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# *Poa densa* (*Poaceae*), an overlooked Turkish steppe grass, and the evolution of bulbs in *Poa*

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**Abstract:** *Poa densa* Troitsky is a characteristic species of the high steppe to low alpine vegetation of Turkey. It was overlooked in the *Flora of Turkey*, and although subsequently reported from a few stations in W part of C Anatolia, is actually relatively common and widespread across the semi-arid C and N steppes. Here we provide a key to related species, a full description, photographs, 2C value of nuclear DNA content, and a distribution map, and discuss its classification in the genus. The synonym *Festuca conferta* is lectotypified. DNA phylogenetic analysis and morphology data indicate *P. densa* is allied to species of *P.* subg. *Poa* sect. *Macropoa*, rather than to the *P. bulbosa* complex of *P.* subg. *Ochlopoa* sect. *Arenariae*, and support multiple origins of the basal bulb in the genus *Poa.*

**Key words:** bulbs, evolution, taxonomy, lectotypification, Turkey, Anatolia, *Poaceae*, *Gramineae*, *Poa*, *Poa densa*, *Festuca conferta*

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## Introduction

*Poa densa* Troitsky was not reported in the *Flora of Turkey* account of *Poa* L. by Edmondson (1985). Tzvelev (1976) was unaware of the occurrence of the species in Turkey. Bor (1970) did not include it in the *Flora Iranica*. Up to the time of these major accounts for grasses it was only known from Transcaucasia [Grossheim (1939: map 231) mapped it from 11 places in Azerbaijan, Georgia and Armenia], Turkmenistan and N Iran (Tzvelev 1976).

The absence of pre-1970s collections of *Poa densa* from Turkey at ANK, B, E, G, ISTE, K, LE and W partially explains the absence of reports for Turkey in the major regional Floras. Curiously, however, as we document here, *P. densa* seems to be a fairly common and characteristic in the mid-to upper steppe zone from SW to NE Turkey. Despite there being at least six collections of the species made between 1973 and 1981, by such prominent collectors as A. Baytop, Y. Akman and M. Doğan, with vouchers deposited at ANK and ISTE (under other species names), the species was overlooked for Turkey until Parolly & al. (2002) reported three newer collections of the species from SW Turkey as a disjunction from the Irano / Caucasian-Turkmenian region. In the checklist of the *Poaceae* of Turkey, Cabi & Doğan (2012) reported 30 *Poa* taxa including *P. densa.* It was also noted more recently in treatments of grasses for Armenia (Gabrieljan 2010) and Iran (Akhani & Scholz 1998) and mapped for Iran (Kavousi & al. 2015). It was reported for Xinjiang, China, by Liu (2003), but no material of this species was found in KUN, NAS, PE or other herbaria surveyed by R.J.S. for the *Flora of China* (Zhu & al. 2006).

Here we report many additional collections of *Poa densa* in Turkey and map them. We also provide a detailed

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description and diagnosis, diagnostic photographs, discuss its lectotypifications, and lectotypify its synonym, *Festuca conferta* Troitsky ex Grossh. We undertook flow-cytometric and phylogenetic investigations to determine its ploidy level and what it might be related to, and in particular how many times bulbs might have arisen within *Poa*.

## Material and methods

Collections of *Poa densa* were sought under this and other names at ANK, ANKF, B, E, EGE, G, ISTE, KNYA and US, with K checked by Maria Vorontsova (herbarium acronyms after Thiers 2015+). New collections were made by some of us in 1991, 1993, 2013, 2014, 2015, and several other specimens were reported in the literature (Parolly & al. 2002) for Turkey. All the Turkish and other specimens known to us are listed in the Taxonomy section.

### *Flow cytometry*

Leaves of field-collected *Poa densa* accessions were used as plant material. Nuclear suspensions were prepared by chopping 0.5 $cm^2$ of leaf tissue of *P. densa* and 0.5 $cm^2$ of internal standard leaves, with a razor blade in a glass Petri dish containing 500 µl isolation buffer (the commercial Partec extraction buffer). *Vicia sativa* 'Orakefe' (2C = 3.65 pg of DNA, Tiryaki & Tuna 2012) was used as an internal reference standard for all samples. Nuclear suspension was then filtered through a 50 µm cell-tricks disposable filter and mixed with 2 ml staining solution and incubated for 30–60 sec. Flow-cytometric analysis was performed using the flow cytometer Partec CyStain UV Precise (code No. 05-5002: Partec GmbH, Germany) at the Department of Field Crops, Faculty of Agriculture of Namık Kemal University. At least 10000 nuclei were analysed per sample. Four individuals were analysed in three different days to avoid errors due to instrumental drift.

### *Molecular analysis*

Thirty-one samples were chosen for the molecular analysis representing 28 species and infraspecific taxa and including three samples of *Poa densa* (Table 1) and seven other bulbous taxa. *Poa* subg. *Sylvestres* (V. L. Marsh ex Soreng) Soreng & L. J. Gillespie (*P. autumnalis* Muhl. ex Elliott, *P. saltuensis* Fernald & Wiegand), well supported as the basal *Poa* clade in previous analyses of *Poa* and subtribe *Poinae* (Gillespie & al. 2007, 2008, 2009; Soreng & al. 2010), was used as the outgroup.

One plastid (*trnT-trnL-trnF* – TLF), and two nuclear ribosomal (nr) DNA markers, internal transcribed spacer (ITS) and external transcribed spacer (ETS), were sequenced. TLF includes two spacer regions and the *trnL* intron (Taberlet & al. 1991). For ETS partial sequences of approximately 500 base pairs at the 3′ end were used (Gillespie & al. 2009). DNA extraction and sequencing protocols, as well as primers, are described in Gillespie & al. (2007, 2008, 2009, 2010).

Sequences were assembled, checked and edited using either Sequencher ver. 4.7 (GeneCodes Corp., http://genecodes.com) or Geneious ver. 6.1.5 (Biomatters Ltd, http://www.geneious.com). Sequences were aligned using the MAFFT ver. 7.017 plugin (Katoh & al. 2002; Katoh & Standley 2013) followed by manual adjustment in Geneious. The three alignments (TLF, ITS, ETS) were concatenated in Geneious.

Maximum parsimony (MP) analyses were performed in PAUP* 4.0b10 (Swofford 2002) on the separate and combined alignments using the heuristic search command with default settings, including tree-bisection reconnection (TBR) swapping and saving all multiple shortest trees (Multrees). Strict consensus trees were computed in PAUP and prepared in FigTree v1.4.0 (Rambaut 2006–2014). Branch support was assessed using MP bootstrap analyses performed in PAUP using a heuristic search strategy with default settings and 1000 bootstrap replicates, each with five random addition sequence replicates. Strict consensus trees were inspected for conflicting topologies, with incongruence identified by branch conflicts having ≥ 70 % MP bootstrap support (BS). Since no supported incongruence was found between the ITS and ETS trees, and subsequently between the ITS+ETS and TLF trees, a final analysis was run on the combined ITS+ETS+TLF dataset.

## Results

### *Cytology*

Our flow-cytometric data suggest that the species is diploid in Turkey (voucher *Soreng & al. 8110,* US, NAKU) with a 2C value of 2.0 pg of DNA (*Vicia* standard), which is intermediate between other studied diploid *Poa* species.

