road to Kalvaz village | Salimov & Safarov RSA 0317 (BAK) | OV140679 | OV139412 | OV140609     |
| Scu030 | DB 45021 | *S. prilipkova* Grossh.             | Azerbaijan, Lerik, on road to Mistan village from Hiveri | Salimov & Safarov RSA 0517 (BAK) | OV140681 | OV139414 | OV140611     |
| Scu047 | DB 45037 | *S. prilipkova* Grossh.             | Azerbaijan, Lerik, the road crossing of Divigac and Pirasora villages | Salimov RSA 1817 (BAK)        | OV140693 | OV139425 | OV140623     |
| Scu048 | DB 45038 | *S. prilipkova* Grossh.             | Azerbaijan, Lerik, around Gosmalian village   | Salimov RSA 1917 (BAK)        | OV140694 | OV139426 | OV140624     |
| Scu105 | DB 45071 | *S. resinoso* Torr.                 | U.S.A., Oklahoma                               | Freeman & Loing 16947 (MO 6377762) | OV140725 | OV139457 | OV140655     |
| Scu038 | DB 45029 | *S. rupetris* Boiss. & Heldr.       | Greece, Arkadia                                | Willing 118505 (B)            | OV140685 | OV139418 | OV140615     |
| Scu094 | DB 45060 | *S. scandens* D. Don               | Nepal, Gandaki zone                            | Suzuki & al. 947024 (MO 6192463) | OV140716 | OV139448 | OV140646     |
| Scu037 | DB 45028 | *S. schweinfurthii* subsp. *pauticola* (Baker) A. J. Paton | Sierra Leone, Loma | Jaeger 8823 (B)          | OV140684 | OV139417 | OV140614     |
| Scu098 | DB 45064 | *S. schweinfurthii* subsp. *pauticola* (Baker) A. J. Paton | Zambia | Harder & al. 1945 (MO 05054043) | OV140718 | OV139450 | OV140648     |
| Scu101 | DB 45067 | *S. scutellariorum* (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, Khanbahan               | Salimov & Safarov RSA 1117 (BAK) | OV140678 | OV139411 | OV140608     |
| Scu043 | DB 45033 | *S. tournefortii* Benth.            | Azerbaijan, Lankaran, Parakand village        | Salimov RSA 0117 (BAK)        | OV140689 | OV139421 | OV140619     |
| Scu044 | DB 45034 | *S. tournefortii* Benth.            | Azerbaijan, on 25 km of road Lankaran-Lerik   | Salimov RSA 0217 (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**

| Scu040 | DB 45031 | S. albida | L. subsp. albida | Iran, Kurdistan | Safikhani 20038 (TARI) 4 LC384604 |
| Scu100 | DB 45066 | S. albida | subsp. condensata (Rech. f.) | Iran, Kurdistan | Safikhani 105477 (TARI) 4 LC384617 |
| Scu077 | DB 45043 | S. albida | subsp. pycnotricha (Rech. f.) Jamzad & Safikhani | Iran, Kurdistan | Safikhani 105480 (TARI) 4 LC384610 |
| Scu078 | DB 45044 | S. albida | subsp. subsimilis (Rech. f.) Jamzad & Safikhani | Iran, Kermanshah | Safikhani 105476 (TARI) 4 LC384614 |
| Scu148 | DB 45078 | S. altaica | Ledeb. ex A. Spreng | China, Xinjiang, Xinyuan | Zhang & al. 17CS16318 (KUN) 7 MN128387 |
| Scu149 | DB 45081 | S. amoena | C. H. Wright | China – | ZDQ17067 (Herbarium Dali University) 5 MN165116 |
| Scu150 | DB 45082 | S. amphichlora | Juz. | Iran, West Azerbaijan | Assadi & al. 68834 (TARI) 4 LC384619 |
| Scu151 | DB 45083 | S. arakensis | Jamzad & Safikhani | Iran, Markazi | Safikhani 105204 (TARI) 3 LC306902 |
| Scu152 | DB 45084 | S. araxensis | Grossh. | Iran, West Azerbaijan | Safikhani 105467 (TARI) 4 LC384608 |
| Scu153 | DB 45085 | S. ariana | Hedge | Iran, Hormozgan | Mozaffarian 58730 (TARI) 4 LC384622 |
| Scu154 | DB 45086 | S. baicalensis | Georgi | China, Heilongjiang | BOP028265 (CMMI) 2 MF521632 |
| Scu155 | DB 45087 | S. barbata | D. Don | China | – |
| Scu156 | DB 45088 | S. bornmuelleri | subsp. mianensis Rech. f. | Iran, East Azerbaijan | Safikhani 105470 (TARI) 4 LC384614 |
| Scu157 | DB 45089 | S. calcarata | C. Y. Wu & H. W. Li | China, Yunnan | Li & al. NJ023 (KUN) 7 MN128385 |
| Scu158 | DB 45090 | S. chamaedrifolia | Hedge & A. J. Paton | Pakistan, Khyber Pakhtunkhwa (Swat) | Lamond 30629 (TARI) 4 MT36254 |
| Scu159 | DB 45091 | S. chorassanica | Bunge | Iran, Khorasan | Assadi & al. 84839 (TARI) 4 LC384624 |
| Scu160 | DB 45092 | S. farsistanica | Rech. f. | Iran, Isfahan | Safikhani 105474 (TARI) 4 LC384621 |
| Scu161 | DB 45093 | S. farsistanica | Rech. f. | Iran, W-Qashqai, Kuhruyeh, Rechinger 47342 (B) 6 MT265267 |
| Scu162 | DB 45094 | S. fragillima | Rech. f. | Iran, Fars | Mozaffarian 83613 (TARI) 4 LC384621 |
| Scu163 | DB 45095 | S. franchetiana | H. Lév. | China – | – |
| Scu164 | DB 45096 | S. galericulata | L. | Iran, Kurdistan | Maroufi & al. 3611 (TARI) 4 LC384620 |
| Scu165 | DB 45097 | S. glechomoides | Boiss. ex Benth. | Iran, N Elbruz | Bornmüller 8048 (B) 6 MT265268 |
| Scu166 | DB 45098 | S. glechomoides | Boiss. ex Benth. | Iran, Tehran | Mozaffarian 78291 (TARI) 4 LC384619 |
| Scu167 | DB 45099 | S. immaculata | Nevski ex Juz. | Uzbekistan, Tianshan | Vatolkina 6757 (B) 6 MT265263 |
