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# The genus *Hedysarum* (Fabaceae; Hedysareae) in Uzbekistan

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**ABSTRACT**

Uzbekistan is one of the centers of species diversity of *Hedysarum* (Fabaceae) in Central Asia, where it occurs mainly in the Tian-Shan and Pamir-Alay Mountains. In this study, we reconstructed the phylogenetic relationships of 26 species occurring in Uzbekistan. The species were classified into three clades in both non-monophyletic ITS and monophyletic plastid trees, corresponding to sections *Hedysarum* (one species) and *Stracheya* (two species), and subsection *Crinifera* (23 species) of section *Multicaulia*. We further assessed the evolutionary status of 22 morphological characters that are used as diagnostic in the taxonomy of *Hedysarum*. The results showed that the majority of morphological characteristics in *Hedysarum* exhibit a high level of homoplasy. Only a few of these characteristics, such as pendent flowers in the raceme (section *Hedysarum*), division of the pod into joints and joint shape and length of pod bristles, serve as synapomorphies for the monophyletic genus and its sections on the plastid tree. Additionally, we propose evaluating additional characters, such as the presence of 1 or 2 pairs of well-developed leaflets of odd-pinnate leaves, long bracts and bracteoles, as apomorphic conditions in some species of subsection *Crinifera*. This article also presents descriptions, nomenclatural information, type citations, and country-level distribution maps of the species of *Hedysarum* in Uzbekistan.

**Key words:** subsection *Crinifera*, phylogeny, morphology, character evolution, synapomorphic and plesiomorphic characteristics

## Introduction

*Hedysarum* L., one of the most species-rich genera in the tribe Hedysareae (Fabaceae), includes over 160 species, mainly occurring in the Mediterranean and warm temperate and continental temperate zones of Eurasia and North America (Lock 2005). Central Asia is considered to be one of the diversity hotspots for *Hedysarum* (Choi and Ohashi 2003; Ranjbar et al. 2006). In total, 81 species are distributed in Central Asia, 46 of them being endemic,

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including 38 species (17 subendemic; 9 endemic) in Kazakhstan (Baitenov 1961, Abdulina 1999), 36 species (20; 7) in Kyrgyzstan (Nikitina 1957; Sultanova 1970, 1973; Lazkov, Sultanova 2014), 18 species (11; 5) in Tajikistan (Karimova 1978), 8 species (one subendemic) in Turkmenistan (Nikitin 1949; Nikitin, Geldykhanov 1988), and 26 species (19, 7) in Uzbekistan. Moreover, the flora of regions surrounding Central Asia also exhibits high species diversity, with 41 species occurring in China (17 endemic; Xu and Choi 2010), 32 species in Iran (16 endemic; Nafisi et al. 2021), 29 species in Turkey (16 endemic; Aytaç 2022), and 14 species in Afghanistan (7 endemic; Podlech 2012).

*Hedysarum* has had a long taxonomic history. Detailed information about it is provided by Duan et al. (2015), Nafisi et al. (2019), and Juramurodov et al. (2023b). In recent years, several large-scale molecular phylogenetic studies have been conducted to ascertain the phylogenetic relationships among the species of *Hedysarum* (Duan et al. 2015; Liu et al. 2017; Nafisi et al. 2019; Juramurodov et al. 2023b). While nuclear gene-based phylogenetic studies suggest that *Hedysarum* is not monophyletic, plastid data indicate that the genus is monophyletic. In our previous study (Juramurodov et al. 2023b), which utilized a combined dataset of nrDNA ITS and plastid markers (*matK, trnL-F, psbA-trnH*) and included approximately 110 taxa of *Hedysarum*, with 36 species from the Tian-Shan and Pamir-Alay Mountains, we estimated the phylogeny of all species (except for *H. kudrjaschevii* Korotkova) in Uzbekistan. In this study, we revised the phylogenetic relationships of *Hedysarum* in Uzbekistan by adding and evaluating additional sequences.

*Hedysarum* includes perennial herbs (rarely semi-shrubs) and can be distinguished from closely related genera by the tricolporate pollen, morphology of the jointed pods, which are flat-compressed or slightly inflated, smooth, glabrous or pubescent, reticulate or transversely ribbed and often covered with short or longer bristles; variations in these features are used to circumscribe infrageneric taxa (Fedtschenko 1902, 1948; Choi and Ohashi 1996, 2003; Ranjbar et al. 2006). Several taxonomic treatments were proposed to determine intersectional relationships within *Hedysarum* (Choi and Ohashi 1996, 2003; Amirahmadi et al. 2014; Nafisi et al. 2019). A recent phylogenetic study by Nafisi et al. (2019) discovered that subsect. *Crinifera* (Boiss.) B.H.Choi & H.Ohashi consists of several groups of species. Those groups and their diagnostic characteristics require a separate in-depth study in Central Asia.

Recent research, with particular focus on projects such as ‘Grid Mapping of the Flora of Uzbekistan’ (Tojibaev et al. 2022) and ‘Taxonomic Revision of Polymorphic Plant Families of the Flora of Uzbekistan’ (Sennikov et al. 2016), has extensively advanced our knowledge of the flora of Uzbekistan. These projects have led to the collection of new specimens and the identification of previously unknown areas of species’ distributions. Utilizing this information, four updated volumes of the ‘Flora of Uzbekistan’ were published between 2016 and 2022 (Sennikov 2016, 2017, 2019, 2022). In these updated volumes, updated treatments of many species with additions have been compiled. Particular attention was paid to nomenclature and typification, and a detailed distribution map of each species was provided. Korotkova's (1955) revision of ‘Flora of Uzbekistan,’ however, was the main source for detailed information on the 19 species of *Hedysarum* in Uzbekistan. However, taxonomic changes in the past 70 years and several discoveries made within the framework of the above-mentioned projects require a complete revision of the species of *Hedysarum* in Uzbekistan.

Recently published taxonomic revisions have provided a better understand of the taxonomy and distribution of species and genera, such as *Eremurus* M.Bieb. (Makhmudjanov et al. 2022), *Tulipa* L. (Tojibaev et al. 2022), *Salvia* L. (Turdiboev et al. 2022), *Iris* L. (Sennikov et al. 2023), and others, in Uzbekistan. In addition to the recently collected specimens, type specimens of *Hedysarum* collected in Central Asia and stored

in the National Herbarium of Uzbekistan (TASH) were reviewed (Juramurodov et al. 2022).

In the study reported here, we reconstructed the phylogenetic relationships of the species of *Hedysarum* in Uzbekistan using ITS and three plastid genes. Additionally, we evaluated the evolutionary status of 22 diagnostic morphological characters used to distinguish 26 *Hedysarum* species in Uzbekistan and provide descriptions of these species, nomenclatural information, type citations and detailed distribution maps. This has allowed us to (1) determine the phylogenetic relationships of the species in Uzbekistan, (2) reconstruct character evolution of the diagnostic morphological traits, (3) revise the taxonomy of *Hedysarum* in Uzbekistan and (4) to compile necessary information on the species for the next edition of the 'Flora of Uzbekistan.'

## Materials and Methods

*Herbarium material and its treatment*

During 2018-2022, more than 100 fresh specimens were collected in Uzbekistan and stored in TASH. In addition, about 400 herbarium specimens from the MW, LE, KUN, FRU, and SAMDU herbaria (herbarium codes follow Thiers (2023, and continuously updated) were checked. Species distribution ranges were inferred from these specimens. The type treatments were based on Juramurodov et al. (2022) and original protologues. Morphological descriptions of the species of *Hedysarum* in the flora of Uzbekistan were compiled based on the works of Fedtschenko (1948, translated into English 1972) and Xu and Choi (2010). The newly collected and old herbarium specimens were cross-checked with detailed descriptions of the various species of *Hedysarum* in the relevant references (Fedtschenko 1948; Korotkova 1955; Baitenov 1961; Sultanova 1973; Kovalevskaya 1981). Botany-oriented geographic regionalization (Fig. 1) of the study area follows the work of Tojibaev et al. (2016). We used Google Earth software for geo-referencing of the collection sites of historical herbarium specimens.

*DNA isolation, PCR, and sequencing*

Total genomic DNA was isolated from silica gel dried leaf material using Plant Genomic DNA Kit (TIANGEN Biotech, Beijing, China), according to the manufacturer's protocol. The genomic DNA was extracted using CTAB protocol with some modifications (Doyle and Doyle 1987). The nrDNA internal transcribed spacer (nrDNA ITS) sequences were amplified using primers ITS1 and ITS4 (White et al. 1990). The cpDNA (*psbA-trnH, trnL-trnF*) regions were amplified using the following primers: psbA 3_F (Sang et al. 1997) and trnHf_05 (Tate and Simpson, 2003), trnL-c and trnL-f (Taberlet et al. 1991), respectively. PCR amplifications were performed according to the protocols of Nafisi et al. (2019).

*Taxon sampling*

In this study, 29 species and 29 accessions were sampled for nrDNA ITS, including 26 species and 26 accessions belonging to *Hedysarum*. For cpDNA, 29 species and 75 accessions were sampled, with 26 species and 67 accessions belonging to *Hedysarum*, including 26 *trnL-F*, 20 *matK*, and 21 *psbA-trnH*. Newly produced sequences included four ITS sequences (*H. popovii* Korotkova, *H. nuratense* Popov, *H. sunhangii* Juram. & Tojibaev, and *H. kudrjaschevii*), as well as sequences for the *trnL-F* and *psbA-trnH* regions of *H. kudrjaschevii*. The remaining sequences, from Juramurodov et al. (2023b), are listed in the Appendix. Three species, *Onobrychis chorassanica* Bunge ex Boiss., *Eversmannia subspinosa* (DC.) B.Fedtsch. and *Caragana grandiflora* DC. were used as outgroups (Duan et al. 2015; Liu et al. 2017; Nafisi et al. 2019).

*Phylogenetic analyses*

Sequences were aligned using MUSCLE (Edgar 2004) as implemented in MEGA X software (Kumar et al. 2018). The plastid data were concatenated using SequenceMatrix

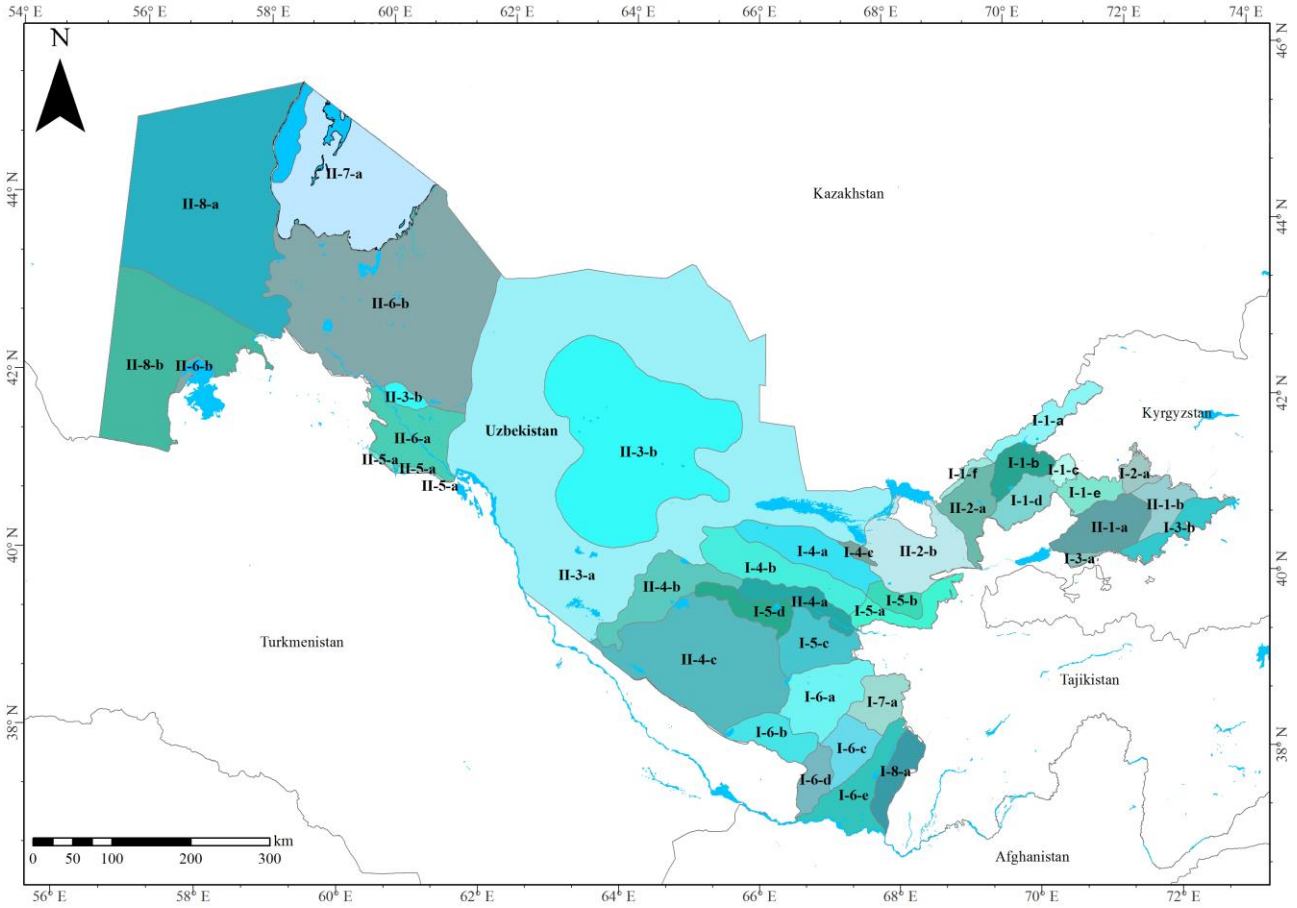


**Fig. 1.** Phytogeographical subdivision of Uzbekistan (according to Tojibaev et al. 2016). **I Central Asian Mountain Province**: I-1 Western Tian-Shan (I-1-a Ugam-Pskem, I-1-b Western Chatkal (Chimgan), I-1-c Arashan, I-1-d Kurama (Akhangaran), I-1-e Chorkesar, I-1-f Tashkent), I-2 Fergana (I-2-a South Chatkal), I-3 Fergana-Alay (I-3-a Western Alay, I-3-b Eastern Alay), I-4 Nuratau (I-4-a Nuratau, I-4-b Aktau, I-4-c Nuratau Relic Mountains), I-5 Kuhistan (I-5-a North Turkestan, I-5-b Malguzar, I-5-c Urgut, I-5-d Ziadin-Zirabulak), I-6Western Hissar (I-6-a Kashkadarya, I-6-b Tarkapchigay, I-6-c Baysun, I-6-d Kuhitang, I-6-e Surkhan-Sherabad), I-7 Hissar-Darvaz (I-7-a Sangardak-Tupalang), I-8 Panj (I-8-a Babatag). **II Turan Province**: II-1 Central Fergana (II-1-a Kayrakum-Yazyavan, II-1-b East Fergana), II-2 Middle Syrdarya (II-2-a Chinaz, II-2-b Mirzachul), II-3 Kyzylkum (II-3-a Kyzylkum, II-3-b Kyzylkum Relic Mountains), II-4 Bukhara (II-4-a Middle Zeravsshan, II-4-b Lower Zeravsshan, II-4-c Karshi-Karnabchul), II-5 Karakum (II-5-a North-East Karakum), II-6 South Aral (II-6-a Khorezm, II-6-b Amudarya Delta), II-7 Aral (II-7-a Aral Sea Bottom), II-8 Ustyurt (II-8-a North Ustyurt, II-8-b South Ustyurt).

software (Vaidya et al. 2011). Phylogenetic reconstructions were conducted based on the nuclear and plastid data separately using Bayesian inference (BI), Maximum Parsimony (MP) and Maximum likelihood (ML). For BI, we used MrBayes v.3.2.7a (Ronquist et al. 2012) with 10 million generations and with random trees sampled every 1000 generations. In the latter analysis, after discarding the first 25% trees as burn-in, a 50% majority-rule consensus tree was constructed from the remaining trees to estimate posterior probabilities (PP). The SYM+G was identified as the best nucleotide substitution model for ITS and TVM+G was identified as the best model for the combined plastid markers according to the Akaike Information Criterion (AIC) using jModelTest2 on XSEDE (www.phylo.org). A maximum likelihood (ML) phylogeny was reconstructed using IQ-TREE

2.1.2 software (Minh et al. 2021) under the above models with 1000 bootstrap replicates. Maximum Parsimony (MP) analysis was done in PAUP* v.4.0a169 with heuristic search, TBR branch-swapping, 1000 bootstrap replicates, random addition sequence with 10 replicates, a maximum of 1000 trees saved per round. The MP and BI bootstrap percentages were labeled on the corresponding branches of the ML tree.

*Morphological analysis*

We used Mesquite v.3.61 (Maddison and Maddison 2019) to infer the ancestral states of 22 morphological characters. The ML tree based on the combined plastid dataset, which demonstrated the monophyly of the genus, was used to conduct ancestral character reconstruction. The morphological characters used in this study (Fig. 2) were obtained through examination of fresh materials in the field, from the literature (Fedtschenko 1948; Korotkova 1955; Nikitina 1957; Baitenov 1961; Sultanova 1973; Karimova 1978; Kovalevskaya 1981) and from more than 420 herbarium specimens deposited in TASH. The characters and character states are listed in Table 1; the data matrix is given in Table 2.

**Table 1.** List of morphological characteristics

| No. | Character | Character states |
|---|---|---|
| a | Life form | herb (0); shrub (1) |
| b | Plant height | ≤ 50 cm (0); > 50 cm (1) |
| c | Plant pubescence (including stem, peduncle and petiole) | glabrous (0); sparse (epidermis visible) (1); dense (epidermis not visible) (2) |
| d | Stem feature | developed (0); short (1); abbreviated (2) |
| e | Leaf length | up to 10 cm (0); up to 20 (1) |
| f | Leaflet pairs per leaf | 1–2 pairs (0); 3–6 pairs (1); up to 7 pairs or more (2) |
| g | Leaflet length | up to 15 mm (0); up to 25 mm (1); up to 50 mm (2) |
| h | Leaflet width | up to 5 mm (0); up to 10 mm (1); up to 30 mm (2) |
| i | Leaflet shape | ovoid (0); ovate (1); oblong (2); oblong-elliptic (3); oblong-ovoid (4); lanceolate (5); rounded (6) |
| j | Orientation of flowers in raceme | pendent (0); vertical or semi-vertical (1) |
| k | Bracts length | ≤ 3 mm (0); up to 6 mm (1); up to 13 mm (2) |
| l | Bracteoles length | ≤ 3 mm (0); > 3 mm (1) |
| m | Pedicel length | < 2 mm (0); ≥ 2 mm (1); > 10 mm (2) |
| n | Calyx teeth length | equal (0); unequal (1) |
| o | Ratio of teeth length to tube in calyx | shorter than tube (0); as long as tube (1); up to 2 times longer than tube (2); up to 4 times longer than tube (3) |
| p | Corolla color | purple (0); pink (1); white (2); yellow (3); violet (4) |
| q | Ratio of standard length to keel | shorter than keel (0); as long as keel (1); longer than keel (2) |
| r | Ratio of wings length to keel | shorter than half of keel (0); as long as half of keel (1); longer than half of keel (2) |
| s | Keel length | up to 15 mm (0); up to 20 mm (1); up to 26 mm (2) |
| t | Number of pod joints | up to 3 (0); up to 6 (1) |
| u | Pod joints shape | rounded or orbicular (0); ovate or linear oblong (1); wide-linear (2); reniform (3) |
| v | Pod pubescence | pubescent and without bristles (0); pubescent and short bristles (1); pubescent and long bristles (2); tomentose and without bristles (3); tomentose and short bristles (4); tomentose and long bristles (5); glabrous (6). |

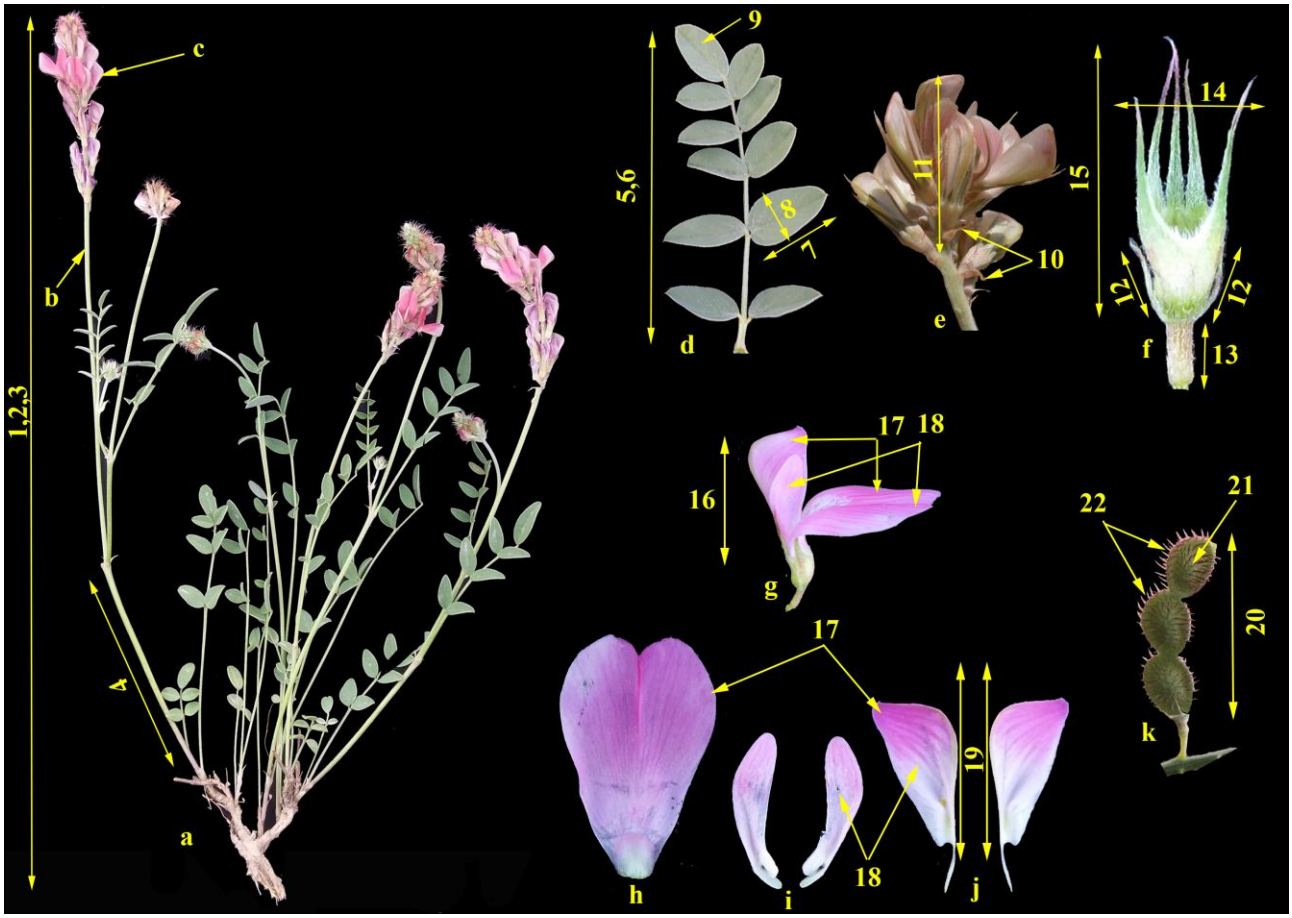


**Fig. 2.** Morphological characters of *Hedysarum* examined: a, complete plant (1, life form; 2, plant height; 3, plant pubescence; 4, stem feature); b, peduncle; c, raceme; d, leaf (5, leaf length; 6, leaflet pairs per leaf; 7, leaflet length; 8, leaflet width; 9, leaflet shape); e, flowers in raceme (10, bracts; 11, state of flowers in raceme); f, calyx (12, bracteoles; 13, pedicel; 14, calyx teeth ratio; 15, the ratio of teeth length to tube of calyx); g, single flower (16, corolla color; 17, ratio of standard length to keel of corolla; 18, ratio of wing length to keel of corolla); h, standard; i, wings; j, keel (19, keel length); k, pod (20, number of pod joints; 21, shape of pod joints; 22, pubescence of joints).