### *Molecular analysis*

The combined ITS+ETS+TLF data matrix comprised 3090 characters, of which 188 were parsimony informative; ITS, ETS and TLF partitions had aligned lengths of 599, 558 and 1933 characters, respectively, of which 54, 67 and 67 were parsimony-informative. The ITS+ETS+TLF analysis resulted in 16 most parsimonious trees, 392 steps long, with a consistency index (CI) excluding uninformative characters of 0.77; the strict consensus tree with bootstrap support values is shown in Fig. 1.

The sampled ingroup *Poa* species form three strongly supported major clades (BS = 100): *P.* subg. *Ochlopoa* (Asch. & Graebn.) Hyl., the separate unclassified lineage called the N-clade (see Gillespie & al. 2009; Soreng & al. 2010), and *P.* subg. *Poa*, with the latter two sister clades (BS = 100). *Poa* subg. *Poa* is further divided into two subclades: *P.* supersect. *Poa* (BS = 86) and *P.* supersect. *Homalopoa* (Dumort.) Soreng & L. J. Gillespie (type:

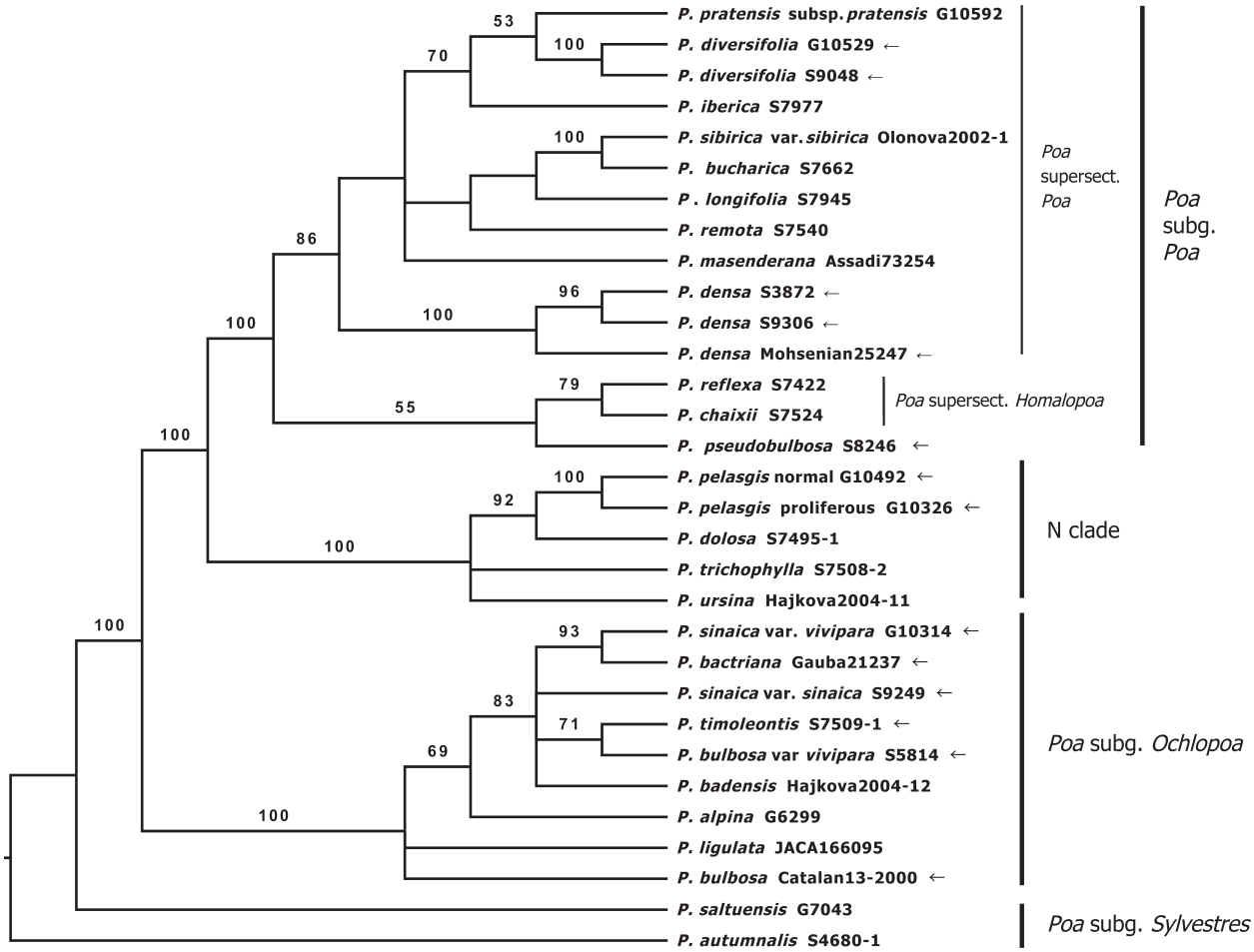


Fig. 1. Strict consensus tree of *Poa* showing the placement of *P. densa* and the distribution of bulbs in the genus, from the combined nuclear ITS and ETS and plastid TLF analysis (16 most parsimonious trees, 392 steps long, CI excl. uninformative chars = 0.77, RI = 0.95). Bootstrap support percentages are shown above the branches. Major clades are labelled on the right. Taxa with bulbous-based shoots are indicated with an arrow.

*P. chaixii* Vill.) (BS =79); note that the classification of *P. pseudobulbosa* Bor is uncertain, although the tree shows weak support for a relationship with *P.* supersect. *Homalopoa*. *Poa densa* resolves in the *P.* subg. *Poa* supersect. *Poa* clade with good support (BS = 86 %). Relationships within the *P.* supersect. *Poa* clade are for the most part weakly supported here, as is the precise position of *P. densa*.

Species with bulbs are distributed in four clades (Fig. 1): (1) *Poa densa* and *P. diversifolia* (Boiss. & Balansa) Hack. ex Boiss. in *P.* supersect. *Poa*; (2) *P. pseudobulbosa* in or near *P.* supersect. *Homalopoa*; (3) *P. pelasgis* H. Scholz in the N-clade; and (4) *P. bactriana* Roshev., *P. bulbosa* L., *P. sinaica* Steud. and *P. timoleontis* Heldr. ex Boiss. in *P.* subg. *Ochlopoa* sect. *Arenariae* (Hegetschw.) Stapf (type: *P. bulbosa* L.) mixed with species of *P.* sect. *Alpinae* (Hegetschw. ex Nyman) Stapf (type: *P. alpina* L.).

