PhytoKeys 196: 1–20 (2022)
doi: 10.3897/phytokeys.196.79566
https://phytokeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

Taxonomic delimitation and molecular identification of clusters within the species *Zanthoxylum nitidum* (Rutaceae) in China

Yunrui Qin[1], Renchuan Hu[1], Hui Zhao[1,3],
Guiyuan Wei[1], Zhiqiang Lu[2], Yunfeng Huang[1,4]

1 *Guangxi Institute of Chinese Medicine and Pharmaceutical Sciences, Nanning 530022, Guangxi, China* **2** *CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, Yunnan, China* **3** *Guangdong Provincial Key Laboratory of Biotechnology for Plant Development, School of Life Sciences, South China Normal University, Guangzhou, 510631, China* **4** *Guangxi Key Laboratory of Traditional Chinese Medicine Quality Standards, Nanning 530022, Guangxi, China*

Corresponding authors: Yunfeng Huang (huangyunfeng2000@126.com), Zhiqiang Lu (luzhiqiang@xtbg.ac.cn)

Academic editor: Hanno Schaefer | Received 20 December 2021 | Accepted 22 April 2022 | Published 12 May 2022

Citation: Qin Y, Hu R, Zhao H, Wei G, Lu Z, Huang Y (2022) Taxonomic delimitation and molecular identification of clusters within the species *Zanthoxylum nitidum* (Rutaceae) in China. PhytoKeys 196: 1–20. https://doi.org/10.3897/phytokeys.196.79566

Abstract

Zanthoxylum nitidum, known as Liang-Mian-Zhen in China, is a traditional Chinese medicinal plant used to treat traumatic injury, rheumatism, paralysis, toothache, stomach ache, and venomous snake bites. Two varieties of the species have been described and three morphological types have been reported within the original variety. However, taxonomic delimitation and molecular markers for distinguishing these varieties and types within this species remain unknown. Since different populations exhibit varying chemical compositions, easy identification of intraspecific taxa is crucial. We collected 420 individuals from 38 natural populations, 3 samples of standard medicinal material, and 17 folk-medicine samples to perform classification and identification within *Zanthoxylum nitidum*. Four distinct genetic clusters (A, B, C, and D) were highly supported by the nuclear barcode. Two distinct chloroplast clusters (A1 and A2) were further detected within A, and three others had one-to-one correspondence with the remaining nuclear clusters. Molecular identification showed that the 17 folk samples comprised A1, A2, B, and D, while the 3 standard samples belonged to A2. The internal transcribed spacer (ITS) region and *rbc*L gene are proposed as barcodes for rapid and accurate identification of the different Liang-Mian-Zhen lineages in China. This study highlights the importance of accurate taxonomic delimitation in combination with rapid and accurate molecular identification of medicinal plants.

Copyright *Yunrui Qin et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Keywords
Classification and identification, Liang-Mian-Zhen, medicinal materials, taxonomic delimitation

Introduction

Medicinal plants are widely used in clinical medications, daily chemical products, and food and drink products in China, and play an important role in people's daily life (Zhu et al. 1983; Hawkins 2008; Bansal et al. 2018; Lu et al. 2020). With the increase in human population and the decrease in natural medicinal resources in recent decades, the market demand for cultivated medicinal plants has been expanding (Zhou and Wu 2006; Hawkins 2008; Techen et al. 2014). Moreover, many substitutes are being used, although their active ingredients are distinctly different from conventionally used substances (Sui et al. 2011; Chao et al. 2014; Dubey and Sawant 2015; Qin et al. 2019). Generally, the active ingredients of any substance are considered to be related to different genetic (or morphological) clusters or species (e.g., Cirak et al. 2007, 2013; Chao et al. 2014; Fan et al. 2015). In our previous study, such a phenomenon was observed among strains within the medical plant Z*anthoxylum nitidum* (Qin et al. 2019). Nine populations covering four morphological clusters were compared and significant differences among the chemical ingredients (e.g., nitidine chloride) were discovered. This suggests that not all *Z. nitidum* proveniences are equally suitable for medicinal use and the identification of intraspecific taxa is crucial.

Zanthoxylum nitidum, known as Liang-Mian-Zhen (两面针) in China, differs from congeneric species in terms of the characteristics of its perianth in two series, 4-merous flowers, 4-carpelled gynoecia, axillary and terminal inflorescences (thyrsiform) pedicel length (rarely reaching 1 cm in fruits), fruit follicles (to 0.9 cm and containing neither prickles nor trichomes), outer part of pericarp (not wider than endocarp), leaflet blades (without oil glands along secondary veins), and leaflet apex retuse (at the tip). Besides the typical variety (*Z. nitidum* var. *nitidum*), a second variety, *Z. nitidum* var. *tomentosum*, has been accepted (Hartley 1966; Editorial Committee of Flora 1997; Zhang et al. 2008; Chinese Pharmacopoeia Commission 2020). Three morphological types have also been proposed for *Z. nitidum* var. *nitidum* (Editorial Committee of Flora 1997). A recent study reported that morphological boundaries between varieties or types within this species should be re-evaluated based on prickle appearance and the density of prickles on the trunk (Qin et al. 2019). In total, the morphological taxonomy of Chinese Liang-Mian-Zhen is disordered owing to the abundance of phenotypic variations and the use of different taxonomic methods (Editorial Committee of Flora 1997; Zhang et al. 2008; Qin et al. 2019). Hence, taxonomic delimitation within the medicinal plant Liang-Mian-Zhen in China remains controversial and more work is needed to disentangle its intraspecific structure.

Molecular identification is widely used in the authentication of medicinal plants (representing a morphological or genetic cluster) [Guo et al. 2013; Chao et al. 2014;

Chen et al. 2015; Osathanunkul et al. 2016; Xin et al. 2018]. Short sequences from a standardized position of the genome are aligned and compared with a known DNA barcode reference library to identify the taxa to which a sample belongs (Chen et al. 2015; Liu et al. 2018). In contrast to traditional taxonomy, there are many advantages to molecular identification using DNA barcodes, such as objectivity, speed, and accuracy, making it more suitable for forensic applications (Chao et al. 2014; Chen et al. 2015). Ideally, an unknown sample can be identified as a specific species – usually as a genetic cluster or lineage – using its DNA barcode sequences based on a reliable reference library (Liu et al. 2018). In practice, before DNA barcode reference libraries are constructed, initial identification based on morphological traits is presupposed to be accurate (Chen et al. 2015). Thus, if taxonomic boundaries of closely related taxa are unresolved, inaccurate reference libraries will be produced, thereby impairing unbiased identification (Liu et al. 2018). Many case studies have reflected this phenomenon in which the taxonomic results based on morphological and molecular evidence are highly inconsistent with traditional taxonomic results (Hu et al. 2015; Su et al. 2015; Lu et al. 2021). Thus, genetic classification using short sequences with high discrimination power, along with the use of barcodes as critical markers for accurate identification, can greatly improve the accuracy of further molecular identification.

Liang-Mian-Zhen is traditionally used in Chinese medicine to treat traumatic injury, rheumatism, paralysis, toothache, stomach ache, and venomous snake bites (Yang and Chen 2008; Feng et al. 2011; Chinese Pharmacopoeia Commission 2020). Many active ingredients are extracted from this species, including nitidine chloride, chelerythrine, ethoxychelerythrine sanguinarium chloride, allocryptopine, and neoherculin (Qin et al. 2019). Owing to its antiviral, anti-inflammatory, analgesic, and antifungal effects, Liang-Mian-Zhen is widely used in the production of daily chemical products (e.g., toothpaste) and clinical medication (e.g., Sanjiuweitai capsules and Liang-Mian-Zhen Zhen Tong tablets); as such, a large number of Liang-Mian-Zhen materials are consumed every year in China (Yang and Chen 2008; Feng et al. 2011; Lu et al. 2020; Qin et al. 2020). However, Liang-Mian-Zhen classification is still controversial in China. Previous studies have shown that DNA barcodes based on nuclear and chloroplast barcodes have large differentiation between strains within Z. *nitidum* (Chen et al. 2013; Ma et al. 2014). Hence, DNA barcodes should be considered as molecular markers to delimit boundaries of different strains within Liang-Mian-Zhen.

In the present study, we conducted extensive sampling of the natural populations of Liang-Mian-Zhen in China, collected standard samples from China Resources Sanjiu, a large state-owned pharmaceutical company, and visited indigenous communities in different geographical regions to obtain folk medicinal samples. Our aim was to establish a standard for the resource classification and identification of Chinese Liang-Mian-Zhen, which will provide a guide for quality, safety, and efficacy during the utilization of medicinal materials. To this end, we asked the following questions: (1) How many genetic clusters can be delimited within this species in China based on nuclear and chloroplast barcodes? (2) Which is the most suitable taxonomic scenario among those currently available? (3) Which barcodes have high discrimination power and are suitable for intraspecific classification and identification of Liang-Mian-Zhen clusters? (4) Which clusters do the Liang-Mian-Zhen used by indigenous people belong to?

Material and methods

Sample collection and specimen identification

We consulted the specimen records of *Z. nitidum* (including two varieties) available in the Chinese Virtual Herbarium (CVH, http://www.cvh.ac.cn/) and also examined all specimens of this species deposited in GXMI of Guangxi Institute of Chinese Medicine and Pharmaceutical Sciences and IBSC of South China Botanical Garden, CAS. Then, we conducted extensive sampling across its whole distribution range in China according to the consulted specimen records to collect enough samples for genetic analyses. All sampled individuals of the same population were spaced more than 50 m apart. Fresh leaves were collected for DNA sequencing and immediately placed in plastic sealed bags with sufficient silica gel to avoid DNA degradation. We also took photos of the trunks, leaves, branchlets and inflorescence of each individual for initial identification. We identified samples of this monophyletic species based on three taxonomic criteria (Figs 1, 2). All voucher specimens and dried leaves for DNA extraction were deposited in GXMI. Geographical information for each location was recorded using a HOLUX M-241 GPS Track instrument (Technology, Inc., Taiwan, China). Finally, 420 individuals from 38 natural populations across the entire distribution in China were collected for genetic analyses (Table 1).

DNA extraction, amplification, and sequencing

The genomic DNA of all samples was extracted from approximately 15 mg of silica gel-dried leaves using the CTAB method (Doyle and Doyle 1990). The quality and concentration of genomic DNA were measured using a NanoDrop 1000 spectrophotometer. Qualified DNA was defined as having values of both 260/280 and 260/230 located in the range 1.6–2.1. Then, each DNA solution was diluted or concentrated to approximately 50 ng/μL for PCR amplification.

Owing to its high discrimination power, nuclear internal transcribed spacer (ITS) sequence fragments are frequently used for plant classification (CBOL Plant Working Group 2011; Pang et al. 2011; Lu et al. 2016), and have been proposed as core barcodes (CBOL Plant Working Group 2011). As core chloroplast barcodes (CBOL Plant Working Group 2009), *mat*K and *rbc*L are widely used for most seed plants (Levin et al. 2003; Kress and Erickson 2007; Fazekas et al. 2008; Kress et al. 2009; Su et al. 2015; Amandita et al. 2019). Other chloroplast fragments (e.g., *ycf*6-*trn*C and *pet*A-*psb*J) have also been used for phylogenetic studies (Shaw et al. 2007; Liu et al. 2012; Sokoloff and Gillespie 2012). Therefore, we used universal primers for the nuclear ITS

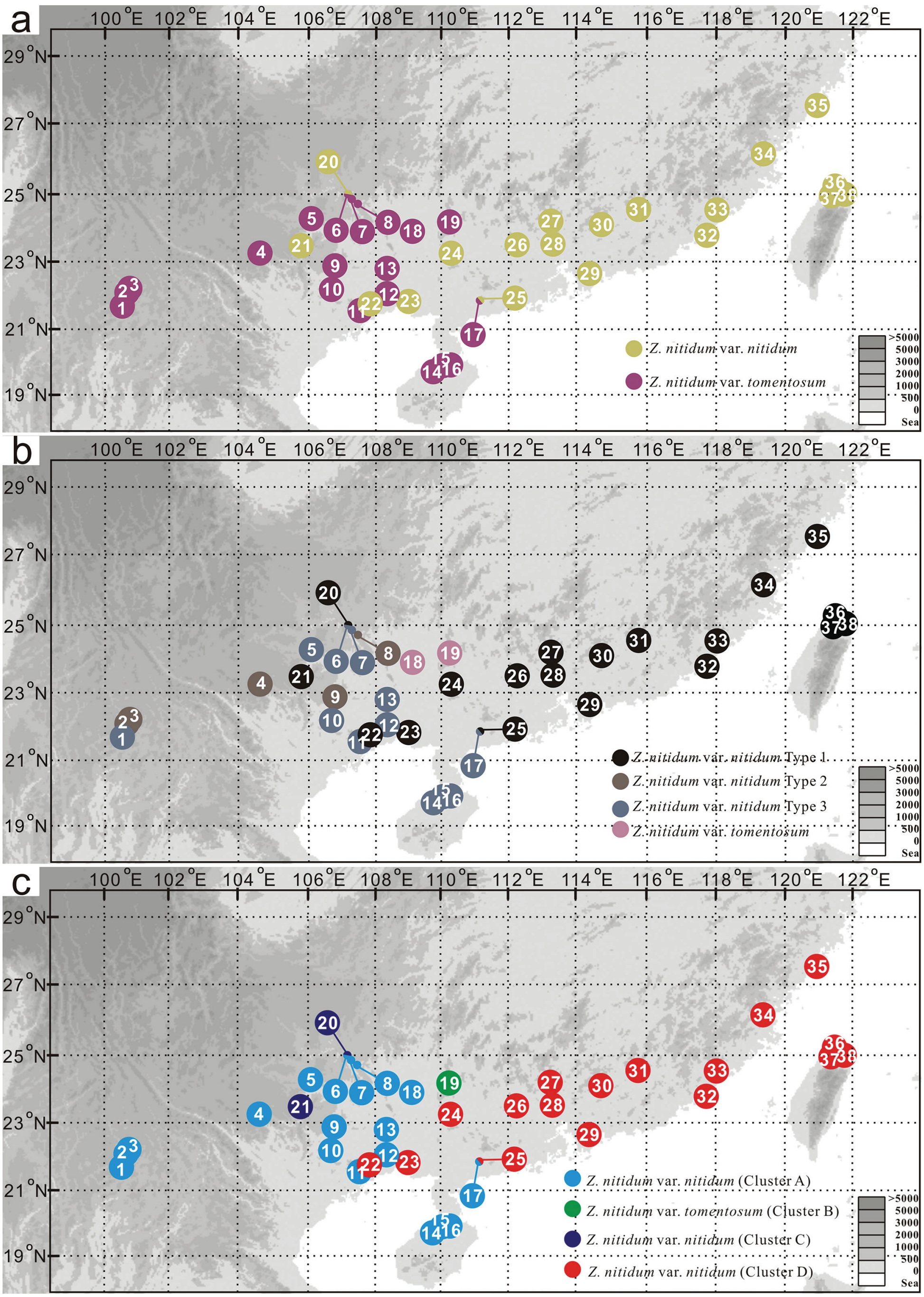

Figure 1. Geographical distribution of 38 *Z. nitidum* populations in China and its taxonomic scenarios currently used based on the presence of hairy or nearly glabrous leaf and rachis in Zhang et al. (2008) (**a**), the description of the Editorial Committee of Flora (1997) (**b**), and trunk appearance in Qin et al. (2020) (**c**).

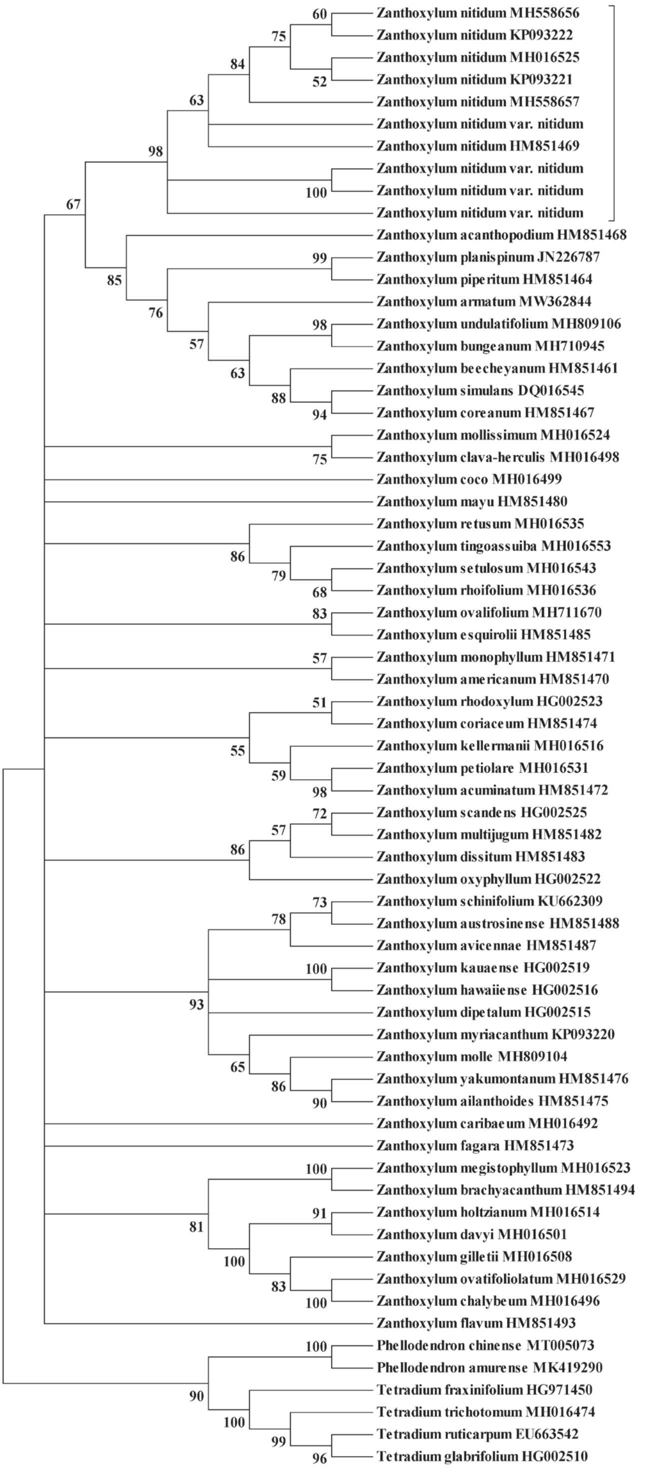

Figure 2. Maximum likelihood (ML) tree of *Zanthoxylum* species based on nuclear internal transcribed spacer (ITS) sequences.

Table 1. Sampling and classification information of *Zanthoxylum nitidum* from natural populations.

Pop. code	Location	GPS Coordinates	Altitude (m)	No. of individuals in internal transcribed spacer (ITS) cluster/type	No. of individuals in cpDNA lineage/haplotype
01 (ML)	Menglun, Yunnan	21.6911, 100.6472	558	2 (A-type5)	2 (A1-H1)
02 (MY)	Mengyang,Yunnan	22.1031, 100.7511	753	5 (A-type5)	5 (A2-H2: A2-H3 = 3:2)
03 (DDG)	Dadugang,Yunnan	22.2019, 100.8806	761	5 (A-type5)	12 (A2-H2: A2-H3 = 1:11)
04 (XC)	Malipo, Yunnan	23.2050, 104.9419	532	2 (A-type6)	5 (A2-H4)
05 (TL)	Tianling,Guangxi	24.2600, 106.0457	479	4 (A-type1)	4 (A2-H2)
06 (TEW)	Tiane, Guangxi	25.0175, 107.1616	535	6 (A-type1)	8 (A2-H2)
07 (TEL)	Tiane, Guangxi	24.9829, 107.1962	260	8 (A-type8:A-type11:A-type12 = 2:3:3)	18 (A2-H2)
08 (ND)	Nandan, Guangxi	24.8437, 107.3397	264	1 (A-type1)	2 (A2-H2)
09 (XL)	Daxin, Guangxi	22.9145, 106.7631	269	6 (A-type1)	11 (A2-H3)
10 (LZ)	Longzhou, Guangxi	22.3742, 106.6117	241	3 (A-type1:A-type6 = 2:1)	5 (A2-H3)
11 (DZ)	Fangcheng, Guangxi	21.6202, 107.5226	261	4 (A-type2:A-type5 = 2:2)	9 (A2-H2)
12 (GT)	Guitai, Guangxi	22.0799, 108.2121	101	9 (A-type3)	13 (A2-H2)
13 (NN)	Nanning, Guangxi	22.9070, 108.2160	160	9 (A-type1)	16 (A2-H2)
14 (HDZ)	Danzhou, Hainan	19.6104, 109.7366	120	8 (A-type2)	14 (A1-H1)
15 (LG)	Chengmai, Hainan	19.8144, 110.1064	47	12 (A-type7:A-type9:A-type10 = 6:3:3)	18 (A1-H1)
16 (HK)	Haikou, Hainan	19.9241, 110.2092	120	12 (A-type4)	19 (A1-H1)
17 (MM)	Maoming, Guangdong	21.8909, 111.1283	84	10 (A-type4:A-type6:A-type8 = 6:2:2)	10(A1-H1:A2-H2 = 6:4)
18 (BY)	Laibing, Guangxi	23.9677, 109.1837	290	9 (A-type2:A-type3 = 6:3)	20 (A2-H2)
19 (JX)	Jinxiu, Guangxi	24.1147, 110.1915	914	20 (B-type1:B-type2:B-type3:B-type4 = 7:6:4:3)	28 (B-H5)
20 (TE)	Tiane, Guangxi	25.0175, 107.1616	535	15 (C-type1:C-type4:C-type6:C-type7 = 9:3:2:1)	28 (C-H6:C-H7 = 20:8)
21 (NP)	Napo, Guangxi	23.3850, 105.8555	1026	13 (C-type2:C-type3:C-type5 = 7:4:2)	15 (C-H6)
22 (FL)	Fulong, Guangxi	21.8489, 107.8954	369	3 (D-type1)	3 (D-H8)
23 (NW)	Qinzhou, Guangxi	21.8856, 108.9255	343	10 (D-type2:D-type5 = 6:4)	13 (D-H8)
24 (BS)	Guiping, Guangxi	23.2028, 110.2032	478	10 (D-type1:D-type2:D-type6 = 3:4:3)	14 (D-H8)
25 (MM)	Maoming, Guangdong	21.8909, 111.1283	84	3 (D-type2)	3 (D-H8)
26 (ZQ)	Zaoqin, Guangdong	23.4534, 112.2185	384	5 (D-type5:D-type7 = 3:2)	7 (D-H8)
27 (YD)	Yingde, Guangdong	24.2411, 113.2146	52	6 (D-type1:D-type2 = 4:2)	10 (D-H8)
28 (GZ)	Guangzhou, Guangdong	23.5139, 113.2190	80	2 (D-type6)	2 (D-H8)
29 (SZ)	Shengzhen, Guangdong	22.6479, 114.3187	275	6 (D-type2:D-type6 D-type7 = 3:1:2)	11 (D-H8)
30 (HY)	Heyuan, Guangdong	24.1123, 114.7886	136	9 (D-type6:D-type8 = 5:4)	18 (D-H8)
31 (MZ)	Meizhou, Guangdong	24.5358, 115.8660	159	7 (D-type1:D-type2:D-type5 = 3:2:2)	12 (D-H8)
32 (ZZ)	Zhangzhou, Fujian	23.7805, 117.6242	10	12 (D-type1:D-type5 = 9:3)	16 (D-H8)
33 (XM)	Xiamen, Fujian	24.4993, 118.0951	202	8 (D-type1:D-type2 = 5:3)	15 (D-H8)
34 (FZ)	Fuzhou, Fujian	26.1026, 119.3183	65	8 (D-type3:D-type4 = 7:1)	9 (D-H8)
35 (RA)	Ruian, Zhejiang	27.4641, 121.0822	44	10 (D-type4)	18 (D-H8)
36 (DSK)	Danshuikou, Taiwan	25.1811, 121.4717	5	1 (D-type3)	1 (D-H8)
37 (WH)	Wanhua, Taiwan	25.0317, 121.5094	20	4 (D-type3)	4 (D-H8)
38 (NG)	Nangang, Taiwan	25.0439, 121.6097	60	2 (D-type4)	2 (D-H8)

fragments and four chloroplast DNA fragments (*mat*K, *rbc*L, *ycf*6-*trn*C, and *pet*A-*psb*J) to amplify and sequence each of the qualified DNA samples (Table 2). The primers were selected based on information from previous studies (White et al. 1990; Kress and Erickson 2007; Shaw et al. 2007; Kress et al. 2009; Liu et al. 2012; Amandita et

Table 2. Primers used in this study.

Primer	Primer sequence	Tm (°C)	Reference
ITS4	TCCTCCGCTTATTGATATGC	52	White et al. 1990
ITS5	GGAAGTAAAAGTCGTAACAAGG		White et al. 1990
*mat*K3F	CGTACAGTACTTTTGTGTTTACGAG	52	Amandita et al. 2019
*mat*K1R	ACCCAGTCCATCTGGAAATCTTGGTTC		Amandita et al. 2019
*rbc*LF	ATGTCACCACAAACAGAGACTAAAGC	55	Kress and Erickson 2007
*rbc*LR	GTAAAATCAAGTCCACCRCG		Kress et al. 2009
*psb*JF	ATAGGTACTGTARCYGGTATT	48	Shaw et al. 2007
*pet*AR	AACARTTYGARAAGGTTCAATT		Shaw et al. 2007
*trn*CF	CCAGTTCRAATCYGGGTG	59	Liu et al. 2012
*ycf*6R	GCCCAAGCRAGACTTACTATATCCAT		Liu et al. 2012

al. 2019). PCR amplification was performed in a 50 μL reaction system with 2 μL of the prepared DNA, 5 μL of 10 × PCR buffer, 0.8 μL of dNTPs (2.5 mmol/ml), 4 μL of the primer, 0.4 μL of rTaq polymerase, and 41.5 μL of ddH_2O. The reaction was programed according to the following procedure: initial template denaturation at 94 °C for 4 min, followed by 38 cycles of 94 °C for 40 s, 48 °C (*pet*A-*psb*J), 52 °C (*mat*K), 55 °C (*rbc*L), 59 °C (*ycf*6-*trn*C) or 60 °C (ITS) for 45 s, and 72 °C for 1.5 min, and final extension at 72 °C for 10 min.

All PCR products were examined by agarose gel electrophoresis and photographed using a UV transilluminator. The products were purified using a TIANquick Midi Purification Kit (TIANGEN, Beijing, China) and the reaction mixtures were sequenced on an ABI 3130xl automated sequencer (Applied Biosystems, Foster City, California, USA). For DNA products that failed direct sequencing, we repeated the extraction, amplification, or sequencing experiment at least three times.

Genetic classification of natural Liang-Mian-Zhen resources in China

We aligned and manually corrected nuclear ITS sequences and chloroplast sequences using MEGA 5 (Tamura et al. 2011). We first analyzed the haplotype relationship using NETWORK 10.0, based on the Median-Join method, for single-barcode and four-chloroplast fragments combined (Bandelt et al. 1999). Owing to the presence of some heterozygous sites in the nuclear ITS dataset, we phased these sequences using DnaSP v5 with default parameters (Librado and Rozas 2009). In addition, we constructed an ML tree of the *Zanthoxylum* species based on ITS sequences downloaded from NCBI (https://www.ncbi.nlm.nih.gov/), using MEGA 5 (Tamura et al. 2011) to further demonstrate the distinctiveness of *Z. nitidum* to the congeneric species. We further identified operational taxonomic units (OTUs) based on DNA barcodes using the Automatic Barcode Gap Discovery (ABGD) method (Puillandre et al. 2012). Indels or heterozygous sites of each fragment were deleted. The ABGD analysis was conducted based on information available online (https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html). We used the Kimura (K80) ts/tv model and set X = 1.5 as the relative barcode gap width. The remaining parameters were retained as the default parameters.

Molecular identification of Liang-Mian-Zhen samples

After genetic classification, we used the barcodes of each nuclear cluster or chloroplast cluster as references for subsequent molecular identification. The Liang-Mian-Zhen used by China Resources Sanjiu was treated as the standard reference because it has a rapid growth rate, a high level of nitidine chloride (Han et al. 2013; Qin et al. 2019), and is widely cultivated. We then visited 10 indigenous individuals who sold Liang-Mian-Zhen in different folk markets in Hainan, Guangxi, and Guangdong, with 1–4 samples obtained from each. We collected only a small number of broken leaves and voucher specimens without the trunk from both China Resources Sanjiu and the indigenous individuals, thereby making visual identification difficult. In total, 20 Liang-Mian-Zhen samples, including 3 standard samples and 17 samples of folk medicinal materials, were used for molecular classification and identification (Table 3). Total DNA was extracted, amplified, and sequenced according to the methods described above. For rapid identification, we directly used the aligned consistent sequences to construct ML trees using MEGA 5 (Tamura et al. 2011). The closely related species *Zanthoxylum armatum* was chosen as an outgroup for phylogenetic analyses within *Z. nitidum* (Accession numbers: MW362848 and MN080708; Chen et al. 2013; Appelhans et al. 2018). Finally, we classified and identified the samples using the nuclear ITS barcode and four chloroplast barcodes.

Results

Genetic classification

We obtained 269 ITS sequences from 420 individuals across 38 natural populations of *Z. nitidum* in China (Fig. 1, Table 1). We recovered 31 different ITS types, and the aligned sequences were 658 bp in length (Table 1). Four genetic clusters (A, B, C, and D) were detected based on the network analysis of these ITS sequences (Fig. 3a). Cluster D was widely distributed across Guangxi, Guangdong, Zhejiang, Fujian, and Taiwan. Cluster C was distributed in North and Southwest Guangxi. Cluster B was narrowly distributed in northeastern Guangxi. Cluster A was widely distributed across Yunnan, Guangxi, Hainan, and Guangdong, and its distribution partially overlapped with that of clusters C and D (Figs 1c, 3a). These genetic classification results are consistent with the third taxonomic scenario based on trunk appearance (Fig. 1c). Phylogenetic analysis confirmed that Liang-Mian-Zhen formed a clade distinct to congeners as the downloaded ITS sequences covered approximately a quarter of the Z*anthoxylum* species (Fig. 2).

After sequencing all four chloroplast barcodes (*mat*K, *rbc*L, *ycf*6-*trn*C, and *pet*A-*psb*J), the aligned sequences of these barcodes were 703, 533, 600, and 1040 bp in length, respectively. In total, 33 substitutions were detected across the 4 chloroplast barcodes. Only 8 cpDNA haplotypes were recovered from the 420 individuals across 38 natural populations, and these haplotypes were divided into 5 clusters (A1, A2, B, C, and D;

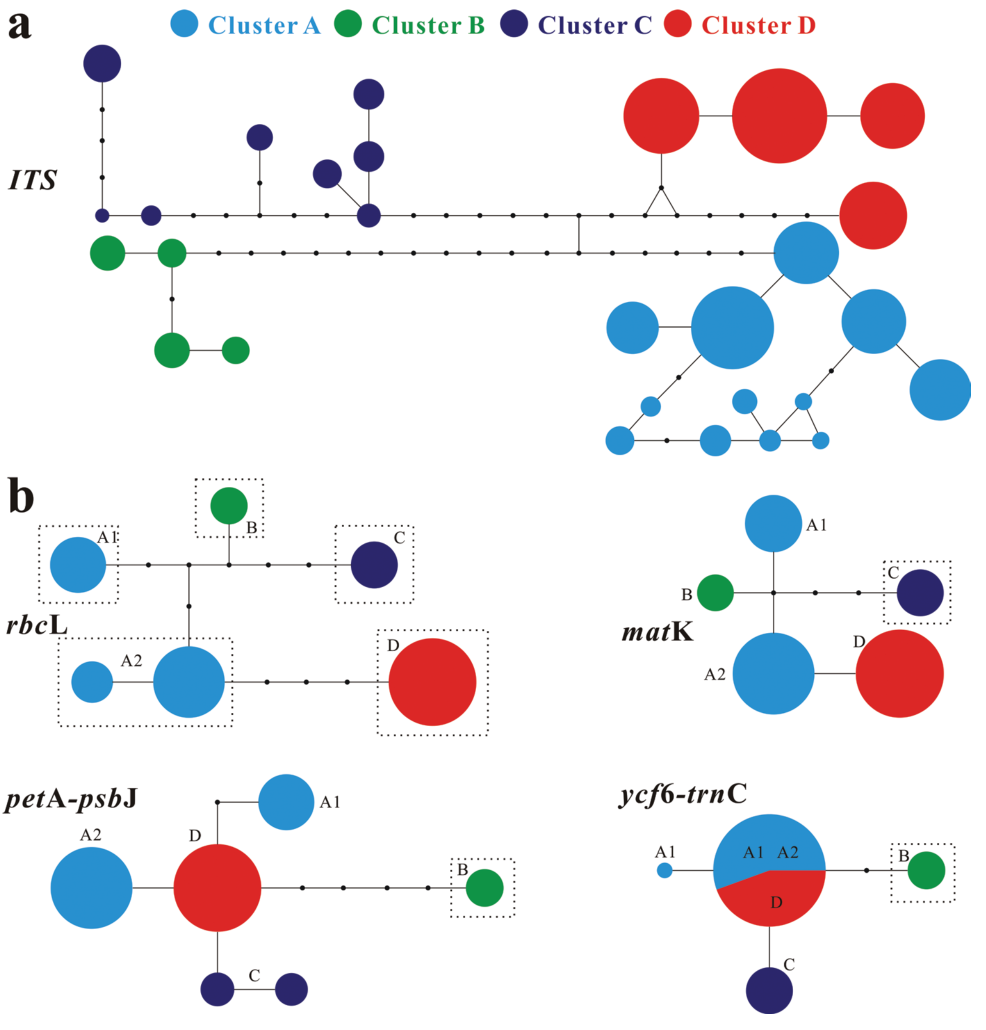

Figure 3. Network analysis of each barcode. Circle size is proportional to the haplotype frequency. Different colors indicate different clusters. The four clusters correspond to four morphological clusters in Fig. 1c.

Fig. 4, Table 1). All five chloroplast clusters were distributed across different geographical regions. Chloroplast clusters B, C, and D corresponded to the three nuclear clusters B, C, and D, respectively. However, two different chloroplast clusters (A1 and A2) were found within A. A1 was mainly found in Hainan and partially extended to southern Guangdong. In addition, it was also found in a preserved individual (coded as pop 1 in table 1) in the Xishuangbanna Tropical Botanical Garden (XTBG; Menglun, Yunnan). A2 was found in the remaining populations within A. We did not find distinct morphological differences between A1 and A2 from voucher specimens based on leaf shape and size, trunk appearance, and flowers. Accession numbers of all nuclear and chloroplast sequences are from MZ769312 to MZ769362 and from MZ773282 to MZ773393, respectively.

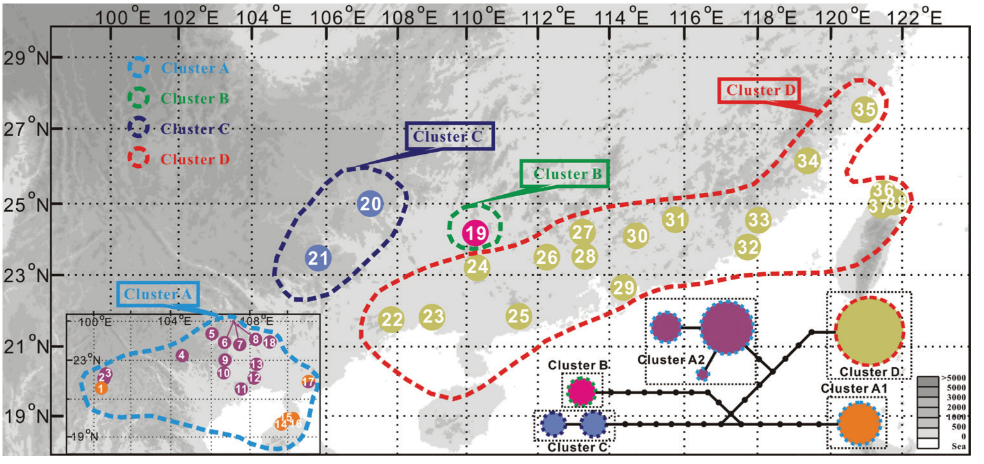

Figure 4. Distribution and network of five chloroplast lineages recovered from *Zanthoxylum nitidum* in China. Dotted lines of different colors indicate different nuclear clusters. Circle size is proportional to the haplotype frequency. Different colored circles indicate different chloroplast clusters.

Additionally, the four OTUs recognized by the ABGD analysis were consistent with four clusters based on the network analysis (Figs 3a, 5), the results of which were highly inconsistent with the two past taxonomic scenarios (Fig. 1a, b) but highly consistent with the recent taxonomic scenario based on trunk appearance (Fig. 1c). For the combined four-chloroplast fragments, the five unveiled chloroplast clusters based on the network analysis were also revealed by the ABGD method (Figs 4, 6). The single chloroplast barcode, *rbc*L, produced the same result as the four fragments combined (Figs 3b, 4). The *mat*K gene only distinguished C from a group comprising the remaining nuclear or chloroplast clusters. Additionally, the other two chloroplast barcodes (*ycf*6-*trn*C and *pet*A-*psb*J) similarly classified this species into two groups: one represented by B, and the other comprising the remaining clusters.

Molecular identification

Molecular identification was determined via phylogenetic analyses. During identification, each sample was delimited into the closest cluster. Four nuclear clusters (A, B, C, and D) and five chloroplast clusters (A1, A2, B, C, and D) were strongly supported by phylogenetic analyses (Fig. 7). The three standard Liang-Mian-Zhen samples from China Resources Sanjiu were identified as cluster A based on the nuclear ITS barcode and as A2 based on the four chloroplast fragments. However, for the 17 folk medicinal samples, three clusters (A, B, and D) were identified based on the nuclear ITS barcode. Four chloroplast clusters (A1, A2, B, and D) were identified based on the four chloroplast fragments. Interestingly, the molecular identification results for the folk medicinal samples were related to the natural distribution of Z. *nitidum* based on nuclear and chloroplast barcodes (Figs 1, 7, Table 1). For example, two folk Liang-Mian-Zhen

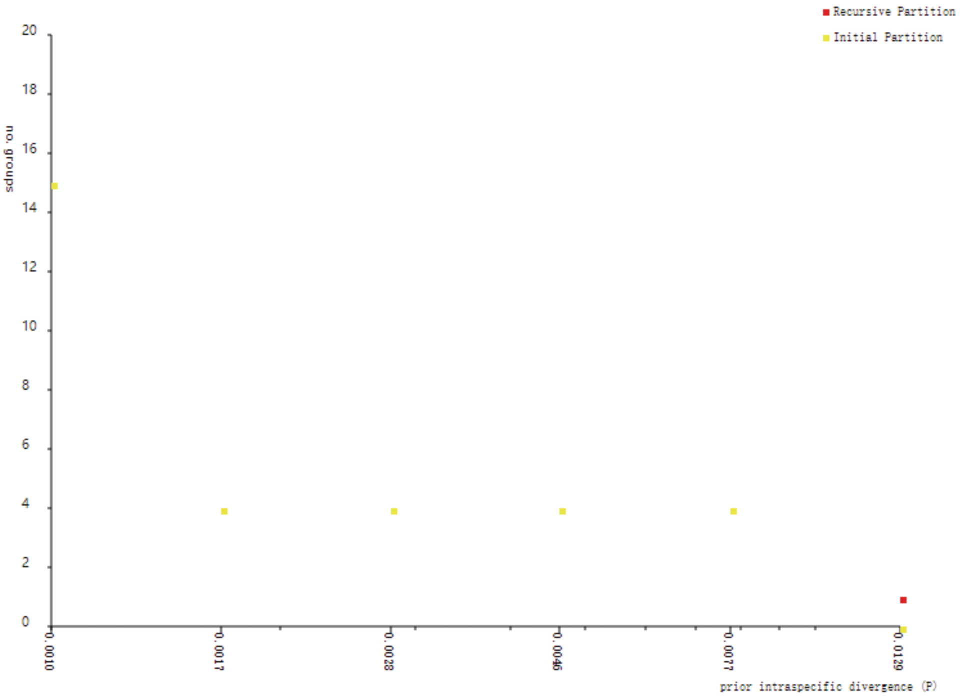

Figure 5. Genetic classification based on nuclear internal transcribed spacer (ITS) sequences using the Automatic Barcode Gap Discovery (ABGD) method.

samples from Jinxiu (Guangxi) were identified as cluster B based on their nuclear ITS sequences and cluster B based on four chloroplast fragments. Similarly, folk Liang-Mian-Zhen samples collected from Guangdong were assigned to nuclear clusters A or D and chloroplast clusters A2 or D. Folk samples collected from southern Guangxi were identified as A or D and A2 or D, and folk samples from Hainan were identified as clusters A and A1. In addition, all folk Liang-Mian-Zhen samples shared chloroplast haplotypes with nearby natural populations (Table 1 and Table 3).

Discussion

Three well-delimited clusters

In this study, we examined the intraspecific delimitation of the commercial medicinal plant *Z. nitidum* using 5 DNA barcodes based on samples from 38 natural populations (Fig. 1). The nuclear ITS sequences classified the species into four distinct genetic clusters (A, B, C, and D; Figs 3a, 5). This finding is consistent with a recent taxonomic scenario based on trunk appearance (Editorial Committee of Flora 1997; Zhang et al. 2008; Qin et al. 2019). However, chloroplast delimitation based on 4 fragments

Table 3. Sampling information and molecular identification results of folk and standard Liang-Mian-Zhen samples.

Code	Location	Internal transcribed spacer (ITS) cluster and No. of individuals	cpDNA lineage/haplotype and No. of individuals
Folk-DX	Dongxing, Guangxi	2 (A:D = 1:1)	2 (A2-H2:D-H8 = 1:1)
Folk-JX	Jingxi, Guangxi	1 (A)	1 (A2-H3)
Folk-NM	Ningming, Guangxi	1 (A)	1 (A2-H3)
Folk-PX-1	Pingxiang, Guangxi	1 (A)	1 (A2-H3)
Folk-PX-2	Pingxiang, Guangxi	1 (A)	1 (A2-H3)
Folk-LZ	Longzhou, Guangxi	1 (A)	1 (A2-H3
Folk-DY	Dayaoshan, Guangxi	2 (B)	2 (B-H5)
Folk-MM-1	Maoming, Guangdong	4 (A:D = 3:1)	4 (A1-H1:D-H8 = 3:1)
Folk-MM-2	Maoming, Guangdong	2 (D)	2 (D-H8)
Folk-HK-1	Haikou, Hainan	2 (A)	2 (A1-H1)
CRS-standard	China resources Sanjiu	3 (A)	3 (A2-H3)

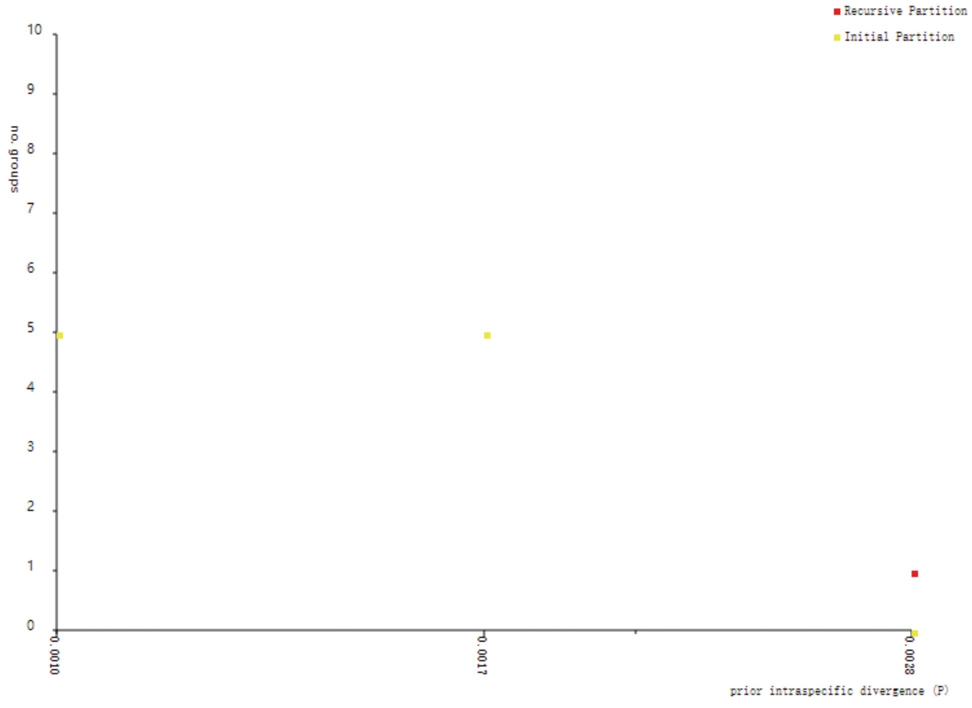

Figure 6. Genetic classification based on four chloroplast barcodes combined using the Automatic Barcode Gap Discovery (ABGD) method.

classified the 38 natural populations of this species into 5 clusters (A1, A2, B, C, and D; Figs 4, 6). The chloroplast clusters B, C, and D correspond one-to-one to the three nuclear clusters B, C, and D. In addition, they also correspond to three different geographical groups. Previous empirical studies have suggested that morphological taxonomy can be supported by molecular evidence (Su et al. 2015; Lu et al. 2021). According

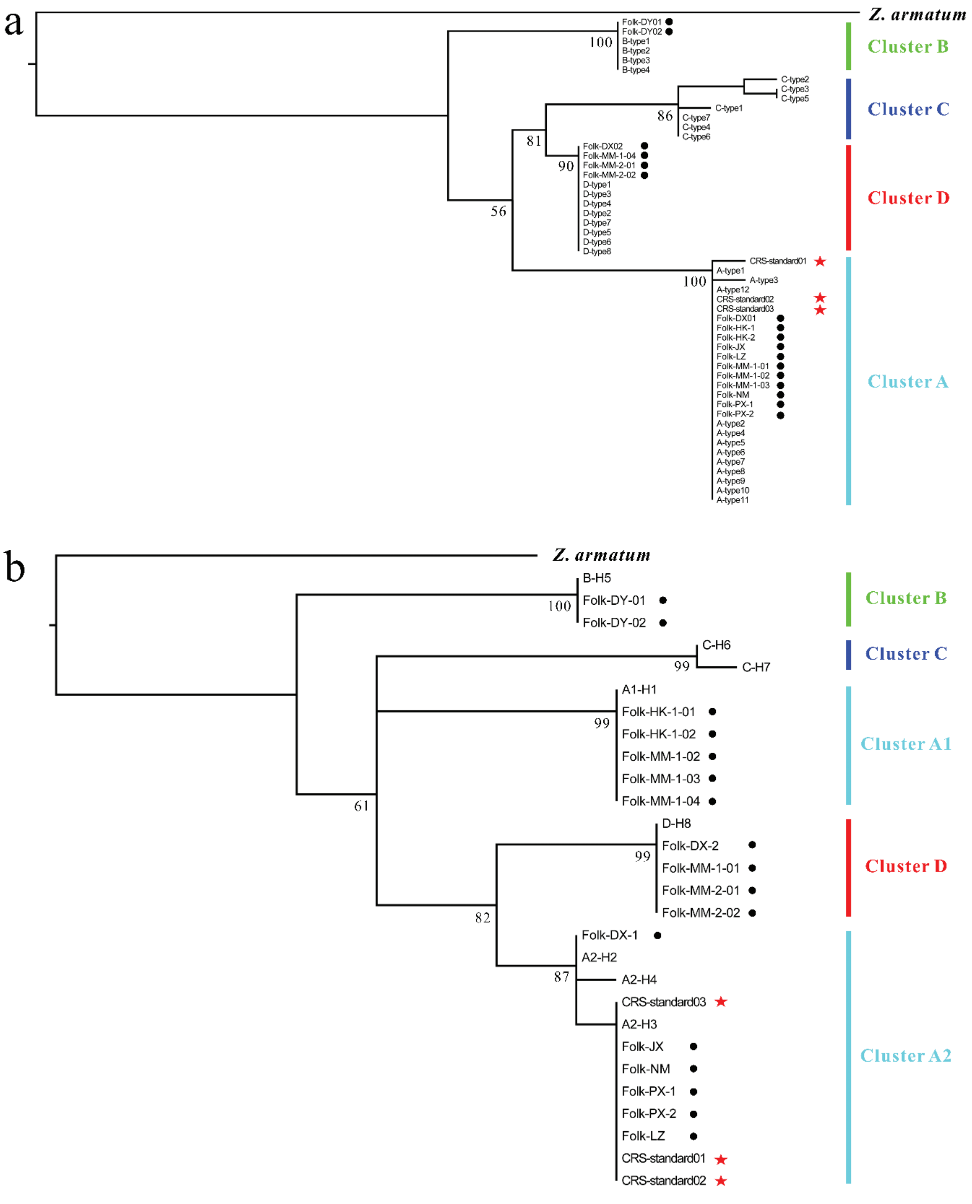

Figure 7. Molecular identification of the Liang-Mian-Zhen samples using Maximum likelihood (ML) trees based on nuclear internal transcribed spacer (ITS) barcodes (**a**) and four chloroplast fragments combined (**b**). Red stars indicate the standard samples obtained from China Resources Sanjiu and black dots indicate folk medicinal samples collected from indigenous individuals in different geographical regions.

to the integrative taxonomic method (Su et al. 2015; Lu et al. 2021; Parker et al. 2021), taxonomic boundaries for clusters B, C, and D were demarcated based on the above evidence and form three well-delimited clusters. However, cluster A identified by nuclear barcode is split into two distinct chloroplast clusters, A1 and A2 (Fig. 4).

Chloroplast cluster A2 is phylogenetically and geographically closer to D, which is a possible indicator for introgression from D to A (Arnold 1997; 2006; Abbott 2017; Lu et al. 2021). However, morphological differences between A1 and A2 were not recognized based on leaf shape and size, trunk appearance, and flowers. Thus, the conflict between nuclear and chloroplast barcodes may be the consequence of cryptic evolutionary units and/or historical chloroplast introgression. Nevertheless, incomplete lineage sorting cannot be completely ruled out as an explanation for this phenomenon (Hollingsworth et al. 2011; Lu et al. 2016; Hu et al. 2019). In fact, the three well-delimited clusters (B, C, and D) can be directly distinguished from each other and from A based on the trunk appearance, while the other two morphological taxonomic scenarios failed in doing this (Fig. 1). However, none of these three scenarios could recognize the two chloroplast clusters (A1 and A2) within A. Hence, the third taxonomic scenario based on the trunk appearance (Fig. 1c) is better than the other two (Fig. 1a, b).

Discrimination power and taxonomic implications

Usually, hybrid introgression and incomplete lineage sorting can induce a low discrimination power for DNA barcodes (Su et al. 2015; Lu et al. 2016, 2021). Nuclear ITS barcodes have shown strong discrimination power in many empirical studies (Pang et al. 2011; Wang et al. 2011; Su et al. 2015; Lu et al. 2016). In this study, both the nuclear ITS barcodes and the four chloroplast fragments combined showed high intraspecific discrimination power, although historical introgression between strains A and D might have occurred (Figs 3, 4, 7). However, a large discrepancy in the discrimination power of different chloroplast fragments was observed (Fig. 3b). For example, only *rbc*L could distinguish all chloroplast clusters, while the other three barcodes could only distinguish one from the remaining chloroplast clusters. Unsurprisingly, using DNA fragments with low discrimination power (e.g., *mat*K, *ycf*6-*trn*C, and *pet*A-*psb*J) to delimit clusters within this species did not yield accurate identification.

In consideration of the large differentiations based on both trunk appearance and molecular markers, whether the clusters in Fig. 1c and Fig. 7a should be treated as separate species or subspecies of Liang-Mian-Zhen remains to be evaluated with more substantial evidence based on genomic data, phenotypic traits, and crossing experiments. Regardless, ITS sequences and *rbc*L are proposed as barcodes for rapid and accurate identification of the different Liang-Mian-Zhen lineages in China.

Molecular identification

Discrepancies in the safety and quality of medicinal materials from different species (or genetic clusters) have been demonstrated in many empirical studies (Bansal et al. 2018; Xin et al. 2018). In the present study, folk Liang-Mian-Zhen samples were shown to comprise several nuclear or chloroplast clusters with regional differences (Figs 3, 4, 7, Tables 1, 3), whereas cultivated Liang-Mian-Zhen material from a state-owned holding pharmaceutical listed company belong to just one of the clusters, suggesting the need to scientifically evaluate the safety and quality for different Liang-Mian-Zhen clusters or lineages. This study is the first to successfully reconcile nuclear molecular evidence (chloroplast conflict exists merely within cluster A) with the morphological taxonomy at the population level and to present accurate resource classification and molecular identification of Liang-Mian-Zhen in China. In summary, there are three major reasons for our accurate molecular identification within this species. First, barcodes with a high level of discrimination power were used to conduct taxonomic delimitation, and to carry out molecular identification. Second, extensive sampling helped to account for overlooked morphological variations and promoted the accuracy of taxonomic delimitation (Linck et al. 2019; Lu et al. 2021). Third, and most importantly, morphological classification or initial identification based on trunk appearance was further supported by integrating evidence from DNA barcodes and geographical distribution. In summary, accurate taxonomic delimitation is the basis for accurate and rapid molecular identification of closely related medicinal plants.

Availability of data

All the data generated in this study are deposited in GenBank under the accession numbers MZ773282–MZ773393 and MZ769312–MZ769362.

Acknowledgements

We thank China Resources Sanjiu for providing the three standard Liang-Mian-Zhen samples, and the 10 indigenous individuals for providing the folk medicinal Liang-Mian-Zhen samples. We are also grateful to the editor, Hanno Schaefer, and reviewers for insightful comments that have improved this manuscript. English language was edited by Editage (www.editage.com). This study was funded by the Guangxi Chinese Medicine Key Disciplines Construction Projects (GZXK-Z-20-69); CAS Light of West China; Biodiversity Survey, Observation and Assessment Program of the Ministry of Ecology and Environment of China (8-3-7-20-5); the National Natural Science Foundation of China (32000264); and The Fourth National Survey of Traditional Chinese Medicine Resources.

References

Abbott RJ (2017) Plant speciation across environmental gradients and the occurrence and nature of hybrid zones. Journal of Systematics and Evolution 55(4): 238–258. https://doi.org/10.1111/jse.12267

Amandita FY, Rembold K, Vornam B, Rahayu S, Siregar IZ, Kreft H, Finkeldey R (2019) DNA barcoding of flowering plants in Sumatra, Indonesia. Ecology and Evolution 9(4): 1858–1868. https://doi.org/10.1002/ece3.4875

Appelhans M, Reichelt N, Groppo M, Paetzold C, Wen J (2018) Phylogeny and biogeography of the pantropical genus *Zanthoxylum* and its closest relatives in the proto-Rutaceae group

(Rutaceae). Molecular Phylogenetics and Evolution 126: 31–44. https://doi.org/10.1016/j.ympev.2018.04.013

Arnold ML (1997) Natural hybridization and evolution. Oxford University Press, New York.

Arnold ML (2006) Evolution through genetic exchange. Oxford University Press, New York. https://doi.org/10.1093/acprof:oso/9780199229031.001.0001

Bandelt HJ, Forster P, Röhl A (1999) Median-joining networks for inferring intraspecific phylogenies. Molecular Biology and Evolution 16(1): 37–48. https://doi.org/10.1093/oxfordjournals.molbev.a026036

Bansal S, Thakur S, Mangal M, Mangal AK, Gupta RK (2018) DNA barcoding for specific and sensitive detection of *Cuminum cyminum* adulteration in *Bunium persicum*. Phytomedicine 50: 178–183. https://doi.org/10.1016/j.phymed.2018.04.023

Chao Z, Zeng W, Liao J, Liu L, Liang ZB, Li XL (2014) DNA barcoding Chinese medicinal *Bupleurum*. Phytomedicine 21(13): 1767–1773. https://doi.org/10.1016/j.phymed.2014.09.001

Chen BB, Song JY, Yao H, Han ZZ, Yang TC, Xing JY (2013) Identification of *Zanthoxyli Radix* and its adulterants using ITS2 barcoding. Chinese Traditional and Herbal Drugs 38(2): 141–148.

Chen J, Jiang ZG, Li CL, Ping XG, Cui SP, Tang SH, Chu HJ, Liu BW (2015) Identification of ungulates used in a traditional Chinese medicine with DNA barcoding technology. Ecology and Evolution 5(9): 1818–1825. https://doi.org/10.1002/ece3.1457

Chinese Pharmacopoeia Commission (2020) The Pharmacopoeia of the People's Republic of China (Part I). Beijing: China Medical Science Press, 176 pp.

Cirak C, Radusiene J, Janulis V, Ivanauskas L (2007) Chemical constituents of some *Hypericum* species growing in Turkey. Journal of Plant Biology 50(6): 632–635. https://doi.org/10.1007/BF03030606

Cirak C, Radusien J, Camas N, Caliskan O, Odabas MS (2013) Changes in the contents of main secondary metabolites in two Turkish *Hypericum* species during plant development. Pharmaceutical Biology 51(3): 391–399. https://doi.org/10.3109/13880209.2012.733012

Doyle JJ, Doyle JL (1990) Isolation of DNA from small amounts of plant tissues. BRL Focus 12: 13–15.

Dubey RB, Sawant BS (2015) Current scenario of adulterants and substitutes of medicinal plants: A review. Journal of Pharmaceutical and Scientific Innovation 4(5): 247–250. https://doi.org/10.7897/2277-4572.04555

Editorial Committee of Flora (1997) Flora Reipublicae Popularis Sinicae (Tomus 43 (2)). Beijing: Science Press, 13–16.

Fan LL, Xu F, Hu JP, Yang DH, Chen HB, Komatsu K, Zhu S, Shang MY, Wang X, Cai SQ (2015) Binary chromatographic fingerprint analysis of Stemonae Radix from three *Stemona* plants and its applications. Journal of Natural Medicines 69(3): 402–410. https://doi.org/10.1007/s11418-015-0887-7

Fazekas AJ, Burgess KS, Kesanakurti PR, Graham SW, Newmaster SG, Husband BC, Percy DM, Hajibabaei M, Barrett SCH (2008) Multiple multilocus DNA barcodes from the plastid genome discriminate plant species equally well. PLoS ONE 3(7): e2802. https://doi.org/10.1371/journal.pone.0002802

Feng J, Zhou JF, Qin FJ, Liang CL, Lai MX, Zhang HY (2011) Studies on the anti-inflammatory and analgesic activities of different polarities from the roots and stems of *Zanthoxylum nitidum* DC. Pharmacology and Clinics of Chinese Materia Medica 27: 60–63.

Guo H, Jin SY, Liu H, Wang ZY (2013) New aspects in Chinese herb materials identification by DNA barcoding. Journal of Microbiology and Biotechnology 5(1): 58–66.

Han ZZ, Tan Y, Qin LF, Lai MX (2013) Comparative Study on the Quality of Wild and Cultivated *Zanthoxylum nitidum* (Roxb.) DC. Research and Practice on Chinese Medicines 2: 65–66.

Hartley TG (1966) A revision of the Malesian species of *Zanthoxylum* (Rutaceae). Journal of the Arnold Arboretum 47(3): 171–221. https://doi.org/10.5962/p.33416

Hawkins B (2008) Plants for life: Medicinal plant conservation and botanic gardens. Botanic Gardens Conservation International, Richmond, UK.

Hollingsworth PM, Forrest LL, Spouge JL, Hajibabaei M, Ratnasingham S, van der Bank M, Chase MW, Cowan RS, Erickson DL, Fazekas AJ, Graham SW, James KE, Kim K-J, Kress WJ, Schneider H, van AlphenStahl J, Barrett SCH, van den Berg C, Bogarin D, Burgess KS, Cameron KM, Carine M, Chacón J, Clark A, Clarkson JJ, Conrad F, Devey DS, Ford CS, Hedderson TAJ, Hollingsworth ML, Husband BC, Kelly LJ, Kesanakurti PR, Kim JS, Kim Y-D, Lahaye R, Lee H-L, Long DG, Madriñán S, Maurin O, Meusnier I, Newmaster SG, Park C-W, Percy DM, Petersen G, Richardson JE, Salazar GA, Savolainen V, Seberg O, Wilkinson MJ, Yi D-K, Little DP, CBOL Plant Working Group (2009) A DNA barcode for land plants. Proceedings of the National Academy of Sciences of the United States of America 106(31): 12794–12797. https://doi.org/10.1073/pnas.0905845106

Hollingsworth PM, Graham SW, Little DP (2011) Choosing and using a plant DNA barcode. PLoS ONE 6(5): e19254. https://doi.org/10.1371/journal.pone.0019254

Hu H, Al-Shehbaz IA, Sun YS, Hao GQ, Wang Q, Liu JQ (2015) Species delimitation in *Orychophragmus* (Brassicaceae) based on chloroplast and nuclear DNA barcodes. Taxon 64(4): 714–726. https://doi.org/10.12705/644.4

Hu YN, Zhao L, Buggs RJA, Zhang XM, Li J, Wang N (2019) Population structure of *Betula albosinensis* and *Betula platyphylla*: Evidence for hybridization and a cryptic lineage. Annals of Botany 123(7): 1179–1189. https://doi.org/10.1093/aob/mcz024

Kress WJ, Erickson DL (2007) A two-locus global DNA barcode for land plants: The coding *rbc*L gene complements the non-coding *trn*H-*psb*A spacer region. PLoS ONE 2(6): e508. https://doi.org/10.1371/journal.pone.0000508

Kress WJ, Erickson DL, Jones FA, Swenson NG, Perez R, Sanjur O, Bermingham E (2009) Plant DNA barcodes and a community phylogeny of a tropical forest dynamics plot in Panama. Proceedings of the National Academy of Sciences of the United States of America 106(44): 18621–18626. https://doi.org/10.1073/pnas.0909820106

Levin RA, Wagner WL, Hoch PC, Nepokroeff M, Pires JC, Zimmer EZ, Sytsma KJ (2003) Family-level relationships of Onagraceae based on chloroplast *rbc*L and *ndh*F data. American Journal of Botany 90(1): 107–115. https://doi.org/10.3732/ajb.90.1.107

Li D-Z, Gao L-M, Li H-T, Wang H, Ge X-J, Liu J-Q, Chen Z-D, Zhou S-L, Chen S-L, Yang J-B, Fu C-X, Zeng C-X, Yan H-F, Zhu Y-J, Sun Y-S, Chen S-Y, Zhao L, Wang K, Yang T, Duan G-W, CBOL Plant Working Group (2011) Comparative analysis of a large dataset indicates that internal transcribed spacer (ITS) should be incorporated into the core barcode for seed plants. Proceedings of the National Academy of Sciences of the United States of America 108(49): 19641–19646. https://doi.org/10.1073/pnas.1104551108

Librado P, Rozas J (2009) DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. Bioinformatics (Oxford, England) 25(11): 1451–1452. https://doi.org/10.1093/bioinformatics/btp187

Linck E, Epperly K, Van Els P, Spellman Jr GM, Mc RWB, Cormack JE, Canales-Del-Castillo R, Klicka J (2019) Dense geographic and genomic sampling reveals paraphyly and a cryptic lineage in a classic sibling species complex. Systematic Biology 68(6): 956–966. https://doi.org/10.1093/sysbio/syz027

Liu PL, Wan Q, Guo YP, Yang J, Rao GY (2012) Phylogeny of the genus *Chrysanthemum* L.: Evidence from single-copy nuclear gene and chloroplast DNA sequences. PLoS ONE 7(11): e48970. https://doi.org/10.1371/journal.pone.0048970

Liu J, Milne RI, Möller M, Zhu GF, Ye LJ, Luo YH, Yang JB, Wambulwa MC, Wang CN, Li DZ, Gao LM (2018) Integrating a comprehensive DNA barcode reference library with a global map of yews (*Taxus* L.) for forensic identification. Molecular Ecology Resources 8(5): 1115–1131. https://doi.org/10.1111/1755-0998.12903

Lu ZQ, Zhang D, Liu SY, Yang XY, Liu X, Liu JQ (2016) Species delimitation of Chinese hop-hornbeams based on molecular and morphological evidence. Ecology and Evolution 6(14): 4731–4740. https://doi.org/10.1002/ece3.2251

Lu Q, Ma RF, Yang Y, Mo ZM, Pu XD, Li CL (2020) *Zanthoxylum nitidum* (Roxb.) DC: Traditional uses, phytochemistry, pharmacological activities and toxicology. Journal of Ethnopharmacology 260: e112946. https://doi.org/10.1016/j.jep.2020.112946

Lu ZQ, Sun YS, Li Y, Yang YZ, Wang GN, Liu JQ (2021) Species delimitation and hybridization history of a hazel species complex. Annals of Botany 127(7): 875–886. https://doi.org/10.1093/aob/mcab015

Ma X, Liu F, Zhan RT, Han ZY, Chen WW (2014) Identification of *Zanthoxylum nitidum* and its adulterants and related species through DNA barcodes. Nanfang Nongye Xuebao 45(1): 12–17.

Osathanunkul M, Suwannapoom C, Osathanunkul K, Madesis P, De Boer H (2016) Evaluation of DNA barcoding coupled high resolution melting for discrimination of closely related species in phytopharmaceuticals. Phytomedicine 23(2): 156–165. https://doi.org/10.1016/j.phymed.2015.11.018

Pang XH, Song JY, Zhu YJ, Xu HX, Huang LF, Chen SL (2011) Applying plant DNA barcodes for Rosaceae species identification. Cladistics 27(2): 165–170. https://doi.org/10.1111/j.1096-0031.2010.00328.x

Parker E, Dornburg A, Struthers CD, Jones CD, Near TJ (2021) Phylogenomic species delimitation dramatically reduces species diversity in an Antarctic adaptive radiation. Systematic Biology 77(1): 58–77.https://doi.org/10.1093/sysbio/syab057

Puillandre N, Lambert A, Brouillet S, Achaz G (2012) ABGD, Automatic Barcode Gap Discovery for primary species delimitation. Molecular Ecology 21(8): 1864–1877. https://doi.org/10.1111/j.1365-294X.2011.05239.x

Qin YR, Jiang ZO, Lai MX, Huang YF, Wang XH (2019) Botanical origin research and simultaneous determination of five effective components of *Zanthoxylum nitidum*. Guangxi Zhi Wu 39(4): 531–539.

Qin F, Wang CY, Hu RC, Wang CG, Wang FF, Zhou MM, Liang D, Liao HB, Lee SK, Wang HS (2020) Anti-inflammatory activity of isobutylamides from *Zanthoxylum nitidum* var. *tomentosum*. Fitoterapia 142: e104486. https://doi.org/10.1016/j.fitote.2020.104486

Shaw J, Lickey EB, Schilling EE, Small RL (2007) Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: The tortoise and the hare III. American Journal of Botany 94(3): 275–288. https://doi.org/10.3732/ajb.94.3.275

Sokoloff PC, Gillespie LJ (2012) Taxonomy of *Astragalus robbinsii* var. *fernaldii* (Fabaceae): Molecular and morphological analyses support transfer to *Astragalus eucosmus*. Botany 90(1): 11–26. https://doi.org/10.1139/b11-077

Su X, Wu GL, Li LL, Liu JQ (2015) Species delimitation in plants using the Qinghai-Tibet Plateau endemic *Orinus* (Poaceae: Tridentinae) as an example. Annals of Botany 116(1): 35–48. https://doi.org/10.1093/aob/mcv062

Sui XY, Huang Y, Tan Y, Guo Y, Long CL (2011) Molecular authentication of the ethnomedicinal plant *Sabia parviflora* and its adulterants by DNA barcoding technique. Planta Medica 77(5): 492–496. https://doi.org/10.1055/s-0030-1250468

Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2011) MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Molecular Biology and Evolution 28(10): 2731–2739. https://doi.org/10.1093/molbev/msr121

Techen N, Parveen I, Pan ZQ, Khan IA (2014) DNA barcoding of medicinal plant material for identification. Current Opinion in Biotechnology 25: 103–110. https://doi.org/10.1016/j.copbio.2013.09.010

Wang Q, Yu QS, Liu JQ (2011) Are nuclear loci ideal for barcoding plants? A case study of genetic delimitation of two sister species using multiple loci and multiple intraspecific individuals. Journal of Systematics and Evolution 49(3): 182–188. https://doi.org/10.1111/j.1759-6831.2011.00135.x

White TJ, Bruns T, Lee S, Taylor J (1990) Analysis of phytogenetic relationships by amplification and direct sequencing of ribosomal RNA genes. In: Innis MA, Gelfand HD, Sninsky JJ, White TJ (Eds) PCR protocols: a guide to methods and applications Academic, New York, 315–322.

Xin TY, Su C, Lin YL, Wang SH, Xu ZC, Song JY (2018) Precise species detection of traditional Chinese patent medicine by shotgun metagenomic sequencing. Phytomedicine 47: 40–47. http://dx.doi.org/10.1016/j.phymed.2018.04.048

Yang GH, Chen DF (2008) Alkaloids from the roots of *Zanthoxylum nitidum* and their antiviral and antifungal effects. Chemistry & Biodiversity 5(9): 1718–1722. https://doi.org/10.1002/cbdv.200890160

Zhang DX, Thomas GH, David JM (2008) Rutaceae. In: Wu ZH, Raven PH (Eds) Flora of China. Vol. 11. Science Press; Miss. Bot. Gard. Press, 55 pp.

Zhou LG, Wu JY (2006) Development and application of medicinal plant tissue cultures for production of drugs and herbal medicinals in China. Natural Product Reports 23(5): 789–810. https://doi.org/10.1039/b610767b

Zhu ZY, Feng YX, Ho LY, Wang YC (1983) Utilization of medicinal plant resources of genus *Stephania* of Menispermaceae in China. Yao Xue Xue Bao 18: 460–467.

PhytoKeys 196: 21–47 (2022)
doi: 10.3897/phytokeys.196.82598
https://phytokeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

Resurrection of *Stipa tremula* and taxonomy of the high-alpine species from the *Stipa purpurea* complex (Poaceae, Pooideae)

Marcin Nobis[1], Marta Krzempek[1], Arkadiusz Nowak[2,3], Polina D. Gudkova[4,5], Ewelina Klichowska[1]

1 *Institute of Botany, Jagiellonian University, Gronostajowa 3, 30–387 Kraków, Poland* **2** *Institute of Biology, University of Opole, 45–052 Opole, Poland* **3** *Botanical Garden, Center for Biological Diversity Conservation, Polish Academy of Sciences, 02–976 Warszawa, Poland* **4** *Research Laboratory 'Herbarium', National Research Tomsk State University, Lenin 36 Ave., 634050 Tomsk, Russia* **5** *Institute of Biology, Altai State University, Lenin 61 Ave., 656049, Barnaul, Russia*

Corresponding authors: Marcin Nobis (m.nobis@uj.edu.pl), Ewelina Klichowska (ewelina.klichowska@uj.edu.pl)

Academic editor: E. Ruiz-Sanchez | Received 22 February 2022 | Accepted 11 April 2022 | Published 13 May 2022

Citation: Nobis M, Krzempek M, Nowak A, Gudkova PD, Klichowska E (2022) Resurrection of *Stipa tremula* and taxonomy of the high-alpine species from the *Stipa purpurea* complex (Poaceae, Pooideae). PhytoKeys 196: 21–47. https://doi.org/10.3897/phytokeys.196.82598

Abstract

Stipa purpurea is a high-alpine species that occurs in cryophilous steppes, semi-deserts and stony slopes, from the Tian Shan and Pamirian Plateau through Qinghai-Xizang Plateau to the Himalayas and is characterised by a great morphological variability. During the revision of specimens of the taxon, we observed that the pattern of this variability is linked to the geographical distribution of the specimens. Numerical analyses (PCA and UPGMA) revealed three groups of OTUs corresponding to three morphotypes within the *S. purpurea* complex. A set of macro- and micromorphological characters, supported by a map of general distributional ranges, are presented to distinguish each of the three taxa within the complex and we reassess the status of *Lasiagrostis tremula* described by Ruprecht in 1869. As a result, *Stipa tremula*, *S. purpurea* and *S. arenosa* were distinguished within the complex. The intermediate characters of *S. arenosa* may suggest its putative hybrid origin (*S. tremula* × *S. purpurea*), whereas the presence of extremely long florets may be an expression of the gigas effect. We propose two new combinations (*S. tremula* and *S. arenosa*), describe a new nothospecies (*S.* ×*ladakhensis*) that originated from hybridisation between *S. klimesii* and *S. purpurea* s.l. and designate the lectotype for *Ptilagrostis semenovii*. An identification key and detailed morphological description of species from the *S. purpurea* complex are also presented.

Keywords

distribution, feathergrasses, hybridisation, *Lasiagrostis*, micromorphology, *Ptilagrostis*, taxonomy, typification

Copyright *Marcin Nobis et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

With ca. 11500 species divided among 750–770 genera (Kellogg 2015; Soreng et al. 2017; Hodkinson 2018), grasses (Poaceae) constitute one of the richest families of flowering plants, widely distributed and covering, as grasslands or bamboo forests, ca. 40% of the Earth's land surface (Gibson 2009; Hodkinson 2018). Grasses occur on all continents and can be found in a wide variety of climates and habitats. Some species of grasses can grow in extreme habitats, such as hot or cold deserts and semi-deserts, grasslands and swards of polar areas or alpine meadows and steppes. Especially interesting are high-alpine species, which, due to strong resistance to cold, drought, wind, high ultraviolet radiation and nutrient poor soils, can grow in severe alpine environments and play an important role in the preservation and stabilisation of high mountain landscape diversity and heterogeneity. Examples of genera with species found in the highest areas of mountains may be: *Calamagrostis* Adans., *Colpodium* Trin., *Elymus* L., *Festuca* Tourn. ex L., *Helictotrichon* Besser, *Leymus* Hochst., *Ptilagrostis* Griseb., *Poa* L., *Puccinellia* Parl. and *Stipa* L. (Bor 1960, 1970; Tzvelev 1976; Cope 1982; Wu et al. 2006; Conti et al. 2020; Kellogg et al. 2020; Liu and Paszko 2020; Nobis et al. 2020).

Within the genus *Stipa* (feathergrasses), *S. purpurea* is an example of high-alpine species with a fairly wide distribution range, being dominant in alpine steppes and an important food component for herbivorous animals (Tzvelev 1968; Wu and Phillips 2006; Yue et al. 2011; Hu et al. 2015; Nobis et al. 2020). It was described by Grisebach (1868) from western Tibet. This species and several other alpine feathergrasses, such as *S. aliena* Keng, *S. basiplumosa* Munro ex Hook. f., *S. capillacea* Keng, *S. dickorei* M. Nobis, *S. klimesii* M. Nobis, *S. penicillata* Hand.-Mazz., *S. regeliana* Hack., *S. roborowskyi* Roshev., *S. subsessiliflora* (Rupr.) Roshev. and *S. zhadaensis* L.Q. Zhao & K. Guo (Nobis et al. 2014, 2016a, 2020; Zhao and Guo 2017), are distributed in the highest elevations of Central Asian mountains (Nobis et al. 2019a, 2020). *Stipa purpurea* occurs in alpine steppes and semi-deserts, stone slopes, gravel or sand terraces and valley sediments (Yue et al. 2011, Nobis et al. 2020) and is distributed from the Tian Shan and Pamir through Kunlun, Karakorum, Qinghai-Xizang Plateau to the Himalayas (Tzvelev 1968; Lu and Wu 1996; Wu and Wang 1999; Wu and Phillips 2006; Ma and Sun 2018; Nobis et al. 2020) at elevations between 1900 and 5240 m (Noltie 2000; Liu et al. 2008; Yue et al. 2011; Nobis et al. 2020). It is a dominant and diagnostic species of high alpine steppes and, in the north-eastern Qinghai-Tibetan Plateau, creates its own plant community, the so-called *Stipa purpurea* steppes (Yue et al. 2011). The species is also characterised by an extremely high morphological variability. In the past centuries, a several taxa that used to be included within the *S. purpurea* complex, namely, *S. purpurea*, *Lasiagrostis tremula* Rupr., *Ptilagtostis semenovii* Krasn., *S. semenowii* Krasn., *S. semenovii* Krasn., *S. pilgeriana* K.S. Hao and *S. purpurea* var. *arenosa* Tzvel. were described (Grisebach 1868; Ruprecht 1869; Krasnow 1887a, 1887b, 1888; Hao 1938; Tzvelev 1968); however, almost all of them were later synonymised with *S. purpurea* (Roshevitz 1934; Tzvelev 1968, 1976; Kuo and Sun 1982, 1987; Freitag 1985; Wu and Phillips 2006; Nobis et al. 2020). The only exception is *S. purpurea* var. *arenosa*, which was accepted by some authors either in the rank of variety or subspecies within *S. purpurea* (Kuo and Sun 1982; Cui 1996; Lu and Wu 1996; Wu and Wang 1999; Nobis et al. 2016a). In recent years, some studies regarding morphological and genetic diversity of the species (Liu et al. 2008, 2016), seed variability (Li et al. 2015), adaptation to drought (Yang et al. 2015), grazing (Zhai et al. 2015) and prediction of distribution models (Ma and Sun 2018) were conducted. However, all of these were focused on populations of *S. purpurea* in the Qinghai-Tibet Plateau and there is a lack of studies that encompass the whole geographical range of the species. In all of the above-mentioned studies, the authors emphasised that *S. purpurea* is an extremely variable taxon, that varied morphologically in relation to latitude, longitude and altitude (Liu et al. 2008, 2016). The phenomenon of this variability within the geographical range is also well illustrated in the morphological descriptions of the species, which can be found in many identification keys, taxonomic elaborations or local floras. Besides the most variable characters, such as length of culms, length of leaf blades, the number of generative shoots or number of spikelets, which depend on local climate, elevation or grazing intensity in particular geographical regions, the variability is also noted within more conservative, species-specific characters, such as the length of ligules on the vegetative shoots, length of florets and length of glumes (cf. Ovchinnikov and Chukavina 1957; Tzvelev 1968; Bor 1970; Cope 1982; Freitag 1985; Kuo and Sun 1987; Cui 1996; Wu and Wang 1999; Noltie 2000; Wu and Phillips 2006).

During the preliminary revision of specimens representing *Stipa purpurea*, we confirmed the high morphological variability, especially regarding the plant height, the shape and length of ligules, the indumentum of lemma and the length of awns and glumes within specimens originating from different localities. We, furthermore, observed that the variability corresponds to the geographical distribution of particular morphotypes. Therefore, we performed a taxonomic revision of the *S. purpurea* complex across its entire geographical range to answer the questions: i) what is the morphological differentiation of the *S. purpurea* morphotypes within the geographical range of the taxon and which characters are the most conservative for them, ii) what are the differences in the distribution patterns of particular morphotypes within the complex, iii) what are the taxonomic relationships between the observed morphotypes and hitherto described taxa within the *Stipa purpurea* complex and iv) what is their taxonomic position?

Methods

This study is based on plant material preserved in the following herbaria: AA, BM, CUH, E, GOET, K, KRA, KUN, LE, M, MSB, MW, MOIS, NY, P, PE, PR, TAD, TK, TASH (acronyms of the herbaria are used according to Index Herbariorum, Thiers 2022). Over 200 sheets with specimens belonging to *Stipa purpurea* complex (including all available types of taxa from the examined complex, i.e. *S. purpurea* – holotype and isotypes, *Lasiagrostis tremula* – holotype, *Ptilagrostis semenovii* – lectotype and isolectotype, *S. pilgeriana* – holotype and *S. purpurea* var. *arenosa* – holotype and paratypes) were reviewed between 2009 and 2020. For comparison purposes, we also reviewed over 60 sheets with specimens representing *S. roborowskyi* and *S. klimesii*. The numerical analyses were based on 77 specimens from the *S. purpurea* complex (see specimens examined below). All specimens used in the analyses were mature and fully developed. Following the assumptions of numerical taxonomy, each specimen was considered as an operational taxonomic unit (OTU). Measurements were taken using a stereomicroscope (Nikon SMZ800) with a graduated scale eyepiece. Principal component analysis, based on the correlation matrix was used to characterise variation within and among taxa and extract the variables that best identify these taxa. Among 53 morphological characters (including: floret length, length of hairs on the ventral part of the lemma, length of hairs on the dorsal part of the lemma, lemma apex (glabrous/with corolla of hairs and length of hairs), callus length, callus base length and width, length of hairs on the dorsal part of the callus, length of hairs on the ventral part of the callus, awn length, lower segment of the awn length, middle segment of the awn length, terminal segment of the awn length, ratio terminal/lower + middle segment of the awn, width of the awn base, length of hairs on the lower segment of the awn, length of hairs on the middle segment of the awn, length of hairs on the terminal segment of the awn, ratio: length of hairs on the terminal segment of the awn/length of hairs on the lower segment of the awn, length of culms, number of culm nodes, distribution of nodes on the culm, length of ligule on the lower culm sheath, length of ligule on the middle culm sheath, length of ligule on the upper culm sheath, length of the lower glume, length of the upper glume, length of the longest ligules on the external leaf-sheaths on the vegetative shoot, length of the longest ligules on the internal leaf-sheaths on the vegetative shoot, character of the lower culm sheaths (glabrous/pubescent and length of hairs), character of leaf-sheaths on the vegetative shoots (glabrous/pubescent and length of hairs), length of panicle, width of panicle, length of the lower pedicles within the panicle, character of pedicles (flexuous/straight), no. of spikelets within the panicle, length of hairs on the adaxial surface of vegetative leaves, length of hairs on the adaxial surface of culm leaves, character of the abaxial surface of leaves (glabrous, scabrous, pilose), length of the vegetative leaves, length of the culm leaves) measured, scored or estimated, the most variable and important for the species identification and with high factor loadings revealed by the initial principal component analysis (PCA), were chosen for further analyses. In consequence, seven characters with factor loadings ≥ 0.65 (Table 1) were chosen for final PCA and ANOVA analyses. However, the results from all the biometric examinations are presented in morphological descriptions of the examined taxa. Subsequently, descriptive statistics of characters for all recognised groups were calculated. To reveal significant differences between means of characters across all examined groups (after using Levene's test to assess the equality of variances), a one-way analysis of variance (ANOVA) and non-parametric Kruskal-Wallis test followed by post-hoc Tukey's HSD test or multiple comparison test were calculated. The cluster analysis (based on the unweighted pair group method with arithmetic mean) was performed on the basis of seven characters

(Table 1). The similarities among OTUs were calculated using Gower's General Similarity Coefficient. The analyses were performed using Statistica 13 (StatSoft Inc. 2011) and PAST v. 3.12 (Hammer et al. 2001).

Micromorphology

Micromorphological structures of the lemma, sampled from the middle parts of the panicles, were observed in examined species (three specimens per taxon). Samples were coated with gold using a JFC-1100E Ion sputter, manufactured by JEOL and photographed with a Hitachi S-4700 scanning electron microscope, at various magnifications.