**Table 2.** Species and morphological characters of *Hedysarum* species

| No. | Species/Characters | A | b | c | d | e | f | g | h | i | j | k | l | m | n | o | p | q | r | s | t | u | v |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | *Hedysarum alaicum* B.Fedtsch. | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 3 | 1 | 1 | 0 | 0 | 1 | 3 | 1 | 2 | 0 | 0 | 0 | 0 | ? |
| 2 | *H. amankutanicum* B.Fedtsch. | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 0 | 3 | 1 | 2 | 1 | 1 | 0 | 0 | 1 |
| 3 | *H. angrenicum* Korotkova | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | 5 | 1 | 1 | 1 | 0 | 0 | 3 | ? | 1 | 2 | 0 | 0 | 0 | 3 |
| 4 | *H. baldshuanicum* B.Fedtsch. | 0 | 1 | 0 | 0 | 1 | 2 | 2 | 2 | 2 | 1 | 2 | 0 | 1 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 2 |
| 5 | *H. bucharicum* B.Fedtsch. | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 1 | 5 | 1 | 0 | 0 | 0 | 0 | 2 | 4 | 0 | 0 | 0 | 0 | 0 | 2 |
| 6 | *H. drobovii* Korotkova | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 0 | 3 | 1 | 1 | 2 | 2 | 0 | 0 | 2 |
| 7 | *H. flavescens* Regel & Schmalh. | 0 | 1 | 0 | 0 | 1 | 2 | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 3 | 1 | 2 | 1 | 1 | 1 | 0 |
| 8 | *H. gypsaceum* Korotkova | 0 | 0 | 2 | 2 | 0 | 0 | 2 | 2 | 6 | 1 | 2 | 1 | 0 | 0 | 3 | 1 | 1 | 2 | 1 | 1 | 0 | 4 |
| 9 | *H. iomuticum* B.Fedtsch. | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 2 | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 4 | 0 | 0 | 2 | 1 | 0 | 4 |
| 10 | *H. jaxarticum* Popov | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 3 | 1 | 0 | 0 | 1 | 1 | 0 | 3 |
| 11 | *H. kudrjaschevii* Korotkova | 0 | 0 | 2 | 0 | 0 | 1 | 2 | 2 | 3 | 1 | 1 | 0 | 1 | 0 | 3 | ? | 1 | 0 | 0 | 0 | 0 | 2 |
| 12 | *H. lehmannianum* Bunge | 0 | 0 | 1 | 2 | 1 | 2 | 1 | 1 | 3 | 1 | 1 | 0 | 0 | 1 | 2 | 4 | 2 | 2 | 1 | 0 | 1 | 0 |
| 13 | *H. magnificum* Kudr. | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 2 | 1 | 1 | 2 | 1 | 0 | 0 | 2 | 2 | 2 | 2 | 2 | 0 | 0 | 6 |
| 14 | *H. minjanense* Rech.f. | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 5 | 1 | 1 | 1 | 0 | 1 | 3 | 4 | 2 | 2 | 0 | 0 | 1 | 3 |
| 15 | *H. mogianicum* (B.Fedtsch.) B.Fedtsch. | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 3 | 1 | 1 | 0 | 1 | 1 | 2 | 0 | 2 | 2 | 1 | 0 | 0 | 2 |
| 16 | *H. montanum* (B.Fedtsch.) B.Fedtsch. | 0 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 3 | 4 | 2 | 0 | 0 | 1 | 0 | 2 |
| 17 | *H. nuratense* Popov | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 2 | 0 | 0 | 1 | 3 | 1 | 1 | 0 | 1 | 1 | 0 | 2 |

| No. | Species/Characters | A | b | c | d | e | f | g | h | i | j | k | l | m | n | o | p | q | r | s | t | u | v |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 18 | *H. olgae* B.Fedtsch. | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 4 | 1 | 1 | 0 | 0 | 1 | 1 | 4 | 2 | 0 | 0 | 0 | 0 | 3 |
| 19 | *H. popovii* Korotkova | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 0 | 3 | ? | 0 | 0 | 1 | 0 | 0 | 3 |
| 20 | *H. plumosum* Boiss. & Hausskn. | 0 | 0 | 2 | 2 | 0 | 0 | 2 | 2 | 6 | 1 | 2 | 1 | 0 | 0 | 3 | 4 | 1 | 1 | 1 | 0 | 0 | 3 |
| 21 | *H. pskemense* Popov ex B.Fedtsch. | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 3 | 1 | 0 | 0 | 0 | 1 | 3 | 0 | 2 | 0 | 0 | 0 | 0 | 4 |
| 22 | *H. santalaschi* B.Fedtsch. | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 5 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 0 | 1 | 0 | 4 |
| 23 | *H. sunhangii* Juram. & Tojibaev | 0 | 0 | 2 | 0 | 1 | 1 | 2 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 3 | 1 | 0 | 0 | 1 | 1 | 0 | 2 |
| 24 | *H. talassicum* Nikitina & Sultanova | 0 | 0 | 2 | 2 | 0 | 2 | 0 | 0 | 2 | 1 | 2 | 1 | 0 | 1 | 3 | 1 | 1 | 1 | 0 | 1 | 0 | 3 |
| 25 | *H. taschkendicum* Popov | 0 | 0 | 1 | 0 | 1 | 2 | 2 | 0 | 2 | 1 | 1 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 5 |
| 26 | *H. turkestanicum* Regel & Schmalh. | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 5 |
| 27 | *Eversmannia subspinosa* (Fisch. ex DC.) B.Fedtsch. | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 3 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 2 | 6 |
| 28 | *Onobrychis chorassanica* Bunge ex Boiss. | 0 | 1 | 2 | 0 | 1 | 2 | 2 | 2 | 1 | 1 | 1 | 0 | 1 | 1 | 2 | 3 | 2 | 0 | 1 | 2 | 3 | 3 |
| 29 | *Caragana grandiflora* DC. | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 4 | 1 | ? | ? | 2 | 1 | 0 | 3 | 2 | 2 | 2 | 2 | 2 | 6 |

## Results and Discussion

*Taxonomic classification of Hedysarum in Uzbekistan*

The first species described as new from Uzbekistan was *Hedysarum bucharicum*, collected by Lipisky in the Yakkabog region on June 16, 1896 and published by Fedtschenko (1902). To date, 15 species have been described as new from Uzbekistan. Three of them (*H. babatagicum* Korotkova, *H. pamiralaicum* Korotkova, and *H. vvedenskyi* Korotkova) were subsequently relegated to synonymy. Additionally, 12 species that were originally described from other countries were later found in Uzbekistan. Detailed information about the species described from or recorded from Uzbekistan is presented in Table 3.

After the treatment of 19 species of *Hedysarum* in the 'Flora of Uzbekistan' (Korotkova 1955), some changes were made to the genus over a period of about seventy years. In 'Conspectus Florae Asiae Mediae,' Kovalevskaya (1981) revised the species of *Hedysarum* in Central Asia based on their morphological characteristics. As a result, several species initially described in the flora of Uzbekistan, including *H. vvedenskyi*, *H. kudrjaschevii* and *H. fedtschenkoanum* Regel, were proposed as synonyms of *H. baldshuanicum*, *H. nuratense* and *H. plumosum*, respectively (Kovalevskaya 1981). Our revision presented here supports this taxonomic treatment, except for the placement of *H. kudrjaschevii*. In addition, we confirmed that *H. hemithamnoides*, which was accepted in 'Flora of Uzbekistan' (Korotkova 1955), is only on Mogoltov Mountain in Tajikistan (Turakulov et al. 2021) and should be excluded from our treatment (Kovalevskaya 1981). Also, *H. denticulatum* Regel was recently published as a new record for Uzbekistan by Tojibaev et al. (2014). However, our molecular analysis based on nrDNA ITS and the combined plastid markers isolated from this species showed that it is most similar to *H. lehmannianum* (Juramurodov et al. 2023b). Our current study, therefore, did not include *H. denticulatum*.

**Table 3.** History of the discovery or reports of species of *Hedysarum* in Uzbekistan.

| No | Species name | First record in Uzbekistan | Record status | Current status | Reference |
|---|---|---|---|---|---|
| 1 | *H. bucharicum* | 1902 | new species | accepted | Fedtschenko 1902 |
| 2 | *H. flavescens* | 1902 | new record | accepted | Fedtschenko 1902 |
| 3 | *H. fedtschenkoanum* | 1902 | new record | synonym of *H. plumosum* | Fedtschenko 1902 |
| 4 | *H. olgae* | 1919 | new species | accepted | Fedtschenko 1919 |
| 5 | *H. nuratense* | 1937 | new species | accepted | Popov 1937 |
| 6 | *H. magnificum* | 1940 | new species | accepted | Kudryashev 1940 |
| 7 | *H. angrenicum* | 1947 | new species | accepted | Korotkova 1947 |
| 8 | *H. babatagicum* | 1947 | new species | synonym of *H. iomuticum* | Korotkova 1947; Kovalevskaya 1981 |

| No | Species name | First record in Uzbekistan | Record status | Current status | Reference |
|---|---|---|---|---|---|
| 9 | *H. drobovii* | 1947 | new species | Accepted | Korotkova 1947 |
| 10 | *H. kudrjaschevii* | 1947 | new species | Accepted | Korotkova 1947 |
| 11 | *H. pamiralaicum* | 1947 | new species | synonym of *H. bucharicum* | Korotkova 1947; Korotkova 1955 |
| 12 | *H. popovii* | 1947 | new species | Accepted | Korotkova 1947 |
| 13 | *H. amankutanicum* | 1949 | new species | Accepted | Fedtschenko 1949 |
| 14 | *H. alaicum* | 1949 | new species | Accepted | Fedtschenko 1949 |
| 15 | *H. gypsaceum* | 1954 | new species | Accepted | Korotkova 1954 |
| 16 | *H. vvedenskyi* | 1954 | new species | synonym of *H. baldshuanicum* | Korotkova 1954; Kovalevskaya 1981 |
| 17 | *H. jaxarticum* | 1955 | new record | Accepted | Korotkova 1955 |
| 18 | *H. lehmannianum* | 1955 | new record | Accepted | Korotkova 1955 |
| 19 | *H. mogianicum* | 1955 | new record | Accepted | Korotkova 1955 |
| 20 | *H. montanum* | 1955 | new record | Accepted | Korotkova 1955 |
| 21 | *H. taschkendicum* | 1955 | new record | Accepted | Korotkova 1955 |
| 22 | *H. pskemense* | 1981 | new record | Accepted | Kovalevskaya 1981 |
| 23 | *H. santalaschi* | 1981 | new record | Accepted | Kovalevskaya 1981 |
| 24 | *H. minjanense* | 2014 | new record | Accepted | Tojibaev et al. 2014 |
| 25 | *H. turkestanicum* | 2014 | new record | Accepted | Tojibaev et al. 2014 |
| 26 | *H. talassicum* | 2021 | new record | Accepted | Tojibaev et al. 2021 |
| 27 | *H. sunhangii* | 2021 | new species | Accepted | Juramurodov et al. 2021 |

*Phylogeny of Hedysarum in Uzbekistan*

According to our previous study (Juramurodov et al. 2023b), species of *Hedysarum* in Uzbekistan belong to three clades, corresponding to sections *Hedysarum*, *Stracheya*, and subsect. *Crinifera* within section *Multicaulia*. In this study, we reconstructed phylogenetic trees using nrDNA ITS and the combined plastid datasets of the species of *Hedysarum* in Uzbekistan (Figs S1–S2). The ITS data showed that the genus was not monophyletic, while the plastid data supported its monophyly as previously reported (Duan et al. 2015; Liu et al. 2017; Nafisi et al. 2019; Juramurodov et al. 2023b).

In our previous study, *H. kudrjaschevii* was not included, but we have now found that it belongs to subsect. *Crinifera* in both trees (Figs S1–S2). In the ITS tree, this species is closely related to *H. nuratense* and *H. sunhangii*, while in the plastid tree, it forms a common subgroup with *H. olgae* and *H. santalaschi*. Although all three methods did not strongly support the relationship of *H. kudrjaschevii* with related species in both trees, its morphological characteristics were more similar to those of *H. nuratense* and *H. sunhangii* (see notes on *H. kudrjaschevii*).

The phylogenetic analysis based on the nrDNA ITS data (Fig. S1) showed that the sectional assignments of individual species were similar to the results obtained in the plastid tree (Fig. S2). According to both ITS and plastid trees, only one Uzbek species, *H. flavescens* belonged to sect. *Hedysarum*, while two species, *H. minjananse* and *H. lehmannianum*, belonged to sect. *Stracheya*. These findings were consistent with those reported in previous studies (Duan et al. 2015; Liu et al. 2017; Nafisi et al. 2019; Juramurodov et al. 2023b). *Hedysarum flavescens* is characterized by the strongly developed stem, pendent flowers in the inflorescence and triangular calyx teeth that are shorter than to as long as the tube. The species of sect. *Stracheya* in Uzbekistan are characterized by an inconspicuous or reduced stem that is usually 5–20 cm tall, leaves with about 5–9 leaflets, violet corolla, wings longer than half of keel, and pubescent or tomentose pods.

Most of the 23 species of *Hedysarum* in Uzbekistan were divided into small groups and formed subsect. *Crinifera* in both the ITS and plastid trees. However, the relationships between the species of subsect. *Crinifera*

differed in both trees, with the topology resolved only for some small clades. The unresolved position of several clades of subsect. *Crinifera* is explained by the low degree of variability in the chosen DNA sequences (Juramurodov et al. 2023a) and the explosive speciation hypothesis proposed in our previous study (Juramurodov et al. 2023b). Our observations suggest that subgroups in the plastid tree have stronger morphological support than in the nrDNA ITS tree, although not across all species. For instance, the subgroup *H. magnificum* (except for *H. montanum*) can be characterized by having large 1 or 2 pairs leaflets, long bracts and bracteoles, calyx teeth of equal length, wings longer than half of the keel, and other similar morphological characters. Similarly, the group between *H. talassicum* and *H. jaxarticum* (except for *H. mogianucum*) is characterized by plant height not exceeding 50 cm, dense hairs (epidermis not visible), short or abbreviated stem, long bracts and bracteoles, calyx teeth several times longer than the tube, pod joints tomentose and without bristles and other characteristics. The group between *H. nuratense* and *H. alaicum* shares common features such as short pedicel, calyx teeth of unequal length, pinkish corolla, wings less than half as long as keel, oblong or oblong-elliptic leaflets.

*Evolution of selected morphological characteristics*

All morphological characters used in this study were found to be highly helpful in identifying the taxa of *Hedysarum*. The delimitation of sections of *Hedysarum* in Uzbekistan based on morphological features was found to exhibit significant homoplasy. Our analysis revealed that only a few characteristics served as synapomorphies for the monophyletic groups of the plastid tree. The majority of the traced characteristics underwent multiple divergences within the group studied. Thus, our findings suggest that morphology alone cannot provide precise insights into the infrageneric relationships among the species of *Hedysarum* in Uzbekistan. Although features of all the characters under study evolved multiple times within *Hedysarum*, some interesting patterns were observed. The evolutionary patterns of all diagnostic morphological traits are discussed below.

Life form (Fig. 3; character ‘a’): our analysis revealed that the perennial (herb) life form is a symplesiomorphic character state for *Hedysarum* in Uzbekistan. Some species. However, are reported to be semi-shrubs, *H. hemithamnoides* Korotkova for example, which is endemic to Tajikistan (Korotkova 1955). Perennial and semishrub life forms can therefore be plesiomorphic characteristics for the whole genus.

Plant height (Fig. 3; character ‘b’): plant height over 50 cm is a plesiomorphic trait for section *Hedysarum* and subsect. *Crinifera*. While most members of subsect. *Crinifera* are less than 50 cm tall, certain species such as *H. montanum, H. magnificum, H. baldshuanicum, H. mogianicum,* and *H. iomuticum* exceed 50 cm (Korotkova 1955; Karimova 1978). In all species of sect. *Stracheya*, however, including species in neighboring countries that were not included in this study (such as *H. cisdarvasicum, H. denticulatum, H. kumaonense, H. wangii* P.L.Liu & Zhao Y.Chang, and *H. tibeticum* (Benth.) B.H.Choi & H.Ohashi), the plant height does not exceed 50 cm (Karimova 1978; Xu and Choi 2010; Liu et al. 2019). Plant height below 50 cm therefore appears to be a symplesiomorphic feature for sect. *Stracheya*.

Plant pubescence (including stems, peduncles and petioles): a glabrous stem is a plesiomorphic state for *Hedysarum* (Fig. 3; character ‘c’). Glabrous stems have probably evolved independently at least 4 or 5 times in subsect. *Crinifera*. However, sparse (epidermis visible) and dense (epidermis not visible) pubescence of the stem are homoplasies for sect. *Stracheya* and subsect. *Crinifera*. Our findings showed that the stem pubescence is not a diagnostic feature among the sections of *Hedysarum*, but can be used to identify species.

Stem feature (Fig. 3; character ‘d’): mapping of this trait revealed that a developed

stem is a plesiomorphic trait in *Hedysarum*. A short, abbreviated stem appears to be a homoplasious character of *Hedysarum*. Despite its homoplasious nature, this trait is useful in distinguishing section *Stracheya* from its likely sister clades, as all species in this section are characterized by the absence or short development of a stem (Choi and Ohashi 2003; Nafisi et al. 2019). Additionally, we found that subsect. *Crinifera* is highly polymorphic in stem characteristics, with all three types of stem features present within this subsection. Furthermore, subsect. *Crinifera* is highly polymorphic in characteristics of the stem, with all the three types of stem features present within this subsection.

Leaf length (Fig. 3; character ‘e’): our findings showed that leaves less than 10 cm long, or under 20 cm long, is a plesiomorphic state for sections *Hedysarum* and *Stracheya* and subsect. *Crinifera* in Uzbekistan. Additionally, we found that changes in stem length evolved several times in subsect. *Crinifera*.

Number of pairs of leaflets per leaf (Fig. 3; character ‘f’): 3–6 pairs, and sometimes 7 or more pairs of leaflets per leaf is considered plesiomorphic in *Hedysarum*. This is because some ancestral species, such as *Onobrychis echidna* Lipsky with 4–5(7) pairs and *Onobrychis micrantha* Schrenk with 5–6 pairs, among others (Korotkova 1955; Karimova 1978), which were not included in this study, were reported to have four or more pairs of leaflets per leaf. In certain species of subsect. *Crinifera*, such as *H. drobovii*, *H. gypsaceum*, *H. magnificum*, and *H. plumosum*, the presence of 1 or 2 well-developed pairs of leaflets on odd-pinnate leaves may indicate an apomorphic condition that differs from their ancestors. For example, *Caragana grandiflora* has 2 pairs of palmate compound leaves, while *Onobrychis tavernierifolia* Stocks ex Boiss. has 1 or 2 pairs of odd-pinnate leaves, but only the odd ones are well developed (Korotkova 1955). Nevertheless, a more extensive taxon sampling that includes more outgroup taxa is necessary to fully evaluate this hypothesis. The taxonomic treatment by Choi and Ohashi (2003) circumscribed subsect. *Crinifera* as consisting of species with 7–15 pairs of leaflets. However, our study reveals that this subsection also includes species with 1 or 2 pairs of leaves, which supports the taxonomic treatment proposed by Nafisi et al. (2019).

Leaflet length (Fig. 3; character ‘g’), leaflet width (Fig. 3; character ‘h’), and leaflet shape (Fig. 3; character ‘i’): the evolution of leaflet length, width, and shape within *Hedysarum* has resulted in a high level of homoplasy. These traits may have evolved independently multiple times from ancestors with leaflets up to 15 mm long and 5 mm wide. The rounded leaflet shape in *H. gypsaceum* and *H. plumosum* seems to be an apomorphic characteristic for *Hedysarum*. However, rounded leaflets also occur in some ancestor species of *Hedysarum*, such as *Onobrychis tavernierifolia* Stocks ex Boiss (Korotkova 1955), that were not included in this study. Similarly, the lanceolate leaflet shape, which we observed in some species of *Hedysarum* in our reconstruction, was also noted in *Onobrychis cornuta* (L.) Desv., *O. micrantha* Schrenk ex Fisch. & C.A.Mey. and other species (Korotkova 1955; Karimova 1978). Thus, leaflet shape may be a plesiomorphic condition for *Hedysarum*. Although these three morphological characteristics may not always be diagnostic, they can be helpful for identification when floral parts or pods are absent.