## Discussion

The centre of distribution of *Poa* subg. *Ochlopoa* sect. *Arenariae*, in which *P. densa* was historically placed, and the only section of the genus characterized by bulbous based shoots, is in the Mediterranean region (11 spp.), with a secondary centre in the C Asian steppes (two to four additional species). Soreng (1998), unaware that *P. diversifolia* was also bulbous, listed 14 species for the section (following Tzvelev 1976; Scholz 1985, 1986; Soreng & al. 1997). *Poa densa* is easily recognized by its indurate thickened basal sheaths forming bulbs, firmer than those that occur in the *P. bulbosa* complex (*P.* sect. *Arenariae* ≡ *P.* sect. *Bolbophorum* Asch. & Graebn., *P.* subsect. *Bulbosae* V. Jirásek), in combination with short (to 0.5 mm long), truncate basal leaf ligules, firm (non-withering), filiform basal leaf blades, and firm, glabrous, 5-veined lemmas. Although Tzvelev (1976) placed it in *P.* sect. *Poa* subsect. *Bulbosae*, along with *P. bactriana*, *P. bulbosa*, *P. sinaica*, *P. timoleontis*, and *P. vvedenskyi* Drobow, Troitsky (1928) originally allied it to *P. diversifolia*, a previously unclassified species of W Turkey and the Levant. Sokolovskaya & Probatova (1979) argued that it belonged to Tzvelev's *P.* sect. *Macropoa* F. Herm. ex Tzvelev (type: *P. longifolia* Trin.), in which they and he included *P. bucharica* Roshev., *P. iberica* Fisch. & C. A. Mey., *P. longi-*

Table 1. *Poa* taxa, our classification, voucher information and GenBank accession numbers for collections in Fig. 1. Sequences with GenBank numbers in **bold** are new in this paper.

| Taxa | Subgenus | Section | Voucher | Country of origin | GenBank accession numbers | | |
|---|---|---|---|---|---|---|---|
| | | | | | ETS | ITS | TLF |
| *P. alpina* L. | *Ochlopoa* | *Alpinae* | *Gillespie 6299* (CAN) | U.S.A.: Colorado | GQ324287 | GQ324483 | DQ353985.2 |
| *P. autumnalis* Elliott | *Sylvestres* | *Sylvestres* | *Soreng 4680* (US) | U.S.A.: Maryland | GQ324294 | EU792379 | DQ353979 |
| *P. bactriana* subsp. *glabriflora* (Roshev.) Tzvelev | *Ochlopoa* | *Arenariae* | *Gauba 21237* (IRAN) | Iran | **KX118716** | **KX118734** | **KX118751** |
| *P. badensis* Haenke ex Willd. | *Ochlopoa* | *Alpinae* | *Hajkova & al. 2004-12* (US) | Bulgaria | GQ324295 | GQ324490 | GQ324402 |
| *P. bucharica* Roshev. | *Poa* (supersect. *Poa*) | *Macropoa* | *Soreng & al. 7662* (US) | Kyrgyzstan | **KX118717** | **KX118735** | **KX118752** |
| *P. bulbosa* L. | *Ochlopoa* | *Arenariae* | *Catalan 13-2000* (Universidad de Zaragoza) | Spain | GQ324297.2 | EU792388 | DQ354034.2, DQ354035.2 |
| *P. bulbosa* var. *vivipara* Koeler | *Ochlopoa* | *Arenariae* | *Soreng 5814* (US) | U.S.A.: Nevada | GQ324298 | GQ324492 | GQ324404 |
| *P. chaixii* Vill. | *Poa* (supersect. *Homalopoa*) | *Homalopoa* s.s. | *Soreng 7524* (US) | Germany | GQ324300 | GQ324493 | GQ324405 |
| *P. densa* Troitsky | *Poa* (supersect. *Poa*) | *Macropoa* | *Mohsenian 25247* (TARI) | Iran | **KX118719** | **KX118737** | **KX118754** |
| *P. densa* | *Poa* (supersect. *Poa*) | *Macropoa* | *Soreng & Cabi 9306* (US) | Turkey | **KX118720** | **KX118738** | **KX118755** |
| *P. densa* | *Poa* (supersect. *Poa*) | *Macropoa* | *Soreng & al. 3872* (US) | Turkey | **KX118718** | **KX118736** | **KX118753** |
| *P. diversifolia* (Boiss. & Balansa) Hack. ex Boiss. | *Poa* (supersect. *Poa*) | *Macropoa* | *Gillespie & al. 10529* (CAN) | Turkey | **KX118721** | **KX118739** | **KX118756** |
| *P. diversifolia* | *Poa* (supersect. *Poa*) | *Macropoa* | *Soreng & Cabi 9048* (US) | Turkey | KX118722 | KX118740 | KX118757 |
| *P. dolosa* Boiss. & Heldr. | N-clade | *Oreinos* s.l. | *Soreng & al. 7495-1* (US) | Greece | GQ324312 | GQ324502 | GQ324414 |
| *P. iberica* Fisch. & C. A. Mey. | *Poa* (supersect. *Poa*) | *Macropoa* | *Soreng & al. 7977* (US) | Russia: Cabardino-Balkaria | **KX118723** | **KX118741** | **KX118758** |
| *P. ligulata* Boiss. | *Ochlopoa* | *Alpinae* | *JACA 166095* | Spain | GQ324346 | GQ324522 | GQ324432, KX118759 |
| *P. longifolia* Trin. subsp. *longifolia* | *Poa* (supersect. *Poa*) | *Macropoa* | *Soreng & al. 7945* (US) | Russia: Cabardino-Balkaria | **KX118724** | **KX118742** | **KX118760** |

(continued on next page)

(Table 1 continued from previous page)

| Taxa | Subgenus | Section | Voucher | Country of origin | GenBank accession numbers | | |
|---|---|---|---|---|---|---|---|
| | | | | | ETS | ITS | TLF |
| *P. masendarana* Freyn & Sint. | *Poa* (supersect. *Poa*) | *Macropoa* | *Assadi 73254* (TARI) | Iran | **KX118725** | **KX118743** | **KX118761** |
| *P. pelasgis* H. Scholz normal | *Ochlopoa* | *Arenariae* | *Gillespie & al. 10492* (CAN) | Turkey | **KX118726** | **KX118744** | **KX118762** |
| *P. pelasgis* proliferous | *Ochlopoa* | *Arenariae* | *Gillespie & Cabi 10326* (CAN) | Turkey | **KX118727** | **KX118745** | **KX118763** |
| *P. pratensis* L. subsp. *pratensis* | *Poa* (supersect. *Poa*) | *Poa* | *Gillespie & al. 10592* (CAN) | Turkey | **KX118728** | **KX118746** | **KX118764** |
| *P. pseudobulbosa* Bor | *Poa* | unclassified | *Soreng & Cabi 8246* (US) | Turkey | **KX118729** | **KX118747** | **KX118765** |
| *P. reflexa* Vasey & Scribn. | *Poa* (supersect. *Homalopoa*) | *Homalopoa* s.l. | *Soreng 7422* (US) | U.S.A.: Colorado | **KX118730** | GQ324543 | GQ324450 |
| *P. remota* Forselles | *Poa* (supersect. *Poa*) | *Homalopoa* s.l. | *Soreng & al. 7540* (US) | Kyrgyzstan | GQ324372 | GQ324545 | GQ324452 |
| *P. saltuensis* Fernald & Wiegand | *Sylvestres* | *Sylvestres* | *Gillespie 7043* (CAN) | Canada: Ontario | GQ324374 | EU792378 | EU792451 |
| *P. sibirica* Roshev. var. *sibirica* | *Poa* (supersect. *Poa*) | *Macropoa* | *Olonova 2002* (CAN) | Russia: Khakasia | GQ324376 | EU792401 | DQ354044, DQ354045 |
| *P. sinaica* Steud. var. *sinaica* | *Ochlopoa* | *Arenariae* | *Soreng & Cabi 9249* (US) | Turkey | **KX118731** | **KX118748** | **KX118766** |
| *P. sinaica* var. *vivipara* Täckh. | *Ochlopoa* | *Arenariae* | *Gillespie & Levin 10314* (CAN) | Turkey | **KX118732** | **KX118749** | **KX118767** |
| *P. timoleontis* Heldr. ex Boiss. | *Ochlopoa* | *Arenariae* | *Soreng & al. 7509* (US) | Greece | **KX118733** | **KX118750** | **KX118768** |
| *P. trichophylla* Heldr. & Sart. ex Boiss. | N-clade | *Nanopoa* | *Soreng & al. 7508* (US) | Greece | GQ324386 | GQ324554 | GQ324461 |
| *P. ursina* Velen. | N-clade | unclassified (*Bolbophorum* in Fl. Eur.) | *Hajkova & al. 2004-11* (US) | Bulgaria | GQ324351 | GQ324526 | GQ324436 |