Table 1. Morphological characters used in the numerical analyses.

Abbreviation	Character	PCA	UPGMA
AL	Length of the floret (*anthecium*) (mm)	+	+
AwL	Length of the awn (mm)	+	+
CL	Length of the callus (mm)	+	+
C/S	Ratio: length of hairs on column to the length of hairs on seta		+
GL	Length of the lower glume (mm)	+	+
LCL	Length of ligules of the middle cauline leaves (mm)	+	+
LVL	Length of ligules of the vegetative shoots (mm)	+	+
SHL	Length of hairs on the lower cauline sheaths (mm)	+	

Results

Numerical analysis

The Principal Component Analysis (PCA) revealed that six of seven analysed characters have high factor loadings ($r \geq 0.7$, Table 2). The first three components account for 88.23% of the total variation. The first component explains 59.17% of the variation, the second 23.4% and all of the analysed characters, i.e. AL, AwL, CL, C/S, GL, LCL, LVL, SHL, displayed high correlations with the first axis (Table 2). The scatter plot of the first two axes in PCA revealed three non-overlapping clusters of OTUs (Fig. 1), corresponding respectively to the typical specimens of *Stipa purpurea*, *S. tremula* and *S. arenosa* (see Taxonomic treatment below), whereas, the OTUs corresponding to types of *Ptilagrostis semenovii* and *Stipa pilgeriana* were placed within the cloud of OTUs of *S. tremula*, what confirms their high morphological similarity to the letter taxon. The results of the one-way ANOVA/Kruskal-Wallis test revealed significant differences in all examined characters (Table 2) and the most significant values of F and H statistics obtained in the ANOVA and Kruskal-Wallis test were CL, LVL, GL and SHL. The results of the post-hoc tests (Tukey's HSD test for variables with normal distribution and multiple comparison tests for characters with non-normal distribution) are presented in Table 2. Depending on the taxon, different characters were found to be significantly significant; however, all examined characters were suitable for distinguishing at least one pair of taxa. The greatest number of characters differentiated *S. purpurea* from *S. tremula*, whereas *S. arenosa* differentiated from *S. tremula* and *S. purpurea* by six and four characters, respectively (Table 2).

Similarly to PCA, the cluster analysis (UPGMA) performed on the basis of seven characters (Table 2), also resulted in the delimitation of three clusters with OTUs belonging to *S. arenosa*, *S. purpurea* and *S. tremula* (Fig. 2). Within each of the revealed clades, the typical specimens for the three above-mentioned species are present (Fig. 2c). In this analysis, the OTUs of *Ptilagrostis semenovii* and *S. pilgeriana* were also located within the *S. tremula* clade.

Table 2. Results of the Principal Component Analysis (PCA) of the *Stipa purpurea* complex, based on seven morphological characters (the highest factor loadings are in bold); one-way ANOVA with F and p values for characters with normal distribution and Kruskal-Wallis test with H and p values for characters with non-normal distribution (the highest F/H values are in bold); the post-hoc tests (Tukey's HSD for characters with normal distribution and multiple comparison tests for characters with non-normal distribution): + – significant, p < 0.05, ns – not significant (abbreviations: *Stipa purpurea* – pur, *S. tremula* – tre, *S. arenosa* – are). For character abbreviations, see Table 1.

Character	PC1	PC2	PC3	*F* / *H** value	*p* value	post-hoc test		
						pur-tre	pur-are	tre-are
AL	**-0.79**	0.49	0.18	35.65*	<0.05	+	ns	+
CL	**-0.75**	0.51	0.28	**50.10**	<0.05	+	+	+
AwL	**-0.73**	0.44	-0.44	23.81	<0.05	+	+	+
LCL	-0.69	-0.57	-0.18	29.92	<0.05	+	+	ns
LVL	**-0.74**	-0.57	0.06	**97.55**	<0.05	+	+	+
LG	**-0.86**	0.14	-0.11	**44.97***	<0.05	+	ns	+
SHL	**-0.78**	-0.50	0.17	**73.26***	<0.05	+	ns	+
Percent variation (%)	59.17	23.40	5.66					
No. of significant differences						7	4	6

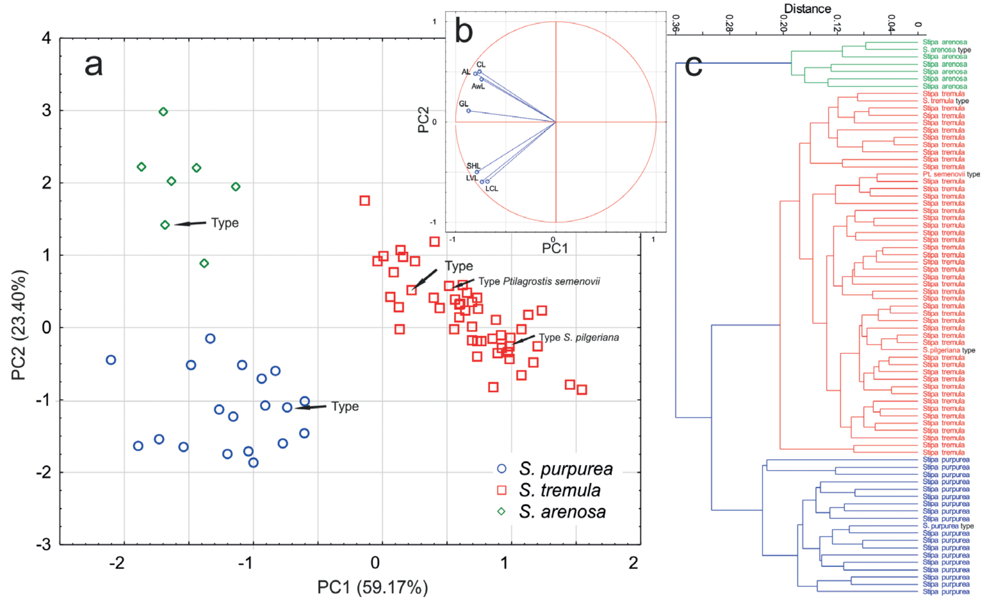

Figure 1. Biplot of the Principal Component Analysis performed on seven quantitative characters: (**a**) with projection of the variables on the factor plane PC1 × PC2; (**b**) and the cluster analysis UPGMA (**c**) of species from the *Stipa purpurea* complex.

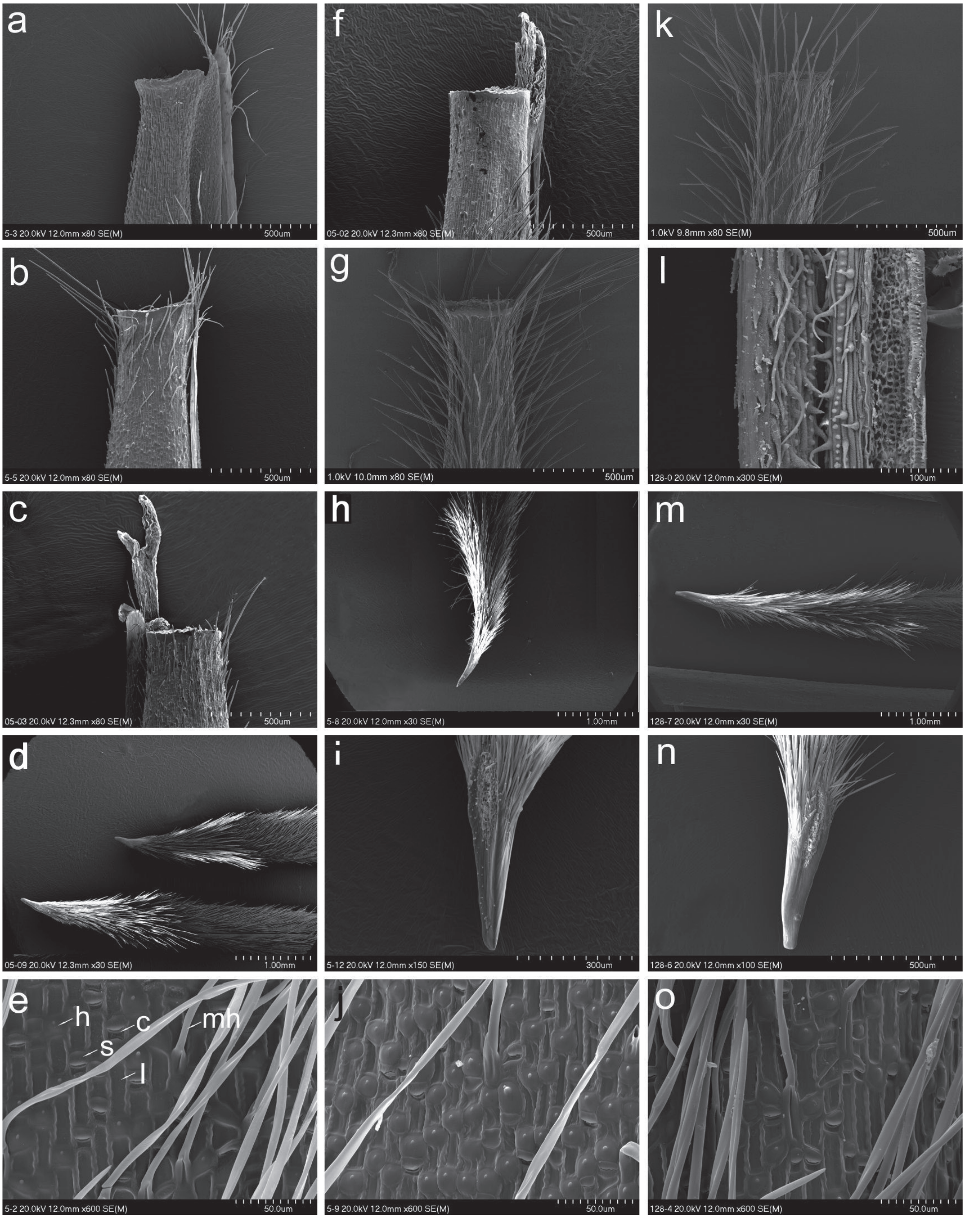

Figure 2. SEM morphology of *Stipa tremula* (**a–e**), *S. purpurea* (**f–j**) and *S. arenosa* (**k–o**). Top of lemma (**a–c, f, g, k**), callus (**d, h, i, m, n**), adaxial surface of leaves (**l**), lemma epidermis (**e, j, o**). Abbreviations: c = cork cell, h = hook, l = long cell, s = silica body, mh = macro-hair. Vouchers: *S. tremula*; Kyrgyzstan, *Pimenov, Kmaishov, Kamsharaeva s.n.* (FRU), Tajikistan, *S.S. Ikonnikov 14896* (LE), China, Shinaihaixiang, *B. Paszko* (KRA); *S. purpurea*: India, *L. Klimeš 619* (KRA), China, *Maizang Team 76-7956* (PE); *S. arenosa*: China, *W.J. Roborowski 318* (KRA 476855), China, *B-z. Guo s.n.* (PE 707226).

Micromorphology of the lemma epidermis

The representatives of the *Stipa purpurea* complex reveal a saw-like lemma epidermal pattern. In all three taxa, the fundamental long cells are rectangular to more or less square (Fig. 2e, j, o). The sidewalls of long cells are raised and undulate. Silica bodies are frequent and ovate to reniform and neighbouring with fairly frequent cork cells. Hooks are frequent and orientated towards the lemma apex, whereas prickles are rather sparse and, if present, occur mostly near the lemma apex. Macro-hairs are straight or bent near the base, (0.05–)0.15–0.80 mm long, cylindrical or string-like and twisted, with a bulbous base and a needle-like apex; they densely cover the lemma surface, from the bottom up to the top. However, the indumentum in the uppermost part of the lemma distinctly varies within and amongt examined species. In specimens of *S. purpurea*, the lemma can be covered by hairs up to the apex (Fig. 2g) or, at the distance of 0.2–0.5 mm to the lemma apex, it is glabrous, surpassed only (but not always) by minute 0.1–0.3 mm long apical lobes (Fig. 2f), whereas, in specimens of *S. tremula*, the lemma is either covered by hairs up to 0.5–1.7(–2.3) mm below the top and above being glabrous (Fig. 2a) or covered by hairs up to 0.5–1.7 mm below the top and above being glabrous, but at 0.2–0.5 mm below the top covered by scattered hairs 0.1–0.8 mm long, creating the corolla (Fig. 2b, c). In *S. arenosa*, all examined specimens have lemmas covered by hairs throughout, from the bottom to the top of the lemma (Fig. 2k).

Distribution range

The clouds of OTUs corresponding with the three examined species, namely *Stipa purpurea*, *S. tremula* and *S. arenosa*, are also well defined by the distribution patterns. The first two seem to be geographical vicariants occupying the highest elevations within the Central Asian Mountains. *Stipa purpurea* occurs mainly within alpine (cryophilous) steppes and semi-deserts, at altitudes between 4000 and 5200 m a.s.l. in south-western China (Xizang) and north India (Ladakh, Sikkim), whereas *S. tremula*, also a species of alpine steppes, occurs at somewhat lower altitudes, between (1900–)3000–4500 (–5100) m a.s.l. within the north-central Asian mountains, in Kyrgyzstan, Tajikistan, north Pakistan, India (Ladakh) and China (Xinjiang, Gansu, Qinghai, Sichuan, western and eastern Xizang; Fig. 3). The ranges of these taxa probably overlap on the area of south-western Qinghai and north-western Xizang and the range borders within the overlapping zones of both species need further studies. *Stipa arenosa* is the rarest taxon within the complex, known only from a few stands in central China (Fig. 3) in the contact zone between *S. purpurea* and *S. tremula*.

Discussion

Although *Stipa purpurea* was described in the middle of the 19th century and has been the subject of many different taxonomical, ecological, phytogeographical and molecular studies (Roshevitz 1934; Tzvelev 1968; Kuo and Sun 1987; Wu and Wang

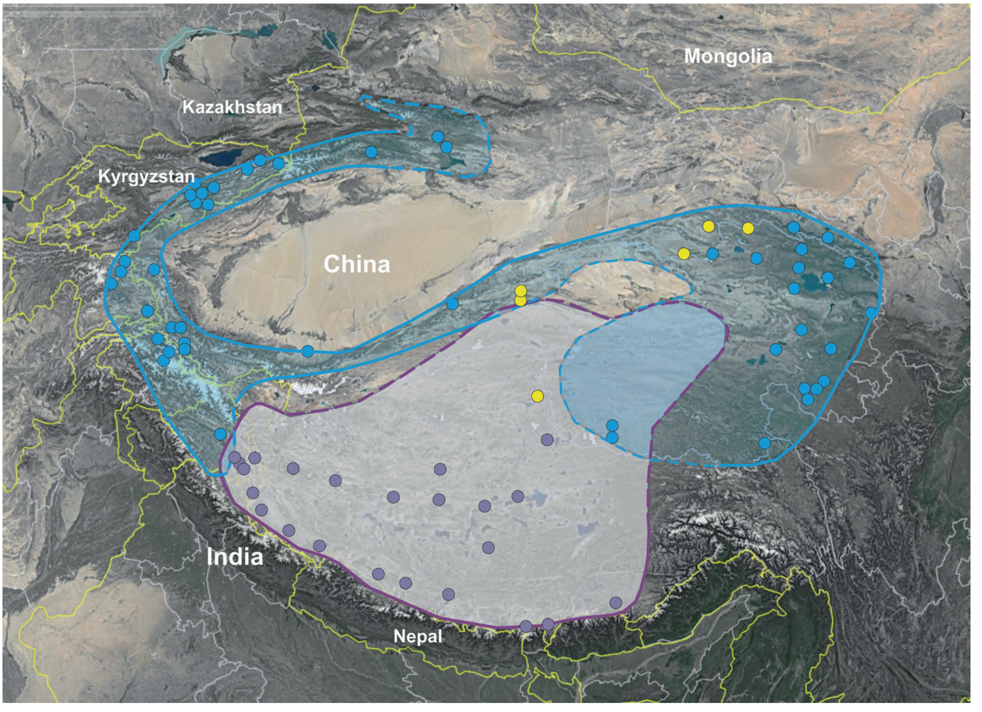

Figure 3. The distribution range of *Stipa purpurea* (purple backgrounds and points), *S. tremula* (blue backgrounds and points) and *S. arenosa* (yellow points).

1999; Wu and Phillips 2006; Liu et al. 2008, 2016; Li et al. 2015; Yang et al. 2015; Zhai et al. 2015; Ma and Sun 2018), to our knowledge, none of them referred to the whole geographical range of the species. Following the description of *S. purpurea* in different (regional) taxonomic treatments (Roshevitz 1934; Nikitina 1950; Ovchinnikov and Chukavina 1957; Kuo and Sun 1982, 1987; Wu and Phillips 2006), we can conclude that *S. purpurea* s.str. was misidentified with *S. tremula* and/or with *S. arenosa*. For instance, Kuo and Sun (1987), Cui (1996) and Wu and Wang (1999) identified the specimens with glumes 17–25 mm long and floret (= *anthecium*: callus+lemma) 12–14 mm long as *S. purpurea* var. *arenosa*, whereas the plants with glumes up to 13–17 mm long, floret 8–10 mm long (and glabrous leaf sheaths, Wu and Wang 1999) as *S. purpurea* var. *purpurea*. Information on the length of ligules on the vegetative shoots are usually not present in morphological descriptions (in Wu and Phillips 2006, the ligules are described as being ca. 1 mm long). The ligules presented on the schematic figures are rather short (ca. 2 mm long in Kuo and Sun 1982, 1987 and Cui 1996) and triangular (somewhat similar to those in *S. tremula*) instead of long and acute as, in fact, are present in *S. purpurea* s.str. (Fig. 4).

Stipa purpurea was transferred by Roshevitz (1934) to the genus *Ptilagrostis* as *P. purpurea* (Griseb.) Roshev.; however, this affiliation was later rejected by the other taxonomists (e.g. Pazij 1968; Tzvelev 1968, 1976; Bor 1970; Kuo and Sun 1987).

The representatives of the examined species from the *S. purpurea* complex reveal a saw-like lemma epidermal pattern, that is typical for representatives of the genus *Stipa* rather than those belonging to *Ptilagrostis* (Barkworth and Everett 1987; Romaschenko et al. 2012; Nobis 2013, 2014; Nobis et al. 2016b, 2019a, 2019b, 2020), whereas the presence of fairly frequent cork cells on the lemma epidermis makes the species more similar to the high mountain, so-called Himalayan feathergrasses from sections *Regelia* Tzvel. or *Pseudoptilagrostis* Tzvel., i.e. *S. regelii*, *S. aliena*, *S. dickorei*, *S. subsessiliflora*, *S. penicillata*, *S. klimesii* or *S. roborowskyi* rather than those from section *Barbatae* A. Junge (Nobis et al. 2015, 2016a, 2019b, 2020), to which the species used to be included (Tzvelev 1974, 1976). This above-mentioned close relationship was also confirmed in molecular phylogenetic studies (Hamasha et al. 2012; Romaschenko et al. 2012; Krawczyk et al. 2017; Nobis et al. 2019c), where *S. purpurea* is placed in one common clade together with other Himalayan species of feathergrasses.

Resurrection of *Stipa tremula*

Stipa tremula was described by Ruprecht (1869) as *Lasiagrostis tremula* and synonymised with *S. purpurea* or with *Ptilagrostis purpurea* by subsequent agrostologists (Roshevitz 1916, 1934; Pazij 1968; Tzvelev 1968, 1976; Bor 1970; Freitag 1985; Kuo and Sun 1987; Wu and Phillips 2006; Nobis et al. 2017, 2020). However, our morphological analysis revealed a set of characters, including the shape and length of ligules of both the vegetative shoots and cauline leaves, characters of sheaths of the vegetative shoots and the lower cauline leaves as well as length of glumes (Fig. 4, Table 3), that led us to distinguish it from *S. purpurea* s.str. and reassess the status of this taxon.

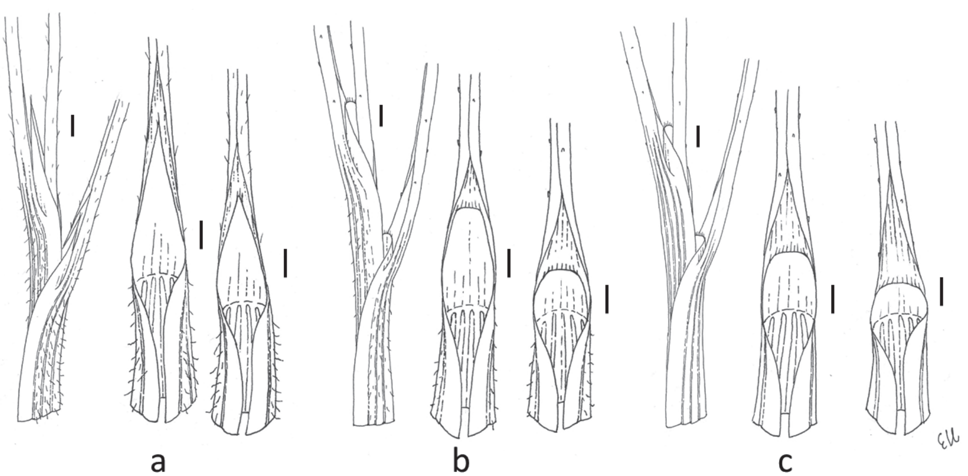

Figure 4. Morphology of the ligules of the internal and external sheaths/leaves of the vegetative shoots in **a** *Stipa purpurea* **b** *S. arenosa* **c** *S. tremula*. Scale bars: 1 mm.

Table 3. A comparison and differences in the main morphological characters of the species from the *Stipa purpurea* complex and allies.

Taxon Character	*Stipa zhadaensis*	*Stipa roborowskyi*	*Stipa klimesii*	*Stipa* × *ladakhensis*	*Stipa tremula*	*Stipa arenosa*	*Stipa purpurea*
Character of sheaths of vegetative shoots	densely pubescent	glabrous and smooth	densely pubescent	densely pubescent	glabrous and smooth	densely pubescent	densely pubescent
The longest ligules on the vegetative shoots [mm]	2–3	0.5–1.5(–2)	(2–)3.5–8(–10)	(1.5–)2–4(–5.5)	(0.5–)1–2(–3)	(1–)1.5–3(–4.5)	(3.8–)4.5–6.5(–8)
Shape of ligules on the vegetative shoots	truncate	truncate	acute	acute	truncate	truncate	acute
Ligules of middle cauline leaves [mm]	ca. 2	(1–)1.5–2.5(–3.5)	(1.5–)2.5–8(–9)	2–4(–5)	(1–)1.5–2.7(–4)	(1.6–)1.9–3.5(–4.5)	(2.2–)4.5–8(–9)
Character of lower cauline leave sheaths	pubescent	glabrous and smooth	densely pubescent	densely pubescent	glabrous and smooth	sparsely pubescent to glabrous	densely pubescent
Panicle	+/- lax	compressed	compressed	+/-compressed	lax	lax	lax
Branches of the panicle	straight	straight	straight	upper straight, lower slightly flexuous	flexuous	flexuous	flexuous
Glumes [mm]	20–28	11–15	13–18	16–19(–20)	(13–)14–17(–19.5)	(19.5–)21–23.5(–25)	(17–)19–26(–28)
Floret [mm]	8–11	(6–)6.5–7.5(–8)	(7–)8.3–9.5(–10.5)	8.5–10.2	(7.5–)8.4–9.5(–11)	(11.5–)12–14(–15)	(8.5–)9.5–11.2(–12.1)
Callus [mm]	ca. 1.5	1.2–2	1.4–2	1.5–1.9	(1.5–)1.6–2(–2.3)	(2–)2.3–3(–3.8)	(1.8–)2–2.4(–2.7)
Awn [mm]	60–90	(40–)47–60(–68)	(25–)35–45(–52)	46–58	(44–)60–74(–90)	(78–)95–112(–130)	(58–)70–91(–105)
Hairs on lower segment of awn (column) [mm]	(0.6–)1–1.5	1.5–2.1	(1.3–)1.5–2(–2.4)	1.7–2.3	(1.3–)1.7–2(–2.3)	(1.5–)1.6–2(–2.3)	(1.5–)1.6–2(–2.2)
Hairs on seta [mm]	0.5–1	(0.3–)0.5–1.1(–1.4)	(1–)1.3–2(–2.3)	1.6–2.1	(1.8–)2.2–2.6(–3.1)	(2.1–)2.3–2.5(–3)	(1.9–)2.1–2.4(–2.7)
Length of hairs on seta to the length of hairs on column	shorter	shorter	shorter	shorter to equal	longer	longer	longer

Within the *S. purpurea* complex, the two additional species, *Ptilagrostis semenovii* (≡ S. *semenovii* and S. *semenowii*) and *S. pilgeriana*, were described respectively by Krasnow [spelled also as Krassnoff or Krassnow] (1887a, 1887b, 1888 [three times!]) from Kyrgyzstan and by Hao (1938) from Gansu in China. However, morphologically, neither taxon differs from *S. tremula* in any of the examined characters. In our analyses, the OTUs of both type species are located in the central part of the cloud within the OTUs of *S. tremula* (Fig. 1); thus, we treat both of them as conspecific with the last-mentioned species.

On the origin of *Stipa arenosa*

Stipa arenosa was described in the rank of variety as *S. purpurea* var. *arenosa* by Tzvelev (1968), who distinguished it from the typical variety, based on the longer glumes (17–22 vs. 12–17 mm long), longer florets (12–13 vs. 8–11 mm long) and longer awns (8–9 vs. 6–8.5 mm long). In our morphological analyses, the OTUs of *S. arenosa* were clustered separately from those of *S. purpurea* and *S. tremula*. The main characters that distinguish *S. arenosa* from *S. purpurea* and *S. tremula* are the length of the floret and the length of callus (Table 3). The other characters are rather intermediate between *S. purpurea* and *S. tremula*. Unlike *S. tremula*, *S. arenosa* has much longer glumes, 19.5–25 mm long and more or less pubescent sheaths of both vegetative and cauline leaves, which makes it similar to *S. purpurea*; however, the presence of fairly short and truncate ligules makes it more similar to *S. tremula* than to *S. purpurea* (Tables 2, 3). These characters may suggest that the taxon originated from hybridisation between *S. tremula* and *S. purpurea*, whereas the presence of such long florets (longer than in both putative parental species) may be a result of genome duplication, which sometimes happens in hybrids and is called as the Gigas effect (Stebbins 1971; Levin and Donald 2002; Soltis et al. 2014; Meeus et al. 2020). Nevertheless, the putative hybrid origin of *S. arenosa* requires confirmation using karyological and integrative morpho-molecular methods, such as those used recently to confirm the origin of other hybrids and cryptic taxa of feathergrasses (Nobis et al. 2019c; Baiakhmetov et al. 2020, 2021; Nie et al. 2020; Tkach et al. 2021).

Taxonomic treatment

A key to the identification of species from the *Stipa purpurea* complex

key 1

1	Sheaths of the vegetative shoots and the lower cauline leaves always glabrous and smooth, glumes (13–)14–17(–19.5) mm long	***S. tremula***
–	Sheaths of the vegetative shoots and the lower cauline leaves more or less densely and shortly pubescent (rarely almost glabrous), glumes (17–)19–26(–28) mm long..	**2**
2	Floret (*anthecium*) (8.5–)9.5–11.2(–12.1) mm long, the longest ligules on the vegetative shoots (3.8–)4.5–6.5(–8.0) mm long, acute with a few cilia at the apex, sheaths of the lower cauline leaves always densely and shortly pubescent...	***S. purpurea***
–	Floret (11.5–)12–14(–15) mm long, the longest ligules on the vegetative shoots (1.0–)1.5–3.0(–4.5) mm long, truncate to slightly acute and ciliate on the apex, sheaths of the lower cauline leaves more or less densely and shortly pubescent rarely almost glabrous...	***S. arenosa***

key 2

1	Sheaths of the lower cauline leaves densely and shortly pubescent, the longest ligules on the vegetative shoots (3.8–)4.5–6.5(–8.0) mm long, acute with a few cilia at the apex...	***S. purpurea***
–	Sheaths of the lower cauline leaves glabrous and smooth or rarely sparsely and shortly pubescent, the longest ligules on the vegetative shoots (0.5–)1.0–3.0(–4.5) mm long, truncate to slightly acute and ciliate at the apex...........	**2**

2 Floret 7.5–11 mm long, sheaths of the vegetative shoots and the lower cauline leaves always glabrous and smooth, glumes (13–)14–17(–19.5) mm long, the longest ligules on the vegetative shoots (0.5–)1.0–2.0(–3.0) mm long, truncate and ciliate on the apex .... ***S. tremula***

– Floret (11.5–)12–14(–15) mm long, sheaths of the vegetative shoots and the lower cauline leaves more or less densely and shortly pubescent (rarely almost glabrous), glumes 19.5–25 mm long, the longest ligules on the vegetative shoots (1.0–)1.5–3.0(–4.5) mm long, truncate to slightly acute and ciliate on the apex .... ***S. arenosa***

Stipa purpurea **Griseb., Nachrichten von der Königlichen Gesellschaft der Wissenschaften und der Georg-Augusts-Universität zu Göttingen 3: 82–83. 1868.**

≡*Ptilagrostis purpurea* (Griseb.) Roshev., Fl. URSS 2: 76. 1934

Type protologue. T. Nari Khorsum, *H. v. Schlagintweit*. **Type:** [China] Tibet, Gnari (Nari) Khorsum, alt. 5000 m, 5–15 Sep 1855, *Schlagintweit 7116* (holotype, GOET!; isotypes, BM 959325!, K 000032088!, LE 9281!, P!).

Description. ***Perennial plants***, densely tufted, with a few culms and numerous vegetative shoots; culms (11.5–)16.0–37.2(–60.0) cm tall, 1–2(–3)-noded, nodes distributed close together in the lowermost part of the culm. ***Leaves of vegetative shoots*****:** sheaths shortly and densely pubescent; ***ligules*** acute, with few cilia at the apex, on the external sheaths (1.5–)3.5–4.5(–6.0) mm long, whereas on the internal sheaths (3.8–)4.5–6.5(–8.0); ***blades*** convolute, green, pale green to greyish, (4.2–)6.0–14.0(–20.0) cm long, 0.3–0.5(–0.7) mm in diameter, adaxial surface covered by dense, 0.15–0.25 mm long hairs, abaxial surface glabrous, scabrous or shortly pilose (grading to almost smooth towards the apex). ***Cauline leaves*****:** lower sheaths densely and shortly pubescent, middle and upper sheath shortly pubescent or glabrous; ***ligules*** acute, on the lower sheaths (2.0–)4.0–7.2(–8.0) mm long, on the middle sheaths (2.2–)4.5–8.0(–9.0) and on the upper sheaths (3.5–)4.8–8.1(–9.2); ***blades*** convolute, green, pale green or greyish (4.5–)4.7–6.1(–7.8) cm long, adaxial surface covered with short hairs, abaxial surface glabrous, scabrous to shortly pubescent. ***Panicle*** (3.5–)9.7–17.5(–20.0) cm long, open, with (3–)6–15(–20) spikelets, at base enclosed by the sheath of the uppermost leaf; branches ascending, flexuous setulose, slightly scabrous, to glabrous and smooth, single or paired, 2–6 cm long. ***Glumes*** subequal (the lower slightly longer than the upper), purplish, (17–)19–26(–28) mm long, lanceolate, with hyaline margins and long tip. ***Floret*** (lemma + callus) (8.5–)9.5–11.2(–12.1) mm long and up to 1.0 mm wide. ***Callus*** (1.8–)2.0–2.4(–2.7) mm long, densely pilose, on ventral part with hairs (0.4–)0.6–0.8(–1.0) mm long, on dorsal with (0.4–)0.5–0.7(–0.8) mm long hairs; callus base 0.5–0.8 mm long and 0.15–0.20 mm wide, sharply pointed, scar narrow-elliptic. ***Lemma*** coriaceous, straw-coloured, purplish or brownish, covered throughout (from the bottom to top) by dense ascending to appressed hairs 0.3–0.8 mm long or the uppermost part of lemma, at 0.2–0.5 mm to the top, completely glabrous (hairless); ***top of lemma*** glabrous or surpassed by a ring of unequal hairs 0.2–0.8 mm long and with (or without) two minute apical lobes 0.1–0.3 mm long. ***Awn*** (58–)70–91(–105) mm long, bigeniculate; ***the lower segment of the awn*** (column) (6.5–)10–13(–16) mm long, twisted, 0.3–0.4 mm wide near the base, with (1.5–)1.6–2.0(–2.2) mm long hairs, ***the middle segment*** of the awn (7–)8–9(–10) mm long, twisted, with (1.7–)2.0–2.3(–2.5) mm long hairs; ***terminal segment*** (seta) slightly arcuate or flexuous (40–)50–69(–80) mm long with hairs longer than those on the column, (1.9–)2.1–2.4(–2.7) mm long, gradually decreasing in length towards the apex. ***Palea*** equalling lemma in length. ***Ovary*** with two styles.

Habitat. High mountain steppes, semi-deserts, stony slopes, gravelly or sandy flats and valley silt, 4000–5200 m a.s.l.

Distribution. Himalayas, southern Karakorum, Tibetan Plateau (Fig. 3); China (Xizang), India (Ladakh, north Sikkim) (Noltie 2000; Liu et al. 2008; Ma and Sun 2018).

Selected specimens examined. China: Xizang Province, Rebang, Ritu County, alt. 4300 m, 28 Aug 1976, *Xizang Team 76-9126* (PE); east of Ando County, around transit station 23, flat landscape, 3 Aug 1961, *S. Wang 3698* (PE); Ali District, Gaer County, Menshi, gritty hillside, 9 Jul 1976, *Maizang Team 76-7956* (PE); Aligaize County, plateau, alt. 4450 m, Aug 1978, *F. Li 015* (PE 707342); Geji County, hillside, *no. 13545* (PE); Zuozuo District, Gar County, Langjiu, Ali, alt. 4650–4700 m, grassland, 10 Aug 1976, *Qing Zang team 76-8646* (PE 707397); alt. 4600 m, 17 Sept 1976, *no. 10333* (PE 707387); alt. 4700–5000 m, 1 Sept 1976, *no. 10106* (PE 707334); alt. 5000 m, 19 Jul 1976, *Xizang team 76-8541* (PE 707339); alt. 4900 m, 21 Aug 1976, *Xizang team 76-9102* (PE 707338); alt. 4400 m, 9 Jul 1976, *Xizang team 76-7956* (PE 707336); alt. 4800 m, 24 Jul 1976, no. 9819 (PE 707332); alt. 5100 m, 13 Sept 1976, *no. 9032* (PE 707337); Xizang Province, alt. 5050 m, 1 Aug 1976, no. 4900 (PE 707390); alt. 5000 m, 17 Aug 1976, no. 10025 (PE 707393); Ritu County, Rebang, gritty land, alt. 4300 m, 28 Aug 1976, *Xizang team 76-9126* (PE 707345); Purang County, Huoer, north slope, hillside grassland, alt. 4860 m, 22 Jul 1976, *Qing zhang team 76-8569* (PE). **India:** NW India, Jammu and Kashmir State, Ladakh, Rupshu, Samad Rokchen, Valley to Rang, alt. 4810–4900 m, 33°15.2'N, 78°05.7'E, 5 Aug 2001, *L. Klimeš 1262,1263* (KRA); NW India, Jammu and Kashmir State, Ladakh, Rupshu, Tso Moriri, slopes along the Luglung River, alt. 5200 m, 23 Aug 1999, 33°2'N, 78°27'E, *L. Klimeš 619* (KRA); NW India, Jammu and Kashmir State, Ladakh, Rupshu, Samad Rokchen, crossing Thukje - Polokongka, Polokongka - Nuruchan, alt.4630–4660 m, 5 Aug 2001, 33°16.6'N, 78°4.6' E, *L. Klimeš 1260* (KRA 479102); Sikkim, Naku La, alt. 16000 ft, 2 Nov 1909, *Ribu & Rhomoo 2769* (CUH).

Stipa tremula **(Rupr.) M. Nobis, comb. nov.**

urn:lsid:ipni.org:names:77297804-1

= *Ptilagrostis semenovii* Krasn. [originally *P. semenovi* Krassn.], Spisok rastenii sobrannykh v vostochnom Tyan-Shane, letom 1886 goda, 125, 1887. Type protologue: Prope fl. sary-Jassy. Type: Ptilagrostis tianschanica Krassn., Ad flumen Sary-Jassy, 1 Aug 1886, *Krassnow s.n.* (lectotype, distinguished here, LE 01009431!, isolectotype, LE 01009430!);

≡ *Stipa semenowii* Krasn. [originally *S. semenowi* Krassn.], Scripta Botanica Horti Universitatis Imperialis Petropolitanae, Botanicheskiia Zapiski 2(1): 22. 1887. Type protologue: In valle fluminis Sary-Jassy in montibus Thian-Schan non procul ab alpe Chan-tengri et in trajectu Turguen-Aksu non rara;

≡ *Stipa semenovii* Krasn. [originally *S. semenovi* Krassn.], Zapiski Imperatorkago Russkago Geograficheskago Obschestva, Opyt' istorii rasvitya flory yuzhnoi chasti vostochnago Tyan-Shanya 19: 341–342. 1888. Type protologue: In valle fluminis Sary-Jassy in montibus Thian-Schan non procul ab alpe Chan-tengri et in trajectu Turguen-Aksu non rara.

= *Stipa pilgeriana* K.S. Hao, Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 68(5): 583–584. 1938. Type protologue: China: Kokonor [Qinghai]: Ming-ke-Shan, Tsi-gi-gen-ba-Gebiete, 3900 m (Nr. 1009 – am 25 August). Type: Kokonor [Qinghai], Mingke, Tsigigenpa, alt. 3900 m, 25 Aug 1930, *Hopkinson 1009* (holotype, PE 707247 [additional no. on the sheet 01940135], [label 2: *S. pilgeriana* Hao sp. nov.]).

Basionym. *Lasiagrostis* (*Leptanthele*) *tremula* Rupr., in Ost.-Sack. & Rupr., Sertum Tianschanicum, Mémories de L'Académie Impériale des Sciences de St.-Pétersbourg, Sér. 7, 14(4): 35. 1869.

Type protologue. Die Gegend des Sarymeki-Flüsschens, 28 Jul 1867, *F. Osten-Sacken s.n.* **Type.** [China] In der Gegend des Flusses Sarymeki, Südlicher Abhang des Tian-Schan, in regione subalpina jugi Thian-Schan, 28/9 Julio 1867, Lib. Baro *Fr. Osten-Sacken s.n.* (lectotype, designated by Tzvelev 1976: 583, LE 01009426!, isolectotypes, P 02241060!, K 000587435!).

Description. ***Perennial plants***, densely tufted, with a few culms and numerous vegetative shoots; culms (11–)20–30(–45) cm tall, 1–2(–3)-noded, nodes distributed close together and only in the lowermost part of the culm. ***Leaves of vegetative shoots*****:** sheaths glabrous and smooth rarely sparsely and shortly pubescent; ***ligules*** truncate, ciliate on the apex, on the external sheaths (0.3–)0.7–1.1(–1.6) mm long, whereas on the internal sheaths, (0.5–)1.0–2.0(–3.0) mm long; ***blades*** convolute, green, pale green to greyish, (3–)4–12(–18) cm long, 0.3–0.5(–0.7) mm in diameter, adaxial surface densely covered by 0.15–0.25 mm long hairs, abaxial surface glabrous or scabrous to shortly pilose and grading to almost smooth towards the apex. ***Cauline leaves*****:** sheaths glabrous and smooth; ***ligules*** on the lower sheaths truncate or acute (0.4–)1.0–1.5(–2.1) mm long, on the middle and upper sheaths acute (1.0–)1.5–2.7(–4.0) and 2.0–3.1(–3.6), respectively; ***blades*** convolute, green, pale green or greyish (2.3–)2.0–3.0(–8.9) cm long, adaxial surface covered with short hairs, abaxial surface glabrous, scabrous to shortly pubescent. ***Panicle*** (7–)11–18(–26) cm long, open, with (3–)6–15(–18) spikelets, at base enclosed by the sheath of the uppermost leaf or rarely exerted; ***branches*** ascending, flexuous, setulose, slightly scabrous to glabrous and smooth, single or paired, 2–6 cm long. ***Glumes*** subequal (the lower slightly longer than the upper), purplish, (13.0–)14–17.0(–19.5) mm long, lanceolate, with hyaline margins and long tip. ***Floret*** (lemma + callus) (7.5–)8.4–9.5(–11.0) mm long and (0.7–)0.8–1.0 mm wide. ***Callus*** (1.5–)1.6–2.0(–2.3) mm long, densely pilose, on ventral part with hairs (0.4–)0.5–0.8(–1.0) mm long, on dorsal with (0.3–)0.4–0.6(–0.8) mm long hairs; callus base 0.5–0.8 mm long and 0.15–0.25 mm in diameter, sharply pointed, scar narrowly elliptic. ***Lemma*** coriaceous, pale-green, purplish or brownish, covered throughout, from the bottom up to 0.5–2.3 mm to the top, by dense ascending to appressed hairs 0.3–0.8 mm long, above being glabrous (hairless) or with scattered hairs just below the apex; ***top of lemma*** glabrous or surpassed by a poorly- to well-developed ring of unequal hairs 0.2–0.5 mm long and with (or without) two minute apical lobes. ***Awn*** (44–)60–74(–90) mm long, bigeniculate; ***the lower segment of the awn*** (column) (6–)11–15(–20) mm long, twisted, 0.3–0.4 mm wide at the base, with (1.3–)1.7–2.0(–2.3) mm long hairs, ***the middle segment of the awn*** (5–)6.5–10(–13) mm long, twisted, with (1.6–)2.0–2.3(–2.6) mm long hairs; ***terminal segment of the awn*** (seta) slightly arcuate or flexuous (26–)39–53(–73) mm long with hairs longer than those on columns, (1.8–)2.2–2.6(–3.1) mm long, gradually decreasing in length towards the apex. ***Palea*** equalling lemma in length. ***Ovary*** with two styles.

Habitat. High mountain steppes, dry grasslands, mats, screes, semi-deserts, stony slopes, gravelly or sandy flats and valleys (1900–)3000–4800(–5100) m a.s.l.

Distribution. Tian Shan, Pamir, Karakorum, eastern Himalayas, Kun-lun, Qilan-Shan, eastern Tibetan Plateau (Fig. 3); Kazakhstan, Kyrgyzstan, Tajikistan, north Pakistan, India (Ladakh), China (Xinjiang, Gansu, Qinghai, Sichuan, western and eastern Xizang) (Pavlov 1956; Ovchinnikov and Chukavina 1957; Lazkov and Sultanova 2014).

Note. *Lasiagrostis tremula* was described from Tian-Shan Mts. by Ruprecht (in Osten-Sacken and Ruprecht 1869), based on the collection of Fr. Osten-Sacken (without indication of type, place of its preservation and the collection number). During the revision of the herbarium material of *Stipa purpurea* s.l., we found three sheets with specimens of *Lasiagrostis tremula* collected by Osten-Sacken, of which the one preserved in LE, previously regarded as type by Tzvelev 1976, Freitag 1985 and Nobis et al. 2020) is here corrected to lectotype. The duplicates preserved in K and P are isolectotypes.

Selected specimens examined. Kyrgyzstan: Tsentralnyi Tyan'-Shan', dolina r. Kuilyu bliz ust'ya r. Oroi-su, na rechnoi terrase, alt. 2100 m, 10 Aug 1956, *I.S. Pushkin s.n.* (MW 803233, 803232); Tian-Schan centr., in valle flum. Sary-tschat, prope glaciem Kolpakovskyi, orientem versus a statione meteorologica, steppum frigidum, alt. ca. 3400 m, *D. Wyschiwkin s.n.* (MW 803231, US 04002929, P 02662772); Narynskii raion, bassein r. Aksai, khr. Kok-kiya, kobrezovyi lug, 15 Aug 1926, *M. Sovetkina, M. Uspenskaya 1745* (MW 803 229); Issykulskie syrty, kovyl'. step, alt. ca. 4000 m, 16 Aug 1953, *N. Trulevich s.n.* (MW 803234); Issykulskie syrty, kovyl'. step, alt. ca. 3000 m, 16 Aug 1953, *N. Trulevich s.n.* (MW 803228); Semirech. obl. Przhevalsk. u. dolina r. Naryna mezhdu r. Bashka-Su i r. Ulan', kamenistye sklony, 20 Jul 1913, *V. Sapozhnikov*

252 (LE); Semirech. obl. Przhevalsk. u. r. Ak-tash', plato, alpiiskaya pustyn. step', 28 Jul 1913, *V. Sapozhnikov 250* (LE, TK); Issyk-Kulskaya obl., Ak-Sulskii raion, khr. Teskei Ala-Too, pravyi bereg r. Sary-Dzhaz, 10 Aug 1988, *Pimenov, Kmaishov, Kamsharaeva s.n.* (KRA, FRU); Naryn prov., At-Bashii reg., Ken-Suu r., 15 Aug 1976, *Abgarova s.n.* (KRA); Tian'-Shan', dolina r. Kuelyu, prav. prit. Sary-Dzhasa, 20–30 Jul 1902, *V. Sapozhnikov s.n.* (LE, TK); Dzhety-Oguzovskii region, Akshiryak, 6–7 km NE of Uzun River, terrace of Cholak River, alt. 3800 m, high mountain steppe, 26 Jul 1935, *I Sanych, G. Sabardina 121* (BM 1191534); Dolina Aksya, Poima r. Terek, Ken-Suu, 1960, *Makarenko s.n.* (FRU, KRA); Semirech. obl. Przhev. u r. Inyl'chek, v 10 v. ot' lednika, 1 Aug 1912, *V. Sapozhnikov, B. Shishkin s.n.* (LE); C Tian'-Shan', verkhie Narynskie syrty, ur. Kum-tala, 23 Aug 1926, *R.I. Abolin 1034* (LE); Semirech. obl. Przhev. u r. Sarydzhas', pri usti r. Myntur', syrty, 28 Jul 1912, *V. Sapozhnikov, B. Shishkin s.n.* (LE, TK, AA); Tian'-shanskaya obl., Terskei khr., pravyi bereg r. Sary-dzhaz, uste r. Kuisyu, 19 Jul 1967, *Pavlova s.n.* (LE); Issykulskaya obl. Pokrovskie syrty, Aug 1957, *Moldoyarov s.n.* (LE); Semirech. obl. Przhev. u r. Dzhangart' srednee techenie, travyanistye sklony, 31 Jul 1913, *B. Shishkin s.n.* (TK); Semirech. obl. Przhev. u Kara-Archa, kamenistye sklony, 6 Aug 1912, *V. Sapozhnikov, B. Shishkin s.n.* (TK); C Tian'-Shan', Khr. Bornokoi, basein r. Karakol, alt. 3700 m, 1949, *M. Tlo[..] s.n.* (AA); Tyan'-shanskaya obl. At-bashinsii raion, bass. r. Ak-saya, stats. Cykanova, Jul 1972, *Nemetskaya s.n.* (FRU); Atbashinskii raion, dolina Ak-sai, pologie sklony, 31 Jul 1939, *Gusarova s.n.* (FRU). **Tajikistan:** Pamir, Kara-kul, dol. Kara-Art, v 5 km ot ust'ya na terrase, alt. 4050 m, 28 Aug 1962, *S.S. Ikonnikov* 14896 (LE, KRA 479099); Pamir, ad lacum Kara-kul, alt. 13500 ft, 5 Jul 1901, *Alexeenko 1392* (LE); Pamir, Shad-Put, peski nizovev dol. r. Up-turukh, alt. 4000 m, 19 Jul 1945, *I. Raikova 159* (LE); Pamir, Rang-Kulskii c/c, 1952, *Sudorov s.n.* (LE); SE Pamir, zap. sklon Ak-tash, Shaimak settl., 29 Aug 1953, *S. Ikonnikov s.n.* (LE); Shot-put, Rang-Kulkii c/c, 20 Jul 1945, *I. Raikova 161* (LE); Pamir, Kara-kul', po krayu lugov u reki Kara-art, 20 Aug 1955, *Sudorov s.n.* (LE). **Pakistan:** S side of Pamir Pass, near Shuwart, alpine steppe, dominated by Gramineae and flat cushions of *Oxytropis* spp., pastures and flushes, grazed, 36°23–25'N, 75°41–43'E, alt. 4420–4520 m, 16 Aug 1991, *G. & S. Miehe 6173* (GOET); Upper Braldu tributary, above Chikor, alpine steppe, dominated by Gramineae and flat cushion of *Oxytropis* spp., 36°22–24'N, 75°22–24'E, alt. 4220 m, 17 Aug 1991, *G. & S. Miehe 6209* (GOET); Khunjerab-pass, alpine steppe, 36°50'N, 75°25'E, alt. 4460 m, 18 Aug 1990, *G. & S. Miehe 2495* (MSB 154127). **India:** NW India, Jammu and Kashmir State, Ladakh, Zanskar, Markha, Hankar Village to Zalung Karpo La, W slopes of Kyangze, alt. 4700 m, 20 Aug1998, 33°44,5'N, 77°29'E, *L. Klimeš* 86 (KRA 479097). **China: Xinjiang province**, Qira Xian, Nor, Yamei, on slope grassland, alt. ca. 3100 m, 3 Jul 1988, *S. Wu, H. Ohba, Y. Wu, Y. Fei 2532* (MOIS 4374351); Qiemo Xian, Kongqibulaker, on desert grassland, alt. ca. 3200 m, 19 Jul 1988, *S. Wu, H. Ohba, Y. Wu, Y. Fei 2591* (MOIS 5660759); alt. 4050 m, 8 Aug 1959, *no. 1685* (PE 707259); 26 Aug 1965, no. 39181 (PE 707280); Qiemo Xian, Kongqibuaker, on arid soil slope, alt. ca. 4000 m, 26 Jul 1988, *S. Wu, H. Ohba, Y. Wu, Y. Fei 2103* (MOIS 4364181); Qiemo Xian, Kongqibulaker, on sparsely grass-covered hill slope, alt. ca. 3150 m, 19 Jul 1988, *S. Wu, H. Ohba, Y. Wu, Y. Fei 2056* (MOIS 4373368); SW Xinjiang, Karakoram, Aghil Shan northern declivity, ca. 7 km northwest of Aghil Pass, gravelly slope, limestone, 36°14'N, 76°34'E, alt. 4200 m, 30 Aug 1986, *B. Dickoré 487* (GOET); SW Xinjiang, Karakoram, Aghil Shan northern declivity, Aghil Valley, at the Kirghiz summer settlement, ca. 19 km SW of Ylik (Yarkand), north-facing limestone cliff, in fissures, 36°15'N, 76°33'E, alt. 4150 m, 29 Aug 1986, *B. Dickoré 472* (GOET); SW Xinjiang, Karakoram, Aghil Shan northen declivity, ca. 3 km NWW of Aghil Pass, gravelly slope, between granite boulders, dry alpine "turf", 36°13'N, 76°35'E, alt. 4520 m, 30 Aug 1986, *B. Dickoré 513* (GOET); Tibet borealis, ozero Orich-nor, yuzhn. bereg, alt. 13500 ft, 18 Jul 1884, *N.M. Przwalski 338* (LE), Kam (Tibet), basein Yan-tszy-tszyan'a (r. Goluboi), 1 Aug 1900, *V.O. Ladygin 434* (LE); Kun-lun, Kashgaria, verkhov'e r. Lapet, 20 Jul 1942, V.I. Serpukhov 474 (LE); Kun-lun, Kashgaria, r. Kara-dshilga, levyi pritok r. Gon-arek, alt. 4000–4500 m, 22 Jul 1942, *V.I. Serpukhov 508* (LE); **Gansu Province**, Yumu Mountain, Dahe District, Sunan County, dry hillside, 5 Aug 1967, *Hexi Team 165* (PE); Kansu, alt. 2600 m, 25 Aug 1967, *no. 274* (PE 707218); Kansu, Richthofen (Nan-Shan), Hung-Shui-Pa-Shang-Ho, alt. ca. 3500 m, 28 Aug 1931, *B. Fries-Johansen 2878* (BM 1031149, 1191537); **Qinghai Province**, Haixi Mongol and Tibetan Autonomous Prefecture, stone gap, alt. 3000 m, 28 Jul 1975, *W. Wong, B. Guo 11742* (PE); near the road G109, 18 km SW of the lake, NE of Dashi Bridge, 3617 m, 36°43'34"N, 99°34'51"E, 24 Jul 2010, *B. Paszko s.n*. (KRA); Mengnan County, Qingshui Town, dry slope, alt. 3100 m, 26 Aug 1975, *W. Wang, Be-z. Guo 12192* (PE); Qaidam, kumirnya Dulan'-Khiti, alt. 10100 ft, 12 Aug 1901, *V.O. Ladygin s.n*. (LE); Yeningou North Mountain, Qilian County, meadow, alt. 3400 m, 5 Sep 1975, *W. Wang, B-z. Guo 12473* (PE 707250); alt. 3700 m, 4 Sep 1975, *W. Wang, B-z. Guo 12411* (PE 707242); alt. 3600 m, 10 Aug 1975, *W. Wang, B-z. Guo 12053* (PE 707240); Dari Xian: Jimai Xian, Huleanma, along Huang, flood plain of Hunag He, tussock grass, 33°43'40"N, 99°21'1"E, alt. 4030 m, 11 Aug 1993, *T-n. Ho, B. Bartholomew 1158* (PE 707267, BM 573601); Shinaihaixiang, alt. 3230 m, 36°59'26,9"N, 99°36'03,0"E, 24 Jul 2010, *B. Paszko s.n*. (KRA); Tibetan Autonomous Prefecture of Haibei, hillside, alt. 3300 m, 29 Aug 1975, *W. Wang, B-z. Guo 12262* (PE 707241); Menyuan County, Gingshizui, dry hillside, alt. 3200 m, 24 Aug 1975, *W. Wang, B-z. Guo 12176* (PE); Qinghai, C Tibet, Tangula Shan N, Upper Yangtse Basin, Bi Qu, Wenquan - Yanshiping (Lhasa – Golmud Rd.), 33°31'N, 91°58'E, alt. 4800 m, 18 Aug 1989, *B. Dickoré 4207* (MSB 152888); Qinghai, C Tibet, Tangula Shan N, Upper Yangtse Basin, Gar Qu Vy. (Mt. Geladandong – Yanshiping), 33°36'N, 91°44'E, alt. 4850 m, 2 Sept 1989, *B. Dickoré 4617* (MSB 152889); Heka area of Xinghai County in Qinghai, dry slope, 35.9 N, 99.9 E, alt. 3300 m, Jul 1965, *P-c. Kuo & T-n. Ho 65-6111* (GOET); Gande (Gadê) Xian, near Shanggongma Xiang, Gande (Gadê) Shan, on road from Dari (Darlag) to Gande (Gadê), flat-bottomed valley with moist alpine meadows on bottom, slopes with rocky outcrops and thick turf, on grassy slope, alt. 4150 m, 33°53'45"N, 99°40'50"E, 9 Aug 1993, *T. Ho, B. Bartholomew & M. Gilbert 952* (E 690603, BM 000573603); Madoi Xian: just E of Malayiwan, on road between Gonghe and Madoi, open *Stipa purpurea* steppe on sandy soil, alt. 4050 m, 35°0'N, 98°30'E, 10 Aug 1996, *T. Ho, B. Bartholomew, M. Watson & M. Gilbert 1585*

(E 125866, PE 707271, BM 573604); Maquin (Maqên) Xian, Naheqingma, Youyun Xiang, between Dari (Darlag) and Huashuxua, consolidated sand dunes with disturbed flat areas, alt. 4190 m, 33°18'39"N, 99°10'53"E, 17 Aug 1993, *T. Ho, B. Bartholomew & M. Gilbert 1342* (E 690703, BM 573602); Dari (Darlag) Xian: Huleanma, Jianshe Xiang, S side of the Huang He and SW of confluence with the Dari He (Dar Qu), flood plain of the Huang He, tussock grass, alt. 4030 m, 33°43'N, 99°21'E, 11 Aug 1993, *T. Ho, B. Bartholomew & M. Gilbert 1158* (E 690604); Maquin (Maqên) Xian, Dawu Xiang, along the Gequ He, N of Maquin (Maqên), Jiangrang, side of valley with steep slope, mostly dry with large tussock grasses and bare soil, shallower slopes with alpine meadow, areas of deeper soil with shrubs, on slope, alt. 3500 m, 34°42'28"N, 100°14'39"E, 31 Jul 1993, *T. Ho, B. Bartholomew & M. Gilbert 623* (E 690605, PE 707268, BM 573600); Yushu Xian, Xiao Surmang Xiang, between Jerikug and the Xizang border, alt. 3550–3650 m, 32°6'N, 97°16'E, 24 Aug 1996, *T. Ho, B. Bartholomew, M. Watson & M. Gilbert 2315* (E 61899); Near the camp XLIV in E Tibet, 15 Jul 1901, *Sv. Heidin 5127* (BM 001191536); **Xizang Province**, near Ranwu District, Basu County, alt. 4000 m, 18 Aug 1980, *no. 1231* (PE 707340); Tibet, alt. 5100 m, 27 Aug 1963, *no 1989* (PE 707466).

***Stipa arenosa* (Tzvelev) M. Nobis, P.D. Gudkova, Krzempek & Klichowska, comb. and stat. nov.**

urn:lsid:ipni.org:names:77297806-1

≡ *Stipa purpurea* subsp. *arenosa* (Tzvelev) D.F. Cui, Flora Xinjiangensis 6: 307. 1996.

Basionym. *Stipa purpurea* var. *arenosa* Tzvelev, Rastenia Tsentral'noi Azii po materialam Botanicheskogo Instituta im. V. L. Komarova 4: 60. 1968.

Type protologue. Tibet bor.-occid., praemontium bor. jugi Przeval'skii, ad 5000 m alt., in steppa arenosa, 24.08.1980, V. Roborovski (LE). **Type:** Thibet boreal.-occid., Kuen-Lun, Khr. Przeval'skogo, severnye peredgorya, 24 Aug 1890, *W.J. Roborowski s.n.* (holotype, LE 01010497!).

Description. ***Perennial plant***, densely tufted, with a few culms and numerous vegetative shoots; culms (14.7–)16.2–39.1(–50.0) cm tall, 1–2(–3)-noded, nodes distributed close together and only in the lowermost part of the culm. ***Leaves of vegetative shoots*:** sheaths shortly and densely pubescent; ***ligules*** truncate to slightly acute, on the external sheaths (0.5–)1.0–1.8(–2.3) mm long, whereas on the internal sheaths (1.0–)1.5–3.0(–4.5); ***blades*** convolute, green, pale green to glaucous, (4.9–)6.1–11.4(–16.0) cm long, 0.4–0.5 mm in diameter, adaxial surface covered by 0.15–0.2 mm long hairs, abaxial surface glabrous, scabrous or setulose. ***Cauline leaves*:** lower sheaths sparsely pubescent to almost glabrous, upper sheath glabrous or almost so; ***ligules*** acute, on the lower sheaths (0.7–)1.2–1.9 mm long, on the middle sheaths (1.6–)1.9–3.5(–4.5) and on the upper 2.0–3.45(–4.5); ***blades*** convolute, green or pale green, (2.5–)3.0–6.5(–7.8) cm long, adaxial surface covered with short hairs, abaxial surface glabrous, scabrous to shortly pubescent. ***Panicle*** (7.6–)8.7–

14.4(–17.8) cm long, open, at base enclosed by the sheath of the uppermost leaf or rarely exerted, branches flexuous, setulose or slightly scabrous or glabrous, single or paired. ***Glumes*** subequal (the lower slightly longer than the upper), purplish, glumes (19.5–)21.0–23.5(–25.0) mm long, narrowly lanceolate. ***Floret*** (lemma + callus) (11.5–)12.0–14.0(–15.0) mm long. ***Callus*** (2.0–)2.3–3.0(–3.8) mm long, densely pilose on the ventral part, with hairs (0.4–)0.6–0.9(–1.0) mm long, on dorsal part sparsely and shortly pilose with straight hairs (0.5–)0.6–0.8(–0.9) mm long; callus base 0.5–0.8 mm long and 0.15–0.25 mm wide, sharply pointed, scar narrow-elliptic. ***Lemma*** coriaceous, pale-green, purplish or brownish, covered throughout (from the bottom to top) by dense ascending to appressed hairs 0.2–0.4 mm long; top of lemma surpassed by a ring of unequal hairs 0.4–0.9 mm long. ***Awn*** (78–)95–112(–130) mm long, bigeniculate, straw-coloured to brownish; **first segment of the awn** (column) (7–)11–22 mm long, twisted, 0.3 mm wide at base, with (1.5–)1.6–2.0(–2.3) mm long hairs, **middle segment of the awn** 10–12(–13) mm long, twisted, with (1.7–)1.9–2.4 mm long hairs; **terminal segment of the awn** (seta) arcuate or flexuous (62–)68–89(–98) mm long and, hairs longer than those on columns, (2.1–)2.3–2.5(–3.0) mm long, gradually decreasing in length towards apex. ***Palea*** equalling lemma in length.

Habitat. High mountain steppes, semi-deserts, 3500–5000 m. a.s.l.

Distribution. China: southern Xinjiang, Qinghai, Gansu, north-western Xizang; Fig. 3 (Tzvelev 1968).

Selected specimen examined. China: Qinghai Province: Kuen-Lun, Dolina r. Sharagol'-dzhin, yr. Paidza-Tologoi, 11000 ft alt., pesch. step', 11 Jul 1894, *W.J. Roborowski 318* (LE 01010495 [label 2: Stipa purpurea Griseb f. robusta, det. R. Roshevitz; Label 3: Stipa kozlovii m. sp. nov. inedit. = S. purpurea var. arenosa m. var. nova, Typus varietis!, XI. 1966, N.N. Tzvelev], LE 01010496, KRA 476855, K, - paratypes); **Xinjiang Province**, Ruoqiang, N of Aqqikkol, on grasslands, ca. 4200 m alt., 21 Aug 1988, *S. Wu, H. Ohba, Y. Wu, Y. Fei 2747* (MOIS 3744710); Xinjiang, Ruoqiang, Yueya River to Aqqikkol, in Stipa grassland on gravel-rich flat places, 21 Aug 1988, *S. Wu, H. Ohba, Y. Wu, Y. Fei 2275* (MOIS 5660755); **Gansu Province**, Subei County, alt. 3500 m, 5 Aug 1956, *B-z. Guo s.n*. (PE 707226); **Xizang Province**, 16 km northeast of Shuanghu County, alt. 5000 m, 27 Jul 1976, *Gansu Agricultural University 111* (PE 2029866).

Note. *Stipa purpurea* var. *arenosa* was described, based on two collections of W.J. Roborowski from Central Asia (Tzvelev 1968). During our research in 2009–2021, in addition to the holotype, we found four sheets (paratypes) with specimens of *Stipa* collected by Roborowski in 1894. The two of the paratypes preserved in LE, were labeled as the type and isotype of *Stipa purpurea* var. *arenosa* by N. Tzvelev in 1966.

A new natural hybrid between *S. klimesii* and *S. tremula*

In western Himalayas (Ladakh, NW India), within high mountain steppes and semi-deserts, *S. kilmesii* and *S. tremula* or *S. purpurea* sometimes co-occur and hybridisation events between the species may occur. During taxonomic revision of the Himalayan feathergrass species, we found a putative product of such hybridisation, that was collected by L. Klimeš in Spangchen Do (Ladakh, NW India) in 2001. The putative hybrid taxon is similar to *S. purpurea* in having long and flexuous branches in the lower part of the panicle; however, in comparison to *S. purpurea*, *S. × ladakhensis* has narrower panicles and shorter awns with hairs on the setae equal or shorter than the hairs on the columns (Table 3). The new taxon also differs from the second parental species, *S. klimesii*, by having longer and flexuous branches, longer glumes and somewhat longer awns (Table 3). Following Nobis et al. (2020), over 30% of species within the genus are of hybrid origin. In feathergrasses, the hybrids are perennial and reproduce vegetatively and, less frequently, sexually (Nobis 2013; Nobis et al. 2017, 2020). Most of them produce some fertile pollen grains and, therefore, may be able to backcross with their parental species, resulting in introgression (Nobis et al. 2017, 2019c; Baiakhmetov et al. 2020, 2021). Thus, for better understanding of the microevolution processes, it is important to detect hybrids and hybridisation events in *Stipa*.

***Stipa* × *ladakhensis* M. Nobis, Klichowska, A. Nowak & P.D. Gudkova, nothosp. nov. (*S. klimesii* × *S. purpurea* s.l.)**
Fig. 5

Type. NW India, Jammu and Kashmir State, Ladakh Region: Zanskar: Zara, Spangchen Do, alt. 4520 m, 1 Sep 2001, 33°22.7'N, 77°45.1'E, code 01-34-13, *L. Klimeš 1474* (holotype KRA 603490!, isotypes PR!, KRA 603487!, 603486!)

Description. ***Plant perennial***, densely tufted, with a few culms and numerous vegetative shoots; culms 35–55 cm tall, 1–2-noded, nodes distributed close together and only in the lowermost part of the culm. ***Leaves of vegetative shoots*:** sheaths shortly and densely pubescent; ***ligules*** acute, on the external sheaths (1.0–)1.2–2.0(–2.8) mm long, whereas, on the internal sheaths (1.5–)2.0–4.0(–5.5) mm long; ***blades*** convolute, green, pale green to glaucous 10–25 cm long, 0.3–0.5 mm in diameter, adaxial surface covered by 0.15–0.2 mm long hairs, abaxial surface scabrous. ***Cauline leaves*:** lower sheaths shortly pubescent, upper scabrous or glabrous; ***ligules*** acute, (1.0–)2.0–4.0(–5.0) mm long; ***blades*** of convolute, green or pale green, adaxial surface shortly pubescent, abaxial surface scabrous or glabrous. ***Panicle*** 17–25 cm long, rather contracted, with 15–23 spikelets, at base enclosed by the sheath of the uppermost leaf or exerted, lower branches 2–6 cm long, straight or slightly flexuous, setulose or glabrous, single or paired. ***Glumes*** subequal, brownish to purplish, glumes 16–19(–20) mm long, narrowly lanceolate, tapering into long hyaline apex. ***Floret*** (lemma + callus) 8.5–10.2 mm long and 0.7–0.9 mm wide. ***Callus*** 1.5–1.9 mm long, densely and long-pilose, the base of callus narrow, peripheral ring 0.15–0.20 mm in diameter, acute, scar narrow elliptic. ***Lemma*** coriaceous, straw-coloured, brownish or purplish; covered throughout (from the bottom to top) by dense ascending to appressed hairs 0.2–0.4 mm long. ***Awn*** 46–58 mm long, bigeniculate, **lower segment of the awn** 8–11 mm long, twisted, with 1.7–2.3 mm long hairs, **middle segment of the awn** 4–9 mm long, twisted, with 1.6–2.2 mm long hairs; **terminal segment of the awn** (seta) flexuous 30–42 mm long with hairs shorter to equal to those on the column, 1.6–2.1 mm long, gradually decreasing in length towards the apex. *Palea* equalling lemma in length.

Habitat. High mountain semi-deserts, on the elevation from 4000 to 5000 m.

Distribution. W Himalayas (NW India).

Figure 5. The holotype of *Stipa* × *ladakhensis* M. Nobis, Klichowska, A. Nowak & P.D. Gudkova.

Acknowledgements

We would like to express our gratitude to the curators of AA, BM, E, GOET, K, KRA, KUN, LE, M, MSB, MW, MOIS, NY, P, PE, PR, TAD, TK and TASH for making their collections of *Stipa* available for study. We are also grateful to Jeffery M. Saarela, Paul M. Peterson and Eduardo Ruiz-Sanchez for their valuable remarks and improvements to the manuscript. The research was funded by the National Science Centre, Poland no 2018/29/B/NZ9/00313 and 2020/39/D/NZ8/02307. The research of P. Gudkova was financed by grant number 19-74-10067.

References

Baiakhmetov E, Nowak A, Gudkova PD, Nobis M (2020) Morphological and genome-wide evidence for natural hybridisation within the genus *Stipa* (Poaceae). Scientific Reports 10(1): 1–14. https://doi.org/10.1038/s41598-020-70582-1

Baiakhmetov E, Ryzhakova D, Gudkova PD, Nobis M (2021) Evidence for extensive hybridisation and past introgression events in feather grasses using genome-wide SNP genotyping. BMC Plant Biology 21(1): e505. https://doi.org/10.1186/s12870-021-03287-w

Barkworth ME, Everett J (1987) Evolution in the Stipeae: identification and relationships of its monophyletic taxa. In: Soderstrom TR, Hilu KW, Campbell CS, Barkworth ME (Eds) Grass systematics and evolution. Smithsonian Institution Press, Washington, 251–264.

Bor NL (1960) Grasses of Burma, Ceylon, India and Pakistan (excluding Bambuseae). Pergamon Press, London, 767 pp.

Bor NL (1970) Graminae. In: Rechinger KH (Ed.) Flora Iranica, 70. Academische Druck-und Verlagsanstalt, Graz-Austria, 573 pp. [& 72 tables]

Conti F, Di Martino L, Bartolucci F (2020) *Poa magellensis* (Poaceae), a new species from Central Apennine (Italy). PhytoKeys 144: 113–124. https://doi.org/10.3897/phytokeys.144.49971

Cope TA (1982) Poaceae. In: Nasir E, Ali SI (Eds) Flora of Pakistan, 143. University of Karachi, Karachi, 678 pp.

Cui DF (1996) *Stipa* L. In: Cui NR (Ed.) Flora Xinjiangensis. Angiospermae, Monocotyledoneae, 6. Xinjiang Science & Technology & Hygiene Publishing House, 291–313.

Freitag H (1985) The genus *Stipa* (Gramineae) in southwest and south Asia. Notes from the Royal Botanic Garden Edinburgh 42: 355–489.

Gibson DJ (2009) Grasses and Grassland Ecology. Oxford University Press.

Grisebach A (1868) Ueber die Gramineen Hochasiens. Nachrichten von der Königlichen Gesellschaft der Wissenschaften und der Georg-Augusts-Universität zu Göttingen 3: 61–93. https://doi.org/10.1007/BF03017184

Hamasha HR, von Hagen KB, Röser M (2012) *Stipa* (Poaceae) and allies in the Old World: Molecular phylogenetics realigns genus circumscription and gives evidence on the origin of American and Australian lineages. Plant Systematics and Evolution 298(2): 351–367. https://doi.org/10.1007/s00606-011-0549-5

Hammer Ø, Harper DA, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4(1): 1–9.

Hao KS (1938) Pflanzengeographische Studien über den Kokonor-See und über das angrenzende Gebeit. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 68(5): 515–668.

Hodkinson TR (2018) Evolution and taxonomy of the grasses (Poaceae): a model family for the study of species-rich groups. Annual Plant Reviews Online: 255–294. https://doi.org/10.1002/9781119312994.apr0622

Hu ZJ, Zhang YL, Yu HB (2015) Simulation of *Stipa purpurea* distribution pattern on Tibetan Plateau based on MaxEnt model and GIS. Ying Yong Sheng Tai Xue Bao 12: 505–511.

Kellogg EA (2015) Flowering plants. In: Kubitski K (Ed.) Monocots: Poaceae. The Families and Genera of Vascular Plants, vol. 13. Springer International, Cham, 1–416.

Kellogg EA, Abbott JR, Bawa KS, Gandhi KN, Kailash BR, Ganeshaiah KN, Shrestha UB, Raven P (2020) Checklist of the grasses of India. PhytoKeys 163: 1–560. https://doi.org/10.3897/phytokeys.163.38393

Krasnow AN (1887a) Spisok rastenii sobrannykh v vostochnom Tyan-Shane, letom 1886 goda. Enumeratio plantarum anno 1886 in Tian Schan orientali lectarum. Petropoli, 1–129.

Krasnow AN (1887b [1888]) Descriptiones plantarum novarum vel minus cognitarum anno 1886 A.A. Krassnow in regionibus Thian Schanicis lectarum. Scripta Botanica Horti Universitatis Imperialis Petropolitanae. Botanicheskiia Zapiski 2(1): 9–22.

Krasnow AN (1888) Opyt' istorii rasvitya flory yuzhnoi chasti vostochnago Tyan-Shanya. Zapiski Imperatorkago Russkago Geograficheskago Obschestva 19: 1–413.

Krawczyk K, Nobis M, Nowak A, Szczecińska M, Sawicki J (2017) Phylogenetic implications of nuclear rRNA IGS variation in *Stipa* L. (Poaceae). Scientific Reports 7(1): 1–11. https://doi.org/10.1038/s41598-017-11804-x

Kuo PC, Sun YH (1982) A preliminary study on the classification, distribution and ecological nature of genus *Stipa* L. of China. Zhiwu Fenlei Xuebao 20: 34–44.

Kuo PC, Sun YH (1987) *Stipa* Linn. In: Kuo PC (Ed.) Flora Reipublicae Popularis Sinicae, Vol. 9(3). Science Press, Beijing, 268–287.

Lazkov GA, Sultanova BA (2014) Checklist of vascular plants of Kyrgyzstan. United Nations Development Programme, Bishkek.

Levin DA, Donald A (2002) The role of chromosomal change in plant evolution. Oxford University Press, USA.

Li X, Yin X, Yang S, Yang Y, Qian M, Zhou Y, Zhang C, Du Y, Yang Y (2015) Variations in seed characteristics among and within *Stipa purpurea* populations on the Qinghai–Tibet Plateau. Botany 93(10): 651–662. https://doi.org/10.1139/cjb-2015-0011

Liu B, Paszko B (2020) *Calamagrostis hongii* (Poaceae, Agrostidinae), a new species from southwestern China. PhytoKeys 166: 41–55. https://doi.org/10.3897/phytokeys.161.53010

Liu WS, Dong M, Song ZP, Wei W (2008) Genetic diversity pattern of *Stipa purpurea* populations in the hinterland of Qinghai-Tibet Plateau. Annals of Applied Biology 154(1): 57–65. https://doi.org/10.1111/j.1744-7348.2008.00274.x

Liu W, Zhao Y, You J, Qi D, Zhou Y, Chen J, Song Z (2016) Morphological and genetic variation along a north-to-south transect in *Stipa purpurea*, a dominant grass on the

Qinghai-Tibetan Plateau: Implications for response to climate change. PLoS ONE 11(8): e0161972. https://doi.org/10.1371/journal.pone.0161972

Lu SL, Wu ZL (1996) On the geographical distribution of the genus *Stipa* L. in China. Zhiwu Fenlei Xuebao 34: 242–253.

Ma B, Sun J (2018) Predicting the distribution of *Stipa purpurea* across the Tibetan Plateau via the MaxEnt model. BMC Ecology 18(1): e10. https://doi.org/10.1186/s12898-018-0165-0

Meeus S, Šemberová K, De Storme N, Geelen D, Vallejo-Marín M (2020) Effect of whole-genome duplication on the evolutionary rescue of sterile hybrid monkeyflowers. Plant Communications 1(6): e100093. https://doi.org/10.1016/j.xplc.2020.100093

Nie B, Jiao BH, Ren LF, Gudkova PD, Chen WL, Zhang WH (2020) Integrative taxonomy recognized a new cryptic species within *Stipa grandis* from Loess Plateau of China. Journal of Systematics and Evolution. https://doi.org/10.1111/jse.12714

Nikitina EV (1950) *Stipa* L. In: Schischkin BK (Ed.) Flora Kirgizskoi SSR. Opredelitel rastenii kirgizskoi SSR, zlaki i osokovye 2. Izdatelstvo Kirfan, SSSR, 47–63.

Nobis M (2013) Taxonomic revision of the *Stipa lipskyi* group (Poaceae: *Stipa* section *Smirnovia*) in the Pamir Alai and Tian-Shan Mountains. Plant Systematics and Evolution 299(7): 1307–1354. https://doi.org/10.1007/s00606-013-0799-5

Nobis M (2014) Taxonomic revision of the Central Asian *Stipa tianschanica* complex (Poaceae) with particular reference to the epidermal micromorphology of the lemma. Folia Geobotanica 49(2): 283–308. https://doi.org/10.1007/s12224-013-9164-2

Nobis M, Nobis A, Nowak A, Nowak S (2014) *Stipa klimesii* (Poaceae), a new species from Western Himalayas (India). Phytotaxa 174(3): 173–180. https://doi.org/10.11646/phytotaxa.174.3.6

Nobis M, Nowak A, Gudkova PD (2015) A new synonym and a new combination in *Stipa aliena* Keng (Poaceae: *Stipa* sect. *Regelia*). Phytotaxa 195(3): 236–242. https://doi.org/10.11646/phytotaxa.195.3.3

Nobis M, Nobis A, Klichowska E, Nowak A, Nowak S, Gudkova PD (2016a) *Stipa dickorei* sp. nov. (Poaceae), three new records and a checklist of feather grasses of China. Phytotaxa 267(1): 29–39. https://doi.org/10.11646/phytotaxa.267.1.3

Nobis M, Klichowska E, Nowak A, Gudkova PD, Rola K (2016b) Multivariate morphometric analysis of the *Stipa turkestanica* group (Poaceae: *Stipa* sect. *Stipa*). Plant Systematics and Evolution 302(2): 137–153. https://doi.org/10.1007/s00606-015-1243-9

Nobis M, Nowak A, Nobis A, Nowak S, Żabicka J, Żabicki P (2017) *Stipa × fallax* (Poaceae: Pooideae: Stipeae), a new natural hybrid from Tajikistan, and a new combination in *Stipa drobovii.* Phytotaxa 303(2): 141–154. https://doi.org/10.11646/phytotaxa.303.2.4

Nobis M, Gudkova PD, Pendry CA (2019a) Synopsis of the tribe Stipeae (Poaceae) in Nepal. PhytoKeys 128: 97–119. https://doi.org/10.3897/phytokeys.128.34637

Nobis M, Gudkova PD, Nowak A (2019b) *Neotrinia* gen. nov. and *Pennatherum* sect. nov. in *Achnatherum* (Poaceae: *Stipeae*). Turczaninowia 22(1): 37–41. https://doi.org/10.14258/turczaninowia.22.1.5

Nobis M, Gudkova PD, Baiakhmetov E, Żabicka J, Krawczyk K, Sawicki J (2019c) Hybridisation, introgression events and cryptic speciation in Stipa (Poaceae): A case study of the

Stipa heptapotamica hybrid-complex. Perspectives in Plant Ecology, Evolution and Systematics 39: e125457. https://doi.org/10.1016/j.ppees.2019.05.001

Nobis M, Gudkova P, Nowak A, Sawicki J, Nobis A (2020) A synopsis of the genus *Stipa* (Poaceae) in Middle Asia, including a key to species identification, an annotated checklist, and phytogeographic analyses. Annals of the Missouri Botanical Garden 105(1): 1–63. https://doi.org/10.3417/2019378

Noltie HJ (2000) Flora of Bhutan, 3(2), The Grasses of Bhutan. Royal Botanic Garden Edinburgh & Royal Government of Bhutan, Edinburgh, 883 pp.

Ovchinnikov PN, Chukavina AP (1957) Kovyl' – *Stipa* L. In: Ovchinnikov PN (Ed.) Flora Tadzhikskoi SSR, 1 – Zlaki. Izdat. Akad. Nauk SSSR, Moskva, 414–431.

Pavlov NV (1956) Flora Kazakhstana 1. Akademiya Nauk Kazakhskoi SSR, Alma-Ata, 353 pp.

Pazij VK (1968) *Stipa* L. In: Kovalevskaya SS (Ed.) Opredelitel rastienii sredniei Azii (Conspectus florae Asiae Mediae) vol. 1. Editio Academiae Scientiarum UzSSR, Taschkent, 64–82, 200–201.

Romaschenko K, Peterson PM, Soreng RJ, Garcia-Jacas N, Futorna O, Susanna A (2012) Systematics and evolution of the needle grasses (Poaceae: Pooideae: Stipeae) based on analysis of multiple chloroplast loci, ITS, and lemma micromorphology. Taxon 61(1): 18–44. https://doi.org/10.1002/tax.611002

Roshevitz RY (1916) Zlaki (Gramineae). In: Fedtschenko BA (Ed.) Flora Aziatskoi Rossii, 12. Pereselencheskoe Upravlenie Ministerstva Zemledeliya, 1–191.

Roshevitz RY (1934) *Ptilagrostis* Griseb., *Stipa* L. In: Komarov VL (Ed.) Flora SSSR, 2. Editio Academiae Scientiarum URSS, Leningrad, 74–112, 740–741.

Ruprecht FJ (1869) Sertum tianschanicum. In: Osten-Sacken F von, Ruprecht FJ (Eds) *Sertum tianschanicum*: Botanische Ergebnisse einer Reise im mittleren Tian-Schan. Memoires de l'Academie Imperiale des Sciences de Saint-Petersbourg 14(4): 1–74.

Soltis PS, Liu X, Marchant DB, Visger CJ, Soltis DE (2014) Polyploidy and novelty: Gottlieb's legacy. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 369(1648): e20130351. https://doi.org/10.1098/rstb.2013.0351

Soreng RJ, Peterson PM, Romaschenko K, Davidse G, Teisher JK, Clark LG, Barberá P, Gillespie LJ, Zuloaga FO (2017) A worldwide phylogenetic classification of the Poaceae (Gramineae) II: An update and a comparison of two 2015 classifications. Journal of Systematics and Evolution 55(4): 259–290. https://doi.org/10.1111/jse.12262

StatSoft Inc. (2011) STATISTICA (data analysis software system), version 13.

Stebbins GL (1971) Chromosomal evolution in higher plants. Chromosomal evolution in higher plants. Addison-Wesley, Reading, Mass., [viii +] 216 pp.

Thiers B (2022[-continuously updated]) Index Herbariorum. A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih [accessed: 14 January 2022]

Tkach N, Nobis M, Schneider J, Becher H, Winterfeld G, Jacobs SW, Röser M (2021) Molecular phylogenetics and micromorphology of australasian Stipeae (Poaceae, subfamily Pooideae), and the interrelation of whole-genome duplication and evolutionary radiations in this grass tribe. Frontiers in Plant Science 11: e2279. https://doi.org/10.3389/fpls.2020.630788

Tzvelev NN (1968) Zlaki (Gramineae). In: Grubov VI (Ed.) Rastieniya Centralnoi Azii. Po materialam Botanicheskogo Instituta im. Komarova VL (Plantae Asiae Centralis, secus materies Instituti botanici nomine Komarovii VL), 4. Nauka, Leningrad, 1–243. [12 maps]

Tzvelev NN (1974) Zametki o tribe *Stipeae* Dum. semeistva zlakov (Poaceae) v SSSR. Novosti Sististematyki Vysshikh Rastenii 11: 4–21.

Tzvelev NN (1976) Zlaki SSSR. Nauka, Leningrad, 788 pp.

Wu ZL, Phillips SM (2006) Tribe Stipae. In: Wu ZY, Raven PH, Hong DY (Eds) Flora of China (Poaceae), 22. Science Press, Beijing and Missouri Botanical Garden Press, St. Louis, 188–212.