Orientation of flowers in raceme (Fig. 3; character ‘j’): the majority of species in *Hedysarum* and its ancestors, with the exception of section *Hedysarum*, exhibit a vertical or semi-vertical flower posture in the raceme, which is considered the plesiomorphic state. In comparison, we found that pendent flowers in the raceme may be the synapomorphic condition for sect. *Hedysarum* based on our examination of hundreds of herbarium specimens (mainly in TASH and KUN), field observations, and review of species images in online databases (www.planatarium.ru, www.iplant.cn, www.gbif.org), including species of sect. *Hedysarum* from adjacent territories not included in this study. Testing this hypothesis, however, will require

greater taxon sampling, including more outgroup taxa.

Bract length (Fig. 3; character ‘k’): bracts ≤ 3 mm and up to 6 mm in length are considered to be plesiomorphic in *Hedysarum*; bracts up to 13 mm in length are apomorphic and diagnostic for subsect. *Crinifera*. Due to changes within the subsect. *Crinifera* clade, not all its members exhibit this trait. Furthermore, bract length is also used as a diagnostic feature for identifying certain species of *Onobrychis* Mill., *Oxytropis* DC., and other genera related to *Hedysarum* (Korotkova 1955; Baitenov 1961).

Bracteole length (Fig. 3; character ‘l’): bracteoles ≤ 3 mm in length are considered plesiomorphic in *Hedysarum* and were observed in multiple instances across the tree. Bracteoles longer than 3 mm are apomorphic and diagnostic for subsect. *Crinifera*, although not all members of the clade exhibit this trait. It is not a reliable diagnostic trait, however, for distinguishing sections in the genus as all three sections have species with bracteoles longer than 3 mm. Nonetheless, bracteole length remains an important character in differentiating certain species of subsect. *Crinifera*, as indicated in the taxonomic key below.

Pedicel length (Fig. 3; character ‘m’): short pedicels (< 2 mm) and long pedicels (≥ 2 mm) are considered plesiomorphic states in *Hedysarum* and have evolved independently multiple times throughout the tree. Pedicels 2 mm long or longer appear to be a symplesiomorphic feature for section *Hedysarum*, as it is similar in most species of this section which were not included in this study (Baitenov 1961; Xu and Choi 2010). Although the short pedicel trait seems to be a symplesiomorphic condition for *Stracheya* in our reconstruction, pedicels longer than 2 mm occur in some species, such as *H. kumaonense* Benth. ex Baker, *Hedysarum denticulatum* Regel and *H. cisdarvasicum* Kamelin & Karimova, which occurs in neighboring territories (Karimova 1978; Xu and Choi 2010).

Length of calyx teeth (Fig. 3; character ‘n’): mapping of this trait revealed that unequal calyx teeth can occur in all sections of *Hedysarum*. Additionally, it appears that calyx teeth of equal length have evolved independently at least 8 to 10 times within subsect. *Crinifera*. While this feature is not exclusive to any particular section, it remains one of the significant characters for distinguishing species such as *H. montanum* and *H. balshuanicum* (see taxonomic key below).

Ratio of length of teeth to tube in calyx (Fig. 3; character ‘o’): the ratio of calyx teeth to calyx tube can be categorized into four types – shorter than tube, as long as tube, up to 2 times longer than tube, and up to 4 times longer than tube – all of which appear to be plesiomorphic traits for *Hedysarum*. Calyx teeth shorter than or rarely equaling the tube are common in related genera, such as *Astragalus*, *Oxytropis* and *Eversmannia*; in most species of *Onobrychis* the calyx teeth are several times longer than tube (Korotkova 1955; Baitenov 1961; Karimova 1978; Xu and Choi 2010). In agreement with Nafisi et al. (2019), calyx teeth several times longer than tube is one of the important diagnostic features in distinguishing subsect. *Crinifera* from other sections in *Hedysarum*, although not all members of the clade possess this trait. Furthermore, Nafisi et al. (2019) provided a taxonomic treatment for subsect. *Crinifera* where it was noted that calyx teeth in this subsection are (1.5-)2 – 3(-4) times longer than the tube. However, our observations revealed that in some species of this subsection, the calyx teeth may be shorter than the tube (as in *H. iomuticum*) or equal to it (as in *H. olgae*).

Corolla color (Fig. 3; character ‘p’): a yellow corolla appears to be ancestral for *Hedysarum*, but most of the species in Uzbekistan exhibit a different color. Similarly, a pink corolla is a plesiomorphic state and has probably evolved at least 8 or 9 times in subsect. *Crinifera*. On comparison, purple and white corollas are derived conditions and are considered to be apomorphic in some species of subsect. *Crinifera* in Uzbekistan. In addition to the taxonomic treatment of Nafisi et al. (2019), we suggest including pink and white corollas for subsect. *Crinifera*. Nafisi et al. (2019)

characterized subsect. *Crinifera* as having purple/violet or leaden-colored corollas. However, our study of the species within this subsection revealed the presence of pink and white corollas (see character 'p' in Fig. 3).

The ratio of the standard length to keel (Fig. 3; character 'q'): our analysis indicates that the trait of the standard being equal to or longer than the keel is a plesiomorphic feature in *Hedysarum*, which is also the case in its ancestors, such as *Oxytropis*, *Onobrychis*, *Alhagi* Tourn. ex Gagnebin and related genera (Korotkova 1955). However, in some species within subsect. *Crinifera* (e.g. *H. taschkendicum, H. turkestanicum, H. bucharicum, H. sunhangii, H. jaxarticum, H. popovii*), there is evidence of an apomorphic condition where the standard is shorter than the keel. This characteristic has also independently evolved at least 6 or 7 times from the ancestral types mentioned earlier. In *H. sunhangii* and *H. nuratense*, we previously reported (Juramurodov et al. 2021) that the ratio of the standard to the keel plays an important role in distinguishing between closely related species.

Ratio of length of wings to keel (Fig. 3; character 'r'): We assessed the ratio of the length of the wings to the length of the keel for three distinct situations (less than half length of keel; half as long as keel; more than half as long as keel). According to our reconstruction, wings that are either less than half as long the keel or more than half as long as keel are considered plesiomorphic for *Hedysarum*. In comparison, in some species of subsect. *Crinifera* in Uzbekistan (*H. plumosum*, *H. talassicum*, *H. amankutanicum* and *H. santalaschi*), wings that are half as long as the keel have evolved at least four times as the apomorphic condition. According to Nafisi et al. (2019), the wings of species within subsect. *Crinifera* are mostly about one half the length of the standard. While their study was based on a large number of species, we found that most of the species of subsect. *Crinifera* that we studied have wings less than half as long as the standard or keel, or in some cases, more than half as long.

Keel length (Fig. 3; character 's'): we determined that the length of the keel in the all three cases we analyzed were plesiomorphic in *Hedysarum*. In only three species, i.e. *H. drobovii*, *H. magnificum* and *H. iomuticum*, the keel up to 26 mm long evolved independently, while lengths up to 15 mm and up to 20 mm evolved in parallel (except in the *H. plumosum* group).

Pod division (Fig. 3; character 't'): the division of the pod into joints can be considered a synapomorphy of *Hedysarum*. This trait may have evolved multiple times in parallel within the genus from ancestors with unilocular or one-jointed pods, resulting in pods that are usually divided into up to 3 or 6 joints. While pods with up to 3- or 6-segments occur in all three sections, the number of joints per pod is not a reliable feature for distinguishing sections.

Shape of pod or pod joints (Fig. 3; character 'u'): the rounded or orbicular pod joints in subsect. *Crinifera* appear to be synapomorphies. Similarly, in our reconstruction ovate or linear-oblong pod joints occurred only in sections *Stracheya* and *Hedysarum* in Uzbekistan. Therefore, it is possible that the shape of these pod joints evolved solely in *Hedysarum*. Ancestral genera related to *Hedysarum*, such as *Onobrychis*, have pods of different shapes, such as reniform, while *Oxytropis* has ovoid, ovoid-oblong, cylindric, and falcate-oblong fruits (Korotkova 1955; Karimova 1978; Xu and Choi 2010). *Eversmannia* has wide, linear fruits (Baitenov 1961). Further taxon sampling, however, including additional outgroup taxa, is necessary to fully test this hypothesis. Additionally, species of *Hedysarum* were not included in this study, but in neighboring territories (Baitenov 1961; Karimova 1978; Xu and Choi 2010), exhibit various pod shapes, such as globose, subglobose, ovoid, ellipsoid, and obovoid.

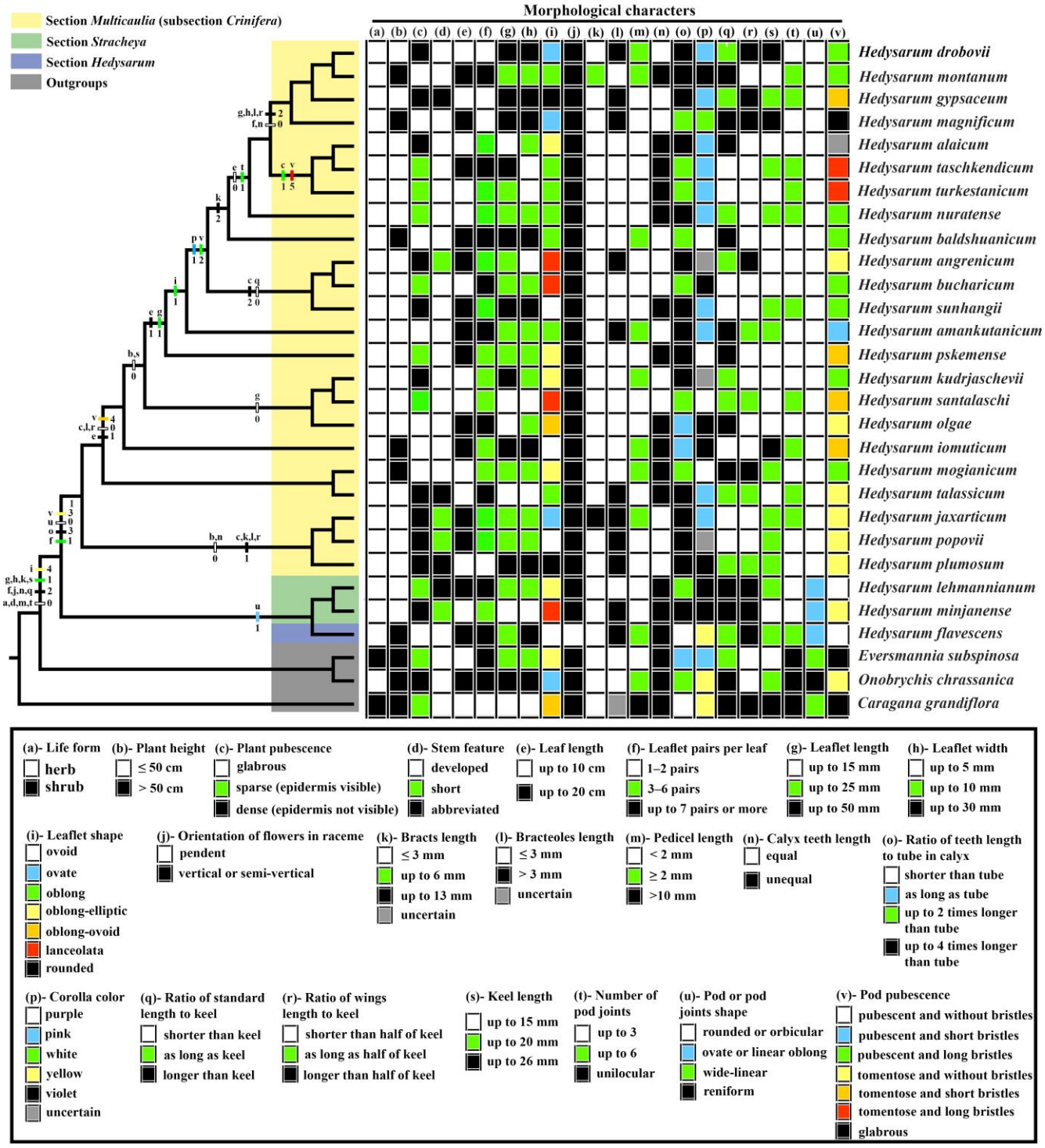


**Fig. 3**. Reconstruction of evolution in selected morphological characters in *Hedysarum* in Uzbekistan based on the strict consensus tree obtained from the maximum likelihood analysis of the plastid data. The character state at the branches indicate the ancestral state of the clade. Characters are shown left/above boxes and their states immediately below. Descriptions of characters and character states are provided in the legend.

Furthermore, the shape of the pod joints can serve as a useful diagnostic trait for distinguishing sections within the genus.

Pod pubescence (Fig. 3; character ‘v’): we categorized the species of *Hedysarum* in Uzbekistan into seven groups based on

pubescence of the pod surface. Our reconstruction analysis of the evolutionary status of pod pubescence showed that this character exhibits a high level of homoplasy within *Hedysarum*. Based on the degree of pubescence of pod joints, glabrous or tomentose or pubescent traits are considered to be ancestral in *Hedysarum*. Conversely, the presence of short or long bristles on the pod joints is a unique and synapomorphic feature for *Hedysarum*, particularly of subsect. *Crinifera*. Additionally, the type of pod pubescence is an important diagnostic trait for identifying species within the genus, as noted by Fedtschenko (1948), Choi and Ohashi (2003), Dehshiri and Goodarzi (2016), and Nafisi et al. (2019).

*Taxonomy*

***Hedysarum*** L., Sp. Pl. 2: 745. (1753).
**Type:**—*Hedysarum alpinum* L. (typ. cons.).
=*Banalia* Bubani in Fl. Pyren. 2: 568 (1899), nom. illeg. (POWO)
=*Sartoria* Boiss. in Diagn. Pl. Orient. 9: 109 (1849).
=*Stracheya* Benth. in Hooker's J. Bot. Kew Gard. Misc. 5: 306 (1853).
**Description:**—Herbs, perennial, or subshrubs, 5–150 cm tall. Stems often strongly developed, branching, sometimes completely abbreviated and inflorescences emerging from short shoots developing from the caudex. Leaves imparipinnate; leaflets usually 5–9 pairs, rarely 1–3-pairs or even with only unpaired leaflets. Inflorescences more or less dense racemes. Flowers: calyx campanulate, teeth shorter than, equaling or longer than tube; corolla longer than calyx, pink, purple, violet or rarely white or yellowish; standard usually equal to or slightly longer than keel, rarely shorter than keel; wings one-fourth to one-half as long as keel, rarely longer; ovules 4–8 per ovary; pods jointed, sometimes some ovules abortive, then pod 1–5-jointed, joints flat-compressed or slightly inflated, smooth, glabrous or often pubescent, reticular or transversely ribbed, often covered with short or long bristles.

**Identification key for the species of *Hedysarum* in Uzbekistan**

1a. Flowers pendent in raceme; corolla yellowish…….. 1. *H. flavescens* (sect. *Hedysarum*)
1b. Flowers horizontally spreading or slightly ascending; corolla pink, purple or violet, rarely white…2

2a. Stem abbreviated; standard longer than keel ……..…3 (sect. *Stracheya*)
2b. Stem usually well developed or sometimes inconspicuous; standard shorter than, equaling or longer than keel ……....4 (subsect. *Crinifera*)

3a. Leaflets 8–12-pairs; bracteoles 3 mm long ……..…..2. *H. lehmannianum*
3b. Leaflets 4–6(–8)-pairs; bracteoles 6–8 mm long ……..…….....3. *H. minjanense*

4a. Stem short or inconspicuous ……..……..... 5
4b. Stem well-developed ……..……..… 10

5a. Calyx teeth shorter than corolla, teeth 3–4 times longer than tube; pods rounded, 4–5 mm long, appressed pilose, without setae …….....4. *H. talassicum*
5b. Calyx teeth as long as corolla, teeth to 4–7 times longer than tube ……...… 6

6a. Leaflets 1 or 2 pairs ……..... 7
6b. Leaflets (2 or)3–7 pairs ……..... 8

7a. Plants 10–25 cm tall; leaflets 1 or 2 pairs; peduncle 7–20 cm long ……...5. *H. gypsaceum*
7b. Plants 5–15 cm tall; leaflets 1 or 2-pairs; peduncle 3–4 cm long ……..……..6. *H. plumosum*

8a. Hairs of peduncle spreading; pods short hairy, with thin transverse veins, without setae and bristles, with very short, barely visible tubercles along margin ……..7. *H. popovii*

8b. Hairs of peduncle appressed; pods short hairy, white tomentose, with tubercles along margins and veins, bristles short or absent ……..……... 9

9a. Wings 5–7–(10) mm long; pods appressed white hairy, transversely ribbed, with long incurved bristles ……..……..…..8. *H. jaxarticum*
9b. Wings 10–12 mm long; pods without setae and bristles, appressed short hairy.....9. *H. angrenicum*

10a. Plants 40–60 cm tall; pods glabrous …….……10. *H. magnificum*
10b. Plants 15–100 cm tall; pods pubescent ……..……..... 11

11a. Leaflets oblong-obovate, 1 or 2 pairs; pods orbicular, prominently nerved, with aculeiform tubercles and bristles .……11. *H. drobovii*
11b. Leaflets ovate, oblong, oblong-elliptic, oblong-ovate or lanceolate, 3–10 pairs; pods elliptic, rounded, orbicular, suborbicular, ovate, transversely ribbed, short or long bristly, rarely without bristles ……. 12

12a. Standard longer than keel ...……..... 13
12b. Standard shorter or as long as keel ……..…..…..…..... 19

13a. Wings more than ½ as long as of keel …… 14
13b. Wings less than ½ as long as keel ..... 15

14a. Plants 70–125 cm tall; calyx teeth unequal; pods with short partly reddish bristles on surface and along sutures ……..…12. *H. mogianicum*
14b. Plants 30–40 cm tall; calyx teeth equal; pods short hairy, gray, with rare short hooks and curved or straight short bristles along margins and sides ……..……..…13. *H. amankutanicum*

15a. Leaflets oblong-ovate; calyx teeth as long as tube; pods marginally short toothed, appressed short hairy, without bristles and setae, with 8–10 transverse veins ……..……..….14. *H. olgae*
15b. Leaflets oblong or oblong-elliptic; calyx teeth one and half or 4 times longer than tube; pods without marginal short teeth…….……..… 16

16a. Leaflets 4–6-pairs, oblong-elliptic; pedicel to 2 mm long …….…… 17
16b. Leaflets 5–10-pairs, oblong; pedicel 2 mm long or more …….. 18

17a. Plants 30–40 cm tall; stem densely pubescent (epidermis not visible); leaves 6–8 cm long; corolla purple.……...15. *H. alaicum*
17b. Plants 25–30 cm tall; stem sparsely pubescent (epidermis visible); leaves 10–15 cm long; corolla pink ……..…16. *H. pskemense*

18a. Calyx teeth of equal length, teeth one and half times longer than tube; corolla violet; pods 1- to 3-jointed, joints glabrous, transversely ribbed, with thin bristles on ribs ……...17. *H. baldshuanicum*
18b. Calyx teeth of unequal length, 4 times longer than tube; corolla purple; pods 3–5-jointed, joints finely pubescent, bristly, bristles at thickened margin longer, incurved.……18. *H. montanum*

19a. Stem glabrous, 60–100 cm tall; calyx teeth as long as tube, upper teeth shorter than tube, lower teeth as long as tube; pods rounded, ribbed, densely short hairy, margins and sides with short hard prickles ……...……...….19. *H. iomuticum*
19b. Stem pubescent, to 50 cm tall; calyx teeth to 2 or 4 times longer than tube …….. 20
20a. Leaflets lanceolate; corolla purple; wings half as long as keel; bracteoles 0.5–0.7 mm long; pods finely appressed hairy, middle part with short (less than l mm) reddish setae .....20. *H. santalaschi*
20b. Leaflets oblong, lanceolate or ovate; corolla violet or pink; wings less than half as long as keel; bracteoles more than 1.2 mm long; pod joints with transverse ribs, with reddish or purple long setae on each…….…..... 21

21a. Bracteoles 1.2–2 mm long; calyx teeth unequal ……..……... 22
21b. Bracteoles 2.5–3 mm; calyx teeth equal ……...21. *H. bucharicum*

22a. Stem sparsely pubescent (epidermis visible) and thin; leaflets 4–7 pairs……..…. 23
22b. Stem densely pubescent (epidermis not visible) and thick; leaflets 2–4 pairs……..... 25

23a. Calyx teeth 3–4 times longer than tube; standard nearly as long as keel …….....24. *H. nuratense*
23b. Calyx teeth 1–3 times longer than tube; standard half to two-thirds as long as keel ……...…. 24

24a. Plants 15–35 cm tall; leaves 3–8 cm long; pods with sparse white hairs and prickles elongated into long reddish hairs……...……22. *H. turkestanicum*
24b. Plants 25–50 cm tall; leaves 10–15 cm long; pods densely pubescent, with large rough bristles on thick nerves, bristles short, not hairlike and not reddish……...23. *H. taschkendicum*

25a. Standard shorter than keel; leaflets ovate or broadly ovate, lower surface of leaflets densely white hairy ……..….25. *H. sunhangii*
25b. Standard as long as keel; leaflets lanceolate or elliptic, both surfaces of leaflets densely white hairy ……..…..……26. *H. kudrjaschevii*

**1. *Hedysarum flavescens*** Regel & Schmalh. in Izv. Imp. Obshch. Lyubit. Estestv. Moskovsk. Univ. 34(2): 21 (1882).

**Type:**—[Tajikistan]. In Kokaniae montibus ad lacum Iskander-kul, 7000’ alt., et in angustiis fluvii Iskander 6500’, *O. Fedtschenko* (holotype LE).