| Scu168 | DB 45100 | S. minor | Ledeb. | Russia, Tuva | – |
| Scu169 | DB 45101 | S. velutina | K. | Ecuador, Loja | Lewis 2256 | (MO 5723133) OV140720 OV139452 OV140650 |
| Scu170 | DB 45102 | S. verticillata | K. | Tanzania, KwaZulu-Natal | Marouf & al. 3611 (TARI) 4 LC384620 |
| Scu171 | DB 45103 | T. aethiopica | Kotschy ex Hook. f. | Tanzania, Kilimanjaro | Kindeketa & al. 2935 | (MO 5993071) OV140699 OV139431 OV140629 |
| Scu172 | DB 45104 | T. galpinii | Briq. | South Africa, Mpumalanga | Bester 8769 | (MO 6342308) OV140700 OV139432 OV140630 |

Downloaded From: https://bioone.org/journals/Willdenowia on 25 Feb 2022
Terms of Use: https://bioone.org/terms-of-use
| Code       | DB No. | Taxon name               | Field / garden origin              | Voucher      | rpl16           | trnL-F         | matK-trnK-psbA |
|------------|--------|--------------------------|------------------------------------|--------------|-----------------|----------------|----------------|
| S. insignis Nakai |       | Korea                    | Yang & al. ZJW-3890 (KUN)          | *NC02853     | *NC02853        | *NC02853       |
| S. kingiana Prain |       | China, Xizang, Cuona     |                                       | MN128389     | MN128389        | MN128389       |
| S. lateriflora L. |       | ?                        | Rechinger 16220 (B)                 | *KY085900    | *KY085900       | *KY085900     |
| S. leptosiphon Neviski |    | Afghanistan, Mazar-e Sharif | Rechinger 30260 (TARI)             | MT265264     |                 |               |
| S. linearis Benth. |       | Pakistan, Khyber Pakhtunkhwa (Kohat) | Rechinger 35513 (B) | MT265270 |                 |               |
| S. linearis Benth. |       | Afghanistan, Khost       | Rechinger 51098 (B)                | MT265271     |                 |               |
| S. litvinovii Bornm. & Sint. |   | Iran, Khorasan           | Assadi & al. 35409 (TARI)          | LC306897     |                 |               |
| S. litvinovii Bornm. & Sint. |   | Iran, Khorasan           | Assadi & al. 50809 (TARI)          | LC384619     |                 |               |
| S. luteoacraulea Bornm. & Sint. |   | China                    | –                                   | MW381011     | MW381011        | MW381011      |
| S. meehanoides C. Y. Wu |   | Iran, Kurdistan           | Safikhani 105478 (TARI)            | LC384615     |                 |               |
| S. megalaspsis Rech. f. |   | Iraq                     | Rechinger 10866 (B)                | MT265287     |                 |               |
| S. moleifolia C. Y. Wu & H. W. Li | | China, Sichuan, Emei    | Chen & al. EM201 (KUN)              | MN128384     | MN128384        | MN128384      |
| S. multicaulis Boiss. subsp. multicaulis var. multicaulis | | Iran, Chaharmahal-o-Bakhtiari | Mohabb 91626 (TARI)                | LC306899     |                 |               |
| S. multicaulis var. gandomanensis Jamzad & Safikhani | | Iran, Chaharmahal-o-Bakhtiari | Assadi 72391 (TARI)                | LC306900     |                 |               |
| S. nepetfolia Benth. |       | Iran, Hamedan             | Safikhani 105464 (TARI)            | LC384612     |                 |               |
| S. orientalis L. |        | Turkey, A8, Murgul-Damar Koyu | Duzenli 756 (TARI)  | LC384625     |                 |               |
| S. orthocaulx. Hand.-Mazz. |         | China, Yunnan             | Zhao & al. ZF015 (KUN)              | MT265283     |                 |               |
| S. patonii Jamzad & Safikhani |   | Iran, Chaharmahal-o-Bakhtiari | Mohabbi 91621 (TARI)              | LC306901     |                 |               |
| S. persica Bornm. |        | Iran, Markazi             | Safikhani K 105472 (TARI)          | LC306896     |                 |               |
| S. pinnatifida subsp. mucida (Stapf) Rech. f. | | Iran, Zanjan              | Fonoughi 1500 (TARI)               | LC384607     |                 |               |
| S. pinnatifida subsp. pichleri (Stapf) Rech. f. | | Iran, Hamedan             | Mozaffarian 64562 (TARI)           | LC384606     |                 |               |
| S. pinnatifida A. Ham. subsp. pinnatifida | | Iran, Kemanshah           | Safikhani 105473 (TARI)            | LC384594     |                 |               |
| S. platystegia Juz. |       | Iran, West Azerbaijan     | Safikhani 105466 (TARI)            | LC384602     |                 |               |
| S. platystegia Juz. |       | Iran, Azerbaijan          | Ghahraman 7697 (TUH)               | MT265278     |                 |               |