Wu YH, Wang QJ (1999) The grasses of Karakorum and Kunlun Mountains. Qinghai People's Publishing House, Xining, 168 pp.

Wu ZY, Raven PH, Hong DY [Eds] (2006) Flora of China. Vol. 22 (Poaceae). Science Press, Beijing, and Missouri Botanical Garden Press, St. Louis.

Yang Y, Dong C, Yang S, Li X, Sun X, Yang Y (2015) Physiological and proteomic adaptation of the alpine grass *Stipa purpurea* to a drought gradient. PLoS ONE 10(2): e0117475. https://doi.org/10.1371/journal.pone.0117475

Yue PP, Lu XF, Ye RR, Zhang CX, Yang SB, Zhou YB, Peng M (2011) Distribution of *Stipa purpurea* steppe in the Northeastern Qinghai-Xizang Plateau (China). Russian Journal of Ecology 42(1): 50–56. https://doi.org/10.1134/S1067413611010140

Zhai XY, Guo YX, Hou FJ, Liu Y, Ma DT, Wang W, Yan XB (2015) Population genetic structure and germplasm conservation of *Stipa purpurea* on Qinghai-Tibetan Plateau under grazing. Biochemical Systematics and Ecology 62: 51–57. https://doi.org/10.1016/j.bse.2015.07.036

Zhao LQ, Guo K (2017) A new species and a new variety of *Stipa* (Poaceae) from Tibet, China. Annales Botanici Fennici 54(1/3): 49–53. https://doi.org/10.5735/085.054.0309

PhytoKeys 196: 49–61 (2022)
doi: 10.3897/phytokeys.196.79673
https://phytokeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

Two new pendulous epiphytic *Columnea* L. (Gesneriaceae) species from the Chocó forests of the Northern Andes

Francisco Tobar[1,2], James F. Smith[3], John L. Clark[4]

1 *Área de Investigación y Monitoreo de Avifauna, Aves y Conservación – BirdLife en Ecuador, Quito, Ecuador* **2** *Instituto Nacional de Biodiversidad, Herbario Nacional del Ecuador QCNE, Quito, Ecuador* **3** *Department of Biological Sciences, Boise State University, 1910 University Drive, Boise, Idaho, 83725, USA* **4** *Science Department, The Lawrenceville School, Lawrenceville, NJ 08648, USA*

Corresponding author: John L. Clark (jclark@lawrenceville.org)

Academic editor: Laura Clavijo | Received 22 December 2021 | Accepted 22 April 2022 | Published 16 May 2022

Citation: Tobar F, Smith JF, Clark JL (2022) Two new pendulous epiphytic *Columnea* L. (Gesneriaceae) species from the Chocó forests of the Northern Andes. PhytoKeys 196: 49–61. https://doi.org/10.3897/phytokeys.196.79673

Abstract

Exploratory field expeditions to the Chocó forests in the northwestern slopes of the Ecuadorian and Colombian Andes resulted in the discovery of two new species of *Columnea* (Gesneriaceae). *Columnea fluidifolia* J.L.Clark & F.Tobar, **sp. nov.**, is described as a narrow endemic from Bosque Protector Mashpi and surrounding areas in the province of Pichincha in northern Ecuador. *Columnea pendens* F.Tobar, J.L.Clark & J.F.Sm., **sp. nov.**, is described from recently discovered populations in the provinces of Carchi and Santo Domingo de los Tsáchilas (Ecuador) and the departments of Cauca and Nariño in southwestern Colombia. The two new species are pendent epiphytes with elongate shoots and shallowly bilabiate to nearly tubular corollas. Descriptions, complete specimen citations, and a distribution map are provided. Based on IUCN guidelines, a preliminary conservation status of Critically Endangered (CR) is provided for *C. fluidifolia* and Endangered (EN) is provided for *C. pendens*.

Resumen

Las expediciones de campo a los bosques del Chocó en las laderas noroccidentales de los Andes de Ecuador y Colombia dieron como resultado el descubrimiento de dos nuevas especies de *Columnea* (Gesneriaceae). *Columnea fluidifolia* J.L.Clark & F.Tobar, **sp. nov.**, descrita como endémica de una reducida área del Bosque Protector Mashpi y zonas circundantes en la provincia de Pichincha. *Columnea pendens* F.Tobar, J.L.Clark & J.F.Sm., **sp. nov.**, se describe a partir de poblaciones recientemente descubiertas en las provincias de Carchi, Santo Domingo de los Tsáchilas (Ecuador) y los departamentos de Cauca y Nariño en el suroeste de Colombia. Las dos nuevas especies son epífitas pendulares con brotes alargados

Copyright *Francisco Tobar et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

y corolas ligeramente bilabiadas a casi tubulares. Descripciones, citaciones completas de los especímenes y mapa de distribución son incluidas. Basados en los criterios de la IUCN, se asigna un estado de conservación preliminar de En Peligro Critico (CR) para *C. fluidifolia* y a *C. pendens* se le asigna la categoría de En Peligro (EN).

Keywords
Chocó, Colombia, Columnea, Ecuador, Gesneriaceae, taxonomy

Introduction

The flowering plant family Gesneriaceae, with more than 3400 species and 150 + genera (Weber 2004; Weber et al. 2013), is in the order Lamiales. The family is divided into three subfamilies and seven tribes (Weber et al. 2013, 2020), which represent monophyletic lineages (Ogutcen et al. 2021). The majority of New World members are in the subfamily Gesnerioideae and are represented by 1200+ species and 77 genera (Clark et al. 2020). *Columnea* L. is classified in the tribe Gesnerieae and subtribe Columneinae (Weber et al. 2013, 2020). The genus *Columnea* is distinguished by fruits that are indehiscent berries in contrast to fleshy bivalved capsules in closely related genera.

Most *Columnea* are epiphytic with primary shoots that are characterized as erect, horizontal, dorsiventral (associated with facultative epiphytes), or pendent. The two species described here are characterized as epiphytes with elongate pendent shoots, a habit more typical of *Columnea* from Central America. In contrast, most *Columnea* in South America are facultative epiphytes with dorsiventral shoots. For example, Panama and Costa Rica have collectively more than 20 species of *Columnea* that are characterized as pendent epiphytes. Some examples of species in the northern Andes with elongate pendent shoots include *Columnea billbergiana* Beurl., *C. kienastiana* Regal., and *C. minor* Hanst. *Columnea fluidifolia* is endemic to the Bosque Protector Mashpi and surrounding areas in the province of Pichincha in northern Ecuador (Fig. 1). *Columnea pendens* is known from the provinces of Carchi and Santo Domingo de los Tsáchilas (Ecuador) and the departments of Cauca and Nariño in southwestern Colombia (Fig. 1). The two species described here have pendent shoots, a habit more typical for *Columnea* in Central America.

Columnea ranges from Mexico south to Bolivia, and is most diverse in the northern Andes of Colombia and Ecuador. With more than 210 species (Clark et al. 2020), *Columnea* is the largest genus in the subfamily Gesnerioideae (Weber et al. 2013, 2020). *Columnea* is strongly supported as a monophyletic genus based on molecular phylogenetic studies (Smith et al. 2013a; Schulte et al. 2014). Most subgeneric ranks are artificially defined and not supported by phylogenetic studies (Smith and Carroll 1997; Smith 2000; Clark and Zimmer 2003; Clark et al. 2012; Smith et al. 2013a; Schulte et al. 2014). Thus, we refrain from classifying the new species into a subgeneric rank.

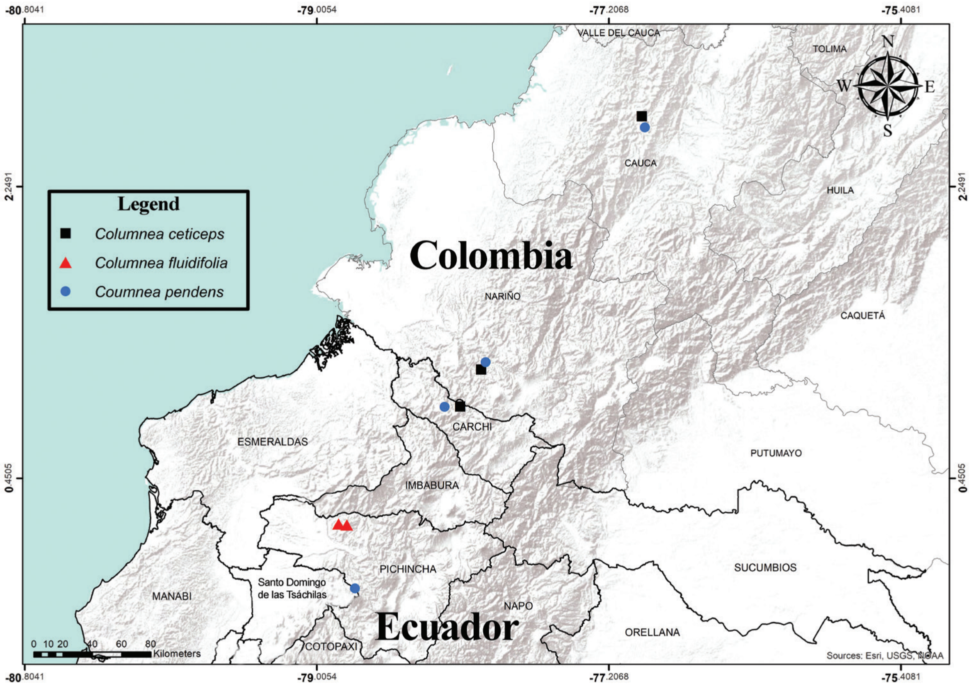

Figure 1. Distribution of *Columnea ceticeps* (squares), *C. fluidifolia* (triangles), and *C. pendens* (circles). Note that range of *C. ceticeps* extends into the Colombian departments of Chocó, Antioquia and Risaralda (not featured here) (map provided by Marco F. Monteros).

Materials and methods

Plants were photographed in the field and subsequently pressed and dried. Specimens are currently deposited at the National Herbarium of Ecuador (QCNE) and the herbarium at the Pontificia Universidad Católica del Ecuador (QCA). Additional specimens will be distributed to the Universidad Estatal Amazónica (ECUAMZ), Marie Selby Botanical Gardens (SEL) and the United States National Herbarium (US). Photographs were taken of live specimens in the field using a Nikon D100 DSLR with a Nikon 105 mm lens. Morphological observations and measurements were made from live collections, alcohol-preserved material, and digital images using the ImageJ program (https://imagej.nih.gov/ij/). Collections from the herbaria QCNE and QCA were consulted as well as type specimens from Jstor Global Plants (https://plants.jstor.org).

We assessed the extinction risk of the two new species following the IUCN Red List Categories and Criteria (2012). We considered observations, collection localities, and population estimates from fieldwork. Species extent of occurrence (EOO) and area of occupancy (AOO) were calculated using *GeoCAT* (Bachman et al. 2011; http://geocat.kew.org/) with the default setting of 2 km^2 grid.

Taxonomic treatment

Columnea fluidifolia **J.L.Clark & F.Tobar, sp. nov.**
urn:lsid:ipni.org:names:77297807-1
Figs 2, 3

Type. Ecuador. Pichincha: cantón Quito, parroquia Pacto, primary road between the town of Pacto and Mashpi Lodge, 0°9'49.3"N, 78°49'14.6"W, 1662 m, 15 Mar 2019, *J.L. Clark & L. Jost 16286* (holotype: US; isotypes: ECUAMZ, QCA, SEL).

Diagnosis. Similar to *Columnea ceticeps*, differing in calyx and corolla uniformly orange (vs. calyx green and corolla bright red in *C. ceticeps*) and corolla shallowly bilabiate (vs. deeply bilabiate in *C. ceticeps*).

Description. Epiphytic herb with elongate pendent shoots, 1.0–1.5 m long, red-brown, with zigzag appearance, densely pilose with gold-colored multicellular trichomes; internodes 2.0–4.0 cm long. Petioles 0.2–0.4 cm long, pilose with multicellular trichomes; leaves opposite, pairs either strongly anisophyllous or isophyllous, sometimes anisophyllous and isophyllous on the same shoot, larger leaf 9.5–10.5 cm long, 3.9–4.5 cm wide, ovate-elliptic, apex long acuminate, base slightly oblique, lateral veins 5–8 per side, adaxially dark-green, with multicellular white-transparent trichomes, abaxially light-green, densely pilose with multicellular white transparent trichomes, more densely pubescent on veins, margin serrulate; smaller leaf 1.3–1.9 cm long, 0.2–0.3 cm wide, lateral veins 2–3 per side, petiole 0.1–0.2 cm long, otherwise similar to larger leaf. Inflorescence reduced to a single axillary flower; bracts not seen, presumably caducous. Pedicels 2.6–3.7 cm long, bright orange, densely pilose with multicellular rust-colored trichomes. Calyx loosely clasping corolla, uniformly bright orange, lobes 2.6–4.2 cm long, 0.4–0.6 cm wide, oblong to narrowly-elliptic, apex acuminate to obtusely acuminate, exterior pilose, with multicellular rust-colored trichomes, more pubescent on veins and margins, interior glabrous, margin serrulate. Corolla 4.5–4.9 cm long, 0.6–0.8 cm at widest point, tubular throughout, inflated near center, slightly gibbous at the base, 0.6–0.7 cm wide before the limb, 0.2–0.4 cm at narrowest point of the base, bright orange externally, densely pubescent with multicellular rust-colored trichomes, interior with short white trichomes; ventral and lateral lobes reflexed, ventral lobe narrowly triangular to oblong, 0.4–0.5 cm long 0.2–0.3 cm wide, dorsal lobes fused, 0.2–0.3 cm long, 0.4–0.5 cm wide, lateral lobes triangular to narrowly triangular, 0.2–0.3 cm long, 0.2–0.3 cm wide. Filaments ca. 4.5 cm long, connate at base for 0.3 cm and adnate to corolla, anthers ca. 1.0 mm long, 1.0 mm wide, included in the corolla throat, quadrangular. Ovary ca. 4.0 mm long, conical, densely pubescent, with multicellular transparent trichomes; style 3.5–4.0 cm long, white with yellow apex, glabrescent; stigma unlobed, papillate, included in corolla tube. Nectary a bilobed dorsal gland. Fruit an indehiscent succulent berry, globose, distally acuminate, uniformly white, pilose; seeds not seen.

Phenology. Flowering during June, August, and November. Mature fruits observed in June.

Etymology. The phyllotaxy in most neotropical Gesneriaceae is opposite with pairs that are either equal in size (isophyllous) or strongly unequal in size (anisophyllous).

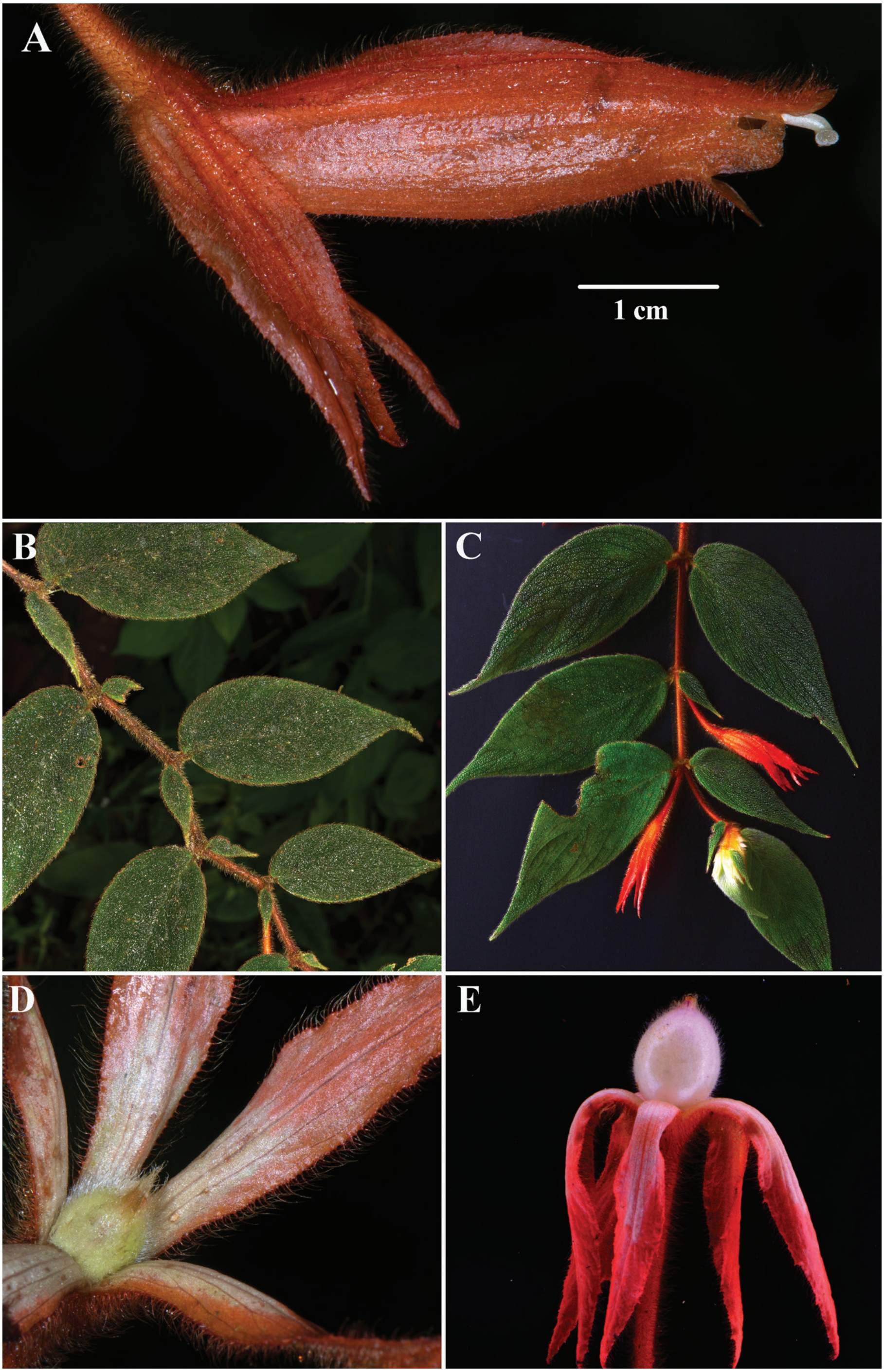

Figure 2. *Columnea fluidifolia* J.L.Clark & F.Tobar **A** lateral view of mature flower **B** anisophyllous leaf pairs **C** isophyllous leaf pairs (base & apex) and anisophyllous leaf pairs (middle) **D** immature berry **E** mature berry (**A, B, D** from *J.L. Clark 16286* **C, E** from *A.J. Perez & F. Tobar sn*). Photos **A, B, D** by J.L. Clark & **C, E** by F. Tobar.

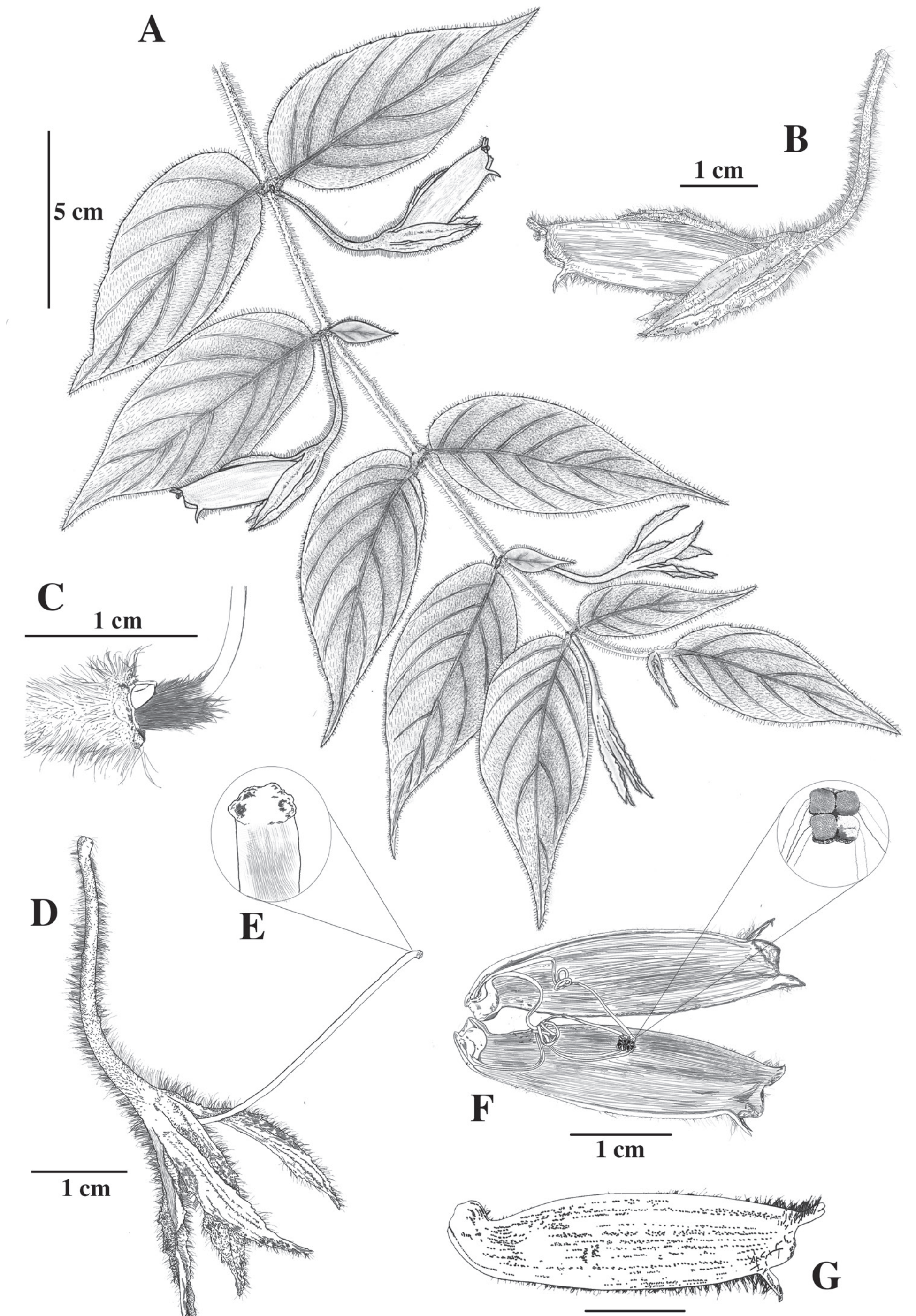

Figure 3. *Columnea fluidifolia* J.L.Clark & F.Tobar **A** pendent shoot **B** lateral view of flower **C** bilobed dorsal nectary gland and ovary **D** mature calyx with style **E** stomatomorphic stigma **F** corolla opened featuring mature anthers **G** mature corolla. Illustration by M.J. Gavilanes.

The leaves in *C. fluidifolia* are unusual for having anisophyllous leaf pairs (Fig. 2B) and isophyllous leaf pairs (Fig. 2C) on the same shoot. The specific epithet reflects the remarkable variability of this vegetative character in *C. fluidifolia*.

Distribution and preliminary assessment of conservation status. *Columnea fluidifolia* is endemic to the northwestern Andean slopes of Ecuador. The only known populations are located in the Mashpi-Pachijal conservation area, in the northwestern province of Pichincha (Fig. 1). The Mashpi-Pachijal conservation area is located in the broadly defined ecoregion referred to as the Chocó Biogeographic Region or the Tumbes-Chocó-Magdalena biodiversity hotspot. According to the vegetation classification system by the Ecosystems of Continental Ecuador (MAE 2012), the vegetation is classified as *Bosque siempreverde piemontano de Cordillera Occidental de los Andes* (*BsPn01*) (premontane evergreen forest) and represents a narrow band between 300 and 1400 meters, that ranges from the Esmeraldas province in the north to the Santo Domingo de los Tsáchilas province in the south. Most remnants of this vegetation have been converted to agriculture crops or livestock. Fewer than 40 individuals of *C. fluidfolia* are known, with a majority in the privately owned reserves of Mashpi and Amagusa. Additional populations of *C. fluidifolia* are known along the primary road that connects the two reserves. Based on the available information and according to the IUCN Red List criteria (IUCN 2012; IUCN Standards and Petitions Committee 2019) *C. fluidifolia* is preliminarily assessed as Critically Endangered (CR) based on an EOO < 100 km^2 (B1), limited geographic range (criteria B1 + 2a, b), and restricted population of fewer than 50 individuals (D).

Comments. *Columnea fluidifolia* differs from most *Columnea* by the presence of pendent elongate shoots and paired leaves that are both anisophyllous (Fig. 2A) and isophyllous (Fig. 2B). In addition, the shallowly bilabiate to tubular corolla and relatively large leaves (> 4 cm long) are not typical for other *Columnea* with pendent elongate shoots. In contrast, most *Columnea* with pendent elongate shoots have corollas that are deeply bilabiate and small leaves (< 4 cm long). *Columnea fluidifolia* is similar to *C. ceticeps*. The calyx lobes and corolla are orange in *C. fluidifolia* (Fig. 2). In contrast, the calyx lobes are green, and the corolla is bright orange in *C. ceticeps* (Fig. 4). The corolla tube in *C. fluidifolia* is nearly tubular without the presence of a bilabiate limb (Figs 2, 3). In contrast, the corolla tube in *C. ceticeps* is deeply bilabiate (Fig. 4).

Ecuador. **Pichincha:** Distrito Metropolitano de Quito, Bosque protector Mashpi, Trasecto Mashpi Laguna 0.169750°N, 78.872120°W, 1150 m, 27 Jun 2017, *F. Tobar et al. 2908* (QCA); Bosque protector Mashpi, Trasecto Mashpi Laguna 0.169750°N, 78.872120°W, 1150 m, 21 Sep 2018, *F. Tobar et al. 3267* (QCA).

Columnea pendens F.Tobar, J.L.Clark & J.F.Sm., sp. nov.

urn:lsid:ipni.org:names:77297808-1
Fig. 5

Type. Ecuador. Carchi, Espejo, road between Goaltal and Chical, near to río Gualpi, 0.890555°N, 78.2188889°W, 1786 m, 12 Sep 2021, *F. Tobar 3638* (holotype: QCA; isotype: QCNE).

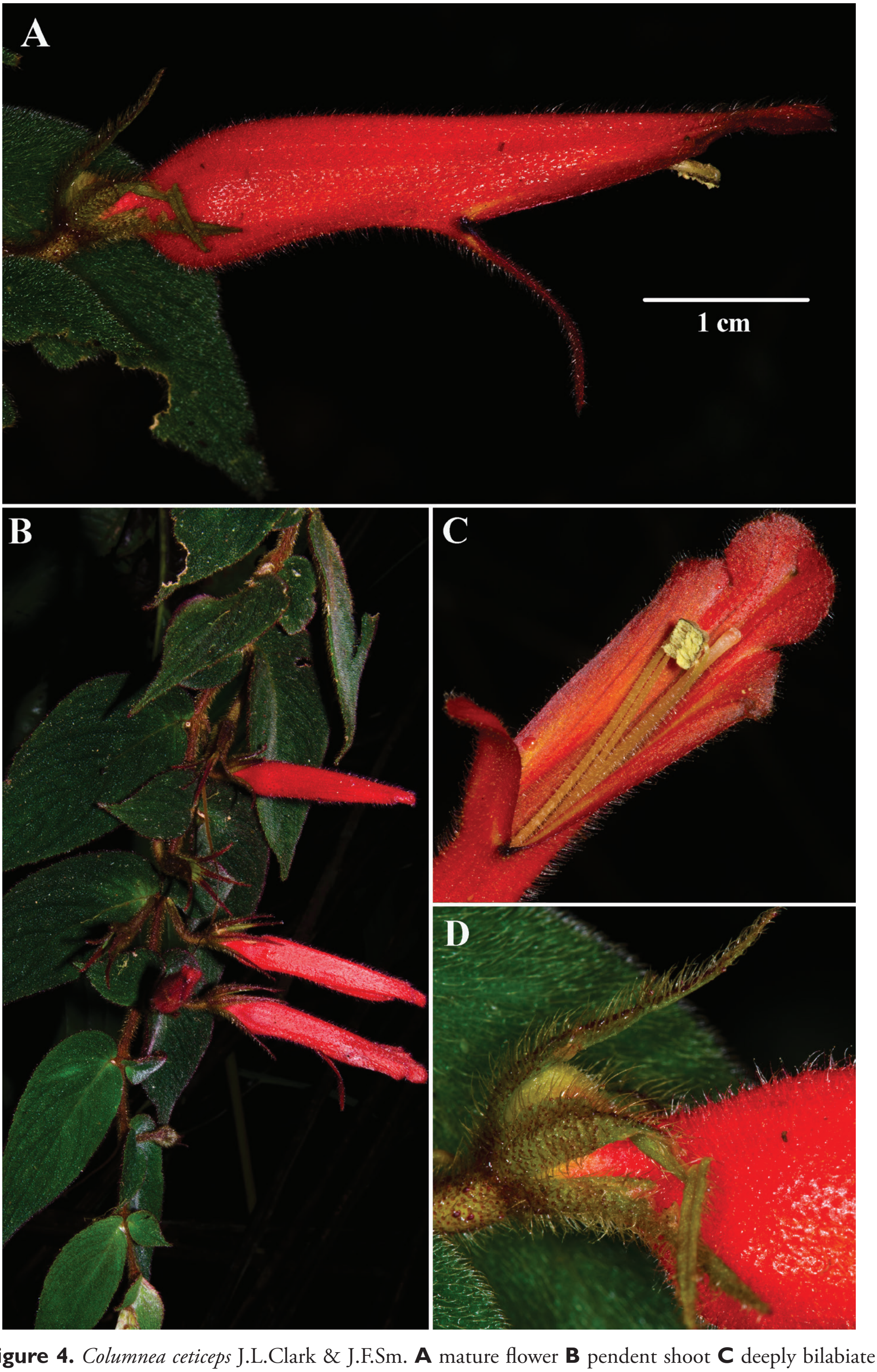

Figure 4. *Columnea ceticeps* J.L.Clark & J.F.Sm. **A** mature flower **B** pendent shoot **C** deeply bilabiate corolla **D** calyx lobes (**A–D** from *J.L. Clark 12950* **D** photos by J.L. Clark.

Diagnosis. Similar to *Columnea ceticeps*, differing in the bright orange corollas (vs. bright red corollas in *C. ceticeps*), calyx lobes broadly ovate (vs. narrowly elongate in *C. ceticeps*), corolla tube ventricose (vs. uniformly tubular in *C. ceticeps*), and corolla tube densely pubescent (vs. corolla tube sparsely pubescent in *C. ceticeps*).

Description. Epiphytic herb with elongate pendent shoots, 1.2–1.5 m long, brown, with zigzag appearance, glabrous near base, pilose with gold-colored trichomes near apex; internodes 2.0–4.5 cm long. Petioles 0.1–0.2 cm long, pilose with multicellular gold-colored trichomes; leaves opposite, pairs usually, nearly equal to isophyllous, rarely anisophyllous, 0.6–6.0 cm long, 0.3–2.3 cm wide, ovate to elliptic, apex acuminate, base slightly oblique, lateral veins 3–8 per side, adaxially dark-green, with white trichomes, abaxially green to red-purple, densely pilose with multicellular gold-colored trichomes and single-celled white trichomes, margin crenulate to serrulate. Inflorescence reduced to 1 or 2 flowers per axil; bracts not seen, presumably caducous. Pedicels 0.3–1.3 cm long, green or red, appressed pilose with multicellular gold-colored trichomes. Calyx clasping, lobes 1.2–2.3 cm long, 0.25 cm wide, triangular-ovate to broadly triangular-ovate, apex long acuminate, exterior densely pilose, with multicellular gold-colored trichomes, interior glabrous, margin serrulate. Corolla 5.2–6.1 cm long, 0.6–1.1 cm at widest point (apex of corolla limb, near throat), tubular, medially ventricose, gibbous at base, 2.8–3.5 mm wide at narrowest point at the base, bright orange externally, interior yellow, exterior densely pubescent with multicellular red-colored trichomes, interior with sparse short trichomes and some stalked glandular trichomes; limb bilabiate, upper lip with two fused dorsal lobes and two lateral lobes, lower limb with an extended ventral lip; dorsal lobes connate, rounded to subquadrate, ca. 6.2 mm long, ca. 6.5 mm wide; lateral lobes triangular to narrowly triangular, ca. 1.5 mm long, ca. 2.0 mm wide; ventral lobe, narrowly oblong to linear ca. 1.9 cm long and ca. 2.8 mm wide, galea 1.9 cm long. Filaments ca. 5.1 cm long, connate for ca. 0.5 cm and adnate to base of corolla, anthers ca. 1.4 mm long, ca. 1.3 mm wide, included in the corolla throat, quadrangular. Ovary 3.4 mm long, conical, pubescent or glabrous, with multicellular transparent trichomes; style pale yellow to white, pilose with multicellular transparent and short stalked glandular trichomes; stigma unlobed, papillate, included in corolla tube. Nectary a bilobed dorsal gland. Mature fruit and seeds not seen.

Phenology. Collected in flower during February-April, and September. Immature fruits observed in April.

Etymology. The specific epithet refers to the pendent epiphytic habit.

Distribution and preliminary assessment of conservation status. *Columnea pendens* is endemic to the western Andean slopes of Ecuador and Colombia (Fig. 1). The forest is located in the broadly defined ecoregion referred to as the Chocó Biogeographic Region or the Tumbes-Chocó-Magdalena biodiversity hotspot.

The Ecuadorian populations are known from the provinces of Santo Domingo de los Tsáchilas and Carchi (Fig. 1). The Ecuadorian population from Santo Domingo de los Tsáchilas is located on the road that connects the village 23 de Julio with San Juan de Chiriboga. Several populations from Carchi are located near Río Gualpi, between

1500 and 1800 m. According to the vegetation classification system by the Ecosystems of Continental Ecuador (MAE 2012), the Ecuadorian forest is classified as *Bosque siempreverde montano bajo de Cordillera Occidental de los Andes* (*BsBn04*) (lower montane evergreen) and represents a narrow band of vegetation between 1400 and 2000 meters, that ranges from the Carchi province in the north to the Santo Domingo de los Tsáchilas province in the south. Current protected areas in Ecuador that correspond to montane evergreen forest include the Ecuadorian national park (Ministerio del Ambiente del Ecuador), Cotacahi-Cayapas Ecological Reserve, and several private reserves such as Los Cedros Biological Reserve, Maquipucuna Cloud Forest Reserve, and Río Guajalito.

The Colombia populations are known from Cerro Plateado, Cerro Pinche, and Munchique in the Cauca department, and La Planada in the Nariño department (Fig. 1). The Colombian forests that host populations of *C. pendens* correspond to premontane, montane, pluvial, and cloud forests along the Pacific slopes of the Cordillera Occidental (western mountain range). Current protected areas in Colombia that correspond to known populations of *C. pendens* include the community-based reserve, La Reserva Natural La Planada, in the Nariño department in southern Colombia. In addition, populations of *C. pendens* are located in the Munchique National Natural Park, part of the Colombian Sistema Nacional de Áreas Protegidas, in the Cauca department.

Based on the available information and According to the IUCN Red List criteria (IUCN 2012; IUCN Standards and Petitions Committee 2019) *C. pendens* is preliminary assessed as Endangered (EN) based on fewer than five known populations (criteria B1 + 2a), EOO < 5000 km^2, and AOO < 500 km^2.

Comments. *Columnea pendens* is similar to *C. ceticeps*, which was recently described from Colombia and northern Ecuador (Smith et al. 2013b). The geographic distribution for these two species overlaps in northern Ecuador and southern Colombia (Fig. 1). *Columnea pendens* has uniformly bright orange corollas (Fig. 5A) in contrast to the uniformly bright red corollas in *C. ceticeps* (Fig. 4A). The calyx lobes of *C. pendens* are broadly ovate (Fig. 5A) in contrast to the narrowly elongate calyx lobes of *C. ceticeps* (Fig. 4A). The corolla in *C. pendens* is medially inflated or ventricose and covered in uniformly dense (nearly tomentose) pubescence (Fig. 5A) in contrast to a sparsely pubescent corolla in *C. ceticeps* (Fig. 4A).

Specimens examined. Colombia. **Cauca:** toward south end of La Depresion, between Cerro Pinche and Cerro Plateado, 26 Sep 1994, *E.L. Core 1358* (US); El Tambo, *O. Haught 5200* (US); El Tambo, Munchique Jul 1948 *S. Yepes Agredo 472* (US). **Nariño:** Reserva Natural La Planada, Ricaurte, on the road near Quebrada Dulce, 3 Mar 1989, *J.F. Smith & P. Galeano 1522*, (COL, WIS). **Ecuador. Carchi:** canton Mira, via Gualchan-El Carmen-Chical, 0.4166667°N, 78.216666°W, 1900–2000 m, 2 Nov 2014, *AJ Perez et al. 7716* (QCA). **Santo Domingo de los Tsáchilas:** cantón Santo Domingo, road between 23 de Julio y San Juan de Chirboga, 0.239444°S, 78.848611°W, 1891 m, 21 April 2021, *F. Tobar & G. Rueda 3644* (QCA).

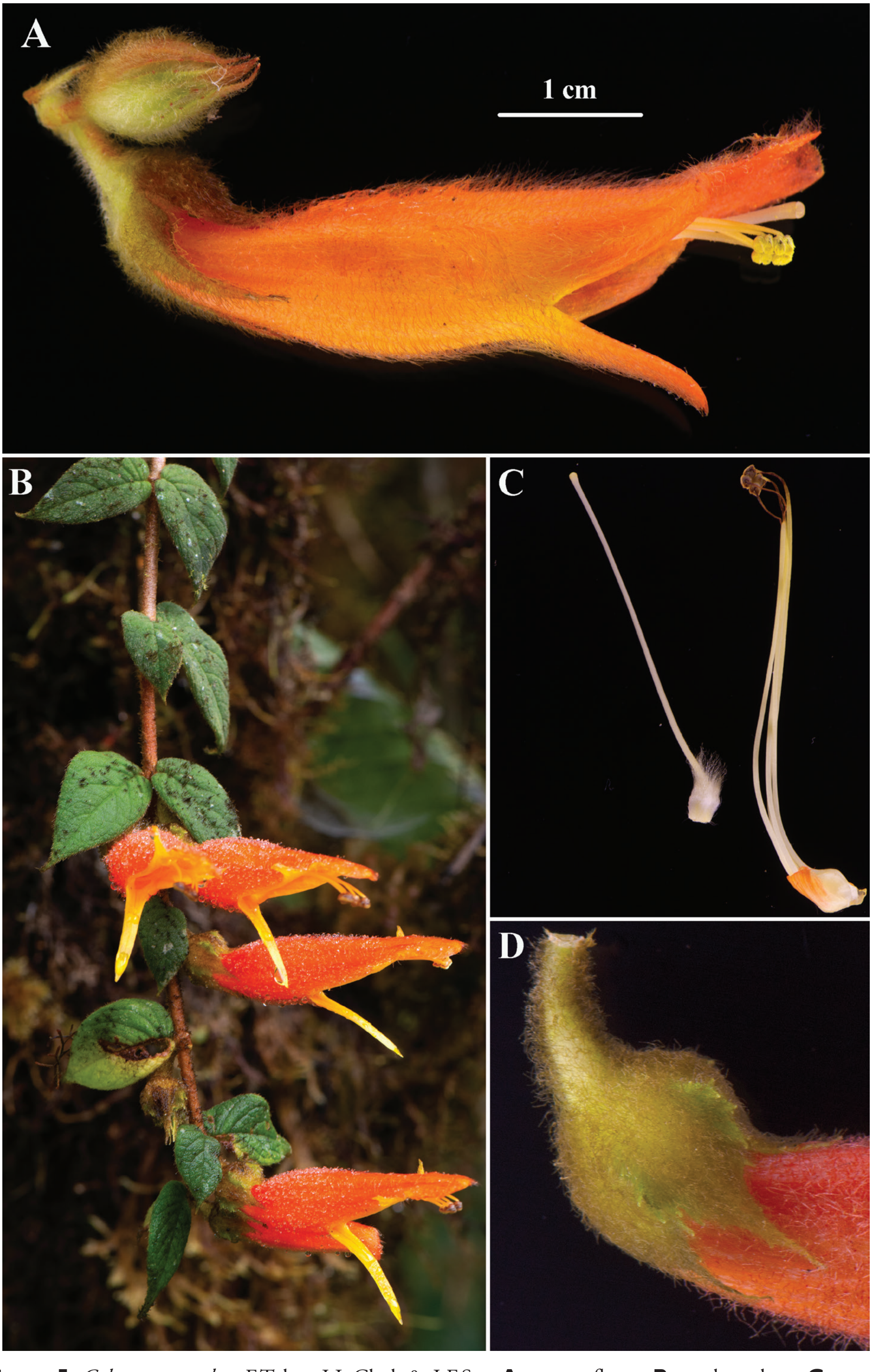

Figure 5. *Columnea pendens* F.Tobar, J.L.Clark & J.F.Sm. **A** mature flower **B** pendent shoot **C** gynoecium and androecium **D** calyx lobes (**A–D** from *F. Tobar* 3638). Photos by F. Tobar.

Acknowledgements

Support for F. Tobar was provided by the Swiss Federal Research Institute (WSL) – National Geographic Society (Grant N° 9952-16); Swiss National Science Foundation (SNF Grant N° 173342) – European Research Council Advanced Grants (ERC Grant N° 787638) Aves y Conservación. We thank the Ministry of the Environment of Ecuador for providing specimen collection and transportation permits (Research permit Aves y Conservación N° 007-2018-IC-FLO-FAU and mobilization permit Aves y Conservación 005-FLO-2019-DPAP-MA). Maria José Gavilanes is acknowledged for illustrating *Columnea fluidifolia* (Fig. 3), and Marco F. Monteros is acknowledged for producing the distribution map (Fig. 1). We thank the Mashpi and Amagusa Reserves for supporting our research by providing access to their forests. We are especially grateful to Mateo Roldan from the Department of Research and Biology – Mashpi Lodge for logistical support during our field research. Brian Keener from the University of West Alabama is acknowledged for suggesting the specific epithet of *fluidifolia*. We thank Christian Feuillet and an anonymous reviewer for providing valuable feedback on an earlier version of this manuscript.

References

Bachman S, Moat J, Hill A, de la Torre J, Scott B (2011) Supporting Red List threat assessments with GeoCAT: Geospatial conservation assessment tool. ZooKeys 150: 117–126. https://doi.org/10.3897/zookeys.150.2109

Clark JL, Zimmer EA (2003) A preliminary phylogeny of *Alloplectus* (Gesneriaceae): Implications for the evolution of flower resupination. Systematic Botany 28: 365–375.

Clark JL, Funke MM, Duffy AM, Smith JF (2012) Phylogeny of a Neotropical clade in the Gesneriaceae: More tales of convergent evolution. International Journal of Plant Sciences 173(8): 894–916. https://doi.org/10.1086/667229

Clark JL, Skog LE, Boggan JK, Ginzbarg S (2020) Index to names of New World members of the Gesneriaceae (Subfamilies Sanangoideae and Gesnerioideae). Rheedea 30: 190–256. https://doi.org/10.22244/rheedea.2020.30.01.14

IUCN (2012) IUCN Red List Categories and Criteria. Version 3.1, 2nd edn. IUCN, Gland, Switzerland and Cambridge, UK.

IUCN Standards and Petitions Committee (2019) Guidelines for using the IUCN Red List Categories and Criteria. Version 14. [Downloadable from:] http://www.iucnredlist.org/documents/RedListGuidelines.pdf

MAE (2012) Ministerio del Ambiente del Ecuador. Sistema de Clasificación de los Ecosistemas del Ecuador Continental. Quito, Ecuador.

Ogutcen E, Christe D, Nishii K, Salamin N, Möller M, Perret M (2021) Phylogenomics of Gesneriaceae using targeted capture of nuclear genes. Molecular Phylogenetics and Evolution 157: e107068. https://doi.org/10.1016/j.ympev.2021.107068

Schulte LJ, Clark JL, Novak SJ, Ooi MT, Smith JF (2014) Paraphyly of Section Stygnanthe (*Columnea*, Gesneriaceae) and a revision of the species of section Angustiflorae, a new section inferred from ITS and chloroplast DNA Data. Systematic Botany 39(2): 613–636. https://doi.org/10.1600/036364414X680861

Smith JF (2000) Phylogenetic resolution with the tribe Episcieae (Gesneriaceae): Congruence of ITS and *ndh*F sequences from parsimony and maximum-likelihood analyses. American Journal of Botany 87(6): 883–897. https://doi.org/10.2307/2656896

Smith JF, Carroll CL (1997) A cladistic analysis of the tribe Episcieae (Gesneriaceae) based on *ndh*F sequences: Origin of morphological characters. Systematic Botany 22(4): 713–724. https://doi.org/10.2307/2419437

Smith JF, Ooi MT, Schulte LJ, Amaya-Márquez M, Pritchard R, Clark JL (2013a) Searching for monophyly in the subgeneric classification systems of *Columnea* (Gesneriaceae). Selbyana 31: 126–142.

Smith JF, Amaya-Márquez M, Marín-Gómez OH, Clark JL (2013b) Four new species of *Columnea* (Gesneriaceae) with primary distributions in Colombia. Journal of the Botanical Research Institute of Texas 7: 667–679.

Weber A (2004) Gesneriaceae. In: Kadereit J (Ed.) The Families and Genera of Vascular Plants. Vol. 7. Flowering Plants. Dicotyledons. Lamiales (Except Acanthaceae Including Avicenniaceae). Springer, Berlin, 63–158. https://doi.org/10.1007/978-3-642-18617-2_8

Weber A, Clark JL, Möller M (2013) A New Formal Classification of Gesneriaceae. Selbyana 31(2): 68–94.

Weber A, Middleton DJ, Clark JL, Möller M (2020) Keys to the infrafamilial taxa and genera of Gesneriaceae. Rheedea 30: 5–47. https://doi.org/10.22244/rheedea.2020.30.01.02

PhytoKeys 196: 63–89 (2022)
doi: 10.3897/phytokeys.196.83176
https://phytokeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

Viola shiweii, a new species of *Viola* (Violaceae) from karst forest in Guizhou, China

Xiao-Chen Li[1,2], Zheng-Wei Wang[1,2], Qi Wang[1,2], Bin-Jie Ge[1,2], Bin Chen[1,2], Ping Yu[3], Xin Zhong[1,2]

1 *Eastern China Conservation Center for Wild Endangered Plant Resources, Shanghai 201602, China* **2** *Shanghai Chenshan Botanical Garden, Shanghai 201602, China* **3** *Guizhou Maolan Karst Forest, Libo 558400, China*

Corresponding author: Xin Zhong (zhongxin@csnbgsh.cn)

Academic editor: Yasen Mutafchiev | Received 6 March 2022 | Accepted 21 April 2022 | Published 16 May 2022

Citation: Li X-C, Wang Z-W, Wang Q, Ge B-J, Chen B, Yu P, Zhong X (2022) *Viola shiweii*, a new species of *Viola* (Violaceae) from karst forest in Guizhou, China. PhytoKeys 196: 63–89. https://doi.org/10.3897/phytokeys.196.83176

Abstract

Viola shiweii Xiao C. Li & Z. W. Wang (Violaceae), a new species from Guizhou, China, is described, based on morphological and molecular evidence. The new species is morphologically most similar to *V. kwangtungensis* Melchior in its glabrous lateral petals and stoloniferous habit, but can be distinguished by its obtuse teeth along the leaf margin, its abaxially greyish-green leaf blade and its broader and entire sepals with a distinct basal appendage.

Keywords

Morphology, phylogeny, sect. *Plagiostigma*, subg. *Viola*

Introduction

Viola L. is the largest genus amongst the Violaceae, comprising approximately 580–620 species (Wahlert et al. 2014; Marcussen et al. 2015), which are widely distributed in temperate regions and tropical high mountain regions worldwide, with south-western China as one of its current centres of diversity (Wahlert et al. 2014). The diversity and high number of species has resulted in an extremely complex interspecific relationship

Copyright *Xiao-Chen Li et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

in this genus due to hybridisation and horizontal evolution amongst sections and species (Marcussen et al. 2015). Since Becker (1925) provided the first infrageneric classification for *Viola*, several infrageneric classifications of the genus have been proposed (Clausen 1927, 1929, 1931, 1964; Gershoy 1934). In the latest taxonomical revision of *Viola* of China, 96 species were recognised as native (Chen et al. 2007). However, delimitation of the species with stolons distributed in southern and south-western China remains highly problematic and new species are still being discovered (Zhou and Xing 2007; Chen and Yang 2008, 2009; Zhou et al. 2008a; Dong et al. 2009; Ning et al. 2012; Huang et al. 2021).

During an expedition to Guizhou Province in November 2019, an unfamiliar violet whose habit was somewhat similar to that of *Viola kwangtungensis* Melchior caught the authors' attention on the karst rock outcrops. Several specimens with cleistogamous flowers were collected from the field and living material was transplanted and cultivated in Chenshan Botanical Garden for further observation.

Materials and methods

In this study, molecular phylogenetic analysis, based on the ITS dataset, was firstly conducted to resolve the phylogenetic position of the unfamiliar violet and its relationship with *V. kwangtungensis* Melchior. Subsequently, morphological characters of this unfamiliar violet and its related species were compared, based on living plants and herbarium specimens, including the digital resource of the Chinese Virtual Herbarium (https://www.cvh.ac.cn/) and the China Field Herbarium (https://www.cfh.ac.cn/). Herbarium specimens were examined in IBK and CSH. Original protologues and relevant literature were also investigated. Leaf material of the putative new species and its related species was collected and stored with silica. Six species, represented by eight individuals, were newly sampled. Voucher specimens were deposited in Chenshan Herbarium (CSH). Total genomic DNA was extracted with the modified CTAB method (Doyle and Doyle 1987) for library construction at Benagen (https://www.benagen.com). Paired-end sequencing of the whole sequences from both ends of 150 bp fragments was performed on the DNBSEQ T7, about 2 Gb clean data for every sample were produced. The nrDNA were de novo assembled using the GetOrganelle pipeline (Jin et al. 2020) and sequences of ITS1-5.8s-ITS2 were extracted with ITSx 1.1.3 (Bengtsson-Palme et al. 2013). Another 31 sample sequences were obtained from NCBI (Gong et al. 2010; Liang and Xing 2010). The sequences of the species and related ones were aligned in Geneious Prime 2021.2.2 (https://www.geneious.com) using MAFFT (Katoh and Standley 2013) by default setting. Phylogenetic construction was conducted by Maximum Likelihood with IQ-Tree 2 software (Minh et al. 2020), selecting the best-fit model of GTR+F+G4 with 2000 bootstraps. The tree file was visualised and annotated on iTOL (https://itol.embl.de/) (Ivica and Peer 2021). All the sequences accession numbers were listed in Table 1.

Table 1. Vouchers of specimens and GenBank accession number.

Taxon	Voucher	Accession no.
Ingroup taxon		
sect. *Diffusae* (W.Becker) C.J.Wang		
ser. *Australasiaticae* Okamoto		
V. mucronulifera Hand.-Mazz.	Lingyun, Guangxi, Zhou J S 311 (IBSC)	FJ002910
V. sumatrana Miq.	Lvchun, Yunnan, Wang Zheng-wei et al.WZW04206 (CSH)	OM406231
V. kwantungensis Melchior	Guidong, Hunan, Huang Cun-zhong LXC01887 (CSH)	OM406227
V. kwantungensis Melchior	Jinyunshan, Chongqing, Huang Yan-shuang HYS210206	OM406230
V.kwangtungensis Melchior	Malipo, Yunnan, Wang Zheng-wei et al. WZW04187 (CSH)	OM618008
V. austrosinensis Y.S.Chen & Q.E.Yang	Tianlin, Guangxi, Li Xiao-chen et al. LXC02318 (CSH)	OM406228
V. davidii Franch.	Mt. Maoershan, Guangxi, Zhou J S 273 (IBSC)	FJ002902
V. davidii Franch.	Mt. Jiulongshan, Zhejiang, Zhong Xin et al. ZX01824 (CSH)	OM406229
V. grandisepala W.Becker	Mt. Emeishan, Sichuan, Zhou J S 425 (IBSC)	FJ002903
V. fargesii H.Boissieu originally published as *V. principis*	Ruyuan, Guangdong, Zhou J S 103 (IBSC)	FJ002904
Viola sp. nov.	Maolan, Guizhou, Li Xiao-chen et al. LXC00927 (CSH)	OM406226
Viola sp. nov.	Maolan, Guizhou, Li Xiao-chen et al. LXC00323 (CSH)	OM406225
Viola sp. nov.	Maolan, Guizhou, Li Xiao-chen et al. LXC00324 (CSH)	OM406224
ser. *Diffusae* (W.Becker) Steenis		
V. nanlingensis J.S.Zhou & F.W.Xing	Mt. Nankunshan, Guangdong, Liang G. X. 0185 (IBSC)	FJ002916
V. yunnanensis W.Becker & H.Boiss.	Mt. Diaoluoshan, Hainan, Zhou J. S. *s.n.* (IBSC)	FJ002915
V. diffusa Ging	Huaiji, Guangdong, Gong Q. 00043 (IBSC)	FJ002917
V. lucens W.Becker	Tanziyan, Guizhou, Zhou J. S. 348 (IBSC)	FJ002913
V. guangzhouensis A.Q.Dong	Conghua, Guangdong, Dong A. Q. 1104 (IBSC)	FJ002918
sect. *Chamaemelanium* Ging		
V. biflora L.	–	FJ002905
V. orientalis (Maximowicz) W.Becker	–	FJ002909
V. delavayi Franch.	Diqing, Yunnan, Zhou J. S. Xing F. W. 487 (IBSC)	FJ002908
sect. *Viola* L.		
V. collina Bess.	–	FJ002880
V. mirabilis L.	–	MK828568
V. rupestris F.W.Schmidt	–	HM851448
V. grypoceras A.Gray	Mt. Lushan, Jianghxi, Liang G. X. 0002 (IBSC)	FJ002881
V. acuminata Ledeb.	–	FJ002884
sect. *Violidium* (K. Koch) Juz.		
V. inconspicua Blume	SCBG, Guangdong, Liang G. X. 0187 (IBSC)	FJ002897
V. japonica Langsdorff ex Candolle	–	EU591965
V. prionantha Bunge	Jinan,Shandong, Zhang R. J., Xing F. W. 17955 (IBSC)	FJ002893
V. hancokii W.Becker	–	FJ002890
V. pekinensis (Regel) W.Becker	–	FJ002892
V. chaerophylloides (Regel) W.Becker	–	FJ002898
V. dissecta Ledeb.	–	FJ002891
V.magnifica C. J. Wang & X.D.Wang	Mt. Lushan, Jiangxi, Liang G. X. 0038 (IBSC)	FJ002899
sect. *Bilobatae* (W.Becker) Juz.		
V. verecunda A.Gray	Mt. Nanling, Guangdong, Zhou J. S. 1553 (IBSC)	FJ002911
V. triangulifolia W.Becker	Mt. Jinggangshan, Jiangxi, Zhou J. S. 140 (IBSC)	FJ002912
outgroup taxon		
Afrohybanthus enneaspermus (L.) Flicker	–	HM483598

Results

Molecular Analysis

The ITS dataset comprises 37 accessions representing 32 species, including *Afrohybanthus enneaspermus* (L.) Flicker selected as an outgroup. The aligned matrix of ITS sequences was 696 bp in total. The result of ML is shown in Fig 1. The samples of the putative new species (pink clade) clustered into a strongly supported monophyletic lineage (clade 1), forming a weak sister relationship with a clade formed by *V. mucronulifera* and *V. sumatrana*. The morphologically most similar *V. kwangtungensis* was resolved on a more distant phylogenetic position (clade 2, blue clade). Based on morphological characters and phylogenetic results, we recognise this unfamiliar violet as a distinct species and described it here as *Viola shiweii* Xiao C. Li & Z.W.Wang.

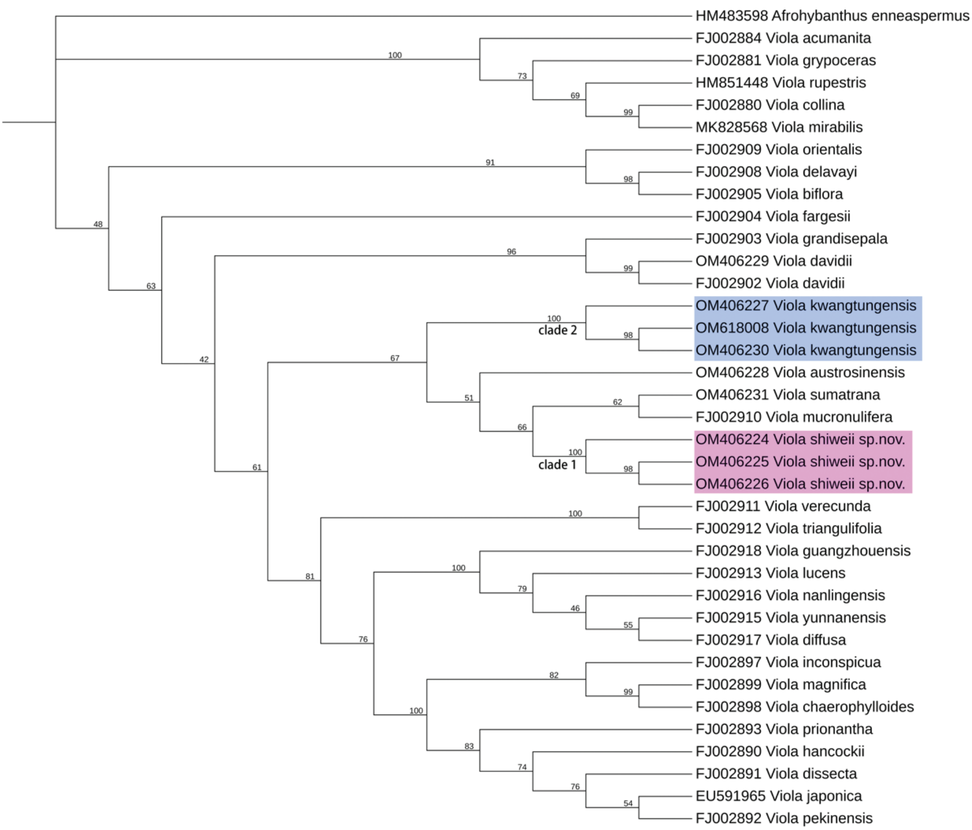

Figure 1. ML tree of the new species *Viola shiweii* sp. nov. and its related species inferred by IQ-Tree 2, based on ITS dataset. Bootstrap values of the Maximum Likelihood are shown along the branches. Outgroup taxon: *Afrohybanthus enneaspermus*.

Taxonomic treatment

Viola shiweii **Xiao C. Li & Z. W. Wang, sp. nov.**
urn:lsid:ipni.org:names:77297809-1
Figs 2, 3, Appendix 1: Figs A1–A12

Type. China. Shanghai Chenshan Botanical Garden, cultivated plants collected from Guizhou, Qiannan Buyi and Miao Autonomous Prefecture (黔南布依族苗族自治区), Libo county (荔波县), Maolan National Nature Reserve (茂兰国家级自然保护区), on the rocks along the karst forest margin, 25°16'39.1039"N, 107°55'2.7598"E, 867 m elevation, 9 Nov 2019, Wang Zheng-wei and Li Xiao-chen, LXC00927 ***Holotype*****:** CSH0182173 (CSH!); ***isotypes*****:** ZJFC!, CSFI!, IBSC!.

Diagnosis. The new species is morphologically most similar to *V. kwangtungensis* Melchior in its glabrous lateral petals and stoloniferous habit, but can be distinguished by its obtuse teeth along the leaf margin, its abaxially pale green leaf blade and its broader and entire sepals with a distinct basal appendage.

Description. Perennial herb, acaulescent, with stolons. Rhizome short, straight or oblique, densely noded, usually covered by brown remains of stipules. **Stipules** free, brown, broadly lanceolate, 5–10 mm long, margin long fimbriate-dentate, lobes remotely dentate. **Basal leaves** glabrous, slightly grooved, with petioles stout, petioles unequal in length; blade thick leathery, ovate or suborbicular, 15–30 × 15–20 mm, base deep cordate, apex usually obtuse, abaxially green, scabrous, abaxially greyish-green, mid-vein distinct above, glabrous on both surfaces, margin glandular-serrate or shallowly glandular-crenate, slightly wavy, teeth obtuse at the apex; **stolon leaves** scattered, smaller. Pedicel equal to or longer than petiole, two bracts narrowly lanceolate, at the middle or lower part of the pedicel. **Sepals** 5, ca. 6 mm long and 2 mm wide, lanceolate, glabrous, margin narrowly membranous, apex somewhat acute, base distinctly decurrent, apex obtuse or shallowly dentate. Flower 1.5–2.5 cm in diameter, **petals** 5, white, posterior and lateral ones obovate, ca. 1.2 cm × 5 mm, narrow at the base, lateral petals purplish near the middle, glabrous, anterior petal shorter, ca. 10 mm (spur included) long, oblong, purple-veined, apex rounded, obtuse, spur saccate, 2–3 mm long and 1.5 mm wide. **Style** clavate, base geniculate, stigmas flattened on top, narrowly margined on lateral sides and abaxially, shortly beaked ventrally. **Capsule** ellipsoid, valves carinate, ca. 10 mm long and 2.5 mm wide, glabrous. **Seeds** black, ca. 2 mm long and 1 mm in diameter.

Distribution and habitat. The species was observed to grow on dry and partially shaded limestone, around the karst forest edge, at 700–900 m elevation.

Additional specimens examined. China, Guizhou, Qiannan Autonomous Prefecture, Libo County, Maolan National Nature Reserve, karst forest, 24 Jul 2008, Zhang Dai-Gui 080724077 (JIU!); **China**, Guizhou, Qiannan Buyi and Miao Autonomous Prefecture, Libo County, Maolan National Nature Reserve, 21 Nov 2021, Li Xiao-chen, Wang Zheng-wei & Wei Hong-jin, LXC02320 (CSH!), LXC02322 (CSH!), LXC02323 (CSH!), LXC02324 (CSH!), LXC02325 (CSH!).

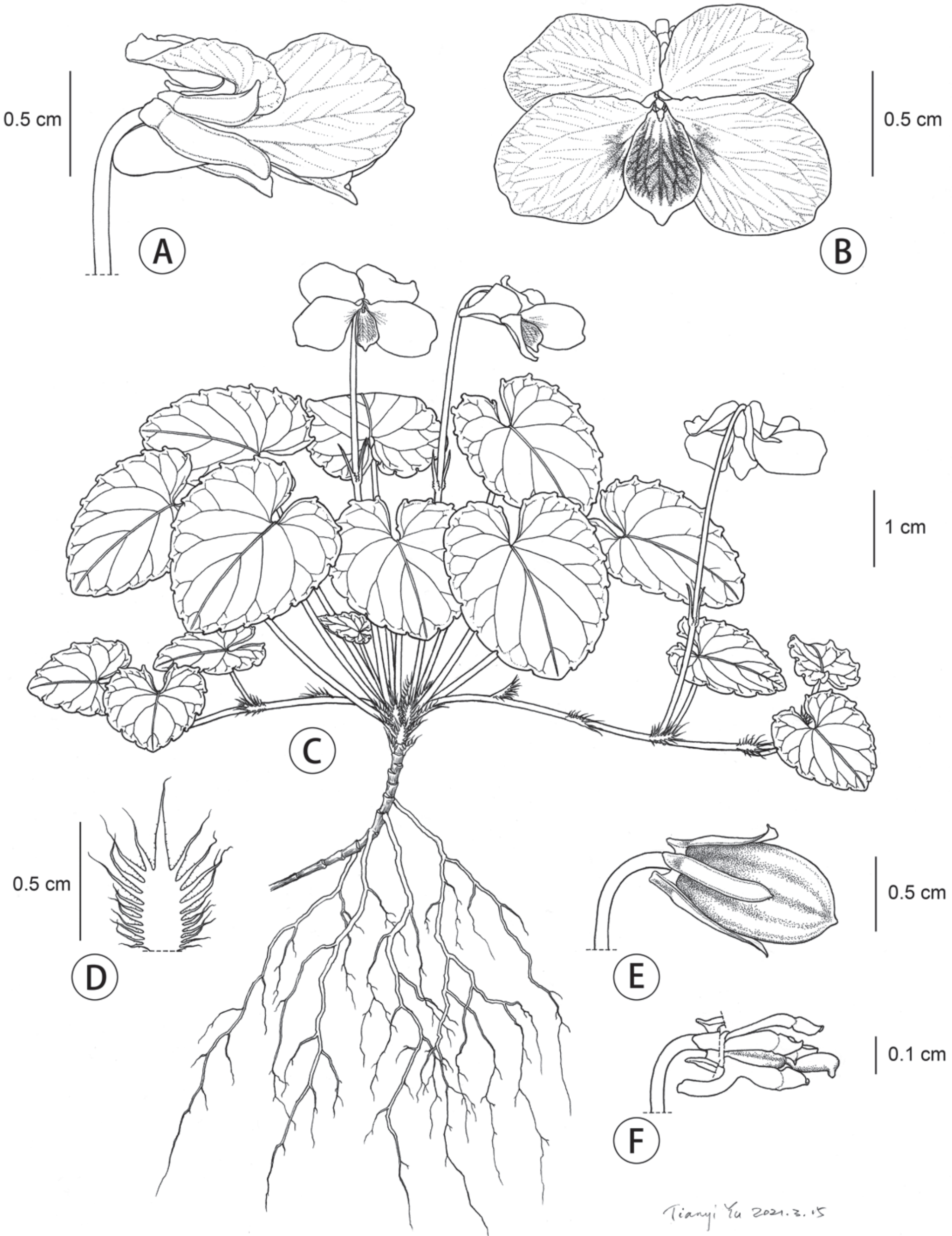

Figure 2. *Viola shiweii* sp. nov. **A** flower side view **B** flower front view **C** habit **D** stipule **E** capsule **F** stamens and pistil.

Phenology. Cultivated plants flower in September-March, fruiting in September.

Etymology. The specific name epithet "*shiweii*" was proposed in memory of Deng Shi-wei (191?-1936), who dedicated his life to the exploration of the flora of Guizhou. The Chinese name is given as "世纬堇菜".

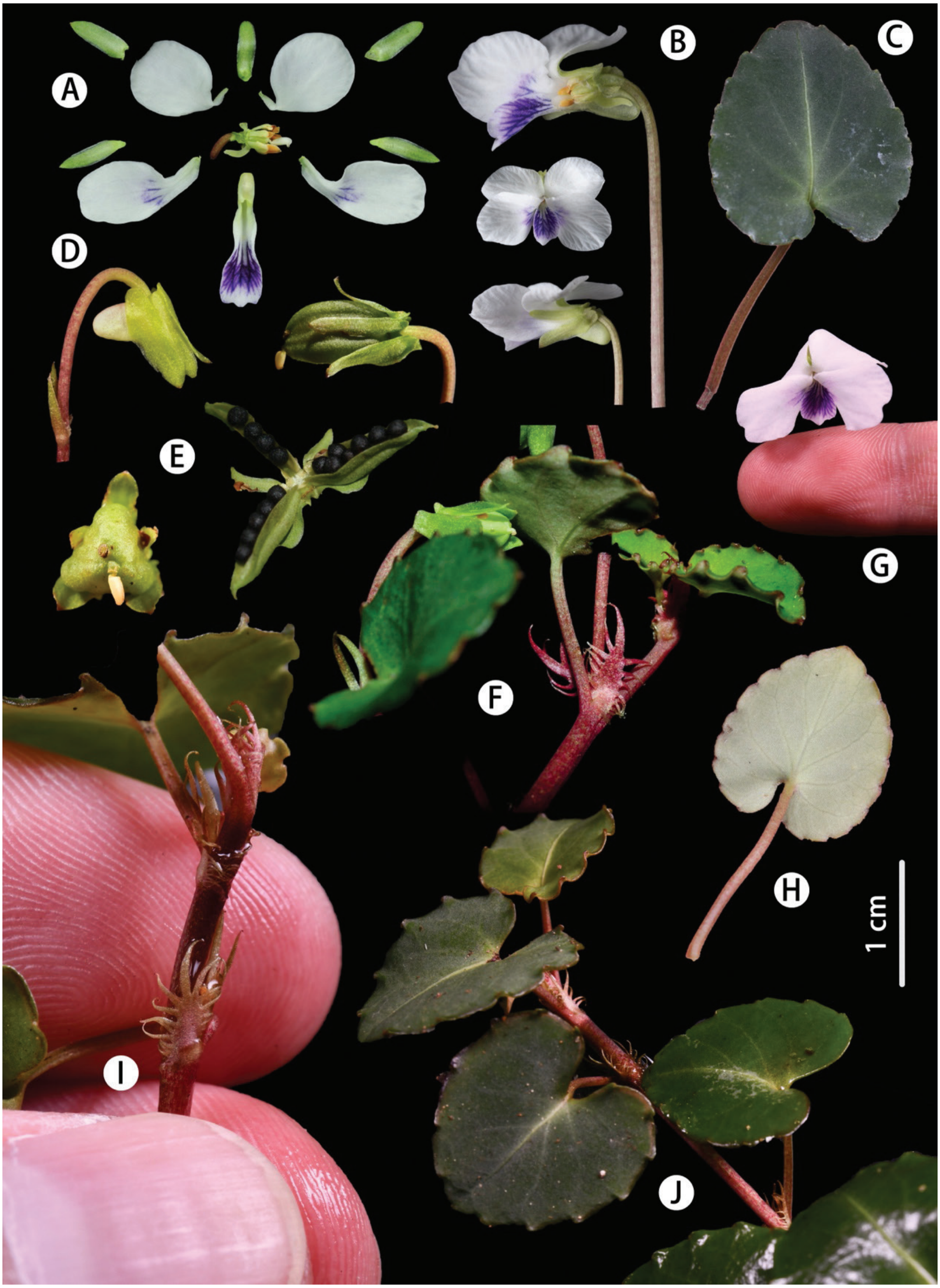

Figure 3. *Viola shiweii* sp. nov. **A** petals, sepals, stamens and pistils **B, G** flower in front view and detail of a longitudinal section in side **C, H** basal leaf adaxially and abaxially **D** cleistogamous flowers **E** capsule and seeds **F** margin teeth **I** stipule **J** leaves on stolons.

Conservation status. Only two populations of *V. shiweii* are currently known from Maolan National Nature Reserve, Libo County, in an area of the karst formation across Guizhou and Guangxi (Fig. 4). This species is represented by no more than 200 large and mature individuals. Due to its rarity, the low number of individuals and habitat vulnerability, *V. shiweii* is considered to be Critically Endangered (CR, B1), according to the IUCN (2019).

Discussion

Although our phylogenetic analysis, based on ITS sequences, did not fully clarify the infrageneric relationships within *Viola*, it produced informative evidence for differentiation amongst lower taxa. *V. shiweii* can be placed in *Viola* ser. *Australasiaticae* (Okamoto et al. 1993), which is characterised by the stolons with scattered leaves, absent aerial stems, short spur of anterior petal and stigma beaked ventrally. The phylogenetic analysis in this study (Fig. 1) also confirmed this conjecture (Fig. 1); however, the monophyly of *Viola* ser. *Australasiaticae* was not supported, which was consistent with a previous study (Gong et al. 2010). *Viola* ser. *Australasiaticae* was proved to be nested in the subg. *Viola* sect. Plagiostigma Godr. (Marcussen et al. 2012).

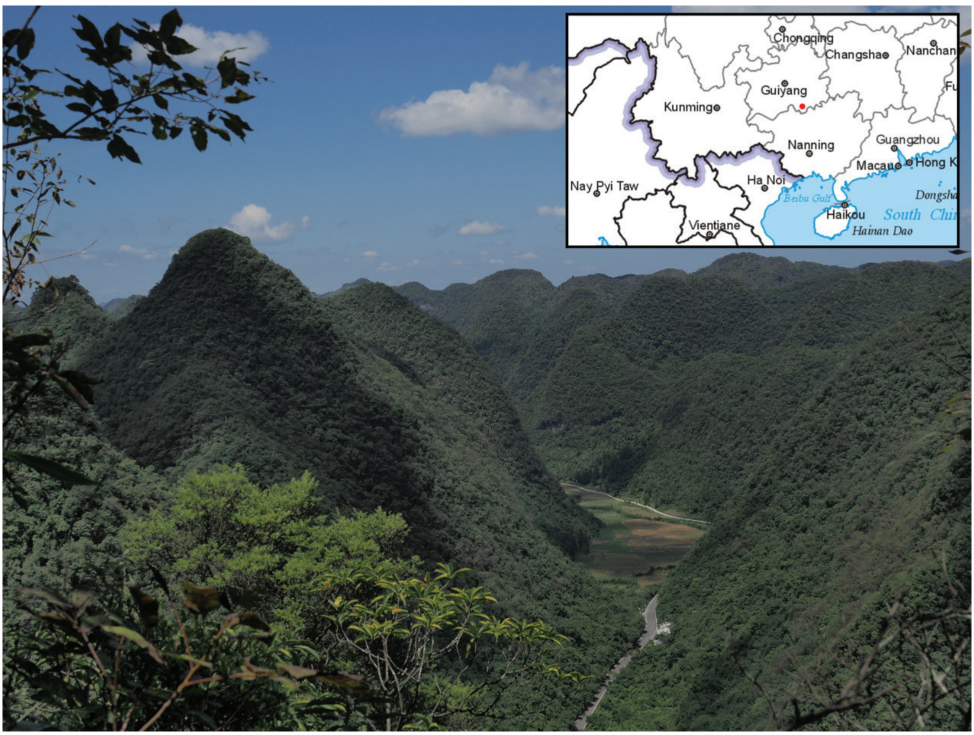

Figure 4. Habitat and distribution of *Viola shiweii*.

Viola ser. *Australasiaticae* comprises ca. 27 species, widely distributed in the Himalayan Region, southern China, south-eastern Asia and Ryukyu Island of Japan, with 14 species occurring in China (Chen 2006), in which *Viola davidii*, *V. schneideri* W.Becker, *V. kwangtungensis*, *V. mucronulifera* and *V. austrosinensis* form a complex in this series and caused mass misidentification due to their high degree of morphological similarity.

Viola davidii Franchet was published by Adrien René Franchet (1885), based on the collection of David from Moupine (Baoxing County, Sichuan, China) (isotype: David#s.n., K000254222) in 1869 [1870]. It is a morphologically variable and widespread species characterised by its ovate or ovate-orbicular leaf blade with 6–8 rounded teeth along each side, bearded lateral petals and short spurred anterior petal. It was originally regarded as species similar to *V. biflora* L., but its beaked stigma (vs. bilobed), white and purple petals (vs. yellow) indicated a distinctly different affiliation amongst the genus. Later, Becker (1921) described a strikingly similar violet with ovate leaves, *V. schneideri* W.Becker, based on the collection of Schneider (isotype: Schneider C.K. #739, G00343327) from Te-chang (De-chang County, Sichuan, China), but the diagnostic leaf shape falls within the morphological variation of *V. davidii* Franchet and, for this reason, it was recently treated as its synonym, which is further supported by overlapping distributions (Chen 2006). The only collection of *V. shiweii* before this study was misidentified as *V. davidii*. *Viola shiweii* shares a similar leaf shape with *V. davidii*, but can be differed by its glabrous lateral petals and obtuse teeth along the leaf margin.

Viola kwangtungensis Melchior, which shows the highest resemblance to *V. shiweii* (Table 2, Figs 5, 6) is an overlooked species frequently being confounded with *V. davidii* or *V. mucronulifera*, but considered as a distinct taxon by Flora of China (Chen et al. 2007). *Viola mucronulifera* Hand.-Mazz. was published by Handel-Mazzetti (1931), based on the collection of R. C. Ching #7016 from Guangxi (holotype: PE00025463, isotypes: NY00097644 & A00067198) and is characterised by the distinctly stipitate tooth glands. Later, *V. kwangtungensis* Melchior (1933) was published, based on a collection of Woon-Young Chun and his assistants (isotype: P. Ko #50326, A00067196) from Guangdong, which can be easily recognised by its characteristic leaf crenation of the leaves, but it was subsequently reduced to a synonym of *V. mucronulifera* in Flora Reipublicae Popularis Sinicae (Wang 1991). *Viola kwangtungensis* has spinules at the apex of the teeth, as the horizontal extension of the teeth, while the spinules of *V. mucronulifera* are perpendicular to the leaf blade and placed between the teeth, which can be distinguished in field observation. *Viola kwangtungensis* also used to be considered conspecific with *V. schneideri* due to morphology transition in the spinose, based only on the specimen observation (Zhou et al. 2008b).

More recently, as the latest supplement of this complex, a new species, *V. austrosinensis*, distinguished from *V. kosanensis* Hayata (ser. Rosulantes Borbas (Y.S.Chen)), was described, of which the leaves were coriaceous, glabrous, not glandular-dotted on the abaxial surface (Chen and Yang 2008). *Viola austrosinensis* is different from *V. shiweii* in its ovate leaf blade and acute anterior petal's apex.

In China, *V. mucronulifera* was found to occur only in the Province of Yunnan and its type locality in Guangxi; its occurrence in Guizhou was a mistake caused by the misidentification of *V. kwangtungensis* in Flora of Guizhou (Yao 1989), as we personally

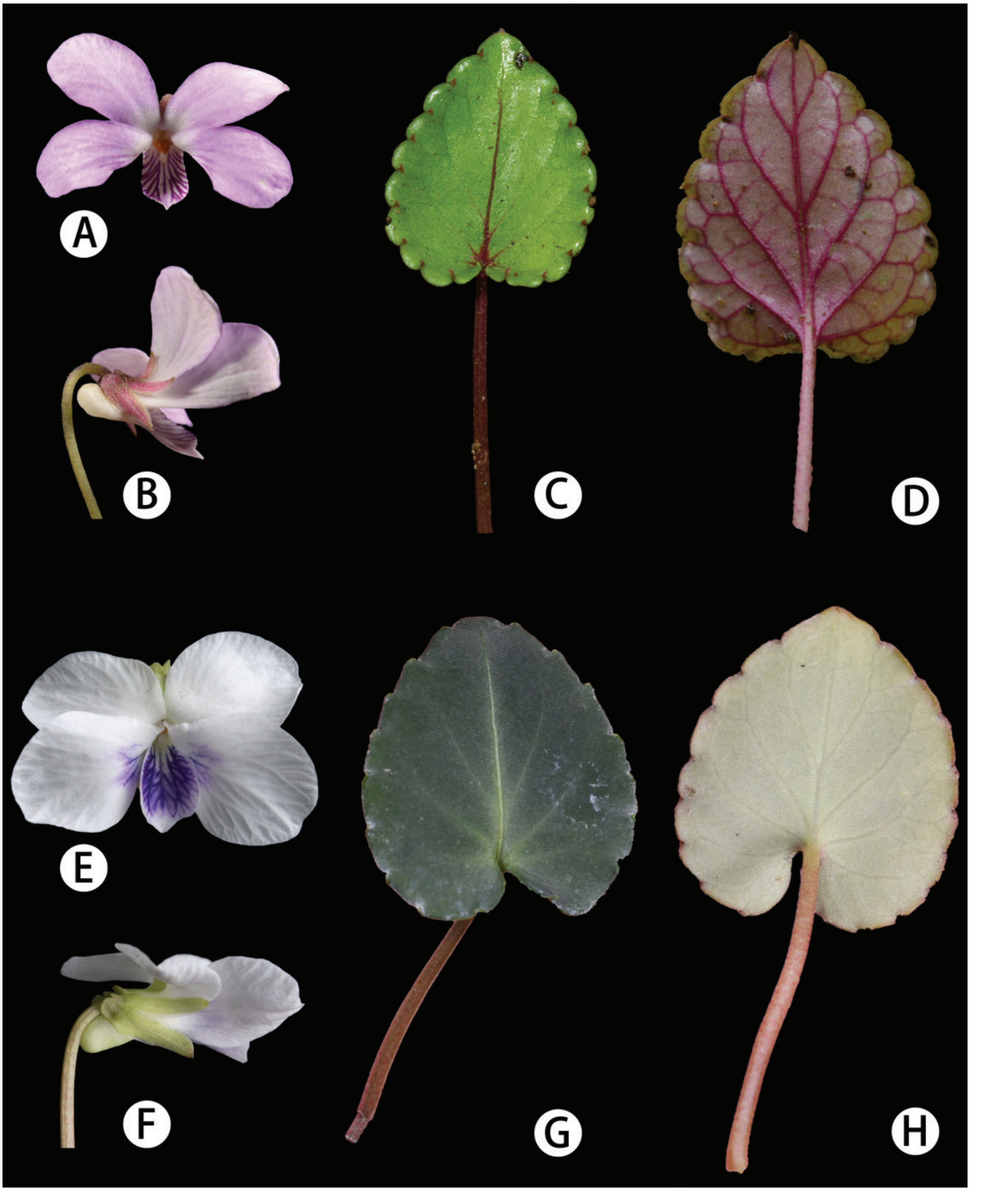

Figure 5. Flowers and leaves of *Viola shiweii* sp. nov. and *Viola kwangtungensis* **A, B** *V. kwangtungensis*, lower, front and side views **C, D** *V. kwangtungensis*, adaxial and abaxial leaf surfaces **E, F** *Viola shiweii*, flower, front and side views **G, H** *V. kwangtungensis*, adaxial and abaxial leaf surfaces.

observed in the locality cited in this work (Fanjingshan, Jiangkou). The morphology and distribution differences between *V. shiweii*, *V. kwangtungensis* and *V. davidii* are listed in Table 2. Comparision of V. shiweii and V. kwangtungensi was visualised in Figs 5, 6. Keys to *V. shiweii* and its allies were also presented.