**Description:**—Herbs, 40–80 cm tall, subglabrous, root somewhat thickened. Stems erect or slightly ascending, cylindrical. Stipules squamiform at base, connate in lower leaves, free in upper, deciduous. Leaves short petiolate, 10–15 cm; leaflets 3–7 pairs, oblong-ovate or elliptic, 10–28 × 5–18 mm, obtuse or rounded at apex. Peduncle longer than leaves. Racemes lax, with many flowers, distinctly longer than leaves, flowers in raceme pendent. Bracts scarious, lanceolate, 2–4 mm long. Bracteoles 2–4.5 mm long. Pedicel 3–4 mm long. Calyx shortly campanulate, 4–5 mm, pubescent; teeth unequal, subulate to triangular at base, slightly shorter than tube. Corolla yellowish; standard 8–18 × 6–7 mm, oblong or oblong-elliptic, slightly apex emarginate; wings 12–16 × 2–2.5 mm; keel 12–18 × 5–7 mm. Ovary pubescent, long stalked; ovules few; pods stipitate, joints 2–4, flattened, pubescent, oblong-elliptic or oblong, tapering at base, finely reticular, with broad complete wing at margin 10–15 × 7–10 mm long. Seeds reniform, flattened, 4–5 × 2.5–4 mm (Figs 4–5).

**Flowering time:**—June-July.

**Fruiting time:**—June-July.

**Habitat:**—On grassy, stony, fine earth slopes, screes, rocks, outcrops of conglomerates, outcrops of red clay in tree and shrub thickets, juniper, birch forests, spruce forests along river valleys, in subalpine meadows, rising to glaciers, in the middle and upper belts of mountains, at 1800–3200 m a.s.l.

**Distribution:**—China (SW Xinjiang), Kazakhstan, Kyrgyzstan, Tajikistan, Uzbekistan. Distribution in Uzbekistan: Fig. 6.

**Specimens examined:**—I-1 **Western Tian-Shan Region**. I-1-a **Ugam-Pskem District**: Pskem ridge (valley of the Pskem River, Urungachsay, 19.07.1963, *Puchkova*; near the Nanai village, Maydantal ridge (Pskem River, Tekeshsay River basin, 02.08.2015, *Tojibaev*); I-1-b **Western Chatkal District**: Chatkal ridge (Chimgan, beyond the Melovoy pass, 22.07.1920, *Vasiliev*; near the Chimgan Botanical Station, on the screen near the Melovoy pass, 14.08.1925, *Gomolitsky 224*, *233*, *236*; near the Chimgan Botanical Station, gorge of the Khadalak River, 07.07.1927, *Linchevsky*; Chatkal River valley, basin of the Akbulak River, upper reaches of the Sagardonsay, Minbulaksay, 30.07.1956, *Korovin 443*; Chimgan tract, pass Melovoy, 08.07.1956, *Granitov, Zuckerwanik 769*; Chimgan, 01.06.1961, *Adylov 1670*; Big Chimgan, 01.07.2019, *Juramurodov*; Big Chimgan, 28.06.1966, *students 16*; the right bank of Tunduksay, 10.08.2019, *Tojibaev, Juramurodov*), 19.06.2020, *Dekhkanov,*

*Ortikov, Turdiev, Juramurodov 19062020090, 19062020089*). I-3 **Fergana- Alay Region.** I-3-b **Eastern Alay District**: Alay ridge (Shakhimardan River basin, Yardansay, bank of the Aksu River, 31.07.1967, *Khalkuziev*). I-7 **Hissar-Darvaz Region**. I-7-a **Sangardak-Tupalang District**: Hissar ridge (Mountains Chor and Ogul, 06.07.1941, *Lopott, Pinkhasov 73*; Tupalang River basin, Kshtut River valley upstream of Tamarkhut village, 19.06.1948, *Pyataeva 1186*). All specimens are at TASH.

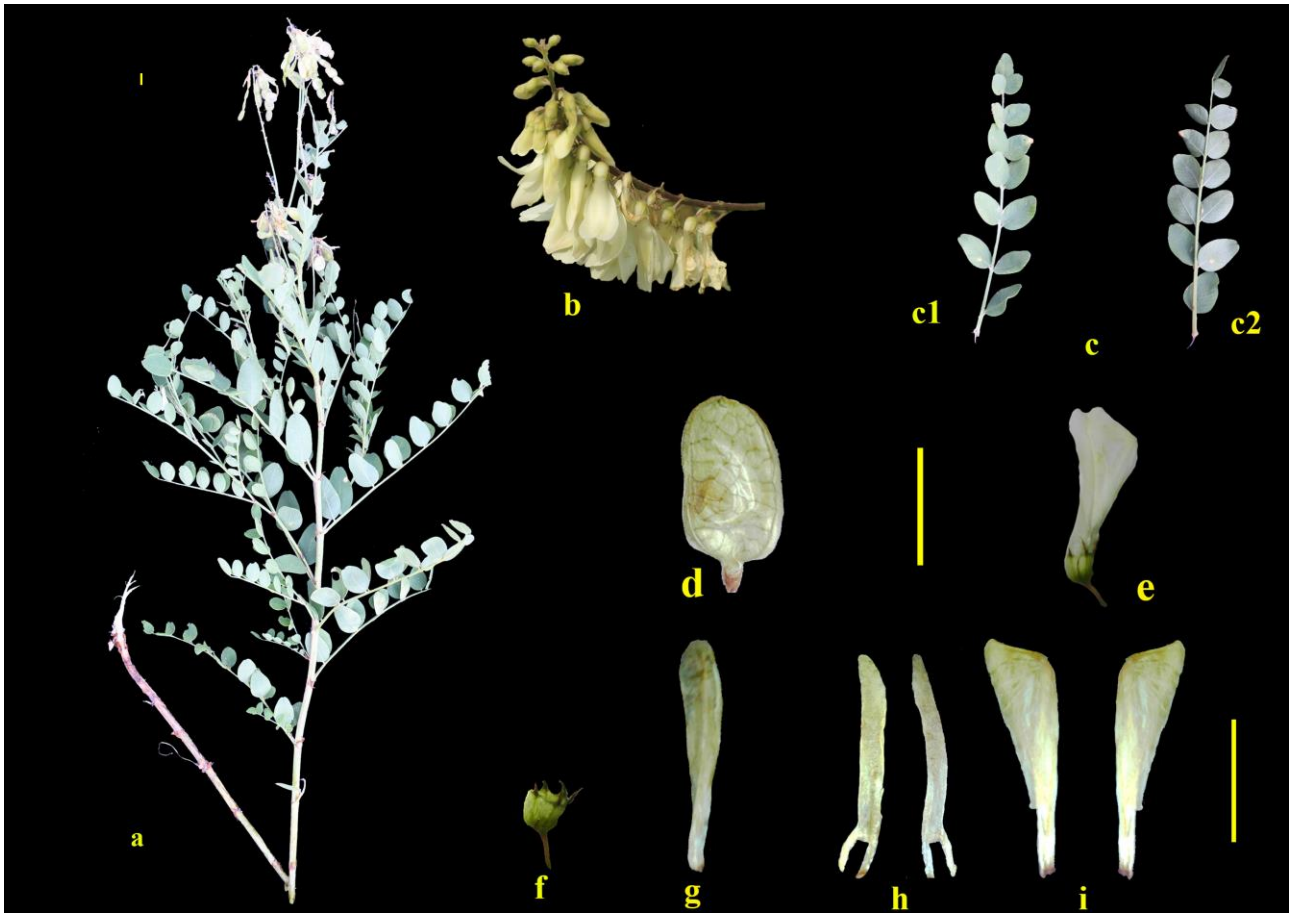


**Fig. 4.** Living plant of *Hedysarum flavescens*: a, entire plant; b, raceme; c, leaflets (c1, upper part and c2, lower part); d, pod; e, flower; f, calyx; f, standard; h, wings; i, keel. Scale bar 1 cm.

**Fig. 5.** Habit of *Hedysarum flavescens*

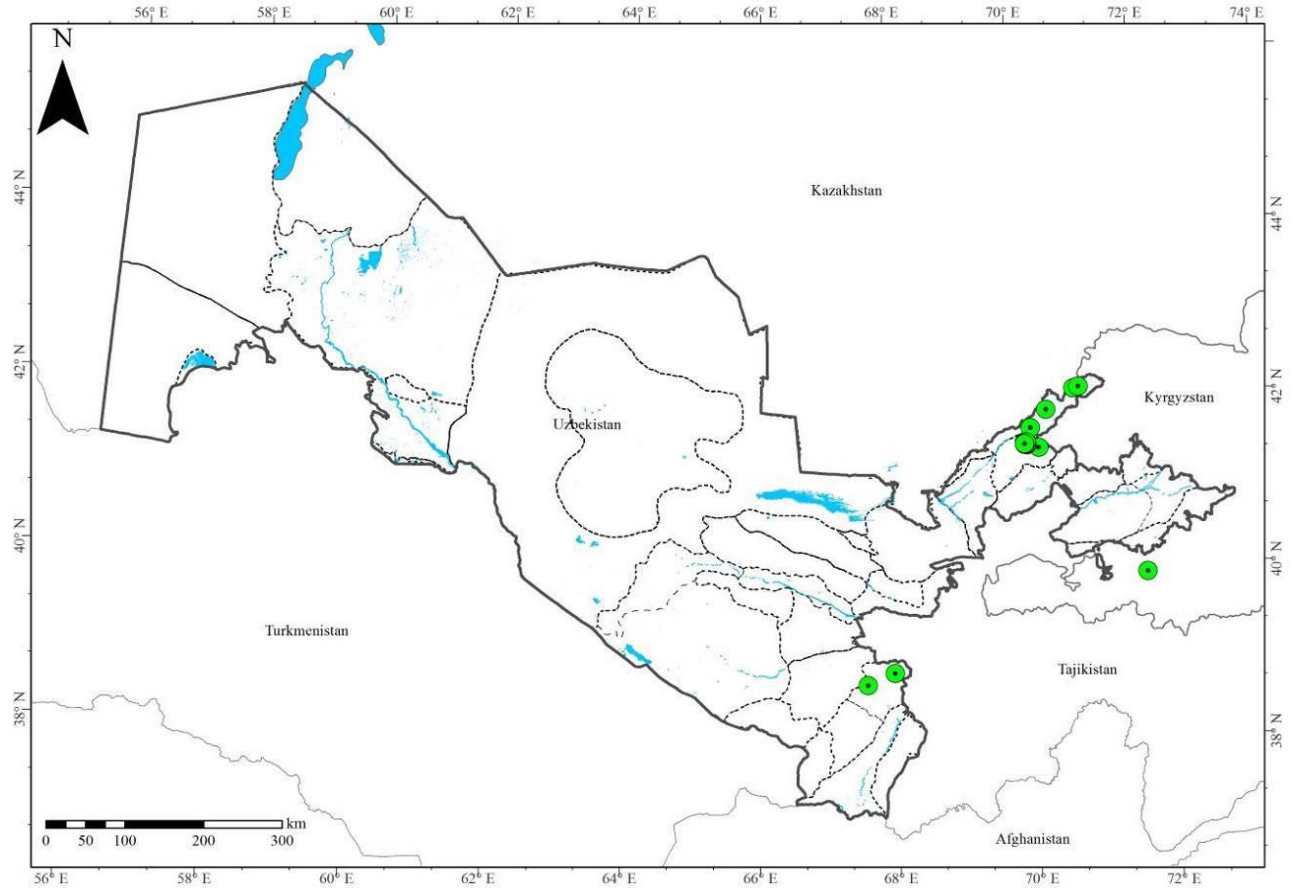


**Fig. 6.** Distribution of *Hedysarum flavescens.*

**2. *Hedysarum lehmannianum*** Bunge, Beitr. Fl. Russl.: 102 (1852).
**Type:**—[Tajikistan]. Described from the basin of Zeravshan River near the village of Fon (holotype P).
= *Hedysarum pulchrum* Nikitina in Fl. Kirgiz. SSR, Suppl. 1: 113 (1967)
**Type:—**[Kyrgyzstan]. Alai Range, Tar River basin, Terek-Suu tract, 18.06.1964, R. Aidarova, N. Gorbunova (FRU).
**Description:**—Herbs, (10) 15–35 cm tall, almost completely appressed hairy. Stems abbreviated. Stipules oblong-lanceolate, brown, connate, appressed hairy. Leaves 10–15 cm; leaflets 8–12 pairs, oblong-elliptic, 10–18 (25) × 5–7 mm, abaxially densely appressed hairy, adaxially pubescent, rarely subglabrous. Peduncle (with raceme) longer than leaves. Racemes rather dense, 12- to 20-flowered. Bracts lanceolate, deciduous post anthesis, 3–8 mm long. Bracteoles ca. 3 mm long. Pedicels 1.5–5 mm long. Calyx spreading hairy, teeth unequal, as long as tube or one and half times longer than tube. Corolla purple; standard 16–24 × 9–12 mm, oblong-ovate; wings lanceolate-oblong, 12–16 × 3–4 mm; keel almost triangular, 16–20 × 6–7 mm, Ovary subsessile, hairy; ovules 3–5. Pods 1–3-jointed, joints unequal-ovate, appressed hairy, reticulate nerved, pubescent, margins dentate, more often without membranous wing along edge, 8–10 × 6.5–7 mm. Seeds dark brown, smooth, 4 × 2.5 mm, ovate-reniform (Fig. 7).


**Fig. 7.** Living plant of *Hedysarum lehmannianum*. a, entire plant; b, pod; c, calyx; d, standard; e, wings; f, keel. Scale bar 1 cm.

**Flowering time:**—June-July.
**Fruiting time:**—August-September.
**Habitat:**—On fine earth and stony slopes, rarely on screes, in the middle belt of mountains among shrubs and trees, up to lower part of the upper belt, occurring there in subalpine meadows.

**Distribution:**—Kyrgyzstan, Tajikistan, Uzbekistan, Afghanistan and Iran. Distribution in Uzbekistan: Fig. 8.

**Specimens examined:**—I-6 **Western Hissar Region**. I-6-c **Baysun District**: Hissar ridge (Mountains of Khodjagurgurat, Irgailisay, 14.07.1934, *Butkov 235*; mountains of Khodjagurgurata, lane Saidjar, 08.08.1934, *Demurina 367*; mountains Ketmen-Chapty, 2900 m, 28.07.1935, *Gordienko* (MW); Chulbair Mountains, alpine vegetation, 01.07.1941, *Popova 868*; Machai River basin, village Yukari Machai, Sharshara tract, 06.06.2012, *Turginov 490*). I-7 **Hissar-Darvaz Region**. I-7-a **Sangardak-Tupalang District**: Hissar ridge (Shargun River, trail to Akjar, at 2410 m a.s.l., 21.07.1987, *Maltsev*). Specimens examined are in TASH unless stated otherwise.

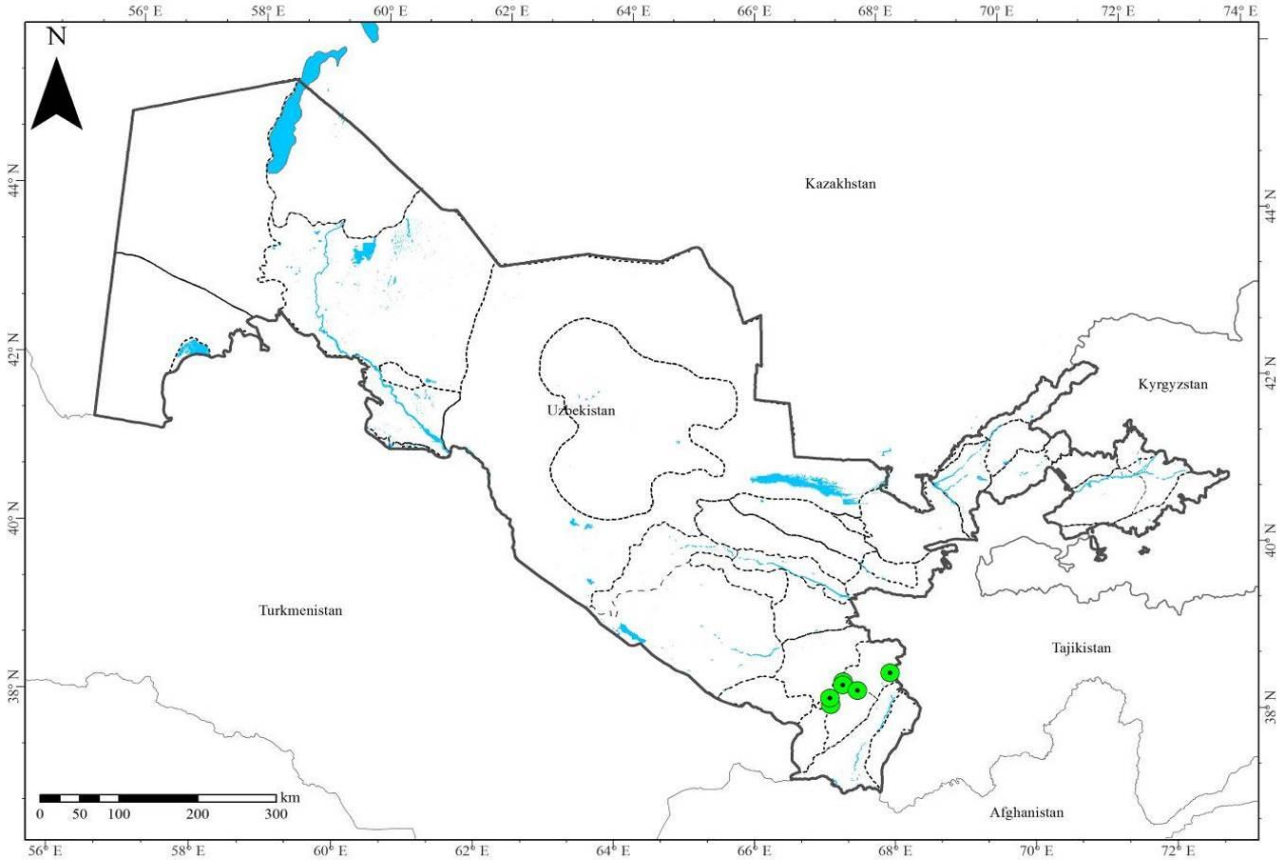


**Fig. 8.** Distribution of *Hedysarum lehmannianum.*

**Notes:**—Upon our examination of the herbarium material, we found specimens collected by Popova in 1941 and by Turginov in 2012 stored in TASH under the name of *H. denticulatum*. However, we found these specimens to be more similar to *H. lehmannianum* based on the presence of 7–9 pairs of leaflets and calyx teeth more than 1–1.5 times longer than the tube. Moreover, molecular analysis of the sample collected by Turginov confirmed its identification as *H. lehmannianum* (Juramurodov et al. 2023b). We therefore reidentified these specimens as *H. lehmannianum*.

**3. *Hedysarum minjanense*** Rech. f. in Biologiske Skrifter 9(3): 185 (1958).

**Type:**—[Afghanistan]. In jugo Manjun, 3600 m, *W. Koelz 12663* (syntypes US, W).

= *Hedysarum cephalotes* Franch. in Ann. Sci. Nat., Bot., Sér. 6, 15: 264 (1883), nom. illeg., non Roxb. 1832.

**Type:**—Tajikistan. Passe de Badraon, vallée des Jagnaous, 06.07.1881, *Capus*; Dachti-Gouibas, 29.06.1881, *Capus* (syntypes P).

**Description:**—Herbs, 8–20(–30) cm tall, densely appressed silvery hairy, rootstock rather thick (18 mm in diameter), strongly branching apically and forming dense tufts,

covered above with relics of petioles and stipules. Annotinous stems barely developed. Stipules connate, membranous, grayish brown, slightly appressed hairy, with distinct longitudinal nerves. Leaves 2–5 cm long; leaflets 4–6(–8) pairs, linear-lanceolate, 4–11(–15) × 0.5–3(–5) mm. Peduncle erect or slightly ascending, longer than leaves, densely appressed hairy. Racemes dense and compressed, somewhat elongating post anthesis, 15- to 30-flowered. Bracts lanceolate or ovoid, 3–6 mm long. Bracteoles filiform, grayish brown, 6–8 mm long. Pedicel to 1 mm long. Calyx short tubular, teeth linear-filiform, ciliate hairy, several times longer than tube, lower tooth slightly longer than others. Corolla lilac-violet; standard broadly ovate, apex emarginate, 13–16 × 10–11 mm; wings lanceolate, 9–11 × 2–3 mm long; keel slightly shorter than standard, obtusely rounded angular, 11–13 × 5–6 mm long. Ovary hairy. Pods transversely rugose, 1- to 3-jointed, joints 5–8 × 4–6 mm, orbicular-tetragonal, densely hairy, ribbed. Seeds 3–3.5 × 2–2.5 mm, broadly reniform, brown (Fig. 9).


**Fig. 9.** Living plant of *Hedysarum minjanense*. a, entire plant; b, pod; c, flower; d, calyx; e, standard; f, wings; g, keel. Scale bar 1 cm. Photo ‘a’ was taken by Gorbunov.

**Flowering time:**—June-August.
**Fruiting time:**—August-September.
**Habitat:**—On rocky and fine earth slopes, outcrops of bedrock in feather-grass-wormwood groups, on alpine lawns, pebbles along river valleys, scree, moraines in the upper mountain belt.

**Distribution:**—Kazakhstan, Kyrgyzstan, Tajikistan, Uzbekistan, Pakistan and Afghanistan. Distribution in Uzbekistan: Fig. 10.

**Specimens examined:**—I-6 **Western Hissar Region**. I-6-c **Baysun District**: Hissar ridge (Mountains of Khodjagurgurata, western side of Belauty pass, 30.06.1961, *Pryakhin* (TASH)).

**Notes:**—There is only one specimen of *Hedysarum minjanense*, collected by Pryakhin in 1961, from Uzbekistan. Our 2018–2022 field research on Khodjagurgurata Mountain to collect additional specimens of this species was unsuccessful.