*folia* and *P. sibirica* Roshev., rather than to his *P*. sect. *Poa* subsect. *Bulbosae*. It differs from *P. diversifolia*, to which it is genetically related (Fig. 1), by its smooth, glabrous lower culms (*P. diversifolia* is minutely scabrous to strigulose below the culm nodes), and short, narrow culm leaf blades (elongate and broader in *P. diversifolia*), and short, densely to slightly loosely contracted panicles. Bulbs are weakly expressed in the rare Turkish endemic *P. pseudobulbosa*, for which Edmondson (1985) noted a relationship to *P. densa* (not then known from Turkey).

Fig. 1 shows that species with bulbs occur in four clades. *Poa densa* and *P. diversifolia* (both bulbous) are closely related to species of *P.* sect. *Macropoa* that are not bulbous, and these are distantly related to other species placed in the *P. bulbosa* complex. *Poa pelasgis* represents a third appearance of a bulbous species in the phylogram. *Poa pseudobulbosa* represents another possible origin of bulbs within *P.* subg. *Poa*, but its position is poorly supported, and we cannot say with confidence that it belongs to *P.* supersect. *Homalopoa.*

The plastid and nrDNA sequences of *Poa densa* from Turkey and Iran are nearly identical, and all the sequences generated are very similar to *P. diversifolia* and *P. longifolia*.

Following our genotype classification (Soreng & al. 2010), *Poa densa* and *P. diversifolia* share "P" plastid genotypes and an "h" nrDNA genotype similar to species of *P.* subg. *Poa* sect. *Macropoa*; *P. bucharica*, *P. iberica*, *P. longifolia*, *P. masenderana* Freyn & Sint. and *P. sibirica*. We place the previous set of species all in *P.* subg. *P.* sect. *Macropoa*. *Poa pratensis* L., of *P.* sect. *Poa*, also characterized as PH, likely picked up part of its allopolyploid genome from *P.* sect. *Macropoa* (see also Patterson & al. 2005). We accept the species of the *P. bulbosa* complex (see Soreng 1998) in *P.* subg. *Ochlopoa* sect. *Arenariae*, where *P. akmanii* Soreng & al., *P. bactriana*, *P. bulbosa*, *P. sinaica* and *P. timoleontis* are characterized as having "OAOA" genotypes, as do members of *P.* sect. *Alpinae* species (incl. *P. alpina*, *P. badensis* Haenke, *P. ligulata* Boiss, etc.). *Poa pelasgis* has an "NN" genotype. The classification of the latter species is under investigation; it was previously reported in DNA studies as *P. sinaica,* by Patterson & al. (2005), or as *P. bulbosa* in part by Soreng (1990) and Gillespie & Soreng (2005). Scholz first described this taxon as *P. sinaica* var. *graeca* H. Scholz, then (in 1985) recognized it as a species related to *P. eigii* Feinbrun and *P. hackelii* Post, still within the *P. bulbosa* complex.

Evidently basal bulbs arose more than once in *Poa*, at least once in *P.* sect. *Arenariae* (OAOA) and again in *P.* sect. *Macropoa* (PH), under similar environmental pressures of arid Mediterranean climate, or the bulbous habit was transferred from one species complex to the other via introgressive hybridization. We are inclined to the former hypothesis based on our DNA results and morphological differences between *P.* sect. *Arenariae* and *P.* sect. *Macropoa*, but cannot categorically reject the latter without deeper genetic analyses. However, for *P. pelasgis* we are inclined to the latter hypothesis, for now, as it is difficult to separate from *P.* sect. *Arenariae* except by its shorter ligules and often strigulose lower sheaths. Curiously, *Poa* is the only genus of grasses with true bulbs; all others with swollen culm bases actually have corms (Kellogg 2015), but some species of *Poa* do have corms: *P. drummondiana* Nees (Australia) and *P. tuberifera* U. J. Faurie ex Hack. (Japan).

## Taxonomy

### Key to *Poa densa* in Turkey (plants with thickened basal sheaths)

1. Spikelets viviparous or normal-flowered; normal lemmas (if any) pubescent on keel and marginal veins, and sometimes between veins; lemmas 3-veined, or obscurely 5-veined; callus with or without a dorsal tuft of hairs (web); ligules of basal leaves 0.5–15 mm long; basal blades soon withering or moderately firm and persisting in form when dry (***P.*** sect. ***Arenariae*****:** ***P. bulbosa*** complex).
– Spikelets normal-flowered; lemmas and calluses totally glabrous; lemmas distinctly 5-veined; ligules all short (c. 1 or less in length) and truncate; basal blades moderately firm and persisting in form when dry (***P.*** sect. ***Macropoa*** s.s. **+** ***P. pseudobulbosa***) . . . . . **2**
2. Culms densely retrorsely or bi-directionally appressed strigulose to aculeolate or finely scabrous just below lower or middle culm leaf nodes; panicles generally loose, long-branched, and many-flowered; basal blades involute, slender, firm; culm blades wider and softer; plants (30–)40–100+ cm tall . . . . . ***P. diversifolia***
– Culms smooth, or at most sparsely scabrous below lower culm nodes (in *P. pseudobulbosa*); panicles contracted or if loose then sparsely flowered, short-branched; culm leaf blades ± like those of basal shoots in form, usually equal in length or shorter; plants 10–60 cm tall . . . . . **3**
3. Panicles loose and sparsely flowered; rachilla internodes elongated, plainly visible; culm leaves well developed, c. equalling the basal blades in length . . . . . ***P. pseudobulbosa***
– Panicles dense, or slightly loose; rachilla internodes contracted, mostly hidden; culm leaf blades similar in form to the basal leaf blades, but shorter, the uppermost very short . . . . . ***P. densa***

### Revision of *Poa densa*

***Poa densa*** Troitsky in Izv. Glavn. Bot. Sada S.S.S.R. 27: 619, f. 1. 1928. – Lectotype (designated by Tzvelev, Zlaki SSSR: 451. 1976): Georgia, Tbilisi region, Gargjiiskaya steppe, 17 Jun 1927, *N. Troitsky* (LE [photo at E!: E00326518]). – Fig. 2.