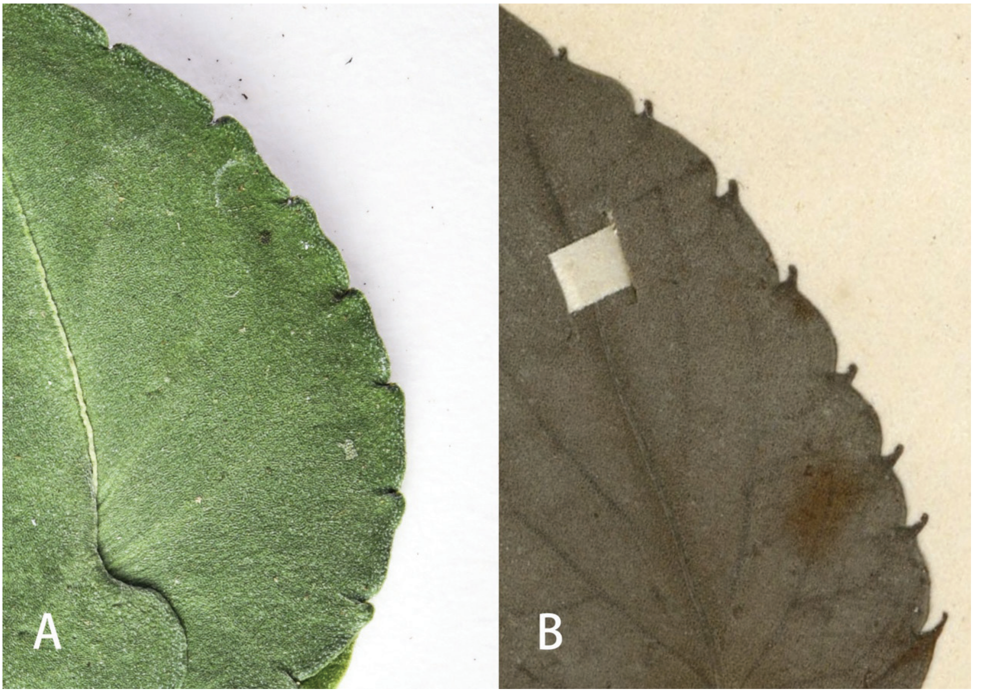

Figure 6. Leaf margin of *V. shiweii* sp. nov. and *V. kwangtungensis* **A** *V. shiweii*, holotype **B** *V. kwangtungensis*, isotype: P. Ko #50326, A00067196.

Table 2. Morphology and distribution comparison between *Viola shiweii* sp. nov., *V. kwangtungensis* and *Viola davidii*.

	Viola shiweii	*Viola kwangtungensis*	*Viola davidii*
Leaf blade	Ovate or orbicular, apex usually obtuse, base deep cordate, greyish-green abaxially.	Ovate to triangularly ovate, base shallowly cordate, apex usually acute, purple abaxially.	Ovate or ovate-orbicular, glaucous abaxially, base deeply coedate, apex rounded or acute.
Leaf margin	Serrate	Crenate	Shallowly 6–8-crenate on each side.
Stipule	Long fimbriate	Fimbriate	Remotely fimbriate-dentate
Sepals	Lanceolate, ca. 6 mm × 2 mm, entire, green, glabrous, basal distinctly decurrent.	Lanceolate, 3–5 mm × 1.5–2 mm, sparsely shallowly dentate, purplish-red, sparsely pubescent, base not decurrent.	Lanceolate or ovate-lanceolate, 5–6 mm × 1.5–2 mm, brown, glabrous, base shortly decurrent, margin narrowly membranous, apex truncate
Posterior and lateral petals	Obovate, base constricted	Obovate-oblong	Oblong-obovate
Seed	Black	Brown	Brown
Habitat	Dry and partially shaded limestone	Humid and shaded stream valley	Shaded place under forest, stream valley, or grassy slope.
Distribution	Guizhou, Guangxi.	Fujian, N Guangdong, Guizhou, Hunan, Jiangxi, Sichuan, Yunnan, and Taiwan (Lu et al. 2019)	Chongqing, Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangxi, Sichuan, SE Xizang, Yunnan, Zhejiang.

Keys to *Viola shiweii* sp. nov. and its related species (ser. Australisiaticae) in China

1	Spur 5–7 mm, anterior petal 2-lobed at apex	***V. formosana***
–	Spur shorter than 5 mm, anterior petal rounded, obtuse or acute at apex	**2**
2	Stipules usually entire, sepals broad ovate, ca. 5 mm wide	***V. grandisepala***
–	Stipules fimbriate, sepals lanceolate, much narrower, not more than 5 mm	**3**
3	Leaf blade spinulose along margin	**4**
–	Leaf blade without spinules along margin	**5**
4	Leaves conspicuously spinose between teeth	***V. mucronulifera***
–	Leaves shortly spinose at apex of teeth	***V. kwangtungensis***
5	Leaves ovate, orbicular or nearly orbicular, apex obtuse	**6**
–	Leaves cordate or oblong-ovate, apex acuminate	**10**
6	Lateral petals beard at base	***V. davidii***
–	Lateral petals glabrous at base	7
7	Leaves serrata, teeth have obtuse apices, apex of anterior petal obtuse	***V. shiweii***
–	Leaves crenate, without obtuse teeth along margin	**8**
8	Leaves coriaceous, base shallowly cordate, anterior petal acute	***V. austrosinensis***
–	Leaves chartaceous, orbicular or nearly orbicular, base deeply cordate, anterior rounded	**9**
9	Leaves adaxially scabrous, sparsely pubescent	***V. duclouxii***
–	Leaves adaxially shiny, glabrous	***V. sikkimensis***
10	Rhizome short, densely noded	**11**
–	Rhizome nodes elongated and stout	**12**
11	Leaves glabrous, shiny adaxially	***V. nitida***
–	Leaves densely pubescent	***V. fargesii***
12	Plant densely pubescent	***V. yunnanensis***
–	Plant glabrous or sparsely pubescent	**13**
13	Leaves blade glabrous, sepals ovate	***V. nuda***
–	Leaves more or less pubescent, sepals lanceolate	**14**
14	Leaves and capsules dot-like brown glandular, lateral petals glabrous	***V. sumatrana***
–	Leaves not glandular, lateral petals bearded	***V. thomsonii***

Acknowledgements

Our deepest gratitude goes to three reviewers Thomas Marcussen, Juliana de Paula-Souza, and Chen You-sheng and Subject editor Yasen Mutafchiev, for their careful work and thoughtful suggestions that have helped improve this paper substantially. The authors are grateful to Mr. Yu Tian-yi for his excellent illustration in the manuscript, Dr. Jiang Kai from Chenshan Botanical Garden for his help in data analysis and

Dr. Huang Yan-shuang from Sun Yat-Sen University, Dr. Zhu Xin-xin from Xinyang Normal University for their generous offer of samples and collection information. The first author is also indebted to Dr. Huang Yu-song and Huang Jin-quan from IBK for hosting our visit and Miss Pi for her company during the epidemic of COVID-19. This study was supported by the project of the National Wild Plant Germplasm Resource Center for Shanghai Chenshan Botanical Garden (ZWGX2102), the project of the Special Fund for Scientific Research of Shanghai Landscaping & City Appearance Administrative Bureau (G212416, G222404).

References

Becker W (1921) Violae novae Asiaticae. Repertorium Specierum Novarum Regni Vegetabilis 17: 784. https://doi.org/10.1002/fedr.19210171907

Becker W (1925) *Viola*. In: Engler A, Prantl K (Eds) Die Natürlichen Pflanzenfamilien (2nd edn.) 21. Duncker & Humblot, Berlin, 363–376.

Bengtsson-Palme J, Ryberg M, Hartmann M, Branco S, Wang Z, Godhe A, De Wit P, Sánchez-García M, Ebersberger I, de Sousa F, Amend AS, Jumpponen A, Unterseher M, Kristiansson E, Abarenkov K, Bertrand YJK, Sanli K, Eriksson KM, Vik U, Veldre V, Nilsson RH (2013) Improved software detection and extraction of ITS1 and ITS 2 from ribosomal ITS sequences of fungi and other eukaryotes for analysis of environmental sequencing data. Methods in Ecology and Evolution 4(10): 914–919. https://doi.org/10.1111/2041–210X.12073

Chen YS (2006) Taxonomic revision of *Viola* L. (Violaceae) in China. PhD Thesis, The Institute of Botany, Chinese Academy of Science, China. https://kreader.cnki.net/Kreader/CatalogViewPage.aspx?dbCode=CDFD&filename=2006189566.nh&tablename=CDFD9908&compose=&first=1&uid=

Chen YS, Yang QE (2008) A new species of *Viola* (Violaceae) from southern China. Botanical Journal of the Linnean Society 158(4): 755–761. https://doi.org/10.1111/j.1095-8339.2008.00935.x

Chen YS, Yang QE (2009) Two new stoloniferous species of *Viola* (Violaceae) from China. Botanical Journal of the Linnean Society 159(2): 349–356. https://doi.org/10.1111/j.1095-8339.2008.00911.x

Chen YS, Yang QE, Ohba H, Nikitin VV (2007) Violaceae. In: Wu ZY, Raven PH (Eds) Flora of China, vol. 13. Science Press, Beijing & Missouri Botanical Garden Press, St. Louis, 72–111.

Clausen J (1927) Chromosome number and the relationship of species in the genus *Viola.* Annals of Botany 41(4): 677–714. https://doi.org/10.1093/oxfordjournals.aob.a090098

Clausen J (1929) Chromosome number and relationship of some North American species of *Viola.* Annals of Botany 43(4): 741–764. https://doi.org/10.1093/oxfordjournals.aob.a090198

Clausen J (1931) Cyto-genetic and taxonomic investigations in *Melanium* violets. Hereditas 15(3): 219–308. https://doi.org/10.1111/j.1601-5223.1931.tb02553.x

Clausen J (1964) Cytotaxonomy and distributional ecology of western North American violets. Maxroño 17: 173–197. https://www.jstor.org/stable/41423141

Dong AQ, Zhou JS, Gong Q (2009) A new species of *Viola* (Violaceae) from Guangdong, China. Novon 19(4): 457–460. https://doi.org/10.3417/2007157

Doyle JJ, Doyle JL (1987) A rapid DNA isolation procedure for small quantities of fresh leaf tissue. Phytochemical Bulletin 19: 11–15. https://webpages.charlotte.edu/~jweller2/pages/BINF8350f2011/BINF8350_Readings/Doyle_plantDNAextractCTAB_1987.pdf

Franchet AR (1885) Plantae Davidianae Ex Sinarum Imperio Plantes Du Thibet Oriental (Province de Moupine). Nouvelles Archives du Muséum d'Histoire Naturelle, sér. 2 8: 203. https://www.biodiversitylibrary.org/page/36875130#page/221/mode/1up

Gershoy A (1934) Studies in North American violets. III. Chromosome numbers and species characters. Vermont Agricultural Experiment Station Bulletin 367: 1–91.

Gong Q, Zhou JS, Zhang YX, Liang GX, Chen HF, Xing FW (2010) Molecular Systematics of Genus *Viola* L. in China. Redai Yaredai Zhiwu Xuebao 18(6): 633–642.

Handel-Mazzetti H (1931) Plantae Novae Chinginae. Sinensia 2(1): 4–5. https://www.cvh.ac.cn/spms/detail.php?id=0755aeb9

Huang YS, Kang N, Zhong XJ, Liao WB, Fan Q (2021) A new species of *Viola* (Violaceae) from Guangdong Province, China. PhytoKeys 176: 67–76. https://doi.org/10.3897/phytokeys.176.65443

IUCN (2019) Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Committee. http://cmsdocs.s3.amazonaws.com/RedListGuidelines.pdf

Ivica L, Peer B (2021) Interactive Tree Of Life (iTOL) v5: An online tool for phylogenetic tree display and annotation. Nucleic Acids Research 49(W1): W293–W296. https://doi.org/10.1093/nar/gkab301

Jin JJ, Yu WB, Yang JB, Song Y, dePamphilis CW, Yi TS, Li DZ (2020) GetOrganelle: A fast and versatile toolkit for accurate de novo assembly of organelle genomes. Genome Biology 21(1): 1–31. https://doi.org/10.1186/s13059-020-02154-5

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Molecular Biology and Evolution 30(4): 772–780. https://doi.org/10.1093/molbev/mst010

Liang GX, Xing FW (2010) Infrageneric phylogeny of the genus *Viola* (Violaceae) Based on trnL-trnF, psbA-trnH, rpL16, ITS Sequences, Cytological and Morphological Data. Yunnan Zhi Wu Yan Jiu 32(6): 477–488.

Lu C, Hung Y, Chen C (2019) *Viola kwangtungensis* Melch. (Violaceae): A new record *Viola* in Taiwan. Taiwan Linye Kexue 34(2): 135–142. https://www.tfri.gov.tw/main/science_in.aspx?siteid=&ver=&usid=&mnuid=5377&modid=1&mode=&noframe=&cid=1228&cid2=2280&nid=6037

Marcussen T, Jakobsen KS, Danihelka J, Ballard HE, Blaxland K, Brysting AK, Oxelman B (2012) Inferring species networks from gene trees in high-polyploid North American and Hawaiian violets (*Viola*, Violaceae). Systematic Biology 61(1): 107–126. https://doi.org/10.1093/sysbio/syr096

Marcussen T, Heier L, Brysting A, Oxelman B, Jakobsen K (2015) From gene trees to a dated allopolyploid network: Insights from the angiosperm genus *Viola* (Violaceae). Systematic Biology 64(1): 84–101. https://doi.org/10.1093/sysbio/syu071

Melchior H (1933) *Viola kwangtungensis*, a new violet from China. Sunyatsenia 1(203): 124–126.

Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, Haeseler A, Lanfear A (2020) IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. Molecular Biology and Evolution 37(5): 1530–1534. https://doi.org/10.1093/molbev/msaa015

Ning ZL, Zeng ZX, Chen L, Xu BQ, Liao JP (2012) *Viola jinggangshanensis* (Violaceae), a new species from Jiangxi, China. Annales Botanici Fennici 49(5): 383–386. https://doi.org/10.5735/085.049.0610

Okamoto M, Okada H, Ueda K (1993) Morphology and chromosome number of *Viola pilosa*, and its systematic position. Taxon 42(4): 781–787. https://doi.org/10.2307/1223263

Wahlert GA, Marcussen T, de Paula-Souza J, Feng M, Ballard Jr HE (2014) A phylogeny of the Violaceae (Malpighiales) inferred from plastid DNA Sequences: Implications for generic diversity and intrafamilial classification. Systematic Botany 39(1): 239–252. https://doi.org/10.1600/036364414X678008

Wang QR (1991) Violaceae. In: Agendae Academiae Sinicae Edita (Eds) Flora Reipublicae Popularis Sinicae Vol. 51. Science Press, Beijing, 95–96. http://www.iplant.cn/info/Viola%20mucronulifera?t=z

Yao LZ (1989) Violaceae. In: Editorial Committee of Flora Guizhouensis (Eds) Flora Guizhouensis, Vol. 4. Sichuan Minorities Press, Chengdu, 228.

Zhou JS, Xing FW (2007) *Viola changii* sp. nov. (Violaceae) from Guangdong, southern China. Nordic Journal of Botany 25(5-6): 303–305. https://doi.org/10.1111/j.0107-055X.2008.00198.x

Zhou JS, Gong Q, Xing FW (2008a) *Viola nanlingensis* (Violaceae), a new species from Guangdong, southern China. Annales Botanici Fennici 45(3): 233–236. https://doi.org/10.5735/085.045.0312

Zhou JS, Li CH, Xing FW (2008b) A revision on several species of *Viola*. Guangxi Zhi Wu 28(5): 573. http://www.guihaia-journal.com/ch/reader/view_abstract.aspx?file_no=20080502&flag=1

Appendix 1. Type specimens of *V. shiweii*.

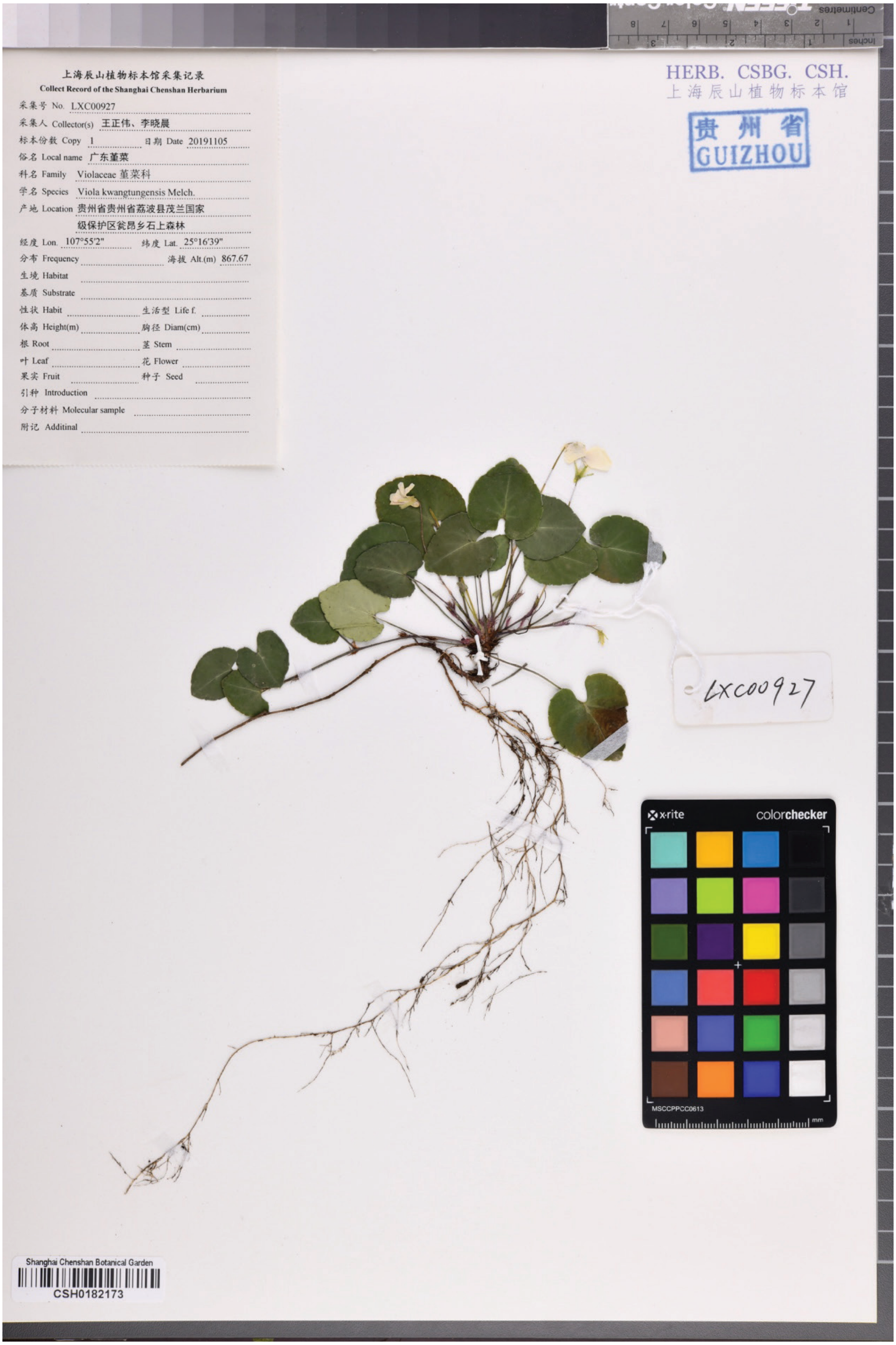

Figure A1. Holotype: LXC00927 (CSH0182173).

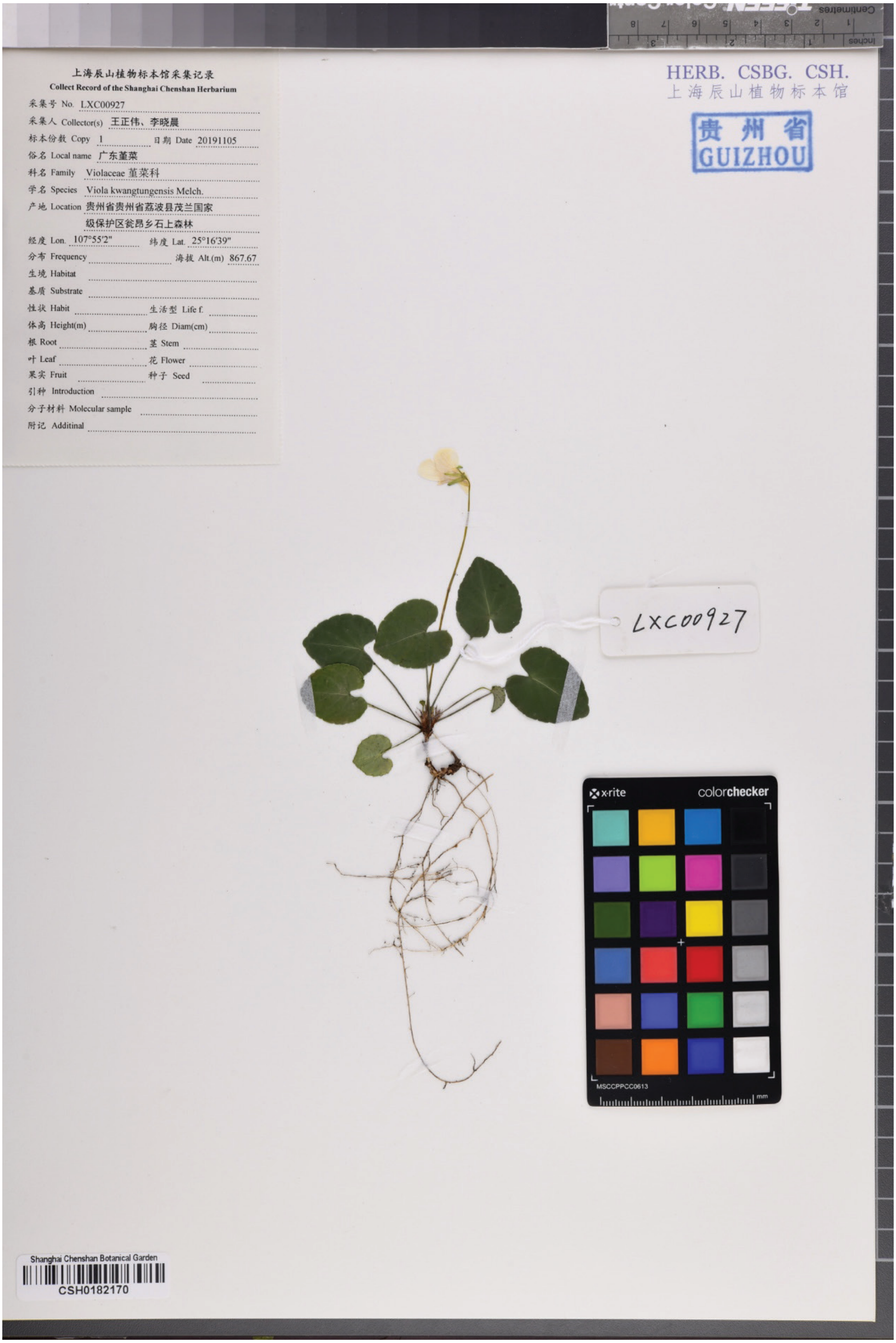

Figure A2. Isotype: LXC00927 (CSH0182170).

Figure A3. Isotype: LXC00927 (CSH0182171).

Figure A4. Isotype: LXC00927 (CSH0182172).

Figure A5. Paratype: LXC02320 (CSH0189181).

Figure A6. Paratype: LXC02322 (CSH0189180).

Figure A7. Paratype: LXC02323 (CSH0189177).

Figure A8. Paratype: LXC02323 (CSH0189178).

Figure A9. Paratype: LXC02323 (CSH0189179).

Figure A10. Paratype: LXC02324 (CSH0189176).

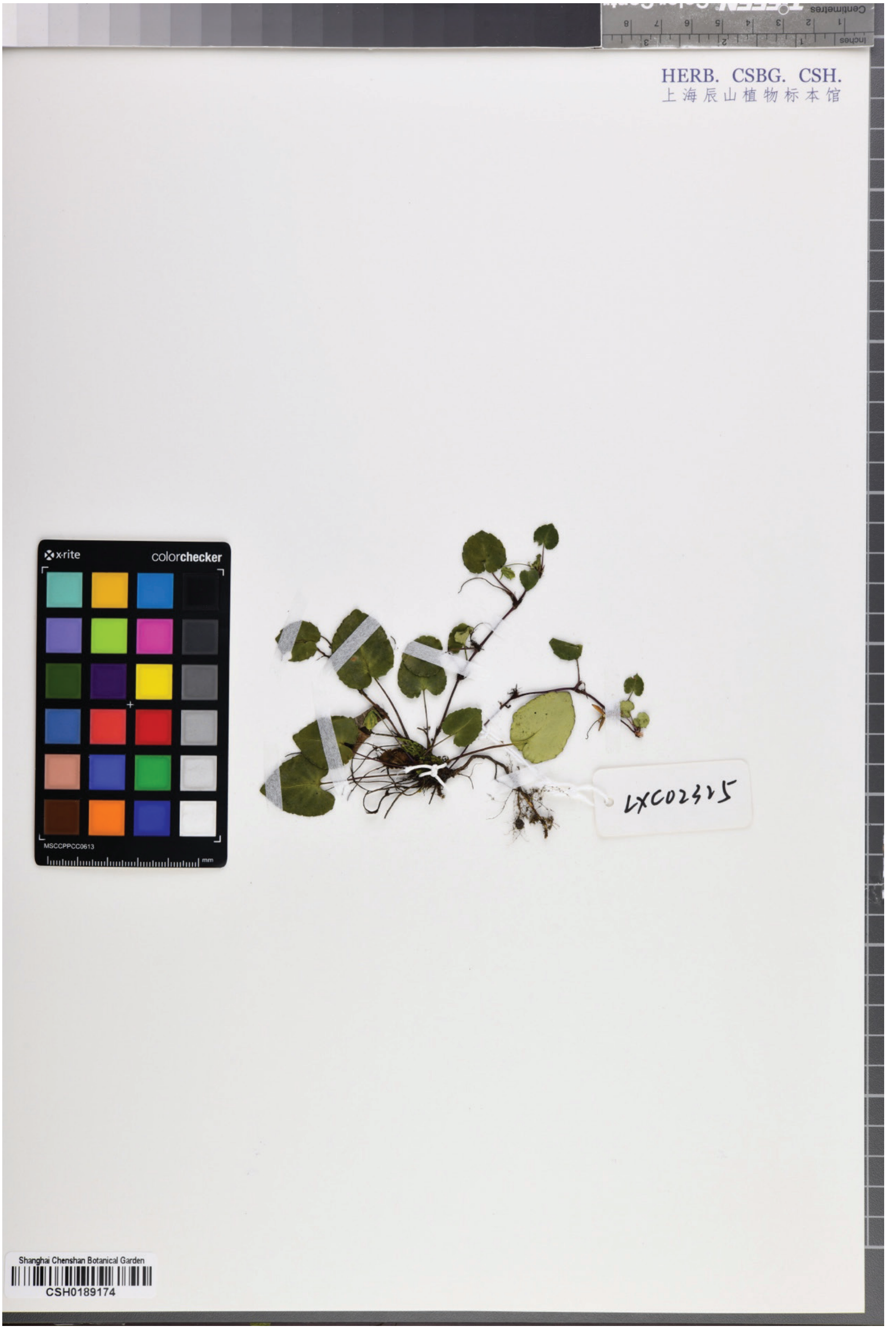

Figure A11. Paratype: LXC02325 (CSH0189174).

Figure A12. Paratype: LXC02325 (CSH0189175).

PhytoKeys 196: 91–214 (2022)
doi: 10.3897/phytokeys.196.77940
https://phytokeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

Taxonomy of *Dianthus* (Caryophyllaceae) – overall phylogenetic relationships and assessment of species diversity based on a first comprehensive checklist of the genus

Georgia Fassou[1], Nadja Korotkova[2], Anush Nersesyan[3], Marcus A. Koch[4], Panayotis Dimopoulos[1], Thomas Borsch[2]

1 *University of Patras, School of Natural Sciences, Department of Biology, Division of Plant Biology, Laboratory of Botany, Patras, Achaia GR-26504, Greece* **2** *Botanischer Garten und Botanisches Museum Berlin, Freie Universität Berlin, Königin-Luise-Strasse 6–8, 14195 Berlin, Germany* **3** *A. Takhtajyan Institute of Botany, Armenian National Academy of Sciences, National Academy of Sciences of the Republic of Armenia, Acharyan st. 1, 0040 Yerevan, Armenia* **4** *Centre for Organismal Studies (COS) Heidelberg, Department of Biodiversity and Plant Systematics/Botanic Garden and Herbarium Heidelberg (HEID), University of Heidelberg Im Neuenheimer Feld 345, 69120 Heidelberg, Germany*

Corresponding author: Thomas Borsch (t.borsch@bo.berlin)

Academic editor: Gian Pietro Giusso del Galdo | Received 12 November 2021 | Accepted 18 March 2022 | Published 23 May 2022

Citation: Fassou G, Korotkova N, Nersesyan A, Koch MA, Dimopoulos P, Borsch T (2022) Taxonomy of *Dianthus* (Caryophyllaceae) – overall phylogenetic relationships and assessment of species diversity based on a first comprehensive checklist of the genus. PhytoKeys 196: 91–214. https://doi.org/10.3897/phytokeys.196.77940

Abstract

In this study, we present an overall phylogenetic framework for *Dianthus* using four plastid regions (*matK-trnK-psbA*, *rpl32-trnL*, *trnQ-rps16*) and nuclear ITS and a species-level checklist for the genus developed by using all available databases and the literature. The trees from the plastid dataset depict a clade of *Dianthus* that also includes *Velezia* and a few taxa of *Petrorhagia*. New combinations in *Dianthus* are provided for these species. The checklist of *Dianthus* in this new delimitation covers 1781 names, with 384 accepted species, 150 subspecies, 12 heterotypic varieties and two forms (not counting autonyms), 1050 synonyms, 22 hybrid names and 172 unresolved names, 3 names were excluded. Implications for the evolution of flower characters, life forms, biogeography, as well as sectional classification are discussed based on the phylogenetic framework.

Keywords

Caryophyllaceae, Caryophyllales, Caucasus, *Dianthus*, EDIT Platform for Cybertaxonomy, Greece, *Petrorhagia*, phylogeny, taxonomy, *Velezia*, World Flora Online

Copyright *Georgia Fassou et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

The genus *Dianthus* L. (pinks and carnations) is after *Silene* L. the second largest genus in the family Caryophyllaceae. It it was considered to contain approximately 300 species mainly distributed in the northern hemisphere, with many range-restricted or narrow-endemic species in the Mediterranean area, SW Asia, the Caucasus and the Irano-Turanian region, and with some species occurring in eastern and southern Africa (Bittrich 1993). *Dianthus* is a genus with many taxonomically complex species groups, which is perhaps the reason that no comprehensive treatment of the whole genus exists. Valente et al. (2010) reported *Dianthus* to be one of the lineages with the highest species diversification rates in flowering plants, which may explain the evolution of numerous narrow-endemic taxa and render *Dianthus* an interesting model for understanding the evolution of north-temperate floras.

Dianthus consists of mostly perennial and a few annual or biennial herbs or shrubs with oblong to ovate or linear and grass-like leaves. According to the widely used circumscription of Pax and Hoffmann (1934), the genus is characterised by hermaphrodite flowers appearing solitary or in more or less dense terminal cymes. The flowers are subtended by 2 to many epicalyx scales and possess a 5-toothed, tubular calyx with 20–60 well-marked parallel nerves. The inclusion of several species formerly classified as *Petrorhagia* (Ser.) Link and *Velezia* L. as suggested by Madhani et al. (2018) adds taxa with fewer (5–15) nerves [*D. candicus* (P.W.Ball & Heywood) Madhani & Heubl., *D. nudiflorus* Griff., *D. recticaulis* Ledeb., and *D. tunicoides* (Ser. ex DC.) Madhani & Heubl). Similarly, the calyx in three of these taxa possesses scarious commissures (*D. candicus*, *D. recticaulis*, *D. tunicoides*) whereas these are missing in *Dianthus* s. str., e.g. as circumscribed by Bittrich (1993), and in *Velezia*. The corolla consists of five distinct petals, with distinct blade and claw. Contrary to the long and pale claw, the limb is brightly coloured (red/pink/purple, yellow) in most species, rarely white. The limb is entire, dentate to laciniate, fimbriate, and without coronal scales. Peltate seeds with a facial hilum and a straight embryo are a characteristic feature of *Dianthus* including *Velezia rigida* L. and apparently all species of *Petrorhagia* (Madhani et al. 2018).

The first infrageneric classification of *Dianthus* was published by Boissier (1867), who recognised six sections, or "sections naturales"; the names he used are considered unranked (Rabeler 1993): *D.* § 5. *Carthusiani* Boiss., *D.* § 4. *Dentati* Boiss., *D.* § 3. *Fimbriati* Boiss., *D.* § 2. *Leiopetali* Boiss. and *D.* § 1. *Verruculosi* Boiss., but this classification was based only on species occurring in the area of his Flora Orientalis. Williams (1893) developed a more comprehensive infrageneric classification system, but apparently did not consider Boissier's work. Williams described the morphology of the genus in detail and recognised three subgenera with eight sections and 22 subsections in total. The most widely used classification until today is the one of Pax and Hoffmann (1934), who recognised seven sections. An overview of the taxonomic history of *Dianthus* is given in Table 1.

The first overall molecular phylogenetic analysis of the Caryophyllaceae (Fior et al. 2006) included *D. furcatus* Balb. and *Dianthus seguieri* Vill. and showed *Velezia rigida* L. as sister to a *Dianthus* clade. Harbaugh et al. (2010) added *D. armeria* L. and an

Table 1. Summary of the infrageneric classification in *Dianthus* as presented by the respective treatments. The names are given as they were used by the authors, not considering some existing earlier names not used by them.

Boissier 1867	Williams 1885	Pax and Hoffmann 1934
	D. subg. *Carthusianastrum* F.N.Williams sect. *Armerium* F.N.Williams	*D.* subg. *Armeriastrum* (Ser.) Pax & K.Hoffm. sect. *Armerium* F.N.Williams
D. § 4. *Dentati* Boiss.	*D.* subg. *Carthusianastrum* F.N.Williams sect. *Suffruticosi* F.N.Williams	*D.* subg. *Armeriastrum* (Ser.) Pax & K.Hoffm. sect. *Suffruticosi* F.N.Williams
D. § 5. *Carthusiani* Boiss.	*D.* subg. *Carthusianastrum* F.N.Williams sect. *Carthusiani* (Boiss.) F.N.Williams [as "*Carthusianum*"]	*D.* subg. *Armeriastrum* (Ser.) Pax & K.Hoffm. sect. *Carthusiani* (Boiss.) F.N.Williams
	D. subg. *Caryophyllastrum* F.N.Williams sect. *Barbulatum* F.N.Williams	*D.* subg. *Caryophyllum* (Ser.) Pax & K.Hoffm. sect. *Barbulatum* F.N.Williams (*D.* sect. *Chamaegarophalon* Griseb.)
	D. subg. *Caryophyllastrum* F.N.Williams sect. *Caryophyllum* Ser. in Candolle	*D.* subg. *Caryophyllum* (Ser.) Pax & K.Hoffm. sect. *Eucaryophyllum* Graebn.
	D. subg. *Caryophyllastrum* F.N.Williams sect. *Imparjugum* F.N.Williams	
D. § 3. *Fimbriati* Boiss.	*D.* subg. *Caryophyllastrum* F.N.Williams sect. *Fimbriati* Boiss. ["*Fimbriatum*"]	*D.* subg. *Caryophyllum* (Ser.) Pax & K.Hoffm. sect. "*Plumaria*" Opiz
D. § 1. *Verruculosi* Boiss.	*D.* subg. *Caryophyllastrum* F.N.Williams sect. "*Tetralepides Leiopetala*" F.N.Williams	*D.* subg. *Caryophyllum* (Ser.) Pax & K.Hoffm. sect. "*Tetralepides Leiopetala*" F.N.Williams
D. § 2. *Leiopetali* Boiss.	*D.* subg. *Proliferastrum* F.N.Williams	in *Tunica* Ludw.

unidentified species of *Dianthus*, but found *Velezia* within the *Dianthus* clade that in turn was sister to *Petrorhagia saxifraga* (L.) Link. After including more species in their plastid and ITS datasets, Valente et al. (2010) concluded that *Dianthus* is monophyletic if *Velezia* is also included. However, this conclusion was premature with respect to *Petrorhagia* since Valente et al. represented this genus of > 30 species with only two species (*P. thessala* (Boiss.) P.W.Ball & Heywood and *P. prolifera* (L.) P.W.Ball & Heywood) as outgroup, not even including *P. saxifraga* (L.) Link, the type of *Petrorhagia*. Greenberg and Donoghue (2011) then largely confirmed these findings using five chloroplast regions (*matK*, *ndhF*, *trnL-trnF*, *trnQ-rps16*, *trnS-trnfM*) and nrITS, although their tree lacked crucial lineages within *Dianthus*.

In a recent synopsis of the genera of the tribe Caryophylleae, Madhani et al. (2018) formally extended the circumscription of *Dianthus* by three species of *Petrorhagia* and *Velezia rigida*, based on trees of plastid *rps16* and nrITS sequences and mapping of selected morphological characters. They recovered *P. armerioides* (Ser. ex DC.) P.W.Ball & Heywood as sister to *V. rigida* based on ITS but the support for a position of this lineage within *Dianthus* was weak (0.77 PP), and only six species of *Dianthus* were sampled, again lacking crucial lineages. Their *rps16* tree shows *Petrorhagia alpina* (Hablitz) P.W.Ball & Heywood, *P. armerioides*, and *P. candica* P.W.Ball & Heywood in a subclade that is nested in a *Dianthus* clade. However, only *Dianthus carthusianorum* L. (only supported by BI, 0.98 PP) and *D. armeria* were included and resolved as successive sisters, whereas *Velezia* was not sampled at all. Moreover, the fact that the authors used different taxa in their plastid and nuclear datasets, some of them crucial for determining generic concepts but represented in only one of the datasets, further limits firm conclusions. The wider circumscription of *Dianthus* proposed by Madhani et al. (2018) is not supported by a morphological synapomorphy because the peltate seeds and straight embryos mentioned therein as important characters for diagnosing *Dianthus* are also found in *Petrorhagia*. The circumscription of *Dianthus* in particular with respect to *Petrorhagia* therefore remains to be clarified by analyses with an improved taxon sampling of both genera and also an increased character base that allows for better resolved trees and statistical support of relevant nodes. These investigations should also consider the Greek and Levant taxa of *Bolanthus* (Ser.) Rchb.. The genus was found closely related to *Dianthus* and *Petrorhagia* based on ITS and *rps16* (Zografidis et al. 2020), which includes *Bolanthus hirsutus* (Labill.) Barkoudah, the type of *Bolanthus*.

Valente et al. (2010) conducted the first comprehensive molecular analysis of *Dianthus*, based on partial *matK*, *psbA-trnK*, *trnH-psbA* and nrITS sequences from 104 species plus some representatives from *Velezia*, *Petrorhagia* and *Saponaria* L. Based on their trees, the authors annotated five major lineages within *Dianthus*. The first branching lineage largely comprised members of *D.* sect. *Armerium* F.N.Williams (e.g. *D. armeria*, *D. deltoides* L., *D. viscidus* Bory & Chaub.), followed by a *Velezia* clade (represented by three different samples of *V. rigida*), and a lineage called "Section *Verruculosi*" with *D. cyri* Fisch & C.A.Mey., *D. strictus* Banks ex Sol. and *D. tripunctatus* Sm. The majority of the species then appeared in a clade annotated as "Eurasian radiation" that was depicted as sister to an African clade. However, the Eurasian clade had almost no internal resolution.

Dianthus has received considerable interest from botanists in recent years, focusing on individual species groups and the description of new taxa or treatments in specific geographic areas (Balao et al. 2009; Kuzmina and Nersesyan 2012; Deniz et al. 2016; Ferrer Gallego and Laguna 2018; Oskay 2018; López-Jurado et al. 2019) and conservation (Kołodziejek et al. 2018; Cogoni et al. 2019). As a result, 54 species and 18 subspecies, mostly from the Euro-Mediterranean area, were described as new to science the last 15 years.

The absence of an overall phylogenetic tree of *Dianthus* as a prerequisite to break up the genus into workable units, in which species level relationships then can be studied in more detail with evolutionary methods, has so far limited the analysis of species limits in *Dianthus*. Also lacking is a comprehensive treatment or checklist, which would be fundamental to inform sampling and provide a basis for synthesising the existing information on *Dianthus*. Considering the wealth of new descriptions, we assumed that the diversity of *Dianthus* may in fact be considerably higher than 300 species as cited by Pax and Hoffmann (1934) and Bittrich (1993). *Dianthus* represents one of the major genera of the order Caryophyllales (Hernández-Ledesma et al. 2015), for which a globally consistent species-level taxonomic backbone is developed by the Caryophyllales Network, which also contributes to the treatments for World Flora Online (WFO, www.worldfloraonline.org) (Borsch et al. 2020).

As a starting point for this study, we took advantage of ongoing research activities in the context of the Caucasus Plant Biodiversity Initiative and the Flora of Greece project (http://portal.cybertaxonomy.org/flora-greece/intro), all covering geographic areas with high species diversity of the genus, and in which *Dianthus* is currently studied. In Greece, *Dianthus* is represented by 44 species and 43 subspecies, of which about half are endemic. Some of them are morphologically and geographically divergent, such as the *D. juniperinus* Sm. and *D. fruticosus* L. groups, which are woody chasmophytes occurring mostly on the island of Crete (Dimopoulos et al. 2013). In the Caucasus, about sixty species are native, of which 20 are endemic (Kuzmina and Nersesyan 2012), and five further endemics occur in NE Turkey and SW Iran.

The specific objectives for this paper are therefore twofold: first, to generate an overall phylogenetic hypothesis for *Dianthus* that covers a broad spectrum of taxa, also extending to putative close relatives (e.g. *Petrorhagia*) to further test the monophyly of *Dianthus*. Due to the extremely low genetic diversity encountered in *Dianthus* as compared to other large genera of flowering plants (e.g. *Campanula*), we sequenced four plastid regions (*matK-trnK-psbA*, *rpl32-trnL*, *trnQ-rps16*) that were selected for high variability and hierarchical phylogenetic signal (Borsch and Quandt 2009) as well as to match existing datasets of Valente et al. (2010). We added nrITS to obtain data from a nuclear region that allows for some first insights to possible hybridisation and reticulate evolution.

The second specific objective is to provide an up-to-date taxonomic backbone for *Dianthus*. This was done using an import that integrated all electronically available sources from the World Flora Online. In this way, an already comprehensive name source was available that we then matched with recent treatments, e.g. major Floras published in the last thirty years, accounts of specific species groups, etc., to have a clear reference for accepting a name or putting it into synonymy. The checklist of *Dianthus* presented here will be also incorporated into the World Flora Online taxonomic backbone and will be updated whenever changes become necessary.

Considering the difficulty in species delimitation and the species diversity of *Dianthus*, we believe that our integrated approach to develop both a taxonomic backbone that includes all names belonging to the genus in a current, monophyletic circumscription, along with a traceable source for the taxon concepts used at species level, will be crucial to understanding evolutionary relationships and species diversification in space and time. Such information is also urgently needed from applied perspectives such as to assess the conservation status of many *Dianthus* species that are local or regional endemics and/or have a critical conservation status.

Methods

Taxon sampling and collection of plant material

Plant material was collected in the field or from well-documented accessions in the living collections of the Botanic Garden Berlin, and from herbarium specimens kept at the herbaria B and ERE. Information on the origin of all samples is provided in Appendix 1. Vouchers are deposited in B, ERE, HEID and UPA.

DNA extraction, amplification and sequencing

Total genomic DNA was extracted from silica-dried leaf material using the NucleoSpin Plant II kit (Macherey Nagel, Düren, Germany) and from herbarium samples using a CTAB protocol with triple extractions (Borsch et al. 2003). DNA fragments were amplified through polymerase chain reaction (PCR) in 50 µl volumes, containing 4 µl of DNA template (concentration c. 10 ng/µl), 5 µl Taq buffer S (PeqLab, Erlangen, Germany), 2 µl of each primer (20 pm/µl), 10 µl dNTPs (each 1.25 mM), 1.5 units of Hot Taq DNA Polymerase (PeqLab), and ultrapure water.

The *matK-trnK-psbA* region was amplified in overlapping halves using the primer pair trnK-F (Wicke and Quandt 2009) and CARYmatK-1440R (Schäferhoff et al. 2009) for the 3' fragment and ACmatK500F (Müller and Borsch 2005), and psbA5'R (Shaw et al. 2005) for the 5' fragment. The use of the reverse primer psbA5'R that anneals to the psbA gene allows the full sequence at the 5' end of the *trnK* intron to be obtained and additionally covers the *trnK-psbA* intergenic spacer. Amplification conditions were: an initial denaturation step of 1 min 30 sec at 96 °C, followed by 34 cycles of denaturation (30 sec at 95 °C), annealing (1 min at 50 °C), extension (1 min 30 sec at 72 °C), and a final extension step (20 min at 72 °C).

The *rpl32-trnL* IGS was amplified using the primers rpl32-F and trnL-UAG (Shaw et al. 2007) and the *trnQ-rps16* IGS was amplified using the primers trnQ2 (Korotkova et al. 2010) and rpl16x1 (Shaw et al. 2007). The PCR conditions were as for *matK-trnK-psbA*, except that the extension step was only 1 minute. ITS was amplified using the primers ITS5 and ITS4 (White et al. 1990), amplification conditions were: 35 cycles of denaturation (1 min at 97 °C), annealing (1 min at 48 °C) and extension (45 s at 72 °C), and a final extension step (7 min at 72 °C).

All PCR products were electrophoresed for 2 hours on a 2% agarose gel and then excised and purified using the Geneaid Gel/PCR DNA Fragments Extraction Kit (Geneaid Biotech Ltd., New Taipei City, Taiwan) and sequenced via standard Sanger sequencing at Macrogen Europe (Amsterdam, The Netherlands). Chromatograms were inspected by eye, erroneous nucleotide calls were manually corrected, and final sequences were assembled using PhyDE v. 0.9971 (Müller et al. 2005+). All sequences were submitted to the European Nucleotide Archive (ENA) https://www.ebi.ac.uk/ena/browser/home under the projects PRJEB48120, PRJEB43752.

Sequence alignment, indel coding and model selection

DNA sequences were aligned in PhyDE following a motif alignment approach and the rules laid out by Löhne and Borsch (2005). Homonucleotide stretches and parts of uncertain homology were excluded from the final matrix prior to the analyses. Indels were coded according to the scheme "Simple Indel Coding" (Simmons and Ochoterena 2000) in SeqState v.1.40 (Müller 2005b).

Phylogenetic analyses

Best-fitting models of nucleotide substitution were selected via the Akaike Information Criterion in jModeltest v.2.1.6 (Darriba et al. 2012). The models that were found to best fit the given DNA sequence data are listed in Table 2. Phylogenetic reconstructions were performed via Maximum Likelihood (ML) and Bayesian Inference (BI). Jackknife (JK) node support was additionally calculated under parsimony in PAUP* v.4.0b10 (Swofford 1998) with 10,000 replicates, branch swapping via tree-bisection-reconnection, a deletion of 36.8% of all characters during replicates, and a retention of one tree per replicate (Müller 2005a).

Tree inference under ML was conducted on the concatenated alignment with RAxML v.8.2.9 (Stamatakis 2014) using the thorough ML optimisation option. The dataset was analysed as a single partition under the nucleotide substitution model GTR+I+G, with branch lengths linked across partitions. Branch support for the ML inference was calculated via 100 bootstrap (BS) replicates using the rapid BS algorithm (Stamatakis et al. 2008).

Bayesian Inference (BI) was conducted with MrBayes v.3.2.2 (Ronquist and Huelsenbeck 2003), using four parallel Markov Chain Monte Carlo (MCMC) runs for a total of 10 million generations on CIPRES. The initial 25% of all MCMC trees were discarded as burn-in, and post-burn-in trees were summarised as majority rule consensus trees. Datasets for BI comprised both DNA sequence data and coded indels; the binary character model was applied for the indel partition. All trees were visualised via TreeGraph2 (Stöver and Müller 2010).

Compilation of the *Dianthus* checklist

The checklist was compiled using the EDIT Platform for Cybertaxonomy (cybertaxonomy.org) (Ciardelli et al. 2009; Berendsohn 2010), which is a suite of open-source software tools and services that covers all aspects of an integrative taxonomic workflow and include tools to capture, process, attribute, document, publish and maintain the data. This way, the already existing interaction with the Global Caryophyllales Synthesis initiative (Borsch et al. 2015) can be used and future dynamic updating is guaranteed.

As a first step, a complete list of *Dianthus* names and their respective World Flora Online (WFO)-IDs were received from the WFO Data Centre in February 2018 and imported into the EDIT Platform. This import included names accepted in the WFO

Table 2. Sequence characteristics of the individual partitions in the plastid dataset. SD = standard deviation.

	rpl32-trnL	*trnQ-rps16*	*trnK intron*	*matK* CDS	*trnK-psbA*	ITS
Dataset including hotspots						
Number of sequences	202	202	202	202	202	145
Aligned length	1372	1166	1229	1536	270	714
Mean length (SD)	786 (89)	688 (120)	815 (163)	1406 (332)	195 (95)	674 (33)
Dataset excluding hotspots						
Aligned length	1236	1068	1186	1537	270	714
Mean length (SD)	755 (78)	653 (114)	793 (160)	1405 (332)	195 (95)	674 (33)
% variable characters	31.5	23.6	16.8	22.4	16.2	33.3
% informative characters	18.8	8.3	5.3	8.8	4.4	27.5
Number of coded indels	106	102	52	17	10	43
jModeltest v.2.1.6, AIC results	GTR+G	TPM1uf+G	TPM1uf+I+G	TPM1uf+I+G	--	SYM+I+G

backbone, their synonyms therein, doubtful names, and names of hybrids, and each of these taxonomic states was preliminarily assigned to the imported names. This dataset was then matched with the World Checklist of Vascular Plants dataset received from the Royal Botanic Gardens, Kew in December 2019 (Kew WCVP 2019), which resulted in some 181 additional, mostly infraspecific names, not yet covered by the WFO backbone, which were manually entered into the EDIT platform as well.

This preliminary list of accepted names and their synonyms was then cross-checked with relevant taxonomic treatments (see below). The resulting circumscription of each taxon is indicated by means of a "secundum" ("sec.") reference (Berendsohn 1995; 1997; Berendsohn and Geoffroy 2007), which is the particular reference for the taxon to be accepted in our taxonomic backbone. For synonyms, the "syn. sec." reference indicates the assignment of the synonym to the concept of either the accepted name or one of its homotypic synonyms; this may or may not be the same reference as that of the taxon's secundum. We selected the secundum reference to be the most comprehensive source of information available for a species or subspecies. Ideally, this was a monographic treatment based on morphology and a detailed revision of type material, as carried out for some Floras. In those cases where a newly described species had not yet been included in any subsequent more inclusive treatment, the original publication served as the secundum reference. The references used as secundum for the Euro-Mediterranean area in the widest sense included the treatments of *Dianthus* in the Euro+Med PlantBase (Marhold 2011), Flora Iberica (Bernal et al. 1990), Vascular Plants of Greece: an annotated checklist (Dimopoulos et al. 2013) and Flora Iranica (Rechinger 1988). Several checklists and Floras were examined for Russia and the Caucasus (Czerepanov 1995; Barkalov and Probatova 2006; Chepinoga et al. 2008; Kuzmina and Nersesyan 2012). For eastern Asia, the sources were the Floras of China (Dequan and Turland 2001), Japan (Zoku 1965) and Pakistan (Ghanzafar and Nasir 1986). The African Plant Database version 3.4.0 (2012) was taken as the primary reference for the African species. These references already covered about 90% of the *Dianthus* species. Further publications reporting taxonomic data were used, such as descriptions of new species (Brullo et al. 2000; Shaulo and Erst 2011; Brullo et al. 2015; Son et al. 2017), nomenclatural notes on certain species or species groups (Peruzzi and Gargano 2006; Bacchetta et al. 2010) and studies on species in single countries (Iamonico 2013; Lazkov 2016). Many new *Dianthus* species were described from Turkey in the last 10–15 years, which were considered through the respective publications (Menemen and Hamzaoğlu 2000; İlçim et al. 2013; Hamzaoğlu et al. 2015; 2017; 2018; Deniz et al. 2016).

In the rare cases of differing taxonomic concepts, we accepted the circumscription with the respective secundum reference that was either the most recent one or the one covering the area where the accepted taxon in question is primarily distributed.

Names that were part of the WFO backbone, treated therein as unresolved names and not found in any of the sources cited above, were also treated as unresolved names in our checklist.

Results

Sequence datasets

The concatenated plastid alignment matrix comprised a total of 202 taxa and 5573 positions, which resulted in a matrix of 5297 nucleotide characters and 287 coded indels. The ITS matrix contained only 136 taxa and was 714 nucleotides in length, with an average length of 674 nucleotides. There were polymorphic sites in about one-third of the generated ITS sequences, including some obvious hybrid sequences which were not readable. For this reason, the ITS matrix only includes unambiguously readable sequences and is therefore smaller than the plastid matrix. Detailed sequence statistics are provided in Table 2.

Trees inferred from the concatenated plastid dataset

Our annotation in the phylogenetic trees uses accepted names as available prior to this study; new names or combinations in order to make *Dianthus* monophyletic are provided below.

The plastid tree (Fig. 1) depicts a maximally supported clade comprising all sampled *Dianthus* taxa as well as *Velezia* and several *Petrorhagia*, which are nested within *Dianthus*. *Petrorhagia alpina* (= *Dianthus recticaulis* Ledeb.) is resolved as sister to the rest of the *Dianthus-Velezia-Petrorhagia* clade. The other *Petrorhagia* samples are resolved in a separate highly supported clade including *P. saxifraga*, the type species of the genus, with *Bolanthus graecus* (Schreb.) Barkoudah sister to the rest of *Petrorhagia*.

A *Dianthus armeria* clade (1 PP, 98% MLBS and 100% JK) is the first branching lineage. The next branching lineages are *Velezia*, *Dianthus candicus*, and a clade comprising *Dianthus cyri*, *D. strictus*, *D. tunicoides* and two further species of *Petrorhagia* (*P. cretica* (L.) P.W.Ball & Heywood and *P. illyrica* (Ard.) P.W.Ball & Heywood). However, the branching order among these clades only receives moderate (BI) to weak support.

The core of *Dianthus* that includes most species (1 PP, 69% MLBS and 65% JK) is composed of three main clades. Clade A (1 PP, < 50% MLBS) contains a wide spectrum of Eurasian taxa. Clade B (1 PP, 90% MLBS and 87% JK) contains mainly Irano-Turanian and Caucasian taxa and all species from southern Africa. Clade C (1 PP, 61% MLBS and 67% JK) consists of *Dianthus juniperinus* and most subspecies of *D. fruticosus*, but *D. fruticosus* subsp. *amorginus* Runemark, subsp. *fruticosus*, and subsp. *rhodius* (Rech. f.) Runemark are resolved in a sublineage of clade A.

Trees inferred from nrITS

The ITS topology (Fig. 2) is hardly resolved at all. Still, the tree depicts a well-resolved core of species of *Petrorhagia* in a clade sister to the *Dianthus* clade. *Dianthus recticaulis* (= *Petrorhagia alpina*) is again depicted as first branch, followed by the *D. armeria* lineage, which is congruent to the plastid tree. *Dianthus cyri*, the species of *Velezia*,

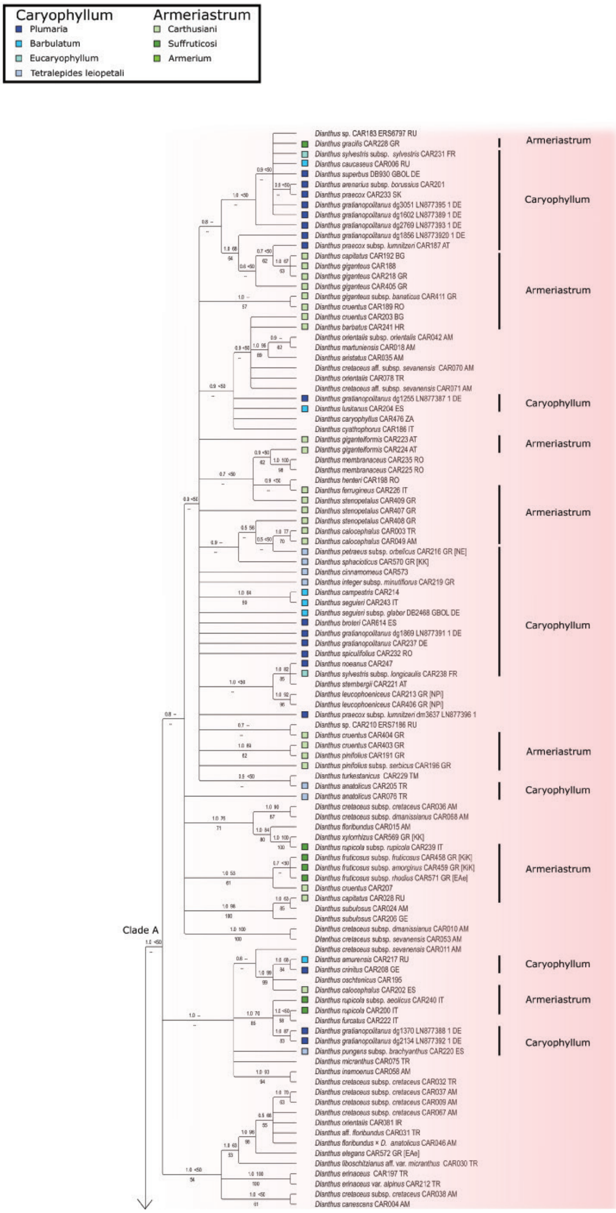

Figure 1. Bayesian majority-rule consensus tree inferred from combined plastid dataset of *trnK/matK*, *trnK-psbA*, *trnQ-rps16*, *rpl32-trnL*. Support values PP (left) and MLBS (right) can be found above branches and JK below; "<50" denotes branches with MLBS support below 50%, "--" denotes a node not found by the respective analysis. Country codes: AM = Armenia, AT = Austria, AZ = Azerbaijan, BG = Bulgaria, CY = Cyprus, DE = Germany, ES = Spain, FR = France, GE = Georgia, GR = Greece (NE = North East, NC = North Central, KK = Kriti and Karpathos, StE = Sterea Ellas, NPi = Norh Pindos, EAe = East Aegean Islands, Pe = Peloponnisos), HR = Croatia, IR = Iran, IT = Italy, RO = Romania, RU = Russia, SK = Slovakia, TR = Turkey, ZA = South Africa. The annotations on the infrageneric classification based on Pax and Hoffmann (1934) are indicated by coloured squares.

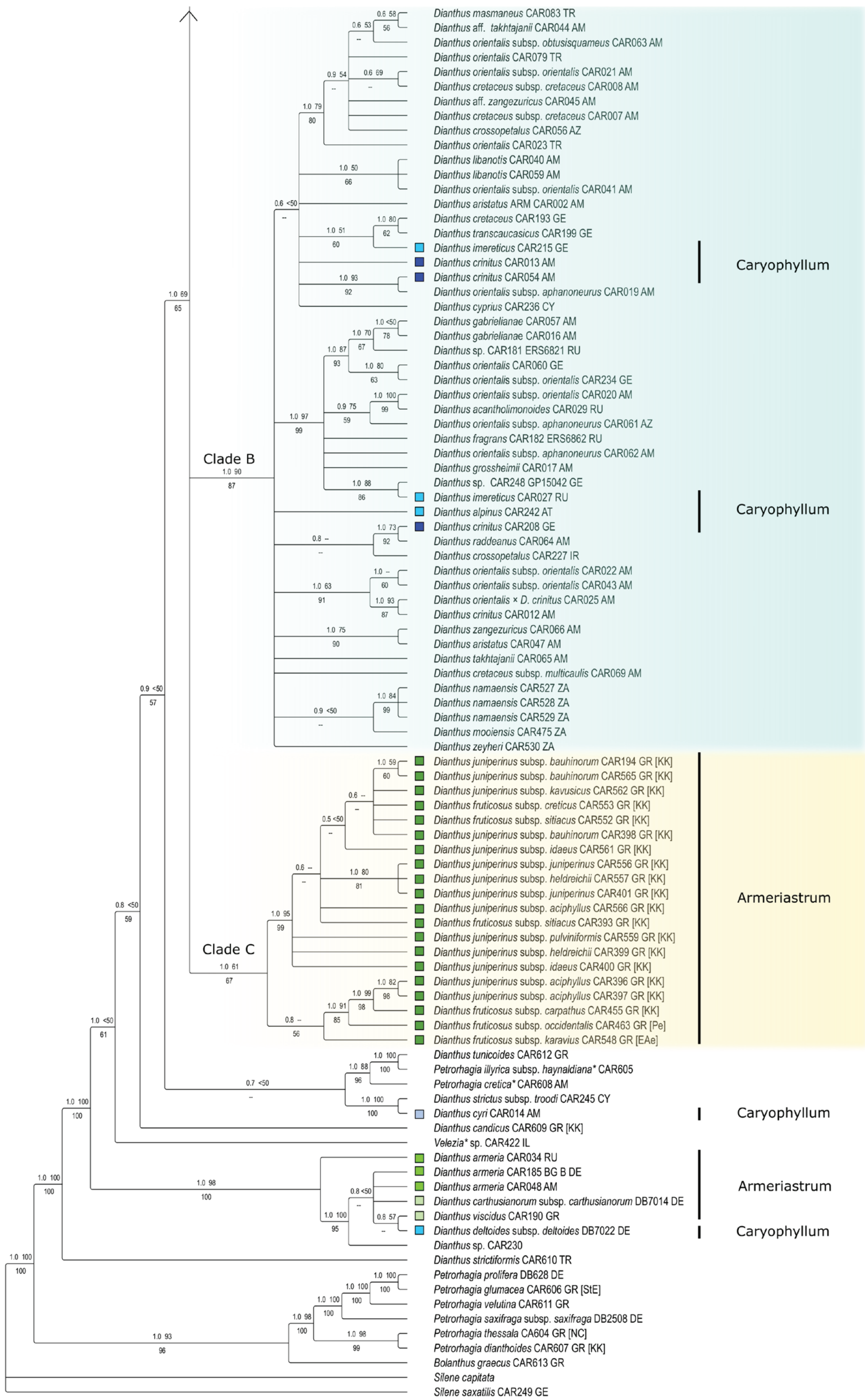

Figure 1. Continued.

Dianthus tunicoides along with *Petrorhagia cretica* and *P. illyrica* are found in a weakly supported clade, inconsistent to their positions in a rather weakly supported grade in the plastid tree. *Bolanthus* (= *Graecobolanthus*) is resolved in the first branch in the tree, albeit with weak support (0.7 BI, 66% JK).

Unlike the plastid sequences, ITS sequence data do not provide resolution within the core of *Dianthus*, although some subclades are evident within a broad polytomy (Fig. 2). The lineage with subspecies of *D. juniperinus* together with *D. fruticosus* subsp. *sitiacus* Runemark corresponds to subclade C in the plastid tree, whereas neither the *D. broteri* Boiss. & Reut. - *D. rupicola* Biv. - *D. lusitanus* Brot. subclade of the ITS tree nor the subclade with *D. caucaseus* Sims, *D. gabrielianae* Nersesian and *D. oschtenica* are recovered by plastid data. Also, the southern African species (e.g. *D. mooiensis* F. N. Williams, *D. zeyheri* Sond) appear within the core polytomy in ITS.

Accepted species names and synonyms

In total, 1781 names are included for a monophyletic genus *Dianthus* as defined here, including *Petrorhagia* p.p. and *Velezia*. The resulting checklist treatment is subdivided into four parts: i) the core checklist that contains the accepted species and infraspecies and their synonyms, ii) hybrid names, iii) unresolved names and iv) excluded names. The core checklist of *Dianthus* including 2 former *Petrorhagia* species and 3 heterotypic subspecies and 6 former *Velezia* species contains 384 total accepted species and 150 accepted heterotypic subspecies, and 1050 names are assigned as synonyms. There are 22 hybrid names, 172 unresolved names, and 3 excluded names.

Discussion

Circumscription and overall relationships of *Dianthus*

Plastid and nuclear data agree on a *Dianthus* clade that includes *Velezia* and further species of *Petrorhagia* (*P. cretica*, *P. illyrica*) as deeply nested (Figs 1, 2) that were not sampled in previous phylogenetic analyses (Valente et al. 2010; Madhani et al. 2018). It is noteworthy that *Dianthus recticaulis* is resolved as sister to all other species of *Dianthus* in both genomic compartments with good support. It is an annual with solitary flowers on conspicuous peduncles (Ball and Heywood 1964) similar to *P. cretica* (Fig. 4A, B). The inflorescence architecture is apparently connected to the annual life form, which evolved independently in different terminal branches in *Dianthus* and allies. *Dianthus recticaulis* is the legitimate name for *P. alpina*, while *Dianthus strictiformis* that was proposed as a new name for *Petrorhagia alpina* by Madhani et al. (2018) is superfluous and illegitimate (Mosyakin and Federonchuk 2018). Their plastid *rpl16* tree, however, depicts this species in an incongruent position as sister to *P. candica* (also transferred to *Dianthus* by the authors), but this may be a spurious signal caused by an imbalanced sampling of *Dianthus* (both species appear nested within the *D. armeria*

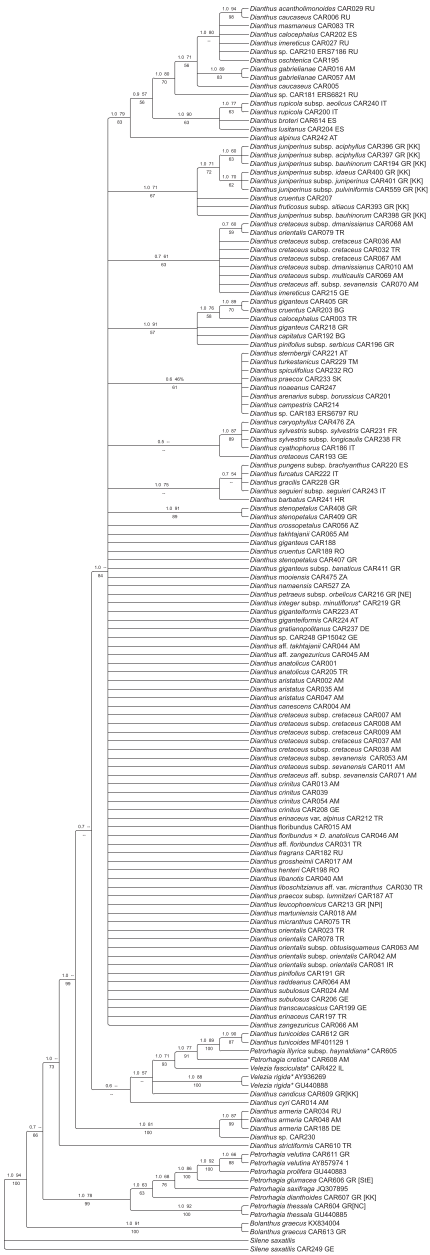

Figure 2. Bayesian majority-rule consensus tree inferred from nuclear ITS datasets. Support values PP (left) and MLBS (right) can be found above branches and JK below; “<50” denotes branches with MLBS support below 50%, “--” denotes a node not found by the respective analysis. Country codes: AM = Armenia, AT = Austria, AZ = Azerbaijan, BG = Bulgaria, CY = Cyprus, DE = Germany, ES = Spain, FR = France, GE = Georgia, GR = Greece (NE = North East, NC = North Central, KK = Kriti and Karpathos, StE = Sterea Ellas, NPi = Norh Pindos, EAe = East Aegean Islands, Pe = Peloponnisos), HR = Croatia, IR = Iran, IT = Italy, RO = Romania, RU = Russia, SK = Slovakia, TR = Turkey, ZA = South Africa. The annotations on the infrageneric classification based on Pax and Hoffmann (1934) are indicated by coloured squares.

clade). Our phylogenetic results confirm the position of these former *Petrorhagia* species within *Dianthus* (Figs 2, 3). Nevertheless, we extended the sampling of *Petrorhagia* and found further species (*P. cretica*, *P. illyrica*) within *Dianthus*, whereas a distant clade of the members of the genus *Petrorhagia* (including the type *P. saxifraga*, and *P. dianthoides* (Sm.) P.W.Ball & Heywood, *P. glumacea* (Bory & Chaub.) P.W.Ball & Heywood, *P. prolifera*, *P. thessala* and *P.dubia* (Raf.) G.López & Romo) receives high support in chloroplast and ITS trees. The taxa that were found nested within *Dianthus* belong to the *Petrorhagia* sect. *Pseudotunica* (Fenzl) Ball & Heywood and *Petrorhagia* sect. *Pseudogypsophila* (A.Braun) P.W.Ball & Heywood, while the *Petrorhagia* taxa that form a distant clade belong to *Petrorhagia* sect. *Petrorhagia* and *Petrorhagia* sect. *Kohlrauschia* (Kunth) P.W.Ball & Heywood (Ball and Heywood 1964). This clade is related to *Bolanthus*, which is inferred as sister with high support in the plastid tree, but is depicted inconsistently in a grade with ITS (Fig. 2). Apart from our now clearer picture of relationships between *Dianthus* and *Petrorhagia*, the genus *Velezia* still plays a role in the monophyletic circumscription of *Dianthus*. Madhani et al. (2018) merged *Velezia* with *Dianthus*, following the suggestion by Valente et al. (2010), but considered only one species, *V. rigida* L., and resurrected the name *Dianthus nudiflorus* Griff. based on a type from Afghanistan. Sequence data of *Velezia* indicate that this former genus consists of more than one species (Fig. 2), with *V. fasciculata* Boiss. in a different position in the ITS tree compared to *V. rigida*, which is in line with the acceptance of six species in the Euro+Med PlantBase (Marhold 2011). Only *V. rigida* is widespread from the western Mediterranean through SW Asia and the Caucasus as well as introduced in North America, specifically in California (Rabeler and Hartmann 1993+), whereas the other species are range-restricted and occur in Greece, Turkey and Syria. Consequently, we propose to also include the remaining *Velezia* species in *Dianthus* (see Nomenclatural Novelties).

The second branch within the *Dianthus* clade is composed of *Dianthus armeria* (incl. *D. viscidus*) and relatives such as *D. carthusianorum* and *D. deltoides*, as congruently inferred by the nuclear and plastid partition and which is also consistent with trees shown by Valente et al. (2010) and Greenberg and Donoghue (2011). The respective positions of the next-branching lineages, i.e. *Velezia* and a lineage of *Dianthus strictus* plus *D. cyri*, are not well supported. Again, our tree topologies agree in principle with the findings of Valente et al. (2010) and Greenberg and Donoghue (2011) but differ in that two former species of *Petrorhagia* as recognised by Madhani et al. (2018) belong here (*P. armerioides* (Ser. ex DC.) P.W.Ball & Heywood, *P. candica* P.W.Ball & Heywood). We show that *P. cretica* and *P. illyrica* are also part of this lineage (Fig. 2) and need to be merged with *Dianthus*.

Our results also agree with a core clade of *Dianthus* that contains the majority of the *Dianthus* species. Contrary to Valente et al. (2010), our results depict three major clades (clades A-C) of core *Dianthus*.

Clade A contains Eurasian taxa and includes the type of the genus, *D. caryophyllus*. Clade A also comprises three subspecies of *D. fruticosus* (subsp. *amorginus*, subsp. *fruticosus* and subsp. *rhodius*) that are apparently convergent in terms of evolving a

Figure 3. Habit, inflorescence and floral morphology in the core lineage of *Dianthus*. From the predominantly Euro-Mediterranean clade A are *D. sphacioticus* (**A**) with solitary flowers enclosed basally by cauline leaves, *D. integer* subsp. *minutiflorus* (**B**) enclosed basally by several slightly coriaceous bracts with an outward-pointing green tip, *D. stenopetalus* (**C**) with several flowers in a condensed terminal inflorescence with many brown scales, *D. critinus* (**D**) with four decussate bracts at the base, and *D. haematocalyx* (**E**). Clade B, which includes many Caucasian and Irano-Turanian species, is represented by *D. gabrielianae* (**F**) and the predominantly Cretan clade C by *D. juniperinus* subsp. *juniperinus* (**G**). *D. juniperinus* is a densely branched, cushion-like subshrub and *D. haematocalyx* is a small cushion plant. Photos: N. Turland (**A**), K. Goula (**B–D**), A. Zografidis (**E**), A. Nersesyan (**F**) and G. Fassou (**G**).

similar life form as the members of clade C. Several terminal sublineages of apparently geographically close samples receive good support such as *D. cretaceus* Adams subsp. *cretaceus* and *D. floribundus* Boiss., but at the same time the samples of *D. gratianopolitanus* Vill. are spread over this clade (Fig. 2).

Clade B contains mostly Irano-Turanian and Caucasian taxa but also *D. cyprius* A.K.Jacks. & Turrill from Cyprus, *D. alpinus* L. from the European Alps and the taxa from tropical and southern Africa (*D. mooiensis*, *D. namaensis* Schinz and *D. zeyheri*). This is in contrast with the claim of Valente et al. (2010) that an African clade is well supported as a sister clade to a Eurasian radiation. According to our data, the African taxa are nested within the Eurasian radiation.

The third clade of the core of *Dianthus* (clade C) consists of the Cretan taxa *Dianthus juniperinus* and some subspecies of *Dianthus fruticosus*. Specifically, the subspecies *D. fruticosus* subsp. *carpathus* Runemark, *D. fruticosus* subsp. *occidentalis* Runemark and *D. fruticosus* subsp. *karavius* Runemark can be found in clade C together with *D. juniperinus*. *Dianthus fruticosus* is not monophyletic; some of its subspecies, *D. fruticosus* subsp. *fruticosus*, *D. fruticosus* subsp. *amorginus* and *D. fruticosus* subsp. *rhodius* are resolved within clade A. There are no apparent morphological differences of *D. fruticosus* subsp. *amorginus* and subsp. *fruticosus* (both from the Cyclades), and *D. fruticosus* subsp. *rhodius* (from Rhodes and other east Aegean islands) compared to the other subspecies of *D. fruticosus* from clade C. This indicates convergent evolution resulting from adaptation to similar coastal rocky habitats.

Infrageneric classification of *Dianthus*

The classification of Pax and Hoffmann (1934) is annotated on the phylogenetic trees in Fig. 1. Even though many species were described later and therefore were not classified into infrageneric entities, it is evident that these subgenera and sections do not represent natural groups. Apart from *D.* sect. *Armerium*, there is little correlation with the taxonomic groups of either Williams (1893) or Pax and Hoffmann (1934).

Dianthus subg. *Armeriastrum* is highly polyphyletic and is represented both in the core of *Dianthus*, namely in clades A and C by *D.* sect. *Carthusiani* and *D.* sect. *Suffruticosi*, but also in the *Dianthus armeria* clade (with *D.* sect. *Armerium*) that belongs to the first branches of *Dianthus*. However, *D.* sect. *Armerium* is paraphyletic to *D. deltoides* (*D.* subg. *Caryophyllum*). Clade C has exclusively taxa from *D.* sect. *Suffruticosi*, but the section itself is not limited to this clade C. It is polyphyletic due to the presence of *D. armeria* outside of the core *Dianthus* clade, the presence of three subspecies of *D. fruticosus*, and two further independent terminal lineages composed by *D. rupicula* and *D. gracilis* in clade A. The suffruticose life form that characterises *D.* sect. *Suffruticosi* must therefore have evolved multiple times.

Dianthus subg. *Caryophyllum* is in the clades A and B, with its sections forming no specific pattern. Although all the sections appear in the core of *Dianthus*, *D.* sect. *Eucaryophyllum* appears exclusively in clade A, while the section "*Tetralepides leiopetala*" can be found in clade A and outside of the core. What was referred to as a clade corresponding to *D.* sect. *Armerium* in Valente et al. (2010) in fact consists of taxa from different sections sensu Pax and Hoffmann (1934). In addition to *D.* sect. *Armerium*, these are *D.* sect. *Carthusiani* (*D. carthusianorum* and *D. viscidus*), although the majority of species from this section are in clade A. *Dianthus deltoides*, which is congruently inferred as part of the *Dianthus armeria* clade by Valente et al. (2010), is classified herein in *D.* subg. *Caryophyllum*.

The early branch of *Dianthus cyri* and *D. strictus* belongs to the section "*Tetralepides leiopetala*" according to Pax and Hoffmann (1934), which was originally described by Williams (1885); see Table 1. The two species *D. cyri* and *D. tripunctatus* (not sampled here) were earlier used by Boissier (1867) to define *D.* § 1. *Verruculosi*, although no type for the sectional name was designated. If we accept *D. cyri* as the type, the name *D.* sect. *Verruculosi* (Boiss.) Schischkin would be correct in terms of priority. This corresponds to the use of this sectional name by Valente et al. (2010), as well as some floristic treatments, e.g. Rechinger (1988). However, Williams (1885; 1893) did not designate any types for his subgeneric or sectional names either. The wide taxon concept of the section "*Tetralepides leiopetala*" sensu Williams (1893) and Pax and Hoffmann (1934) can only be adjusted after the application of a validly published name and its typification. This section is polyphyletic and its species are found across all our clades (Fig. 1).

Implications for the evolution of floral and inflorescence morphology

The inflorescences in *Dianthus*, *Petrorhagia* and related genera possess a cymose principal structure as in most Caryophyllaceae, and these inflorescences exhibit various levels of complexity. The spectrum ranges from solitary flowers on more or less unbranched stems (e.g. *D. sphacioticus* Boiss. & Heldr., Fig. 3A), over more or less richly branched inflorescences (e.g. *D. deltoides*, *D. juniperinus*, Figs 3G, 4C, 4E) to somewhat condensed (e.g. *D. armeria*, Fig. 4D) or strongly condensed terminal head-like inflorescences (e.g. *D. stenopetalus* Griseb., Fig. 3C). These complex inflorescences have evolved independently in different lineages within *Dianthus*, such as the early-branching *Dianthus armeria* clade (*D. armeria*, *D. carthusianorum*) and within clade A of the core group (*D. cruentus* Griseb., *D. giganteus* d'Urv., *D. pinifolius* Sm., *D. stenopetalus*) and also within clade B (*D. asperulus* Boiss. & A.Huet, *D. transcaucasicus* Schischk.). In a similar way, the condensed inflorescences in *Petrorhagia prolifera* and relatives (Fig. 1C, Fig. 4F; Ball and Heywood 1964) mark convergent evolution in a terminal clade, whereas *P. saxifraga* has solitary flowers subtended by four decussate bracts, like in several species of *Dianthus* in core clades A-C (Fig. 3). Within the inflorescences, cauline herbaceous leaves more or less gradually become narrower, more scarious or papery in texture and with a more distinctly excurrent midrib (Figs 3D, 4E) toward the tip of the branches. The position of the uppermost pair of these leaf organs can be distinctly below the calyx as in *Petrorhagia cretica*, and in this case they differ only slightly in their morphology from cauline leaves. Alternatively, these leaf organs arise directly at the base of the calyx, resulting from a reduced peduncle and shortened uppermost internodes of the inflorescence branches or stems (Figs 3 B, D, 4E). This seems to be the most common state in *Dianthus*, which is present in all major lineages. These "subtending" modified leaf organs usually differ more abruptly from the upper leaves on stems and inflorescence branches and have been called "epicalyx scales" or "epicalyx bracts" (Ball and Heywood 1964; Tutin 1964; Madhani et al. 2018;). Condensed inflorescences with multiple flowers do not only have such "epicalyx scales" but also additional, usually brown, scarious bracts (Fig. 3C) that create a firm, head-like appearance.

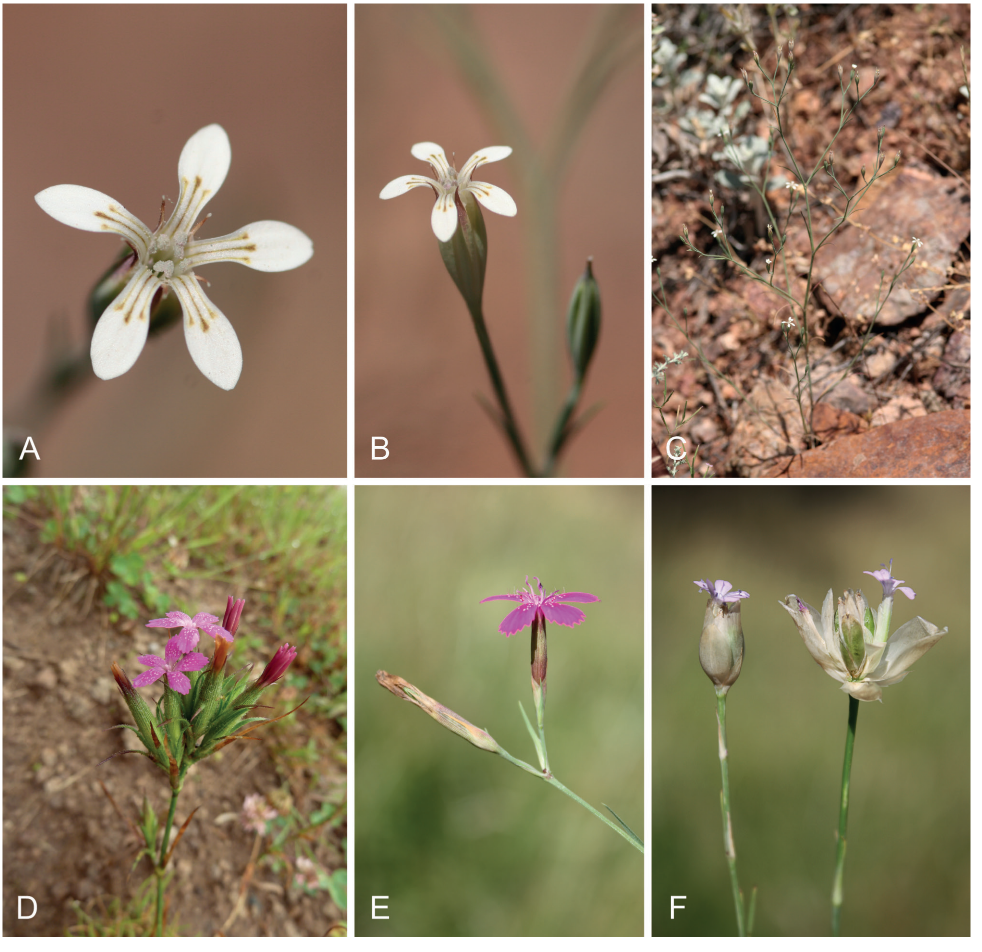

Figure 4. Habit, inflorescence and floral morphology in early-branching lineages of *Dianthus* and *Petrorhagia*. The *Dianthus tunicoides* clade is represented by *D. pachygonus* (= *Petrorhagia cretica*), which has solitary flowers (**A, B**) in diffusely branched inflorescences (**C**). The *Dianthus armeria* clade is represented by *D. armeria* (**D**), which has condensed terminal inflorescences and flowers supported by reflexed, bract-like leaves, and *D. deltoides*, which has lax inflorescences with solitary flowers each supported by two opposite bracts (**E**). The core clade of *Petrorhagia* is represented by *P. prolifera*, which has highly condensed terminal inflorescences with broadly ovate and thinly scarious bracts enclosing the flowers (**F** with opened inflorescence to the right). Photos: A. Nersesyan (**A-D**), T. Borsch (**E, F**).