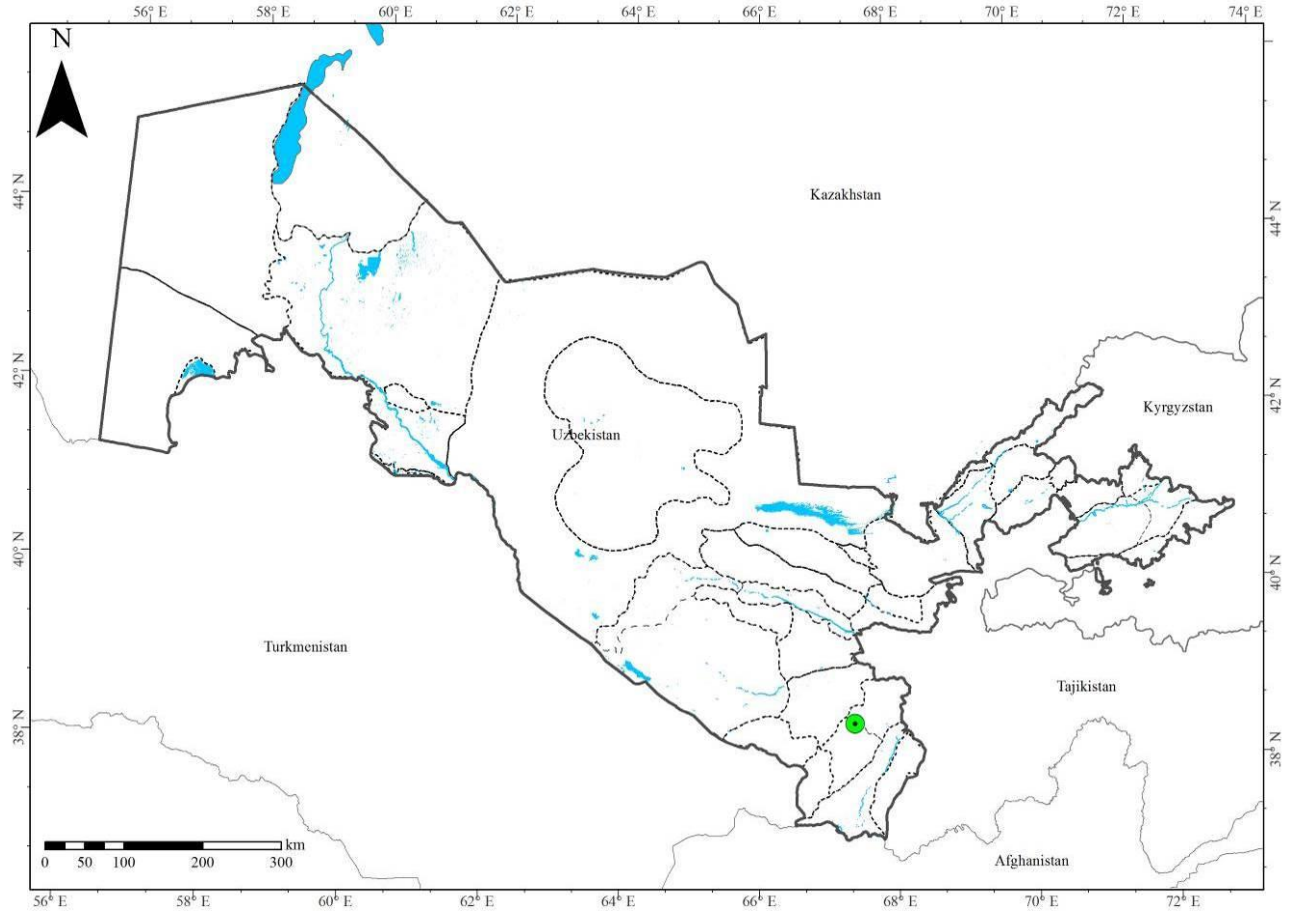


**Fig. 10.** Distribution of *Hedysarum minjanense.*

**4. *Hedysarum talassicum*** Nikitina & Sultanova in Mater. Fl. Kirg.: 43 (1973).

**Type:**—[Kyrgyzstan]. Ala-Tau Talassicus, systema fl. Kalba, locus Ters-Bulak dictus, 29.07.1954, *J.V. Vychodzev* (holotype FRU [photo!]).

**Description:**—Herbs, 10–25 cm tall, acaulescent. Stipules pale brown, appressed hairy, 5–10 mm long. Leaves 6–10 cm long; leaflets 9–15 pairs, oblong-narrowly elliptic, 10–15 × 3–5 mm, abaxially sparsely pilose, adaxially densely pilose. Peduncle longer than leaves, pilose. Racemes dense, multi flowered. Bracts lanceolate 5–10 mm long, pilose. Bracteoles lanceolate, 4–8 mm long, divaricate pilose. Pedicel 0.5–1 mm long. Calyx campanulate, densely curled pilose, calyx teeth subulate, shorter than corolla, teeth 3–4 times longer than tube. Corolla bright pink; standard rounded, 12–15 × 9–11 mm; wings 5–6 mm long; keel as long as or slightly longer than standard. Pods 2- to 4-jointed, joints rounded, 4–5 mm long, appressed pilose, without setae (Figs 11–12).

**Flowering time:**—July-August.

**Fruiting time:**—August.

**Habitat:**—Stony slopes at 2800–3400 m a.s.l. (Fig. 11).

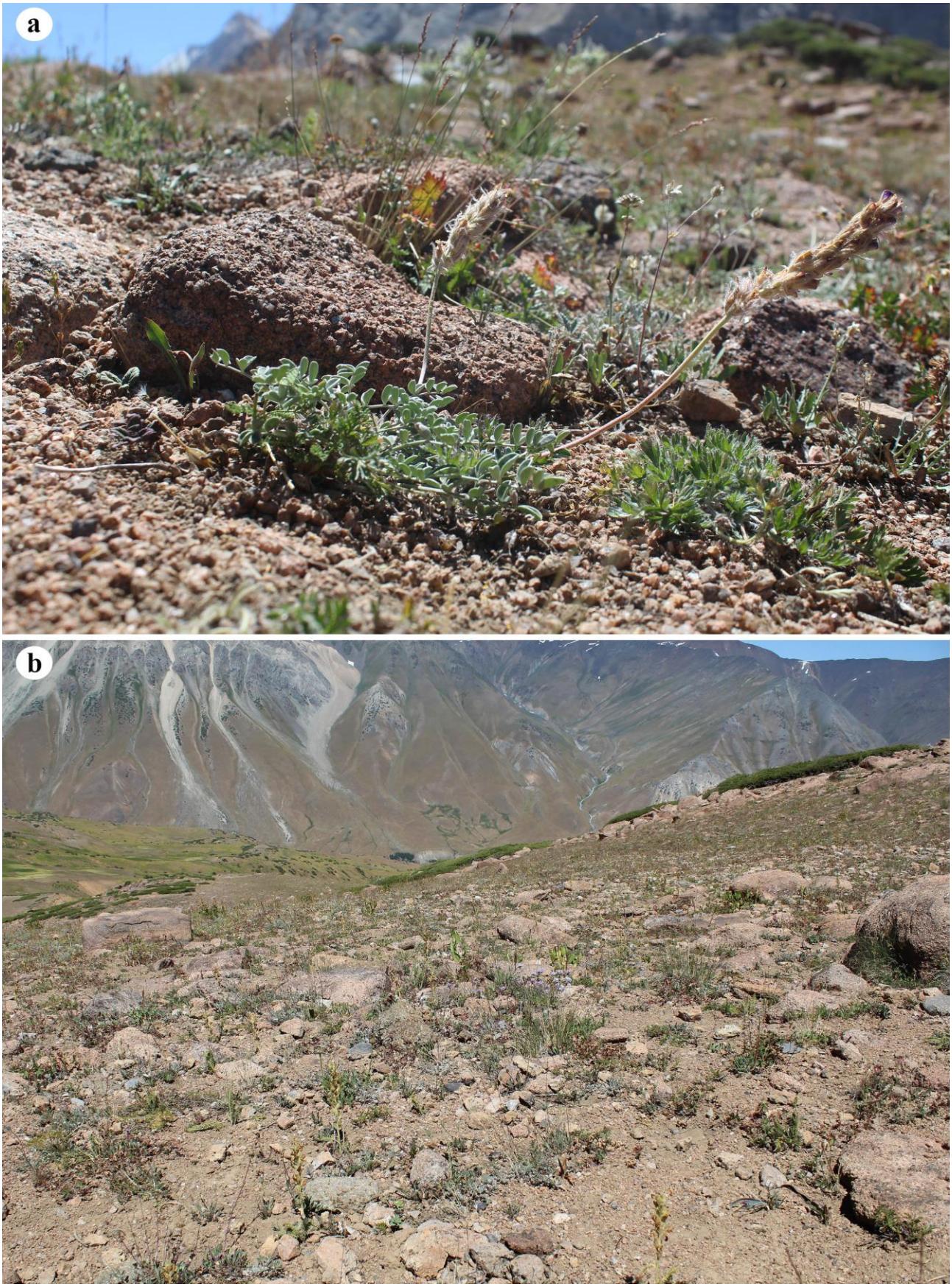


**Fig. 11.** *Hedysarum talassicum* —a–b: habit of plant.

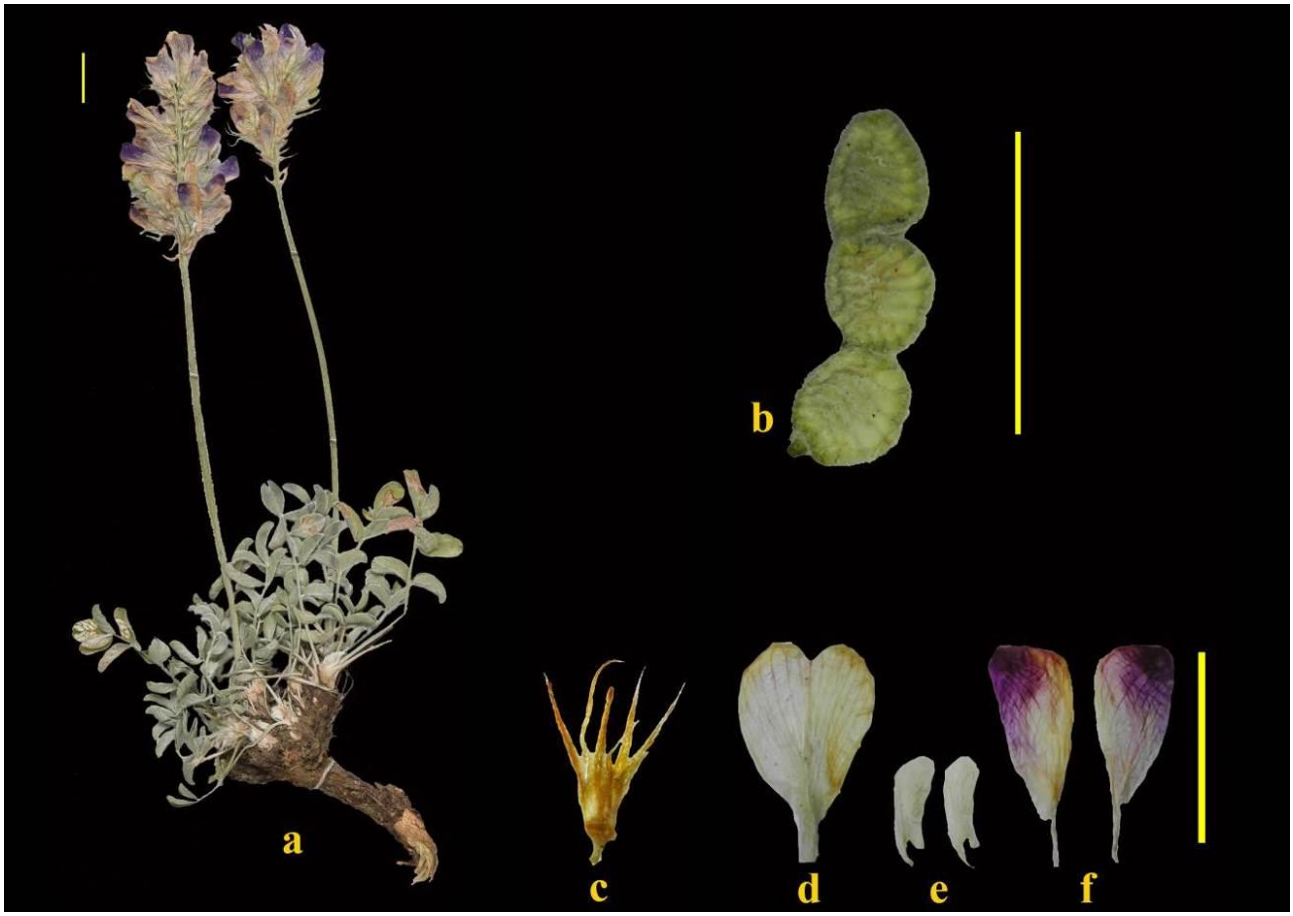


**Fig. 12.** Living plant of *Hedysarum talassicum*. a, entire plant; b, pod; c, calyx; d, standard; e, wings; f, keel. Scale bar 1 cm.

**Distribution:**—Kyrgyzstan and Uzbekistan. Distribution in Uzbekistan: Fig. 13.

**Specimens examined:**—I-1 **Western Tian-Shan Region**. I-1-a **Ugam-Pskem District**: Pskem ridge (Mid point of Oygaing River, between Koksu and Tundyk gorges, rocky slope, 16.08.1954, *Pavlov 216* (MW); The upper reaches of the gorge Barkraksay, 21.08.1958, *Pavlov 88* (MW); Oigaing River valley, the upper reaches of the gorge Barkraksay, 11.08.2019, *Tojibaev, Juramurodov №1108116, 1108117, 1108118, 1108149* (TASH)).

**5. *Hedysarum gypsaceum*** Korotkova in Bot. Mater. Gerb. Inst. Bot. Akad. Nauk Uzbeksk. S.S.R. 14: 13 (1954).

**Type**:—[Uzbekistan]. Uzbek SSR, Chartak District, Naritansky State Farm, on slopes with gypsum clay at an altitude of 800–900 m, in association with Tau-sagys, 06.06.1951, fl., *M. M. Nabiev* (holotype TASH barcode 001929!).

**Description:**—Herbs, acaulescent, 10–25 cm tall. Leaves 5–10 cm long, with 1 or 2 pairs of leaflets; leaflets nearly round, broadly elliptic or broadly ovate, 2.5–3.5 × 1–2 cm. Peduncles very densely hairy, almost equal to upper petiole, 3–10 cm long. Raceme thick, oblong, 4–10 cm long. Bracts lanceolate, 7–10 mm long. Bracteoles linear, silky, almost as long as or 3 times longer than calyx tube, 3–5 mm long. Pedicel 2 mm long. Calyx campanulate, 14–18 mm long, teeth almost equal, up to 4 times longer than tube; corolla pale purple; standard broadly elliptic, 16–18 × 11–15 mm; wings 14–16.5 × 4.5–6 mm; keel almost triangular, 17–18 × 9–9.5 mm. Pods 2- to 4-jointed; joints nearly round, 5–7 × 4.5–5 mm, with dense short bristles (Figs 14–15).

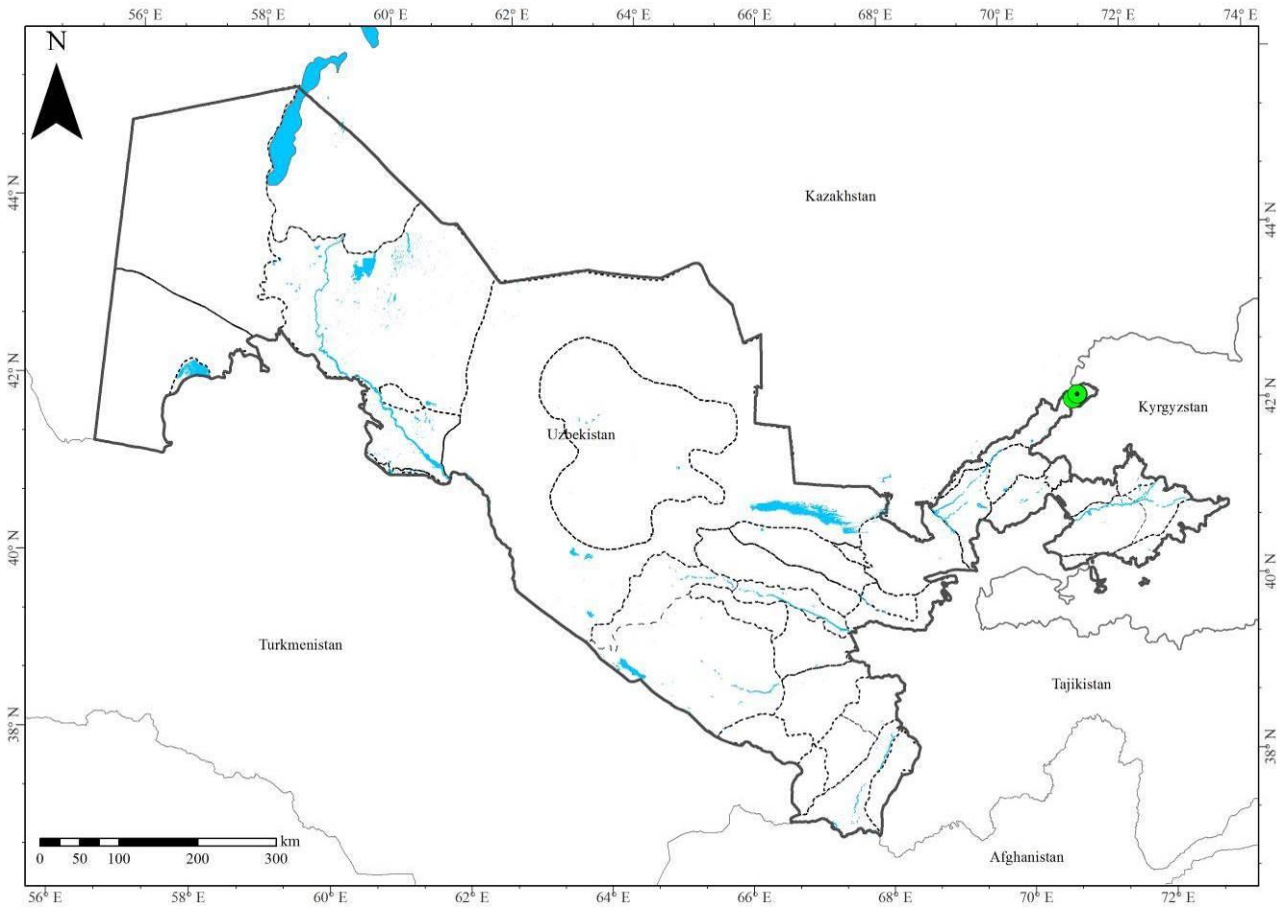


**Fig. 13.** Distribution of *Hedysarum talassicum.*

**Flowering time:**—May-June.
**Fruiting time:**—June-July.
**Habitat:**—On gypsum slopes at 700–1000 m a.s.l. (Fig. 14).
**Distribution:**—Central Asia: Kyrgyzstan, Uzbekistan. Distribution in Uzbekistan: Fig. 16.
**Specimens examined:**—I-1 **Western Tian-Shan Region**. I-1-e: I-1-e **Chorkesar District**: Chatkal ridge (tract Djidasay, 16.05.1950, *Arifkhanova 219*; Fergana valley, tract Djidasay, 22.05.1952, *Arifkhanova, Gringof 842, 899*; Fergana valley, tract Djidasay, 23.05.1952, *Arifkhanova 940*). I-2 **Fergana Region**. I-2-a **Southern Chatkal District**: Chatkal ridge (Arbagish village, 23.05.2015, *Tojibaev, Nuralieva, Karimov 2305201521*; Fergana valley, Chartak District, Arbagish village, 1000 m, 23.05.2019, *Juramurodov, Gulomov 045-1, 045-2*; Namangan Province, Chartak District, Arbagich hill, 05.06.2020, *Dekhkonov, Batashov, Khoshimov, Gulomov 29*; Fergana valley, Chartak District, Arbagish village, 990 m, 29.05.2021, *Juramurodov, Gulomov 2905202101, 2905202104*). All specimens are at TASH.