| S. przewalskii Juz. |       | China, Xinjiang, Aletai   | Chen & al. YC_Z027 (KUN)           | MT265279     |                 |               |
| S. przewalskii Juz. |       | Kyrgyzstan, Tianschan     | Durbay 1755 (B)                    | MT265279     |                 |               |
| S. quadrilobulata Y. Z. Sun | | China, Yunnan, Xinping    | Li & al. XP965 (KUN)               | MN128381     | MN128381        | MN128381      |
| Species                                    | Collection Details                          | Accession Numbers |
|--------------------------------------------|---------------------------------------------|-------------------|
| *S. rehderiana* Diels                      | China                                        | MT982397          |
| *S. spongiosa* Fisch. ex Schrank           |                                              |                   |
| *S. squarrosa* Nevek.                     | Iran, West Azerbaijan                        |                   |
| *S. stockei* Boiss.                       | Arab.                                        |                   |
| *S. terebrata* Bentol.                    | Iran, Gilan                                  |                   |
| *S. terebrata* C. Y. Wu & S. Chow         | China, Beijing                               |                   |
| *S. tuberifera* C. Y. Wu & C. Chen        |                                              |                   |
| *S. velutina* Juz. & Vved.                 | Tajikistan                                   |                   |
| *S. xylorrhiza* Bornm.                    | Iran, Isfahan                                |                   |
| *H. sarahitzii* Retz.                     |                                              |                   |
| *G. tetrahit* L.                          |                                              |                   |
| *H. longifolius* Miq.                     |                                              |                   |
| *M. japonicus* L.                         |                                              |                   |
| *M. longifolia* L.                        |                                              |                   |
| *M. spicata* L.                           |                                              |                   |
| *M. spicata* L.                           |                                              |                   |
| *S. przewalskii* Maxim.                   |                                              |                   |
| *S. rosmarinus* Spenn.                    |                                              |                   |
| *S. sylvatica* L.                         |                                              |                   |
| *T. mascatense* Boiss. subsp.              |                                              |                   |
| *T. stocksianum* Boiss.                   |                                              |                   |
| *W. alternifolia* C. Y. Wu & S. Chow     |                                              |                   |
| *A. reptans* L.                           |                                              |                   |
| *G. tetrahit* L.                          |                                              |                   |
| *H. longifolius* Miq.                     |                                              |                   |
| *M. japonicus* L.                         |                                              |                   |
| *M. longifolia* L.                        |                                              |                   |
| *M. spicata* L.                           |                                              |                   |
| *S. przewalskii* Maxim.                   |                                              |                   |
| *S. rosmarinus* Spenn.                    |                                              |                   |
| *S. sylvatica* L.                         |                                              |                   |
| *T. mascatense* Boiss. subsp.              |                                              |                   |
| *T. stocksianum* Boiss.                   |                                              |                   |
| *W. alternifolia* C. Y. Wu & S. Chow     |                                              |                   |

Downloaded From: https://bioone.org/journals/Willdenowia on 25 Feb 2022
Terms Of Use: https://bioone.org/terms-of-use