This was noted by Tutin (1964), who stated that bracts occur in species with capitate inflorescences and should be distinguished from epicalyx scales. Specialised inflorescence types have also evolved in other genera of Caryophyllales, such as the head-like synflorescences composed of several paracladia that are supported by pseudanthial leaves in *Gomphrena*, Amaranthaceae (Ortuño Limarino and Borsch 2020). Therefore, complex evolution of inflorescences is present in the Caryophyllales, and occurs multiple times within the respective genera. The absence or presence of "epicalyx bracts" as discussed by Ball and Heywood (1964) and Madhani et al. (2018) can therefore not be used as diagnostic to delimit *Dianthus* from *Petrorhagia* and as such does not represent a homologous character. Nevertheless, the evolution of complex inflorescence types, which possess additional modified leaf organs compared to the subtending opposite leaves in dichasial inflorescence structures, may be more accurately reconstructed once there is a fully resolved tree of *Dianthus*.

The conspicuous species with plumose petals (Fig. 3) were early on classified as "*Dianthus* sect. *Plumaria*", a name published by Opiz (1852), albeit a nomen nudum and therefore invalid. It largely corresponds to *D.* sect. *Fimbriati* (Boiss.) F.N.Williams. This section is highly polyphyletic, and points to multiple evolutionary origins of plumose petals in *Dianthus*, such as in *D. superbus* (core clade A) and *D. crinitus* or *D. libanotis*, (core clade B), and there are also transitional petals slightly plumose at the tip (e.g. *D. cyprius*, *D. namaensis*).

Implications for biogeography and diversification patterns

A striking biogeographic feature within *Dianthus* is the Cretan *D. juniperinus*-*D. fruticosus* clade (clade C). The highly fragmented form of the Aegean region with many islands is the result of a series of geological events. Between the Lower Oligocene and before the Serravallian, there was a land mass, Aegea. Since Serravallian and until Upper Tortonian times (12–5 MYA), the sea slowly invaded and formed the mid-Aegean Trench, which divided the eastern and central-western parts of Aegea. During the Messinian Salinity Crisis (5.96–5.33 MYA), the Mediterranean Sea almost dried up, creating routes between some isolated areas. Nevertheless, Crete remained isolated from the Cyclades and Peloponnese due to deep trenches with high salinity. At the beginning of the Pliocene (5.3 Ma), the sea level rose again and resulted in a highly fragmented Aegea. Crete was almost submerged and only the peaks of the mountains remained as isolated islands. Since the Middle Pliocene until the upper Pliocene-Lower Pleistocene, the Aegean islands and Crete took their present form, with minor changes. The palaeogeographic history of the Aegean Sea has a major contribution to the biogeographic patterns of all recent taxa of these areas (Sfenthourakis and Triantis 2017). The bisection of *D. fruticosus* into two different clades, with *D. fruticosus* subsp. *fruticosus*, *D. fruticosus* subsp. *amorginus* and *D. fruticosus* subsp. *rhodius* belonging to clade A and the rest of the subspecies nested in the C with *D. juniperinus*, follows the fragmentation of Aegea due to the formation of the Mid-Aegean Trench. Moreover, Crete was connected to the mainland during most of the Miocene and was mostly isolated during the Pliocene, forming its own unique biogeographic patterns. The Aegean region is a biologically very diverse archipelago, but the way in which the islands and plant groups have interacted and evolved is not yet sufficiently understood. There are some recent studies, e.g. Kougioumoutzis et al. (2016) that address the biogeographic studies in the area, but further research is nonetheless crucial.

The tropical and southern African *Dianthus* taxa appear in our clade C within the Eurasian taxa, although, due to lack of resolution, we cannot yet infer the closest relatives of the southern African species. *Dianthus* shows a pattern like other species from the northern hemisphere with African high-mountain clades nested within Eurasian clades, as shown for, e.g., *Carex* and *Ranunculus* (Gehrke and Linder 2009). Many cases suggest not only migration from the northern hemisphere, but the recurrence of that (Bleeker et al. 2002; Carlsen et al. 2009), which could explain the presence of the African taxa within the clades of Eurasian taxa. The tropical-alpine and tropical-montane floras, as suggested by Linder (2014), show strong relations with the flora of Eurasia. One probable migration route from Eurasia to southern Africa for these taxa is through the Arabian Peninsula and the high mountains of eastern and southern Africa (Koch et al. 2006), which fits well with the pattern observed in this study that African *Dianthus* are part of a clade dominated by the Eurasian and Irano-Turanian taxa.

Dianthus is suggested to be one of the fastest species radiations of flowering plants (Valente et al. 2010). These authors calculated diversification rates by using a rather conservative estimate of 300 species. Considering that the number of species in *Dianthus* as assessed here is distinctly higher, the true speciation rates may also even be higher. On the other hand, there is not a single "Eurasian radiation" as suggested by Valente et al. (2010). Rather, our data point to three sub-radiations in the core of *Dianthus*, which seem to have evolved different numbers of species in different geographic areas. It is noteworthy that *Dianthus* has not evolved a high number of species in tropical and southern Africa. The smallest is the radiation of *D. juniperinus* and allies on Crete (our clade C). However, the number of species in this lineage is still difficult to assess because the current classification includes many subspecies and because species as currently classified do not represent biological entities.

Compared to the other lineages of *Dianthus*, clade C shows a high phylogenetic structure and apparently some geographic patterns. Future analyses will therefore test how far speciation was triggered through geographic and ecological isolation on Crete. The two much more species-rich clades A and B have colonised vast geographic areas, offering many more ecological opportunities and potential areas for spatial isolation.

Phylogenetic signal at species level and speciation in *Dianthus*

Genetic distances in *Dianthus* are very low, which limits resolution in phylogeny reconstruction at species level and may be attributed to the core clade of *Dianthus* representing a rapid radiation (Valente et al. 2010) that did not yet allow for the accumulation of mutations in the genomic regions sequenced, while the evolution of phenotypic characters occurred more quickly. Sequence divergence is particularly low in the ribosomal array (Fig. 2). Nevertheless, the overall phylogenetic tree of *Dianthus* (Fig. 2) reveals deep nodes with significant statistical support. The core *Dianthus* clade exhibits a deep sharing of plastid haplotypes in some species, for example in *D. gratianopolitanus*, where individuals from geographically different populations in central Europe are resolved in various sublineages of clade A. The pattern in this species is particularly striking since there were no noticeable morphological differences among these individuals. Another species complex with deeply shared plastid haplotypes is *D. orientalis* Adams (Fig. 1, clade B), although here considerable morphological variation is present that has led to the acceptance of several subspecies. Again, the haplotypes are shared only within subclade C, and not across the genus. Such a pattern could be explained by a combination of shared ancestral variation and continuous secondary genetic contact, which took place within certain major lineages of *Dianthus* and within certain geographic areas. *Dianthus* seems to be one of the most extreme cases of deep chloroplast-sharing in flowering plants, similar to what has been observed in the rapid postglacial evolution of relatives of *Arabidopsis thaliana* (L.) Heynh. during the last 800,000 years (Hohmann and Koch 2017; Novikova et al. 2016).

Future research will therefore have to employ phylogenomic approaches to better understand species-level relationships and species limits in *Dianthus*. In addition to sequencing a broad set of nuclear loci, the analysis of complete plastid genomes will reveal how far plastid genomes are really shared between extant species, considering that our current limited sampling of the plastid regions may not depict the full complexity and divergence patterns of this maternally inherited organellar genome.

Species diversity of *Dianthus*

Our *Dianthus* checklist contains 384 accepted species, and 147 accepted heterotypic subspecies. The unresolved names section of the checklist contains a further 172 species names that were not assessed, and a number of them may be good species as well. Therefore, the often-quoted number of 300 species (Pax and Hoffmann 1934; Bittrich 1993; Hernández-Ledesma et al. 2015) is underestimated. It should be noted that we present a compilation of names, not a genus-wide treatment, which we nevertheless consider to be an accurate estimate of the species diversity since it is based on available detailed treatments. It is therefore much more accurate compared to the previous World Flora Online backbone based on The Plant List in terms of accepted species and synonyms. About 50 names that were unresolved in the original WFO backbone could be resolved in our checklist. The remaining 172 unresolved names are in part old names, described in the 19th century and apparently not used in subsequent treatments. But there are also a number of names described from south-eastern Europe, which would have to be assessed in more detail by local experts.

It is both noteworthy and unexpected that taxon concepts are congruent between different treatments, despite some geographic overlap. The widely distributed species are accepted under the same name in different Floras, while subspecies are normally geographically restricted and therefore only accepted in one Flora. In total, differing taxonomic concepts affect fewer than 10 taxa in the whole checklist.

So far, only one species complex within *Dianthus* has been analysed with an evolutionary approach. Farsi et al. (2013) used a combination of sequence data and morphological characters to assess species limits in the *D. polylepis* Bien. complex, concluding that *D. binaludensis* Rech.f. could not be separated from *D. polylepis* but should be better treated as its subspecies. Our present study provides insights into the *Dianthus fruticosus* and *D. juniperinus* groups, but aside from that, basically all other species limits in *Dianthus* are still based on classical morphology, and so are the numerous recent descriptions of new species.

Nomenclatural novelties

The three species of *Petrorhagia* that were found nested in *Dianthus* (*P. armerioides*, *P. candica* and *P. alpina*) were already transferred to *Dianthus* by Madhani et al. (2018). We found two additional *Petrorhagia* species to be part of the *Dianthus* clade although they have no name in *Dianthus*. Of the three subspecies of *P. illyrica*, we sampled only one. They all are morphologically very similar (Ball and Heywood 1964) and therefore can be expected to be closely related, although we are aware that is not true for the subspecies of *Dianthus fruticosus* that we showed to be unrelated. Nevertheless, we provide new combinations for the other two *P. illyrica* subspecies so that these subspecies can be classified in *Dianthus*. Their phylogenetic placement remains to be tested.

Velezia rigida, the nomenclatural type of *Velezia*, was found to be nested within the *Dianthus* clade by Madhani et al. (2018) and therefore Velezia cannot be accepted as a separate genus any longer. We therefore provide new names in *Dianthus* for the five remaining *Velezia* species; their phylogenetic placement however remains to be confirmed.

The complete homotypic and heterotypic synonymy for each of the species is given in the checklist; here we provide only the basionyms and the former names in *Petrorhagia* or *Velezia*.

***Dianthus antalyensis* Fassou, N.Korotkova, Dimop. & Borsch, nom. nov.**
urn:lsid:ipni.org:names:77297792-1

≡ *Velezia tunicoides* P.H.Davis in Notes Roy. Bot. Gard. Edinburgh 22: 166. 1957.

Holotype. Turkey, Prov. Antalya, distr. Kemer (Lycia): Gönük, by dry stream bed, 7 Jul 1949, *Davis*, *Bilger & Attila D. 15009* (K-000077456!; isotype: E-00301891!).

Note. The name *Dianthus tunicoides* Madhani & Heubl in Taxon 67(1): 103. 2018) was already published as a new name for *Gypsophila armerioides* Ser. ex DC. ≡ *Petrorhagia armerioides* (Ser. ex DC.) P.W.Ball & Heywood. This new name refers to the province of Antalya, Turkey, from where the species was described.

Dianthus hispidus **(Boiss. & Balansa) Fassou, N.Korotkova, Dimop. & Borsch, comb. nov.**
urn:lsid:ipni.org:names:77297793-1

≡ *Velezia hispida* Boiss. & Balansa in Boissier, Diagn. Pl. Orient., ser. 2, 5: 57. 1856.

Syntypes. Turkey, Yaïla de Bozdagh (Tmolus occidental), dans les vergers, 27 Jul 1854, *Balansa 117* (GOET-000717!, P-04998030!, P-04998031!, P-04998036!, WAG-0000421!).

Dianthus illyricus **(Ard.) Fassou, N.Korotkova, Dimop. & Borsch, comb. nov.**
urn:lsid:ipni.org:names:77297794-1

≡ *Saponaria illyrica* Ard., Animadv. Bot. Spec. Alt.: 24. 1764 ≡ *Petrorhagia illyrica* (Ard.) P.W.Ball & Heywood in Bull. Brit. Mus. (Nat. Hist.), Bot. 3: 133. 1964.

Lectotype (designated here). locality and date unknown, *Arduino s.n.*, Herb. Linnaeus No. 580.7 (LINN!). This specimen was mentioned by Ball and Heywood (1964). The sheet has two distinct specimens, one of which is labelled "Ard.", and the typification refers to this specimen. Ball & Heywood mentioned that it "may be regarded at least as an isotype", but did not formally designate it as a type.

Dianthus illyricus subsp. *illyricus*

Dianthus illyricus **subsp.** ***angustifolius*** **(Poir.) Fassou, N.Korotkova, Dimop. & Borsch, comb. nov.**
urn:lsid:ipni.org:names:77297795-1

≡ *Silene angustifolia* Poir., Voy. Barbarie 2: 164. 1789 ≡ *Petrorhagia illyrica* subsp. *angustifolia* (Poir.) P.W.Ball & Heywood in Bull. Brit. Mus. (Nat. Hist.), Bot. 3: 136. 1964.

Neotype (designated here). locality and date unknown, *Poiret 32* (P-00286897!). This specimen might be original material for the name.

Dianthus illyricus **subsp.** ***haynaldianus*** **(Nyman) Fassou, N.Korotkova, Dimop. & Borsch, comb. nov.**
urn:lsid:ipni.org:names:77297796-1

≡ *Tunica haynaldiana* [Borbás in Mat. Term. Közlem. 13: 46. 1877, pro. syn; in Just's Bot. Jahresber. 4(2): 1067. 1878, provisional name] Nyman, Consp. Fl. Eur. Suppl. 2(1): 57. 1889 ≡ *T. illyrica* var. *haynaldiana* (Nyman) Hayek, Prodr. Fl. Penins. Balcan. 1: 222. 1924 ≡ *Petrorhagia illyrica* subsp. *haynaldiana* (Nyman) P.W.Ball & Heywood in in Bull. Brit. Mus. (Nat. Hist.), Bot. 3: 134. 1964.

Type: Romania, in rupestribus versus portam ferram ad Danubium inferiorem infra Orsova jam in Vallachia sitis frequens, 28 Jun 1870, *Janka* #Iter banaticum s.n. (B-100365631!).

***Dianthus illyricus* subsp. *taygeteus* (Boiss.) Fassou, N.Korotkova, Dimop. & Borsch, comb. nov.**
urn:lsid:ipni.org:names:77297799-1

≡ *Tunica illyrica* var. *taygetea* Boiss., Fl. Orient. 1: 521. 1867 ≡ *Petrorhagia illyrica* subsp. *taygetea* (Boiss.) P.W.Ball & Heywood in Bull. Brit. Mus. (Nat. Hist.), Bot. 3: 137. 1964.

Syntypes. Greece, Peloponnisos, Androuvista, Montis Taygeti, Jun-Jul 1844, *Heldreich s.n.*, (G-00227046!, G-00227047!, BR0000006981167!, BR0000006981495!, BM, CGE, K fide Ball and Heywood 1964).

***Dianthus fasciculatus* (Boiss.) Fassou, N.Korotkova, Dimop. & Borsch, comb. nov.**
urn:lsid:ipni.org:names:77297800-1

≡ *Velezia fasciculata* Boiss., Diagn. Pl. Orient., ser. 1, 8: 92. 1849.

Syntypes. Syria, locality as given in the protologue: "Hab. in montosis Syriae borealis inter fluvium Orontem et urbem Laodiceam", Jun 1846, *Boissier s.n.* (K-000077457!, K-000077458!, LECB-0000587!, P-04998034!, P-04998035!).

Note. The name *Dianthus fasciculatus* Gilib., Fl. Lit. Inch. 2: 161. 1782 was not validly published.

***Dianthus pachygonus* (Fisch & C.A.Mey.) Fassou, N.Korotkova, Nersesian & Borsch, comb. nov.**
urn:lsid:ipni.org:names:77297801-1

≡ *Tunica pachygona* Fisch. & C.A.Mey., Index Sem. Hort. Bot. Petropol. 4: 50. 1838
= *Saponaria cretica* L., Sp. Pl., ed. 2, 1: 584. 1762 ≡ *Petrorhagia cretica* (L.) P.W.Ball & Heywood in Bull. Brit. Mus. (Nat. Hist.), Bot. 3: 142. 1964.

Type. not designated

Lectotype. (designated by Davis in Notes Roy. Bot. Gard. Edinburgh 22: 164. 1957): locality, date and collector unknown, Herb. Linnaeus No. 580.4 (LINN!).

Davis (1957) had pointed out the name *Tunica cretica* (L.) Fisch. & C.A.Mey. (basionym: *Saponaria cretica* L.) had been misapplied, whereas in fact the type of the name (the specimen in LINN) is an annual species that was later named *Tunica pachygona* Fisch. & C.A.Mey. Accordingly, the correct name in *Dianthus* would be *D. pachygonus*, the new combination published here because the epithet of *Saponaria cretica* is preoccupied in *Dianthus* by *D. creticus* Tausch. which is now treated as *Dianthus fruticosus* subsp. *creticus* (Tausch) Runemark.

***Dianthus pseudorigidus* (Hub.-Mor.) Fassou, N.Korotkova, Dimop. & Borsch, comb. nov.**
urn:lsid:ipni.org:names:77297802-1

≡ *Velezia pseudorigida* Hub.-Mor. in Bauhinia 2: 195. 1963.

Holotype. Turkey, Prov. Antalya, Distr. Antalya, *Poterium-Cistus*-Macchie in der Bucht von Atbükü, 5 km nördlich von Cirali, 10–50 m, auf Serpentin, 26 May 1950, *Huber-Morath 9666* (E 00301890!).

***Dianthus quadridentatus* (Sm.) Fassou, N.Korotkova, Dimop. & Borsch, comb. nov.**
urn:lsid:ipni.org:names:77297803-1

≡ *Velezia quadridentata* Sm. in Sibthorp & Smith, Fl. Graec. Prodr. 1: 283. 1809.

Type. not designated; original material: "In Asiâ minori", *Sibthorp s.n.* (OXF Sib-FG Sib-0954!, K000077455!).

Checklist

***Dianthus* L., Sp. Pl. 1: 409. 1753.** Sec. this publication
≡ *Caryophyllus* Mill., Gard. Dict. Abr., ed. 4: [textus s.n.]. 1754, nom. illeg. syn. sec. IPNI
≡ *Caryophyllus* Tourn. ex Moench, Methodus: 58. 1794 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.
= *Velezia* L., Sp. Pl.: 332. 1753 syn. sec. Madhani et al. (2018). Type: *Velezia rigida* L.
= *Cylichnanthus* Dulac, Fl. Hautes-Pyrénées: 260. 1867 syn. sec. Madhani et al. (2018)
– *Diosanthos* St.-Lag. in Ann. Soc. Bot. Lyon 7: 87. 1880, nom. inval. syn. sec. Kew WCVP (2019)

Core checklist

***Dianthus acantholimonoides* Schischk. in Byull. Gosud. Muz. Gruzii 5: 121. 1930.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus acicularis* Fisch. ex Ledeb., Fl. Ross. 1: 284. 1842.** Sec. Czerepanov (1995)
= *Dianthus tauscheri* Eversm. ex Ledeb., Fl. Ross. 1: 284. 1842 syn. sec. Dequan & Turland (2001)

***Dianthus acrochlorus* Stapf in Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. 51: 5. 1886.** Sec. Marhold (2011)
– *Dianthus acrochlonis* Stapf in Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. 51: 5. 1886 syn. sec. Marhold (2011) [is misspelling for *Dianthus acrochlorus* Stapf]

***Dianthus aculeatus* Hamzaoğlu in Biol. Diversity Conservation 7(2): 160. 2014.** Sec. Hamzaoğlu et al. (2014)

***Dianthus afghanicus* Rech.f. in Bot. Jahrb. Syst. 75: 360. 1951.** Sec. Rechinger (1988)

***Dianthus agrostolepis* Rech.f. in Plant Syst. Evol. 142: 246. 1983.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus akdaghensis* Gemici & Leblebici in Candollea 50: 43. 1995.** Sec. Gemici & Leblebici (1995)

***Dianthus albens* Aiton, Hort. Kew. 2: 90. 1789.** Sec. African Plant Database (version 3.4.0)
= *Dianthus incurvus* Thunb., Prodr. Pl. Cap. 1: 81. 1794 syn. sec. African Plant Database (version 3.4.0)

***Dianthus algetanus* Graells ex F.N.Williams in J. Bot. 23: 347. 1885.** Sec. Bernal et al. (1990)
≡ *Dianthus pyrenaicus* subsp. *algetanus* (Graells ex F.N.Williams) Malag., Sin. Fl. Ibér. 20: 318. 1975 syn. sec. Bernal et al. (1990) ≡ *Dianthus costae* subsp. *algetanus* (Graells ex F.N.Williams) M.Laínz, Muñoz Garm. & Soriano in Anales Jard. Bot. Madrid 43: 473. 1986 ["1987"] syn. sec. Bernal et al. (1990)
= *Dianthus algetanus* var. *toletanorum* Pau in Cavanillesia 1: 63. 1928 syn. sec. Bernal et al. (1990)

Dianthus algetanus* subsp. *algetanus

***Dianthus algetanus* subsp. *turolensis* (Pau) M.Bernal, Laínz & Muñoz Garm. in Anales Jard. Bot. Madrid 45: 575. 1988 ["1989"].** Sec. Bernal et al. (1990)
≡ *Dianthus turolensis* Pau in Bol. Real Soc. Esp. Hist. Nat. 21: 142. 1921 syn. sec. Bernal et al. (1990) ≡ *Dianthus algetanus* var. *turolensis* (Pau) Pau in Bortéria, Sér. Bot. 22: 111. 1926 syn. sec. Bernal et al. (1990) ≡ *Dianthus costae* subsp. *turo-*

lensis (Pau) M.Laínz & Muñoz Garm in Anales Jard. Bot. Madrid 43: 473. 1986 ["1987"] syn. sec. Bernal et al. (1990)

***Dianthus alpinus* L., Sp. Pl.: 412. 1753.** Sec. Marhold (2011)
= *Dianthus alpinus* lusus *angustifolius* Regel in Bull. Soc. Imp. Naturalistes Moscou 34(2): 530. 1862 syn. sec. Marhold (2011)
= *Dianthus alpinus* lusus *latifolius* Regel in Bull. Soc. Imp. Naturalistes Moscou 34(2): 530. 1862 syn. sec. Marhold (2011)
= *Dianthus alpinus* var. *meyeri* Regel in Bull. Soc. Imp. Naturalistes Moscou 34(2): 530. 1862 syn. sec. Kew WCVP (2019)

***Dianthus altaicus* L.X.Dong & Chang Y.Yang in Acta Bot. Boreal.-Occid. Sin. 28(12): 2355. 2008.** Sec. Dong et al. (2008)

***Dianthus amurensis* Jacques in J. Soc. Imp. Centr. Hort. 7: 625. 1861.** Sec. Barkalov & Probatova (2006)
≡ *Dianthus chinensis* var. *amurensis* (Jacques) Kitag., Neo-Lineam. Fl. Manshur.: 266. 1979 syn. sec. this publication

***Dianthus anatolicus* Boiss., Diagn. Pl. Orient. ser. 1 1: 22. 1843.** Sec. Marhold (2011)
= *Dianthus parviflorus* Boiss., Diagn. Pl. Orient. ser. 1 1: 21. 1843 syn. sec. Marhold (2011)
≡ *Dianthus anatolicus* var. *parviflorus* (Boiss.) Boiss., Fl. Orient. 1: 490. 1867 syn. sec. Dimopoulos et al. (2013)
= *Dianthus kotschyanus* Boiss. & Heldr. in Boissier, Diagn. Pl. Orient., ser. 1, 8: 68. 1849 syn. sec. Marhold (2011)

***Dianthus ancyrensis* Hausskn. & Bornm. in Repert. Spec. Nov. Regni Veg. Beih. 89: 94. 1936.** Sec. Marhold (2011)

***Dianthus andronakii* Woronow ex Schischk., Fl. URSS 6: 841. 1936.** Sec. Kuzmina & Nersesyan (2012)
≡ *Dianthus tristis* Woronow in Věstn. Tiflissk. Bot. Sada 10: 25. 1908 syn. sec. WFO 2018

***Dianthus androsaceus* (Boiss. & Heldr.) Hayek in Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Kl., Denkschr. 94: 141. 1918.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus lilacinus* var. *androsaceus* Boiss. & Heldr. in Boissier, Fl. Orient. Suppl.: 81. 1888 syn. sec. WFO 2018

***Dianthus andrzejejowskianus* (Zapał.) Kulcz., Fl. Polska 2: 156. 1921.** Sec. Czerepanov (1995)

≡ *Dianthus capitatus* subsp. *andrzejowskianus* Zapał. in Rozpr. Wydz. Mat.-Przyr Polsk Akad. Umiejetn., Dzial A/B, Nauki Mat-Fiz. Biol. 11: 25. 1911 syn. sec. Czerepanov (1995)
= *Dianthus capitatus* var. *pancicianus* F.N.Williams in J. Bot. 23: 342. 1885 syn. sec. Kew WCVP (2019)
= *Dianthus andrzejejowskianus* subsp. *orientalis* Kleopow in Izv. Kievsk. Bot. Sada 14: 104. 1932 syn. sec. Kew WCVP (2019)

***Dianthus angolensis* Hiern ex F.N.Williams in J. Bot. 24: 301. 1886.** Sec. African Plant Database (version 3.4.0)

***Dianthus angrenicus* Vved. in Bot. Mater. Gerb. Bot. Inst. Uzbekistansk. Fil. Akad. Nauk S.S.S.R. 3: 9. 1941.** Sec. WFO 2018

***Dianthus angulatus* Royle ex Benth., Ill. Bot. Himal. Mts.: 79. 1834.** Sec. Rechinger (1988)
≡ *Dianthus orientalis* var. *angulatus* (Royle ex Benth.) Majumdar, Fl. India 2: 532. 1993 syn. sec. WFO 2018
= *Dianthus incertus* Jacquem. ex Edgew. & Hook.f., Fl. Brit. India 1: 215. 1874 syn. sec. WFO 2018

Dianthus angulatus* subsp. *angulatus

***Dianthus angulatus* subsp. *subangulatus* Rech.f., Fl. Iranica 163: 183. 1988.** Sec. Rechinger (1988)

***Dianthus antalyensis* Fassou, N.Korotkova, Dimop. & Borsch.** Sec. this publication 118
≡ *Velezia tunicoides* P.H.Davis in Notes Roy. Bot. Gard. Edinburgh 22: 166. 1957. Syn. sec. this publication

***Dianthus anticarius* Boiss. & Reut., Pugill. Pl. Afr. Bor. Hispan.: 19. 1852.** Sec. Bernal et al. (1990)
≡ *Dianthus cintranus* subsp. *anticarius* (Boiss. & Reut.) Malag., Pl. Sennen. I: Dianthus 6. 1974 syn. sec. Bernal et al. (1990)
= *Dianthus gaditanus* Boiss., Diagn. Pl. Orient., ser. 2, 1: 67. 1854 syn. sec. Bernal et al. (1990)
= *Dianthus hornemannii* Salzm. ex Boiss., Diagn. Pl. Orient., ser. 2, 1: 67. 1854 syn. sec. Marhold (2011)
= *Dianthus schousboei* Coss. ex Ball in J. Linn. Soc., Bot. 16: 355. 1877 syn. sec. WFO 2018

Dianthus anticarius* subsp. *anticarius

***Dianthus anticarius* subsp. *saorinii* Sánchez-Gómez, M.L.Rodr., López Esp., J.B.Vera & J.F.Jiménez in Anales Biol., Fac. Biol., Univ. Murcia 27: 101. 2005.** Sec. New taxa described to the Flora Iberica region after publication of the respective volumes. Published at http://www.floraiberica.es/eng/miscelania/nuevos_taxones.php

***Dianthus arenarius* L., Sp. Pl.: 412. 1753.** Sec. Czerepanov (1995)
≡ *Tunica arenaria* (L.) Scop., Fl. Carniol., ed. 2, 1: 301. 1771 ≡ *Silene arenaria* (L.) E.H.L.Krause, Deutschl. Fl. Abbild., ed. 2, 5: 115. 1901, nom. illeg. syn. sec. Kew WCVP (2019);
= *Dianthus arenarius* var. *glaucus* Blocki in Oesterr. Bot. Z. 34: 72. 1884 syn. sec. Kew WCVP (2019)
= *Dianthus krylovianus* Juz. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 13: 71. 1950 syn. sec. Czerepanov (1995)
= *Dianthus arenarius* var. *suecicus* Novák syn. sec. Czerepanov (1995)

Dianthus arenarius* subsp. *arenarius

***Dianthus arenarius* subsp. *borussicus* Vierh. in Izv. Kievsk. Bot. Sada 12–13: 34. 1931.** Sec. Marhold (2011)
≡ *Dianthus borussicus* (Vierh.) Juz. syn. sec. Marhold (2011)
= *Dianthus arenarius* var. *bohemicus* Novák syn. sec. Kew WCVP (2019) ≡ *Dianthus arenarius* subsp. *bohemicus* (Novák) O.Schwartz in Mitt. Thüring. Bot. Ges. 1: 99. 1949 syn. sec. Kew WCVP (2019)

***Dianthus arenarius* subsp. *pseudoserotinus* (Blocki) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 190. 1963.** Sec. Czerepanov (1995)
≡ *Dianthus pseudoserotinus* Blocki syn. sec. Czerepanov (1995) ≡ *Dianthus serotinus* var. *pseudoserotinus* (Blocki) Zapał., Consp. Fl. Gallic. Crit. 3: 150. 1911 syn. sec. Kew WCVP (2019)

***Dianthus arenarius* subsp. *pseudosquarrosus* (Novák) Kleopow in Izv. Kievsk. Bot. Sada 12–13: 35. 1931.** Sec. Marhold (2011)
≡ *Dianthus arenarius* f. *pseudosquarrosus* Novák in Mem. Soc. Sci. De Bohem 1: 9. 1925 syn. sec. Kew WCVP (2019) ≡ *Dianthus pseudosquarrosus* (Novák) Klokov, Fl. RSS Ucr. 4: 639. 1952 syn. sec. Marhold (2011)

***Dianthus aristatus* Boiss., Asie Min., Bot. 1: 222. 1860.** Sec. Kuzmina & Nersesyan (2012)
≡ *Dianthus zonatus* var. *aristatus* (Boiss.) Reeve, Notes Roy. Bot. Gard. Edinb. 28: 21. 1967 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus preobrazhenskii* Klokov in Trudy Silsko-Gosp. Bot. 1(3): 170. 1927 syn. sec. Kuzmina & Nersesyan (2012)

***Dianthus armeria* L., Sp. Pl.: 410. 1753.** Sec. Marhold (2011)

≡ *Caryophyllus armerius* (L.) Moench, Methodus: 59. 1794 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. ≡ *Dianthus armeria* subsp. *armeria* syn. sec. WFO 2018

= *Dianthus hirsutus* Lam., Fl. Franç. 2: 533. 1779 syn. sec. Bernal et al. (1990)

= *Dianthus hirtus* Lam., Fl. Franç. 2: 533. 1779 syn. sec. WFO 2018

= *Dianthus villosus* Gilib., Fl. Lit. Inch. 2: 160. 1782 syn. sec. WFO 2018

= *Dianthus carolinianus* Walter, Fl. Carol.: 140. 1788 syn. sec. WFO 2018

= *Gypsophila armeria* var. *nanus* Boenn., Prodr. Fl. Monast. Westphal.: 124. 1824 syn. sec. Kew WCVP (2019)

= *Dianthus hybridus* F.W.Schmidt ex Tausch in Flora 13: 245. 1830 syn. sec. WFO 2018

= *Dianthus vivariensis* Jord. ex Boreau, Fl. Centre France ed. 3, 2: 91. 1857 syn. sec. WFO 2018

= *Dianthus armeria* var. *laevis* Heuff. in Verh. Zool.-Bot. Ges. Wien 8: 68. 1858 syn. sec. Kew WCVP (2019)

= *Dianthus armeriastrum* Wolfner in Oesterr. Bot. Z. 8: 318. 1858 syn. sec. WFO 2018 ≡ *Dianthus armeria* subsp. *armeria*strum (Wolfner) Velen., Fl. Bulg. Suppl. 1: 42. 1898 syn. sec. WFO 2018

= *Dianthus epirotus* Halácsy in Verh. K. K. Zool.-Bot. Ges. Wien 48: 708. 1898 syn. sec. WFO 2018

= *Silene vaga* E.H.L.Krause, Deutschl. Fl. Abbild., ed. 2, 5: 109. 1901 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.

= *Dianthus pseudocorymbosus* Velen. in Sitzungsber. Königl. Böhm. Ges. Wiss., Math.-Naturwiss. Cl. 8: 6. 1910 ["1911"] syn. sec. Dimopoulos et al. (2013)

= *Dianthus armeria* f. *acaulis* Bolzon in Bull. Soc. Bot. Ital. 1911: 56. 1911 syn. sec. Kew WCVP (2019)

= *Dianthus armeria* f. *caespitosa* Bolzon in Bull. Soc. Bot. Ital. 1911: 56. 1911 syn. sec. Kew WCVP (2019)

= *Dianthus armeria* f. *albiviridis* Lehr in Bull. Torrey Bot. Club 90: 207. 1963 syn. sec. WFO 2018

= *Dianthus armeria* f. *glabrissimus* Sigunov in Glasn. Prir. Muz. Beogradu, C 10: 23. 1977 syn. sec. WFO 2018

= *Dianthus armeria* f. *alba* Stritch in Castanea 48: 58. 1983 syn. sec. WFO 2018

***Dianthus arpadianus* Ade & Bornm. in Repert. Spec. Nov. Regni Veg. 36: 385. 1934.** Sec. Dimopoulos et al. (2013)

***Dianthus arrosti* C.Presl, Delic. Prag.: 60. 1822.** Sec. Marhold (2011)

≡ *Dianthus caryophyllus* var. *arrosti* (C.Presl) Tanfani, Fl. Ital. 9: 283. 1892 syn. sec. WFO 2018 ≡ *Dianthus caryophyllus* subsp. *arrosti* (C.Presl) Arcang., Comp. Fl. Ital. ed. 2: 306. 1894 syn. sec. Marhold (2011) – *Dianthus arrostii* C.Presl, Delic. Prag.: 60. 1822 syn. sec. Marhold (2011) [is orthographic variant for *Dianthus arrosti* C.Presl]

= *Dianthus contractus* Jan ex Lojac., Fl. Sicul. 1: 164. 1889 syn. sec. WFO 2018

***Dianthus* ×*artignanii* Sennen in Bol. Soc. Ibér. Ci. Nat. 25: 145. 1926.** Sec. Bernal et al. (1990)

***Dianthus aticii* Hamzaoğlu in Phytokeys 48: 22. 2015.** Sec. Hamzaoğlu et al. (2015)

***Dianthus atlanticus* Pomel, Nouv. Mat. Fl. Atl. 1: 332. 1874.** Sec. African Plant Database (version 3.4.0)
≡ *Dianthus liburnicus* var. *atlanticus* (Pomel) Chabert in Bull. Soc. Bot. France 38: 383. 1892 ["1891"] syn. sec. Kew WCVP (2019)

***Dianthus atschurensis* Sosn. in Vestn. Tiflissk. Bot. Sada n.s. 1: 74. 1923.** Sec. Kuzmina & Nersesyan (2012)
– *Dianthus azkurensis* Sosn. in Vestn. Tiflissk. Bot. Sada n.s. 1: 74. 1923 syn. sec. this publication [is misspelling for *Dianthus atschurensis* Sosn.]

***Dianthus austroiranicus* Lemperg in Repert. Spec. Nov. Regni Veg. 50: 260. 1941.** Sec. Rechinger (1988)

***Dianthus awaricus* Kharadze in Zametki Sist. Geogr. Rast. 16: 50. 1951.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus aydogdui* Menemen & Hamzaoğlu in Ann. Bot. Fenn. 37: 285. 2000.** Sec. Menemen & Hamzaoğlu (2000)

***Dianthus aytachii* C.Vural in Bot. J. Linn. Soc. 158: 55. 2008.** Sec. Vural (2008)

***Dianthus balansae* Boiss., Fl. Orient. 1: 488. 1867.** Sec. Marhold (2011)

***Dianthus barbatus* L., Sp. Pl.: 409. 1753.** Sec. Marhold (2011)
≡ *Caryophyllus barbatus* (L.) Moench, Methodus: 59. 1794 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. ≡ *Cylichnanthus barbatus* (L.) Dulac, Fl. Hautes-Pyrénées: 261. 1867 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. ≡ *Silene barbata* (L.) E.H.L.Krause, Deutschl. Fl. Abbild., ed. 2, 5: 108. 1901 syn. sec. Kew WCVP (2019); ≡ *Dianthus barbatus* var. *barbatus*
= *Tunica barbata* Scop., Fl. Carniol., ed. 2, 1: 298. 1771 syn. sec. Marhold (2011)
= *Dianthus hispanicus* Dum.Cours. in Bot. Cult. 3: 168. 1802 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus latifolius* Willd., Enum. Pl.: 466. 1809 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus aggregatus* Poir., Encycl. Suppl. 4: 124. 1816 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus corymbosus* F.Dietr., Nachtr. Vollst. Lex. Gärtn. 2: 667. 1816 syn. sec. Kuzmina & Nersesyan (2012)

= *Dianthus barbatus* var. *latifolius* Ser., Prodr. 1: 356. 1824 syn. sec. Kew WCVP (2019)
= *Dianthus barbatus* var. *paniculatus* Ser., Prodr. 1: 356. 1824 syn. sec. Kew WCVP (2019)
= *Dianthus barbatus* var. *pedunculosus* Ser., Prodr. 1: 356. 1824 syn. sec. Kew WCVP (2019)
= *Dianthus pulcherrimus* Loisel., Dict. Sci. Nat. ed. 2, 35: 417. 1825 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus splendidissimus* Hoffmanns. in Verz. Pfl.-Kult. Nachtr: 27. 1842 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus girardinii* Lamotte in Bull. Soc. Bot. France 21: 120. 1874 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus barbatus* var. *asiaticus* Nakai, Tyosen-Syokubutsu: 143. 1914 syn. sec. Marhold (2011)

Dianthus barbatus* subsp. *barbatus

***Dianthus barbatus* subsp. *compactus* (Kit. ex Schult.) Nyman, Consp. Fl. Eur. Suppl. 2(1): 58. 1889.** Sec. Marhold (2011)
≡ *Dianthus compactus* Kit. ex Schult., Oestr. Fl. ed. 2, 1: 654. 1814 syn. sec. Marhold (2011) ≡ *Dianthus barbatus* var. *compactus* (Kit. ex Schult.) Heuff. in Verh. K. K. Zool.-Bot. Ges. Wien 8: 68. 1858 syn. sec. Kuzmina & Nersesyan (2012)

***Dianthus basianicus* Boiss. & Hausskn. ex Boiss., Fl. Orient. Suppl.: 77. 1888.** Sec. Rechinger (1988)

***Dianthus basuticus* Burtt Davy in Bull. Misc. Inform. Kew 1922: 220. 1922.** Sec. African Plant Database (version 3.4.0)
= *Dianthus micropetalus* var. *galpinii* Burtt Davy syn. sec. WFO 2018

Dianthus basuticus* subsp. *basuticus

***Dianthus basuticus* subsp. *fourcadei* S.S.Hooper, Hooker's Icon. Pl. 7 [1]: 20–22. 1959.** Sec. African Plant Database (version 3.4.0)

***Dianthus basuticus* var. *grandiflorus* S.S.Hooper, Hooker's Icon. Pl. 7 [1]: 19. 1959.** Sec. African Plant Database (version 3.4.0)

***Dianthus benearnensis* Loret in Bull. Soc. Bot. France 5: 327. 1858.** Sec. Bernal et al. (1990)
≡ *Dianthus furcatus* subsp. *benearnensis* (Loret) Kerguélen in Lejeunia 120: 79. 1987 syn. sec. IPNI

***Dianthus bessarabicus* (Kleopow) Klokov in Bot. Zhurn. (Kiev) 5: 28. 1948.** Sec. Czerepanov (1995)
≡ *Dianthus polymorphus* subsp. *bessarabicus* Kleopow in Izv. Kievsk. Bot. Sada 14: 114. 1932 syn. sec. Czerepanov (1995)

= *Dianthus polymorphus* var. *bessarabicus* Sanda syn. sec. Czerepanov (1995)

***Dianthus bicolor* Adams in Beitr. Naturk. 1: 55. 1805.** Sec. Kuzmina & Nersesyan (2012)
= *Dianthus caucasicus* M.Bieb., Fl. Taur.-Caucas. 1: 327. 1808 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus bicolor* var. *minor* Ser., Prodr. 1: 361. 1824 syn. sec. Kew WCVP (2019)

***Dianthus biflorus* Sm., Fl. Graec. Prodr. 1(2): 285. 1809.** Sec. Dimopoulos et al. (2013)
= *Dianthus binatus* Bartl. ex Rchb., Fl. Germ. Excurs.: 810. 1832 syn. sec. WFO 2018
= *Dianthus cinnabarinus* Spruner ex Boiss., Diagn. Pl. Orient. ser. 1, 6: 22. 1846 syn. sec. WFO 2018
= *Dianthus samaritani* Heldr. ex Halácsy, Consp. Fl. Graec. 1: 213. 1900 syn. sec. WFO 2018 ≡ *Dianthus biflorus* subsp. *samaritanii* (Heldr. ex Halácsy) Maire & Petitm syn. sec. Dimopoulos et al. (2013) – *Dianthus samaritani* Heldr. ex Boiss., Fl. Orient. 1: 511. 1867, nom. inval. syn. sec. Dimopoulos et al. (2013)

***Dianthus boissieri* Willk., Icon. Descr. Pl. Nov. 1: 22. 1853.** Sec. Bernal et al. (1990)
≡ *Dianthus caryophyllus* var. *boissieri* (Willk.) Emb. & Maire, Fl. Afr. Nord 10: 318. 1963 syn. sec. Bernal et al. (1990) ≡ *Dianthus sylvestris* subsp. *boissieri* (Willk.) Dobignard in J. Bot. Soc. Bot. France 20: 37. 2002 syn. sec. WFO 2018
= *Dianthus sylvestris* Boiss., Fl. Orient. 1: 701. 1867 syn. sec. WFO 2018
= *Dianthus caryophyllus* var. *brevifolius* Rouy, Obs. Dianthus France: 3. 1882 syn. sec. Kew WCVP (2019) ≡ *Dianthus caryophyllus* f. *brevifolius* (Rouy) Maire, Fl. Afrique N. 10: 319. 1963 syn. sec. Kew WCVP (2019)
= *Dianthus caryophyllus* var. *longifolius* Rouy, Obs. Dianthus France: 3. 1882 syn. sec. Kew WCVP (2019) ≡ *Dianthus caryophyllus* f. *longifolius* (Rouy) Maire, Fl. Afrique N. 10: 319. 1963 syn. sec. Kew WCVP (2019)
= *Dianthus caryophyllus* var. *longifolius* Maire in Bull. Soc. His. Nat. Afrique N. 22: 36. 1931, nom. illeg. syn. sec. Kew WCVP (2019)
= *Dianthus charmelii* Sennen & Mauricio, Diagn. Nouv.: 246. 1936 syn. sec. WFO 2018 ≡ *Dianthus caryophyllus* f. *charmelii* (Sennen & Mauricio) Maire, Fl. Afr. Nord 10: 319. 1963 syn. sec. WFO 2018
= *Dianthus caryophyllus* var. *tenuicaulis* Maire in Bull. Soc. His. Nat. Afrique N. 30: 333. 1939 syn. sec. Kew WCVP (2019)
– *Dianthus caryophyllus* f. *grandiflorus* Pau & Font Quer, Iter Marocc. 1928: no. 102. 1829, nom. inval. syn. sec. Kew WCVP (2019)
– *Dianthus caryophyllus* f. *emancipatus* Pau & Font Quer, Iter Marocc. 1927: no. 195. 1928, nom. inval. syn. sec. Kew WCVP (2019)

***Dianthus bolusii* Burtt Davy in Bull. Misc. Inform. Kew 1922: 218. 1922.** Sec. African Plant Database (version 3.4.0)

Dianthus borbasii **Vandas in Oesterr. Bot. Z. 36: 193. 1886.** Sec. Kuzmina & Nersesyan (2012)

Dianthus borbonicus **Brullo, C.Brullo, Colombo, Giusso, Ilardi & R.Perrone in Phytotaxa 233: 50. 2015.** Sec. Brullo et al. (2015)

Dianthus brachycalyx **A.Huet & É.Huet ex Bacch., Brullo, Casti & Giusso in Nordic J. Bot. 28: 142. 2010.** Sec. Bacchetta et al. (2010)

Dianthus brevicaulis **Fenzl, Pug. Pl. Nov. Syr.: 10. 1842.** Sec. Bacchetta et al. (2010)

Dianthus brevicaulis **subsp.** ***brevicaulis***

Dianthus brevicaulis **subsp.** ***setaceus*** **Reeve in Notes Roy. Bot. Gard. Edinburgh 28: 21. 1967.** Sec. Marhold (2011)

Dianthus brevipetalus **Vved. in Bot. Mater. Gerb. Bot. Inst. Uzbekistansk. Fil. Akad. Nauk S.S.S.R. 3: 9. 1941.** Sec. Czerepanov (1995)

Dianthus broteri **Boiss. & Reut., Pugill. Pl. Afr. Bor. Hispan.: 22. 1852.** Sec. Bernal et al. (1990)

≡ *Dianthus fimbriatus* Brot., Fl. Lusit. 2: 177. 1805, nom. illeg. syn. sec. Bernal et al. (1990)

= *Dianthus serrulatus* var. *barbatus* Boiss., Elench. Pl. Nov.: 19. 1838 syn. sec. Bernal et al. (1990) ≡ *Dianthus serrulatus* subsp. *barbatus* (Boiss.) Greuter & Burdet in Willdenowia 13: 281. 1983 [“1984”] syn. sec. Bernal et al. (1990)

= *Dianthus valentinus* Willk., Icon. Descr. Pl. Nov. 1: 14. 1852 syn. sec. Bernal et al. (1990) ≡ *Dianthus malacitanus* var. *valentinus* (Willk.) Losa & Rivas Goday in Arch. Inst. Aclim. Cons. Super. Invest. Ci. 13(2): 150. 1974 syn. sec. Bernal et al. (1990) ≡ *Dianthus broteri* subsp. *valentinus* (Willk.) Rivas Mart. et al. in Rivasgodaya 6: 29. 1991 syn. sec. Bernal et al. (1990)

= *Dianthus malacitanus* Haens. ex Boiss., Fl. Orient. 1: 85. 1867 syn. sec. Bernal et al. (1990)

= *Dianthus serrulatus* Boiss., Fl. Orient. 1: 84. 1867 syn. sec. Bernal et al. (1990)

= *Dianthus eusebii* Sennen, Diagn. Nouv.: 264. 1936 syn. sec. Bernal et al. (1990)

= *Dianthus absconditus* Fern.Casas in Fontqueria 3: 35. 1983 syn. sec. WFO 2018

= *Dianthus subbaeticus* Fern.Casas in Fontqueria 3: 37. 1983 syn. sec. WFO 2018 ≡ *Dianthus broteri* subsp. *subbaeticus* (Fern.Casas) Fern.Casas, M.Laínz & Muñoz Garm. in Anales Jard. Bot. Madrid 44: 573. 1987 syn. sec. Bernal et al. (1990) ≡ *Dianthus anticarius* subsp. *subbaeticus* (Fern.Casas) Rivas Mart. et al. in Rivasgodaya 6: 28. 1991 syn. sec. Bernal et al. (1990)

= *Dianthus hinoxianus* Gallego in Lagascalia 14: 71. 1986 syn. sec. Bernal et al. (1990) ≡ *Dianthus broteri* subsp. *hinoxianus* (Gallego) Rivas Mart. in Lagascalia 15(Extra): 116. 1988 syn. sec. Bernal et al. (1990)

***Dianthus brutius* Brullo, Scelsi & Spamp., Portugaliae Act. Biol., Sér. B, Sist. 19: 304. 2000.** Sec. Brullo et al. (2000)

Dianthus brutius* subsp. *brutius

***Dianthus brutius* subsp. *pentadactyli* Brullo, Scelsi & Spamp., Portugaliae Act. Biol., Sér. B, Sist. 19: 306. 2000.** Sec. Brullo et al. (2000)

***Dianthus bukovinensis* (Zapał.) Klokov, Fl. RSS Ucr. 4: 606. 1952.** Sec. Czerepanov (1995)
≡ *Dianthus carthusianorum* var. *bucovinensis* Zapał., Consp. Fl. Gallic. Crit. 3: 113. 1911 syn. sec. WFO 2018 – *Dianthus bucoviensis* (Zapał.) Klokov syn. sec. WFO 2018 [is orthographic variant for *Dianthus bukovinensis* (Zapał.) Klokov] – *Dianthus carthusianorum* var. *bucoviensis* Zapał. syn. sec. Czerepanov (1995) [is orthographic variant for *Dianthus carthusianorum* var. *bucovinensis* Zapał.]

***Dianthus burchellii* Ser., Prodr. 1: 359. 1824.** Sec. African Plant Database (version 3.4.0)

***Dianthus burdurensis* Hamzaoğlu & Koç in Phytotaxa 233: 197. 2015.** Sec. Hamzaoğlu & Koç (2015)

***Dianthus busambrae* Soldano & F.Conti, Annot. Checkl. Italian Vasc. Fl.: 18. 2005.** Sec. Bacchetta et al. (2010)
= *Dianthus paniculatus* Lojac. in Malpighia 20: 188. 1906 syn. sec. Bacchetta et al. (2010)

***Dianthus cachemiricus* Edgew. & Hook.f., Fl. Brit. India 1: 214. 1874.** Sec. Rechinger (1988)

***Dianthus caespitosus* Thunb., Prodr. Pl. Cap. 1: 81. 1794.** Sec. African Plant Database (version 3.4.0)

Dianthus caespitosus* subsp. *caespitosus

***Dianthus caespitosus* subsp. *pectinatus* (E.Mey. ex Sond.) S.S.Hooper in Hookers Icon. Pl. 37: 37. 1959.** Sec. African Plant Database (version 3.4.0)
≡ *Dianthus pectinatus* E.Mey. ex Sond., Fl. Cap. 1: 124. 1860 syn. sec. African Plant Database (version 3.4.0)
= *Dianthus prostratus* Jacq., Pl. Hort. Schoenbr. 3: 11. 1798 syn. sec. African Plant Database (version 3.4.0)
= *Dianthus albens* Eckl. & Zeyh., Enum. Pl. Afric. Austral. 1: 32. 1835 syn. sec. WFO 2018
= *Dianthus crenatus* S.T.Edw. syn. sec. African Plant Database (version 3.4.0)

***Dianthus callizonus* Schott & Kotschy in Bot. Zeitung (Berlin) 9: 192. 1851.** Sec. Marhold (2011)

***Dianthus calocephalus* Boiss., Diagn. Pl. Orient. ser. 1, 6: 23. 1846.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus campestris* M.Bieb., Fl. Taur.-Caucas. 1: 326. 1808.** Sec. Marhold (2011)
= *Dianthus hypanicus* Besser ex Rchb., Fl. Germ. Excurs.: 809. 1832 syn. sec. WFO 2018
= *Dianthus pseudoversicolor* Klokov, Fl. RSS Ucr. 4: 660. 1952 syn. sec. WFO 2018
= *Dianthus campestris* subsp. *arenarius* Širj. syn. sec. WFO 2018
= *Dianthus campestris* subsp. *serbanii* Prodán syn. sec. Marhold (2011) ≡ *Dianthus serbanii* (Prodán) Prodán, Fl. Reipubl. Popul. Roman. 2: 670. 1953 syn. sec. Marhold (2011)

Dianthus campestris* subsp. *campestris

***Dianthus campestris* subsp. *laevigatus* (Gruner) Klokov, Fl. RSS Ucr. 4: 625. 1952.** Sec. Marhold (2011)
≡ *Dianthus campestris* var. *laevigatus* Gruner in Bull. Soc. Imp. Naturalistes Moscou 41(2): 124. 1868 syn. sec. Marhold (2011) ≡ *Dianthus laevigatus* (Gruner) Klokov in Novosti Sist. Vyssh. Nizsh. Rast. 1980: 99. 1980 syn. sec. Marhold (2011)

***Dianthus campestris* subsp. *steppaceus* Širj. in Širj. & Lavrenko, Consp. Crit. Fl. Prov. Charkov.: 1. 1926.** Sec. Marhold (2011)

***Dianthus candicus* (P.W.Ball & Heywood) Madhani & Heubl in Taxon 67(1): 103. 2018.** Sec. Madhani et al. (2018)
≡ *Petrorhagia candica* P.W.Ball & Heywood in Bull. Brit. Mus. (Nat. Hist.), Bot. 3: 141. 1964 syn. sec. Kew WCVP (2019); ≡ *Fiedleria candica* (P.W.Ball & Heywood) Ovcz., Fl. Tadzhikskoi S.S.R. 3: 608. 1968 syn. sec. Kew WCVP (2019).

***Dianthus canescens* K.Koch in Linnaea 15: 710. 1841.** Sec. Kuzmina & Nersesyan (2012)
≡ *Dianthus fimbriatus* var. *canescens* (K.Koch) Boiss., Fl. Orient. 1: 496. 1867 syn. sec. Kuzmina & Nersesyan (2012)

***Dianthus capitatus* Balb. ex DC., Cat. Pl. Horti Monsp.: 103. 1813.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus capitatus* J.St.-Hil., Pl. France 3: 70. 1809.** Sec. Czerepanov (1995)
= *Dianthus cephalotes* Ser., Prodr. 1: 356. 1824 syn. sec. Czerepanov (1995)
= *Dianthus glaucophyllus* Boiss., Fl. Orient. 1: 514. 1867 syn. sec. Czerepanov (1995)
= *Dianthus capillatus* Meinsh., Beitr. Pfl. Geogr. Sued-Ural-Geb.: 6 syn. sec. Czerepanov (1995)

Dianthus capitellatus **Klokov, Fl. RSS Ucr. 4: 659. 1952.** Sec. Kuzmina & Nersesyan (2012)
≡ *Dianthus borbasii* subsp. *capitellatus* (Klokov) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 192. 1963 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus pseudomembranaceus* Schischk. ex Grossh., Fl. Cauc. 2(3): 282. 1945 syn. sec. Kuzmina & Nersesyan (2012)

Dianthus carbonatus **Klokov in Sc. Mag. Biol. 1927: 15. 1927.** Sec. Czerepanov (1995)

Dianthus carmelitarum **Reut. ex Boiss., Fl. Orient. 1: 512. 1867.** Sec. Kuzmina & Nersesyan (2012)
= *Dianthus artwinensis* Schischk. ex Grossh., Fl. Cauc. 2(3): 284. 1945 syn. sec. Kuzmina & Nersesyan (2012)

Dianthus carthusianorum **L., Sp. Pl.: 409. 1753.** Sec. Marhold (2011)
≡ *Tunica carthusianorum* (L.) Scop., Fl. Carniol., ed. 2, 1: 299. 1771 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. ≡ *Caryophyllus carthusianorum* (L.) Moench, Methodus: 59. 1794 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. ≡ *Silene carthusianorum* (L.) E.H.L.Krause, Deutschl. Fl. Abbild., ed. 2, 5: 110. 1901 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.;
= *Dianthus atrorubens* All., Fl. Pedem. 2: 75. 1785 syn. sec. Marhold (2011) ≡ *Caryophyllus atrorubens* (All.) Moench, Suppl. Meth.: 23. 1802 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. ≡ *Dianthus carthusianorum* var. *atrorubens* (All.) Ser., Prodr. 1: 357. 1824 syn. sec. this publication ≡ *Dianthus carthusianorum* subsp. *atrorubens* (All.) Hegi in Allg. Bot. Z. Syst. 17: 15. 1911 syn. sec. Marhold (2011)
= *Dianthus vaginatus* Chaix, Hist. Pl. Dauphiné 1: 330. 1786 syn. sec. WFO 2018 ≡ *Cylichnanthus vaginatus* (Chaix) Dulac, Fl. Hautes-Pyrénées: 261. 1867 syn. sec. Kew WCVP (2019)
= *Dianthus montanus* F.W.Schmidt in Neuere Abh. Königl. Böhm. Ges. Wiss. 1: 30. 1791 syn. sec. WFO 2018
= *Dianthus clavatus* Spreng., Neue Entdeck. Pflanzenk. 2: 169. 1821 syn. sec. WFO 2018
= *Dianthus carthusianorum* var. *anisopodus* Ser., Prodr. 1: 357. 1824 syn. sec. Kew WCVP (2019)
= *Dianthus carthusianorum* var. *nanus* Ser., Prodr. 1: 357. 1824 syn. sec. Kew WCVP (2019)
= *Dianthus nanus* Sweet, Hort. Brit.: 41. 1826 syn. sec. WFO 2018
= *Dianthus atrorubens* var. *intermedius* Gaudin, Fl. Helv. 3: 146. 1828 syn. sec. Kew WCVP (2019)
= *Dianthus carthusianorum* var. *pygmaeus* Gaudin, Fl. Helv. 3: 145. 1828 syn. sec. Kew WCVP (2019)

= *Dianthus allionii* Colla, Herb. Pedem. 1: 297. 1833 syn. sec. WFO 2018
= *Dianthus sanguineus* Vis., Index Seminum (PAD) 1845: 1. 1845 syn. sec. Marhold (2011) ≡ *Dianthus atrorubens* var. *sanguineus* (Vis.) Arcang., Comp. Fl. Ital.: 84. 1882 syn. sec. this publication ≡ *Dianthus carthusianorum* var. *sanguineus* (Vis.) Tanfani, Fl. Ital. 9: 254. 1892 syn. sec. this publication ≡ *Dianthus carthusianorum* subsp. *sanguineus* (Vis.) Hegi in Ill. Fl. Mitt. Eur. 3: 323. 1910 syn. sec. Marhold (2011)
= *Dianthus ferrugineus* Pourr. ex Gren. & Godr., Fl. France 1: 232. 1847 syn. sec. WFO 2018
= *Dianthus gramineus* Schur in Verh. Mitth. Siebenbürg. Vereins Naturwiss. Hermannstadt 4: 11. 1853 syn. sec. WFO 2018
= *Dianthus congestus* Boreau, Fl. Centre France ed. 3, 2: 90. 1857 syn. sec. WFO 2018
= *Dianthus carthusianorum* var. *campestris* Heuff. in Verh. Zool.-Bot. Ges. Wien 8: 68. 1858 syn. sec. Kew WCVP (2019)
= *Dianthus carthusianorum* var. *ternatus* Heuff. in Verh. Zool.-Bot. Ges. Wien 8: 68. 1858 syn. sec. Kew WCVP (2019)
= *Dianthus graminifolius* Schur in Verh. Mitth. Siebenbürg. Vereins Naturwiss. Hermannstadt 10: 144. 1859 syn. sec. WFO 2018
= *Dianthus tenuifolius* Schur in Verh. Mitth. Siebenbürg. Vereins Naturwiss. Hermannstadt 10: 143. 1859 syn. sec. WFO 2018 ≡ *Dianthus carthusianorum* subsp. *tenuifolius* (Schur) Hegi syn. sec. Marhold (2011)
= *Dianthus carthusianorum* var. *saxigenus* Schur, Enum. Pl. Transsilv.: 93. 1866 syn. sec. WFO 2018 ≡ *Dianthus carthusianorum* subsp. *saxigenus* (Schur) Dostál in Folia Mus. Rerum Nat. Bohemiae Occid., Bot. 21: 5. 1984 syn. sec. WFO 2018
= *Dianthus chloaephyllus* Schur, Enum. Pl. Transsilv.: 95. 1866 syn. sec. WFO 2018
= *Dianthus rupicola* Schur, Enum. Pl. Transsilv.: 93. 1866 syn. sec. Schur (1866)
= *Dianthus rupicolus* Schur, Enum. Pl. Transsilv.: 93. 1866 syn. sec. WFO 2018
= *Dianthus subneglectus* Schur, Enum. Pl. Transsilv.: 95. 1866 syn. sec. WFO 2018
= *Dianthus carthusianorum* var. *puberulus* Simonk., Mat. Term. Közlem. 15: 531. 1878 syn. sec. Marhold (2011) ≡ *Dianthus carthusianorum* subsp. *puberulus* (Simonk.) Soó in Feddes Repert. 83: 161. 1972 syn. sec. Marhold (2011) ≡ *Dianthus puberulus* (Simonk.) A.Kern. syn. sec. Marhold (2011)
= *Dianthus atropurpureus* Gromov ex Trautv. in Trudy Imp. S.-Peterburgsk. Bot. Sada 8: 130. 1883 syn. sec. WFO 2018
= *Dianthus carpathicus* Woł., Spraw. Komis. Fizjogr. 22(2): 214. 1888 syn. sec. WFO 2018
= *Dianthus semperflorens* Voss in Gartenflora 44: 514. 1895 syn. sec. WFO 2018
= *Dianthus carthusianorum* var. *brachyanthus* Dörfl. & Hayek in Oesterr. Bot. Z. 70: 12. 1921 syn. sec. Kew WCVP (2019)
= *Dianthus carthusianorum* var. *longisquamis* Kulcz., Fl. Polska 2: 159. 1921 syn. sec. WFO 2018
= *Dianthus ceretanicus* Sennen in Bol. Soc. Ibér. Ci. Nat. 25: 147. 1926 syn. sec. WFO 2018
= *Dianthus carthusianorum* var. *tenorei* Lacaita in Nuovo Giorn. Bot. Ital. n.s., 34: 188. 1927 syn. sec. WFO 2018 ≡ *Dianthus carthusianorum* subsp. *tenorei* (Lacaita) Pignatti in Giorn. Bot. Ital. 111: 46. 1977 syn. sec. Marhold (2011)

= *Dianthus montivagus* Domin in Acta Bot. Bohem. 8: 53. 1929 syn. sec. WFO 2018
= *Dianthus velebiticus* Borbás ex Degen, Fl. Veleb. 2: 97. 1937 syn. sec. WFO 2018
= *Dianthus carthusianorum* var. *capillifrons* Borbás syn. sec. Marhold (2011) ≡ *Dianthus capillifrons* (Borbás) H.Neumayer in Oesterr. Bot. Z. 91: 236. 1942 syn. sec. WFO 2018 ≡ *Dianthus carthusianorum* subsp. *capillifrons* (Borbás) Soó in Acta Bot. Acad. Sci. Hung. 23: 391. 1977 [“1978”] syn. sec. Marhold (2011)
= *Dianthus carthusianorum* var. *parviflorus* Čelak. syn. sec. WFO 2018 ≡ *Dianthus carthusianorum* subsp. *parviflorus* (Čelak.) Dostál in Folia Mus. Rerum Nat. Bohemiae Occid., Bot. 21: 5. 1984 syn. sec. WFO 2018
= *Dianthus sanguineus* var. *atrisquamatus* Novák syn. sec. WFO 2018 ≡ *Dianthus carthusianorum* f. *atrisquamatus* (Novák) Gajić, Fl. SR Srbije 9: 64. 1977 syn. sec. WFO 2018
– *Dianthus fasciculatus* Gilib., Fl. Lit. Inch. 2: 161. 1782, nom. inval. syn. sec. WFO 2018

Dianthus carthusianorum* subsp. *carthusianorum

***Dianthus carthusianorum* subsp. *latifolius* (Griseb. & Schenk) Hegi in Allg. Bot. Z. Syst. 17: 13. 1911.** Sec. Marhold (2011)
≡ *Dianthus carthusianorum* var. *latifolius* Griseb. & Schenk in Arch. Naturgesch. 18: 300. 1852 syn. sec. WFO 2018
= *Dianthus montivagus* var. *carsticus* Novák syn. sec. Kew WCVP (2019) ≡ *Dianthus carthusianorum* subsp. *carsticus* (Novák) Dostál in Folia Mus. Rerum Nat. Bohemiae Occid., Bot. 21: 5. 1984 syn. sec. Kew WCVP (2019)

***Dianthus carthusianorum* subsp. *polonicus* (Zapał.) Kovanda in Preslia 56: 297. 1984.** Sec. WFO 2018
≡ *Dianthus polonicus* Zapał., Consp. Fl. Gallic. Crit. 3: 122. 1911 syn. sec. WFO 2018 ≡ *Dianthus carthusianorum* var. *polonicus* (Zapał.) Kulcz., Fl. Polska 2: 159. 1921 syn. sec. WFO 2018

***Dianthus carthusianorum* subsp. *sudeticus* Kovanda in Preslia 52: 122. 1980.** Sec. Marhold (2011)

***Dianthus caryophyllus* L., Sp. Pl.: 410. 1753.** Sec. Marhold (2011)
≡ *Silene caryophylla* (L.) E.H.L.Krause, Deutschl. Fl. Abbild., ed. 2, 5: 111. 1901 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.; ≡ *Dianthus caryophyllus* var. *coronarius* L., Sp. Pl. 1: 410. 1753 syn. sec. Domina et al. (2021) ≡ *Dianthus caryophyllus* subsp. *coronarius* (L.) Maire, Fl. Afrique N. 10: 318. 1963 syn. sec. this publication ≡ *Tunica caryophyllus* (L.) Scop., Fl. Carniol., ed. 2, 1: 301. 1771 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.; – *Dianthus coronarius* (L.) Burm.f., Fl. Ind. Prodr. Fl. Cap.: 13. 1768, nom. illeg. syn. sec. Domina et al. (2021) – *Dianthus coronarius* Lam., Fl. Franç. 2: 536. 1779, nom. illeg. syn. sec. Domina et al. (2021)
= *Caryophyllus tunica* Garsault, Fig. Pl. Méd.: t. 203. 1764 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.

= *Dianthus moschatus* J.F.Gmel., Syst. Nat.: 711. 1791 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus caryophyllus* var. *minor* Gray, Nat. Arr. Brit. Pl. 2: 644. 1822 ["1821"] syn. sec. Kew WCVP (2019)
= *Dianthus caryophyllus* var. *carduinus* Ser., Prodr. 1: 359. 1824 syn. sec. Kew WCVP (2019)
= *Dianthus corsicus* Link ex Spreng., Syst. Veg., ed. 16, 2: 376. 1825 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus arbuscula* Lindl. in Bot. Reg. 13: t. 1086. 1827 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus arrectus* Dumort., Fl. Belg.: 196. 1827 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus caryophyllus* var. *wakefieldii* C.Morren, Hort. Belge 2: 7. 1834 syn. sec. Kew WCVP (2019)
= *Dianthus multinervis* Vis., Fl. Dalmat. 3: 164. 1850 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus longicaulis* Costa, Introd. Fl. Cataluña: 36. 1864 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus acinifolius* Schur, Enum. Pl. Transsilv.: 97. 1866 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus binatus* Schur, Enum. Pl. Transsilv.: 97. 1866 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus kayserianus* Schur, Enum. Pl. Transsilv.: 97. 1866 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus miniatus* A.Huet ex Nyman, Consp. Fl. Eur. 1: 105. 1878 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus caryophyllus* f. *intermedius* Pamp. in Boll. Mus. Republ. San Marino 1: 142. 1917 syn. sec. Kew WCVP (2019)

***Dianthus caucaseus* Sims in Bot. Mag. 21: t. 795. 1804.** Sec. Kuzmina & Nersesyan (2012)
= *Dianthus discolor* Sims in Bot. Mag. 29: t. 1162. 1808 syn. sec. Kuzmina & Nersesyan (2012)

***Dianthus charidemi* Pau in Bull. Acad. Int. Geogr. Bot. 16(206): 74. 1906.** Sec. Bernal et al. (1990)
≡ *Dianthus cintranus* subsp. *charidemi* (Pau) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 190. 1963 syn. sec. Bernal et al. (1990)

***Dianthus chimanimaniensis* S.S.Hooper in Kew Bull. 13: 318. 1958.** Sec. African Plant Database (version 3.4.0)

***Dianthus chinensis* L., Sp. Pl.: 411. 1753.** Sec. Dequan & Turland (2001)

= *Dianthus sequieri* Chaix, Vill. Fl. Dauph. 1: 330. 1786 syn. sec. Dequan & Turland (2001)
= *Dianthus pulcher* Salisb., Prodr. Stirp. Chap. Allerton: 303. 1796 syn. sec. Dequan & Turland (2001)
= *Dianthus scaber* Schleich. ex Suter, Helvet. Fl. 1: 259. 1802 syn. sec. Dequan & Turland (2001) ≡ *Dianthus serratus* var. *scaber* (Schleich. ex Suter) DC., Fl. Franç., ed. 3, 5: 601. 1815 syn. sec. this publication ≡ *Dianthus collinus* var. *scaber* (Schleich. ex Suter) Gaudin, Fl. Helv. 3: 147. 1828 syn. sec. this publication
= *Dianthus tataricus* Fisch., Cat. Jard. Gorenki ed. 2: 59. 1812 syn. sec. Dequan & Turland (2001)
= *Dianthus umbellatus* DC., Cat. Pl. Horti Monsp.: 104. 1813 syn. sec. Dequan & Turland (2001)
= *Dianthus ibericus* Willd., Enum. Pl., Suppl.: 24. 1814 syn. sec. Dequan & Turland (2001)
= *Dianthus patens* Willd., Enum. Pl., Suppl.: 24. 1814 syn. sec. Dequan & Turland (2001)
= *Dianthus fischeri* Spreng., Pl. Min. Cogn. Pug. 2: 62. 1815 syn. sec. Dequan & Turland (2001)
= *Dianthus ruthenicus* Roem. ex Poir., Encycl. Suppl. 4: 131. 1816 syn. sec. Dequan & Turland (2001)
= *Dianthus ochroleucus* Link, Enum. Hort. Berol. Alt. 1: 420. 1821 syn. sec. Dequan & Turland (2001)
= *Dianthus versicolor* Fisch. ex Link, Enum. Hort. Berol. Alt. 1: 420. 1821 syn. sec. Dequan & Turland (2001) ≡ *Dianthus chinensis* var. *versicolor* (Fisch. ex Link) Y.C.Ma, Fl. Intramongolica 2: 191. 1978 ["1979"] syn. sec. Dequan & Turland (2001) ≡ *Dianthus chinensis* subsp. *versicolor* (Fisch. ex Link) Vorosch., Florist. Issl. Razn. Rayonakh SSSR: 167. 1985 syn. sec. Dequan & Turland (2001)
= *Dianthus willdenowii* Link, Enum. Hort. Berol. Alt. 1: 420. 1821 syn. sec. Dequan & Turland (2001)
= *Dianthus schraderi* Rchb. in Iconogr. Bot. Exot. 1: 24. 1824 syn. sec. Dequan & Turland (2001)
= *Dianthus dentosus* Fisch. ex Rchb. in Iconogr. Bot. Pl. Crit. 6: 32. 1828 syn. sec. Dequan & Turland (2001) ≡ *Dianthus chinensis* var. *dentosus* (Fisch. ex Rchb.) Debeaux in Act. Simpo. Internac. Bot. Pius Font Quer 31: 124. 1876 syn. sec. Dequan & Turland (2001) ≡ *Dianthus seguieri* var. *dentosus* (Fisch. ex Rchb.) Franch., Pl. David. 1: 46. 1884 syn. sec. Dequan & Turland (2001) ≡ *Dianthus sequieri* var. *dentosus* (Fisch. ex Rchb.) Franch., Pl. David. 1: 46. 1884 syn. sec. Dequan & Turland (2001)
= *Dianthus sinensis* Link, Handbuch 2: 237. 1831 syn. sec. Dequan & Turland (2001)
= *Dianthus chinensis* var. *sylvaticus* W.D.J.Koch, Syn. Fl. Germ. Helv.: 96. 1835 syn. sec. Dequan & Turland (2001)
= *Dianthus altaicus* Willd. ex Ledeb., Fl. Ross. 1: 278. 1842 syn. sec. Dequan & Turland (2001)

= *Dianthus jeniseensis* Less. ex Ledeb., Fl. Ross. 1: 278. 1842 syn. sec. Dequan & Turland (2001)
= *Dianthus chinensis* var. *macrosepalus* Franch. ex L.H.Bailey, Cycl. Amer. Hort.: 100. 1900 syn. sec. Dequan & Turland (2001)
= *Dianthus laciniatus* Makino in Bot. Mag. (Tokyo) 17: 60. 1903 syn. sec. Dequan & Turland (2001)
= *Dianthus morii* Nakai in Bot. Mag. (Tokyo) 28: 302. 1914 syn. sec. Dequan & Turland (2001) ≡ *Dianthus chinensis* var. *morii* (Nakai) Y.C.Chu, Fl. Plant. Herb. Chinae bor.-or. 3: 49. 1975 syn. sec. Dequan & Turland (2001)
= *Dianthus pineticola* Kleopow in Izv. Kievsk. Bot. Sada 12–13: 161. 1931 syn. sec. Dequan & Turland (2001)
= *Dianthus versicolor* var. *alpinus* Krylov, Fl. Zapadnoi Sibiri 5: 1104. 1931 syn. sec. Kew WCVP (2019)
= *Dianthus chinensis* var. *longisquama* Nakai & Kitag. in Rep. Exped. Manchoukou Sect. IV, 1: 23. 1934 syn. sec. Dequan & Turland (2001)
= *Dianthus chinensis* var. *ignescens* Nakai in Rep. Exped. Manchoukou Sect. IV, 4(2): 15. 1935 syn. sec. Dequan & Turland (2001) ≡ *Dianthus chinensis* f. *ignescens* (Nakai) Kitag. in J. Jap. Bot. 34: 5. 1959 syn. sec. Dequan & Turland (2001)
= *Dianthus subulifolius* Kitag. in Rep. Exped. Manchoukou Sect. IV, 2: 16. 1935 syn. sec. Dequan & Turland (2001) ≡ *Dianthus versicolor* var. *subulifolius* (Kitag.) Y.C.Chu, Fl. Plant. Herb. Chinae bor.-or. 3: 50. 1975 syn. sec. Dequan & Turland (2001) ≡ *Dianthus chinensis* var. *subulifolius* (Kitag.) Y.C.Ma, Fl. Intramongolica 2: 191. 1978 ["1979"] syn. sec. Dequan & Turland (2001)
= *Dianthus subulifolius* f. *leucopetalus* Kitag. in Rep. Exped. Manchoukou Sect. IV, 2: 17. 1935 syn. sec. Dequan & Turland (2001) ≡ *Dianthus versicolor* f. *leucopetalus* (Kitag.) Y.C.Chu, Fl. Plant. Herb. Chinae bor.-or. 3: 50. 1975 syn. sec. Dequan & Turland (2001)
= *Dianthus chinensis* var. *liaotungensis* Y.C.Chu, Fl. Plant. Herb. Chinae bor.-or. 3: 227. 1975 syn. sec. Dequan & Turland (2001)
= *Dianthus chinensis* subsp. *paracampestris* Vorosch. in Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. n.s., 83(5): 116. 1978 syn. sec. Dequan & Turland (2001)
= *Dianthus versicolor* var. *ninelli* Peschkova, Fl. Tsentralnoi Sibiri 1: 334. 1979 syn. sec. Dequan & Turland (2001) ≡ *Dianthus versicolor* subsp. *ninelli* (Peschkova) Baikov & N.V.Vlassova, Rast. Mir Aziatsk. Rossii 3(23): 21. 2016 syn. sec. Kew WCVP (2019)
= *Dianthus chinensis* var. *trinervis* D.Q.Lu in Bull. Bot. Res., Harbin 15: 185. 1995 syn. sec. Dequan & Turland (2001)
= *Dianthus chinensis* var. *jingpoensis* G.Y.Zhang & X.Y.Yuan in Bull. Bot. Res., Harbin 18: 10. 1998 syn. sec. Dequan & Turland (2001)
= *Dianthus chinensis* var. *shandongensis* J.X.Li & F.Q.Zhou in Bull. Bot. Res., Harbin 21: 511. 2001 syn. sec. Dequan & Turland (2001)
= *Dianthus chinensis* f. *albiflora* Y.N.Lee in Bull. Korea Pl. Res. 4: 28. 2004 syn. sec. Dequan & Turland (2001)

= *Dianthus chinensis* var. *serpens* Y.N.Lee in Bull. Korea Pl. Res. 4: 29. 2004 syn. sec. Dequan & Turland (2001)

***Dianthus chouardii* Dobignard in J. Bot. Soc. Bot. France 48: 15. 2009.** Sec. African Plant Database (version 3.4.0)

***Dianthus cibrarius* Clementi in Mem. Reale Accad. Sci. Torino II 16: 20. 1855.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus ciliatus* Guss., Ind. Sem. Horto Boccad. 1825: 5. 1825.** Sec. Marhold (2011)
= *Dianthus litoralis* Host, Fl. Austriaca 1: 522. 1827 syn. sec. WFO 2018

Dianthus ciliatus* subsp. *ciliatus

***Dianthus ciliatus* subsp. *dalmaticus* (Čelak.) Hayek in Repert. Spec. Nov. Regni Veg. Beih. 30(1): 246. 1924.** Sec. Marhold (2011)
≡ *Dianthus dalmaticus* Čelak. in Oesterr. Bot. Z. 35: 189. 1885 syn. sec. Marhold (2011)
= *Dianthus racemosus* Vis. in Flora 12(1 Erg.): 12. 1829 syn. sec. Marhold (2011) ≡ *Dianthus ciliatus* subsp. *racemosus* (Vis.) Hayek in Repert. Spec. Nov. Regni Veg. Beih. 30(1): 246. 1924 syn. sec. Marhold (2011)

***Dianthus ciliatus* subsp. *medunensis* (Beck & Szyszyl.) Trinajstić in Suppl. Fl. Anal. Jugosl. 6: 8. 1979.** Sec. Marhold (2011)
≡ *Dianthus medunensis* Beck & Szyszył., Pl. Cernagor. Lect.: 65. 1888 syn. sec. WFO 2018 – *Dianthus ciliatus* subsp. *medunensis* (Beck & Szyszyl.) Trinajstić in Suppl. Fl. Anal. Jugosl. 5: 751. 1979, nom. inval. syn. sec. this publication

***Dianthus* ×*cincinnatus* Lem. in Ill. Hort. 11: t. 388. 1864.** Sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.
= *Dianthus* ×*isensis* Hirahata & Kitam. in Acta Phytotax. Geobot. 20: 205. 1962 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. ≡ *Dianthus* ×*cincinnatus* f. *isensis* (Hirahata & Kitam.) M.Hiroe, Pl. Bashos & Busons Hokku Lit. 8: 489. 1971 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.
= *Dianthus* ×*cincinnatus* f. *longipetalus* M.Hiroe, Pl. Bashos & Busons Hokku Lit. 8: 489. 1971 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.
= *Dianthus* ×*cincinnatus* f. *rosalbus* M.Hiroe, Pl. Bashos & Busons Hokku Lit. 8: 489. 1971 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.