≡ *Festuca conferta* Troitsky ex Grossh., Fl. Kavkaza 1: 115. 1928 (post 20 Nov 1927) [non *Poa conferta* Elliott


Fig. 2. *Poa densa* (*E. Cabi 5135*) – A: habit; B: inflorescence; C: spikelet; D: culm upper node; E: basal bulbous shoots; F: ligule. – Photographs by E. Cabi.

1816, nec Blytt 1861]. – **Lectotype (designated here):** Georgia, Tbilisi region, Gargjiiskaya steppe, 17 Jun 1927, *N. Troitsky* (LE [photo at E!: E00326518]).

*Description* — *Herbs* perennial, hermaphroditic, without rhizomes or stolons, tufted, tufts dense, green to bluish green; culm base with innermost lateral sheaths thick, coriaceous-cartilaginous, elongate-bulbous (bulbs 1–3 cm long), usually exposed, tillers all intravaginal, cataphylls absent, prophylls elongated (c. 1 cm long?). *Culms* (15–)25–60 cm tall, erect, slender, several per tuft, slightly decumbent, smooth or lightly scabrous below panicle, smooth below nodes, glabrous. Leaves mostly basal; leaf sheaths slightly to strongly compressed, strongly imbricated at base; inner ones thickened (elongate bulbous), outer ones papery to scarious, loose, those on culm tightly clasping, flag-leaf sheath 8–14 cm long, margins fused for 36–53 % of their length; ligules of culm leaves 0.5–1.1 mm long, scarious, whitish, abaxially densely scabrous, apex truncate to slightly rounded, asperous, of sterile shoots 0.2–0.7(–1) mm long; blades of culm 0–5 cm long, 0.5–1(–1.5) mm wide, much shorter than their sheath, folded with involute margins, abaxially scabrous along keel and sometimes along some veins, adaxially smooth, apex narrowly prow-tipped, reduced distally, upper one sometimes rudimentary or absent, of sterile shoots 2–10 cm long, fairly firm, involute, capillary (c. 0.5 mm in diam.), lowest with few distinct whitish ribs expressed abaxially, scabridulous between ribs. *Panicles* 2.5–8 cm long, 0.8–1.5 cm wide, contracted, or slightly spreading in anthesis, mostly congested, with (10–)40–60 spikelets, peduncle and axis moderately to densely scabrous, axis with (2 or)3–5 branches at lowest nodes; primary branches, erect to ascending, weakly angled, moderately to densely scabrous, pedicels mostly less than ¼ their spikelets in length, longest branches 0.5–2 cm long, with 4–8

spikelets per branch. *Spikelets* 3.6–5.5(–9) mm long, lanceolate (to broadly ovate); vivipary absent (in Turkey); florets 2 or 3(–7); rachilla internodes 0.5–1 mm long, densely muriculate to sparsely scabrous, glabrous; glumes unequal, keels scabrous distally, margins narrowly hyaline, surfaces sometimes and edges scabridulous distally, thinly chartaceous, thinner than lemmas; lower glumes 1.9–2.5(–3) mm long, lanceolate, 1–3-veined; upper glumes 2.5–3.2(–3.7) mm long, 3-veined, margins and apex hyaline; callus glabrous; lemmas 3.2–4.2(–4.9) mm long, 5-veined, chartaceous to subcoriaceous, lanceolate, green or commonly violaceous, distinctly keeled, glabrous, keel and marginal veins scabrous, intermediate surfaces muriculate, distally and marginally scabridulous, intermediate veins faint to moderately distinct extending to near apex, margins very narrowly hyaline, edges finely scabridulous, apex acute, sharply pointed; palea equalling lemma, keels scabrous, intercostal zone muriculate to sparsely scabridulous. *Flowers* bisexual; anthers 1.5–2.2(–3) mm long; caryopses c. 2.5 mm long, ventrally distinctly sulcate, hard, glabrous, tightly adherent to palea; hilum oval (c. 0.5 mm long). Chromosome number: $2n = 14$.

*Phenology* — Flowering from June to July.

*Ecology* — High steppe grasslands to low alpine, 1100–2550 m, calcareous, gypseous, serpentine and igneous substrates. Commonly associated with shrubby *Astragalus* L. species, *Thymus marschallianus* Willd., *Bellardiochloa* Chiov., *Festuca* L. and *Koeleria* Pers. species, normal-flowered *Poa sinaica* and viviparous varieties of *P. sinaica*, *P. timoleontis* and *P. bulbosa* (the last sometimes of ambiguous species determination and called "*Poa bulbosa* viviparous aggregate" by us).

*Distribution* — Mapped in Fig. 3: Armenia, Azerbaijan, Georgia, Iran, Turkey, to SW Turkmenistan (Kopetdağ; Kovalevskaja 1968).

*Lectotypifications* — *Festuca conferta* was published in Grossheim's *Flora Kavkaza* (1928) sometime after the signature page dated "20 Nov 1927". Troitsky's *Poa densa* was published sometime in 1928. We do not know which publication came first, and neither author mentioned the name of the other's taxon, so *P. densa* was not an avowed replacement name (non *P. conferta* Ell., as implied by Tzvelev 1976, but not by Grossheim 1939). *Festuca conferta* was validated in a key to the genus in Russian [English translation: "Low internodes thickened, bulbous. Densely turfed. Culms 30–50 cm tall. Leaves stiff, green. Panicle 3–8 cm with short branches. Lemma obscurely keeled. Georgia: Tiflis, Armenia: Erevan. On dry slopes of the middle mountain zone. [No.] 420. *Festuca conferta* Troitsky (ined.)"]. Grossheim did not cite any specimens, and *Festuca conferta* has remained untypified, but, as the diagnosis and distribution agree with Troitsky's publication of *P. densa*, and the names have been treated as synonyms since accounts by Roshevitz (1934) and Grossheim (1939), we tie the two names together by lectotypifying the former name on the lectotype of the latter.

The lectotypification history of *Poa densa* is a bit convoluted. Troitsky (1928) cited four collections (syntypes) in "Horti Petrop.", "Horti Tifl." and "Musei Agric. Armeniae". Roshevitz (Fl. SSSR 2: 378. 1934) chose one of these as type: "(Tiflisskii Raion, Garedzhinskaya Steppe, 17 June 1927, *N. Trotizky*) Type in Tiflis [now TBI], cotype in Lenningrad". Apparently, Roshevitz either did not realize the "17 June 1927" sheet at LE was not duplicated in the Tiflis herbarium, or the duplicate there was lost. Evidently, there are two original *Troitsky* sheets at TBI, TBI-1025700 and TBI-1025701, collected on "11 June 1926", but none collected on "17 June 1927". Both the 11 June 1926, and the 17 June 1927, collections at LE have Roshevitz's printed annotation slips with "*Poa densa* Troitsky" and the date of "1930" hand-written. Tzvelev (1976: 451), without explanation for the change of herbarium, cited the 17 June 1927 sheet as the "Type in LE". Although the 17 June 1927 sheet at LE was not found by R.J.S. in 2010, its existence is confirmed by an old photograph at E (E00326518). E. T. Gabrieljan's herbarium annotations of 2003 on the 11 June 1926 gathering noted TBI-1025700 as the lectotype and TBI-1025701 and the LE duplicate as isolectotypes (images available via JSTOR Global Plants: http://plants.jstor.org/), but she subsequently accepted the 17 Jun 1927 *Troitsky* specimen at LE as the lectotype (Gabrieljan 2010).