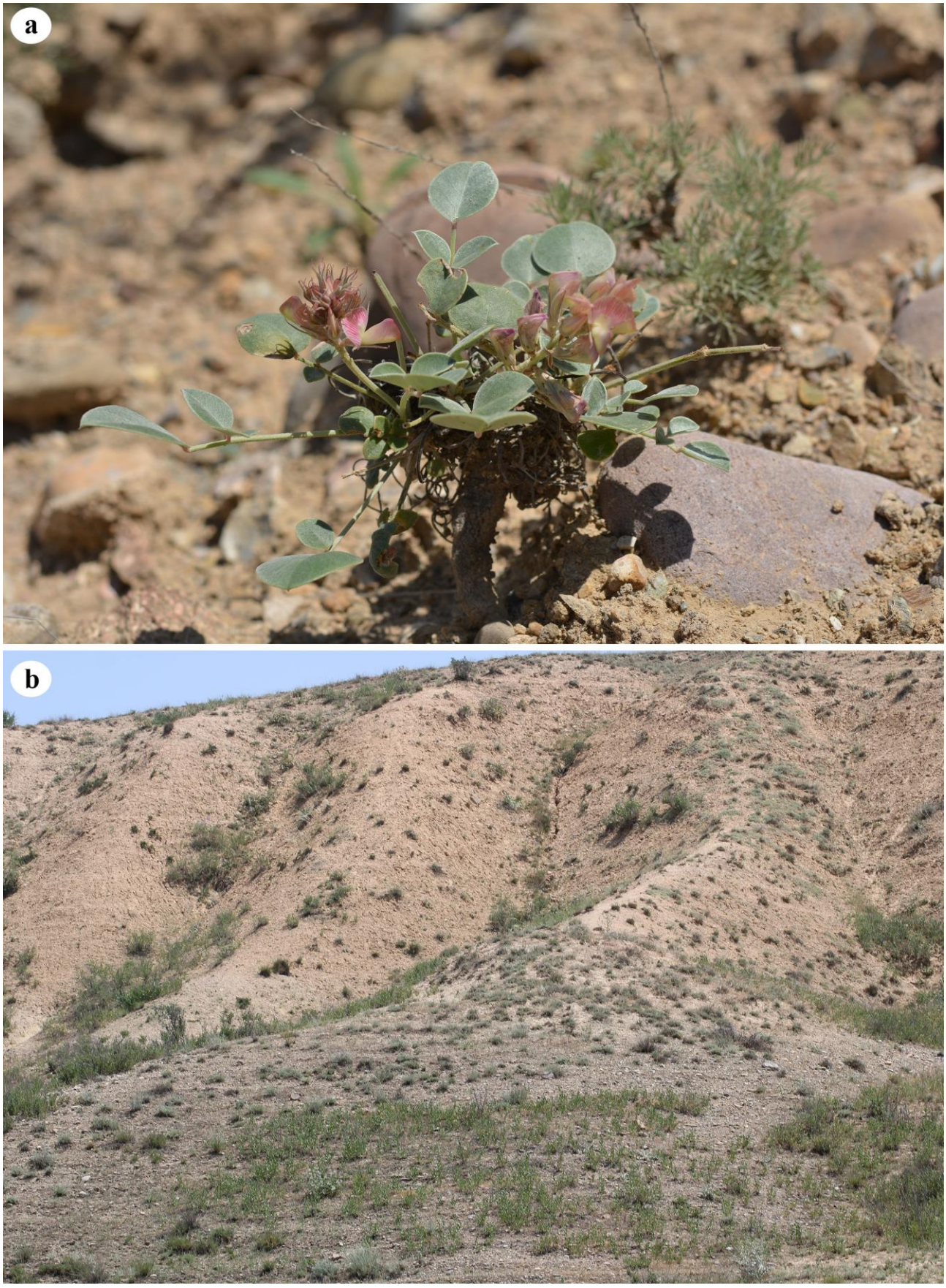


**Fig. 14.** *Hedysarum gypsaceum* —a–b: habit of plant.

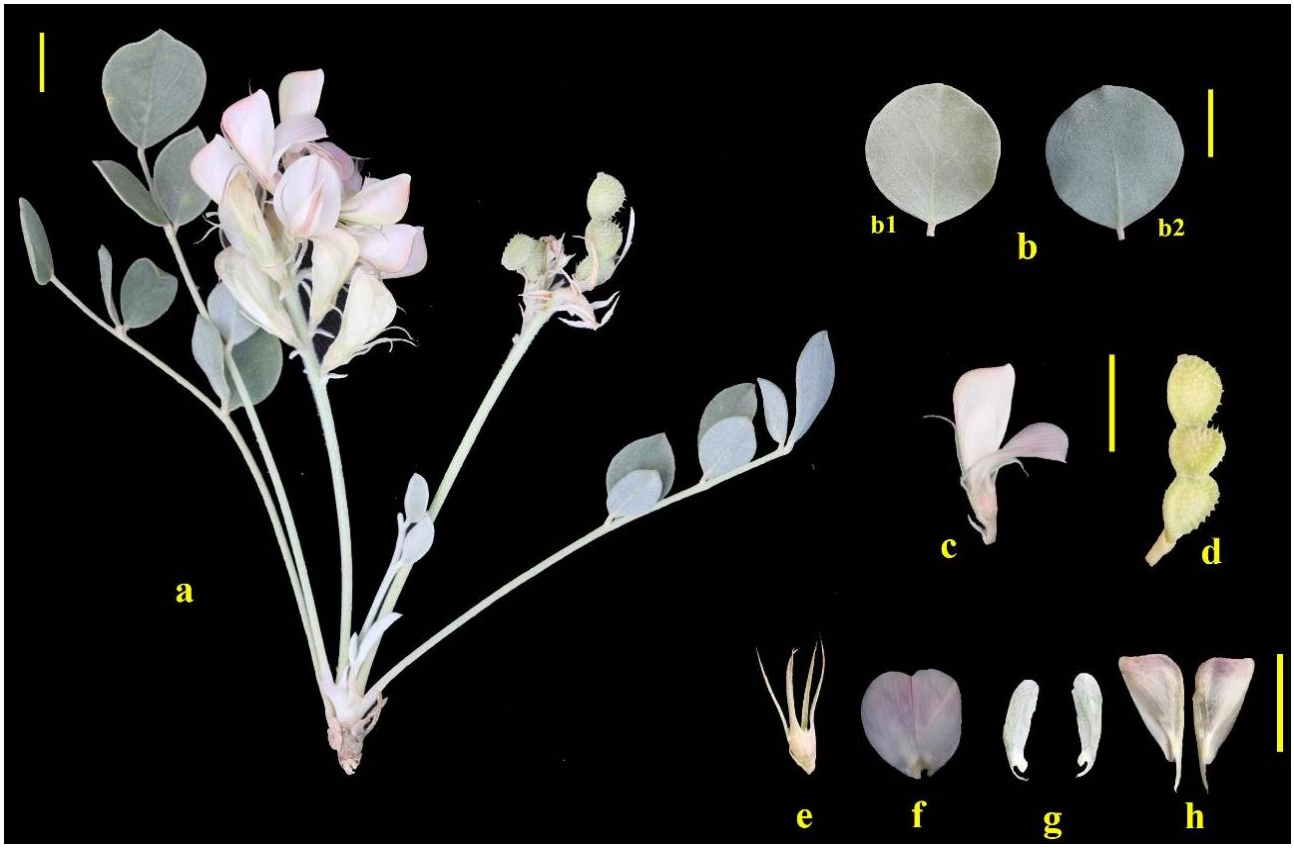


**Fig. 15.** Living plant of *Hedysarum gypsaceum*. a, entire plant; b, leaflet (b1, upper part and b2, lower part); c, flower; d, pod; e, calyx; f, standard; g, wings; h, keel. Scale bar 1 cm.

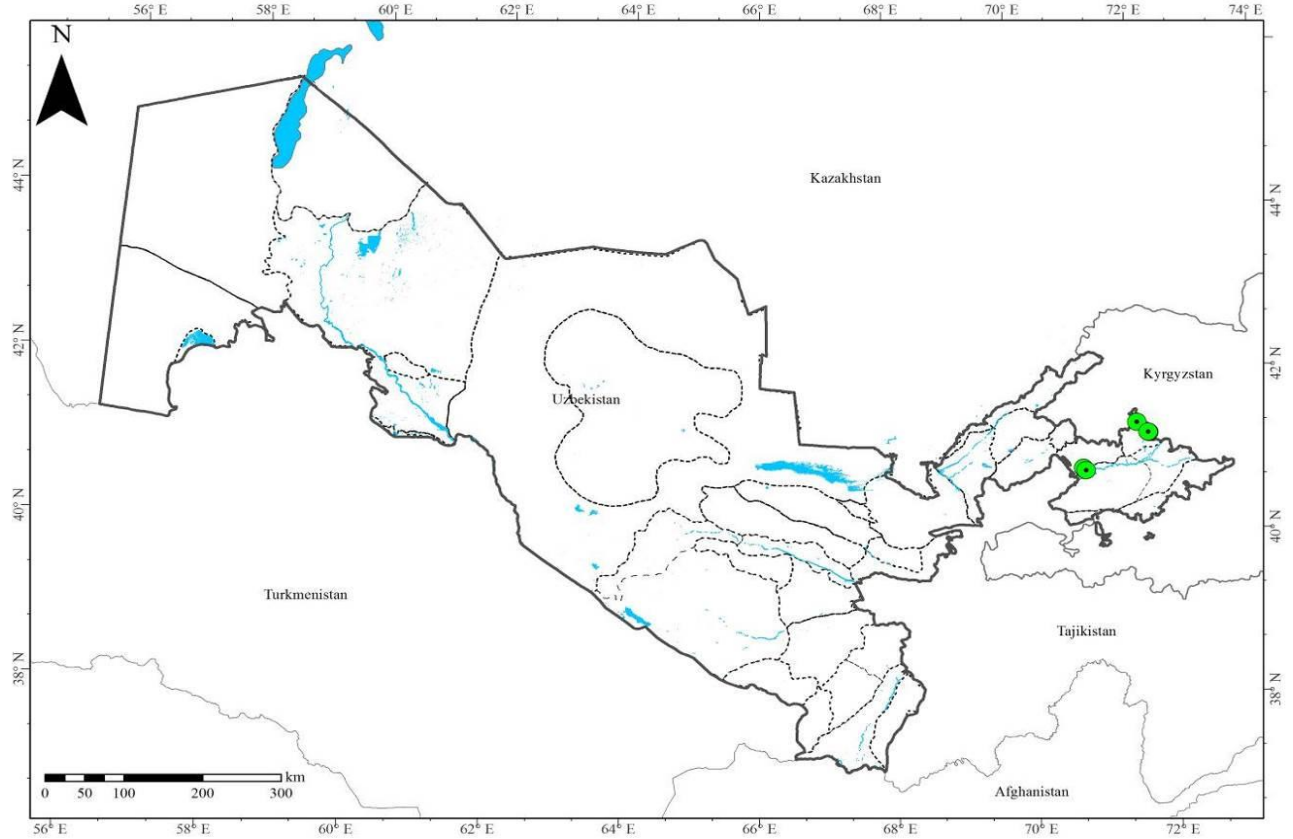


**Fig. 16.** Distribution of *Hedysarum gypsaceum*.

**6. *Hedysarum plumosum*** Boiss. & Hausskn., Fl. Orient. 2: 515 (1872).
**Type:**—[Iran]. Kellal, Sistr. Bachtiarioum, 09.1868, *C. Haussknecht* (holotype P, barcode 02765690).
= *H. fedtschenkoanum* Regel in Izv. Imp. Obshch. Lyubit. Estestv. Moskovsk. Univ. 34 (2): 23 (1882).
**Type:**—Alai, Karatau and Zeravschan Ranges (syntypes LE).
= *Hedysarum dshambulicum* Pavlov in Vestn. Akad. Nauk Kazakhsk. S.S.R. 1949 (1): 33 (1949).
**Type:**—Kazakhstan. Karatau Mts., Ulkun-Burun Mt., 27.05.1948, *N.V. Pavlov 79* (holotype AA).
= *Hedysarum kuhitangi* Boriss. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 10: 82 (1947).
**Type:**—Turkmenistan. Jugum Kuhitang, prope p. Chodsha-fil-ata, 27.06.1931, *S.A. Nevski* (holotype LE).
= *Hedysarum parvum* Sultanova in Mater. Fl. Kirg.: 44 (1973).
**Type:**—Kyrgyzstan. North-West side of Chatkal Range, Tegerek-saz, 14.08.1967, *N. Gorbunova* (holotype FRU; isotype TASH barcode 001978!).
**Description:**—Herbs, 5–15 cm tall, rootstock elongate, buried among stones or in rock crevices, branching distally and bearing many short shoots, with decayed stipules and petioles. Stems abbreviated. Stipules lanceolate, more or less connate, long acuminate, broad at base, white hairy. Leaves tufted, 1–3 cm long; leaflets 1 or 2 pairs, sometimes only terminal leaflet developed, oblong-ovate or elliptic, abaxially densely silvery hairy, adaxially less so, surface punctulate, considerably variable in size, terminal leaflet 40 × 20 mm, lateral leaflets 10 to 20 mm long. Peduncle (with raceme) slightly longer than leaves, with dense appressed or spreading hairs, 3–4 cm long. Racemes dense, many-flowered, 3–4 cm long. Bracts membranous, lanceolate, transparent along margins, abaxially hairy, 7 × 4 mm. Bracteoles linear, silky, almost as long or 2 times longer than calyx tube, 6–8 mm long. Pedicel 1–1.2 mm long. Calyx short campanulate, teeth unequal in length, filiform, 3–5 times longer than tube, nearly as long as corolla, long hairy. Corolla bright violet; standard broadly ovate, apex emarginate, 10–20 × 8–12 mm; wings 5–8 × 2–3 mm, apex rounded, obliquely angled, ovate; keel nearly triangular, nearly straight along upper edge, slightly curved along lower edge, apex blunt, 12–20 × 5–6 mm. Pods 1- to 3-jointed, joints 4–6 × 4–5 mm, short haired, without setae and bristles, with fine transverse veins. Seeds reniform-ovate, 2.5 × 3 mm, smooth, dark brown (Fig. 17). **Flowering time:**—June-July.
**Fruiting time:**—July-August.
**Habitat:**—On stony and gravelly slopes, screes, outcrops of variegated rocks and limestones, along sandy-pebbly riverbeds from lower to upper belts of mountains (Fig. 18).
**Distribution:**—Kazakhstan, Kyrgyzstan, Turkmenistan, Tajikistan, Uzbekistan, Afghanistan and Iran. Distribution in Uzbekistan: Fig. 19.
**Specimens examined:**—I-1 **Western Tian-Shan Region**. I-1-a **Ugam-Pskem District**: Ugam ridge (Khumsan, Naudale Mountains, 14.08.1920, *Popov 1248*; Ugam River valley, soft western slope, 15.06.1928, *Kultiasov 648*; in the upper reaches of the Navalisay gorge, on dry rocky slopes, 3000 m a.s.l., 20.07.1953, *Pavlov 416* (MW); upper gorge Kurdenytsay, rocky slope, 3050 m a.s.l., 30.08.1958, *Pavlov 187* (MW)), Pskem ridge (Valley of the Pskem River, right bank upper belt of Mountains, 26.06.1975, *Khalmukhamedova 135, 174, 182, 186, 188, 196, 198*; slopes of Aksarsay peak, 27.07.1949, *Pavlov 237* (MW)); I-1-b **Western Chatkal District**: Chatkal ridge (Big Chimgan, 25.07.1919, *Ambrak*; big Chimgan, 22.07.1920, *Vasiliev*; big Chimgan, 01.08.1922, *Simonov*; big Chimgan, 14.08.1922, *Batuev*; near Chimgan Botanical Station, 01.08.1924, *Yakimov*; tract Chimgan, stony, Podvinskaya scree in the subalpine region of Greater Chimgan, 22.08.1924, *Gomolitsky*; near the Chimgan Botanical station, 24.07.1925, *Gomolitsky 106*; near the Chimgan Botanical station, Big Chimgan, 12.08.1926, *Baranov, Raikova*; Big Chimgan at 3000 m above sea level, 18.07.1934, *Alekseeva 515*; the tract

Myndzhilke, Nurekata River, 21.07.1936, *Korotkova* and *Titov 1622*; River Kzyldarya, on the west south from the village Kzyltam, 10.07.1941, *Koshurnikova 302*; Chimgan, Pioneer camp, 1947, *Titov*; Palatkhan, 29.07.1959, *Petrov*; river valley Chatkal, Akbulak River basin, Aktakhtai pass, 21.07.1965, *Butkov, Mogilevsky 21*; river valley Chatkal, Akbulak River basin, Aktakhtai pass, 14.08.1965, *Butkov, Mogilevsky 533*; Polatkhan, 06.08.1970, *Blazhevich*); I-1-d **Kurama District**: Kurama ridge (basin of the Angren River, 2 km from the Kamchik pass, 02.08.1954, *Nabiev, Li 505*). **I-5 Kuhistan Region.** I-5-a **Northern Turkestan District**: Turkestan ridge (Shaibek pass, 26.06.1920, *Balabaev 1015*; Auchi village, 08.07.1927, *Drobov 136*; Zaaminsu River basin, Kizylmazar tract, 21.06.1935, *Zakrzhevsky 515*; Kulsay, near Kizylmazar, 02.07.1938, *Korotkov 556*; Guralash reserve, middle part of the Kulsay valley, 12.07.1940, *Pyataev 60*; Tuyatashsay, 15.06.1944, *Nazarenko*; Guralash reserve, in the lower part of Kulsay, 15.06.1947, *Nazarenko;* Kulsay, in the lower part of the Guralash reserve, 21.06.1947, *Nazarenko 273*; Jizzakh forestry, Kulsay valley, 25.07.1958, *Gorzova*; Jizzakh forestry, Kulsay valley, 05.08.1958, *Gorzova*; reserve Guralash, 1959, *Pyataeva, Yuldashev 64*; Zaamin reserve, Guralash pass, 22.08.1977, *Levichev*; Zaamin National Park, on red outcrops, near Kizylmazar, 22.06.2019, *Juramurodov 004a, 004b*; Kulsay gorge, gravel slope, 08.06.2020, *Ortikov, Pulatov, Turdiev, Juramurodov, Makhmudjanov 8062020483, 8062020484, 8062020485*; Kizylmazar, Kulsay, 13.06.1914, *Mikhelson* (LE); Guralash Nature Reserve southeast slope, northwest of Kulsay, 12.07.1940, *Pyataeva 60* (LE); reserve Guralash watershed between Kulsay and Tuyatashsay, 15.07.1940, *Kulttiasov* (MW)). I-6 **Western Hissar Region**. I-6-a **Kashkadarya District**: Hissar ridge (village Wardan, 04.07.1927, *Kultiasov, Granitov 949, 955*; Khantakhta tract, 09.07.1931, *Granitov,*

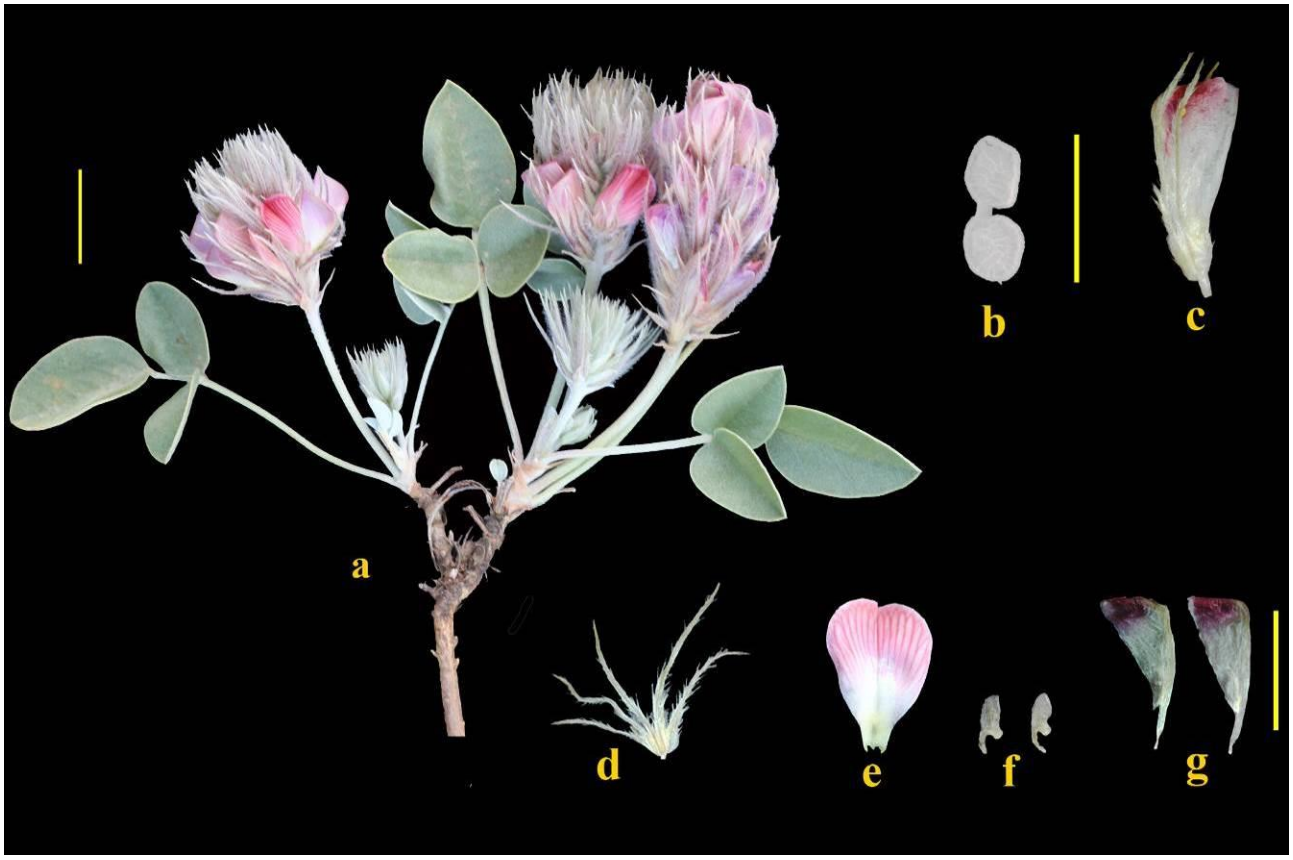


**Fig. 17.** Living plant of *Hedysarum plumosum*. a, entire plant; b, pod; c, flower; d, calyx; e, standard; f, wings; g, keel. Scale bar 1 cm.


**Fig. 18.** *Hedysarum plumosum* —a–c, e: habit of plant, d, raceme. (Photo ‘c’ was taken by N. Beshko).

*Demurina 1355*; Kattauru River, gypsum outcrops in the upper reaches of Kizilsay, 09.06.1935, *Lepeshkin 11*; Beshnau Mountains, 25.06.1937, *Kudryashev 793*; between Cholmazar and the Tashkurgan villages, 23.07.1948, *Korotkova*; valley of the Guzardarya River, 12 km from the village of Igrisu, 06.07.1955, *Pyataeva 1638*; village Kul, 10.07.1959, *Khalikov 25*; basin of the Kashkadarya River, 2 km south of the Kul village, 10.07.1959, *Li* and *Zakirov 1245*; Vuari village, 11.07.1959, *Li* and *Zakirov 1251*; upper reaches of the river Tankhazdarya, near to Shurasan village, Beshnau Mountains, Kainarsay, 29.06.1988, *Pimenov, Vasileva, Lavrova, Kuznetsova 178* (MW)); I-6-c **Baysun District**: Hissar ridge (Mountains of Khodjagurgurat, upper reaches of Chakmaksay, 16.08.1934, *Demurina 745* (TASH); vicinity of Baysun, Gaza lane, 22.06.1941, *Popova 748*; mountains Ketmenchapty, near the pass Gaza, rocky slope, 2800 m, 20.07.1935, *Gordienko 95* (MW)). I-7 **Hissar-Darvaz Region**. I-7-a **Sangardak-Tupalang District**: Hissar ridge (upper reaches of the Sangardak River, gypsum outcrops along Kizilsay, 09.09.1935, *Lepeshkin 7*). Specimens in TASH unless otherwise specified.