***Dianthus cinnamomeus* Sm., Fl. Graec. Prodr. 1(2): 287. 1809.** Sec. Dimopoulos et al. (2013)

Dianthus cinnamomeus* subsp. *cinnamomeus

***Dianthus cinnamomeus* subsp. *naxensis* Runemark ex Strid in Strid & Tan, Fl. Hellenica 1: 352. 1997.** Sec. Dimopoulos et al. (2013)

***Dianthus cintranus* Boiss. & Reut., Pugill. Pl. Afr. Bor. Hispan.: 20. 1852.** Sec. Bernal et al. (1990)

***Dianthus cintranus* subsp. *atrosanguineus* (Emb. & Maire) Greuter & Burdet in Willdenowia 12: 186. 1982.** Sec. Marhold (2011)
≡ *Dianthus gaditanus* subsp. *atrosanguineus* Emb. & Maire, Mém. Soc. Sci. Nat. Maroc 21–22: 26. 1930 syn. sec. Marhold (2011) ≡ *Dianthus anticarius* subsp. *atrosanguineus* (Emb. & Maire) Valdés & Mateos in Lagascalia 29: 157. 2009 syn. sec. WFO 2018

***Dianthus cintranus* subsp. *barbatus* R.Fern. & Franco in Franco, Nova Fl. Portugal 1: 159. 1971.** Sec. Bernal et al. (1990)

***Dianthus cintranus* subsp. *byzacenus* (Burollet) Greuter & Burdet in Willdenowia 12: 186. 1982.** Sec. Marhold (2011)
≡ *Dianthus byzacenus* Burollet, Sahel Sousse: 35. 1927 syn. sec. Marhold (2011) ≡ *Dianthus gaditanus* subsp. *byzacenus* (Burollet) Maire, Fl. Afrique N. 10: 307. 1963 syn. sec. Kew WCVP (2019)

Dianthus cintranus* subsp. *cintranus

***Dianthus cintranus* subsp. *jahandiezii* (Maire) Greuter & Burdet in Willdenowia 12: 186. 1982.** Sec. Marhold (2011)
≡ *Dianthus gaditanus* subsp. *jahandiezii* Maire, Mém. Soc. Sci. Nat. Maroc 15: 17. 1927 syn. sec. WFO 2018 ≡ *Dianthus anticarius* subsp. *jahandiezii* (Maire) Valdés & Mateos in Lagascalia 29: 157. 2009 syn. sec. WFO 2018

***Dianthus cintranus* subsp. *maroccanus* (F.N.Williams) Greuter & Burdet in Willdenowia 12: 186. 1982.** Sec. Marhold (2011)
≡ *Dianthus gaditanus* var. *maroccanus* F.N.Williams in J. Linn. Soc., Bot. 29: 423. 1893 syn. sec. Marhold (2011) ≡ *Dianthus gaditanus* subsp. *maroccanus* (F.N.Williams) Maire, Mém. Soc. Sci. Nat. Maroc 15: 17. 1927 syn. sec. Kew WCVP (2019) ≡ *Dianthus anticarius* subsp. *maroccanus* (F.N.Williams) Valdés & Mateos in Lagascalia 29: 157. 2009 syn. sec. WFO 2018
= *Dianthus gaditanus* var. *rifeus* Pau & Sennen, Cat. Fl. Rif Orient.: 19. 1933 syn. sec. Kew WCVP (2019)

***Dianthus cintranus* subsp. *mauritanicus* (Pomel) Greuter & Burdet in Willdenowia 12: 186. 1982.** Sec. Marhold (2011)

≡ *Dianthus mauritanicus* Pomel, Nouv. Mat. Fl. Atl. 1: 333. 1874 syn. sec. Marhold (2011) ≡ *Dianthus serrulatus* subsp. *mauritanicus* (Pomel) Batt., Fl. Algérie, Dicot.: 145. 1888 syn. sec. Kew WCVP (2019) ≡ *Dianthus gaditanus* subsp. *mauritanicus* (Pomel) Maire, Mém. Soc. Sci. Nat. Maroc 21–22: 26. 1930 syn. sec. Kew WCVP (2019) ≡ *Dianthus anticarius* subsp. *mauritanicus* (Pomel) Valdés & Mateos in Lagascalia 29: 157. 2009 syn. sec. WFO 2018

***Dianthus cintranus* subsp. *mentagensis* (Maire) Greuter & Burdet in Willdenowia 12: 186. 1982.** Sec. Marhold (2011)

≡ *Dianthus gaditanus* subsp. *mentagensis* Maire in Bull. Soc. His. Nat. Afrique N. 23: 168. 1932 syn. sec. Marhold (2011) ≡ *Dianthus anticarius* subsp. *mentagensis* (Maire) Valdés & Mateos in Lagascalia 29: 157. 2009 syn. sec. WFO 2018

***Dianthus cintranus* subsp. *occidentalis* (Quézel) Mathez in Willdenowia 13: 280. 1983 ["1984"].** Sec. Marhold (2011)

≡ *Dianthus gaditanus* subsp. *occidentalis* Quézel in Bull. Soc. His. Nat. Afrique N. 44: 197. 1953 syn. sec. Marhold (2011) ≡ *Dianthus anticarius* subsp. *occidentalis* (Quézel) Valdés & Mateos in Lagascalia 29: 157. 2009 syn. sec. WFO 2018

***Dianthus collinus* Waldst. & Kit. in Descr. Icon. Pl. Hung. 1: 51. 1800.** Sec. Czerepanov (1995)

≡ *Dianthus carthusianorum* subsp. *collinus* (Waldst. & Kit.) Pers., Syn. Pl. 1: 493. 1805 syn. sec. Kew WCVP (2019) ≡ *Dianthus asper* var. *collinus* (Waldst. & Kit.) Ser., Prodr. 1: 357. 1824 syn. sec. Kew WCVP (2019) ≡ *Dianthus seguieri* var. *collinus* (Waldst. & Kit.) W.D.J.Koch, Syn. Fl. Germ. Helv. 1: 96. 1835 syn. sec. Kew WCVP (2019) ≡ *Dianthus seguieri* subsp. *collinus* (Waldst. & Kit.) Arcang., Comp. Fl. Ital.: 84. 1882 syn. sec. Kew WCVP (2019)

= *Dianthus collinus* var. *minor* Gaudin, Fl. Helv. 3: 147. 1828 syn. sec. Kew WCVP (2019)

= *Dianthus seguieri* subsp. *scaber* Čelak., Prodr. Fl. Böhmen: 507. 1875 syn. sec. Czerepanov (1995)

***Dianthus commutatus* (Zapał.) Klokov, Fl. RSS Ucr. 4: 607. 1952.** Sec. Czerepanov (1995)

≡ *Dianthus carthusianorum* var. *commutatus* Zapał., Fl. Galic. Crit.: 119. 1911 syn. sec. Czerepanov (1995)

***Dianthus corymbosus* Sm., Fl. Graec. Prodr. 1(2): 285. 1809.** Sec. Dimopoulos et al. (2013)

= *Dianthus corymbosus* Poir., Encycl. Suppl. 4: 124. 1816 syn. sec. WFO 2018

= *Dianthus poiretianus* Ser., Prodr. 1: 360. 1824 syn. sec. WFO 2018

= *Dianthus chalcidicus* Halácsy in Verh. K. K. Zool.-Bot. Ges. Wien 48: 707. 1898 syn. sec. WFO 2018

***Dianthus costae* Willk., Prodr. Fl. Hispan. 3: 683. 1878.** Sec. Bernal et al. (1990)
≡ *Dianthus pyrenaicus* subsp. *costae* (Willk.) O.Bolòs & Vigo in Butl. Inst. Catalana Hist. Nat., Secc. Bot. 38(1): 187. 1974 syn. sec. Bernal et al. (1990) ≡ *Dianthus algetanus* subsp. *costae* (Willk.) Romo, Fl. Veg. Montsec: 98. 1989, nom. illeg. syn. sec. Kew WCVP (2019)
= *Dianthus ciliatus* Costa, Introd. Fl. Cataluña: 36. 1864 syn. sec. Bernal et al. (1990)
= *Dianthus marianii* Sennen, Diagn. Nouv.: 32. 1936 syn. sec. WFO 2018

***Dianthus crassipes* R.Roem. in Linnaea 25: 11. 1852.** Sec. Bernal et al. (1990)
= *Dianthus serenaeus* Coincy in J. Bot. (Morot) 12: 53. 1898 syn. sec. Bernal et al. (1990) ≡ *Dianthus crassipes* subsp. *serenaeus* (Coincy) Rivas Mart. et al. in Rivasgodaya 6: 29. 1991 syn. sec. this publication

***Dianthus crenatus* Thunb., Prodr. Pl. Cap. 1: 81. 1794.** Sec. African Plant Database (version 3.4.0)
= *Dianthus inaequalis* E.Mey., Zwei Pflanzengeogr. Dokum.: 178. 1843 syn. sec. WFO 2018

***Dianthus cretaceus* Adams in Beitr. Naturk. 1: 56. 1805.** Sec. Kuzmina & Nersesyan (2012)
= *Dianthus petraeus* M.Bieb., Fl. Taur.-Caucas. 1: 328. 1808 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus bracteatus* Willd. ex Ser., Prodr. 1: 360. 1824 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus liboschitzianus* Ser., Prodr. 1: 360. 1824 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus siemienkiewiczii* Bordz. in Repert. Spec. Nov. Regni Veg. 30: 364. 1932 syn. sec. this publication

Dianthus cretaceus* subsp. *cretaceus

***Dianthus cretaceus* subsp. *dmanissianus* (M.Kuzmina) Nersesian in Nov. Syst. Vyssh. Rast. 42: 113. 2011.** Sec. Kuzmina & Nersesyan (2012)
≡ *Dianthus dmanissianus* M.Kuzmina in Bot. Zhurn. (Moscow & Leningrad) 81(8): 80. 1996 syn. sec. Kuzmina & Nersesyan (2012)

***Dianthus cretaceus* subsp. *multicaulis* (Boiss. & A.Huet) Nersesian in Novosti Sist. Vyssh. Rast. 42: 112. 2011.** Sec. Kuzmina & Nersesyan (2012)
≡ *Dianthus multicaulis* Boiss. & A.Huet in Boissier, Diagn. Pl. Orient., ser. 2, 5: 53. 1856 syn. sec. Kuzmina & Nersesyan (2012) ≡ *Dianthus liboschitzianus* var. *multicaulis* (Boiss. & A.Huet) Boiss., Fl. Orient. 1: 487. 1867 syn. sec. Kuzmina &

Nersesyan (2012) ≡ *Dianthus cretaceus* var. *multicaulis* (Boiss. & A.Huet) Grossh., Fl. Cauc. 2: 430. 1930 syn. sec. Kuzmina & Nersesyan (2012)

***Dianthus cretaceus* subsp. *sevanensis* Nersesian in Nov. Syst. Vyssh. Rast. 42: 113. 2011.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus cribrarius* Clementi in Mem. Reale Accad. Sci. Torino II 16: 20. 1855.** Sec. Marhold (2011)

***Dianthus crinitus* Sm. in Trans. Linn. Soc. London 2: 300. 1794.** Sec. Rechinger (1988)
= *Dianthus fimbriatus* Hohen. in Bull. Soc. Imp. Naturalistes Moscou 6: 232. 1833 syn. sec. Rechinger (1988)
= *Dianthus ibericus* Steven ex Ledeb., Fl. Ross. 1: 283. 1842 syn. sec. Rechinger (1988)
= *Dianthus amoenus* Pomel, Nouv. Mat. Fl. Atl. 1: 210. 1874 syn. sec. Rechinger (1988) ≡ *Dianthus crinitus* var. *amoenus* (Pomel) Maire, Fl. Afrique N. 10: 300. 1963 syn. sec. Kew WCVP (2019)
= *Dianthus crinitus* var. *flaviflorus* Emb. in Bull. Soc. Sci. Nat. Maroc 15: 196. 1935 syn. sec. Kew WCVP (2019)

***Dianthus crinitus* subsp. *baldzhuanicus* (Lincz.) Rech.f. in Plant Syst. Evol. 151: 285. 1986.** Sec. Rechinger (1988)
≡ *Dianthus baldzhuanicus* Lincz. in Trudy Tadzhikistansk. Bazy 8: 629. 1940 syn. sec. Rechinger (1988)

Dianthus crinitus* subsp. *crinitus

***Dianthus crinitus* subsp. *kermanensis* Rech.f., Pl. Syst. Evol. 151(3–4): 286. 1986.** Sec. Rechinger (1988)

***Dianthus crinitus* subsp. *nuristanicus* (Gilli) Rech.f. in Plant Syst. Evol. 151: 285. 1986.** Sec. Rechinger (1988)
≡ *Dianthus nuristanicus* Gilli in Feddes Repert. Spec. Nov. Regni Veg. 59: 162. 1956 syn. sec. Rechinger (1988)

***Dianthus crinitus* subsp. *soongoricus* (Schischk.) Kozhevn. in Novosti Sist. Vyssh. Rast. 22: 112. 1985.** Sec. Rechinger (1988)
≡ *Dianthus soongoricus* Schischk., Fl. URSS 6: 899. 1936 syn. sec. Rechinger (1988)

***Dianthus crinitus* subsp. *tetralepis* (Nevski) Rech.f. in Plant Syst. Evol. 151: 286. 1986.** Sec. Rechinger (1988)
≡ *Dianthus tetralepis* Nevski, Fl. URSS 6: 899. 1936 syn. sec. Rechinger (1988)

Dianthus crinitus **subsp.** ***turcomanicus*** **(Schischk.) Rech.f. in Plant Syst. Evol. 151: 287. 1986.** Sec. Rechinger (1988)
≡ *Dianthus turcomanicus* Schischk., Fl. URSS 6: 899. 1936 syn. sec. Rechinger (1988)

Dianthus crinitus **var.** ***argaeus*** **Aytaç & H.Duman in Ann. Bot. Fenn. 41: 217. 2004.** Sec. Rechinger (1988)

Dianthus crossopetalus **(Fenzl ex Boiss.) Grossh., Fl. Kavkaza 2: 428. 1930.** Sec. Kuzmina & Nersesyan (2012)
≡ *Dianthus crinitus* var. *crossopetalus* Fenzl ex Boiss., Fl. Orient. 1: 496. 1867 syn. sec. Kuzmina & Nersesyan (2012)

Dianthus cruentus **Griseb., Spic. Fl. Rumel. 1: 186. 1843.** Sec. Dimopoulos et al. (2013)
= *Dianthus cruentus* var. *micropetalus* Pančić in Verh. Zool.-Bot. Vereins Wien 6: 501. 1856 syn. sec. Kew WCVP (2019)
= *Dianthus consanguineus* Schur, Enum. Pl. Transsilv.: 93. 1866 syn. sec. WFO 2018
= *Dianthus fastigiatus* Pant. in Verh. Vereins Natur- Heilk. Presburg n.s., 2: 105. 1871 syn. sec. WFO 2018
= *Dianthus holzmannianus* Heldr. & Hausskn. ex Nyman, Consp. Fl. Eur. Suppl. 2(1): 58. 1889 syn. sec. WFO 2018
= *Dianthus cibrarius* var. *leucolepis* Hausskn. in Mitth. Thüring. Bot. Vereins n.f., 5: 54. 1893 syn. sec. WFO 2018 ≡ *Dianthus brachyzonus* Borbás ex Formánek in Verh. Naturf. Vereins Brünn 35: 194. 1897 syn. sec. WFO 2018
= *Dianthus quadrangulus* Velen. in Sitzungsber. Königl. Böhm. Ges. Wiss., Math.-Naturwiss. Cl. 1892: 372. 1893 syn. sec. WFO 2018
= *Dianthus turcicus* Velen. in Sitzungsber. Königl. Böhm. Ges. Wiss., Math.-Naturwiss. Cl. 1892: 273. 1893 syn. sec. WFO 2018 ≡ *Dianthus cruentus* subsp. *turcicus* (Velen.) Stoj. & Acht., Fl. Bulg. ed. 3: 405. 1948 syn. sec. WFO 2018
= *Dianthus lateritius* Halácsy, Consp. Fl. Graec. 1: 213. 1900 syn. sec. WFO 2018
= *Dianthus baldaccii* Degen in Magyar Bot. Lapok 5: 275. 1906 syn. sec. WFO 2018
= *Dianthus cruentus* var. *pancicii* Stoj. & Acht., Krit. Stud. Nelk. Bulg.: 56. 1935 syn. sec. WFO 2018
= *Dianthus hyalolepis* Acht. & Lindtner in Izv. Carsk. Prir. Inst. Sofija 13: 195. 1940 syn. sec. WFO 2018
= *Dianthus calocephalus* var. *villiger* Bornm. syn. sec. WFO 2018 ≡ *Dianthus villiger* (Bornm.) Bornm. in Allg. Bot. Z. Syst. 32: 27. 1926 ["1927"] syn. sec. WFO 2018 ≡ *Dianthus brachyzonus* subsp. *villiger* (Bornm.) Micevski in Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 8: 45. 1987 ["1990"] syn. sec. WFO 2018

Dianthus cyathophorus **Moris, Index Seminum (TO) 1852: 32. 1852.** Sec. Bacchetta et al. (2010)
≡ *Dianthus siculus* subsp. *cyathophorus* (Moris) Arrigoni in Parlatorea 7: 20. 2005 syn. sec. Bacchetta et al. (2010)

= *Dianthus minae* Mazzola, Raimondo & Ilardi in Bocconea 17: 307. 2004 syn. sec. Bacchetta et al. (2010) ≡ *Dianthus cyathophorus* subsp. *minae* (Mazzola, Raimondo & Ilardi) Raimondo in Quad. Bot. Amb. Appl. 21: 189. 2010 syn. sec. this publication

***Dianthus cyprius* A.K.Jacks. & Turrill in Bull. Misc. Inform. Kew 1938: 462. 1938.** Sec. Marhold (2011)

***Dianthus cyri* Fisch. & C.A.Mey. in Index Seminum St. Petersburg (Petropolitanus) 4: 34. 1838.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus daghestanicus* Kharadze in Zametki Sist. Geogr. Rast. 16: 47. 1951.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus darvazicus* Lincz.** Sec. Czerepanov (1995)

***Dianthus deltoides* L., Sp. Pl.: 411. 1753.** Sec. Marhold (2011)

≡ *Caryophyllus deltoides* (L.) Moench, Methodus: 59. 1794 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. ≡ *Cylichnanthus deltoides* (L.) Dulac, Fl. Hautes-Pyrénées: 262. 1867 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. ≡ *Silene deltoides* (L.) E.H.L.Krause, Deutschl. Fl. Abbild., ed. 2, 5: 113. 1901 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.;

= *Dianthus deltoides* var. *montanus* Klett & Richt., Fl. Leipzig: 376. 1830 syn. sec. Kew WCVP (2019)

= *Dianthus albus* Schkuhr ex Steud., Nomencl. Bot., ed. 2, 1: 498. 1840 syn. sec. WFO 2018

= *Dianthus endressii* Zahlbr. ex Conrath in Oesterr. Bot. Z. 38: 51. 1888 syn. sec. WFO 2018

= *Dianthus glaucus* L., Sp. Pl.: 411. 1753 syn. sec. WFO 2018 ≡ *Caryophyllus glaucus* (L.) Moench, Methodus: 59. 1794 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. ≡ *Dianthus deltoides* var. *glaucus* (L.) Trevir., Index Seminum (WROCL, Wratislaviensi) 1818: 3. 1818 syn. sec. Kew WCVP (2019) ≡ *Dianthus deltoides* f. *glaucus* (L.) P.D.Sell, Fl. Gr. Brit. Ireland 1: 686. 2018 syn. sec. Kew WCVP (2019)

= *Dianthus supinus* Lam., Fl. Franç. 2: 534. 1779 syn. sec. WFO 2018

= *Dianthus crenatus* Gilib., Fl. Lit. Inch. 2: 161. 1782 syn. sec. WFO 2018

= *Dianthus volgensis* Ser., Prodr. 1: 361. 1824 syn. sec. WFO 2018

***Dianthus deltoides* subsp. *degenii* (Bald.) Strid in Willdenowia 13: 280. 1983 ["1984"].** Sec. Marhold (2011)

≡ *Dianthus degenii* Bald. in Nuovo Giorn. Bot. Ital. n.s., 6: 27. 1899 syn. sec. Marhold (2011)

Dianthus deltoides* subsp. *deltoides

***Dianthus denaicus* Assadi in Iranian J. Bot. 3: 17. 1985.** Sec. Rechinger (1988)

***Dianthus desideratus* Strid, Fl. Hellenica 1: 371. 1997.** Sec. Dimopoulos et al. (2013)

***Dianthus diffusus* Sm., Fl. Graec. Prodr. 1(2): 285. 1809.** Sec. Dimopoulos et al. (2013)
= *Dianthus pubescens* Sm., Fl. Graec. Prodr. 1(2): 286. 1809 syn. sec. WFO 2018
= *Dianthus rupestris* Friv. ex Griseb., Spic. Fl. Rumel. 1: 191. 1843 syn. sec. WFO 2018
= *Dianthus cylleneus* Boiss. & Heldr. in Boissier, Diagn. Pl. Orient., ser. 2, 1: 63. 1854 syn. sec. WFO 2018
= *Dianthus syriacus* F.N.Williams in J. Bot. 23: 346. 1885 syn. sec. WFO 2018
= *Dianthus glandulosopubescens* Halácsy in Verh. K. K. Zool.-Bot. Ges. Wien 48: 706. 1898 syn. sec. WFO 2018

***Dianthus dilepis* Rech.f. in Bot. Jahrb. Syst. 75: 361. 1951.** Sec. Rechinger (1988)

***Dianthus diversifolius* Assadi in Iranian J. Bot. 3: 40. 1985.** Sec. Rechinger (1988)

***Dianthus dobrogensis* Prodán in Bul. Acad. Stud. Agron. Cluj 5(1): 97. 1934.** Sec. Marhold (2011)

***Dianthus* ×*dufftii* Hausskn. ex Asch. in Oesterr. Bot. Z. 26: 259. 1876**

***Dianthus edetanus* (M.B.Crespo & Mateo) M.B.Crespo & Mateo in Flora Montiber. 40: 64. 2008.** Sec. Mateo Sanz & Crespo (2008)
≡ *Dianthus hispanicus* subsp. *edetanus* M.B.Crespo & Mateo in Flora Montiber. 20: 7. 2002 syn. sec. Mateo Sanz & Crespo (2008)

***Dianthus elatus* Ledeb., Fl. Altaic. 2: 136. 1830.** Sec. Dequan & Turland (2001)

***Dianthus elbrusensis* Kharadze in Zametki Sist. Geogr. Rast. 21: 48. 1959.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus eldivenus* Czeczott in Acta Soc. Bot. Poloniae 9: 33. 1932.** Sec. Marhold (2011)

***Dianthus elegans* d'Urv., Mém. Soc. Linn. Paris 1: 302. 1822.** Sec. Dimopoulos et al. (2013)
= *Dianthus actinopetalus* Fenzl, Pug. Pl. Nov. Syr.: 11. 1842 syn. sec. WFO 2018
= *Dianthus cous* Boiss., Diagn. Pl. Orient. ser. 1 1: 20. 1843 syn. sec. WFO 2018
= *Dianthus wawrae* Freyn ex Boiss., Fl. Orient. Suppl.: 79. 1888 syn. sec. WFO 2018

***Dianthus elymaiticus* Hausskn. & Bornm. in Beih. Bot. Centralbl. 19(2): 213. 1905.** Sec. Rechinger (1988)

***Dianthus engleri* Hausskn. & Bornm. in Mitt. Geogr. Ges. (Thüringen) Jena 9: 15. 1891.** Sec. Marhold (2011)

***Dianthus eretmopetalus* Stapf in Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. 51: 349. 1886.** Sec. Marhold (2011)

***Dianthus erinaceus* Boiss., Diagn. Pl. Orient. ser. 1 1: 21. 1843.** Sec. Marhold (2011)
= *Dianthus webbianus* Parl. ex Vis. in Atti Riunione Sci. Ital. 2: 180. 1841 syn. sec. Marhold (2011)

***Dianthus ernesti-mayeri* Micevski & Matevski in Razpr. Slov. Akad. Znan. Umetn., Razr. Nar. Vede 42: 155. 2001.** Sec. WFO 2018

***Dianthus erythrocoleus* Boiss., Fl. Orient. 1: 493. 1867.** Sec. Rechinger (1988)

***Dianthus eugeniae* Kleopow in Izv. Kievsk. Bot. Sada 12–13: 157. 1931.** Sec. Czerepanov (1995)
= *Dianthus tesquicola* Klokov in Bot. Zhurn. (Kiev) 5: 26. 1948 syn. sec. Czerepanov (1995)

***Dianthus excelsus* S.S.Hooper in Hookers Icon. Pl. 37: 13. 1959.** Sec. African Plant Database (version 3.4.0)
= *Dianthus angolensis* subsp. *orientalis* Turrill in Kew Bull. 9: 49. 1954 syn. sec. African Plant Database (version 3.4.0)

***Dianthus falconeri* Edgew. & Hook.f., Fl. Brit. India 1: 214. 1874.** Sec. Ghanzafar & Nasir (1986)

***Dianthus ×fallens* Timb.-Lagr. in Bull. Soc. Bot. France 5: 329. 1858.** Sec. Bernal et al. (1990)
≡ *Dianthus ×tener* subsp. *fallens* (Timb.-Lagr.) Nyman, Consp. Fl. Eur.: 104. 1878 syn. sec. Bernal et al. (1990) ≡ *Dianthus ×monspessulanus* var. *fallens* (Timb.-Lagr.) Pau in Bol. Soc. Aragonesa Ci. Nat. 4: 187. 1905 syn. sec. Bernal et al. (1990)
= *Dianthus ×borderei* Rouy & Foucaud, Fl. France 3: 183. 1896 syn. sec. Kew WCVP (2019) – *Dianthus ×borderi* Rouy & Foucaud, Fl. France 3: 183. 1896 syn. sec. Bernal et al. (1990) [is misspelling for *Dianthus ×borderi* Rouy & Foucaud]

***Dianthus fasciculatus* (Boiss.) Fassou, N.Korotkova, Dimop. & Borsch.** Sec. this publication 141
≡ *Velezia fasciculata* Boiss., Diagn. Pl. Orient., ser. 1, 8: 92. 1849

***Dianthus ferrugineus* Mill., Gard. Dict., ed. 8: 9. 1768.** Sec. Marhold (2011)
= *Dianthus balbisii* Ser., Prodr. 1: 356. 1824 syn. sec. Marhold (2011) ≡ *Dianthus carthusianorum* var. *balbiosii* (Ser.) Tanfani, Fl. Ital. 9: 253. 1892 syn. sec. Kew WCVP (2019)
= *Dianthus balbisii* var. *paniculatus* Ser., Prodr. 1: 356. 1824 syn. sec. Kew WCVP (2019)
= *Dianthus glaucophyllus* Hornem. ex Ser., Prodr. 1: 356. 1824 syn. sec. WFO 2018
= *Dianthus propinquus* Schur, Enum. Pl. Transsilv.: 94. 1866 syn. sec. WFO 2018
= *Dianthus ligusticus* Willd. ex Nyman, Consp. Fl. Eur. 1: 103. 1878 syn. sec. WFO 2018
= *Dianthus rosulatus* Borbás ex Nyman, Consp. Fl. Eur. 1: 103. 1878 syn. sec. WFO 2018
= *Dianthus albaceteanus* Huter in Oesterr. Bot. Z. 54: 339. 1904 syn. sec. Peruzzi & Gargano (2006)

Dianthus ferrugineus* subsp. *ferrugineus

***Dianthus ferrugineus* subsp. *liburnicus* (Bartl.) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 191. 1963.** Sec. Marhold (2011)
≡ *Dianthus liburnicus* Bartl. in Beitr. Bot. 2: 52. 1825 syn. sec. Marhold (2011) ≡ *Dianthus balbisii* subsp. *liburnicus* (Bartl.) Pignatti in Giorn. Bot. Ital. 111: 45. 1977 syn. sec. Marhold (2011)
= *Dianthus liburnicus* var. *albiflorus* Caldesi in Nuovo Giorn. Bot. Ital. 11: 338. 1879 syn. sec. Kew WCVP (2019)

***Dianthus floribundus* Boiss., Asie Min., Bot. 1: 221. 1860.** Sec. Kuzmina & Nersesyan (2012)
= *Dianthus schischkinii* Grossh. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 11: 83. 1949 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus woronowii* Schischk. in sched. herb. LE syn. sec. Kuzmina & Nersesyan 2012 syn. sec. Kuzmina & Nersesyan (2012)

***Dianthus formanekii* Borbás ex Formánek in Verh. Naturf. Vereins Brünn 32: 39. 1894.** Sec. Dimopoulos et al. (2013)

***Dianthus fragrans* Adams in Weber u. Mohr, Beitr. Naturk. 1: 56. 1805.** Sec. Kuzmina & Nersesyan (2012)
= *Dianthus fragrans* M.Bieb., Fl. Taur.-Caucas. 1: 331. 1808 syn. sec. this publication
= *Dianthus liboschitzianus* Hohen. ex Boiss., Fl. Orient. 1: 491. 1867 syn. sec. Czerepanov (1995)
= *Dianthus tichomirovii* Devyatov, Taisumov & Teimurov in Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. n.s. 104(2): 37. 1999 syn. sec. Kuzmina & Nersesyan (2012)
Notes: – Although Bieberstein (1808) didn't mention Adams (1805) as an author of *D. fragrans* in his 1st volume of the Flora Taurica-Caucasica, the descriptions are very similar and very likely refer to the same species.

***Dianthus freynii* Vandas in Sitzungsber. Königl. Böhm. Ges. Wiss., Math.-Naturwiss. Cl. 1889(2): 255. 1890.** Sec. Marhold (2011)

***Dianthus fruticosus* L., Sp. Pl.: 413. 1753.** Sec. Dimopoulos et al. (2013)
= *Dianthus frutescens* Houtt., Nat. Hist. 2(5): 109. 1775 syn. sec. WFO 2018

***Dianthus fruticosus* subsp. *amorginus* Runemark in Bot. Not. 133(4): 485. 1980.** Sec. Dimopoulos et al. (2013)

***Dianthus fruticosus* subsp. *carpathus* Runemark in Bot. Not. 133(4): 487. 1980.** Sec. Dimopoulos et al. (2013)

***Dianthus fruticosus* subsp. *creticus* (Tausch) Runemark in Bot. Not. 133(4): 488. 1980.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus creticus* Tausch in Flora 13: 247. 1830 syn. sec. WFO 2018

Dianthus fruticosus* subsp. *fruticosus

***Dianthus fruticosus* subsp. *karavius* Runemark in Bot. Not. 133(4): 487. 1980.** Sec. Dimopoulos et al. (2013)

***Dianthus fruticosus* subsp. *occidentalis* Runemark in Bot. Not. 133: 483. 1980.** Sec. Dimopoulos et al. (2013)

***Dianthus fruticosus* subsp. *rhodius* (Rech.f.) Runemark in Bot. Not. 133: 486. 1980.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus rhodius* Rech.f. in Denkschr. Akad. Wiss. Wien, Math.-Naturwiss. Kl. 105: 156. 1943 syn. sec. WFO 2018

***Dianthus fruticosus* subsp. *sitiacus* Runemark in Bot. Not. 133(4): 488. 1980.** Sec. Dimopoulos et al. (2013)

***Dianthus furcatus* Balb., Mém. Acad. Sci. Turin, Sci. Phys. 10–11: 13. 1804.** Sec. Marhold (2011)
= *Dianthus alpester* Balb., Mém. Acad. Sci. Turin, Sci. Phys. 1: 13. 1802 syn. sec. Marhold (2011) ≡ *Dianthus carthusianorum* subsp. *alpester* (Balb.) Pers., Syn. Pl. 1: 493. 1805 syn. sec. Kew WCVP (2019)
= *Dianthus pungens* Gren. & Godr., Fl. France 1: 234. 1847 syn. sec. WFO 2018

***Dianthus furcatus* subsp. *dissimilis* (Burnat) Pignatti in Giorn. Bot. Ital. 107: 209. 1973.** Sec. Marhold (2011)
≡ *Dianthus furcatus* var. *dissimilis* Burnat, Fl. Alpes Marit. 1: 230. 1892 syn. sec. Marhold (2011)

Dianthus furcatus* subsp. *furcatus

***Dianthus furcatus* subsp. *gyspergerae* (Rouy) Burnat ex Briq., Prodr. Fl. Corse 1: 572. 1910.** Sec. Marhold (2011)
≡ *Dianthus gyspergerae* Rouy in Rev. Bot. Syst. Géogr. Bot. 1: 132. 1903 syn. sec. Marhold (2011)

***Dianthus furcatus* subsp. *lereschii* (Burnat) Pignatti in Giorn. Bot. Ital. 107: 209. 1973.** Sec. Marhold (2011)
≡ *Dianthus furcatus* var. *lereschii* Burnat, Fl. Alpes Marit. 1: 230. 1892 syn. sec. Marhold (2011)
= *Dianthus tener* Balb., Mém. Acad. Sci. Turin, Sci. Phys. 1: 14. 1802 syn. sec. Marhold (2011) ≡ *Dianthus strictus* var. *tener* (Balb.) Tanfani, Fl. Ital. 9: 272. 1892 syn. sec. Kew WCVP (2019) ≡ *Dianthus furcatus* subsp. *tener* (Balb.) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 189. 1963 syn. sec. Marhold (2011)

***Dianthus gabrielianiae* Nersesian in Takhtajania 1: 45. 2011.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus gasparrinii* Guss., Fl. Sicul. Syn. 1: 479. 1843.** Sec. Bacchetta et al. (2010)
≡ *Dianthus caryophyllus* subsp. *gasparrinii* (Guss.) Arcang., Comp. Fl. Ital. ed. 2: 306. 1894 syn. sec. Bacchetta et al. (2010)

***Dianthus geminiflorus* Loisel., Fl. Gall. 2: 725. 1807.** Sec. Bernal et al. (1990)
≡ *Dianthus furcatus* subsp. *geminiflorus* (Loisel.) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 189. 1963 syn. sec. WFO 2018

***Dianthus genargenteus* Bacch., Brullo, Casti & Giusso in Nordic J. Bot. 28: 145. 2010.** Sec. Bacchetta et al. (2010)

***Dianthus giganteiformis* Borbás in Oesterr. Bot. Z. 41: 32. 1891.** Sec. Marhold (2011)
≡ *Dianthus sabuletarum* Heuff. in Oesterr. Bot. Z. 8: 26. 1858 syn. sec. WFO 2018
= *Dianthus pontederae* A.Kern., Sched. Fl. Exs. Austro-Hung. 2: 539. 1882 ["1883"] syn. sec. WFO 2018 ≡ *Dianthus carthusianorum* subsp. *pontederae* (A.Kern.) Hegi in Allg. Bot. Z. Syst. 17: 16. 1911 syn. sec. WFO 2018 ≡ *Dianthus giganteiformis* subsp. *pontederae* (A.Kern.) Soó in Acta Bot. Acad. Sci. Hung. 15: 339. 1969 ["1970"] syn. sec. WFO 2018 ≡ *Dianthus sabuletorum* subsp. *pontederae* (A.Kern.) Holub in Folia Geobot. Phytotax. 19: 214. 1984 syn. sec. WFO 2018
= *Dianthus tenuifolius* subsp. *serpentini* Podp., Spisy Přír. Fak. Masarykovy Univ. 12: 20. 1922 syn. sec. WFO 2018 ≡ *Dianthus sabuletorum* subsp. *serpentini* (Podp.) Holub in Folia Geobot. Phytotax. 19: 214. 1984 syn. sec. WFO 2018

= *Dianthus urziceniensis* Prodán, Fl. Reipubl. Popul. Roman. 2: 667. 1953 syn. sec. WFO 2018
= *Dianthus diutinus* Rchb., Icon. Fl. Germ. Helv. 6: 44. 1844, nom illeg syn. sec. WFO 2018
= *Dianthus giganteiformis* var. *comanae* Prodán syn. sec. WFO 2018 ≡ *Dianthus comanae* (Prodán) Prodán, Fl. Reipubl. Popul. Roman. 2: 284. 1953 syn. sec. WFO 2018

Dianthus giganteiformis **subsp.** ***giganteiformis***

Dianthus giganteiformis **subsp.** ***kladovanus*** **(Degen) Soó in Feddes Repert. 83: 161. 1972.** Sec. Marhold (2011)
≡ *Dianthus kladovanus* Degen in Magyar Bot. Lapok 4: 122. 1905 syn. sec. Marhold (2011) ≡ *Dianthus sabuletorum* subsp. *kladovanus* (Degen) Holub in Folia Geobot. Phytotax. 19: 214. 1984 syn. sec. Marhold (2011)

Dianthus giganteus **d'Urv., Mém. Soc. Linn. Paris 1: 301. 1822.** Sec. Dimopoulos et al. (2013)
= *Dianthus intermedius* Boiss., Fl. Orient. 1: 515. 1867 syn. sec. Marhold (2011)
= *Dianthus haynaldianus* Borbás in Oesterr. Bot. Z. 38: 144. 1888 syn. sec. Marhold (2011) ≡ *Dianthus giganteus* subsp. *haynaldianus* (Borbás) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 69: 191. 1963 syn. sec. WFO 2018
= *Dianthus subgiganteus* Borbás ex Formánek in Verh. Naturf. Vereins Brünn 32: 181. 1894 syn. sec. WFO 2018 ≡ *Dianthus giganteus* subsp. *subgiganteus* (Borbás ex Formánek) Hayek in Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. 94: 138. 1917 syn. sec. WFO 2018

Dianthus giganteus **subsp.** ***banaticus*** **(Heuff.) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 191. 1963.** Sec. Marhold (2011)
≡ *Dianthus carthusianorum* var. *banaticus* Heuff. syn. sec. Marhold (2011) ≡ *Dianthus banaticus* (Heuff.) Dörfl., Exsicc. (Herb. Norm.) 1894: 3018. 1894 syn. sec. Marhold (2011)

Dianthus giganteus **subsp.** ***croaticus*** **(Borbás) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 70: 4. 1964.** Sec. Marhold (2011)
≡ *Dianthus croaticus* Borbás in Bot. Jahresber. (Just) 4: 1059. 1877 syn. sec. Marhold (2011)

Dianthus giganteus **subsp.** ***giganteus***

Dianthus giganteus **subsp.** ***vandasii*** **(Velen.) Stoj. & Acht., Sborn. Blghar. Akad. Nauk 29: 43. 1935.** Sec. Marhold (2011)
≡ *Dianthus vandasii* Velen. in Sitzungsber. Königl. Böhm. Ges. Wiss., Math.-Naturwiss. Cl. 1892: 16. 1893 syn. sec. Marhold (2011)

***Dianthus glabriusculus* (Kit.) Borbás in Verh. Bot. Vereins Prov. Brandenburg 19: 19. 1877.** Sec. Czerepanov (1995)
≡ *Dianthus collinus* var. *glabriusculus* Kit. in Linnaea 32: 528. 1863 syn. sec. Czerepanov (1995) ≡ *Dianthus collinus* subsp. *glabriusculus* (Kit.) Thaisz in Bot. Közlem. 8: 252. 1910 syn. sec. Czerepanov (1995)
= *Dianthus glabriusculus* subsp. *moldavicus* Prodán in Bul. Soc. Sti. Cluj. 10: 158. 1948 syn. sec. Czerepanov (1995) ≡ *Dianthus piatra-neamtzui* Prodán, Fl. Reipubl. Popul. Roman. 2: 234. 1953 syn. sec. Czerepanov (1995)
= *Dianthus collinus* subsp. *glabriusculus* Soó syn. sec. Czerepanov (1995)

***Dianthus glacialis* Haenke in Collectanea 2: 84. 1788.** Sec. Marhold (2011)
≡ *Dianthus alpinus* var. *glacialis* (Haenke) Regel in Bull. Soc. Imp. Naturalistes Moscou 34(2): 533. 1862, nom. illeg.
= *Dianthus glacialis* var. *acaulis* Ser., Prodr. 1: 362. 1824 syn. sec. Kew WCVP (2019)
= *Dianthus glacialis* var. *latifolius* Ser., Prodr. 1: 362. 1824 syn. sec. Kew WCVP (2019)
= *Dianthus alpinus* var. *subacaulis* Roth, Enum. Pl. Phaen. Germ. 1(2): 282. 1827 syn. sec. Kew WCVP (2019)
= *Dianthus glacialis* f. *reducta* Fornac. in Giorn. Bot. Ital. 107: 246. 1973 syn. sec. WFO 2018

***Dianthus glacialis* subsp. *gelidus* (Schott, Nyman & Kotschy) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 190. 1963.** Sec. Marhold (2011)
≡ *Dianthus gelidus* Schott, Nyman & Kotschy in Schott, Analecta Bot.: 54. 1854 syn. sec. Marhold (2011)

Dianthus glacialis* subsp. *glacialis

***Dianthus glutinosus* Boiss. & Heldr. in Boissier, Diagn. Pl. Orient., ser. 2, 1: 61. 1854.** Sec. Dimopoulos et al. (2013)
= *Dianthus pubescens* d'Urv., Mém. Soc. Linn. Paris 1: 303. 1822 syn. sec. WFO 2018

***Dianthus goekayi* Kaynak, Yılmaz & Daşkın in Ann. Bot. Fenn. 48: 74. 2011.** Sec. Yılmaz et al. (2011)

***Dianthus goerkii* Hartvig & Strid in Bot. Jahrb. Syst. 108: 321. 1987.** Sec. Hamzaoğlu & Koç (2021)
= *Dianthus leucophaeus* var. *patens* Reeve syn. sec. Hamzaoğlu & Koç (2021)

***Dianthus gracilis* Sm., Fl. Graec. Prodr. 1(2): 288. 1809.** Sec. Dimopoulos et al. (2013)

***Dianthus gracilis* subsp. *armerioides* (Griseb.) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 191. 1963.** Sec. Marhold (2011)

≡ *Dianthus gracilis* var. *armerioides* Griseb., Spic. Fl. Rumel. 1: 190. 1843 syn. sec. Marhold (2011)
= *Dianthus suskalovicii* Adamović in Oesterr. Bot. Z. 55: 179. 1905 syn. sec. Marhold (2011)
= *Dianthus callosus* Velen. in Sitzungsber. Königl. Böhm. Ges. Wiss., Math.-Naturwiss. Cl. 8: 5. 1910 ["1911"] syn. sec. Marhold (2011)
= *Dianthus achtarovii* Stoj. & Kitan. in Izv. Bulg. Bot. Druzh. 9: 94. 1943 syn. sec. Marhold (2011) ≡ *Dianthus gracilis* subsp. *achtarovii* (Stoj. & Kitanov) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 191. 1963 syn. sec. Marhold (2011)

***Dianthus gracilis* subsp. *drenowskianus* (Rech.f.) Strid in Willdenowia 13: 281. 1983 ["1984"].** Sec. Marhold (2011)
≡ *Dianthus drenowskianus* Rech.f. in Repert. Spec. Nov. Regni Veg. 31: 158. 1932 syn. sec. Marhold (2011)

***Dianthus gracilis* subsp. *friwaldskyanus* (Boiss.) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 191. 1963.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus friwaldskyanus* Boiss., Diagn. Pl. Orient., ser. 2, 1: 65. 1854 syn. sec. Dimopoulos et al. (2013)

Dianthus gracilis* subsp. *gracilis
= *Dianthus albanicus* Wettst. in Biblioth. Bot. 26: 34. 1892 syn. sec. Dimopoulos et al. (2013)
= *Dianthus athous* Rech.f. in Repert. Spec. Nov. Regni Veg. 31: 159. 1932 syn. sec. Marhold (2011)

***Dianthus gracilis* subsp. *xanthinus* (Davidov) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 191. 1963.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus xanthinus* Davidov in Trav. Soc. Bulg. Sci. Nat. 8: 56. 1915 syn. sec. this publication – *Dianthus xanthianus* Davidov in Trav. Soc. Bulg. Sci. Nat. 8: 56. 1915 syn. sec. this publication [is orthographic variant for *Dianthus xanthinus* Davidov] – *Dianthus gracilis* subsp. *xanthianus* (Davidov) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 191. 1963 syn. sec. this publication [is orthographic variant for *Dianthus gracilis* subsp. *xanthinus* (Davidov) Tutin]

***Dianthus graminifolius* C.Presl, Fl. Sicul. 1: 147. 1826.** Sec. Bacchetta et al. (2010)
≡ *Dianthus arrosti* var. *graminifolius* (C.Presl) Lojac., Fl. Sicul. 1: 164. 1889 syn. sec. Bacchetta et al. (2010) – *Dianthus arrostii* var. *graminifolius* (C.Presl) Lojac., Fl. Sicul. 1: 164. 1889 syn. sec. Bacchetta et al. (2010) [is orthographic variant for *Dianthus arrosti* var. *graminifolius* (C.Presl) Lojac.]

***Dianthus graniticus* Jord., Observ. Pl. Nouv. 7: 13. 1849.** Sec. Marhold (2011)

≡ *Dianthus hirtus* subsp. *graniticus* (Jord.) Rouy & Foucaud in Rouy, Fl. France 3: 177. 1896 syn. sec. Marhold (2011)

***Dianthus gratianopolitanus* Vill., Hist. Pl. Dauphiné 3: 598. 1789.** Sec. Marhold (2011)
= *Dianthus caesius* Sm., Engl. Bot. [1]: t. 62. 1792 syn. sec. Marhold (2011) ≡ *Silene caesia* (Sm.) E.H.L.Krause, Deutschl. Fl. Abbild., ed. 2, 5: 112. 1901, nom. illeg.
= *Dianthus caesius* subsp. *adscendens* Gaudin, Fl. Helv. 3: 158. 1828 syn. sec. Kew WCVP (2019)
= *Dianthus caesius* subsp. *montanus* Gaudin, Fl. Helv. 3: 159. 1828 syn. sec. Kew WCVP (2019)
= *Dianthus caesius* var. *nanus* Gaudin, Fl. Helv. 3: 159. 1828 syn. sec. Kew WCVP (2019)
= *Dianthus flaccidus* Fieber in Flora 17: 633. 1834 syn. sec. WFO 2018

***Dianthus gredensis* Pau ex Caball. in Anales Jard. Bot. Madrid 5: 513. 1945.** Sec. Bernal et al. (1990)
≡ *Dianthus langeanus* subsp. *gredensis* (Pau ex Caball.) Rivas Mart., Fern.Gonz. & Sánchez Mata in Opusc. Bot. Pharm. Complut. 2: 108. 1986 syn. sec. Bernal et al. (1990) ≡ *Dianthus pungens* subsp. *gredensis* (Pau ex Caball.) Crespí, C.P.Fern., A.Castro, Bernardos & Amich in Ann. Bot. Fenn. 44: 253. 2007 syn. sec. this publication

***Dianthus grossheimii* Schischk. in Trudy Bot. Inst. Akad. Nauk S.S.S.R., ser. 1, Fl. Sist. Vyssh. Rast. 2: 278. 1936.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus guessfeldtianus* Muschl., Man. Fl. Egypt 1: 330. 1912.** Sec. Marhold (2011)

***Dianthus guliae* Janka in J. Bot. 12: 338. 1874.** Sec. Peruzzi & Gargano (2006)
≡ *Dianthus liburnicus* var. *guliae* (Janka) Arcang., Comp. Fl. Ital.: 85. 1882 syn. sec. Peruzzi & Gargano (2006) ≡ *Dianthus carthusianorum* var. *guliae* (Janka) Tanfani, Fl. Ital. 9: 254. 1892 syn. sec. Peruzzi & Gargano (2006)

***Dianthus guttatus* M.Bieb., Fl. Taur.-Caucas. 1: 328. 1808.** Sec. Czerepanov (1995)
= *Dianthus pseudogrisebachii* Grecescu, Consp. Fl. Roman.: 100. 1898 syn. sec. WFO 2018
= *Dianthus guttatus* subsp. *mariae* Kleopow in Zhurn. Inst. Bot. Vseukraïns'k. Akad. Nauk 21–22: 244. 1939 syn. sec. WFO 2018 ≡ *Dianthus mariae* (Kleopow) Klokov in Bot. Zhurn. (Kiev) 5: 27. 1948 syn. sec. WFO 2018

***Dianthus guttatus* subsp. *dicaricatus* Prodán, Fl. Republ. Popul. Român. 2: 669. 1953.** Sec. Jalas & Suominen (1988)

Dianthus guttatus* subsp. *guttatus

Dianthus haematocalyx **Boiss. & Heldr. in Boissier, Diagn. Pl. Orient., ser. 2, 1: 68. 1854.** Sec. Dimopoulos et al. (2013)
= *Dianthus haematocalyx* f. *olympica* Stoj. & Jordanov in God. Sofiisk. Univ. Fiz.-Mat. Fak. 34: 178. 1938 syn. sec. Kew WCVP (2019)

Dianthus haematocalyx **subsp.** ***haematocalyx***

Dianthus haematocalyx **subsp.** ***phitosianus*** **Constantin. in Phyton (Horn) 39(2): 279. 1999.** Sec. Dimopoulos et al. (2013)

Dianthus haematocalyx **subsp.** ***pindicola*** **(Vierh.) Hayek in Repert. Spec. Nov. Regni Veg. Beih. 30(1): 240. 1924.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus pindicola* Vierh. in Verh. K. K. Zool.-Bot. Ges. Wien 47: 31. 1897 syn. sec. Dimopoulos et al. (2013) ≡ *Dianthus haematocalyx* subsp. *pinidicola* (Vierh.) Hayek in Repert. Spec. Nov. Regni Veg. Beih. 30(1): 240. 1924 syn. sec. Dimopoulos et al. (2013)
= *Dianthus pineticola* var. *jacupicensis* Košanin syn. sec. WFO 2018

Dianthus haematocalyx **subsp.** ***pruinosus*** **(Boiss. & Orph.) Hayek in Repert. Spec. Nov. Regni Veg. Beih. 30(1): 240. 1924.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus pruinosus* Boiss. & Orph. in Boissier, Diagn. Pl. Orient. ser. 2, 6: 28. 1859 syn. sec. Dimopoulos et al. (2013)

Dianthus haematocalyx **subsp.** ***ventricosus*** **Maire & Petitm. in Bull. Soc. Sci. Nancy III, 9: 193. 1908.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus ventricosus* Heldr. ex Halácsy, Consp. Fl. Graec. 1: 204. 1900, nom. illeg. syn. sec. Marhold (2011)
= *Dianthus sibthorpii* Vierh. in Verh. K. K. Zool.-Bot. Ges. Wien 47: 33. 1897 syn. sec. Marhold (2011) ≡ *Dianthus haematocalyx* subsp. *sibthorpii* (Vierh.) Hayek in Repert. Spec. Nov. Regni Veg. Beih. 30(1): 240. 1924 syn. sec. Marhold (2011)

Dianthus hafezii **Assadi in Iranian J. Bot. 3: 23. 1985.** Sec. Rechinger (1988)

Dianthus halisdemirii **Hamzaoğlu & Koç in KSÜ Tarim Doga Derg. 21: 548. 2018.** Sec. Hamzaoğlu et al. (2018)

Dianthus hamzaoglui **Koç in Phytotaxa 439(1): 58. 2020.** Sec. Koç (2020)

Dianthus harrissii **Rech.f. in Plant Syst. Evol. 142: 240. 1983.** Sec. Rechinger (1988)

Dianthus helenae **Vved. in Bot. Mater. Gerb. Bot. Inst. Uzbekistansk. Fil. Akad. Nauk S.S.S.R. 3: 10. 1941.** Sec. Czerepanov (1995)

Dianthus ×hellwigii **Borbás ex Čelak. in Sitzungsber. Königl. Böhm. Ges. Wiss., Math.-Naturwiss. Cl. 1878: 20. 1879.** Sec. IPNI
≡ *Dianthus ×hellwigii* Borbás ex Asch. in Oesterr. Bot. Z. 26: 258. 1876;

Dianthus ×helveticorum **M.Laínz in Anales Jard. Bot. Madrid 42: 549. 1985 ["1986"].** Sec. Bernal et al. (1990)

Dianthus henteri **Heuff. ex Griseb. & Schenk in Arch. Naturgesch. 18(1): 303. 1852.** Sec. Marhold (2011)

Dianthus hispidus **(Boiss. & Balansa) Fassou, N.Korotkova, Dimop. & Borsch.** Sec. this publication 150
≡ *Velezia hispida* Boiss. & Balansa in Boissier, Diagn. Pl. Orient., ser. 2, 5: 57. 1856 syn. sec. this publication

Dianthus hoeltzeri **C.Winkl. in Gartenflora 30: 1. 1881.** Sec. Dequan & Turland (2001)

Dianthus holopetalus **Turcz. in Bull. Soc. Imp. Naturalistes Moscou 27(2): 369. 1854.** Sec. African Plant Database (version 3.4.0)

Dianthus humilis **Willd. ex Ledeb., Fl. Ross. 1: 280. 1842.** Sec. Czerepanov (1995)
= *Dianthus hirtus* M.Bieb., Fl. Taur.-Caucas. 1: 326. 1808 syn. sec. WFO 2018
= *Dianthus virgineus* Hablitz ex M.Bieb., Fl. Taur.-Caucas. 1: 326. 1808 syn. sec. WFO 2018
= *Dianthus sterilis* Steven ex Boiss., Fl. Orient. 1: 505. 1867 syn. sec. WFO 2018

Dianthus hymenolepis **Boiss., Diagn. Pl. Orient., ser. 1, 8: 64. 1849.** Sec. Rechinger (1988)

Dianthus hypanicus **Andrz., Ischisl. Rast. Podolsk. Gub. 1: 18. 1860.** Sec. Czerepanov (1995)

Dianthus hyrcanicus **Rech.f. in Plant Syst. Evol. 142: 241. 1983.** Sec. Rechinger (1988)

Dianthus hyssopifolius **L., Cent. Pl. I: 11. 1755.** Sec. Bernal et al. (1990)
= *Dianthus monspeliacus* L., Syst. Nat., ed. 10 2: 1029. 1759 syn. sec. WFO 2018
= *Dianthus ambiguus* Salisb., Prodr. Stirp. Chap. Allerton: 303. 1796 syn. sec. WFO 2018
= *Dianthus saxatilis* Pers., Syn. Pl. 1: 494. 1805 syn. sec. WFO 2018
= *Dianthus alpestris* Sternb., Deutschl. Fl.: 28. 1809 syn. sec. WFO 2018 ≡ *Dianthus monspessulanus* var. *alpestris* (Sternb.) Arcang., Comp. Fl. Ital.: 87. 1882 syn. sec. Kew WCVP (2019)

= *Dianthus plumosus* DC. ex Spreng., Pl. Min. Cogn. Pug. 2: 64. 1815 syn. sec. WFO 2018 ≡ *Dianthus monspessulanus* var. *plumosus* (DC. ex Spreng.) Gaudin, Fl. Helv. 6: 355. 1830 syn. sec. Kew WCVP (2019)
= *Dianthus suaveolens* Spreng., Novi Provent.: 16. 1818 syn. sec. Bernal et al. (1990) ≡ *Dianthus monspessulanus* var. *suaveolens* (Spreng.) Trevir., Index Seminum (WROCL, Wratislaviensi) 1821(App. 3): 1. 1821 syn. sec. Kew WCVP (2019)
= *Dianthus monspessulanus* var. *brevifolius* Ser., Prodr. 1: 365. 1824 syn. sec. Kew WCVP (2019)
= *Dianthus acuminatus* Tausch, Syll. Pl. Nov. 2: 242. 1828 syn. sec. WFO 2018
= *Dianthus controversus* Gaudin, Fl. Helv. 3: 157. 1828 syn. sec. WFO 2018 ≡ *Dianthus seguieri* var. *controversus* (Gaudin) W.D.J.Koch, Syn. Fl. Germ. Helv. 1: 96. 1835 syn. sec. Kew WCVP (2019) ≡ *Dianthus seguieri* subsp. *controversus* (Gaudin) Arcang., Comp. Fl. Ital.: 84. 1882 syn. sec. Kew WCVP (2019)
= *Dianthus sprengelii* G.Don, Gen. Hist. 1: 394. 1831 syn. sec. WFO 2018
= *Dianthus odoratissimus* Vest ex Rchb., Fl. Germ. Excurs.: 807. 1832 syn. sec. WFO 2018
= *Dianthus monspessulanus* var. *alpicola* W.D.J.Koch, Syn. Fl. Germ. Helv. 1: 99. 1835 syn. sec. Kew WCVP (2019)
= *Dianthus condensatus* Kil. in Linnaea 32: 532. 1863 syn. sec. WFO 2018
= *Dianthus oreades* Balb. ex Nyman, Consp. Fl. Eur. 1: 104. 1878 syn. sec. WFO 2018
= *Dianthus eynensis* Sennen in Bol. Soc. Ibér. Ci. Nat. 25: 148. 1926 syn. sec. WFO 2018
= *Dianthus monspessulanus* var. *jacetanus* P.Monts. in Bull. Soc. Échange Pl. Vasc. Eur. Occid. Bassin Médit. 18: 72. 1981 syn. sec. WFO 2018

***Dianthus hyssopifolius* subsp. *gallicus* (Pers.) M.Laínz & Muñoz Garm in Anales Jard. Bot. Madrid 44: 572. 1987.** Sec. Bernal et al. (1990)
≡ *Dianthus gallicus* Pers., Syn. Pl. 1: 495. 1805 syn. sec. Bernal et al. (1990) ≡ *Dianthus monspeliacus* subsp. *gallicus* (Pers.) M.Laínz & Muñoz Garm in Anales Jard. Bot. Madrid 42: 259. 1985 syn. sec. Bernal et al. (1990)

Dianthus hyssopifolius* subsp. *hyssopifolius

***Dianthus ichnusae* Bacch., Brullo, Casti & Giusso in Nordic J. Bot. 28: 146. 2010.** Sec. Bacchetta et al. (2010)

Dianthus ichnusae* subsp. *ichnusae

***Dianthus ichnusae* subsp. *toddei* Bacch., Brullo, Casti & Giusso in Nordic J. Bot. 28: 147. 2010.** Sec. Bacchetta et al. (2010)

***Dianthus illyricus* (Ard.) Fassou, N.Korotkova, Dimop. & Borsch.** Sec. this publication 151

≡ *Saponaria illyrica* Ard., Animadv. Bot. Spec. Alt.: 24. 1764 syn. sec. this publication ≡ *Tunica illyrica* (Ard.) Fisch. & C.A.Mey., Index Sem. Hort. Petrop. 4: 49. 1838 syn. sec. this publication ≡ *Fiedleria illyrica* (Ard.) Rchb., Icon. Fl. Germ. Helv. 6: 42, t. 246. 1844 syn. sec. this publication (2019) ≡ *Petrorhagia illyrica* (Ard.) P.W.Ball & Heywood in Bull. Brit. Mus. (Nat. Hist.), Bot. 3: 133. 1964 syn. sec. this publication

***Dianthus illyricus* subsp. *angustifolius* (Poir.) Fassou, N.Korotkova, Dimop. & Borsch.** Sec. this publication 152

≡ *Silene angustifolia* Poir., Voy. Barbarie 2: 164. 1789 syn. sec. this publication (2019); ≡ *Tunica angustifolia* (Poir.) Briq., Prodr. Fl. Corse 1: 544. 1910 syn. sec. this publication ≡ *Tunica illyrica* subsp. *angustifolia* (Poir.) Maire in Bull. Soc. His. Nat. Afrique N. 30: 265. 1939 syn. sec. this publication

= *Gypsophila compressa* Desf., Fl. Atlant. 1: 343, t. 97. 1798 syn. sec. this publication ≡ *Tunica compressa* (Desf.) Fisch. & C.A.Mey., Index Sem. Hort. Petrop. 4: 50. 1838 syn. sec. this publication ≡ *Dianthella compressa* (Desf.) Pomel, Mat. Fl. Atl.: 9. 1860 syn. sec. this publication (2019)

= *Tunica davaeana* Coss. in Bull. Soc. Bot. France 36: 103. 1889 syn. sec. this publication

= *Tunica scoparia* Pamp. in Arch. Bot. (Forlì) 12: 25. 1936 syn. sec. this publication (2019)

***Dianthus illyricus* subsp. *haynaldianus* (Janka) Fassou, N.Korotkova, Dimop. & Borsch.** Sec. this publication 152

≡ *Gypsophila haynaldiana* Janka in Oesterr. Bot. Z. 20: 316. 1870 syn. sec. this publication (2019) ≡ *Tunica haynaldiana* (Janka) Borbás in Math. Term. Közlem. 12: 165. 1876 syn. sec. this publication (2019) ≡ *Gypsophila haynaldiana* Janka ex Nyman, Consp. Fl. Eur. 1: 100. 1878 syn. sec. IPNI ≡ *Tunica illyrica* var. *haynaldiana* (Janka) Hayek, Prodr. Fl. Penins. Balcan. 1: 222. 1924 syn. sec. this publication ≡ *Tunica illyrica* subsp. *haynaldiana* (Janka) Prodán in Savulescu, F. Roman. P. R. 2: 215. 1953 syn. sec. this publication ≡ *Petrorhagia illyrica* subsp. *haynaldiana* (Janka) P.W.Ball & Heywood in Bull. Brit. Mus. (Nat. Hist.), Bot. 3: 134. 1964 syn. sec. this publication

= *Tunica rhodopea* Velen. in Abh. Böhm. Ges. Wiss. 1894 (29): 4. 1895 syn. sec. Kew WCVP (2019)

Dianthus illyricus* subsp. *illyricus

***Dianthus illyricus* subsp. *taygeteus* (Boiss.) Fassou, N.Korotkova, Dimop. & Borsch.** Sec. this publication 152

≡ *Tunica illyrica* var. *taygetea* Boiss., Fl. Orient. 1: 521. 1867 syn. sec. this publication; ≡ *Tunica taygetea* (Boiss.) P.H.Davis in Notes Roy. Bot. Gard. Edinburgh 22: 165. 1957 syn. sec. this publication (2019) ≡ *Petrorhagia illyrica* subsp. *taygetea* (Boiss.)

P.W.Ball & Heywood in Bull. Brit. Mus. (Nat. Hist.), Bot. 3: 137. 1964 syn. sec. this publication ≡ *Tunica cretica* var. *taygetea* (Boiss.) Halácsy syn. sec. this publication

***Dianthus imereticus* (Rupr.) Schischk. in Byull. Gosud. Muz. Gruzii 5: 123. 1928 ["1930"].** Sec. Kuzmina & Nersesyan (2012)
≡ *Dianthus montanus* f. *imereticus* Rupr., Fl. Caucasi: 173. 1869 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus charadzeae* Gagnidze & Gvin. in Zametki Sist. Geogr. Rast. 37: 25. 1981 syn. sec. Kuzmina & Nersesyan (2012)

***Dianthus inamoenus* Schischk., Fl. URSS 6: 897. 1936.** Sec. Kuzmina & Nersesyan (2012)
= *Dianthus lenkoranicus* Kharadze in Zametki Sist. Geogr. Rast. 16: 46. 1951 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus pallens* subsp. *inamoenus* Sanda syn. sec. Kuzmina & Nersesyan (2012)

***Dianthus ingoldbyi* Turrill in Bull. Misc. Inform. Kew 1924: 314. 1924.** Sec. Dimopoulos et al. (2013)

***Dianthus insularis* Bacch., Brullo, Casti & Giusso in Nordic J. Bot. 28: 156. 2010.** Sec. Bacchetta et al. (2010)

***Dianthus integer* Vis. in Flora 12(1 Erg.): 11. 1829.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus petraeus* subsp. *integer* (Vis.) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 190. 1963 syn. sec. WFO 2018
= *Dianthus nicolai* Beck & Szyszył., Pl. Cernagor. Lect.: 65. 1888 syn. sec. WFO 2018
= *Dianthus prenjus* Beck in Wiss. Mitt. Bosnien & Herzegovina 11: 488. 1909 syn. sec. WFO 2018

Dianthus integer* subsp. *integer

***Dianthus integer* subsp. *macedonicus* Trinajstić in Suppl. Fl. Anal. Jugosl. 6: 8. 1979.** Sec. Marhold (2011)
– *Dianthus integer* subsp. *macedonicus* Trinajstić in Suppl. Fl. Anal. Jugosl. 5: 737. 1979, nom. inval. syn. sec. this publication

***Dianthus integer* subsp. *minutiflorus* (Halácsy) Bornm. ex Strid, Mount. Fl. Greece 1: 182. 1986.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus minutiflorus* Halácsy, Consp. Fl. Graec. 1: 216. 1900 syn. sec. Marhold (2011) ≡ *Dianthus petraeus* subsp. *minutiflorus* (Halácsy) Greuter & Burdet in Willdenowia 12: 187. 1982 syn. sec. Marhold (2011)
= *Dianthus strictus* var. *minutiflorus* Borbás in Verh. Naturf. Vereins Brünn 34: 85. 1896 syn. sec. WFO 2018

Dianthus integerrimus **Bunge in Mém. Acad. Imp. Sci. St-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 7: 583. 1858.** Sec. Kuzmina & Nersesyan (2012)
≡ *Dianthus liboschitzianus* var. *integerrimus* (Bunge) Boiss., Fl. Orient. 1: 487. 1867 syn. sec. Kuzmina & Nersesyan (2012) ≡ *Dianthus cretaceus* var. *integerrimus* (Bunge) Grossh., Fl. Cauc. 2: 430. 1930 syn. sec. Kuzmina & Nersesyan (2012)

Dianthus jacobsii **Rech.f. in Plant Syst. Evol. 142: 243. 1983.** Sec. Kuzmina & Nersesyan (2012)

Dianthus jacquemontii **Edgew. & Hook.f., Fl. Brit. India 1: 214. 1874.** Sec. Ghanzafar & Nasir (1986)

Dianthus ×jaczonis **Asch. in Oesterr. Bot. Z. 26: 257. 1876.** Sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.

Dianthus japigicus **Bianco & S.Brullo in Braun-Blanquetia 2: 31. 1988.** Sec. Bacchetta et al. (2010)

Dianthus japonicus **Thunb., Syst. Veg. ed. 14: 417. 1784.** Sec. Zoku (1965)
= *Dianthus ellipticus* Turcz. in Bull. Soc. Imp. Naturalistes Moscou 27(2): 369. 1854 syn. sec. Zoku (1965)
= *Dianthus nipponicus* Makino in Bot. Mag. (Tokyo) 17: 58. 1903 syn. sec. Zoku (1965)
= *Dianthus japonicus* f. *albiflorus* J.Ohara ex Nakan. in J. Geobot. 16: 116. 1968 syn. sec. WFO 2018
= *Dianthus japonicus* f. *albiflorus* Honda & Koike in J. Jap. Bot. 46: 75. 1971, nom. illeg. syn. sec. WFO 2018
= *Dianthus japonicus* f. *albiflorus* Konta & S.Matsumoto in Bull. Natl. Sci. Mus., Tokyo, B. 31(1): 23. 2005, nom. illeg. syn. sec. Zoku (1965)

Dianthus jaroslavii **Galushko in Novosti Sist. Vyssh. Rast. 6: 213. 1970.** Sec. Kuzmina & Nersesyan (2012)

Dianthus ×javorkae **Kárpáti in Borbásia 5–6: 87. 1946.** Sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.

Dianthus juniperinus **Sm. in Trans. Linn. Soc. London 2: 303. 1794.** Sec. Dimopoulos et al. (2013)

Dianthus juniperinus **subsp. *aciphyllus* (Sieber ex Ser.) Turland in Bull. Brit. Mus. (Nat. Hist.), Bot. 22: 168. 1992.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus aciphyllus* Sieber ex Ser. in Candolle, Prodr. 1: 358. 1824 syn. sec. WFO 2018

***Dianthus juniperinus* subsp. *bauhinorum* (Greuter) Turland in Bull. Brit. Mus. (Nat. Hist.), Bot. 22: 168. 1992.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus aciphyllus* var. *bauhinorum* Greuter in Candollea 20: 190. 1965 syn. sec. WFO 2018
– *Dianthus arboreus* L., Sp. Pl.: 413. 1753, nom. rej. syn. sec. WFO 2018

***Dianthus juniperinus* subsp. *heldreichii* Greuter in Candollea 20: 187. 1966.** Sec. Dimopoulos et al. (2013)

***Dianthus juniperinus* subsp. *idaeus* Turland in Bull. Brit. Mus. (Nat. Hist.), Bot. 22(2): 168. 1992.** Sec. Dimopoulos et al. (2013)

Dianthus juniperinus* subsp. *juniperinus

***Dianthus juniperinus* subsp. *kavusicus* Turland in Bull. Brit. Mus. (Nat. Hist.), Bot. 22(2): 168. 1992.** Sec. Dimopoulos et al. (2013)

***Dianthus juniperinus* subsp. *pulviniformis* (Greuter) Turland in Bull. Brit. Mus. (Nat. Hist.), Bot. 22: 166. 1992.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus pulviniformis* Greuter in Candollea 20: 189. 1965 syn. sec. WFO 2018

***Dianthus juzeptchukii* M.Kuzmina in Bot. Zhurn. (Moscow & Leningrad) 81: 80. 1996.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus kapinaensis* Markgr. & Lindtner in Glasn. Skopsk. Naucn. Drustva 18(6): 125. 1938.** Sec. Marhold (2011)

***Dianthus karami* (Boiss.) Mouterde in Bull. Soc. Bot. France 104: 511. 1958.** Sec. Marhold (2011)
≡ *Dianthus hypochlorus* var. *karami* Boiss., Fl. Orient. Suppl.: 80. 1888 syn. sec. Marhold (2011)

***Dianthus karataviensis* Pavlov in Sovetsk. Bot. 1934(1): 22. 1934.** Sec. Czerepanov (1995)

***Dianthus kastembeluensis* Freyn & Sint. in Oesterr. Bot. Z. 43: 375. 1893.** Sec. Marhold (2011)

***Dianthus khamiesbergensis* Sond., Fl. Cap. 1: 124. 1860.** Sec. African Plant Database (version 3.4.0)

***Dianthus kirghizicus* Schischk., Fl. URSS 6: 896. 1936.** Sec. Czerepanov (1995)

Dianthus kiusianus **Makino in Bot. Mag. (Tokyo) 26: 178. 1912.** Sec. Zoku (1965)
= *Dianthus hachijoensis* Nakai in Bot. Mag. (Tokyo) 35: 150. 1921 syn. sec. Zoku (1965)

Dianthus klokovii **Knjasev in Bot. Zhurn. (Moscow & Leningrad) 82(11): 80. 1997.** Sec. Knjasev (1997)

Dianthus knappii **(Pant.) Asch. & Kanitz ex Borbás, Mat. Term. Közlem. 13: 196. 1877.** Sec. Marhold (2011)
≡ *Dianthus liburnicus* var. *knappii* Pant. in Oesterr. Bot. Z. 23: 4. 1873 syn. sec. Marhold (2011) ≡ *Dianthus balbisii* subsp. *knappii* (Pant.) Peruzzi & Uzunov in Phytol. Balcan. 14: 48. 2008 syn. sec. Marhold (2011)

Dianthus koreanus **D.C.Son & K.H.Lee in Phytotaxa 303(1): 71. 2017.** Sec. Son et al. (2017)

Dianthus kubanensis **Schischk. in Trudy Bot. Inst. Akad. Nauk S.S.S.R., ser. 1, Fl. Sist. Vyssh. Rast. 3: 184. 1937.** Sec. Kuzmina & Nersesyan (2012)

Dianthus kuschakewiczii **Regel & Schmalh. in Trudy Imp. S.-Peterburgsk. Bot. Sada 5: 244. 1877.** Sec. Dequan & Turland (2001)

Dianthus kusnezowii **Marcow. in Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 4: 31. 1923.** Sec. Kuzmina & Nersesyan (2012)
= *Dianthus abchasicus* Gvin. in Zametki Sist. Geogr. Rast. 27: 78. 1969 syn. sec. Kuzmina & Nersesyan (2012)

Dianthus lactiflorus **Fenzl in Asie Min., Bot. 1: 215. 1860.** Sec. Marhold (2011)

Dianthus laingsburgensis **S.S.Hooper in Hookers Icon. Pl. 37: 30. 1959.** Sec. African Plant Database (version 3.4.0)

Dianthus lanceolatus **Steven ex Rchb., Pl. Crit. 6: 34. 1828.** Sec. Kuzmina & Nersesyan (2012)

Dianthus langeanus **Willk., Prodr. Fl. Hispan. 3: 690. 1878.** Sec. Bernal et al. (1990)

Dianthus laricifolius **Boiss. & Reut., Diagn. Pl. Nov. Hisp.: 7. 1842.** Sec. Bernal et al. (1990)

Dianthus laricifolius **subsp.** ***caespitosifolius*** **(Planellas) M.Laínz, Aport. Conocim. Fl. Gallega 6: 6. 1968.** Sec. Bernal et al. (1990)
≡ *Dianthus caespitosifolius* Planellas, Ensayo Fl. Gallega: 118. 1852 syn. sec. Bernal et al. (1990)

= *Dianthus planellae* Willk., Icon. Descr. Pl. Nov. 1: 79. 1854 syn. sec. Bernal et al. (1990)

Dianthus laricifolius* subsp. *laricifolius

***Dianthus laricifolius* subsp. *marizii* (Samp.) Franco in Ann. Bot. Fenn. 23: 91. 1986.** Sec. Bernal et al. (1990)
≡ *Dianthus graniticus* var. *marizii* Samp. in Ann. Sci. Nat. (Oporto) 10: 14. 1906 syn. sec. Bernal et al. (1990) ≡ *Dianthus marizii* (Samp.) Samp. in Bol. Soc. Brot. II, 1: 134. 1922 syn. sec. Bernal et al. (1990) ≡ *Dianthus merinoi* subsp. *marizii* (Samp.) Rivas Mart. & Penas in Itinera Geobot. 15: 700. 2002 syn. sec. WFO 2018 – *Dianthus graniticus* var. *maritzii* Samp. in Ann. Sci. Nat. (Oporto) 10: 14. 1906 syn. sec. Kew WCVP (2019) [is misspelling for *Dianthus graniticus* var. *marizii* Samp.]

***Dianthus laricifolius* subsp. *merinoi* (M.Laínz) M.Laínz in Anales Jard. Bot. Madrid 43: 197. 1986.** Sec. Bernal et al. (1990)
≡ *Dianthus merinoi* M.Laínz, Comun. I. N. I. A., Sér. Recurs. Nat. 2: 3. 1974 syn. sec. Bernal et al. (1990)

***Dianthus legionensis* (Willk.) F.N.Williams in J. Bot. 23: 346. 1885.** Sec. Bernal et al. (1990)
≡ *Dianthus lusitanus* var. *legionensis* Willk., Prodr. Fl. Hispan. 3: 684. 1878 syn. sec. Bernal et al. (1990)
= *Dianthus toletanus* var. *cutandae* Pau in Bol. Soc. Ibér. Ci. Nat. 22: 87. 1923 syn. sec. Bernal et al. (1990) ≡ *Dianthus cutandae* (Pau) Pau in Cavanillesia 1: 63. 1928 syn. sec. Bernal et al. (1990) ≡ *Dianthus scaber* subsp. *cutandae* (Pau) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 190. 1963 syn. sec. Bernal et al. (1990)

***Dianthus leptoloma* Steud. ex A.Rich., Tent. Fl. Abyss. 1: 42. 1847.** Sec. African Plant Database (version 3.4.0)
= *Dianthus abyssinicus* R.Br., Voy. Abyss. App: lxiv. 1814 syn. sec. WFO 2018

***Dianthus leptopetalus* Willd., Enum. Pl.: 468. 1809.** Sec. Kuzmina & Nersesyan (2012)
= *Dianthus pomeridianus* M.Bieb., Fl. Taur.-Caucas. 1: 329. 1808 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus pubescens* Fisch., Cat. Jard. Gorenki ed. 2: 59. 1812 syn. sec. WFO 2018
= *Dianthus bicolor* Hornem. in Hort. Bot. Hafn. 1: 407. 1813 syn. sec. WFO 2018

***Dianthus leucophaeus* Sm., Fl. Graec. Prodr. 1(2): 288. 1809.** Sec. Marhold (2011)
= *Dianthus olympicus* Sibth. ex Boiss., Fl. Orient. 1: 487. 1867 syn. sec. Kew WCVP (2019)
= *Dianthus ilgazensis* Czeczott in Acta Soc. Bot. Poloniae 9: 32. 1932 syn. sec. Marhold (2011)

Dianthus leucophoeniceus **Dörfl. & Hayek in Oesterr. Bot. Z. 70: 13. 1921.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus giganteus* subsp. *leucophoeniceus* (Dörfl. & Hayek) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 191. 1963 syn. sec. Dimopoulos et al. (2013)

Dianthus libanotis **Labill. in Icon. Pl. Syr. 1: 14. 1791.** Sec. Kuzmina & Nersesyan (2012)
= *Dianthus atomarius* Boiss., Diagn. Pl. Orient., ser. 1, 8: 71. 1849 syn. sec. Kuzmina & Nersesyan (2012)

Dianthus lindbergii **Riedl in Ann. Naturhist. Mus. Wien 65: 30. 1962.** Sec. Rechinger (1988)

Dianthus longicalyx **Miq. in J. Bot. Néerl. 1: 127. 1861.** Sec. Dequan & Turland (2001)
= *Dianthus oreadum* Hance in Ann. Sci. Nat., Bot. V, 5: 207. 1866 syn. sec. Dequan & Turland (2001) ≡ *Dianthus superbus* var. *oreadum* (Hance) Pamp. in Nuovo Giorn. Bot. Ital. n.s., 17: 265. 1910 syn. sec. Dequan & Turland (2001)
= *Dianthus superbus* f. *longicalycinus* Maxim. in Trudy Imp. S.-Peterburgsk. Bot. Sada 11: 64. 1890 syn. sec. Dequan & Turland (2001) ≡ *Dianthus superbus* var. *longicalycinus* (Maxim.) F.N.Williams in J. Linn. Soc., Bot. 34: 411. 1899 syn. sec. Dequan & Turland (2001) ≡ *Dianthus superbus* subsp. *longicalycinus* (Maxim.) Kitam. in Acta Phytotax. Geobot. 20: 205. 1962 syn. sec. WFO 2018
= *Dianthus superbus* var. *latifolius* Nakai in Bot. Mag. (Tokyo) 43: 457. 1929 syn. sec. WFO 2018 ≡ *Dianthus superbus* f. *latifolius* (Nakai) Kitag. in J. Jap. Bot. 40: 138. 1965 syn. sec. WFO 2018
= *Dianthus taiwanensis* Masam. in Trans. Nat. Hist. Soc. Taiwan 33: 618. 1943 syn. sec. Dequan & Turland (2001) ≡ *Dianthus superbus* var. *taiwanensis* (Masam.) T.S.Liu & S.S.Ying, Fl. Taiwan 2: 334. 1976 syn. sec. Dequan & Turland (2001)
= *Dianthus superbus* f. *tricolor* Honda in Acta Phytotax. Geobot. 20: 18. 1962 syn. sec. WFO 2018
= *Dianthus superbus* var. *pycnophyllus* Kitag. in J. Jap. Bot. 55: 266. 1980 syn. sec. WFO 2018

Dianthus longiglumis **Delile in Ann. Sci. Nat., Bot. II, 20: 89. 1843.** Sec. African Plant Database (version 3.4.0)

Dianthus longivaginatus **Rech.f. in Plant Syst. Evol. 142: 244. 1983.** Sec. Rechinger (1988)

Dianthus ×lorberi **Kubát & Abtová in Severoceskou Prír. 21: 5. 1988.** Sec. Danihelka et al. (2012)

Dianthus lucae **Asch. in Oesterr. Bot. Z. 26: 259. 1876**
= *Dianthus* ×*lucae* var. *novakii* Graebn., Syn. Mitteleur. Fl. 5(2): 451. 1922 syn. sec. Kew WCVP (2019) ≡ *Dianthus* ×*novakii* (Graebn.) Novák in Vestn. Král. Ceské Spolecn. Nauk. Tr. Mat.-Prír. 9: 47. 1927 syn. sec. Kew WCVP (2019)

Dianthus lusitanus **Brot., Fl. Lusit. 2: 177. 1805.** Sec. Bernal et al. (1990)
= *Dianthus bolivaris* Sennen in Butl. Inst. Catalana Hist. Nat. 32: 96. 1932 syn. sec. WFO 2018
= *Dianthus lusitanus* var. *imberbis* Maire in Bull. Soc. His. Nat. Afrique N. 28: 342. 1937 syn. sec. Kew WCVP (2019)

Dianthus lusitanus **subsp.** ***lusitanus***

Dianthus lusitanus **subsp.** ***sidi-tualii*** **(Font Quer) Dobignard in J. Bot. Soc. Bot. France 20: 39. 2002.** Sec. African Plant Database (version 3.4.0)
≡ *Dianthus sidi-tualii* Font Quer in Cavanillesia 7: 149. 1935 syn. sec. African Plant Database (version 3.4.0)
= *Dianthus lusitanus* var. *latifolius* Maire in Bull. Soc. His. Nat. Afrique N. 24: 204. 1933 syn. sec. Kew WCVP (2019)
= *Dianthus lusitanus* var. *tamarutii* Caball., App. Discurs. Univ. Madrid: 2. 1935 syn. sec. Kew WCVP (2019)
= *Dianthus atlanticus* Romo in Bot. J. Linn. Soc. 108: 205. 1992 syn. sec. African Plant Database (version 3.4.0)

Dianthus lydus **Boiss., Diagn. Pl. Orient. ser. 1 1: 20. 1843.** Sec. Marhold (2011)

Dianthus macranthoides **Hausskn. ex Bornm. in Beih. Bot. Centralbl. 19(2): 213. 1906.** Sec. Rechinger (1988)

Dianthus macranthus **Boiss., Diagn. Pl. Orient. ser. 1 1: 23. 1843.** Sec. Rechinger (1988)

Dianthus macroflorus **Hamzaoğlu in Syst. Bot. 40: 210. 2015.** Sec. Hamzaoğlu et al. (2015)

Dianthus mainensis **Shaulo & Erst in Feddes Repert. 122: 345. 2011.** Sec. Shaulo & Erst (2011)

Dianthus marschallii **Schischk. in J. Bot. Gard. Nikita 10(2): 39. 1928.** Sec. Czerepanov (1995)
= *Dianthus bicolor* M.Bieb., Fl. Taur.-Caucas. 1: 329. 1808 syn. sec. Czerepanov (1995)
= *Dianthus pallens* subsp. *marschallii* Sanda syn. sec. Czerepanov (1995)

***Dianthus martuniensis* M.Kuzmina in Bot. Zhurn. (Moscow & Leningrad) 81(8): 81. 1996.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus masmenaeus* Boiss., Diagn. Pl. Orient., ser. 2, 5: 51. 1856.** Sec. Kuzmina & Nersesyan (2012)
= *Dianthus mutabilis* Boiss. in Ann. Sci. Nat., Bot. IV, 2: 44. 1854 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus asperulus* Boiss. & A.Huet in Boissier, Diagn. Pl. Orient., ser. 2, 5: 51. 1856 syn. sec. Kuzmina & Nersesyan (2012)

***Dianthus mazanderanicus* Rech.f. in Plant Syst. Evol. 142: 245. 1983.** Sec. Rechinger (1988)

***Dianthus ×melandrioides* Pau in Not. Bot. Fl. Españ. 1: 29. 1887.** Sec. Bernal et al. (1990)
= *Dianthus ×carolipaui* M.B.Crespo & Mateo in Anales Jard. Bot. Madrid 47: 506. 1989 ["1990"] syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.