*Remarks* — The first collections of *Poa densa* in Turkey that we are aware of were made near Beypazari, Ankara Region, by Asuman Baytop & Yildirim Akman (s.n.) and SE of the city of Erzurum by Adem Tatlı (s.n.) in 1973. We now have identified 30 records for Turkey from across a wide swath of the country. Tzvelev (1974, 1976: 451) noted *P. densa* to be rarely viviparous (var. *vivipara* Tzvelev), but that the viviparous material (type from Azerbaijan) may represent hybridization between *P. densa* and *P. bulbosa* s.l. Gabrieljan (2010) mentioned that vivipary occurs sometimes in *P. sinaica* and usually in *P. bulbosa*, but wrote nothing about it in *P. densa* in Armenia. Although there are viviparous plants of the *P. bulbosa* complex just about everywhere in Turkey, and *P. densa* and *P. sinaica* are commonly sympatric or parapatric, we have not seen any viviparous material we would ascribe to *P. densa*, nor any specimens that seemed intermediate between *P. densa* and other bulbous-based species in the field or in herbaria. Kelley & al. (2009) indicated *P. densa* might be a nanoploid apomict, but we suspect their sample (PI 380984) to represent another species (possibly a contaminant), since it differs from two independent estimates that *P. densa* is diploid: Sokolovskaya & Probatova (1979) reported *P. densa* as diploid, $2n = 14$, and our flow-cytometry data agree with that.

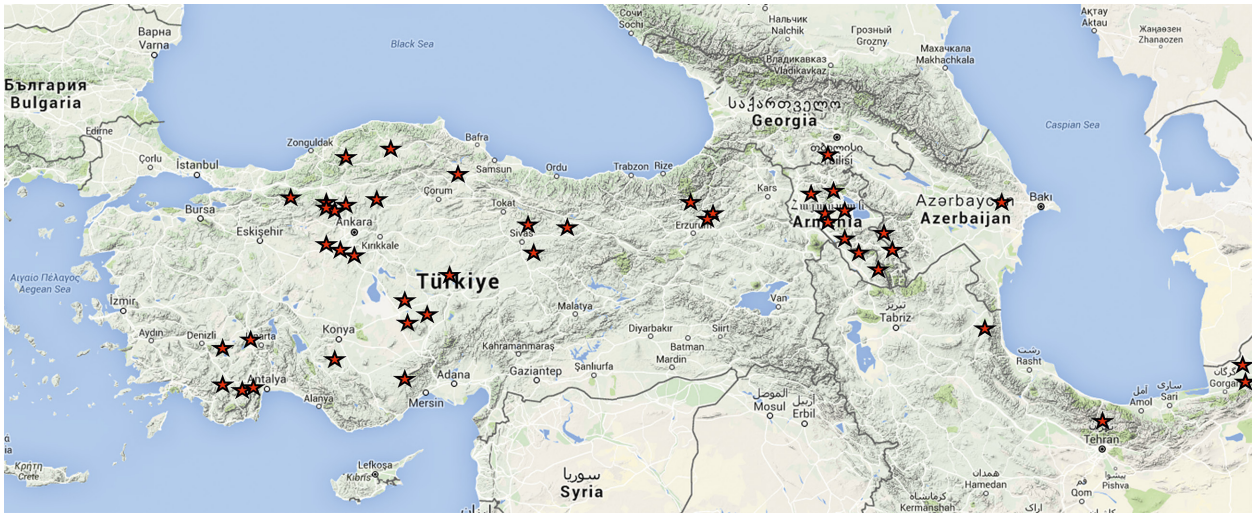

Fig. 3. Map of the occurrences of *Poa densa* in Turkey and its distribution in SW Asia – See Table 1 for vouchers.

*Specimens examined* — (* = DNA vouchers).
Turkey: A3 Bolu: Abant Peak, N side, near microwave tower, E of Abant Lake, Ovacık village, Kurtaran hill, 1600 m, 19 Jun 1980, *M. Doğan hb. no. 1006* (ANK). — A3 Ankara: Beypazarı, Nuh Lake, c. 30 km SE of Bolu, 40.6045°N, 31.3207°E, 1787 m, low alpine/steppe, bald hill, limestone, 11 Jun 2013, *R. J. Soreng & al. 8110* (CAN, NAKU, US); Beypazarı, Nuh Hoca mansion, Kös Yolu, 1450 m, 26 May 1973; *A. Baytop & Y. Akman s.n.* (ANK); Beypazarı, Kel Tepe, 40.27926°N, 31.80766°E, 1528 m, grassy ridge-top meadows in *Pinus nigra* forest, conglomerate rocks, 16 May 2015, *R. J. Soreng & M. Kaya 9299* (NAKU, US). — A4 Ankara: c. 100 km SE of Ankara, Küre Dağı below national forest land, 39.23°N, 33.30°E, 1600 m, steppe vegetation below *Quercus pubescens/Pinus nigra* forest, loamy soil, 30 % slopes, N-exposed, with *Astragalus*, *Poa*, *Thymus*, 12 Jun 1991, *R. J. Soreng & al. 3860* (ANK, US); Beynam forest, on road to Karaali, 39.68083°N, 32.91425°E, 1333 m, *Astragalus* steppe vegetation at lower *Quercus pubescens/Pinus nigra* forest, serpentine, 17 May 2015, *R. J. Soreng & E. Cabi 9306* (NAKU, US*); c. 20 km NE of Kızılcahamam, Köroğlu Dağları, near Işık Dağı massif, 40.62°N, 32.83°E, 1600 m, moist mountain valley, deep loamy soils in grassy meadow along river with *Carex*, *Geum*, *Melampyrum*, *Ranunculus*, *Thalictrum*, 14 Jun 1991, *R. J. Soreng & al. 3872* (ANK, US*); Hasanoğlan, İdris Dağı, 1400–1700 m, 27 Jun 1989, *N. Tanker s.n.* (ANK 1006); c. 7 km WNW of Haymana, 39.4664°N, 32.4519°E, 1098 m, steppe-covered hills, grassy slopes with *Crataegus*, *Dactylis*, *Festuca*, *Hordeum bulbosum*, *Koeleria*, *Poa*, *Stipa holosericea*, 12 Jun 1991, *R. J. Soreng 3860* (ANK, US); c. 60 km SW of Ankara, c. 5 km N of Haymana, on highway to Polatlı, 39.47°N, 32.42°E, 1300 m, steppe, shallow slightly gypseous loam on gentle limestone slope, with *Helianthemum canum*, 13 Jun 1991, *R. J. Soreng & al. 3868-b* (ANK, US); Ayaş Dağları, opening in forest of *Pinus nigra*, 1500 m, 19 Jun 1975, *A. Baytop & Y. Akman s.n.* (ANK). — A4 Karabük: Keltepe, above the forest belt, 41.08596°N, 32.46819°E, 1750 m, 19 Jul 2013, *E. Cabi 5151* (NAKU). — A5 Amasya: Akdağ, summit, 40.77898°N, 36.01817°E, 1496 m, 21 Jul 2013, *E. Cabi 5135* (NAKU). — A6 Kastamonu: Ilgaz Dağları, around the TV towers, 1900 m., 25 Jul 1981, *E. Yurdakul & al.* (ANK 11472). — A6 Sivas: Köse Dağları pass, 28 Jul 2014, *R. J. Soreng & al. 8898a* (CAN, NAKU, US). — A8 Erzurum: İspir, pass S of Pazaryolu along hwy 925, 2236 m, 3 Aug 2014, *R. J. Soreng & al. 8980* (CAN, NAKU, US); Palandöken Da., 5 Aug 1973, *A. Tatlı* (ISTE). — A8 Gümüşhane: along E97 hwy, between Gümüşhane (51 km E of) and Bayburt, c. 1 km W of Aksar, 40.3447°N, 39.8958°E, 1829 m, N-facing limestone hill, shrub and juniper grasslands, *Astragalus*, *Avenula*, *Cotoneaster*, *Rosa*, *Sesleria*, 1 Aug 1993, *R. J. Soreng & al. 4216* (ANK, US). — B3 Isparta: Barla Dağı, *Eren & Parolly 3342* (AKDU, B). — B5 Niğde: Melendiz Dağı E end, Güresentepe pass, above Tepeköy, c. 15 km (direct) NNW of Niğde, 2072 m, volcanic rocks, high steppe grass shrubland, S-exposed, 14 Jun 2013, *R. J. Soreng & al. 8154* (CAN, NAKU*, US). — B5 Aksaray: Hasan Dağı, above Helvadere, 38.15914°N, 34.16556°E, 2021–2100 m, alpine steppe, 22 Jun 2014, *E. Cabi St6*, (NAKU). — B5/C5 Niğde: Ulukışla, Taurus mts, Bolkar Dağları, N slope, along Kayak Evi road toward Bolkar and Toros Dağı, WSW of Maden, 37.4322°N, 34.5782°E, 2294 m, high-elevation steppe grasslands along ridge, E-exposed, 5–30 % slopes, shale, 16 Jun 2013, *R. J. Soreng & al. 8186* (CAN, NAKU, US). — B6 Kayseri: Pınarbaşı, Kaynar, Hınzır Dağı, above Kara Amet, 1700 m, Mar 1980, *A. Baytop s.n.* (ISTE). — B6 Sivas: Kangal, 4 km S of Kurtgölü, 38.35808°N, 37.84757°E, 1582 m, limestone scarps in *Artemisia-Astragalus-Festuca* steppe, 2 May 2015, *R. J. Soreng & E. Cabi 9208* (US). — B7 Sivas: İmranlı, S of Çalıyurt Köyü, 39.93377°N, 38.2512°E, 1978 m, alpine steppes, 13 Jul 2008, *S. Aslan & al. 2939* (GAZI). — C2 Denizli: Honaz Dağı, *Eren & Parolly 7481* (B, ISTE, herb. Parolly); ibid., *Eren & Parolly 7514* (B, herb. Parolly), ibid., *Eren & Parolly 3048* (AKDU, GAZI). — C2 Muğla: Fethiye, Girdev Dağı, Jun