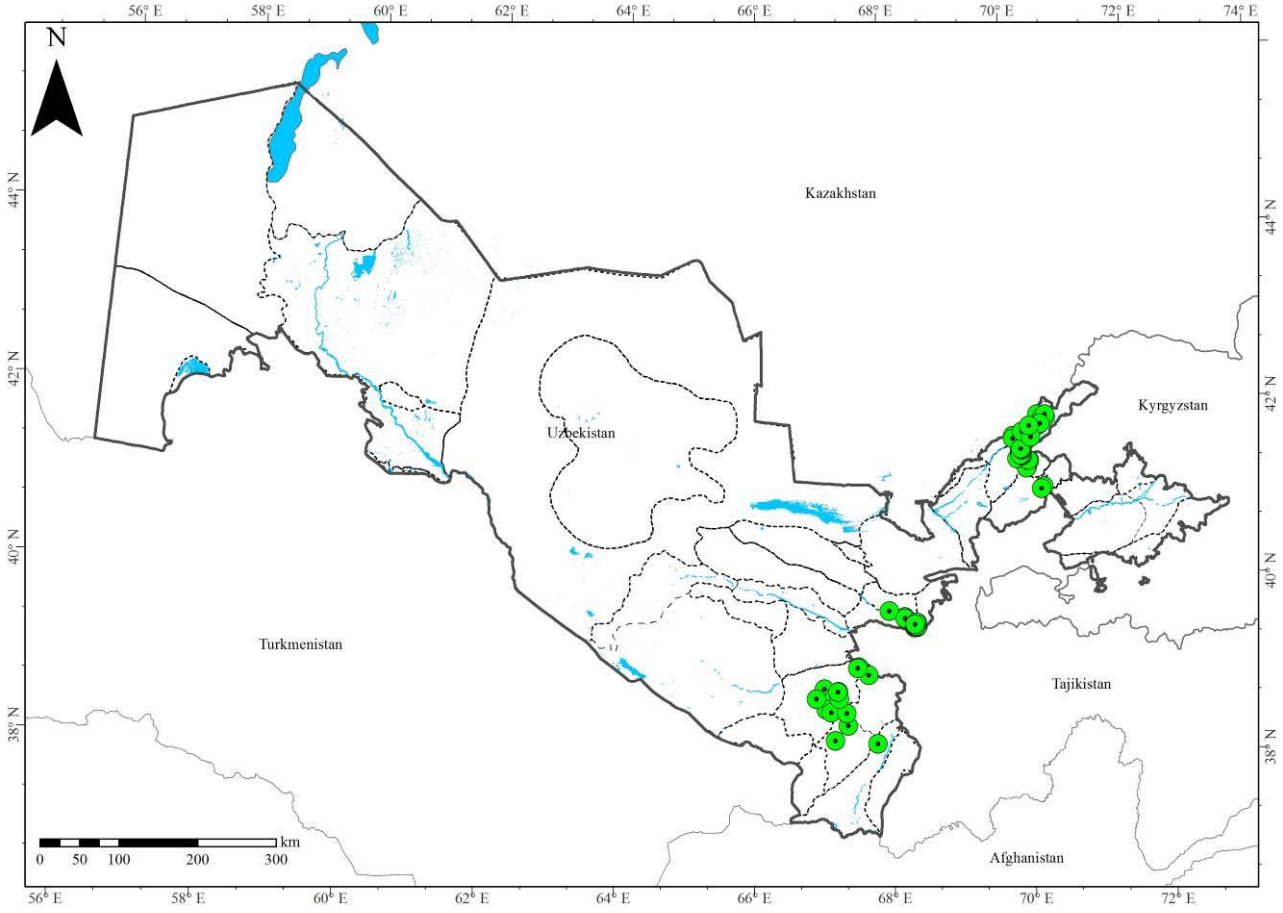


**Fig. 19.** Distribution of *Hedysarum plumosum*.

**7. *Hedysarum popovii*** Korotkova in Bot. Mater. Gerb. Inst. Bot. Zool. Akad. Nauk Uzbeksk. S.S.R. 9: 13 (1947).

**Type:**—[Uzbekistan]. Right bank of the Angren River, lower reaches of the Arasan River, screes of clayey sandstones and conglomerates, 14.08.1924, fl., *E. P. Korovin 662* (holotype TASH barcode 001979!; Fig. 20).

**Description:**—Herbs, 10–18 cm tall. Stems 2–5 cm long. Lower stipules brown, upper half fused, white, membranous, apex long acuminate, 10–12 mm long, hairy outside.


**Fig. 20.** Holotype specimen of *Hedysarum popovii*.

Leaves appearing silvery, petiolate, 8–14.5 cm long; leaflets 1, 2 or 3 pairs, identical or terminal leaflet slightly larger, ovate, adaxially rarely silky, abaxially densely appressed silky, 16–25 × 5–10 mm. Peduncle (with raceme) slightly longer than leaves, spreading hairy, 6.5–10 cm long. Racemes dense, many-flowered, 3–4 cm long. Bracts membranous, lanceolate, white, hairy outside, apiculate, ca. 10 × 2–2.5 mm. Bracteoles 5–8 mm long. Pedicel pubescent, 2–3 mm long. Calyx campanulate, densely hairy; teeth almost equal, longer than corolla, 12–20 mm long, tube 3 mm long. Standard 12–15 × 9–17 mm, obovate, nearly rounded; wings 5–7.5 × 2.5–3 mm, claw curved, apex rounded, ovoid or ovate; keel 13–16 mm long, nearly quadrangular. Pods 1–3-jointed, joints 5–6 × 4.5–5 mm, short hairy, with thin transverse veins, without setae and bristles, margins with short barely visible tubercles. Seeds reniform-ovate, 3 × 3 mm, smooth, dark brown.

**Flowering time:**—June-July.
**Fruiting time:**—July-August.
**Habitat:**—On screes of sandstones and conglomerates in lower mountain belt.
**Distribution:**—Uzbekistan (Fig. 21).
**Specimens examined:**—I-1 **Western Tian-Shan Region**. I-1-d **Kurama District**: Kurama ridge (right bank of the Angren River, lower reaches of the Arashan River, 14.08.1924, *Korovin 661*, *662*; on the right bank of the Arashan River, 14.08.1924, *Sovetkina 149*). All specimens are at TASH.
**Notes:**—Only two specimens of *Hedysarum popovii*, collected by Korovin in 1924, are known. They are from the type locality on the Kurama ridge between Tashkent and Namangan Provinces, Uzbekistan. Unfortunately, our searches in the area around the Arashan River from 2018 to 2021 to collect new specimens of this species were unsuccessful.

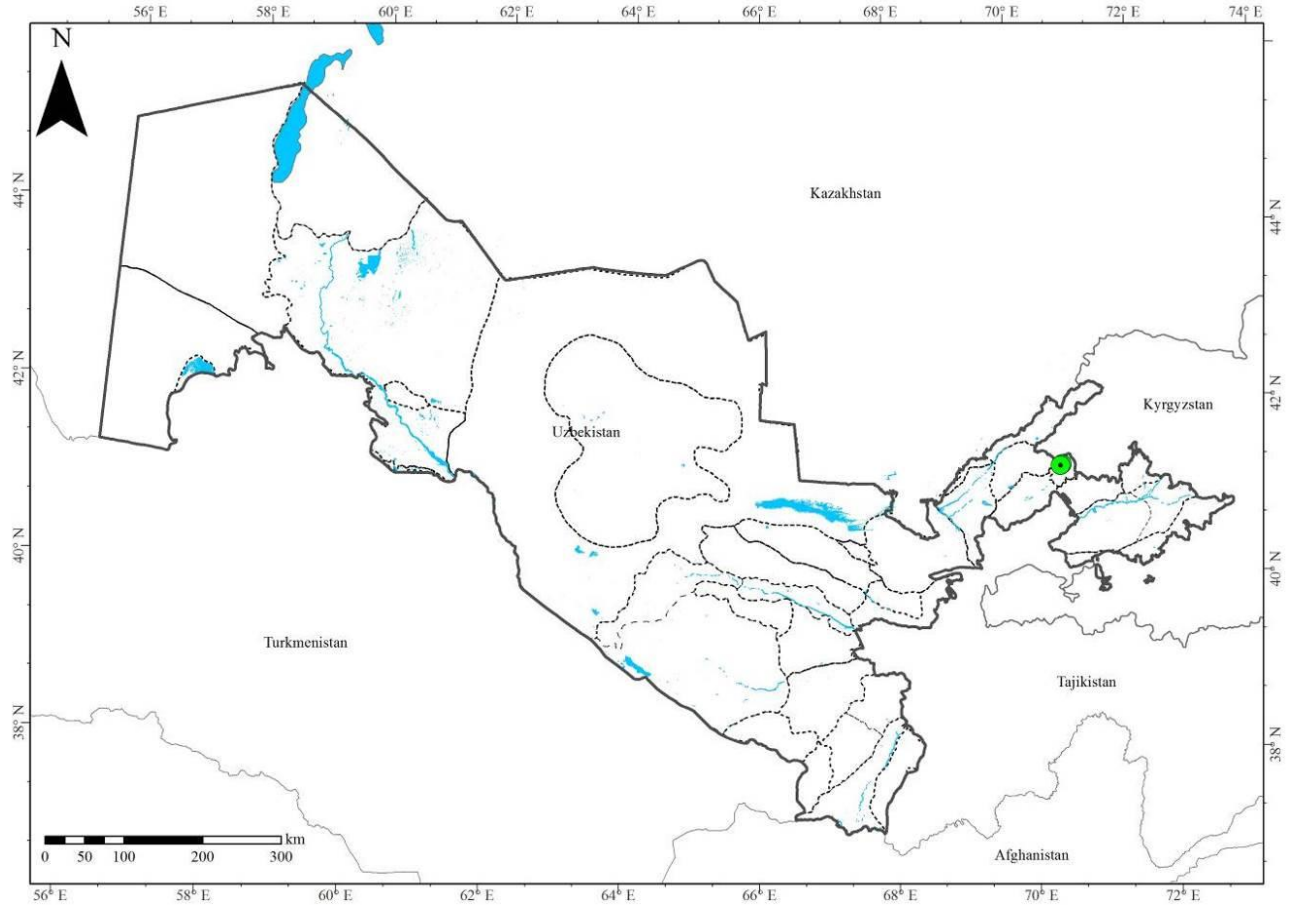


**Fig. 21.** Distribution of *Hedysarum popovii*.

**8. *Hedysarum jaxarticum*** Popov in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 7: 13 (1937).

**Type:**—[Kazakhstan]. 60 km NE from Tashkent city, between Uzun-bulak and Sok-sok wells, outcrops of variegated rocks, 13.05.1926, *Popov* (lectotype TASH barcode 001954!, designated by Juramurodov et al. (2022: 16); Fig. 22).

**Description:**—Herbs, 12–15 cm tall, rootstock thin, bearing bundles of leaves; stems 2 or 3 short or obsolete. Stems appressed white hairy, 2–3(4) cm long. Stipules brown, lanceolate, base connate, apex free. Petioles elongate. densely white pubescent, 10–15 cm long; leaflets 3–5 pairs, broadly ovate or obovate, apex somewhat attenuate or obtuse, 10–25 × 6–12 mm, yellowish green, adaxially sparingly pubescent or glabrous, abaxially densely silvery hairy. Peduncle (with raceme) longer or shorter than leaves. Racemes dense. Bracts grayish brown, lower one lanceolate, upper ones linear-subulate, long hairy, shorter than to longer than calyx (before flowering), 7–12 mm long. Bracteoles 3–6 mm long. Pedicel ca. 2 mm long. Calyx short campanulate, long sericeous hairy, teeth linear-subulate, three to four times as long as tube, nearly as long as corolla (before anthesis) or shorter (post anthesis). Corolla light pink mixed with yellow; standard oblong-ovate, 12–13(–18) × 8–13 mm; wings 5–7(–10) × 2–4 mm; lower margin of keel subrectangular, (12–)15–18 × 7–9 mm long. Pods 1- to 3-jointed, joints 5–6 × 5 mm, appressed white hairy, transversely ribbed, with long incurved prickles. Seeds reniform, brown.

**Flowering time:**—May.

**Fruiting time:**—June.

**Habitat:**—On clay hills, outcrops of red clays and sandstones on plains and in foothills.

**Distribution:**—Kazakhstan and Uzbekistan. Distribution in Uzbekistan: Fig. 23.

**Specimens examined:**—I-1 **Western Tian-Shan Region**. I-1-b **Western Chatkal District**: Chatkal ridge (Tashkent Alatau, Parkent District, Karamansay, 16.06.1953, *Maylun, Nabiev, Zuckerwanik 782* (TASH)).

**9. *Hedysarum angrenicum*** Korotkova in Bot. Mater. Gerb. Inst. Bot. Zool. Akad. Nauk Uzbeksk. S.S.R. 9: 6 (1947).

**Type:**—[Uzbekistan]. Angren, Itelgesay, on the northern slope of the stony mountains, abundant, 27.06.1931, defl., *A. Matskevich 203* (holotype TASH barcode 001949!).

**Description:**—Herbs, ca. 20 cm tall. Stem abbreviated. Leaves 10–16 cm long; leaflets 3 or 4 pairs, lanceolate, (7–)10–22 × 4–6 mm, adaxially slightly hairy or nearly glabrous, often punctate, abaxially densely appressed hairy, silvery-silky, lateral veins weakly expressed. Peduncle 10–18 cm long, appressed hairy, gray, slightly ribbed, straight, strong. Racemes dense, 2–7 cm long. Bracts hairy outside, gray, lanceolate, acute, 4–6 mm long. Bracteoles ca. 8 mm long. Pedicel ca. 1–2 mm long. Calyx long hairy; teeth linear-subulate nearly equal, almost as long as or very slightly longer than corolla, long hairy, 4–5 times longer than tube. Standard 13–14 × 9–11 mm, broadly obovate or ovate oblong, apex notched; wings 10–12 × 3–3.5 mm, oblong, apex rounded or slightly narrowed; keel 13–14 × 6 mm, nearly triangular. Pods 1- to 3-jointed; joints 5 × 4.5 mm, short hairy, without setae and bristles, with weakly expressed transverse veins. Seeds unknown.

**Flowering time:**—June-July.

**Fruiting time:**—July-August.

**Habitat:**—North-facing stony slopes in middle mountainous zone.

**Distribution:**—Uzbekistan (Fig. 24).

**Specimens examined:**—I-1 **Western Tian-Shan Region**. I-1-d **Kurama District**: Chatkal ridge (near the Aksu gorge, 11.07.1916, *Balabaev* (TASH); Angren, Itelgesay, on the northern slope of the stony mountains, abundantly covering the slopes, 27.06.1931, defl., *Matskevich 203* (holotype, TASH; Fig. 25)).

**Notes:**—*Hedysarum angrenicum* has been classified as a ‘Disappearing species’ in the Red Data Book of the Republic of Uzbekistan (Khassanov 2019). Apart from the two specimens cited above, we also observed one from Kyrgyzstan: ‘Chatkal Ridge, watershed between the rivers Karagayli and Karasu, alpine

zone, 29.07.1927, *Uspenskaya 33* (sub nom. *Hedysarum pumilum* (Ledeb.) B.Fedtsch. / *Hedysarum angrenicum* Korotkova. I 1977, Determ. S. Kovalevskaya)' (TASH). We are aware of only the three specimens of this species. No specimens of this species have been collected in the past 90 years.