***Dianthus membranaceus* Borbás in Oesterr. Bot. Z. 26: 125. 1876.** Sec. Kuzmina & Nersesyan (2012)
= *Dianthus rehmannii* Blocki in Kosmos (Lvov) 5: 494. 1880 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus pseudobarbatus* Besser ex Blocki in Deutsche Bot. Monatsschr. 3(9): 131. 1885 syn. sec. Kuzmina & Nersesyan (2012)

***Dianthus mercurii* Heldr. in Atti Congr. Int. Bot. Firenze 1874: 237. 1876.** Sec. Dimopoulos et al. (2013)

***Dianthus micranthus* Boiss. & Heldr. in Boissier, Diagn. Pl. Orient., ser. 1, 8: 69. 1849.** Sec. Marhold (2011)
= *Dianthus haussknechtii* Boiss., Fl. Orient. 1: 489. 1867 syn. sec. Marhold (2011)

***Dianthus microlepis* Boiss., Diagn. Pl. Orient. ser. 1 1: 22. 1843.** Sec. Marhold (2011)
= *Dianthus pumilus* Friv. ex Boiss., Diagn. Pl. Orient. ser. 1 1: 22. 1843 syn. sec. WFO 2018
= *Dianthus brachyanthus* Schur, Enum. Pl. Transsilv.: 96. 1866 syn. sec. WFO 2018
= *Dianthus pumilio* Degen & Urum. in Magyar Bot. Lapok 13: 177. 1914 ["1915"] syn. sec. Marhold (2011)
= *Dianthus microlepis* f. *alba* Delip. & Dimitrov in Feddes Repert. 83: 490. 1972 ["1973"] syn. sec. WFO 2018
= *Dianthus microlepis* var. *degenii* Stoj. & Acht. syn. sec. WFO 2018 ≡ *Dianthus microlepis* subsp. *degenii* (Stoj. & Acht.) Peev & Zlatkova in Phytologia Balcan. 1: 38. 1995 syn. sec. WFO 2018

= *Dianthus microlepis* var. *musalae* Velen. syn. sec. WFO 2018 ≡ *Dianthus musalae* (Velen.) Velen. in Sitzungsber. Königl. Böhm. Ges. Wiss., Math.-Naturwiss. Cl. 8: 6. 1910 [“1911”] syn. sec. WFO 2018

***Dianthus micropetalus* Ser., Prodr. 1: 359. 1824.** Sec. African Plant Database (version 3.4.0)

***Dianthus moesiacus* Vis. & Pančić in Mem. Reale Ist. Veneto Sci. 15: 17. 1870.** Sec. Marhold (2011)

≡ *Dianthus carthusianorum* var. *moesiacus* (Vis. & Pančić) F.N.Williams in J. Linn. Soc., Bot. 29: 376. 1893 syn. sec. Kew WCVP (2019)

= *Dianthus burgasensis* Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 192. 1963 syn. sec. WFO 2018

***Dianthus moesiacus* subsp. *grancarovii* (Urum.) Stoj. & Acht. in Sborn. Bălg. Akad. Nauk. 29(2): 53. 1935.** Sec. Marhold (2011)

≡ *Dianthus grancarovii* Urum. in Sborn. Bălg. Akad. Nauk. 22(1): 22. 1926 syn. sec. Marhold (2011) ≡ *Dianthus moesiacus* var. *grancarovii* Urum. ex Stoj. & Stef., Fl. Bulg. ed. 2: 368. 1933 syn. sec. this publication

Dianthus moesiacus* subsp. *moesiacus

***Dianthus moesiacus* subsp. *sevlievensis* (Degen & Nejceff) Stoj. & Acht. in Sborn. Bălg. Akad. Nauk. 29(2): 54. 1935.** Sec. Marhold (2011)

≡ *Dianthus vandasii* var. *sevlievensis* Degen & Nejceff in Period. Spis. Bulg. Knizh. Druzh. 69: 74. 1908 syn. sec. Marhold (2011)

***Dianthus moesiacus* subsp. *skobelevii* (Velen.) Stoj. & Acht. in Sborn. Bălg. Akad. Nauk. 29(2): 53. 1935.** Sec. Marhold (2011)

≡ *Dianthus moesiacus* var. *skobelevii* Velen., Fl. Bulg. Suppl.: 45. 1898 syn. sec. Marhold (2011)

***Dianthus monadelphus* Vent., Choix Pl.: t. 39. 1807.** Sec. Dimopoulos et al. (2013)

= *Dianthus ochroleucus* Pers., Syn. Pl. 1: 494. 1805 syn. sec. WFO 2018

***Dianthus monadelphus* subsp. *judaicus* (Boiss.) Greuter & Burdet in Willdenowia 12: 186. 1982.** Sec. Marhold (2011)

≡ *Dianthus judaicus* Boiss., Diagn. Pl. Orient., ser. 1, 8: 66. 1849 syn. sec. Marhold (2011)

= *Dianthus auraniticus* Post in J. Linn. Soc., Bot. 24: 422. 1888 syn. sec. Marhold (2011)

Dianthus monadelphus* subsp. *monadelphus

***Dianthus monadelphus* subsp. *pallens* (Sm.) Greuter & Burdet in Willdenowia 12: 187. 1982.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus pallens* Sm., Fl. Graec. Prodr. 1(2): 286. 1809 syn. sec. WFO 2018
= *Dianthus procumbens* Vent., Choix Pl.: Index. 1808 syn. sec. WFO 2018
= *Dianthus rhodopeus* Velen. in Sitzungsber. Königl. Böhm. Ges. Wiss., Math.-Naturwiss. Cl. 1890(2): 40. 1890 syn. sec. WFO 2018

***Dianthus monspessulanus* L., Amoen. Acad. 4: 1313. 1759.** Sec. Marhold (2011)

***Dianthus monspessulanus* subsp. *marsicus* (Ten.) Novák, Spisy Prir. Fak. Karlovy Univ. 21: 25. 1924.** Sec. Marhold (2011)
≡ *Dianthus marsicus* Ten., Fl. Napol. 4: 61. 1830 syn. sec. Marhold (2011) ≡ *Dianthus monspessulanus* var. *marsicus* (Ten.) Arcang., Comp. Fl. Ital.: 87. 1882 syn. sec. this publication ≡ *Dianthus sternbergii* subsp. *marsicus* (Ten.) Pignatti in Giorn. Bot. Ital. 107: 209. 1973 syn. sec. Marhold (2011) ≡ *Dianthus waldsteinii* subsp. *marsicus* (Ten.) Greuter & Burdet in Willdenowia 12: 188. 1982 syn. sec. Marhold (2011)

Dianthus monspessulanus* subsp. *monspessulanus

***Dianthus mooiensis* F.N.Williams in J. Bot. 27: 199. 1889.** Sec. African Plant Database (version 3.4.0)
≡ *Dianthus moviensis* F.N.Williams in J. Bot. 27: 199. 1889 syn. sec. African Plant Database (version 3.4.0)
= *Dianthus nelsonii* F.N.Williams in J. Bot. 27: 200. 1889 syn. sec. WFO 2018

***Dianthus mooiensis* subsp. *kirkii* (Burtt Davy) S.S.Hooper in Hookers Icon. Pl. 37: 54. 1959.** Sec. African Plant Database (version 3.4.0)
≡ *Dianthus kirkii* Burtt Davy in Bull. Misc. Inform. Kew 1922: 220. 1922 syn. sec. African Plant Database (version 3.4.0) ≡ *Dianthus moviensis* subsp. *kirkii* (Burtt Davy) S.S.Hooper in Hookers Icon. Pl. 37: 54. 1959 syn. sec. this publication

Dianthus mooiensis* subsp. *mooiensis

***Dianthus mooiensis* var. *dentatus* Burtt Davy in Bull. Misc. Inform. Kew 1922: 222. 1922.** Sec. African Plant Database (version 3.4.0)
– *Dianthus moviensis* var. *dentatus* Burtt Davy in Bull. Misc. Inform. Kew 1922: 222. 1922 syn. sec. this publication [is misspelling for *Dianthus mooiensis* var. *dentatus* Burtt Davy]

***Dianthus moravicus* Kovanda in Preslia 54: 241. 1982.** Sec. Marhold (2011)
≡ *Dianthus gratianopolitanus* subsp. *moravicus* (Kovanda) Holub in Folia Geobot. Phytotax. 18: 205. 1983 syn. sec. this publication

***Dianthus morisianus* Vals. in Boll. Soc. Sarda Sci. Nat. 24: 333. 1985.** Sec. Bacchetta et al. (2010)
≡ *Dianthus siculus* subsp. *morisianus* (Vals.) Arrigoni in Parlatorea 7: 20. 2005 syn. sec. Bacchetta et al. (2010)

***Dianthus mossanus* Bacch. & Brullo in Portugaliae Act. Biol., Sér. B, Sist. 19: 296. 2000.** Sec. Bacchetta & Brullo (2000)
≡ *Dianthus siculus* subsp. *mossanus* (Bacch. & Brullo) Arrigoni in Parlatorea 7: 20. 2005 syn. sec. WFO 2018

***Dianthus muglensis* Hamzaoğlu & Koç in Phytotaxa 491(4): 291. 2021.** Sec. Hamzaoğlu & Koç (2021)
≡ *Dianthus elegans* var. *gramineus* R.M.Burton in Karaca Arbor. Mag. 3: 184. 1997 syn. sec. Hamzaoğlu & Koç (2021)

***Dianthus multiaffinis* Pau in Bol. Real Soc. Esp. Hist. Nat. 21: 142. 1921.** Sec. Bernal et al. (1990)
≡ *Dianthus pungens* var. *multiaffinis* (Pau) O.Bolòs & Vigo in Butl. Inst. Catalana Hist. Nat., Secc. Bot. 38(1): 88. 1974 syn. sec. Bernal et al. (1990) ≡ *Dianthus costae* subsp. *multiaffinis* (Pau) M.Laínz in Anales Jard. Bot. Madrid 43: 473. 1986 ["1987"] syn. sec. Bernal et al. (1990) ≡ *Dianthus multiceps* subsp. *multiaffinis* (Pau) Rivas Mart. in Itinera Geobot. 15: 700. 2002 syn. sec. WFO 2018

***Dianthus multiceps* Costa ex Willk. in Linnaea 30: 88. 1859.** Sec. WFO 2018
≡ *Dianthus cintranus* subsp. *multiceps* (Costa ex Willk.) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 190. 1963 syn. sec. Marhold (2011) ≡ *Dianthus pungens* subsp. *multiceps* (Costa ex Willk.) O.Bolòs & Vigo in Butl. Inst. Catalana Hist. Nat., Secc. Bot. 38(1): 88. 1974 syn. sec. Marhold (2011) ≡ *Dianthus pungens* var. *multiceps* (Costa ex Willk.) O.Bolòs & Vigo in Butl. Inst. Catalana Hist. Nat., Secc. Bot. 38: 88. 1974 syn. sec. Kew WCVP (2019)
= *Dianthus* ×*bergadensis* Sennen in Bol. Soc. Ibér. Ci. Nat. 25: 144. 1926 syn. sec. Bernal et al. (1990)
= *Dianthus* ×*corberae* Sennen in Bol. Soc. Ibér. Ci. Nat. 25: 143. 1926 ["1927"] syn. sec. Bernal et al. (1990)
= *Dianthus* ×*notabilis* Sennen in Bol. Soc. Ibér. Ci. Nat. 25: 207. 1926 ["1927"] syn. sec. Bernal et al. (1990)

Dianthus multiceps* subsp. *multiceps

***Dianthus multiceps* subsp. *praepyrenaicus* M.Bernal in Anales Jard. Bot. Madrid 44: 569. 1987.** Sec. Bernal et al. (1990)

***Dianthus multiflorus* Deniz & Aykurt in Phytokeys 63: 3. 2016.** Sec. Deniz et al. (2016)

***Dianthus multisquamatus* F.N.Williams in J. Bot. 23: 344. 1885.** Sec. Williams (1893)

***Dianthus multisquameus* Bondarenko & R.M.Vinogr., Opred. Rast. Sred. Azii 2: 327. 1971.** Sec. Czerepanov (1995)

***Dianthus muschianus* Kotschy ex Boiss., Fl. Orient. 1: 510. 1867.** Sec. Marhold (2011)

***Dianthus myrtinervius* Griseb., Spic. Fl. Rumel. 1: 194. 1843.** Sec. Dimopoulos et al. (2013)
= *Dianthus myrtinervius* subsp. *zupancicii* Micevski & E.Mayer in Razpr. Slov. Akad. Znan. Umetn., Razr. Nar. Vede 43: 411. 2002 syn. sec. WFO 2018

***Dianthus myrtinervius* subsp. *caespitosus* Strid & Papan. in Ann. Mus. Goulandris 4: 219. 1978.** Sec. Dimopoulos et al. (2013)
= *Dianthus myrtinervius* var. *oxylepis* Boiss., Fl. Orient. 1: 509. 1867 syn. sec. this publication ≡ *Dianthus oxylepis* (Boiss.) Kümmerle & Jáv., Balkán-Kutat Tud. Eredm. 3: 233. 1926 syn. sec. Dimopoulos et al. (2013)
= *Dianthus kajmaktzalanicus* Mitsevski in Fragm. Balcan. Mus. Macedon. Sci. Nat. 10(4): 29. 1977 syn. sec. Dimopoulos et al. (2013)

Dianthus myrtinervius* subsp. *myrtinervius

***Dianthus namaensis* Schinz in Bull. Herb. Boiss. 5(App. 3): 84. 1897.** Sec. African Plant Database (version 3.4.0)
= *Dianthus pearsonii* Burtt Davy in Bull. Misc. Inform. Kew 1922: 215. 1922 syn. sec. African Plant Database (version 3.4.0)

***Dianthus namaensis* var. *dinteri* (Schinz) S.S.Hooper.** Sec. African Plant Database (version 3.4.0)
= *Dianthus dinteri* Schinz in Vierteljahrsschr. Naturf. Ges. Zürich 74: 110. 1929 syn. sec. African Plant Database (version 3.4.0)

***Dianthus namaensis* var. *junceus* (Burtt Davy) S.S.Hooper in Hookers Icon. Pl. 37: 30. 1959.** Sec. African Plant Database (version 3.4.0)
≡ *Dianthus junceus* Burtt Davy in Bull. Misc. Inform. Kew 1922: 219. 1922 syn. sec. African Plant Database (version 3.4.0)

Dianthus namaensis* var. *namaensis

***Dianthus nangarharicus* Rech.f. in Plant Syst. Evol. 142: 240. 1983.** Sec. Rechinger (1988)

***Dianthus nanshanicus* Chang Y.Yang & L.X.Dong in Bull. Bot. Res., Harbin 28: 644. 2008.** Sec. Dequan & Turland (2001)

***Dianthus nardiformis* Janka in Oesterr. Bot. Z. 23: 195. 1873.** Sec. Marhold (2011)

***Dianthus nihatii* Güner, Fl. Turkey 11: 318. 2000 [“2001”].** Sec. Güner (2000)

***Dianthus nitidus* Waldst. & Kit. in Descr. Icon. Pl. Hung. 2: 209. 1805.** Sec. Marhold (2011)

***Dianthus noeanus* Boiss., Diagn. Pl. Orient., ser. 2, 5: 52. 1856.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus strictus* subsp. *noeanus* (Boiss.) Stoj. & Acht. in Sborn. Bulg. Akad. Nauk. 29: 81. 1935 syn. sec. Dimopoulos et al. (2013) ≡ *Dianthus petraeus* subsp. *noeanus* (Boiss.) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 190. 1963 syn. sec. WFO 2018

***Dianthus nudiflorus* Griff., Not. Pl. Asiat. 4: 466. 1854.** Sec. Madhani et al. (2018)
= *Velezia rigida* L., Sp. Pl.: 332. 1753 syn. sec. Kew WCVP (2019)
= *Velezia rigida* var. *glabrata* Regel in Izv. Imp. Obshch. Lyubit. Estestv. Moskovsk. Univ. 34(2): 13. 1882 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.
= *Velezia rigida* var. *sessiliflora* F.N.Williams in J. Bot. 37: 28. 1899 syn. sec. Kew WCVP (2019)

***Dianthus oliastrae* Bacch., Brullo, Casti & Giusso in Nordic J. Bot. 28: 171. 2010.** Sec. Bacchetta et al. (2010)

***Dianthus orientalis* Adams in Beitr. Naturk. 1: 54. 1805.** Sec. Kuzmina & Nersesyan (2012)
= *Dianthus fimbriatus* M.Bieb., Fl. Taur.-Caucas. 1: 332. 1808 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus pogonopetalus* Boiss. & Kotschy in Boissier, Diagn. Pl. Orient. ser. 2, 6: 29. 1859 syn. sec. Kuzmina & Nersesyan (2012)

***Dianthus orientalis* subsp. *aphanoneurus* Rech.f. in Plant Syst. Evol. 151: 290. 1986.** Sec. Kuzmina & Nersesyan (2012)
≡ *Dianthus aphanoneurus* (Rech.f.) M.Kuzmina in Bot. Zhurn. (Moscow & Leningrad) 81: 82. 1996 syn. sec. Kuzmina & Nersesyan (2012)

***Dianthus orientalis* subsp. *gilanicus* Rech.f. in Pl. Syst. Evol. 151(3–4): 289. 1986.** Sec. Rechinger (1988)

***Dianthus orientalis* subsp. *gorganicus* Rech.f. in Pl. Syst. Evol. 151(3–4): 291. 1986.** Sec. Rechinger (1988)

***Dianthus orientalis* subsp. *ketzkhovelii* (Makaschv.) Nersesian, Konspekt Fl. Kavkaza 3(2): 194. 2012.** Sec. Kuzmina & Nersesyan (2012)
≡ *Dianthus ketzkhovelii* Makaschv. in Soobshch. Akad. Nauk Gruzinsk. S.S.R. 8(7): 447. 1947 syn. sec. Kuzmina & Nersesyan (2012)

***Dianthus orientalis* subsp. *macropetalus* (Boiss.) Rech.f. in Plant Syst. Evol. 151: 289. 1986.** Sec. Kuzmina & Nersesyan (2012)
≡ *Dianthus fimbriatus* var. *macropetalus* Boiss., Fl. Orient. Suppl.: 77. 1888 syn. sec. Kuzmina & Nersesyan (2012)

***Dianthus orientalis* subsp. *nassireddinii* (Stapf) Rech.f. in Plant Syst. Evol. 151: 292. 1986.** Sec. Kuzmina & Nersesyan (2012)
≡ *Dianthus nassireddinii* Stapf in Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. 51: 279. 1886 syn. sec. WFO 2018
= *Dianthus dumulosus* Boiss. & A.Huet in Boissier, Diagn. Pl. Orient., ser. 2, 5: 53. 1856 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus fimbriatus* var. *brachyodontus* Boiss. & A.Huet in Boissier, Diagn. Pl. Orient., ser. 2, 5: 53. 1856 syn. sec. Kuzmina & Nersesyan (2012) ≡ *Dianthus brachyodontus* (Boiss. & A.Huet) Grossh., Fl. Cauc., ed. 2, 3: 294. 1945 syn. sec. Kuzmina & Nersesyan (2012)

***Dianthus orientalis* subsp. *obtusisquameus* (Boiss.) Rech.f. in Plant Syst. Evol. 151: 291. 1986.** Sec. Kuzmina & Nersesyan (2012)
≡ *Dianthus fimbriatus* var. *obtusisquameus* Boiss., Fl. Orient. 1: 495. 1867 syn. sec. Kuzmina & Nersesyan (2012)

Dianthus orientalis* subsp. *orientalis

***Dianthus orientalis* subsp. *scoparius* (Fenzl ex Boiss.) Bornm. in Beih. Bot. Centralbl. 28(2): 134. 1911.** Sec. Rechinger (1988)
≡ *Dianthus scoparius* Fenzl ex Boiss., Fl. Orient. 1: 494. 1867 syn. sec. Kuzmina & Nersesyan (2012)
= *Dianthus fallax* Rech.f. & Esfand. in Bot. Jahrb. Syst. 75: 362. 1951 syn. sec. Rechinger (1988)

***Dianthus orientalis* subsp. *stenocalyx* (Boiss.) Rech.f. in Plant Syst. Evol. 151: 292. 1986.** Sec. Rechinger (1988)
≡ *Dianthus fimbriatus* var. *stenocalyx* Boiss., Fl. Orient. 1: 495. 1867 syn. sec. Rechinger (1988)
= *Dianthus macronyx* Fenzl ex Boiss., Fl. Orient. 1: 495. 1867 syn. sec. Rechinger (1988)

= *Dianthus pulverulentus* Stapf in Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. 51: 279. 1886 syn. sec. Rechinger (1988)

***Dianthus oschtenicus* Galushko in Novosti Sist. Vyssh. Rast. 2: 118. 1965.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus pachygonus* (Fisch. & C.A.Mey.) Fassou, N.Korotkova, Nersesian & Borsch.** Sec. this publication 167
≡ *Tunica pachygona* Fisch. & C.A.Mey., Index Sem. Hort. Bot. Petropol. 4: 50. 1838 syn. sec. this publication;
= *Saponaria cretica* L., Sp. Pl., ed. 2 1: 584. 1762 syn. sec. this publication ≡ *Tunica cretica* (L.) Fisch. & C.A.Mey., Index Sem. Hort. Bot. Petropol. 4: 49. 1837 syn. sec. Kew WCVP (2019) ≡ *Petrorhagia cretica* (L.) P.W.Ball & Heywood in Bull. Brit. Mus. (Bot.) 3(4): 142. 1964 ≡ *Fiedleria cretica* (L.) Ovcz., Fl. Tadzhiksk. S.S.R. 3: 608. 1968 syn. sec. this publication

***Dianthus paghmanicus* Rech.f. in Bot. Jahrb. Syst. 75: 362. 1951.** Sec. Rechinger (1988)

***Dianthus palinensis* S.S.Ying, Col. Ill. Fl. Taiwan 2: 693. 1987.** Sec. Dequan & Turland (2001)

***Dianthus pallidiflorus* Ser., Prodr. 1: 358. 1824.** Sec. Marhold (2011)
≡ *Dianthus campestris* subsp. *pallidiflorus* (Ser.) Schmalh., Fl. Sredn. Yuzhn. Rossii 1: 447. 1895 syn. sec. Marhold (2011)
= *Dianthus paniculatus* Gueldenst., Reis. Russland 1: 68. 1787 syn. sec. WFO 2018
= *Dianthus pallens* M.Bieb., Fl. Taur.-Caucas. 1: 325. 1808 syn. sec. WFO 2018
= *Dianthus saxatilis* Pall. ex M.Bieb., Fl. Taur.-Caucas. 1: 329. 1808 syn. sec. WFO 2018
= *Dianthus emarginatus* Ser., Prodr. 1: 359. 1824 syn. sec. WFO 2018
= *Dianthus parviflorus* Willd. ex Ledeb., Fl. Ross. 1: 279. 1842 syn. sec. WFO 2018
= *Dianthus aridus* Griseb. ex Janka in Oesterr. Bot. Z. 23: 196. 1873 syn. sec. Marhold (2011)
= *Dianthus maeoticus* Klokov in Sc. Mag. Biol. 1927: 13. 1927 syn. sec. Marhold (2011)

***Dianthus pamiralaicus* Lincz. in Novosti Sist. Vyssh. Rast. 1: 76. 1964.** Sec. Czerepanov (1995)

***Dianthus pancicii* Velen. in Sitzungsber. Königl. Böhm. Ges. Wiss., Math.-Naturwiss. Cl. 1886(Extr.): 9. 1886.** Sec. Marhold (2011)
≡ *Dianthus stenopetalus* var. *pancicii* (Velen.) F.N.Williams in J. Linn. Soc., Bot. 29: 389. 1893 syn. sec. this publication ≡ *Dianthus cruentus* var. *pancicii* (Velen.) Stoj. & Acht., Krit. Stud. Nelk. Bulg.: 56. 1935 syn. sec. this publication ≡ *Dianthus cruentus* subsp. *pancicii* (Velen.) Stoj. & Stef., Fl. Bulg., ed. 3: 405. 1948 syn. sec. Marhold (2011)

= *Dianthus tristis* Velen. in Sitzungsber. Königl. Böhm. Ges. Wiss., Math.-Naturwiss. Cl. 1890(2): 41. 1890 syn. sec. Marhold (2011)

***Dianthus* ×*paradoxus* Rouy & Foucaud, Fl. France 3: 187. 1896.** Sec. WFO 2018

***Dianthus patentisquameus* Bondarenko & R.M.Vinogr., Opred. Rast. Sred. Azii 2: 327. 1971.** Sec. Czerepanov (1995)

***Dianthus pavlovii* Lazkov in Bot. Zhurn. (Moscow & Leningrad) 87(12): 113. 2002.** Sec. Lazkov (2006)
– *Dianthus attenuatus* Pavlov, Fl. Kazakhst. 3: 426. 1960, nom. inval. syn. sec. Lazkov (2002)

***Dianthus pavonius* Tausch in Flora 22: 145. 1839.** Sec. Marhold (2011)
= *Dianthus neglectus* Loisel. in J. Bot. (Paris) 2: 321. 1809 syn. sec. Marhold (2011) ≡ *Cylichnanthus neglectus* (Loisel.) Dulac, Fl. Hautes-Pyrénées: 262. 1867

***Dianthus pelviformis* Heuff. in Flora 36: 625. 1853.** Sec. Marhold (2011)
= *Dianthus bulgaricus* Velen., Fl. Bulg.: 78. 1891 syn. sec. Marhold (2011)
= *Dianthus zernyi* Hayek in Repert. Spec. Nov. Regni Veg. Beih. 30(1): 237. 1924 syn. sec. Marhold (2011)

***Dianthus pendulus* Boiss. & Blanche in Boissier, Diagn. Pl. Orient. ser. 2, 6: 28. 1859.** Sec. Rechinger (1988)

***Dianthus persicus* Hausskn. in Mitt. Geogr. Ges. (Thüringen) Jena 9: 16. 1891.** Sec. Rechinger (1988)

***Dianthus petraeus* Waldst. & Kit. in Descr. Icon. Pl. Hung. 3: 246. 1807.** Sec. Dimopoulos et al. (2013)
= *Dianthus bohemicus* Mayer ex Tausch in Flora 13: 246. 1830 syn. sec. WFO 2018
= *Dianthus bebius* Vis. ex Rchb. in Icon. Fl. Germ. Helv. 6: 47. 1844 syn. sec. WFO 2018
= *Dianthus integripetalus* Schur, Enum. Pl. Transsilv.: 98. 1866 syn. sec. WFO 2018
= *Dianthus pseudocaesius* Schur, Enum. Pl. Transsilv.: 98. 1866 syn. sec. WFO 2018
= *Dianthus liliodorus* Pančić, Fl. Serbiae: 176. 1874 syn. sec. Marhold (2011) ≡ *Dianthus petraeus* f. *liliodorus* (Pančić) Hayek in Repert. Spec. Nov. Regni Veg. Beih. 30(1): 252. 1924 syn. sec. Kew WCVP (2019)
= *Dianthus kitaibelii* Janka ex Beck in Ann. K. K. Naturhist. Hofmus. 2: 192. 1889 syn. sec. WFO 2018
= *Dianthus skorpilii* Velen. in Sitzungsber. Königl. Böhm. Ges. Wiss., Math.-Naturwiss. Cl. 1890(2): 40. 1890 syn. sec. WFO 2018

***Dianthus petraeus* subsp. *orbelicus* (Velen.) Greuter & Burdet in Willdenowia 12: 187. 1982.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus strictus* subsp. *orbelicus* Velen., Fl. Bulg. Suppl. 1: 40. 1898 syn. sec. Marhold (2011)
= *Dianthus strictus* Sm., Fl. Graec. Prodr. 1(2): 288. 1809 syn. sec. Marhold (2011)
= *Dianthus simonkaianus* Péterfi in Magyar Bot. Lapok 15: 14. 1916 syn. sec. Marhold (2011) ≡ *Dianthus petraeus* subsp. *simonkaianus* (Péterfi) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 190. 1963 syn. sec. Marhold (2011)
= *Dianthus suendermannii* Bornm. in Repert. Spec. Nov. Regni Veg. 17: 40. 1921 syn. sec. WFO 2018
= *Dianthus stefanoffii* Eig in J. Bot. 75: 191. 1937 syn. sec. Dimopoulos et al. (2013) ≡ *Dianthus petraeus* subsp. *stefanoffii* (Eig) Greuter & Burdet in Willdenowia 12: 187. 1982 syn. sec. Dimopoulos et al. (2013)

Dianthus petraeus* subsp. *petraeus

***Dianthus pinifolius* Sm., Fl. Graec. Prodr. 1(2): 284. 1809.** Sec. Marhold (2011)
= *Dianthus brevifolius* Friv. in Flora 18: 334. 1835 syn. sec. WFO 2018 ≡ *Dianthus pinifolius* subsp. *brevifolius* (Friv.) Stoj. & Stef., Fl. Bulg., ed. 3: 406. 1948 syn. sec. Marhold (2011)
= *Dianthus rumelicus* Velen., Fl. Bulg.: 78. 1891 syn. sec. Marhold (2011) ≡ *Dianthus pinifolius* subsp. *rumelicus* (Velen.) Stoj. & Acht., Sborn. Bălg. Akad. Nauk. 29(2): 66. 1935 syn. sec. Marhold (2011)
= *Dianthus pinifolius* subsp. *smithii* Wettst. in Biblioth. Bot. 26: 33. 1892 syn. sec. Marhold (2011)
= *Dianthus serresianus* Halácsy & Charrel in Oesterr. Bot. Z. 42: 271. 1892 syn. sec. Marhold (2011)
= *Dianthus smithii* Wettst. in Biblioth. Bot. 26: 33. 1892 syn. sec. this publication
= *Dianthus rhodopeus* Davidov in Trav. Soc. Bulg. Sci. Nat. 8: 55. 1915, nom. illeg. syn. sec. Kew WCVP (2019)
= *Dianthus serresianus* Hayek in Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. 94: 140. 1917 syn. sec. Marhold (2011)
= *Dianthus serulis* Kulcz. in Rozpr. Wydz. Mat.-Przyr Polsk Akad. Umiejetn., Dzial A/B, Nauki Mat-Fiz. Biol. 59: 361. 1923 syn. sec. Marhold (2011) ≡ *Dianthus pinifolius* subsp. *serulis* (Kulcz.) Trinajstić in Suppl. Fl. Anal. Jugosl. 6: 9. 1979 syn. sec. Marhold (2011) – *Dianthus pinifolius* subsp. *serulis* (Kulcz.) Trinajstić in Suppl. Fl. Anal. Jugosl. 5: 753. 1979, nom. inval. syn. sec. this publication

***Dianthus pinifolius* subsp. *lilacinus* (Boiss. & Heldr.) Wettst. in Biblioth. Bot. 26: 33. 1892.** Sec. Marhold (2011)
≡ *Dianthus lilacinus* Boiss. & Heldr. in Boissier, Diagn. Pl. Orient., ser. 2, 1: 63. 1854 syn. sec. Marhold (2011)

Dianthus pinifolius **subsp.** ***pinifolius***

Dianthus pinifolius **subsp.** ***serbicus*** **Wettst. in Biblioth. Bot. 26: 34. 1892.** Sec. Marhold (2011)

≡ *Dianthus serbicus* (Wettst.) Hayek in Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Kl., Denkschr. 94: 141. 1918 syn. sec. this publication

Dianthus pinifolius **subsp.** ***tenuicaulis*** **(Turrill) Strid, Fl. Hellenica 1: 368. 1997.** Sec. Marhold (2011)

≡ *Dianthus tenuicaulis* Turrill in Bull. Misc. Inform. Kew 1929: 224. 1929 syn. sec. Marhold (2011)

Dianthus plumarius **L., Sp. Pl.: 411. 1753.** Sec. Marhold (2011)

≡ *Tunica plumaria* (L.) Scop., Fl. Carniol., ed. 2, 1: 300. 1771 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.; ≡ *Caryophyllus plumarius* (L.) Moench, Methodus: 59. 1794 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. ≡ *Cylichnanthus plumarius* (L.) Dulac, Fl. Hautes-Pyrénées: 262. 1867 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. ≡ *Silene plumaria* (L.) E.H.L.Krause, Deutschl. Fl. Abbild., ed. 2, 5: 114. 1901 syn. sec. Kew WCVP (2019);

= *Dianthus hortensis* Schrad. ex Willd., Enum. Pl.: 469. 1809 syn. sec. WFO 2018 ≡ *Dianthus plumarius* var. *hortensis* (Schrad. ex Willd.) Trevir., Index Seminum (WROCL, Wratislaviensi) 1818: 3. 1818 syn. sec. Kew WCVP (2019)

= *Dianthus portensis* Libosch. ex Ser., Prodr. 1: 363. 1824 syn. sec. WFO 2018 ≡ *Dianthus plumarius* var. *portensis* Ser., Prodr. 1: 363. 1824 syn. sec. Kew WCVP (2019)

= *Dianthus plumarius* var. *blandus* Rchb., Fl. Germ. Excurs.: 807. 1832 syn. sec. Marhold (2011) ≡ *Dianthus blandus* (Rchb.) Hayek, Fl. Steiermark 1: 320. 1908 syn. sec. Marhold (2011)

= *Dianthus odoratus* Vest ex Steud., Nomencl. Bot., ed. 2, 1: 500. 1840 syn. sec. WFO 2018

= *Plumaria vulgaris* Opiz, Seznam: 75. 1852 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.

= *Dianthus plumarius* var. *parviflorus* Kauffm., Index Seminum (MHA, Mosquensis) 1868: 9. 1868 syn. sec. Kew WCVP (2019)

= *Dianthus hoppei* Port. ex Hayek, Fl. Steiermark 1: 320. 1908 syn. sec. Marhold (2011)

= *Dianthus neilreichii* Hayek syn. sec. Marhold (2011)

= *Dianthus dubius* Hornem. ex DC., Cat. Pl. Horti Monsp.: 103. 1813, nom. illeg. syn. sec. Marhold (2011) – *Dianthus dubius* Hornem. in Hort. Bot. Hafn. 1: 408. 1813 syn. sec. WFO 2018 [is later isonym of *Dianthus dubius* Hornem. ex DC.]

Dianthus plumarius* subsp. *plumarius

***Dianthus plumarius* subsp. *regis-stephani* (Rapaics) Baksay in Bot. Közlem. 57: 215. 1970.** Sec. Marhold (2011)
≡ *Dianthus regis-stephani* Rapaics syn. sec. WFO 2018 ≡ *Dianthus hungaricus* subsp. *regis-stephani* (Rapaics) Holub in Folia Geobot. Phytotax. 9: 273. 1974 syn. sec. WFO 2018

***Dianthus plumbeus* Schischk. in Izv. Tomsk. Gosud. Univ. 81: 451. 1928.** Sec. Marhold (2011)

***Dianthus polylepis* Bien. ex Boiss., Fl. Orient. 1: 497. 1867.** Sec. Rechinger (1988)

***Dianthus polylepis* subsp. *binaludensis* (Rech.f.) Vaezi & Behrooz. in Pl. Syst. Evol. 299: 1430. 2013.** Sec. Farsi et al. (2013)
≡ *Dianthus binaludensis* Rech.f. in Plant Syst. Evol. 142: 242. 1983 syn. sec. Farsi et al. (2013)

Dianthus polylepis* subsp. *polylepis

***Dianthus polymorphus* M.Bieb., Fl. Taur.-Caucas. 1: 324. 1808.** Sec. Kuzmina & Nersesyan (2012)
= *Dianthus dichotomus* Pall., Reise Südl. Statthaltersch. Russ. Reich. 2: 335. 1801 syn. sec. WFO 2018
= *Dianthus diutinus* Kit. ex Schult., Oestr. Fl. ed. 2, 1: 655. 1814 syn. sec. WFO 2018
≡ *Dianthus polymorphus* var. *diutinus* (Kit.) Ser., Prodr. 1: 356. 1824 syn. sec. this publication
= *Dianthus atratus* Beaupré ex Ser., Prodr. 1: 356. 1824 syn. sec. WFO 2018
= *Dianthus ponticus* Wahlenb., Isis (Oken) 21: 985. 1828 syn. sec. WFO 2018
= *Dianthus glomeratus* Pall. ex Ledeb., Fl. Ross. 1: 276. 1842 syn. sec. WFO 2018
= *Dianthus intermedius* Willd. ex Ledeb., Fl. Ross. 1: 276. 1842 syn. sec. WFO 2018
= *Dianthus autumnalis* Kit. in Linnaea 32: 530. 1863 syn. sec. WFO 2018
= *Dianthus sabuli* Kit. in Linnaea 32: 530. 1863 syn. sec. WFO 2018
= *Dianthus platyodon* Klokov in Bot. Zhurn. (Kiev) 5: 27. 1948 syn. sec. WFO 2018
= *Dianthus polymorphus* var. *platyodon* Sanda syn. sec. WFO 2018

***Dianthus praecox* Willd. ex Spreng., Syst. Veg., ed. 16, 2: 381. 1825.** Sec. Marhold (2011)
≡ *Dianthus plumarius* subsp. *praecox* (Willd. ex Spreng.) Domin syn. sec. Marhold (2011)
= *Dianthus hungaricus* Pers., Syn. Pl. 1: 494. 1805 syn. sec. WFO 2018

***Dianthus praecox* subsp. *lumnitzeri* (Wiesb.) Kmeťová, Biol. Práce Slov. Akad. Vied. 5: 63. 1985.** Sec. Marhold (2011)

≡ *Dianthus lumnitzeri* Wiesb. in Bot. Centralbl. 26: 85. 1886 syn. sec. Marhold (2011) ≡ *Dianthus hungaricus* subsp. *lumnitzeri* (Wiesb.) Holub in Folia Geobot. Phytotax. 9: 272. 1974 syn. sec. WFO 2018 ≡ *Dianthus plumarius* subsp. *lumnitzeri* (Wiesb.) Domin syn. sec. Marhold (2011)

= *Dianthus plumarius* f. *palaviensis* Novák syn. sec. WFO 2018 ≡ *Dianthus lumnitzeri* subsp. *palaviensis* (Novák) Dostál in Folia Mus. Rerum Nat. Bohemiae Occid., Bot. 21: 5. 1984 syn. sec. WFO 2018

Dianthus praecox* subsp. *praecox

***Dianthus praecox* subsp. *pseudopraecox* (Novák) Kmeťová, Biol. Práce Slov. Akad. Vied. 5: 69. 1985.** Sec. Marhold (2011)

≡ *Dianthus plumarius* f. *pseudopraecox* Novák syn. sec. Marhold (2011) ≡ *Dianthus lumnitzeri* subsp. *pseudopraecox* (Novák) Dostál in Folia Mus. Rerum Nat. Bohemiae Occid., Bot. 21: 4. 1984 syn. sec. Marhold (2011)

***Dianthus pratensis* M.Bieb., Fl. Taur.-Caucas. 3: 300. 1819.** Sec. Marhold (2011)

≡ *Dianthus seguieri* lusus *pratensis* (M.Bieb.) Regel in Bull. Soc. Imp. Naturalistes Moscou 34(2): 526. 1862 syn. sec. Kew WCVP (2019)

= *Dianthus chloroleucus* Fisch. in Hort. Bot. Hafn. Suppl: 137. 1819 syn. sec. WFO 2018

= *Dianthus seguieri* lusus *angustifolius* Regel in Bull. Soc. Imp. Naturalistes Moscou 34(2): 526. 1862 syn. sec. Kew WCVP (2019)

= *Dianthus seguieri* lusus *humilis* Regel in Bull. Soc. Imp. Naturalistes Moscou 34(2): 526. 1862 syn. sec. Kew WCVP (2019)

Dianthus pratensis* subsp. *pratensis

***Dianthus pratensis* subsp. *racovitzae* (Prodán) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 189. 1963.** Sec. Marhold (2011)

≡ *Dianthus racovitzae* Prodán, Bul. Soc. St. Cluj 10(2): 162. 1948 syn. sec. Marhold (2011)

***Dianthus pseudarmeria* M.Bieb., Fl. Taur.-Caucas. 1: 323. 1808.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus pseudobarbatus* Besser ex Ledeb.** Sec. Czerepanov (1995)

= *Dianthus trifasciculatus* subsp. *euponticus* Kleopow syn. sec. Czerepanov (1995)

***Dianthus pseudocrinitus* Behrooz. & Joharchi in Phytotaxa 156: 69. 2014.** Sec. Vaezi et al. (2014)

***Dianthus pseudorigidus* (Hub.-Mor.) Fassou, N.Korotkova, Dimop. & Borsch.** Sec. this publication 173
≡ *Velezia pseudorigida* Hub.-Mor. in Bauhinia 2: 195. 1963 syn. sec. this publication

***Dianthus pungens* L., Mant. Pl. 2: 240. 1771.** Sec. Bernal et al. (1990)
= *Dianthus purpureus* Poir., Encycl. 4: 523. 1798 syn. sec. WFO 2018
= *Dianthus serratus* Lapeyr., Hist. Pl. Pyrénées: 241. 1813 syn. sec. Marhold (2011)
≡ *Dianthus asper* var. *serratus* (Lapeyr.) Ser., Prodr. 1: 357. 1824 syn. sec. Kew WCVP (2019)
= *Dianthus insignitus* Timb.-Lagr. in Bull. Soc. Bot. France 11: 143. 1864 syn. sec. WFO 2018

***Dianthus pungens* subsp. *brachyanthus* (Boiss.) B.Fern.Casas, G.López & M.Laínz in Anales Jard. Bot. Madrid 44: 180. 1987.** Sec. Bernal et al. (1990)
≡ *Dianthus brachyanthus* Boiss., Fl. Orient. 1: 701. 1867 syn. sec. Bernal et al. (1990)
≡ *Dianthus subacaulis* subsp. *brachyanthus* (Boiss.) P.Fourn., Quatre Fl. France: 331. 1936 syn. sec. Bernal et al. (1990) ≡ *Dianthus strictus* var. *brachyanthus* (Boiss.) Boiss. syn. sec. this publication
= *Dianthus attenuatus* Xatard ex Walp., Repert. Bot. Syst. 1: 267. 1842 syn. sec. WFO 2018
= *Dianthus pungens* J.Gay ex Boiss., Fl. Orient. 1: 85. 1867 syn. sec. WFO 2018
= *Dianthus brachyanthus* var. *maroccanus* Pau & Font Quer, Iter Marocc. 1927: 197. 1928 syn. sec. WFO 2018 ≡ *Dianthus subacaulis* var. *maroccanus* (Pau & Font Quer) Maire, Fl. Afrique N. 10: 314. 1963 syn. sec. Kew WCVP (2019)
= *Dianthus brachyanthus* subsp. *cantabricus* Font Quer in Collect. Bot. (Barcelona) 3: 355. 1953 syn. sec. Marhold (2011) ≡ *Dianthus subacaulis* subsp. *cantabricus* (Font Quer) Laínz in Bol. Inst. Estud. Adsturianos, Supl. Ci. 15: 12. 1970 syn. sec. Marhold (2011)
= *Dianthus brachyanthus* var. *nivalis* Willk. syn. sec. WFO 2018 ≡ *Dianthus subacaulis* subsp. *nivalis* (Willk.) Malag., Subesp. Variac. Geogr.: 6. 1973 syn. sec. WFO 2018

***Dianthus pungens* subsp. *hispanicus* (Asso) O.Bolòs & Vigo in Butl. Inst. Catalana Hist. Nat., Secc. Bot. 38(1): 188. 1974.** Sec. Bernal et al. (1990)
≡ *Dianthus hispanicus* Asso, Syn. Stirp. Aragon.: 53. 1779 syn. sec. Bernal et al. (1990)
≡ *Dianthus pungens* var. *hispanicus* (Asso) Ser., Prodr. 1: 360. 1824 syn. sec. this publication
= *Dianthus brachyanthus* subsp. *tarraconensis* (Costa) Rivas Mart. ex M.B.Crespo & Mateo in Flora Montiber. 45: 90. 2010 syn. sec. Bernal et al. (1990) ≡ *Dianthus brachyanthus* var. *tarraconensis* Costa in Anales Soc. Esp. Hist. Nat. 3: 183. 1874 syn. sec. Bernal et al. (1990) ≡ *Dianthus pungens* subsp. *tarraconensis* (Costa) O.Bolòs & Vigo in Butl. Inst. Catalana Hist. Nat., Secc. Bot. 38(1): 88. 1974 syn. sec. Bernal et al. (1990) ≡ *Dianthus hispanicus* subsp. *tarraconensis* (Costa) Molero in Folia Bot. Misc. 3: 12. 1982 syn. sec. Bernal et al. (1990)

Dianthus pungens **subsp.** ***pungens***

Dianthus pungens **subsp.** ***ruscinonensis*** **(Boiss.) M.Bernal, Laínz & Muñoz Garm. in Anales Jard. Bot. Madrid 44: 571. 1987.** Sec. Bernal et al. (1990)

≡ *Dianthus brachyanthus* var. *ruscinonensis* Boiss., Fl. Orient. 1: 86. 1867 syn. sec. Bernal et al. (1990) ≡ *Dianthus ruscinonensis* (Boiss.) Sennen in Trab. Mus. Ci. Nat., Ser. Bot., 15: 48. 1931 syn. sec. Bernal et al. (1990) ≡ *Dianthus subacaulis* subsp. *ruscinonensis* (Boiss.) G.Bosc & Kerguélen in Lejeunia 120: 80. 1987 syn. sec. Bernal et al. (1990)

Dianthus purpureimaculatus **Podlech in Mitt. Bot. Staatssamml. München 16: 544. 1980.** Sec. Rechinger (1988)

Dianthus pygmaeus **Hayata in Icon. Pl. Formosan. 3: 34. 1913.** Sec. Dequan & Turland (2001)

= *Dianthus pygmaeus* var. *albiflorus* S.S.Ying in Quart. J. Chin. Forest. 8(4): 120. 1975 syn. sec. Dequan & Turland (2001) ≡ *Dianthus pygmaeus* f. *albiflorus* (S.S.Ying) S.S.Ying, Fl. Taiwan ed. 2, 2: 356. 1996 syn. sec. Dequan & Turland (2001)

Dianthus pyrenaicus **Pourr., Mém. Acad. Sci. Toulouse 3: 318. 1788.** Sec. Marhold (2011)

= *Dianthus cognobilis* (Timb.-Lagr.) Timb.-Lagr. in Bull. Soc. Bot. France 11: 143. 1864 syn. sec. WFO 2018 ≡ *Dianthus requienii* var. *cognobilis* Timb.-Lagr. syn. sec. WFO 2018 ≡ *Dianthus pungens* subsp. *cognobilis* (Timb.-Lagr.) O.Bolòs & Vigo in Butl. Inst. Catalana Hist. Nat., Secc. Bot. 38(1): 88. 1974 syn. sec. WFO 2018

= *Dianthus maritimus* (Rouy) P.Fourn., Quatre Fl. France: 332. 1936, nom. illeg. syn. sec. Marhold (2011) ≡ *Dianthus pyrenaicus* subsp. *maritimus* (Rouy) Kerguélen, Coll. Patrim. Nat. 8: 13. 1993 syn. sec. WFO 2018

= *Dianthus pungens* subsp. *fontqueri* O.Bolòs & Vigo in Butl. Inst. Catalana Hist. Nat., Secc. Bot. 38(1): 88. 1974 syn. sec. WFO 2018 ≡ *Dianthus hispanicus* subsp. *fontqueri* (O.Bolòs & Vigo) A.Barber, M.B.Crespo & Mateo, Contr. Coneix. Fl. Fitogeogr. Lit. Comarca Marina Alta: 77. 1999 syn. sec. WFO 2018

Dianthus pyrenaicus **subsp.** ***attenuatus*** **(Sm.) M.Bernal, Laínz & Muñoz Garm. in Anales Jard. Bot. Madrid 45: 364. 1988.** Sec. Bernal et al. (1990)

≡ *Dianthus attenuatus* Sm. in Trans. Linn. Soc. London 2: 301. 1794 syn. sec. WFO 2018

= *Dianthus longiflorus* Poir., Encycl. 4: 522. 1798 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.

= *Dianthus attenuatus* var. *catalaunicus* Willk. & Costa syn. sec. WFO 2018 ≡ *Dianthus catalaunicus* (Willk. & Costa) Pourr. ex Willk. & Lange, Prodr. Fl. Hispan. 3: 684. 1878 syn. sec. WFO 2018 ≡ *Dianthus pyrenaicus* subsp. *catalaunicus* (Willk. & Costa) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 190. 1963 syn. sec. WFO 2018

Dianthus pyrenaicus* subsp. *pyrenaicus

***Dianthus quadridentatus* (Sm.) Fassou, N.Korotkova, Dimop. & Borsch.** Sec. this publication 175
≡ *Velezia quadridentata* Sm. in Sibthorp & Smith, Fl. Graec. Prodr. 1: 283. 1809 syn. sec. this publication
= *Velezia clavata* d'Urv. in Mém. Soc. Linn. Paris 1: 284. 1822 syn. sec. Kew WCVP (2019)

***Dianthus raddeanus* Vierh. in Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1, 57(1): 1145. 1898.** Sec. Kuzmina & Nersesyan (2012)
= *Dianthus trautvetteri* Woronow in Izv. Kavkazsk. Muz. 7: 346. 1913 syn. sec. Kuzmina & Nersesyan (2012)

***Dianthus ramosissimus* Pall. ex Poir., Encycl. Suppl. 4: 130. 1816.** Sec. Dequan & Turland (2001)

***Dianthus recognitus* Schischk. in Trudy Bot. Inst. Akad. Nauk S.S.S.R., ser. 1, Fl. Sist. Vyssh. Rast. 3: 187. 1937.** Sec. Czerepanov (1995)

***Dianthus recticaulis* Ledeb., Fl. Ross. 1(2): 287. 1842.** Sec. Mosyakin & Fedoronchuk (2018)

***Dianthus repens* Willd., Sp. Pl. 2: 681. 1799.** Sec. Dequan & Turland (2001)
≡ *Dianthus alpinus* var. *repens* (Willd.) Regel in Bull. Soc. Imp. Naturalistes Moscou 34(2): 531. 1862 syn. sec. Kew WCVP (2019) ≡ *Dianthus alpinus* subsp. *repens* (Willd.) Kozhevn. in Novosti Sist. Vyssh. Rast. 18: 238. 1981 syn. sec. Czerepanov (1995) ≡ *Dianthus chinensis* subsp. *repens* (Willd.) Vorosch., Florist. Issl. Razn. Rayonakh SSSR: 167. 1985 syn. sec. WFO 2018 ≡ *Dianthus repens* var. *repens* syn. sec. WFO 2018
= *Dianthus repens* var. *scabripilosus* Y.Z.Zhao in Acta Sci. Nat. Univ. Intramongol. 20: 110. 1989 syn. sec. Dequan & Turland (2001)

Dianthus repens* subsp. *repens

***Dianthus repens* subsp. *schistosus* Kuvaev, Fl. Subarkt. Gor Evraz.: 144. 2006.** Sec. Kuvaev (2006)

***Dianthus rigidus* M.Bieb., Fl. Taur.-Caucas. 1: 325. 1808.** Sec. Czerepanov (1995)
≡ *Tunica rigida* (M.Bieb.) Raf., Fl. Tellur. 2: 54. 1837 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.

***Dianthus robustus* Boiss. & Kotschy ex Boiss., Fl. Orient. 1: 492. 1867.** Sec. Marhold (2011)
= *Dianthus superbiens* Kotschy ex Boiss., Fl. Orient. 1: 492. 1867 syn. sec. WFO 2018

***Dianthus rogowiczii* Kleopow in Izv. Kievsk. Bot. Sada 12–13: 160. 1931.** Sec. Czerepanov (1995)

***Dianthus roseoluteus* Velen. in Oesterr. Bot. Z. 36: 226. 1886.** Sec. Marhold (2011)
≡ *Dianthus campestris* subsp. *roseoluteus* (Velen.) Stoj. & Acht., Sborn. Blghar. Akad. Nauk 29(2): 16. 1935 syn. sec. Marhold (2011)
= *Dianthus purpureoluteus* Velen., Fl. Bulg.: 73. 1891 syn. sec. Marhold (2011)

***Dianthus rudbaricus* Assadi in Iranian J. Bot. 3: 38. 1985.** Sec. Rechinger (1988)

***Dianthus rupicola* Biv., Sicul. Pl. 1: 31. 1806.** Sec. Bernal et al. (1990)
= *Dianthus bisignanii* Ten., Cat. Piante Barra: 13. 1805 syn. sec. Bernal et al. (1990)
= *Dianthus suffruticosus* Willd., Enum. Pl.: 466. 1809 syn. sec. WFO 2018
= *Dianthus involucratus* Poir., Encycl. Suppl. 4: 132. 1816 syn. sec. WFO 2018
= *Dianthus arborescens* Hoffmanns., Verz. Pfl.-Kult.: 56. 1824 syn. sec. WFO 2018
= *Dianthus bertolonii* J.Woods, Tourists Fl.: 45. 1850 syn. sec. Kew WCVP (2019) ≡ *Dianthus rupicola* var. *bertolonii* (J.Woods) Arcang., Comp. Fl. Ital.: 85. 1882 syn. sec. Kew WCVP (2019)
= *Dianthus hermaeensis* Coss., Ill. Fl. Atlant. 1: 129. 1890 syn. sec. Bernal et al. (1990) ≡ *Dianthus rupicola* var. *hermaeensis* (Coss.) F.N.Williams in J. Linn. Soc., Bot. 29: 363. 1893 syn. sec. Kew WCVP (2019) ≡ *Dianthus rupicola* subsp. *hermaeensis* (Coss.) O.Bolòs & Vigo in Butl. Inst. Catalana Hist. Nat., Secc. Bot. 38(1): 187. 1974 syn. sec. Bernal et al. (1990)

***Dianthus rupicola* subsp. *aeolicus* (Lojac.) Brullo & Miniss. in Inform. Bot. Ital. 33: 539. 2001 [“2002”].** Sec. Iamonico (2013)
≡ *Dianthus aeolicus* Lojac., Fl. Sicul. 1(1): 163. 1888 syn. sec. Iamonico (2013)

***Dianthus rupicola* subsp. *bocchoriana* L.Llorens & Gradaille in Candollea 46: 389. 1991.** Sec. New taxa described to the Flora Iberica region after publication of the respective volume. Published at http://www.floraiberica.es/eng/miscelania/nuevos_taxones.php

***Dianthus rupicola* subsp. *lopadusanus* Brullo & Miniss. in Inform. Bot. Ital. 33: 541. 2002 [“2001”].** Sec. Iamonico (2013)

Dianthus rupicola* subsp. *rupicola

***Dianthus ruprechtii* Schischk. ex Grossh., Fl. Kavkaza 2: 432. 1930.** Sec. Kuzmina & Nersesyan (2012)
= *Dianthus carthusianorum* var. *caucasicus* Rupr., Fl. Caucasi: 174. 1869 syn. sec. Kuzmina & Nersesyan (2012)

***Dianthus sachalinensis* Barkalov & Prob., Fl. Ross. Dalnego Vostoka: 444. 2006.** Sec. Barkalov & Probatova (2006)

***Dianthus saetabensis* Rouy in Bull. Soc. Bot. France 29: 44. 1882.** Sec. Mateo Sanz & Crespo (2008)

***Dianthus saetabensis* subsp. *contestanus* (M.B.Crespo & Mateo) M.B.Crespo & Mateo in Flora Montiber. 40: 65. 2008.** Sec. Mateo Sanz & Crespo (2008)
≡ *Dianthus hispanicus* subsp. *contestanus* M.B.Crespo & Mateo in Flora Montiber. 20: 8. 2002 syn. sec. Mateo Sanz & Crespo (2008)

Dianthus saetabensis* subsp. *saetabensis

***Dianthus sahandicus* Assadi in Iranian J. Bot. 3: 45. 1985.** Sec. Rechinger (1988)

***Dianthus sajanensis* (Baikov) Czepinoga, Konspekt Fl. Irkutsk. Obl.: 116. 2008.** Sec. Chepinoga et al. (2008)
≡ *Dianthus superbus* subsp. *sajanensis* Baikov in Bot. Zhurn. (Moscow & Leningrad) 77(9): 80. 1992 syn. sec. Chepinoga et al. (2008)

***Dianthus sancarii* Hamzaoğlu & Koç in Biol. Diversity Conservation 11(1): 31. 2018.** Sec. Hamzaoğlu & Koç (2018)

***Dianthus sardous* Bacch., Brullo, Casti & Giusso in Feddes Repert. 116: 271. 2005.** Sec. Bacchetta et al. (2010)

***Dianthus ×saxatilis* F.W.Schmidt in Neuere Abh. Königl. Böhm. Ges. Wiss. 1: 28. 1790.** Sec. WFO 2018

***Dianthus scardicus* Wettst. in Biblioth. Bot. 26: 31. 1891.** Sec. Marhold (2011)
= *Dianthus scardicus* var. *incisus* Micevski in Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 8: 44. 1987 [“1990”] syn. sec. WFO 2018
= *Dianthus nitidus* subsp. *lakusicii* Wraber in Biol. Vestn. 36: 97. 1988 syn. sec. WFO 2018

***Dianthus schemachensis* Schischk. in Trudy Geobot. Obsl. Pastb. S.S.R. Azerbaidzhn, Ser. A., Zimn. Pabstb. 7: 90. 1931.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus seguieri* Vill., Hist. Pl. Dauphiné 1: 330. 1786.** Sec. Bernal et al. (1990)
≡ *Silene seguieri* (Vill.) E.H.L.Krause, Deutschl. Fl. Abbild., ed. 2, 5: 109. 1901 syn. sec. Kew WCVP (2019)
= *Dianthus asper* Willd., Enum. Pl.: 466. 1809 syn. sec. WFO 2018 ≡ *Dianthus seguieri* var. *asper* (Willd.) W.D.J.Koch, Syn. Fl. Germ. Helv. 1: 96. 1835 syn. sec. Kew WCVP (2019)

= *Dianthus asper* var. *angustifolius* Ser., Prodr. 1: 357. 1824 syn. sec. Kew WCVP (2019)
= *Dianthus seguieri* f. *longibracteatus* Regel, Index Seminum (St. Petersburg, Petropolitanus) 1863: 34. 1863 syn. sec. Kew WCVP (2019)
= *Dianthus seguieri* var. *viscidus* Regel, Index Seminum (St. Petersburg, Petropolitanus) 1863: 40. 1863 syn. sec. Kew WCVP (2019)
= *Cylichnanthus ciliatus* Dulac, Fl. Hautes-Pyrénées: 261. 1867 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.
= *Dianthus sylvaticus* var. *pseudocollinus* P.Fourn., Quatre Fl. France: 330. 1936 syn. sec. Kew WCVP (2019) ≡ *Dianthus seguieri* subsp. *pseudocollinus* (P.Fourn.) Jauzein, Biocosme Mésogéen 27: 114. 2010 syn. sec. Kew WCVP (2019)
= *Dianthus seguieri* var. *subaggregatus* Albov syn. sec. IPNI ≡ *Dianthus subaggregatus* (Albov) Schischk. ex Kem.-Nath. in Vestn. Tiflissk. Bot. Sada, n.s., 5: 12. 1931 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.

***Dianthus seguieri* subsp. *glaber* Čelak., Prodr. F. Böhmen 3: 507. 1875.** Sec. Marhold (2011)

***Dianthus seguieri* subsp. *requienii* (Godr.) M.Bernal, Laínz & Muñoz Garm. in Anales Jard. Bot. Madrid 44: 569. 1987.** Sec. Bernal et al. (1990)
≡ *Dianthus requienii* Godr., Fl. France 1: 234. 1847 syn. sec. Bernal et al. (1990) ≡ *Dianthus furcatus* subsp. *requienii* (Godr.) Kerguélen in Lejeunia 120: 80. 1987 syn. sec. Bernal et al. (1990)
= *Cylichnanthus unibiflorus* Dulac, Fl. Hautes-Pyrénées: 261. 1867 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.
= *Dianthus arragonensis* Timb.-Lagr. ex Nyman, Consp. Fl. Eur. 1: 105. 1878 syn. sec. WFO 2018
= *Dianthus gerundensis* Sennen & Pau in Bol. Soc. Aragonesa Ci. Nat. 4: 309. 1905 syn. sec. WFO 2018 ≡ *Dianthus seguieri* var. *gerundensis* (Sennen & Pau) O.Bolòs & Vigo in Butl. Inst. Catalana Hist. Nat., Secc. Bot. 38(1): 88. 1974 syn. sec. WFO 2018
= *Dianthus gautieri* Sennen in Bull. Acad. Int. Geogr. Bot. 21: 107. 1911 syn. sec. Bernal et al. (1990) ≡ *Dianthus seguieri* subsp. *gautieri* (Sennen) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 189. 1963 syn. sec. Bernal et al. (1990) ≡ *Dianthus seguieri* var. *gautieri* (Sennen) O.Bolòs & Vigo in Butl. Inst. Catalana Hist. Nat., Secc. Bot. 38: 88. 1974 syn. sec. this publication
= *Dianthus cadevallii* Sennen & Pau in Bull. Acad. Int. Geogr. Bot. 24: 237. 1914 syn. sec. Bernal et al. (1990) ≡ *Dianthus seguieri* subsp. *cadevallii* (Sennen & Pau) O.Bolòs & Vigo in Butl. Inst. Catalana Hist. Nat., Secc. Bot. 38(1): 88. 1974 syn. sec. Bernal et al. (1990)
= *Dianthus* ×*paui* Sennen in Bull. Acad. Int. Geogr. Bot. 24: 236. 1914 syn. sec. Bernal et al. (1990)
= *Dianthus queraltii* Sennen in Bol. Soc. Ibér. Ci. Nat. 25: 210. 1926 [“1927”] syn. sec. WFO 2018 ≡ *Dianthus seguieri* var. *queraltii* (Sennen) O.Bolòs & Vigo in Butl. Inst. Catalana Hist. Nat., Secc. Bot. 38(1): 88. 1974 syn. sec. WFO 2018

Dianthus seguieri* subsp. *seguieri

***Dianthus seidlitzii* Boiss., Fl. Orient. 1: 506. 1867.** Sec. Rechinger (1988)
= *Dianthus pusillus* Freyn & Sint. in Bull. Herb. Boiss. 3: 75. 1895 syn. sec. Rechinger (1988)

***Dianthus semenovii* (Regel & Herder) Vierh. in Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1, 107: 1147. 1898.** Sec. Dequan & Turland (2001)
≡ *Dianthus alpinus* var. *semenovii* Regel & Herder in Bull. Soc. Imp. Naturalistes Moscou 39(1): 531. 1866 syn. sec. Dequan & Turland (2001)

***Dianthus seravschanicus* Schischk., Fl. URSS 6: 898. 1936.** Sec. Czerepanov (1995)

***Dianthus serotinus* Waldst. & Kit. in Descr. Icon. Pl. Hung. 2: 188. 1804.** Sec. Czerepanov (1995)

***Dianthus serpentinus* Hamzaoğlu in Nordic J. Bot. 33: 59. 2014.** Sec. Hamzaoğlu et al. (2015)

***Dianthus serratifolius* Sm., Fl. Graec. Prodr. 1(2): 287. 1809.** Sec. Dimopoulos et al. (2013)
= *Dianthus nazaraeus* E.D.Clarke, Trav. Var. Eur. 2: 420. 1812 syn. sec. WFO 2018

***Dianthus serratifolius* subsp. *abbreviatus* (Heldr. ex Halácsy) Strid, Mount. Fl. Greece 1: 179. 1986.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus serratifolius* var. *abbreviatus* Heldr. ex Halácsy syn. sec. Dimopoulos et al. (2013)

Dianthus serratifolius* subsp. *serratifolius

***Dianthus serrulatus* Desf., Fl. Atlant. 1: 346. 1798.** Sec. Marhold (2011)
= *Dianthus serrulatus* var. *strictus* Maire in Bull. Soc. His. Nat. Afrique N. 23: 169. 1932 syn. sec. Kew WCVP (2019)
= *Dianthus serrulatus* var. *subsimplex* F.N.Williams ex Maire in Bull. Soc. His. Nat. Afrique N. 23: 169. 1932 syn. sec. Kew WCVP (2019)
= *Dianthus taygeteus* Quézel & Contandr. in Taxon 16: 239. 1967 syn. sec. Marhold (2011)

***Dianthus serrulatus* subsp. *cyrenaicus* (Pamp.) Maire, Fl. Afr. Nord 10: 303. 1963.** Sec. Marhold (2011)
≡ *Dianthus serrulatus* var. *cyrenaicus* Pamp. in Arch. Bot. (Forlì) 12: 24. 1936 syn. sec. Marhold (2011)

***Dianthus serrulatus* subsp. *macranthus* Maire.** Sec. Marhold (2011)
= *Dianthus serrulatus* var. *broteri* Batt., Fl. Algérie Tunisie: 61. 1905 syn. sec. Kew WCVP (2019)
= *Dianthus mesanidum* Litard. & Maire, Mém. Soc. Sci. Nat. Maroc 6: 7. 1924 syn. sec. Marhold (2011) ≡ *Dianthus serrulatus* var. *mesanidum* (Litard. & Maire) Maire, Fl. Afrique N. 10: 303. 1963 syn. sec. Kew WCVP (2019)

Dianthus serrulatus* subsp. *serrulatus

***Dianthus sessiliflorus* Boiss., Fl. Orient. Suppl.: 78. 1888.** Sec. Marhold (2011)

***Dianthus setisquameus* Hausskn. & Bornm. in Mitt. Geogr. Ges. (Thüringen) Jena 9: 15. 1891.** Sec. Marhold (2011)

***Dianthus shinanensis* (Yatabe) Makino in Bot. Mag. (Tokyo) 17: 58. 1903.** Sec. Zoku (1965)
≡ *Dianthus barbatus* var. *shinanensis* Yatabe in Bot. Mag. (Tokyo) 6: 132. 1892 syn. sec. Zoku (1965)
= *Dianthus takenakae* Honda in Bot. Mag. (Tokyo) 44: 670. 1930 syn. sec. Zoku (1965)
= *Dianthus shinanensis* f. *alpinus* Hid.Takah. ex T.Shimizu, Fl. Nagano Pref.: 1505. 1997 syn. sec. WFO 2018

***Dianthus siculus* C.Presl, Delic. Prag.: 59. 1822.** Sec. Bacchetta et al. (2010)
≡ *Dianthus caryophyllus* subsp. *siculus* (C.Presl) Arcang., Comp. Fl. Ital. ed. 2: 306. 1894 syn. sec. Bacchetta et al. (2010) ≡ *Dianthus caryophyllus* var. *siculus* (C.Presl) Fiori, Fl. Italia 1: 379. 1898 syn. sec. Bacchetta et al. (2010) ≡ *Dianthus sylvestris* subsp. *siculus* (C.Presl) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 190. 1963 syn. sec. Bacchetta et al. (2010)
= *Dianthus kremeri* Boiss. & Reut., Pugill. Pl. Afr. Bor. Hispan.: 21. 1852 syn. sec. African Plant Database (version 3.4.0)
= *Dianthus siculus* var. *lanceolatus* Pau in Trab. Mus. Ci. Nat., Ser. Bot., 11: 22. 1917 syn. sec. African Plant Database (version 3.4.0) ≡ *Dianthus caryophyllus* var. *lanceolatus* (Pau) Maire, Cat. Pl. Maroc 2: 238. 1932 syn. sec. African Plant Database (version 3.4.0)
= *Dianthus caryophyllus* var. *transiens* Maire in Bull. Soc. His. Nat. Afrique N. 20: 16. 1929 syn. sec. African Plant Database (version 3.4.0) ≡ *Dianthus caryophyllus* f. *transiens* (Maire) Maire, Fl. Afrique N. 10: 319. 1963 syn. sec. this publication
= *Dianthus caryophyllus* var. *puberulus* Faure & Maire in Bull. Soc. His. Nat. Afrique N. 22: 280. 1931 syn. sec. African Plant Database (version 3.4.0)
= *Dianthus mauritii* Sennen, Diagn. Nouv.: 295. 1936 syn. sec. African Plant Database (version 3.4.0)
= *Dianthus kremeri* var. *trichodontus* Faure & Maire in Bull. Soc. His. Nat. Afrique N. 30: 333. 1939 syn. sec. African Plant Database (version 3.4.0)

***Dianthus simulans* Stoj. & Stef. ex Stef. & Jordanov in Magyar Bot. Lapok 32: 1. 1933.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus gracilis* subsp. *simulans* (Stoj. & Stef.) Stoj. & Acht. in Sborn. Bălg. Akad. Nauk. 29(2): 71. 1935 syn. sec. Dimopoulos et al. (2013)

***Dianthus sinaicus* Boiss., Diagn. Pl. Orient. ser. 1 1: 23. 1843.** Sec. Marhold (2011)
= *Dianthus multisquamatus* Hochst. ex Boiss., Fl. Orient. 1: 497. 1867 syn. sec. WFO 2018

***Dianthus siphonocalyx* Blakelock in Kew Bull. 3: 397. 1948 ["1949"].** Sec. Rechinger (1988)

***Dianthus somanus* Oskay in Phytotaxa 347: 264. 2018.** Sec. Oskay (2018)

***Dianthus sphacioticus* Boiss. & Heldr. in Boissier, Diagn. Pl. Orient., ser. 1, 8: 70. 1849.** Sec. Dimopoulos et al. (2013)
= *Dianthus leucophaeus* Sieber, Reise Kreta 2: 320. 1823, nom. illeg. syn. sec. WFO 2018 [non *Dianthus leucophaeus* Sm.]

***Dianthus spiculifolius* Schur, Enum. Pl. Transsilv.: 98. 1866.** Sec. Czerepanov (1995)

***Dianthus squarrosus* M.Bieb., Fl. Taur.-Caucas. 1: 331. 1808.** Sec. Czerepanov (1995)
= *Dianthus arenarius* Pall., Reise Russ. Reich. 3: 600. 1776 syn. sec. Czerepanov (1995) [non *Dianthus arenarius* L.]
= *Dianthus mussini* Hornem. in Hort. Bot. Hafn. 1: 408. 1813 syn. sec. Czerepanov (1995)
= *Dianthus recurvus* Fisch. ex Ledeb., Fl. Ross. 1: 284. 1842 syn. sec. Czerepanov (1995)
= *Dianthus sabulosus* Willd. ex Ledeb., Fl. Ross. 1: 284. 1842 syn. sec. Czerepanov (1995)

***Dianthus stamatiadae* Rech.f. in Bot. Not. 124: 77. 1971.** Sec. Dimopoulos et al. (2013)

***Dianthus stapfii* Lemperg in Repert. Spec. Nov. Regni Veg. 50: 261. 1941.** Sec. Rechinger (1988)

***Dianthus stellaris* Camarda in Parlatorea 6: 87. 2003.** Sec. Camarda (2003)
≡ *Dianthus siculus* subsp. *stellaris* (Camarda) Arrigoni in Parlatorea 7: 20. 2005 syn. sec. WFO 2018

***Dianthus stenocephalus* Boiss., Diagn. Pl. Orient. ser. 1 1: 19. 1843.** Sec. Rechinger (1988)
= *Dianthus macrolepis* Fenzl ex Boiss., Diagn. Pl. Orient., ser. 1, 8: 64. 1849 syn. sec. WFO 2018

***Dianthus stenopetalus* Griseb., Spic. Fl. Rumel. 1: 187. 1843.** Sec. Dimopoulos et al. (2013)
= *Dianthus geticus* Kulcz. in Rozpr. Wydz. Mat.-Przyr Polsk Akad. Umiejetn., Dzial A/B, Nauki Mat-Fiz. Biol. 59: 37. 1923 syn. sec. WFO 2018

***Dianthus stepanovae* Barkalov & Prob., Fl. Ross. Dalnego Vostoka: 444. 2006.** Sec. Barkalov & Probatova (2006)

***Dianthus sternbergii* Sieber ex Capelli, Cat. Stirp.: 24. 1821.** Sec. Marhold (2011)
≡ *Dianthus monspessulanus* var. *sternbergii* (Sieber ex Capelli) Tanfani, Fl. Ital. 9: 276. 1892 syn. sec. Kew WCVP (2019) ≡ *Dianthus hyssopifolius* subsp. *sternbergii* (Sieber ex Capelli) Graebn. & P.Graebn. in Ascherson & Graebn., Syn. Mitteleur. Fl. 5(2): 436. 1922 syn. sec. Marhold (2011)
= *Dianthus waldsteinii* Sternb. in Flora 9(1 Beibl.): 73. 1826 syn. sec. Marhold (2011)
= *Dianthus monspessulanus* subsp. *sternbergii* Hegi syn. sec. Marhold (2011)

***Dianthus stramineus* Boiss. & Heldr. in Boissier, Diagn. Pl. Orient., ser. 1, 8: 70. 1849.** Sec. Marhold (2011)

***Dianthus stribrnyi* Velen. in Sitzungsber. Königl. Böhm. Ges. Wiss., Math.-Naturwiss. Cl. 1892: 15. 1893.** Sec. Marhold (2011)
≡ *Dianthus moesiacus* subsp. *stribrnyi* (Velen.) Stoj. & Acht. in Sborn. Bălg. Akad. Nauk. 29(2): 53. 1935 syn. sec. Marhold (2011)

***Dianthus strictus* Banks & Sol., Nat. Hist. Aleppo ed. 2, 2: 252. 1794.** Sec. Rechinger (1988)
= *Dianthus polycladus* Boiss., Diagn. Pl. Orient., ser. 1, 8: 65. 1849 syn. sec. Rechinger (1988)
= *Dianthus quadrilobus* Boiss., Asie Min., Bot. 1: 222. 1860 syn. sec. Rechinger (1988)
= *Dianthus sulcatus* Boiss., Fl. Orient. 1: 483. 1867 syn. sec. Rechinger (1988)
= *Dianthus halepensis* Bornm. in Repert. Spec. Nov. Regni Veg. Beih. 89: 91. 1936 syn. sec. Rechinger (1988)

***Dianthus strictus* subsp. *multipunctatus* (Ser.) Mouterde ex Greuter & Burdet in Willdenowia 12: 187. 1982.** Sec. Rechinger (1988)
≡ *Dianthus multipunctatus* Ser., Prodr. 1: 362. 1824 syn. sec. Rechinger (1988)
= *Dianthus lineolatus* Bové ex Delile in Ann. Sci. Nat., Bot. II, 7: 286. 1837 syn. sec. Rechinger (1988)

Dianthus strictus* subsp. *strictus

***Dianthus strictus* subsp. *sublaevis* D.F.Chamb. in Edinburgh J. Bot. 51: 56. 1994.** Sec. Chamberlain et al. (1994)

***Dianthus strictus* subsp. *troodi* (Post) B.F.Osoriol & Seraphim ex Greuter & Burdet in Willdenowia 12: 187. 1982.** Sec. Rechinger (1988)
≡ *Dianthus multipunctatus* var. *troodi* Post in Mém. Herb. Boissier 1(18): 91. 1900 syn. sec. Rechinger (1988) ≡ *Dianthus strictus* var. *troodi* (Post) S.S.Hooper, Fl. Cyprus 1: 806. 1977 syn. sec. Rechinger (1988)

***Dianthus strictus* subsp. *velutinus* (Boiss.) Mouterde ex Greuter & Burdet in Willdenowia 12: 187. 1982.** Sec. Rechinger (1988)
≡ *Dianthus multipunctatus* var. *velutinus* Boiss., Diagn. Pl. Orient., ser. 1, 8: 65. 1849 syn. sec. Rechinger (1988)

***Dianthus strictus* var. *axilliflorus* (Fenzl) Reeve in Notes Roy. Bot. Gard. Edinburgh 28: 19. 1967.** Sec. Rechinger (1988)
≡ *Dianthus axilliflorus* Fenzl, Pug. Pl. Nov. Syr.: 10. 1842 syn. sec. Rechinger (1988) ≡ *Dianthus multipunctatus* var. *axilliflorus* (Fenzl) Boiss., Fl. Orient. 1: 483. 1867 syn. sec. Rechinger (1988)
= *Dianthus bitlisianus* Kotschy ex Boiss., Fl. Orient. 1: 483. 1867 syn. sec. Rechinger (1988)

***Dianthus strictus* var. *gracilior* (Boiss.) Reeve in Notes Roy. Bot. Gard. Edinburgh 28: 19. 1967.** Sec. Rechinger (1988)
≡ *Dianthus multipunctatus* var. *gracilior* Boiss., Fl. Orient. 1: 483. 1867 syn. sec. Rechinger (1988)
= *Dianthus striatellus* Fenzl, Pug. Pl. Nov. Syr.: 10. 1842 syn. sec. Rechinger (1988)
= *Dianthus paniculatus* Pau in Trab. Mus. Ci. Nat., Ser. Bot., 14: 9. 1918 syn. sec. Rechinger (1988)

***Dianthus strictus* var. *subenervis* (Boiss.) Reeve in Notes Roy. Bot. Gard. Edinburgh 28: 19. 1967.** Sec. Rechinger (1988)
≡ *Dianthus multipunctatus* var. *subenervis* Boiss., Fl. Orient. 1: 483. 1867 syn. sec. Rechinger (1988)

***Dianthus strymonis* Rech.f. in Bot. Jahrb. Syst. 69: 450. 1939.** Sec. Dimopoulos et al. (2013)

***Dianthus subacaulis* Vill., Hist. Pl. Dauphiné 3: 597. 1789.** Sec. Marhold (2011)
≡ *Dianthus virgineus* var. *subacaulis* (Vill.) Ser., Prodr. 1: 361. 1824 syn. sec. this publication

Dianthus subaphyllus **(Lemperg) Rech.f., Fl. Iran. 163: 170. 1988.** Sec. Rechinger (1988)

≡ *Dianthus tabrisianus* var. *subaphyllus* Lemperg in Repert. Spec. Nov. Regni Veg. 50: 259. 1941 syn. sec. Rechinger (1988)

Dianthus ×subfissus **Rouy & Foucaud, Fl. France 3: 184. 1896.** Sec. Bernal et al. (1990)

Dianthus subscabridus **Lincz., Fl. Uzbekist. 2: 525. 1953.** Sec. Czerepanov (1995)

Dianthus subulosus **Conrath & Freyn in Bull. Herb. Boiss. 3: 76. 1895.** Sec. Nersesyan (2011)

Dianthus superbus **L., Amoen. Acad. 4: 272. 1759.** Sec. Dimopoulos et al. (2013)

≡ *Caryophyllus superbus* (L.) Moench, Methodus: 59. 1794 syn. sec. Kew WCVP (2019); ≡ *Silene superba* (L.) E.H.L.Krause, Deutschl. Fl. Abbild., ed. 2, 5: 116. 1901 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.; ≡ *Dianthus superbus* var. *superbus* syn. sec. WFO 2018 – *Plumaria superba* (L.) Opiz, Seznam: 75. 1852, nom. inval. syn. sec. Kew WCVP (2019);

= *Dianthus fimbriatus* Lam., Fl. Franç. 2: 538. 1779 syn. sec. WFO 2018 ≡ *Cylichnanthus fimbriatus* (Lam.) Dulac, Fl. Hautes-Pyrénées: 262. 1867 syn. sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.