2011, *L. J. Gillespie & al. 10581* (CAN, NAKU, US). — C3 Antalya: Bey Dağları, forest reserve, N side of main range, on trail to Kızlar Sivrisi, 36.5981°N, 30.0833°E, 1986–2180 m, subalpine shrub-steppe, N-exposed, limestone 30–50 % slopes, 20 Jun 2013, *R. J. Soreng & al. 8208* (CAN, NKU, US); ibid., Kızlar Sivrisi, 27 Jun 2014, *E. Cabi s.n.* (NAKU); Bakırlı Dağı, 2200–2550 m, *Eren 6507* (AKDU, B, herb. Parolly). — C4 Konya: Bozkır, Haydar Da. 37.06585°N, 32.16796°E, 1839 m, limestone slopes, *Astragalus-Berberis* steppe, 25 Jun 2014, *R. J. Soreng & al. 8850* (CAN, NKU, US). — C5 Mersin: NW of Mersin, Arslanköy to Fındıkpınarı, 1850 m, calcareous slopes, 15 Jun 2006, *E. Cabi s.n.* (NAKU).

Armenia: Delizhan distr., in pascuis pagi Nadezhdino, 1926, *M. Timofeew & W. Kiurktschan* (ERE [not seen]; syntype of *Poa densa*); Pambakski Khrebet in vicinitate oppida Sevan, 1900–2200 m, 17 Jul 1975, *V. Vasik s.n.* (B); Yerevan distr., in pascuis Elidja, 1926, *A. Schelkownikow* (ERE [not seen]; syntype of *Poa densa*).

Georgia: Tiflis, Garedzenskaya steppe, 11 Jun 1926, *N. Troitsky s.n.* (LE [photo K-969/167], TBI-1025700 [image], TBI-1025701 [image]; syntypes of *Poa densa*); Tbilisi region, Gargjiiskaya steppe, 17 Jun 1927, *N. Troitsky s.n.* (LE [photo at E: E00326518]; lectotype of *Poa densa* and *Festuca conferta*).

Iran: Golestan, *Mohsenian 25247* (IRAN*); Khorasan, *Akhani 11010* (B).

## Conclusions

Within Turkey, *Poa densa* is readily recognizable, widespread, and characteristic of the high steppe regions of C to NE Anatolia. Its distribution extends more or less continuously N from the W Taurus mountains, and to the NE into the mountainous regions S of the Karadeniz Dağları (Pontic Mountains), occurring between 1000 and 2250(–2500) m in altitude. The number of new records of this distinctive species of *Poa* in Turkey suggests the flora of the high Anatolian steppes is not as sufficiently documented as one might have expected and calls for more systematic collecting in this region. *Poa densa* is here reclassified from *P.* sect. *Arenariae* to *P.* sect. *Macropoa*. Bulbs in *Poa* appear to have arisen at least twice, or as many as four times.

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## References

Akhani H. & Scholz H. 1998: Studies on the flora and vegetation of the Golestan National Park, NE Iran II. A new *Poa* and some new and noteworthy grass records for Iran. – Edinburgh J. Bot. **55:** 443–453.

Bor N. L. 1970: *Poa* L. – Pp. 20–46 in: Rechinger K. H. (ed.), Flora iranica **70.** – Graz: Akademische Druk- und Verlagsanstalt.

Cabi E. & Doğan M. 2012: *Poaceae* – Pp. 690–756 in: Güner A., Aslan S., Ekim T., Vural M. & Babaç M. T. (ed.), Türkiye Bitkileri Listesi (Damarlı Bitkiler). – İstanbul: Nezahat Gökyiğit Botanik Bahçesi ve Flora Araştırmaları Derneği Yayını.

Edmondson J. R. 1985: *Poa* L. – Pp. 470–486 in: Davis P. H. (ed.), Flora of Turkey and the East Aegean Islands **9.** – Edinburgh: University Press.

Gabrieljan E. T. 2010: *Poa* L. – Pp. 258–273 in: Gabrieljan E. T. & Oganesian M. E. (ed.), *Poaceae* in: Takhtajan A. L. (ed.), Flora Armenii **11.** – Ruggell: A.R.G. Gantner.