= *Dianthus multifidus* Gilib., Fl. Lit. Inch. 2: 162. 1782 syn. sec. WFO 2018

= *Dianthus contortus* Sm., Cycl.: 11. 1808 syn. sec. WFO 2018

= *Dianthus superbus* var. *rubicundus* Ser., Prodr. 1: 365. 1824 syn. sec. Kew WCVP (2019)

= *Dianthus plumarius* Gunnerus ex Spreng., Syst. Veg., ed. 16, 2: 379. 1825 syn. sec. WFO 2018

= *Dianthus schizopetalus* Wallr. in Linnaea 14: 570. 1840 syn. sec. WFO 2018

= *Dianthus wimmeri* Wich. in Jahresber. Schles. Ges. Vaterl. Cult. 1854: 75. 1854 syn. sec. WFO 2018

= *Dianthus superbus* var. *subobtusus* Regel & Herder in Bull. Soc. Imp. Naturalistes Moscou 39(1): 532. 1866 syn. sec. Kew WCVP (2019)

= *Dianthus superbus* subsp. *silvestris* Čelak., Prodr. Fl. Böhmen 3: 508. 1875 syn. sec. Kew WCVP (2019)

= *Dianthus szechuensis* F.N.Williams in J. Linn. Soc., Bot. 34: 428. 1899 syn. sec. WFO 2018

= *Dianthus superbus* f. *albiflorus* Iljinski in Trudy Bot. Muz. Imp. Akad. Nauk 14: 25. 1915 syn. sec. WFO 2018

= *Dianthus superbus* f. *albiflorus* Honda in Bot. Mag. (Tokyo) 52: 140. 1938, nom. illeg. syn. sec. Dimopoulos et al. (2013)

= *Dianthus superbus* f. *albiflorus* Tatew., Veg. Shikotan Is.: 32. 1940, nom. illeg. syn. sec. Dimopoulos et al. (2013)

= *Dianthus superbus* f. *albus* Popov in Konspekt Fl. Pober. Baikal: 213. 1966 syn. sec. Kew WCVP (2019)
= *Dianthus superbus* f. *leucanthus* T.Shimizu in J. Phytogeogr. Taxon. 37: 120. 1989 syn. sec. WFO 2018
= *Dianthus superbus* subsp. *norvegicus* M.Kuzmina, Fl. Vostoch. Evropy 11: 294. 2004 syn. sec. WFO 2018
= *Dianthus revolutus* Tausch in Flora 13: 245. 1830 syn. sec. WFO 2018 – *Plumaria revoluta* (Tausch) Opiz, Seznam: 75. 1852, nom. inval. syn. sec. Kew WCVP (2019)

Dianthus superbus **subsp.** ***alpestris*** **Kablík. ex Čelak., Prodr. Fl. Böhmen: 508. 1875.** Sec. Marhold (2011)
= *Dianthus superbus* var. *speciosus* Rchb., Fl. Germ. Excurs.: 808. 1832 syn. sec. WFO 2018 ≡ *Dianthus speciosus* (Rchb.) Rchb. in Icon. Fl. Germ. Helv. 6: 46. 1844 syn. sec. WFO 2018 ≡ *Dianthus superbus* subsp. *speciosus* (Rchb.) Hayek, Sched. Fl. Stiriac. 11–12: 9. 1907 syn. sec. Marhold (2011) ≡ *Dianthus superbus* f. *speciosus* (Rchb.) Bolzon in Nuovo Giorn. Bot. Ital., n.s., 21: 180. 1914 syn. sec. Kew WCVP (2019)
= *Dianthus superbus* var. *monticola* Makino in Bot. Mag. (Tokyo) 17: 59. 1903 syn. sec. WFO 2018
= *Dianthus superbus* var. *bibracteolata* Koidz. in Icon. Pl. Koisikav. 3(4): t. 183. 1916 syn. sec. WFO 2018 ≡ *Dianthus superbus* f. *bibracteolata* (Koidz.) Tatew. in J. Sapporo Soc. Agric. 121: 256. 1934 syn. sec. WFO 2018
= *Dianthus superbus* f. *chionanthus* Okuyama in J. Jap. Bot. 30: 42. 1955 syn. sec. WFO 2018

Dianthus superbus **subsp.** ***autumnalis*** **Oberd., Pfl. Exkurs. Fl., ed. 4: 359. 1979.** Sec. Marhold (2011)

Dianthus superbus **subsp.** ***stenocalyx*** **(Trautv. ex Juz.) Kleopow in Izv. Kievsk. Bot. Sada 14: 137. 1932.** Sec. Marhold (2011)
≡ *Dianthus stenocalyx* Trautv. ex Juz. in Mem. Inst. Agron. For. Belarus 4: 212. 1925 syn. sec. Marhold (2011)

Dianthus superbus **subsp.** ***superbus***

Dianthus superbus **var.** ***amoena*** **Nakai in Bot. Mag. (Tokyo) 44: 520. 1930.** Sec. Kew WCVP (2019)
≡ *Dianthus superbus* var. *alpestris* Nakai in Bot. Mag. (Tokyo) 36: 63. 1922, nom. illeg. syn. sec. Kew WCVP (2019)

Dianthus sylvaticus **Hoppe ex Willd., Enum. Pl.: 467. 1809.** Sec. Danihelka et al. (2012)
≡ *Dianthus seguieri* var. *sylvaticus* (Hoppe ex Willd.) W.D.J.Koch, Syn. Fl. Germ. Helv. 1: 96. 1835 syn. sec. this publication ≡ *Dianthus seguieri* subsp. *sylvaticus* (Hoppe ex Willd.) Arcang., Comp. Fl. Ital.: 84. 1882 syn. sec. this publication

Dianthus sylvestris **Wulfen in Collectanea 1: 237. 1786.** Sec. Dimopoulos et al. (2013)

≡ *Dianthus caryophyllus* subsp. *sylvestris* (Wulfen) Rouy & Foucaud, Fl. France 3: 193. 1896 syn. sec. Kew WCVP (2019) ≡ *Silene sylvestris* (Wulfen) E.H.L.Krause, Deutschl. Fl. Abbild., ed. 2, 5: 112. 1901, nom. illeg. syn. sec. Kew WCVP (2019);

= ?*Dianthus caryophyllus* var. *inodorus* L., Sp. Pl. 1: 410. 1753 syn. sec. Domina et al. (2021) ≡ ?*Dianthus inodorus* (L.) Gaertn., Fruct. Sem. Pl. 2: 227. 1791 syn. sec. Domina et al. (2021)

= *Dianthus rupestris* L.f., Suppl. Pl.: 240. 1782 syn. sec. WFO 2018

= *Dianthus caryophylloides* Schult., Observ. Bot.: 78. 1809 syn. sec. WFO 2018

= *Dianthus wulfenii* F.Dietr., Nachtr. Vollst. Lex. Gärtn. 2: 669. 1816 syn. sec. WFO 2018

= *Dianthus frigidus* Zucc. in Flora 7: 283. 1824 syn. sec. WFO 2018

= *Dianthus sylvestris* var. *imbricatus* Gaudin, Fl. Helv. 3: 152. 1828 syn. sec. Kew WCVP (2019)

= *Dianthus sylvestris* var. *uniflorus* Gaudin, Fl. Helv. 3: 152. 1828 syn. sec. Kew WCVP (2019)

= *Dianthus sylvestris* var. *humilior* W.D.J.Koch, Syn. Fl. Germ. Helv. 1: 97. 1835 syn. sec. Kew WCVP (2019)

= *Dianthus sylvestris* var. *subacaulis* W.D.J.Koch, Syn. Fl. Germ. Helv. 1: 97. 1835 syn. sec. Kew WCVP (2019)

= *Dianthus saxicola* Jord., Mém. Acad. Sci. Lyon, Sect. Sci. 1: 241. 1851 syn. sec. WFO 2018

= *Dianthus aggericola* Jord., Annot. Fl. France Allemagne: 48. 1855 syn. sec. Kew WCVP (2019)

= *Dianthus aggericolus* Jord., Annot. Fl. France Allemange: 48. 1855 syn. sec. WFO 2018

= *Dianthus consimilis* Jord., Annot. Fl. France Allemange: 47. 1855 syn. sec. WFO 2018

= *Dianthus guyetanii* Jord., Annot. Fl. France Allemange: 46. 1855 syn. sec. WFO 2018

= *Dianthus orophilus* Jord., Annot. Fl. France Allemange: 43. 1855 syn. sec. WFO 2018

= *Dianthus reuteri* Jord., Annot. Fl. France Allemange: 49. 1855 syn. sec. WFO 2018

= *Dianthus papillosus* Vis. & Pančić in Mem. Reale Ist. Veneto Sci. 10: 434. 1861 syn. sec. Marhold (2011) ≡ *Dianthus sylvestris* f. *papillosus* (Vis. & Pančić) Beck in Glasn. Zemaljsk. Muz. Bosni Hercegovini 21: 175. 1909 syn. sec. this publication

= *Dianthus brevicalyx* Beck in Ann. K. K. Naturhist. Hofmus. 2: 63. 1887 syn. sec. Marhold (2011)

= *Dianthus juratensis* Jord., Icon. Fl. Eur. 3: 32. 1903 syn. sec. WFO 2018

= *Dianthus sylvestris* f. *albiflorus* Micevski in Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 8: 44. 1987 ["1990"] syn. sec. WFO 2018

= *Dianthus sylvestris* var. *alpestris* Micevski in Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 8: 42. 1987 ["1990"] syn. sec. WFO 2018

Dianthus sylvestris **subsp.** ***alboroseus*** **F.K.Mey. in Haussknechtia, Beih. 15: 53. 2011.** Sec. Meyer (2011)

Dianthus sylvestris **subsp.** ***aristidis*** **(Batt.) Greuter & Burdet in Willdenowia 12: 187. 1982.** Sec. Marhold (2011)
≡ *Dianthus aristidis* Batt., Fl. Algérie Dicot.(App. 2): v. 1888 syn. sec. Marhold (2011) ≡ *Dianthus caryophyllus* subsp. *aristidis* (Batt.) Maire, Fl. Afrique N. 10: 320. 1963 syn. sec. Kew WCVP (2019)

Dianthus sylvestris **subsp.** ***bertisceus*** **Rech.f. in Repert. Spec. Nov. Regni Veg. 38: 150. 1935.** Sec. Marhold (2011)
≡ *Dianthus bertisceus* (Rech.f.) E.Mayer & Trpin in Biol. Vestn. 13: 57. 1965 syn. sec. Marhold (2011)

Dianthus sylvestris **subsp.** ***kozjakensis*** **Micevski in Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 8: 43. 1987 ["1990"].** Sec. Marhold (2011)

Dianthus sylvestris **subsp.** ***longibracteatus*** **(Maire) Greuter & Burdet in Willdenowia 12: 187. 1982.** Sec. Marhold (2011)
≡ *Dianthus caryophyllus* subsp. *longibracteatus* Maire in Bull. Soc. His. Nat. Afrique N. 19: 33. 1928 syn. sec. Marhold (2011)
= *Dianthus caryophyllus* var. *mogadorensis* Maire in Bull. Soc. His. Nat. Afrique N. 20: 16. 1929 syn. sec. African Plant Database (version 3.4.0)
= *Dianthus caryophyllus* var. *volubilitanus* Maire, Cat. Pl. Maroc 2: 238. 1932 syn. sec. WFO 2018 ≡ *Dianthus caryophyllus* f. *mogadorensis* (Maire) Maire, Fl. Afr. Nord 10: 319. 1963 syn. sec. WFO 2018

Dianthus sylvestris **subsp.** ***longicaulis*** **(Ten.) Greuter & Burdet in Willdenowia 12: 187. 1982.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus longicaulis* Ten., Cat. Hort. Neapol. 1813 App. 2: 77. 1819 syn. sec. Dimopoulos et al. (2013) ≡ *Dianthus caryophyllus* var. *longicaulis* (Ten.) Trevir., Index Seminum (WROCL, Wratislaviensi) 1821: 1. 1821 syn. sec. this publication ≡ *Dianthus caryophyllus* subsp. *longicaulis* (Ten.) Arcang., Comp. Fl. Ital. ed. 2: 306. 1894 syn. sec. Dimopoulos et al. (2013)
= *Dianthus virgineus* Gren. & Godr. in Bot. Mag. 42: t. 1740. 1815 syn. sec. Dimopoulos et al. (2013)
= *Dianthus caryophyllus* var. *tenuifolius* Moris, Fl. Sardoa 1: 231. 1837 syn. sec. Dimopoulos et al. (2013) ≡ *Dianthus siculus* subsp. *tenuifolius* (Moris) Arrigoni in Parlatorea 7: 20. 2005 syn. sec. Dimopoulos et al. (2013)
= *Dianthus scheuchzeri* Jord., Mém. Acad. Sci. Lyon, Sect. Sci. 1: 241. 1851 syn. sec. Dimopoulos et al. (2013)
= *Dianthus collivagus* Jord., Annot. Fl. France Allemange: 46. 1855 syn. sec. Dimopoulos et al. (2013)

= *Dianthus godronianus* Jord., Annot. Fl. France Allemange: 45. 1855 syn. sec. Dimopoulos et al. (2013) ≡ *Dianthus caryophyllus* subsp. *godronianus* (Jord.) P.Martin in Bull. Soc. Échange Pl. Vasc. Eur. Occid. Bassin Médit. 19: 93. 1984 syn. sec. Dimopoulos et al. (2013) ≡ *Dianthus sylvestris* var. *godronianus* (Jord.) Kerguélen in Lejeunia 120: 81. 1987 syn. sec. Dimopoulos et al. (2013)

***Dianthus sylvestris* subsp. *nodosus* (Tausch) Hayek in Repert. Spec. Nov. Regni Veg. Beih. 30(1): 247. 1924.** Sec. Marhold (2011)
≡ *Dianthus nodosus* Tausch, Syll. Pl. Nov. 2: 243. 1828 syn. sec. Marhold (2011)

Dianthus sylvestris* subsp. *sylvestris

***Dianthus sylvestris* subsp. *tergestinus* (Rchb.) Hayek in Repert. Spec. Nov. Regni Veg. Beih. 30(1): 247. 1924.** Sec. Marhold (2011)
≡ *Dianthus virgineus* var. *tergestinus* Rchb., Icon. Fl. Germ. Helv. 6: 47, t. 5049b. 1844 syn. sec. Marhold (2011) ≡ *Dianthus tergestinus* (Rchb.) A.Kern., Sched. Fl. Exs. Austro-Hung.: no. 545. 1882 syn. sec. Marhold (2011) ≡ *Dianthus caryophyllus* var. *tergestinus* (Rchb.) Tanfani, Fl. Ital. 9: 283. 1892 syn. sec. this publication

***Dianthus szowitsianus* Boiss., Fl. Orient. 1: 503. 1867.** Sec. Rechinger (1988)
= *Dianthus pallens* var. *oxylepis* Boiss., Fl. Orient. 1: 485. 1867 syn. sec. Rechinger (1988)

***Dianthus tabrisianus* Bien. ex Boiss., Fl. Orient. 1: 496. 1867.** Sec. Rechinger (1988)
= *Dianthus pachypetalus* Stapf in Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. 51: 278. 1886 syn. sec. Rechinger (1988)

***Dianthus tabrisianus* var. *coloratus* (Bornm.) Rech.f., Fl. Iran. 163: 147. 1988.** Sec. Rechinger (1988)
≡ *Dianthus pachypetalus* var. *coloratus* Bornm. in Verh. K. K. Zool.-Bot. Ges. Wien 60: 80. 1910 syn. sec. Rechinger (1988) ≡ *Dianthus coloratus* (Bornm.) Hand.-Mazz., Ann. K. K. Naturhist. Hofmus. 26: 153. 1912 syn. sec. Rechinger (1988)

Dianthus tabrisianus* var. *tabrisianus

***Dianthus takhtajanii* Nersesian in Takhtajania 1: 47. 2011.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus talyschensis* Boiss. & Buhse in Nouv. Mém. Soc. Imp. Naturalistes Moscou 12: 34. 1860.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus tarentinus* Lacaita in Nuovo Giorn. Bot. Ital. n.s., 18: 511. 1911.** Sec. Bacchetta et al. (2010)

= *Dianthus sylvestris* var. *garganicus* Ten., Fl. Napol. 2: 208. 1830 syn. sec. Bacchetta et al. (2010) ≡ *Dianthus caryophyllus* subsp. *garganicus* (Ten.) Grande in Boll. Soc. Bot. Ital. 1912: 178. 1912 syn. sec. Bacchetta et al. (2010) ≡ *Dianthus caryophyllus* var. *garganicus* (Ten.) Fiori, Nuov. Fl. Italia 1: 512. 1924 syn. sec. Bacchetta et al. (2010) ≡ *Dianthus sylvestris* subsp. *garganicus* (Ten.) Pignatti in Giorn. Bot. Ital. 107: 211. 1973 syn. sec. Bacchetta et al. (2010) ≡ *Dianthus garganicus* (Ten.) Brullo in Braun-Blanquetia 2: 31. 1988 syn. sec. Bacchetta et al. (2010)

***Dianthus tenuiflorus* Griseb., Spic. Fl. Rumel. 1: 189. 1843.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus corymbosus* subsp. *tenuiflorus* (Griseb.) Trinajstić in Suppl. Fl. Anal. Jugosl. 5: 746. 1979 syn. sec. Dimopoulos et al. (2013)

***Dianthus thunbergii* S.S.Hooper in Hookers Icon. Pl. 37: 38. 1959.** Sec. African Plant Database (version 3.4.0)
= *Dianthus hirtus* Vill., Syst. Pl. Eur. 1: 41. 1785 syn. sec. WFO 2018
= *Dianthus scaber* Chaix, Hist. Pl. Dauphiné 1: 331. 1786 syn. sec. WFO 2018
= *Dianthus scaber* Thunb., Prodr. Pl. Cap. 1: 81. 1794 syn. sec. African Plant Database (version 3.4.0)
= *Dianthus prostratus* Eckl. & Zeyh., Enum. Pl. Afric. Austral. 1: 32. 1835 syn. sec. WFO 2018
= *Dianthus ramentaceus* Fenzl ex Sond., Fl. Cap. 1: 122. 1860 syn. sec. WFO 2018

***Dianthus thunbergii* f. *maritimus* S.S.Hooper, Hooker's Icon. Pl. 7 [1]: 38–40. 1959.** Sec. African Plant Database (version 3.4.0)

Dianthus thunbergii* f. *thunbergii

***Dianthus tianschanicus* Schischk., Fl. URSS 6: 897. 1936.** Sec. Czerepanov (1995)

***Dianthus tlaratensis* Husseinov in Bot. Zhurn. (Moscow & Leningrad) 75: 234. 1990.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus toletanus* Boiss. & Reut., Diagn. Pl. Nov. Hisp.: 7. 1842.** Sec. Bernal et al. (1990)
≡ *Dianthus scaber* subsp. *toletanus* (Boiss. & Reut.) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 190. 1963 syn. sec. Bernal et al. (1990)

***Dianthus transcaucasicus* Schischk. in Izv. Tomsk. Gosud. Univ. 80: 452. 1929.** Sec. Nersesyan (2011)

***Dianthus transvaalensis* Burtt Davy in Bull. Misc. Inform. Kew 1922: 215. 1922.** Sec. African Plant Database (version 3.4.0)

= *Dianthus scaber* var. *graminifolius* Fenzl ex Szyszyl. syn. sec. African Plant Database (version 3.4.0)

***Dianthus trifasciculatus* Kit. ex Schult., Oestr. Fl. ed. 2, 1: 654. 1814.** Sec. Marhold (2011)

= *Dianthus lancifolius* Tausch in Flora 14: 215. 1831 syn. sec. WFO 2018

= *Dianthus danubialis* Griseb. & Schenk in Arch. Naturgesch. 18(1): 301. 1852 syn. sec. WFO 2018

= *Dianthus heptaneurus* Griseb. & Schenk in Arch. Naturgesch. 18(1): 302. 1852 syn. sec. WFO 2018

= *Dianthus biternatus* Schur in Verh. Mitth. Siebenbürg. Vereins Naturwiss. Hermannstadt 4: 11. 1853 syn. sec. WFO 2018

= *Dianthus transsylvanicus* Schur in Verh. Mitth. Siebenbürg. Vereins Naturwiss. Hermannstadt 5: 82. 1854 syn. sec. WFO 2018

= *Dianthus pruinosus* Janka, Index Seminum (WU) 1858: 4. 1858 syn. sec. WFO 2018

= *Dianthus banaticus* Kit. in Linnaea 32: 527. 1863 syn. sec. WFO 2018

***Dianthus trifasciculatus* subsp. *parviflorus* Stoj. & Acht., Sborn. Blghar. Akad. Nauk 29: 40. 1935.** Sec. Marhold (2011)

= *Dianthus trifasciculatus* var. *deserti* Prodán syn. sec. WFO 2018 ≡ *Dianthus deserti* (Prodán) Prodán, Fl. Reipubl. Popul. Roman. 2: 232. 1953 syn. sec. Marhold (2011) ≡ *Dianthus trifasciculatus* subsp. *deserti* (Prodán) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 190. 1963 syn. sec. Marhold (2011)

***Dianthus trifasciculatus* subsp. *pseudobarbatus* (Schmalh.) Jalas in Ann. Bot. Fenn. 22: 219. 1985.** Sec. Marhold (2011)

≡ *Dianthus chinensis* subsp. *pseudobarbatus* Schmalh., Fl. Sredn. Yuzhn. Rossii 1: 125. 1895 syn. sec. Marhold (2011) ≡ *Dianthus pseudobarbatus* (Schmalh.) Besser ex Klok., Fl. S.S.S.R. 4: 609. 1952 syn. sec. Marhold (2011)

= *Dianthus euponticus* Zapał., Consp. Fl. Gallic. Crit. 3: 141. 1911 syn. sec. Marhold (2011)

Dianthus trifasciculatus* subsp. *trifasciculatus

***Dianthus tripunctatus* Sm., Fl. Graec. Prodr. 1(2): 286. 1809.** Sec. Dimopoulos et al. (2013)

= *Dianthus barati* Duval-Jouve in Bull. Soc. Bot. France 2: 350. 1855 syn. sec. WFO 2018

***Dianthus tunicoides* Madhani & Heubl in Taxon 67(1): 103. 2018.** Sec. Madhani et al. (2018)

≡ *Tunica sibthorpii* Boiss., Diagn. Pl. Orient., ser. 1, 8: 61. 1849, nom. illeg. syn. sec. Madhani et al. (2018) ≡ *Gypsophila armerioides* Ser. ex DC., Prodr. 1: 353. 1824 syn. sec. Madhani et al. (2018) ≡ *Tunica armerioides* (Ser. ex DC.) Halácsy, Consp. Fl. Graec. 1: 194. 1900 syn. sec. Madhani et al. (2018) ≡ *Petrorhagia armerioides*

(Ser. ex DC.) P.W.Ball & Heywood in Bull. Brit. Mus. (Nat. Hist.), Bot. 3: 139. 1964 syn. sec. Madhani et al. (2018) ≡ *Fiedleria armerioides* (Ser. ex DC.) Ovcz., Fl. Tadzhikskoi S.S.R. 3: 608. 1968 syn. sec. Madhani et al. (2018).

***Dianthus turkestanicus* Preobr. in Izv. Imp. Bot. Sada Petra Velikago 15: 366. 1915.** Sec. Czerepanov (1995)
≡ *Dianthus versicolor* subsp. *turkestanicus* (Preobr.) Kozhevn. in Novosti Sist. Vyssh. Rast. 22: 113. 1985 syn. sec. Czerepanov (1995)
= *Dianthus alatavicus* Popov in Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. n.s., 47: 86. 1938 syn. sec. Czerepanov (1995)

***Dianthus tymphresteus* (Boiss. & Spruner) Heldr. & Sart. ex Boiss., Diagn. Pl. Orient. ser. 2, 6: 27. 1859.** Sec. Dimopoulos et al. (2013)
≡ *Dianthus viscidus* var. *tymphresteus* Boiss. & Spruner in Boissier, Diagn. Pl. Orient., ser. 1, 8: 64. 1849 syn. sec. WFO 2018

***Dianthus ucarii* Hamzaoğlu & Koç in Turkish J. Bot. 41: 487. 2017.** Sec. Hamzaoğlu et al. (2017)

***Dianthus ugamicus* Vved. in Bot. Mater. Gerb. Bot. Inst. Uzbekistansk. Fil. Akad. Nauk S.S.S.R. 3: 10. 1941.** Sec. Czerepanov (1995)

***Dianthus uniflorus* Forssk., Fl. Aegypt.-Arab.: cxi. 1775.** Sec. WFO 2018

***Dianthus uralensis* Korsh. in Trudy Glavn. Bot. Sada 43: 310. 1930.** Sec. Czerepanov (1995)

***Dianthus urumoffii* Stoj. & Acht., Fl. Bulg. ed. 2: 364. 1933.** Sec. WFO 2018

***Dianthus uzbekistanicus* Lincz., Fl. Uzbekist. 2: 526. 1953.** Sec. Czerepanov (1995)

***Dianthus vanensis* Behçet & Ilçim in Turkish J. Bot. 37: 219. 2013.** Sec. İlçim et al. (2013)

***Dianthus varankii* Hamzaoğlu & Koç in KSÜ Tarim Doga Derg. 21: 546. 2018.** Sec. Hamzaoğlu et al. (2018)

***Dianthus ×varians* Rouy & Foucaud, Fl. France 3: 186. 1896.** Sec. Bernal et al. (1990)
≡ *Dianthus ×saxatilis* nothosubsp. *varians* (Rouy & Foucaud) M.Bernal, Laínz & Muñoz Garm. in Anales Jard. Bot. Madrid 45: 367. 1988 syn. sec. Bernal et al. (1990)

***Dianthus vigoi* M.Laínz in Anales Jard. Bot. Madrid 42: 551. 1985 ["1985"].** Sec. Bernal et al. (1990)

≡ *Dianthus seguieri* subsp. *vigoi* (M.Laínz) O.Bolòs, Fl. Països Catalans 2: 757. 1990 syn. sec. Marhold (2011)

***Dianthus virgatus* Pasq. in Ann. Accad. Aspir. Naturalisti III, 1: 28. 1861.** Sec. Bacchetta et al. (2010)
≡ *Dianthus caryophyllus* subsp. *virgatus* (Pasq.) Arcang., Comp. Fl. Ital. ed. 2: 306. 1894 syn. sec. Bacchetta et al. (2010)

***Dianthus virgineus* L., Sp. Pl.: 412. 1753.** Sec. Domina et al. (2021)
≡ *Tunica virginea* (L.) Scop., Fl. Carniol., ed. 2, 1: 302. 1771 syn. sec. Domina et al. (2021); ≡ *Dianthus caryophyllus* var. *virgineus* (L.) Fiori, Fl. Italia 1(2): 379. 1898 syn. sec. Domina et al. (2021) ≡ *Dianthus rupestris* Lam., Fl. Franç. 2: 536. 1779, nom. illeg. syn. sec. Domina et al. (2021) ≡ *Dianthus scheuchzeri* Rchb., Fl. Germ. Excurs.: 811. 1832 syn. sec. Domina et al. (2021)

***Dianthus viridescens* Clementi in Atti Riunione Sci. Ital. 3: 520. 1841.** Sec. Marhold (2011)

***Dianthus viscidus* Bory & Chaub., Nouv. Fl. Pélop.: 26. 1838.** Sec. Dimopoulos et al. (2013)
= *Dianthus olympicus* Boiss., Diagn. Pl. Orient. 1: 19. 1843 syn. sec. Kew WCVP (2019)
= *Dianthus grisebachii* Boiss., Diagn. Pl. Orient., ser. 2, 1: 62. 1854 syn. sec. WFO 2018
= *Dianthus parnassicus* Boiss. & Heldr. in Boissier, Diagn. Pl. Orient., ser. 2, 1: 64. 1854 syn. sec. WFO 2018
= *Dianthus heldreichii* Bornm. in Bot. Jahrb. Syst. 59: 393. 1924 syn. sec. WFO 2018
= *Dianthus viscidus* subsp. *elatior* (Halácsy) Hayek in Repert. Spec. Nov. Regni Veg. Beih. 30(1): 227. 1924 syn. sec. Dimopoulos et al. (2013)
= *Dianthus viscidus* subsp. *grisebachii* (Boiss.) Hayek in Repert. Spec. Nov. Regni Veg. Beih. 1: 226. 1924 syn. sec. Dimopoulos et al. (2013)
= *Dianthus viscidus* var. *glandulosus* Micevski in Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 8: 44. 1987 ["1990"] syn. sec. WFO 2018

***Dianthus vladimirii* Galushko in Novosti Sist. Vyssh. Rast. 11: 298. 1974.** Sec. Kuzmina & Nersesyan (2012)

***Dianthus volgicus* Juz. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 13: 73. 1950.** Sec. Czerepanov (1995)

***Dianthus vulturius* Guss. & Ten., Index Seminum (NAP) 1837: 3. 1837.** Sec. Marhold (2011)
≡ *Dianthus carthusianorum* var. *vulturius* (Guss. & Ten.) Tanfani, Fl. Ital. 9: 253. 1892 syn. sec. Kew WCVP (2019) ≡ *Dianthus balbisii* subsp. *vulturius* (Guss. & Ten.) Maire in Bull. Soc. His. Nat. Afrique N. 23: 169. 1932 syn. sec. Marhold (2011) ≡

Dianthus ferrugineus subsp. *vulturius* (Guss. & Ten.) Tutin in Feddes Repert. Spec. Nov. Regni Veg. 68: 191. 1963 syn. sec. Marhold (2011)

Dianthus vulturius **subsp.** ***aspromontanus*** **Brullo, Scelsi & Spamp. in Portugaliae Acta Biol., Sér. B, Sist. 19: 310. 2000.** Sec. Brullo et al. (2000)

Dianthus vulturius **subsp.** ***vulturius***

Dianthus ×warionii **Timb.-Lagr. in Bull. Soc. Agric. Sci. Litt. Pyrén.-Orient. 25: 20. 1881.** Sec. Bernal et al. (1990)
≡ *Dianthus richteri* nothovar. *warionii* (Timb.-Lagr.) Rouy & Foucaud, Fl. France 3: 183. 1896 syn. sec. Bernal et al. (1990)
= *Dianthus ×richteri* Rouy & Foucaud, Fl. France 3: 182. 1896 syn. sec. Bernal et al. (1990)

Dianthus woroschilovii **Barkalov & Prob., Fl. Ross. Dalnego Vostoka: 76. 2006.** Sec. Barkalov & Probatova (2006)
≡ *Dianthus chinensis* subsp. *reflexus* Vorosch. in Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. n.s., 83(5): 116. 1978 syn. sec. Barkalov & Probatova (2006)

Dianthus xylorrhizus **Boiss. & Heldr. in Boissier, Diagn. Pl. Orient., ser. 1, 8: 67. 1849.** Sec. Dimopoulos et al. (2013)

Dianthus zangezuricus **Nersesian in Novosti Sist. Vyssh. Rast. 42: 115. 2011.** Sec. Kuzmina & Nersesyan (2012)

Dianthus zederbaueri **Vierh. in Ann. K. K. Naturhist. Hofmus. 20: 391. 1905.** Sec. Marhold (2011)

Dianthus zeyheri **Sond., Fl. Cap. 1: 124. 1860.** Sec. African Plant Database (version 3.4.0)
= *Dianthus albens* Turcz. in Bull. Soc. Imp. Naturalistes Moscou 27(2): 369. 1854 syn. sec. WFO 2018
= *Dianthus serpae* Ficalho & Hiern in Trans. Linn. Soc. London, Bot. 2: 17. 1881 syn. sec. African Plant Database (version 3.4.0)
= *Dianthus mecistocalyx* F.N.Williams in J. Bot. 27: 199. 1889 syn. sec. African Plant Database (version 3.4.0)

Dianthus zeyheri **subsp.** ***natalensis*** **S.S.Hooper in Hookers Icon. Pl. 37: 48. 1959.** Sec. African Plant Database (version 3.4.0)
= *Dianthus colensoi* F.N.Williams in J. Bot. 23: 344. 1885 syn. sec. African Plant Database (version 3.4.0)

Dianthus zeyheri **subsp.** ***zeyheri***

Dianthus zonatus **Fenzl, Pug. Pl. Nov. Syr.: 11. 1842.** Sec. Dimopoulos et al. (2013)
= *Dianthus hypochlorus* Boiss. & Heldr. in Boissier, Diagn. Pl. Orient., ser. 1, 8: 67. 1849 syn. sec. WFO 2018

Hybrids

Dianthus ×ambrozy-migazzianus **Boros in Magyar Bot. Lapok 23: 33. 1924 ["1925"].** Sec. WFO 2018

Dianthus ×arvernensis **Rouy & Foucaud, Fl. France 3: 185. 1896.** Sec. WFO 2018

Dianthus ×brivatensis **Blanch., Jardin 6: 174. 1892.** Sec. WFO 2018

Dianthus ×burciae **Péterfi & Gürtler in Magyar Bot. Lapok 15: 20. 1916.** Sec. WFO 2018

Dianthus ×calalpinus **Farrer in Engl. Rock Gard. 1: 283. 1919**

Dianthus ×callizonoides **Sünd. in Allg. Bot. Z. Syst. 12: 91. 1906.** Sec. Kew WCVP (2019)

Dianthus ×courtoisii **Rchb., Fl. Germ. Excurs.: 806. 1832.** Sec. WFO 2018
= *Dianthus ×wolfii* Vetter in Bull. Murith. Soc. Valais. Sci. Nat. 11: 132. 1883 syn. sec. Kew WCVP (2019)

Dianthus ×digeneus **Rouy & Foucaud, Fl. France 3: 184. 1896.** Sec. WFO 2018

Dianthus ×ebneri **Heimerl, Fl. Brixen: 105. 1911.** Sec. WFO 2018

Dianthus ×gabrielae **Domin in Vestn. Král. Ceské Spolecn. Nauk. Tr. Mat.-Prír. 13: 4. 1927 ["1926"].** Sec. WFO 2018

Dianthus ×genersichii **Györffy in Magyar Bot. Lapok 23: 70. 1924 ["1925"].** Sec. WFO 2018

Dianthus ×josephinae **Font Quer in Cavanillesia 1: 34. 1928.** Sec. WFO 2018

Dianthus ×julii-wolfii **Marton in Magyar Bot. Lapok 15: 19. 1916.** Sec. WFO 2018

Dianthus ×krasanii **A.Kern. ex Dalla Torre & Sarnth., Fl. Tirol 6(2): 209. 1909.** Sec. WFO 2018

***Dianthus* ×*lacinulatus* Zapał., Consp. Fl. Gallic. Crit. 3: 161. 1911.** Sec. WFO 2018

***Dianthus* ×*lamyi* Rouy & Foucaud, Fl. France 3: 176. 1896.** Sec. WFO 2018

***Dianthus* ×*laucheanus* Bolle ex Bolle & Asch. in Verh. Bot. Vereins Prov. Brandenburg 33: 102. 1892.** Sec. WFO 2018

***Dianthus* ×*loretii* Rouy & Foucaud, Fl. France 3: 176. 1896.** Sec. WFO 2018

***Dianthus* ×*mammingiorum* Murr in Allg. Bot. Z. Syst. 13: 23. 1907.** Sec. WFO 2018

***Dianthus* ×*nigritus* Hirahata & Kitam. in Acta Phytotax. Geobot. 20: 205. 1962.** Sec. WFO 2018

***Dianthus* ×*paradoxus* Keller ex Schröt. in Ber. Schweiz. Bot. Ges. 14: 117. 1905.** Sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.

***Dianthus* ×*ponsi* Rouy & Foucaud, Fl. France 3: 184. 1896.** Sec. WFO 2018

***Dianthus* ×*pritchardii* Farrer, Engl. Rock Gard. 1: 300. 1919**

***Dianthus* ×*saxatilis* F.W.Schmidt in Neuere Abh. Königl. Böhm. Ges. Wiss. 1: 28. 1790.** Sec. WFO 2018

***Dianthus* ×*zarencznianus* Zapał., Consp. Fl. Gallic. Crit. 3: 149. 1911.** Sec. WFO 2018

Unresolved names

***Dianthus acuminatus* F.W.Williams in J. Bot. 23: 347. 1885.** Sec. WFO 2018

***Dianthus adulterinus* Sweet, Hort. Brit. ed. 2: 50. 1830.** Sec. WFO 2018

***Dianthus ambiguus* Pančić, Fl. Serbiae: 178. 1874.** Sec. WFO 2018

***Dianthus ambiguus* Pančić ex F.N.Williams in J. Bot. 23: 342. 1885.** Sec. WFO 2018

***Dianthus andersonii* F.N.Williams in J. Bot. 23: 346. 1885.** Sec. WFO 2018

***Dianthus aragonensis* Timb.-Lagr., Mém. Acad. Sci. Toulouse VI, 5: 242. 1867.** Sec. WFO 2018

***Dianthus arenarius* var. *gigas* Novák.** Sec. WFO 2018
≡ *Dianthus arenarius* subsp. *gigas* (Novák) Soó in Feddes Repert. 83: 161. 1972 syn. sec. WFO 2018

***Dianthus armerioides* Raf. in J. Bot. Agric. 4: 269. 1814.** Sec. WFO 2018

***Dianthus attenuatus* proles *maritimus* Rouy.** Sec. Kew WCVP (2019)

***Dianthus banaticiformis* Prodán in Bul. Soc. Sti. Cluj 10: 152. 1948.** Sec. WFO 2018

***Dianthus basalticus* (Domin) Fritsch, Exkursionsfl. Oesterreich ed. 2: 215. 1909.** Sec. WFO 2018
≡ *Dianthus carthusianorum* var. *basalticus* Domin syn. sec. this publication

***Dianthus behriorum* Bornm. in Repert. Spec. Nov. Regni Veg. 41: 188. 1936.** Sec. WFO 2018

***Dianthus bolfae* Sennen in Bol. Soc. Ibér. Ci. Nat. 25: 149. 1926.** Sec. WFO 2018

***Dianthus bornmuelleri* Hausskn. in Mitt. Geogr. Ges. (Thüringen) Jena 9: 16. 1891.** Sec. WFO 2018

***Dianthus borzaeanus* Prodán in Bul. Inform. Grad. Bot. Univ. Cluj 5: 41. 1925.** Sec. WFO 2018

***Dianthus bottemeri* Bouchard in Bull. Soc. Bot. France 97: 220. 1951.** Sec. WFO 2018

***Dianthus brachyanthus* Gren. & Godr., Fl. France 1: 235. 1847.** Sec. WFO 2018

***Dianthus brachycarpus* Velen. in Abh. Königl. Böhm. Ges. Wiss. 7(Folge 1): 9. 1886.** Sec. WFO 2018

***Dianthus brevilimbis* Boiss. ex Trautv. in Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 506. 1873.** Sec. WFO 2018

***Dianthus brevior* Gand., Contr. Fl. Terr. Slav. Merid. 1: 5. 1883.** Sec. WFO 2018

***Dianthus brevistylus* Timb.-Lagr. & Jeanb. in Bull. Soc. Agric. Sci. Litt. Pyrén.-Orient. 25: 24. 1881.** Sec. WFO 2018

***Dianthus bucovinensis* Prodán & Morariu in Bul. Sti. Acad. Republ. Populare Romîne, Sect. Biol. Sti. Agric. Ser. Bot., 9: 301. 1957.** Sec. WFO 2018

Dianthus buergeri **Miq. in Ann. Mus. Bot. Lugduno-Batavi 2: 77. 1865.** Sec. WFO 2018

Dianthus callichrous **Jord., Icon. Fl. Eur. 3: 30. 1903.** Sec. WFO 2018

Dianthus callizonoides **Sünd. in Allg. Bot. Z. Syst. 12: 91. 1906.** Sec. WFO 2018

Dianthus calverti **Boiss., Asie Min., Bot. 1: 223. 1860.** Sec. WFO 2018

Dianthus camboi **Sennen, Diagn. Nouv.: 42. 1936.** Sec. WFO 2018

Dianthus camusii **Sennen, Diagn. Nouv.: 9. 1936.** Sec. WFO 2018

Dianthus carneus **Jord., Icon. Fl. Eur. 3: 25. 1903.** Sec. WFO 2018

Dianthus carpaticus **Woloszack.** [publication] Sec. WFO 2018

Dianthus caucasicus **Spreng., Adumbr. Pl. Hort. Hal.: 23. 1806.** Sec. WFO 2018

Dianthus chlorostomus **Jord., Icon. Fl. Eur. 3: 31. 1903.** Sec. WFO 2018

Dianthus collincola **Spreng. in Bot. Gart. Halle Nachtr. 1: 20. 1801.** Sec. WFO 2018

Dianthus companyoi **Sennen in Bol. Soc. Ibér. Ci. Nat. 25: 208. 1926 [“1927”].** Sec. WFO 2018

Dianthus corymbosus **Andrz. in Trudy Komiss. Vys. Uchr., Kiev 1: 18. 1860.** Sec. WFO 2018

Dianthus costei **Sennen in Bull. Acad. Int. Geogr. Bot. 24: 237. 1914.** Sec. WFO 2018

Dianthus cruentus **Fisch. ex Planch., Fl. Serres Jard. Eur. 5: t. 488. 1849.** Sec. WFO 2018

Dianthus curticeps **Borbás in Oesterr. Bot. Z. 40: 97. 1890.** Sec. WFO 2018

Dianthus decrescens **Borbás in Oesterr. Bot. Z. 27: 378. 1877.** Sec. WFO 2018

Dianthus deserti **Post, Pl. Postianae 2: 6. 1891.** Sec. WFO 2018

Dianthus deserti **Kotschy in Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1, 52(1): 262. 1866.** Sec. WFO 2018

Dianthus dissimilis **(Burnat) Landolt, Fl. Indicativa: 268. 2010.** Sec. WFO 2018

Dianthus divaricatus **d'Urv., Mém. Soc. Linn. Paris 1: 302. 1822.** Sec. WFO 2018

Dianthus dostalii **Novák in Repert. Spec. Nov. Regni Veg. 38: 304. 1935.** Sec. WFO 2018

Dianthus egregius **Jord., Icon. Fl. Eur. 3: 23. 1903.** Sec. WFO 2018

Dianthus elegans **M.Bieb. ex Rupr., Fl. Caucasi: 174. 1870.** Sec. WFO 2018

Dianthus elongatus **C.A.Mey., Verz. Caucasus Pfl.: 211. 1849.** Sec. WFO 2018

Dianthus erubescens **Roth, Enum. Pl. Phaen. Germ. 1(2): 279. 1827.** Sec. WFO 2018

Dianthus exilis **Posp., Fl. Oesterr. Küstenl. 1: 452. 1897.** Sec. WFO 2018

Dianthus fallacinus **Rouy & Foucaud, Fl. France 3: 190. 1896.** Sec. WFO 2018

Dianthus faurei **Arv.-Touv. in Bull. Soc. Dauphin. Échange Pl. 7: 263. 1880.** Sec. WFO 2018

Dianthus fauriei **H.Lév. & Vaniot in Repert. Spec. Nov. Regni Veg. 7: 200. 1909.** Sec. WFO 2018

Dianthus flabellatus **Jord., Icon. Fl. Eur. 3: 29. 1903.** Sec. WFO 2018

Dianthus flahaultii **Braun-Blanq. in Annuaire Conserv. Jard. Bot. Genève 21: 32. 1919.** Sec. WFO 2018

Dianthus flexicaulis **Jord., Icon. Fl. Eur. 3: 26. 1903.** Sec. WFO 2018

Dianthus floribundus **Sennen in Bull. Soc. Bot. France 73: 645. 1926 ["1927"].** Sec. WFO 2018

Dianthus foliosus **Turcz. in Bull. Soc. Imp. Naturalistes Moscou 5: 184. 1832.** Sec. WFO 2018

Dianthus galicicae **Micevski in Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 8: 40. 1987 ["1990"].** Sec. WFO 2018

Dianthus gelcenii **Gelcenis ex Sennen in Bull. Soc. Bot. France 73: 646. 1926 ["1927"].** Sec. WFO 2018

***Dianthus gizellae* Borbás in Oesterr. Bot. Z. 27: 378. 1877.** Sec. WFO 2018

***Dianthus glaucophyllus* Colla in Mem. Reale Accad. Sci. Torino 35: 187. 1831.** Sec. WFO 2018

***Dianthus grandiflorus* Poir., Encycl. 4: 515. 1798.** Sec. WFO 2018

***Dianthus gremblichii* Asch. in Sitzungsber. Bot. Vereins Prov. Brandenburg 19: 28. 1877.** Sec. WFO 2018

***Dianthus gustavii* Sennen, Diagn. Nouv.: 9. 1936.** Sec. WFO 2018

***Dianthus handelii* Hayek in Ann. K. K. Naturhist. Hofmus. 28: 157. 1914.** Sec. WFO 2018

***Dianthus hanryi* Burnat, Fl. Alpes Marit. 1: 223. 1892.** Sec. WFO 2018

***Dianthus hazaricus* F.N.Williams in Bull. Herb. Boissier, sér. 2, 1: 892. 1901.** Sec. WFO 2018

***Dianthus helwigii* Asch.** [publication] Sec. WFO 2018

***Dianthus hendersonianus* Paxton in Fl. Mag. (London) 14: 126. 1848.** Sec. WFO 2018

***Dianthus heterophyllus* Rouy & Foucaud, Fl. France 3: 172. 1896.** Sec. WFO 2018

***Dianthus hornemannii* Ser., Prodr. 1: 262. 1824.** Sec. WFO 2018
= *Dianthus geminatus* Kit. ex Schult., Oestr. Fl. ed. 2, 1: 656. 1814 syn. sec. WFO 2018

***Dianthus huebneri* Seehaus in Verh. Bot. Vereins Prov. Brandenburg 33: 95. 1892.** Sec. WFO 2018

***Dianthus hypoleucus* Jord., Icon. Fl. Eur. 3: 31. 1903.** Sec. WFO 2018

***Dianthus impunctatus* Jord., Icon. Fl. Eur. 3: 29. 1903.** Sec. WFO 2018

***Dianthus inoxianus* Gallego in Lagascalia 14: 71. 1986.** Sec. WFO 2018

***Dianthus istriacus* Gand., Contr. Fl. Terr. Slav. Merid. 1: 5. 1883.** Sec. WFO 2018

***Dianthus italicus* Jan ex Pasq., Index Seminum (NAP): 1866. 1866.** Sec. WFO 2018

***Dianthus jablanicensis* Micevski in Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 8: 31. 1987 [“1990”].** Sec. WFO 2018

***Dianthus jacupicensis* (Košanin) Micevski in Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 8: 41. 1987 [“1990”].** Sec. WFO 2018

***Dianthus japigicum* Bianco & Brullo.** Sec. WFO 2018

***Dianthus jugoslavicus* Micevski in Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 8: 33. 1987 [“1990”].** Sec. WFO 2018

***Dianthus ×laucheanus* Bolle in Gartenflora 53: 393. 1904.** Sec. WFO 2018

***Dianthus laxus* Tausch, Hort. Canal. 2: t. 17. 1825.** Sec. WFO 2018

***Dianthus lereschii* (Burnat) Landolt, Fl. Indicativa: 268. 2010.** Sec. WFO 2018

***Dianthus levieri* Borbás in Oesterr. Bot. Z. 27: 231. 1877.** Sec. WFO 2018

***Dianthus lisae* Burnat, Fl. Alpes Marit. 1: 233. 1892.** Sec. WFO 2018

***Dianthus longicaulis* St.-Lag. in Ann. Soc. Bot. Lyon 7: 144. 1880.** Sec. WFO 2018

***Dianthus longifolius* Jord., Icon. Fl. Eur. 3: 32. 1903.** Sec. WFO 2018

***Dianthus macedonicus* Micevski in Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 8: 35. 1987 [“1990”].** Sec. WFO 2018

***Dianthus macrophyllus* Jord., Icon. Fl. Eur. 3: 30. 1903.** Sec. WFO 2018

***Dianthus magyari* Dorsch, Kert. Szemle 5: 241. 1933.** Sec. WFO 2018

***Dianthus marginatus* Poir., Encycl. Suppl. 4: 131. 1816.** Sec. WFO 2018

***Dianthus maris* Willd. ex B.S.Williams in Bot. J. Linn. Soc. 29(203): 415. 1893.** Sec. WFO 2018

***Dianthus marisensis* Simonk. in Term. Füz. 9: 37. 1885.** Sec. WFO 2018

***Dianthus maritimus* Jord., Icon. Fl. Eur. 3: 25. 1903.** Sec. WFO 2018

***Dianthus massiliensis* Jord., Icon. Fl. Eur. 3: 25. 1903.** Sec. WFO 2018

***Dianthus mayeri* C.Presl in Abh. Königl. Böhm. Ges. Wiss. V, 3: 448. 1845.** Sec. WFO 2018

***Dianthus medius* Besser ex Nyman, Consp. Fl. Eur. 1: 103. 1878.** Sec. WFO 2018

***Dianthus microcheilus* B.S.Williams in Oesterr. Bot. Z. 41: 176. 1891.** Sec. WFO 2018

***Dianthus mikii* Reichardt in Verh. K. K. Zool.-Bot. Ges. Wien 17: 331. 1867.** Sec. WFO 2018

***Dianthus minimus* Javeiol in Curr. Sci. 42: 692. 1973.** Sec. WFO 2018

***Dianthus minor* Porta in Nuovo Giorn. Bot. Ital. 11: 278. 1879.** Sec. WFO 2018

***Dianthus moldavicus* Grinţ. in Bul. Inform. Grad. Bot. Univ. Cluj 4: 57. 1924.** Sec. WFO 2018

***Dianthus monteuilii* Burnat, Fl. Alpes Marit. 1: 221. 1891.** Sec. WFO 2018

***Dianthus morrisii* Hance in London J. Bot. 7: 472. 1848.** Sec. WFO 2018
≡ *Tunica morrisii* (Hance) Walp. in Ann. Bot. Syst. 2: 101. 1851 syn. sec. Kew WCVP (2019);

***Dianthus nevadensis* Sennen, Diagn. Nouv.: 210. 1936.** Sec. WFO 2018

***Dianthus nicaeensis* Jord., Icon. Fl. Eur. 3: 30. 1903.** Sec. WFO 2018

***Dianthus nobilis* Anon. in Gartenflora 81: 94. 1932.** Sec. WFO 2018

***Dianthus novakii* J.Sojak, Čas. Nár. Mus., Odd. Přír. 148: 77. 1979 ["1980"].** Sec. WFO 2018

***Dianthus obtusifolius* Scheele in Flora 26: 428. 1843.** Sec. WFO 2018

***Dianthus oculatus* Boiss. in Ann. Sci. Nat., Bot. IV, 2: 245. 1854.** Sec. WFO 2018

***Dianthus ×oenipontanus* A.Kern. in Oesterr. Bot. Z. 15: 209. 1865.** Sec. WFO 2018

***Dianthus ohridanus* Micevski in Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 8: 34. 1987 ["1990"].** Sec. WFO 2018

***Dianthus pancicii* F.N.Williams.** [publication] Sec. WFO 2018

Dianthus parciflorus **Jord., Icon. Fl. Eur. 3: 28. 1903.** Sec. WFO 2018

Dianthus pedemontanus **Rouy, Fl. France 3: 188. 1896.** Sec. WFO 2018

Dianthus penrynae **Sweet, Hort. Brit. ed. 2: 51. 1830.** Sec. WFO 2018

Dianthus petteri **Boiss., Diagn. Pl. Orient., ser. 2, 1: 66. 1854.** Sec. WFO 2018

Dianthus platyphyllus **Turcz. in Bull. Soc. Imp. Naturalistes Moscou 27(2): 368. 1854.** Sec. WFO 2018

Dianthus pomeridianus **L., Sp. Pl., ed. 2 2: 1673. 1763.** Sec. WFO 2018
= *Dianthus tricolor* Adams ex Ser., Prodr. 1: 360. 1824 syn. sec. WFO 2018

Dianthus ponticola **Bornm. in Bot. Jahrb. Syst. 59: 398. 1924.** Sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.

Dianthus ponticolus **Bornm. in Bot. Jahrb. Syst. 59: 398. 1924.** Sec. WFO 2018

Dianthus portae **A.Kern. ex Huter in Oesterr. Bot. Z. 54: 339. 1904.** Sec. WFO 2018

Dianthus praevertens **B.S.Williams in Bot. J. Linn. Soc. 29(203): 408. 1893.** Sec. WFO 2018

Dianthus prilepensis **Micevski in Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 8: 39. 1987 ["1990"].** Sec. WFO 2018

Dianthus puberulus **F.N.Williams in J. Bot. 23: 344. 1885.** Sec. WFO 2018

Dianthus puberulus **Jord., Icon. Fl. Eur. 3: 31. 1903.** Sec. WFO 2018

Dianthus pulchellus **Pers., Syn. Pl. 1: 495. 1805.** Sec. WFO 2018

Dianthus pulverulentus **Wettst. in Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1, 98: 382. 1889 ["1896"].** Sec. WFO 2018

Dianthus pumilus **Vahl, Symb. Bot. 1: 32. 1790.** Sec. WFO 2018

Dianthus punctatus **Spreng., Neue Entdeck. Pflanzenk. 2: 169. 1821.** Sec. WFO 2018

Dianthus pungens **Poir., Encycl. 4: 526. 1798.** Sec. WFO 2018

Dianthus purpureus **F.N.Williams in J. Bot. 23: 343. 1885.** Sec. WFO 2018

***Dianthus pusillus* F.W.Schmidt in Neuere Abh. Königl. Böhm. Ges. Wiss. 1: 29. 1791.** Sec. WFO 2018

***Dianthus quetierii* Carrière ex Herincq, Hort. Franç. 1866: 43. 1866.** Sec. WFO 2018

***Dianthus ramiger* Jord., Icon. Fl. Eur. 3: 28. 1903.** Sec. WFO 2018

***Dianthus rigidulus* Jord., Icon. Fl. Eur. 3: 27. 1903.** Sec. WFO 2018

***Dianthus rubicundus* Jord., Icon. Fl. Eur. 3: 24. 1903.** Sec. WFO 2018

***Dianthus ruscinonensis* Foucaud & Gaut., Cat. Fl. Pyrénées-orientales: 108. 1898.** Sec. WFO 2018

***Dianthus sallentii* Sennen in Bull. Acad. Int. Geogr. Bot. 24: 236. 1914.** Sec. WFO 2018

***Dianthus schlosseri* F.N.Williams in J. Bot. 23: 342. 1885.** Sec. WFO 2018

***Dianthus ×seehausianus* Asch. ex Seehaus in Verh. Bot. Vereins Prov. Brandenburg 34: 12. 1893.** Sec. WFO 2018

***Dianthus seguieri* Costa ex Willk. & Lange, Prodr. Fl. Hispan. 3: 681. 1878.** Sec. WFO 2018

***Dianthus seisuimontanus* Masam. in Trans. Nat. Hist. Soc. Taiwan 31: 343. 1941.** Sec. WFO 2018

***Dianthus serrulatus* Schloss. & Vuk., Fl. Croat.: 321. 1869.** Sec. WFO 2018

***Dianthus silenoides* Poir., Encycl. 4: 514. 1798.** Sec. WFO 2018

***Dianthus singuliflorus* Jord., Icon. Fl. Eur. 3: 26. 1903.** Sec. WFO 2018

***Dianthus sintenisii* Freyn in Oesterr. Bot. Z. 43: 376. 1893.** Sec. WFO 2018

***Dianthus skopjensis* Micevski in Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 8: 36. 1987 ["1990"].** Sec. WFO 2018

***Dianthus slavonicus* B.S.Williams in Bot. J. Linn. Soc. 29(203): 380. 1893.** Sec. WFO 2018

***Dianthus souliei* Sennen in Bull. Soc. Bot. France 73: 646. 1926 ["1927"].** Sec. WFO 2018

Dianthus spurius **A.Kern. ex Borbás in Rad Jugoslav. Akad. Znan. 36: 173. 1876.** Sec. WFO 2018

Dianthus suavis **Willd., Enum. Pl., Suppl.: 24. 1814.** Sec. WFO 2018

Dianthus subalbidus **Jord., Icon. Fl. Eur. 3: 24. 1903.** Sec. WFO 2018

Dianthus subbarbatus **Schur, Enum. Pl. Transsilv.: 92. 1866.** Sec. WFO 2018

Dianthus subulatus **Timb.-Lagr. in Bull. Soc. Agric. Sci. Litt. Pyrén.-Orient. 25: 13. 1881.** Sec. WFO 2018

Dianthus syriacus **Steud., Nomencl. Bot., ed. 2, 1: 501. 1840.** Sec. WFO 2018

Dianthus taniacensis **Gueldenst. ex Ledeb., Fl. Ross. 1: 287. 1842.** Sec. WFO 2018

Dianthus tatrae **Borbás in Term. Füz. 12: 221. 1889.** Sec. WFO 2018

Dianthus tenuidens **Jord., Icon. Fl. Eur. 3: 28. 1903.** Sec. WFO 2018

Dianthus tenuis **F.N.Williams in Bull. Misc. Inform. Kew 1914: 205. 1914.** Sec. WFO 2018

= *Dianthus tenorei* F.N.Williams in Bull. Misc. Inform. Kew 1914: 206. 1914 syn. sec. WFO 2018

Dianthus tergestinus **Simonk., Magyar Növényt. Lapok 12: 21. 1888.** Sec. WFO 2018

Dianthus thessalus **Orph. in Bull. Congr. Bot. Petersb. 1969: 123. 1870.** Sec. WFO 2018

Dianthus tzopae **Prodán, Fl. Reipubl. Popul. Roman. 2: 671. 1953.** Sec. WFO 2018

Dianthus varciorovensis **Prodán, Fl. Reipubl. Popul. Roman. 2: 671. 1953.** Sec. WFO 2018

Dianthus variegatus **Jord., Icon. Fl. Eur. 3: 27. 1903.** Sec. WFO 2018

Dianthus velenovskyi **Borbás in Term. Füz. 14: 46. 1893.** Sec. WFO 2018

Dianthus verschaffeltii **Lem. in Ill. Hort. 6: t. 220. 1859.** Sec. WFO 2018

Dianthus vesulanus **Jord., Icon. Fl. Eur. 3: 27. 1903.** Sec. WFO 2018

Dianthus vodnensis **Micevski in Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 8: 38. 1987 ["1990"].** Sec. WFO 2018

Dianthus vukotinovicii **Borbás in Rad Jugoslav. Akad. Znan. 36: 172. 1876.** Sec. WFO 2018

Dianthus wettsteinii **Bornm. in Bull. Herb. Boissier, sér. 2, 5: 60. 1905.** Sec. WFO 2018

Dianthus winterlianus **Priszter in Bot. Közlem. 54: 153. 1967.** Sec. WFO 2018

Dianthus wolfii **Vetter in Bull. Murith. Soc. Valais. Sci. Nat. 11: 132. 1883.** Sec. WFO 2018

Kohlrauschia sibthorpii **Kunth, Fl. Berol., ed. 2, 1: 109. 1838**
= *Kohlrauschia sibthorpii* Kunth, Fl. Berol., ed. 2, 1: 109. 1838 syn. sec. Kew WCVP (2019);

Tunica argentii **Meikle in Kew Bull. 9: 106. 1954**

Velezia arabica **Hochst. & Steud. ex Steud., Nomencl. Bot., ed. 2, 2(2–5): 746. 1841**

Excluded names

Dianthus alpinus **var.** ***glacialis*** **Trautv. in Trudy Imp. S.-Peterburgsk. Bot. Sada 2: 505. 1873.** Sec. Kuzmina & Nersesyan (2012)

Wrongly attributed to Trautvetter l.c., who had cited *Dianthus alpinus* var. *glacialis* (Haenke) Regel in Bull. Soc. Imp. Naturalistes Moscou 34(II): 533. 1862

Dianthus argentii **(Meikle) Govaerts.** Sec. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew.

Listed as ined. in Plants of the World Online, with a remark that the name has been published in Skvortsovia, but no such name was found in this journal.

Dianthus hypoleucus **var.** ***karami*** **Boiss., Fl. Orient., Suppl.: 80. 1888.** Sec. TPL (2013)

Erroneous TPL record for *Dianthus hypochlorus* var. *karami* Boiss.

Acknowledgements

We thank Walter Berendsohn and the EDIT Platform developer team Andreas Müller, Andreas Kohlbecker and Katja Luther for their continuous commitment in developing and maintaining the Platform and for their help with database imports and queries, data cleaning, implementing Platform features and generating the checklist as a database output. We are very grateful to Nicholas Turland for his advice on nomenclatural questions and for many helpful comments on the manuscript. We further thank the Royal Botanic Gardens, Kew for providing what was at that time an unpublished dataset of the World Checklist of Vascular Plants, as well as William Ulate of the World Flora Online team at the Missouri Botanical Garden for facilitating the WFO backbone data for *Dianthus*. We thank Katerina Goula, Nicholas Turland and Aris Zografidis for providing photographs. The Berlin laboratory team, especially Kim Govers, Julia Dietrich and Annika Richtering helped with generating the sequences and Gabi Dröge assisted with sample metadata management and ENA sequence submission. We thank Alexandra Winizuk, Florian Michling and Nora Walden (Heidelberg) for assistance in generating, annotating and submitting plastome sequence data. Material and *trnK/matK* sequences for German *Dianthus* and *Petrorhagia* were generated in the GBOL I – *German Barcode of Life* project funded by the German Federal Ministry of Education and Research (FKZ 01LI1101). Sampling of the Caucasian species and the corresponding laboratory work was carried out as part of the project *Developing tools for conserving the plant diversity of the South Caucasus* funded by VolkswagenStiftung (reference AZ85021 and AZ89950). In this context, we also thank Zhirair Vardanyan and Anahit Ghukasyan, both former heads of the Institute of Botany, Yerevan, Armenia for their continuous support of this project. We are also highly indebted to the Kuban State University Krasnodar (Russia) and Svetlana A. Litvinskaya for support of field work in the Krasnodar Region, Russia. We further acknowledge financial support from the Verein der Freunde des Botanischen Gartens und des Botanischen Museums Berlin for field work in Russia and Greece as well as financial support from from the Green Fund and the Hellenic Botanical Society (Greece) for a part of this study. Financial support from the Stiftung Naturschutzfond Baden-Württemberg (M Koch, 27.8831.27/546) is also greatly acknowledged for processing of plastome data of Cheddar pink. We thank, Richard K. Rabeler, University of Michigan for his numerous helpful suggestions on this manuscript.

References

African Plant Database (2012) Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute, Pretoria. http://www.ville-ge.ch/musinfo/bd/cjb/africa/ [version 3.4.0, accessed January through February 2020]

Bacchetta G, Brullo S (2000) *Dianthus mossanus* (Caryophyllaceae), a new species from Sardinia. Portugaliae Acta Biologica 19: 295–301.

Bacchetta G, Brullo S, Casti M, Pietro Giusso del Galdo G (2010) Taxonomic revision of the *Dianthus sylvestris* group (Caryophyllaceae) in central-southern Italy, Sicily and Sardinia. Nordic Journal of Botany 28(2): 137–173. https://doi.org/10.1111/j.1756-1051.2009.00459.x

Balao F, Casimiro-Soriguer R, Talavera M, Herrera J, Talavera S (2009) Distribution and diversity of cytotypes in *Dianthus broteri* as evidenced by genome size variations. Annals of Botany 104(5): 965–973. https://doi.org/10.1093/aob/mcp182

Ball PW, Heywood VH (1964) A revision of the genus *Petrorhagia*. Bulletin of the British Museum (Natural History). Botany 3: 119–172.

Barkalov VJ, Probatova NS (2006) Род Гвоздика - *Dianthus* L. In: Kojevnikov AE, Probatova NS (Eds) Флора Российского дальнего востока (Flora of the Russian Far East). Dal'nauka, Vladivostok, 74–77.

Berendsohn WG (1995) The concept of "potential taxa" in databases. Taxon 44(2): 207–212. https://doi.org/10.2307/1222443

Berendsohn WG (1997) A taxonomic information model for botanical databases: The IOPI Model. Taxon 46(2): 283–309. https://doi.org/10.2307/1224098

Berendsohn WG (2010) Devising the EDIT Platform for Cybertaxonomy. In: Nimis PL, Vignes-Lebbe R (Eds) Tools for identifying Biodiversity: Progress and Problems. EUT - Edizioni Università di Trieste, 1–6.

Berendsohn WG, Geoffroy M (2007) Networking taxonomic concepts – uniting without "unitaryism". In: Curry G, Humphries C (Eds) Biodiversity databases - techniques, politics, and applications. CRC Taylor & Francis, Baton Rouge, 13–22. https://doi.org/10.1201/9781439832547.ch3

Bernal M, Laínz M, Muñoz Garmendia F (1990) *Dianthus* L. In: Castroviejo S, Laínz M, López Gonzáles G, Montserrat P, Muñoz Garmendia F, Paiva J, Villar L (Eds) Flora Iberica. Plantas vasculares de la Península Ibérica e Islas Baleares, Vol 2. Real Jardín Botánico, C.S.I.C., Madrid, 426–462.

Bittrich V (1993) Caryophyllaceae. In: Kubitzki K, Rohwer G, Bittrich V (Eds) The Families and Genera of Vascular Plants II Flowering Plants - Dicotyledons Magnoliid, Hamamelid and Caryophyllid Families. Springer-Verlag, Berlin Heidelberg, 206–236. https://doi.org/10.1007/978-3-662-02899-5_21

Bleeker W, Franzke A, Pollmann K, Brown AHD, Hurka H (2002) Phylogeny and biogeography of southern Hemisphere high-mountain *Cardamine* species (Brassicaceae). Australian Systematic Botany 15(4): 575–581. https://doi.org/10.1071/SB01026

Boissier E (1867) Flora Orientalis. H. Georg, Basel & Geneve.

Borsch T, Quandt D (2009) Mutational dynamics and phylogenetic utility of noncoding chloroplast DNA. Plant Systematics and Evolution 282(3–4): 169–199. https://doi.org/10.1007/s00606-009-0210-8

Borsch T, Hilu KW, Quandt D, Wilde V, Neinhuis C, Barthlott W (2003) Noncoding plastid *trnT-trnF* sequences reveal a well resolved phylogeny of basal angiosperms. Journal of Evolutionary Biology 16(4): 558–576. https://doi.org/10.1046/j.1420-9101.2003.00577.x

Borsch T, Hernandez-Ledesma P, Berendsohn WG, Flores-Olvera H, Ochoterena H, Zuloaga FO, von Mering S, Kilian N (2015) An integrative and dynamic approach for monographing species-rich plant groups - Building the global synthesis of the angiosperm order Caryophyllales. Perspectives in Plant Ecology, Evolution and Systematics 17(4): 284–300. https://doi.org/10.1016/j.ppees.2015.05.003

Borsch T, Berendsohn W, Dalcin E, Delmas M, Demissew S, Elliott A, Fritsch P, Fuchs A, Geltman D, Güner A, Haevermans T, Knapp S, le Roux MM, Loizeau P-A, Miller C, Miller J, Miller JT, Palese R, Paton A, Parnell J, Pendry C, Qin H-N, Sosa V, Sosef M, von Raab-Straube E, Ranwashe F, Raz L, Salimov R, Smets E, Thiers B, Thomas W, Tulig M, Ulate W, Ung V, Watson M, Jackson PW, Zamora N (2020) World Flora Online: Placing taxonomists at the heart of a definitive and comprehensive global resource on the world's plants. Taxon 69(6): 1311–1341. https://doi.org/10.1002/tax.12373

Brullo S, Scelsi F, Spampinato G (2000) New taxa belonging to *Dianthus vulturius* Guss. & Ten. group (Caryophyllaceae) from S Calabria (Italy). Portugaliae Acta Biologica 19: 303–317.

Brullo S, Brullo C, Colombo P, Galdo GGD, Ilardi V, Perrone R (2015) *Dianthus borbonicus* (Caryophyllaceae), a new species from Sicily. Phytotaxa 233(1): 46–60. https://doi.org/10.11646/phytotaxa.233.1.3

Camarda I (2003) *Thymus catharinae* (Lamiaceae), *Dianthus stellaris* (Cariophyllaceae) e *Rubus limbarae* (Rosaceae) species novae di Sardegna. Parlatorea 6: 83–93.

Carlsen T, Bleeker W, Hurka H, Elven R, Brochmann C (2009) Biogeography and phylogeny of *Cardamine* (Brassicaceae). Annals of the Missouri Botanical Garden 96(2): 215–236. https://doi.org/10.3417/2007047

Chamberlain DF, Clement RA, Lamond J (1994) Studies in the Flora of Arabia: XXVIII. Some new taxa from the Arabian Peninsula. Edinburgh Journal of Botany 51(1): 49–58. https://doi.org/10.1017/S0960428600001700

Chepinoga VV, Stepantsova AV, Grebenyuk AV, Verhozina AV, Vinkoskaya OP, Gnutikov AA, Dulepova NA, Enuschenko IV, Zarubin AM, Kazanovskiy SG, Konovalov AS, Korobkov AA, Luferov AN, Rosbakh SA (2008) Конспект флоры Иркутской области (сосудистые растения) The checklist of the flora of Irkutsk oblast' (vascular plants). Irkutskiy Gosudarstvennyi Universitet, Irkutsk.

Ciardelli P, Kelbert P, Kohlbecker A, Hoffmann N, Güntsch A, Berendsohn WG (2009) The EDIT Platform for Cybertaxonomy and the taxonomic workflow: Selected components. Lecture Notes in Informatics 154: 625–638. [LNI]

Cogoni D, Sulis E, Bacchetta G, Fenu G (2019) The unpredictable fate of the single population of a threatened narrow endemic Mediterranean plant. Biodiversity and Conservation 28(7): 1799–1813. https://doi.org/10.1007/s10531-019-01757-0

Czerepanov SK (1995) Vascular plants of Russia and adjacent states (the former USSR). Cambridge University Press.

Danihelka J, Chrtek JJ, Kaplan Z (2012) Checklist of vascular plants of the Czech Republic. Preslia 84: 647–811.

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: More models, new heuristics and parallel computing. Nature Methods 9(8): 772–772. https://doi.org/10.1038/nmeth.2109

Davis PH (1957) New turkish species of *Tunica*, *Velezia* and *Potentilla*. Notes from the Royal Botanic Garden Edinburgh 22: 163–171.

Deniz İG, Aykurt C, Genç İ, Aksoy A (2016) A new species of *Dianthus* (Caryophyllaceae) from Antalya, South Anatolia, Turkey. PhytoKeys 63: 1–12. https://doi.org/10.3897/phytokeys.63.8033

Dequan L, Turland NJ (2001) *Dianthus*. Flora of China 6 - Caryophyllaceae through Lardizabalaceae. efloras.org.

Dimopoulos P, Raus T, Bergmeier E, Constantinidis T, Iatrou G, Kokkini S, Strid A, Tzanoudakis D (2013) Vascular plants of Greece - an annotated checklist. Botanic Garden and Botanical Museum Berlin-Dahlem and the Hellenic Botanical Society, Berlin.

Domina G, Astuti G, Barone G, Gargano D, Minuto L, Varaldo L, Peruzzi L (2021) Lectotypification of the Linnaean name *Dianthus virgineus* (Caryophyllaceae) and its taxonomic consequences. TAXON 70(5): 1096–1100. https://doi.org/10.1002/tax.12563

Domina G, Astuti G, Bacchetta G, Barone G, Rešetnik I, Terlević A, Thiébaut M, Peruzzi L (2021) Typification of 14 names in the *Dianthus virgineus* group (Caryophyllaceae). PhytoKeys 187: 1–14. https://doi.org/10.3897/phytokeys.187.75534

Dong L-X, Yang C-Y, Wang M-X, Huang M-R, Cai Y-M (2008) A new species of the genus *Dianthus* from Xinjiang, China. Xibei Zhiwu Xuebao 28: 2355–2358.

Farsi M, Behroozian M, Vaezi J, Joharchi MR, Memariani F (2013) The evolution of *Dianthus polylepis* complex (Caryophyllaceae) inferred from morphological and nuclear DNA sequence data: One or two species? Plant Systematics and Evolution 299(8): 1419–1431. https://doi.org/10.1007/s00606-013-0804-z

Ferrer Gallego PP, Laguna E (2018) *Dianthus* × *ossetianus* (Caryophyllaceae), a new hybrid for the Valencian flora. Flora Montibérica 70: 67–72.

Fior S, Karis PO, Casazza G, Minuto L, Sala F (2006) Molecular phylogeny of the Caryophyllaceae (Caryophyllales) inferred from chloroplast *matK* and nuclear rDNA its sequences. American Journal of Botany 93(3): 399–411. https://doi.org/10.3732/ajb.93.3.399

Gehrke B, Linder PH (2009) The scramble for Africa: Pan-temperate elements on the African high mountains. Proceedings. Biological Sciences 276(1667): 2657–2665. https://doi.org/10.1098/rspb.2009.0334

Gemici Y, Leblebici E (1995) Seven new species for the Flora of Turkey. Candollea 50: 41–50.

Ghanzafar SA, Nasir YJ (1986) Caryophyllaceae. In: Nasir E, Ali SI (Eds) Flora of Pakistan 175. University of Karachi, Karachi, 1–25.

Güner A (2000) *Dianthus* L. In: Güner A, Özhatay N, Ekim T, Başer KHC (Eds) Flora of Turkey and the East Aegean Islands, Vol. 11, Suppl 2. Edinburgh University Press, Edinburgh, 48–49.

Greenberg AK, Donoghue MJ (2011) Molecular systematics and character evolution in Caryophyllaceae. Taxon 60(6): 1637–1652. https://doi.org/10.1002/tax.606009

Hamzaoğlu E, Koç M (2015) *Dianthus burdurensis* (Caryophyllaceae), a new species from South-western Turkey. Phytotaxa 233(2): 5. https://doi.org/10.11646/phytotaxa.233.2.8

Hamzaoğlu E, Koç M (2018) *Dianthus sancarii* (Caryophyllaceae), a new species from eastern Turkey. Biological Diversity and Conservation 11: 30–34.

Hamzaoğlu E, Koç M (2021) *Dianthus muglensis* nom. nov. and notes on *D. goerkii*, the correct name for *D. leucophaeus* var. *patens* (Caryophyllaceae). Phytotaxa 491: 291–296. https://doi.org/10.11646/phytotaxa.491.4.4

Hamzaoğlu E, Koç M, Aksoy A (2014) A new pricking carnation (Caryophyllaceae) grows on tuff from Turkey: *Dianthus aculeatus* sp. nov. Biological Diversity and Conservation 7: 159–162.

Hamzaoğlu E, Koç M, Aksoy A (2015) *Dianthus aticii*, a new species from Turkey (Caryophyllaceae). PhytoKeys 48: 21–28. https://doi.org/10.3897/phytokeys.48.4446

Hamzaoğlu E, Koç M, Büyük İ (2017) *Dianthus ucarii* (Caryophyllaceae): A new species from the northwest of Turkey. Turkish Journal of Botany 41: 486–492. https://doi.org/10.3906/bot-1612-41

Hamzaoğlu E, Koç M, Büyük İ (2018) Two new spiny species of *Dianthus* (Caryophyllaceae) from Turkey. KSÜ Tarım ve Doğa Dergisi 21: 545–554.

Harbaugh DT, Nepokroeff M, Rabeler RK, McNeill J, Zimmer EA, Wagner WL (2010) A new lineage-based tribal classification of the family Caryophyllaceae. International Journal of Plant Sciences 171(2): 185–198. https://doi.org/10.1086/648993

Hernández-Ledesma P, Berendsohn WG, Borsch T, von Mering S, Akhani H, Arias S, Castañeda-Noa I, Eggli U, Eriksson R, Flores-Olvera H, Fuentes-Bazán S, Kadereit G, Klak C, Korotkova N, Nyffeler R, Ocampo G, Ochoterena H, Oxelman B, Rabeler RK, Sanchez A, Schlumpberger BO, Uotila P (2015) A taxonomic backbone for the global synthesis of species diversity in the angiosperm order Caryophyllales. Willdenowia 45(3): 281–383. https://doi.org/10.3372/wi.45.45301

Hohmann N, Koch MA (2017) An *Arabidopsis* introgression zone studied at high spatio-temporal resolution: Interglacial and multiple genetic contact exemplified using whole nuclear and plastid genomes. BMC Genomics 18(1): e810. https://doi.org/10.1186/s12864-017-4220-6

Iamonico D (2013) Italian endemic Caryophyllaceae: A review. Lagascalia 33: 275–298.

İlçim A, Behçet L, Mükemre M (2013) *Dianthus vanensis* (Caryophyllaceae), a new species from Turkey. Turkish Journal of Botany 37: 219–224.

Jalas J, Suominen J (1988) Atlas Florae Europaeae: Distribution of vascular plants in Europe. Cambridge University Press, Cambridge.

Kew WCVP (2019) Dataset export of the World Checklist of Vascular Plants database. [dated 19 December 2019]

Knjasev MC (1997) О новом виде рода *Dianthus* (Caryophyllaceae) намеченном к описанию М. В. Клоковым [On a new species of the genus *Dianthus* (Caryophyllaceae) suggested but not described by M. Klokov]. Botanicheskii Zhurnal 82: 80–83.

Koç M (2020) Morphological and molecular evidence for a new species of *Dianthus* (Caryophyllaceae) from Turkey. Phytotaxa 439: 56–66. doi:https://doi.org/10.11646/phytotaxa.439.1.3

Koch MA, Kiefer C, Ehrich D, Vogel J, Brochmann C, Mummenhoff K (2006) Three times out of Asia Minor: The phylogeography of *Arabis alpina* L. (Brassicaceae). Molecular Ecology 15(3): 825–839. https://doi.org/10.1111/j.1365-294X.2005.02848.x

Kołodziejek J, Patykowski J, Wala M (2018) An experimental comparison of germination ecology and its implication for conservation of selected rare and endangered species of *Dianthus* (Caryophyllaceae). Botany 96(5): 319–328. https://doi.org/10.1139/cjb-2017-0213

Korotkova N, Zabel L, Quandt D, Barthlott W (2010) A phylogenetic analysis of *Pfeiffera* and the reinstatement of *Lymanbensonia* as an independently evolved lineage of epiphytic Cactaceae within a new tribe Lymanbensonieae. Willdenowia 40(2): 151–172. https://doi.org/10.3372/wi.40.40201

Kougioumoutzis K, Valli AT, Georgopoulou E, Simaiakis SM, Triantis KA, Trigas P (2016) Network biogeography of a complex island system: The Aegean Archipelago revisited. Journal of Biogeography 44(3): 651–660. https://doi.org/10.1111/jbi.12920

Kuvaev VB (2006) Флора субарктических гор Евразии и высотное распределение ее видов [The flora of subarctic mountains in Eurasia and the altitudinal distribution of its species]. KMK publishing, Moscow.

Kuzmina ML, Nersesyan A (2012) *Dianthus* L. In: Takhtajan AL (Ed.) Конспект флоры Кавказа (Caucasian Flora Conspectus), Vol. 3. KMK Scientific Press, Saint Petersburg, Moscow, 182–196.

Lazkov GA (2002) New species of Caryophyllaceae. Botanicheskii Zhurnal 87: 112–115.

Lazkov GA (2006) Семейство гвоздичных (Caryophyllaceae) во флоре Кыргыстана [The carnation family (Caryophyllaceae) in the flora on Kyrgyzstan]. KMK publishing, Moscow.

Lazkov GA (2016) Typification of taxa of subfamily *Silenoideae* (Caryophyllaceae Juss.) from Siberia and Russian Far East based on materials kept in the Herbarium of the Komarov Botanical Institute (LE). Turczaninowia 19(2): 50–53. https://doi.org/10.14258/turczaninowia.19.2.5

Linder PH (2014) The evolution of African plant diversity. Frontiers in Ecology and Evolution 2: e38. https://doi.org/10.3389/fevo.2014.00038

Löhne C, Borsch T (2005) Molecular evolution and phylogenetic utility of the *petD* group II intron: A case study in basal angiosperms. Molecular Biology and Evolution 22(2): 317–332. https://doi.org/10.1093/molbev/msi019

López-Jurado J, Mateos-Naranjo E, Balao F (2019) Niche divergence and limits to expansion in the high polyploid *Dianthus broteri* complex. New Phytologist: 1076–1087. https://doi.org/10.1111/nph.15663

Madhani H, Rabeler R, Pirani A, Oxelman B, Heubl G, Zarre S (2018) Untangling phylogenetic patterns and taxonomic confusion in tribe Caryophylleae (Caryophyllaceae) with special focus on generic boundaries. Taxon 67(1): 83–112. https://doi.org/10.12705/671.6

Marhold K (2011) Caryophyllaceae. Euro+Med Plantbase - the information resource for Euro-Mediterranean plant diversity. https://europlusmed.org/

Mateo Sanz G, Crespo MB (2008) Novedades taxonómicas y nomenclaturales para la flora valenciana. Flora Montiberica 40: 60–70.

Menemen Y, Hamzaoğlu E (2000) A new species of *Dianthus* (Caryophyllaceae) from Salt Lake, Central Anatolia, Turkey. Annales Botanici Fennici 37: 285–287.

Meyer FK (2011) Beiträge zur Flora von Albanien. Hausknechtia Beiheft 15. Thüringische Botanische Gesellschaft e.V., Jena.

Mosyakin SL, Fedoronchuk MM (2018) *Dianthus recticaulis*, the correct name for *Gypsophila stricta* and *G. alpina* (≡ *Petrorhagia alpina*) (Caryophyllaceae). Phytotaxa 347: 297–300. https://doi.org/10.11646/phytotaxa.347.4.7

Müller KF (2005a) The efficiency of different search strategies in estimating parsimony jackknife, bootstrap, and Bremer support. BMC Evolutionary Biology 5(1): e58. https://doi.org/10.1186/1471-2148-5-58

Müller KF (2005b) SeqState - primer design and sequence statistics for phylogenetic DNA data sets. Applied Bioinformatics 4: 65–69. https://doi.org/10.2165/00822942-200504010-00008

Müller KF, Borsch T (2005) Phylogenetics of Amaranthaceae based on *matK*/*trnK* sequence data - Evidence from Parsimony, likelihood, and Bayesian analyses. Annals of the Missouri Botanical Garden 92: 66–102.

Müller J, Müller KF, Neinhuis C, Quandt D (2005+) PhyDE: Phylogenetic Data Editor. www.phyde.de

Nersesyan A (2011) The genus *Dianthus* L. (Caryophyllaceae) in Southern Transcaucasia. Takhtajania 1: 44–51.

Novikova PY, Hohmann N, Nizhynska V, Tsuchimatsu T, Ali J, Muir G, Guggisberg A, Paape T, Schmid K, Fedorenko OM, Holm S, Säll T, Schlötterer C, Marhold K, Widmer A, Sese J, Shimizu KK, Weigel D, Krämer U, Koch MA, Nordborg M (2016) Sequencing of the genus *Arabidopsis* identifies a complex history of nonbifurcating speciation and abundant trans-specific polymorphism. Nature Genetics 48(9): 1077–1082. https://doi.org/10.1038/ng.3617

Opiz FM (1852) Šeznam Rostlin Květeny České. Praha.

Ortuño Limarino T, Borsch T (2020) *Gomphrena* (Amaranthaceae, Gomphrenoideae) diversified as a C4 lineage in the New World tropics with specializations in floral and inflorescence morphology, and an escape to Australia. Willdenowia 50(3): 345–381. https://doi.org/10.3372/wi.50.50301

Oskay D (2018) *Dianthus somanus* (Caryophyllaceae), a new species from Turkey. Phytotaxa 347(4): 263–271. https://doi.org/10.11646/phytotaxa.347.4.2

Pax F, Hoffmann K (1934) Caryophyllaceae. In: Engler A, Harms H (Eds) Die natürlichen Pflanzenfamilien. Verlag von Wilhelm Engelmann, Leipzig, 275–364.

Peruzzi L, Gargano D (2006) *Dianthus ferrugineus* Mill. vs. *D. guliae* Janka: Nomenclatural considerations on the Italian yellow carnation. Taxon 55(3): 781–784. https://doi.org/10.2307/25065652

Rabeler RK (1993) Infrageneric nomenclature: Corrections and additions in the Caryophyllaceae. Contributions from the University of Michigan Herbarium 19: 149–164.

Rabeler RK, Hartman RL *Dianthus*. In: Flora of North America Editorial Committee (Eds) 1993+ Flora of North America North of Mexico [Online]. 22+ vols. New York and Oxford. Vol. 5. http://floranorthamerica.org/Dianthus [accessed 4 Mar 2022]

Rechinger KH (1988) *Dianthus*. In: Rechinger KH (Ed.) Flora Iranica vol. 163. Akademische Druck-und Verlangsanstalt, Graz, 128–188.

Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics (Oxford, England) 19(12): 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Schäferhoff B, Müller KF, Borsch T (2009) *Caryophyllales* phylogenetics: Disentangling *Phytolaccaceae* and *Molluginaceae* and description of *Microteaceae* as a new isolated family. Willdenowia 39(2): 209–228. https://doi.org/10.3372/wi.39.39201

Sfenthourakis S, Triantis KA (2017) The Aegean archipelago: A natural laboratory of evolution, ecology and civilisations. Journal of Biological Research (Greece) 24(1): 1–13. https://doi.org/10.1186/s40709-017-0061-3

Shaulo DN, Erst AS (2011) A new species of *Dianthus* L. (Caryophyllaceae) from the West Sayan, Altai-Sayan Mountains, Russia. Feddes Repertorium 122(5–6): 344–350. https://doi.org/10.1002/fedr.201100007

Shaw J, Lickey EB, Beck JT, Farmer SB, Liu W, Miller J, Siripun KC, Winder CT, Schilling EE, Small RL (2005) The tortoise and the hare II: Relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. American Journal of Botany 92(1): 142–166. https://doi.org/10.3732/ajb.92.1.142

Shaw J, Lickey EB, Schilling EE, Small RL (2007) Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: The tortoise and the hare III. American Journal of Botany 94(3): 275–288. https://doi.org/10.3732/ajb.94.3.275

Simmons MP, Ochoterena H (2000) Gaps as characters in sequence-based phylogenetic analyses. Systematic Biology 49(2): 369–381. https://doi.org/10.1093/sysbio/49.2.369

Son DC, Kim H-J, Chang KS, Lee D-H, Lee K-H (2017) A new species of *Dianthus* (Caryophyllaceae) from Republic of Korea. Phytotaxa 303(1): 71–76. https://doi.org/10.11646/phytotaxa.303.1.6

Stamatakis A (2014) RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics (Oxford, England) 30(9): 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Stamatakis A, Hoover P, Rougemont J (2008) A rapid bootstrap algorithm for the RAxML web servers. Systematic Biology 57(5): 758–771. https://doi.org/10.1080/10635150802429642

Stöver B, Müller K (2010) TreeGraph 2: Combining and visualizing evidence from different phylogenetic analyses. BMC Bioinformatics 11(1): e7. https://doi.org/10.1186/1471-2105-11-7

Swofford DL (1998) PAUP*. Phylogenetic Analysis Using Parsimony (*and other Methods). Sinauer Associates, Sunderland, Massachussets.

TPL (2013) TPL 2013: The Plant List v. 1.1. http://www.theplantlist.org/ [accessed 2019–2020]

Tutin TG (1964) *Dianthus* L. In: Tutin TG, Burges NA, Chater AO, R. EJ, Heywood VH, Moore DM, Valentine DH, Walters SM (Eds) Flora Europaea, Vol. 1. Cambridge University Press, Cambridge, 188–204.

Vaezi J, Behroozian M, Memariani F, Joharchi MR (2014) Dianthus pseudocrinitus (Caryophyllaceae), a new species from Northeast of Iran identified by morphological and molecular data. Phytotaxa 156(2): 59–73. https://doi.org/10.11646/phytotaxa.156.2.1

Valente LM, Savolainen V, Vargas P (2010) Unparalleled rates of species diversification in Europe. Proceedings. Biological Sciences 277(1687): 1489–1496. https://doi.org/10.1098/rspb.2009.2163

Vural C (2008) A new species of *Dianthus* (Caryophyllaceae) from Mount Erciyes, central Anatolia, Turkey. Botanical Journal of the Linnean Society 158(1): 55–61. https://doi.org/10.1111/j.1095-8339.2008.00843.x

WFO (2018) World Flora Online taxonomic backbone data export for Caryophyllales. received from William Ulate, Missouri Botanical Garden. [dated 22 oct 2018]

White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis DGM, Sninsky J, White T (Eds) PCR protocols: A guide to methods and applications. Academic Press, San Diego, California, 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Wicke S, Quandt D (2009) Universal primers for the amplification of the plastid *trnK*/*matK* region in land plants. Anales del Jardin Botanico de Madrid 66(2): 285–288. https://doi.org/10.3989/ajbm.2231

Williams FN (1885) Enumeratio specierum varietatumque generis *Dianthus*; characteres communes sectionibus includens. Le Journal de Botanique 23: 340–352.

Williams FN (1893) A monograph of the genus *Dianthus*, Linn. Botanical Journal of the Linnean Society 29(203): 346–469. https://doi.org/10.1111/j.1095-8339.1893.tb02037.x

Yılmaz Ö, Kaynak G, Daşkın R, Meriçlioğlu A (2011) *Dianthus goekayi* (Caryophyllaceae), a new species from Turkey. Annales Botanici Fennici 48(1): 74–78. https://doi.org/10.5735/085.048.0111

Zografidis A, Fragman-Sapir O, Strid A, Dimopoulos P (2020) Notes on the generic name *Graecobolanthus* (Caryophylleae, Caryophyllaceae). Taxon 69(5): 992–997. https://doi.org/10.1002/tax.12292

Zoku N (1965) *Dianthus* L. In: Ōi J, Meyer FG, Walker EH (Eds) Flora of Japan. Smithsonian Institution, Washington D. C., 431–432.

Supplementary material 1

Appendix 1

Authors: Georgia Fassou, Nadja Korotkova, Anush Nersesyan, Marcus A. Koch, Panayotis Dimopoulos, Thomas Borsch

Data type: Xlsx file.

Explanation note: Voucher information and ENA accession numbers.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/phytokeys.196.77940.suppl1