Gillespie L. J., Archambault A. & Soreng R. J. 2007: Phylogeny of *Poa* (*Poaceae*) based on *trnT-trnF* sequence data: major clades and basal relationships. – Aliso **23:** 420–434.

Gillespie L. J. & Soreng R. J. 2005: A phylogenetic analysis of the bluegrass genus *Poa* based on cpDNA restriction site data. – Syst. Bot. **30:** 84–105.

Gillespie L. J., Soreng R. J., Bull R. D., Jacobs S. W. L. & Refulio-Rodriguez N. F. 2008: Phylogenetic relationships in subtribe *Poinae* (*Poaceae*, *Poeae*) based on nuclear ITS and plastid *trnT-trnL-trnF* sequences. – Botany **86:** 938–967.

Gillespie L. J., Soreng R. J., & Jacobs S. W. L. 2009: Phylogenetic relationships of Australian *Poa* (*Poaceae*: *Poinae*), including molecular evidence for two new genera, *Saxipoa* and *Sylvipoa*. – Austral. Syst. Bot. **22:** 413–436.

Gillespie L. J., Soreng R. J., Paradis M. & Bull R. D. 2010: Phylogeny and reticulation in subtribe *Poinae* and related Subtribes (*Poaceae*) Based on nrITS, ETS, and *trnTLF* data. – Pp. 589–615 in: Seberg O., Petersen S., Barfod A. S. & Davis J. I. (ed.), Diversity, phylogeny and evolution in the Monocotyledons. – Aarhus: Aarhus University Press.

Grossheim A. A. 1928: Flora Kavkaza **1.** – Tiflis: Trudy Bot. Sada S.S.R. Armenii.

Grossheim A. A. 1939: *Gramineae* – Pp. 103–402 + maps 93–324 + index I–XXI in: Grossheim A. A., Fl. Kavkaza, ed. 2, **1.** – Baku: Akademiia Nauk S.S.S.R. Azerbaidzhanskii filial.

Katoh K., Misawa K., Kuma K. & Miyata T. 2002: MAFFT: A novel method for rapid multiple sequence alignment based on fast Fourier transform. – Nucl. Acids Res. **30:** 3059–3066.

Katoh K. & Standley D. M. 2013: MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. – Molec. Biol. Evol. **30:** 772–780.

Kavousi M., Assadi M. & Nejadsattari T. 2015: Taxonomic revision of the genus *Poa* L. in Iran, new additions to *Flora iranica*, and a new identification key. – Turkish J. Bot. **39:** 105–127.

Kelley A. M., Johnson P. G., Waldron B. L. & Peel M. D. 2009: A survey of apomixis and ploidy levels among *Poa* L. (*Poaceae*) using flow cytometry. – Crop Sci. (Logan) **49:** 1395–1402.

Kellogg E. A. 2015: *Poaceae*. – Pp. i–xv, 1–416 in: K. Kubitzki (ed.), The families and genera of vascular plants **13.** – Berlin: Springer.

Kovalevskaja S. S. 1968: *Poa* L. [in Russian]. – In: Opred. Rast. Srednei Azii **1:** 127–138.

Liu L. 2003: *Poa* L. – Pp. 91–226 in: Liu L. (ed.), Fl. Reipubl. Popularis Sin. **9(2):** 91–226.

Parolly G., Eren Ö. & Scholz H. 2002: – Pp. 206–207 in: Greuter W. R. & Raus T. (ed.), Med-Checklist Notulae 21. – Willdenowia **32:** 195–208.

Patterson J., Larson S. R. & Johnson P. G. 2005: Genome relationships in polyploid *Poa pratensis* and other *Poa* species inferred from phylogenetic analysis of nuclear and chloroplast DNA sequences. – Genome **48:** 76–87.

Rambaut A. 2006–2014: Tree figure drawing tool version 1.4.2. – Edinburgh: Institute of Evolutionary Biology, University of Edinburgh. – Published at http://tree.bio.ed.ac.uk/

Roshevitz R. Y. 1934: *Gramineae* – In: Komarov V. L. (ed.), Flora S.S.S.R. **2.** – Leningrad: Akademii Nauk SSSR.

Scholz H. 1985: *Poa*-Studien 4. – Über *Poa hackelii* Post und *P. pelasgis* species nova (*Gramineae*). – Willdenowia **15:** 91–97.

Scholz H. 1986: *Poa* Studies 5. – The genus *Poa* (*Gramineae*) in Greece: annotated check-list and key to the species. – Willdenowia **15:** 393–400.

Sokolovskaya A. P. & Probatova N. S. 1979: Chromosome numbers of some grasses (*Poaceae*) in the Flora U.S.S.R. III. – Bot. Zhurn. (Moscow & Leningrad) **64:** 1245–1258.

Soreng R. J. 1990: Chloroplast-DNA phylogenetics and biogeography in a reticulating group: study in *Poa*. – Amer. J. Bot. **77:** 1383–1400.

Soreng R. J. 1998: An infrageneric classification for *Poa* in North America and other notes on sections, species, and subspecies of *Poa*, *Puccinellia* and *Dissanthelium* (*Poaceae*). – Novon **8:** 187–202.

Soreng R. J., Bull R. D. & Gillespie L. J. 2010: Phylogeny and reticulation in *Poa* based on plastid *trnTLF* and nrITS sequences with attention to diploids. – Pp. 619–644 in: Seberg O., Peterson G., Barfod A. S. & Davis J. I. (ed.), Diversity, Phylogeny, Evolution Monocots. – Aarhus: Aarhus University Press.

Soreng R. J., Hein P. & Scholz H. 1997: *Poa akmanii* (*Poaceae*), a new species from Turkey. – Willdenowia **27:** 195–198.

Swofford D. L. 2002: PAUP*: Phylogenetic analysis using parsimony (and other methods), version 4.0b10. – Sunderland: Sinauer Associates.

Taberlet P., Gielly L., Pautou G., & Bouvet J. 1991: Universal primers for amplification of three noncoding regions of chloroplast DNA. – Pl. Molec. Biol. **17:** 1105–1109.

Thiers B. 2015+ [continuously updated]: Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's virtual herbarium. – Published at http://sweetgum.nybg.org/science/ih/ [last accessed 13 Jul 2016].

Tiryaki İ. & Tuna M. 2012: Determination of intraspecific nuclear DNA content variation in common vetch (*Vicia sativa* L.) lines and cultivars based on two distinct internal reference standards. – Turk. J. Agric. Forest. **36:** 645–653.

Troitsky N. A. 1828: Dva novyh vida rastenij iz Zakavkazya. – Izv. Glavn. Bot. Sada S.S.S.R. **27:** 619–625.

Tzvelev N. N. 1974: De Genere *Poa* L. in URSS [in Russian with Latin descriptions of new taxa]. – Novosti Sist. Vyssh. Rast. **11:** 24–41.

Tzvelev N. N. 1976: Zlaki SSSR. – Leningrad: Nauka Publishers.

Zhu G. H., Liu L., Soreng R. J. & Olonova M. V. 2006: *Poa* L. – Pp. 257–309 in: Wu C. Y., Raven P. H. & Hong D. Y. (ed.), Fl. China **22.** – Beijing & St. Louis: Science Press & Missouri Botanical Garden Press.

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