**Fig. 22.** Lectotype specimen of *Hedysarum jaxarticum.*

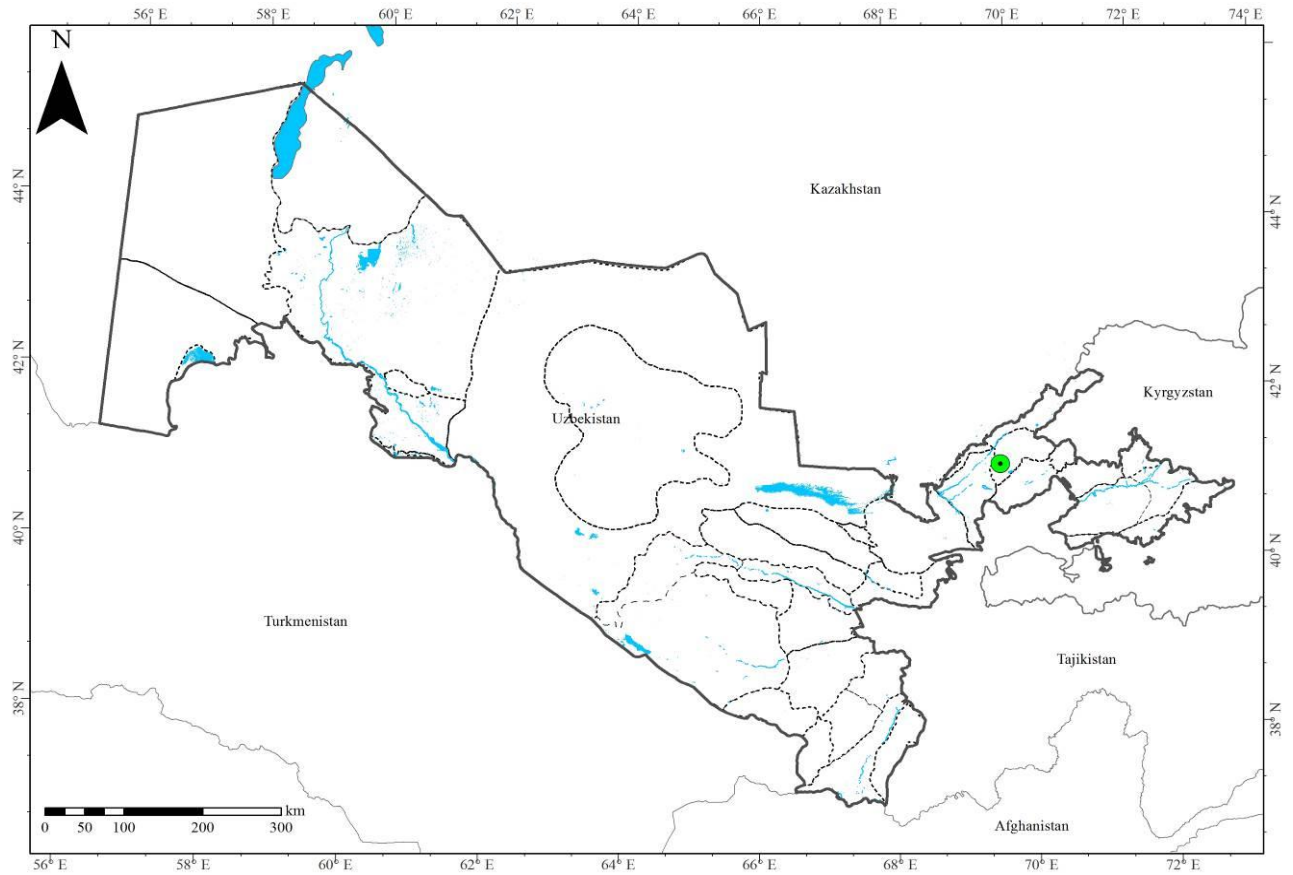


**Fig. 23.** Distribution of *Hedysarum jaxarticum*.

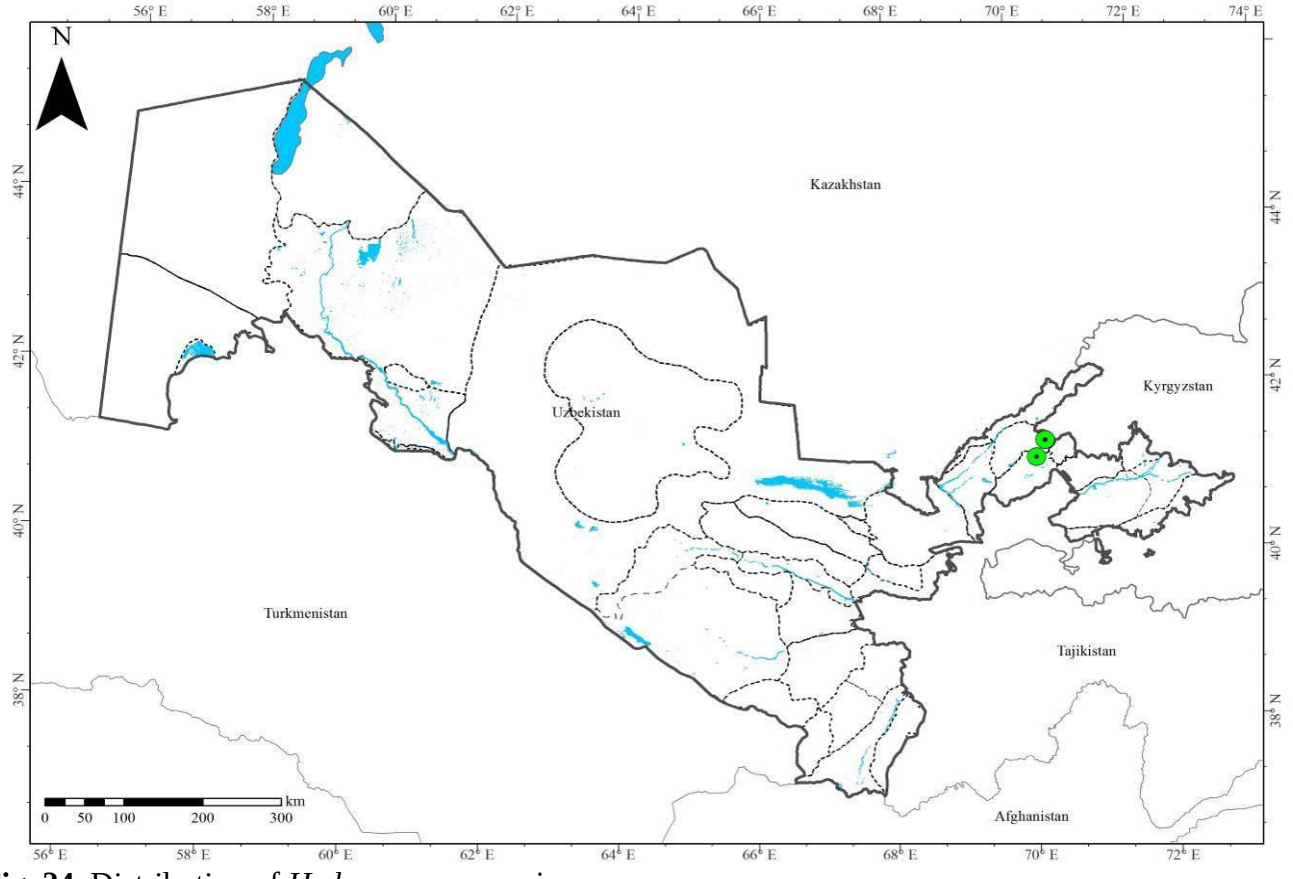


**Fig. 24.** Distribution of *Hedysarum angrenicum*.

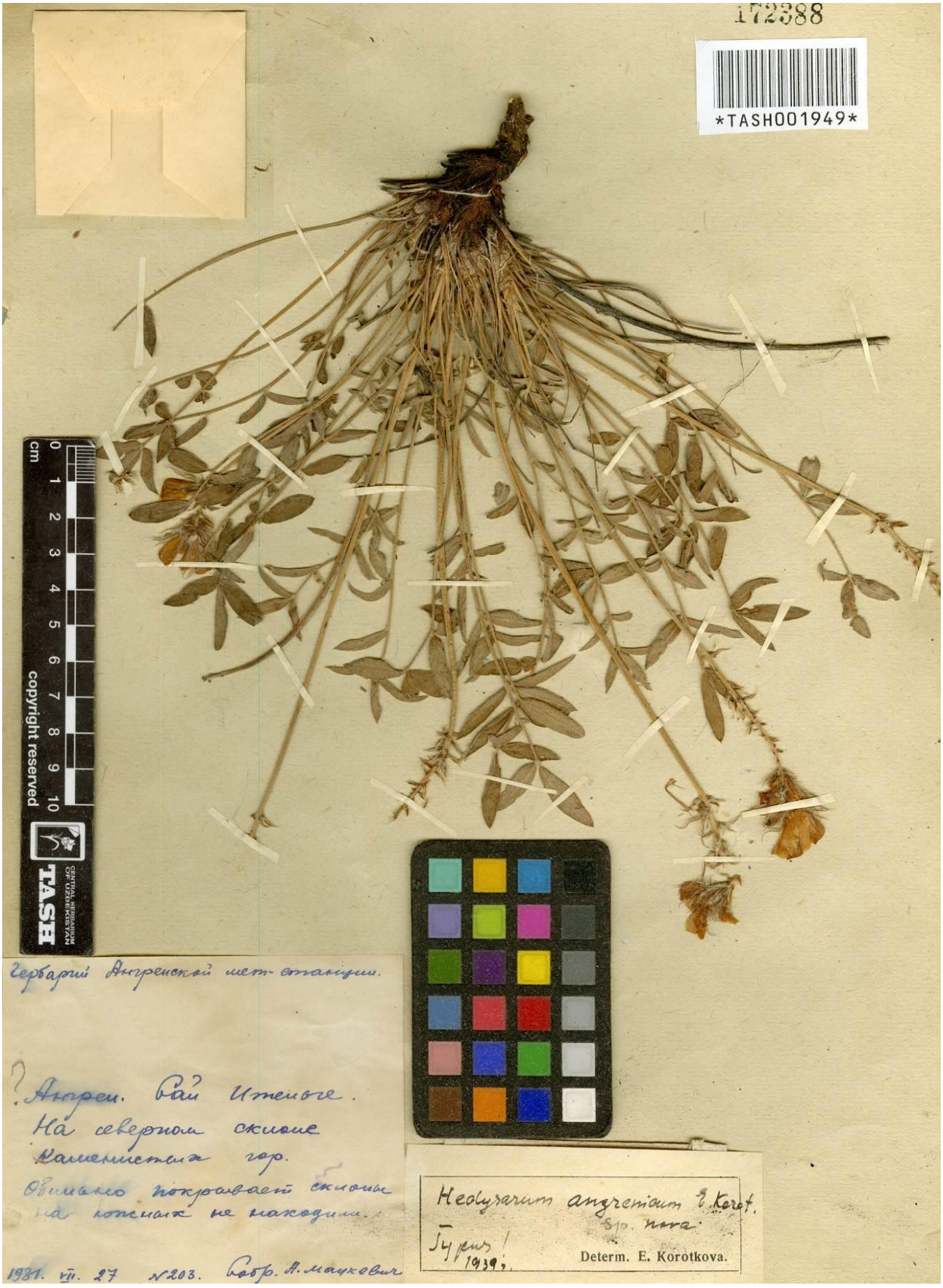


**Fig. 25**. Holotype specimen of *Hedysarum angrenicum.*

**10.** ***Hedysarum magnificum*** Kudr. in Bot. Mater. Gerb. Bot. Inst. Uzbekistansk. Fil. Akad. Nauk S.S.S.R. 1: 3 (1940).

**Type:**—[Uzbekistan]. Northern side of Hissar Range, Kashka-Darya River basin, middle part of Tankhasa River, between Shurdzhi and Kiyaki, red clay outcrops, 26.06.1937, fl., fr., *S.N. Kudryashov 843* (lectotype TASH barcode 001965!, designated by Juramurodov et al. (2022: 20)).

**Description:**—Herbs, 40–60 cm tall. Stems few, erect, branching, diverging from caudex, glabrous or sparsely short hairy, lower internodes short. Leaves more or less thick, glabrous, 10–19 cm long; leaflets 2 or 3 pairs, ovate or oblong-ovate, adaxially finely punctate, leaflets of lower leaves larger, 4–5.5 × 1.7–3.5 cm, leaflets of upper leaves 2–3 cm long. Peduncles 17–30 cm long. Racemes lax, bilateral, 7- or 8-flowered. Bracts white membranous, lanceolate, 8–10 mm long. Bracteoles ca. 5 mm long. Pedicel ca. 0.5 mm long. Calyx campanulate, glabrous, teeth narrowly lanceolate, wider at base, 1.5 times longer than tube. Corolla bright white or whitish pink; standard 25–28 × 17–21 mm, limb obovate, apex rounded; wings 13–19 × 5–7 mm, oblong-ovate; keel obovate-triangular, 21–26 × 9–13 mm. Pods stipitate, 1- or 2-jointed, joints transversely ribbed, ovate, glabrous. Seeds dark brown, rather convex, tuberous, 4 × 3 mm (Fig. 26).

**Flowering time:**—May.

**Fruiting time:**—June.

**Habitat:**—On outcrops of variegated rocks, gypsum and red sandstones in grass-forb groups in foothills, rarely on mountains in juniper forests, at 1500–2200 m a.s.l.

**Distribution:**—Turkmenistan and Uzbekistan. Distribution in Uzbekistan: Fig. 27.


**Fig. 26.** Living plant of *Hedysarum magnificum*: a, habit (photo was taken by Orzimad Turginov); b, flower; c, pod; d, calyx; e, standard; f, wings; g, keel. Scale bar 1 cm.

**Specimens examined:**—I-6 **Western Hissar Region**. I-6-a **Kashkadarya District**: Hissar ridge (Yakkabag bekstvo near the village Tashkurgan, 05.1916, *Popov* (LE); village Tashkurgan, 29.05.1916, *Popov 1071*; 5 km C from the village of Shurdzhi, 06.07.1927, *Kultiasov, Granitov 222, 686*; in the vicinity of the village Tashkurgan, 24.06.1936, *Bochantsev, Butkov 1066*; village Kokbulak, 25.06.1954, *Pyataeva*; valley of the Aksu River, between the villages of Kyzyl kishlak and Kyzyl mechat, 15.05.1972, *Nabiev, Shermatov, Kazakboev 577*); I-6-b **Tarkapchigay District**: Hissar ridge (near to village Akrabad, 30.04.1916, *Popov 1073*; Talli pass, 19.05.1968 *Mustafaev*; between Akrabat and Shurchi, 14.05.1976, *Pratov, Zuckerwanik, Makhmedov 481*; near to pass Akrabat, 1380 m.s.l., 05.04.2019, *Beshko*; Dehkhanabad District, 4 km from village Chamanzar, 24.05.2019, *Abduraimov*; Dehkhanabad District, Tolli pass, 27.04.2019, *Abduraimov*; low pass, Kurukdagan Mountains, gypsum, 18.05.1967, *Bochantsev 69* (LE); low mountains southeast of the village of Dehkhanabad, outcrops of variegated rocks between village Kurgantash and the Tarkapchigai River, 1300-1500 m, 08.05.1975, *Bochantsev 17* (LE); Tarqapchigay River basin, Talli pass, 02.05.1976, *Pimenov, Klyuykov, Baranova, Vasilieva 336* (MW)); I-6-c **Baysun District**: Hissar ridge (Khodja-Gurgurata Mountains, upper reaches of the Turgandarya River, Kizilsay, 11.07.1934, *Butkov 217, 435*; above the village of Yukary Machai, 08.06.1947, *Korotkov 217*; village Khangaron northeast slope, 22.06.1968, *Mustafaev 839;* river Machai, near the Urtamachay village, 23.05.1978, *Nabiev, Li, Zuckerwanik 25*; near the Kyzylnaur village, 20.05.2019, *Juramurodov*; near the village Amankhana, 12.06.2019, *Turginov, Pulatov, Jabbarov*; Asholmurat Mountains, 18.07.2019, *Juramurodov*; near the Urtamachay village, 28.05.2020, *Pulatov, Juramurodov, Jabborov, Rakhmatov, Makhmudjanov, Madaminov*;

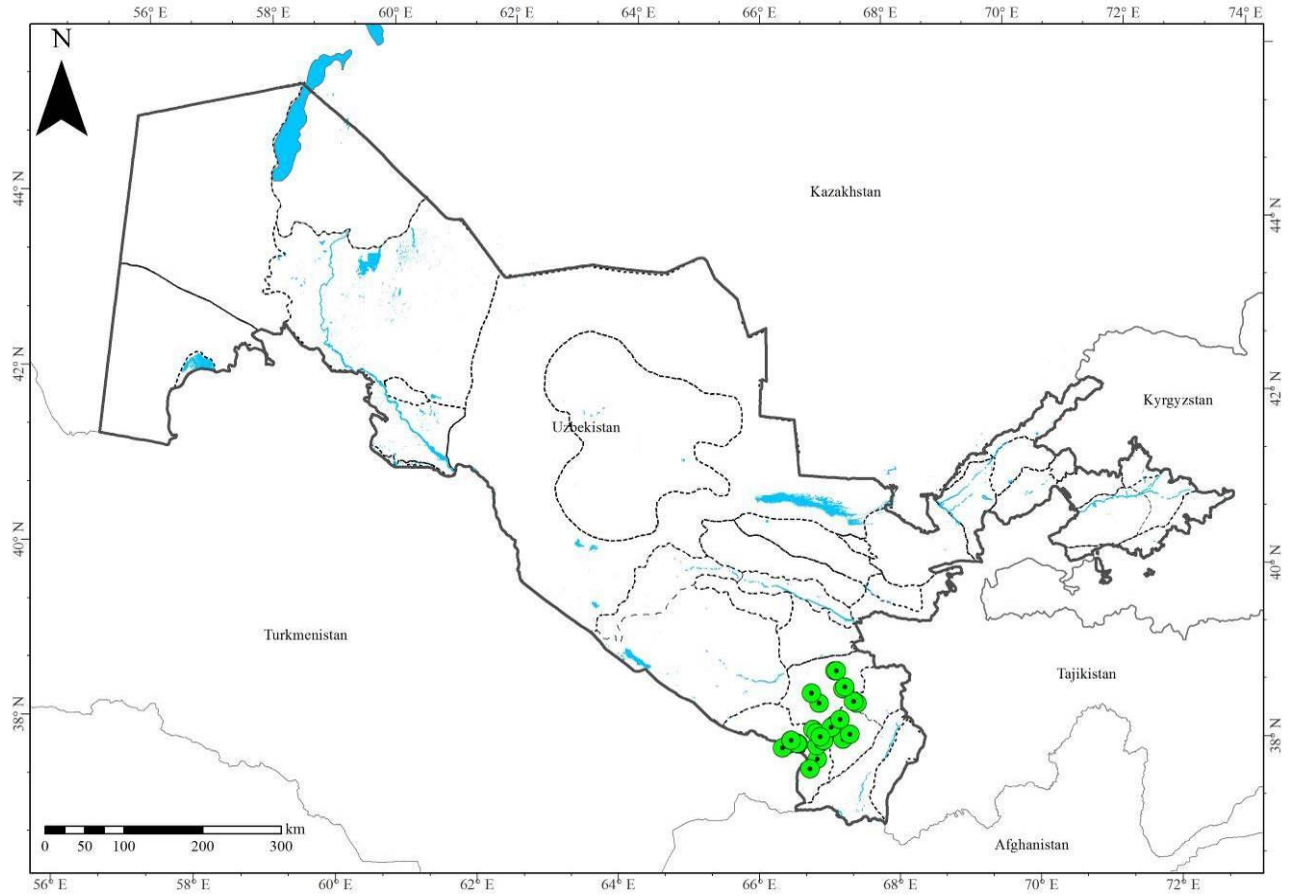


**Fig. 27.** Distribution of *Hedysarum magnificum*.

southwest of Machai village, between Kyzylbulak and Pasmachai villages, 04.05.1979, *Pimenov, Klyuykov, Baranova, Vasilyeva 354* (MW)); I-6-d **Kuhitang District**: Kuhitangtau ridge (Baysun Mountains, passes between Akrabat and the Shurab village, 18.05.1972, *Nabiev, Shermatov, Kazakboev 73, 120, 381*; Baysuntau, pass between Shurab and Akrabat, 06.06.1972, *Allanazarova, Butkov 85, 284*; environs of the village Shurab, 13.05.1976, *Pratov, Zuckerwanik, Makhmedov 253*; Khatak village, 15.05.1978, *Nabiev, Li, Zuckerwanik 160*; Around the road between Shorab and Khamkan villages, 28.04.2013, *Tojibaev 140*; Between villages Akrabat and Shurob, red sandstone slopes in low mountains, 26.05.1973, *Bochantsev 62* (LE)). Specimens in TASH unless otherwise specified.

**Notes:**—'The Red Data Book of the Republic of Uzbekistan' has classified *Hedysarum magnificum* as 'Declining' (Khassanov 2019). In our field research, however, we discovered around 15,000–20,000 individuals in Boysun, Khodja-Gurgurata and the Kuhitang Mountain ranges. Accordingly, we recommend removing this species from the Red Book of the Republic of Uzbekistan.

**11.** ***Hedysarum drobovii*** Korotkova in Bot. Mater. Gerb. Inst. Bot. Zool. Akad. Nauk Uzbeksk. S.S.R. 9: 9 (1947).

**Type:**—[Uzbekistan]. Chotkal River near Brich-Mulla village, slope along the left bank, 18.06.1921, fl., *V. P. Drobov 18* (lectotype TASH barcode 001922!, designated by Juramurodov et al. (2022: 13)).

**Description:**—Herbs, 30–35(–50) cm tall, appressed silvery hairy. Stems numerous or few, angular, grooved. Stipules triangular-lanceolate, apex gradually acuminate, entire, foliaceous, nearly free, 12–15 × 2–5 mm. Leaves 7–10 cm long; leaflets 1 or 2 pairs, oblong-obovate, 25–50 × 15–30 mm, base rounded or broadly cuneate, apex rounded abruptly tapering to short beak, both surfaces dotted, abaxially prominently nerved; terminal leaflet distinctly larger than lateral, 60 × 40 mm. Peduncles axillary, longer than leaves, 15–22 cm long (with raceme). Racemes loose. Bracts linear-lanceolate, apex gradually acuminate, nearly as long as calyx, 10–13 mm long; Bracteoles ca. 2 mm long. Calyx teeth linear-lanceolate, two to three times as long as tube, 11–14 mm long. Corolla pink, persistent in fruit; standard oblong-obovate, 21–24 × 11–15 mm, about as long as keel, apex emarginate, base cuneate; wings oblong, 13–14 × 3–4 mm; keel 20–23 × 8–9 mm, triangular, upper margin rounded, apex obtuse, base tapering to claw, 5–6 mm long. Pods subsessile, 15–25 mm long, joints 3, 6–8 x 6–7 mm, orbicular, prominently nerved, with aculeiform tubercles and bristles. Seeds suborbicular, 3–4 x 3 mm, blackish brown or brown, smooth (Fig. 28).

**Flowering time:**—June.

**Fruiting time:**—July.

**Habitat:**—On outcrops of red sandstones and variegated rocks in foothills and on slopes in the middle mountain belt at 1500–1800 m a.s.l.

**Distribution:**—Uzbekistan (Fig. 29).

**Specimens examined:**—I-1 **Western Tian-Shan Region**. I-1-a **Ugam-Pskem District**: Ugam ridge (left bank of the Ugam River, 01.07.1960, *Pratov 323*; Tashkent Province, Bostanlyk region, left bank of the Ugam River, in the middle belt of mountains, 01.07.1960, *Pratov, Kovalevskaya 394* (LE); near the Khumsan village, 14.06.1962, *Karimov*; Khumsan village, left bank of the Ugam River, 19.06.1962, *Nabiev, Pratov, Tulyaganova*; between Khumsan and Bechit villages, Kattazhar tract, on red sandstones, 19.06.1962, *Pratov* (LE, MW); near the Khumsan village, right bank of the Ugam River, upper reaches of the Kamavsay, 19.06.1962, *Nabiev, Pratov, Tulyaganova*); I-1-b **Western Chatkal District**: Chatkal ridge (near the village of Brichmulla, northeast slope of the left bank of the Chatkal River, between the village of Kalaga and the Khadalak gorge, 30.07.1950, *Pyataeva 54*; valley of the Chatkal River, Kuylyuksay near the Yangikurgan village, 15.06.1957, *Butkov, Maylun, Nabiev 9*; along the road from Charvak to the Brichmulla village, 13.06.1984, *Khamidov*; at the confluence of the Chatkal River with the Charvak Reservoir, left bank of the river,

08.08.2008, *Tojibaev*; at the confluence of the Chatkal River with the Charvak reservoir, left bank of the river, rocky-rubbly slope, opposite the Obirakhmat tract, 11.06.2019, *Juramurodov 1106a, 1106b*; ibid, 19.06.2020, *Dekhkanov, Ortikov, Turdiev, Juramurodov 19062020117, 19062020118, 19062020119, 19062020120*). Specimens in TASH unless otherwise specified.

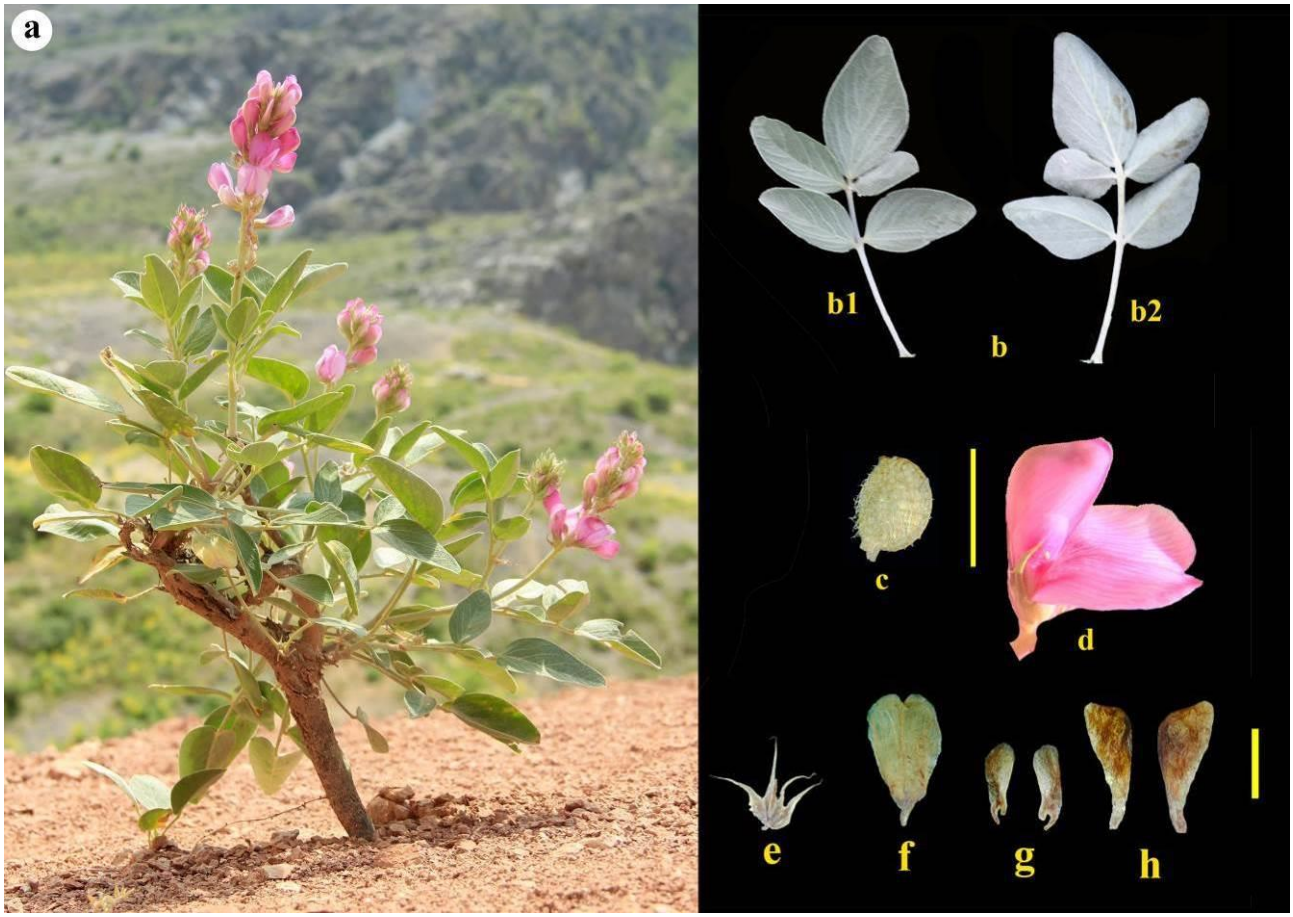


**Fig. 28.** Living plant of *Hedysarum drobovii*: a, habit; b, leaflets (b1, upper part and b2, lower part); c, pod; d, flower; e, calyx; f, standard; g, wings; h, keel. Scale bar 1 cm.

**Notes:**—*Hedysarum drobovii* was classified as 'Disappearing' in the Red Data Book of the Republic of Uzbekistan (Hassanov 2019). Th Red Data Book contains information that indicates the total number of individuals does not exceed 200, and that 50 percent of the population is on the banks of the Chotkal River. Additionally, herbarium data suggests that it can also be found arround the village of Khumsan near the Ugam River. Despite attempts to it around the village of Khumsan between 2017 and 2022, we were unable to locate any individuals. Furthermore, the absence of new specimens collected in the vicinity of the village of Khumsan for over 60 years leads us to conclude that it may have become extinct in this area, with populations potentially surviving only in the vicinity of the villages of Burchmulla and Yangikurgan on the banks of the Chotkal River. Unfortunately, this area is also heavily impacted by human activities; for instance, in 2020, the construction of a road in the region where the *H. drobovii* population was present resulted in the loss of over 50 percent of individuals (Figs 30–31). Given that this species is endemic to the Uzbekistan flora and has only one population, we suggest implementing stringent conservation measures to safeguard this area. Furthermore, future studies should assess the status of this species based on IUCN criteria and categories.

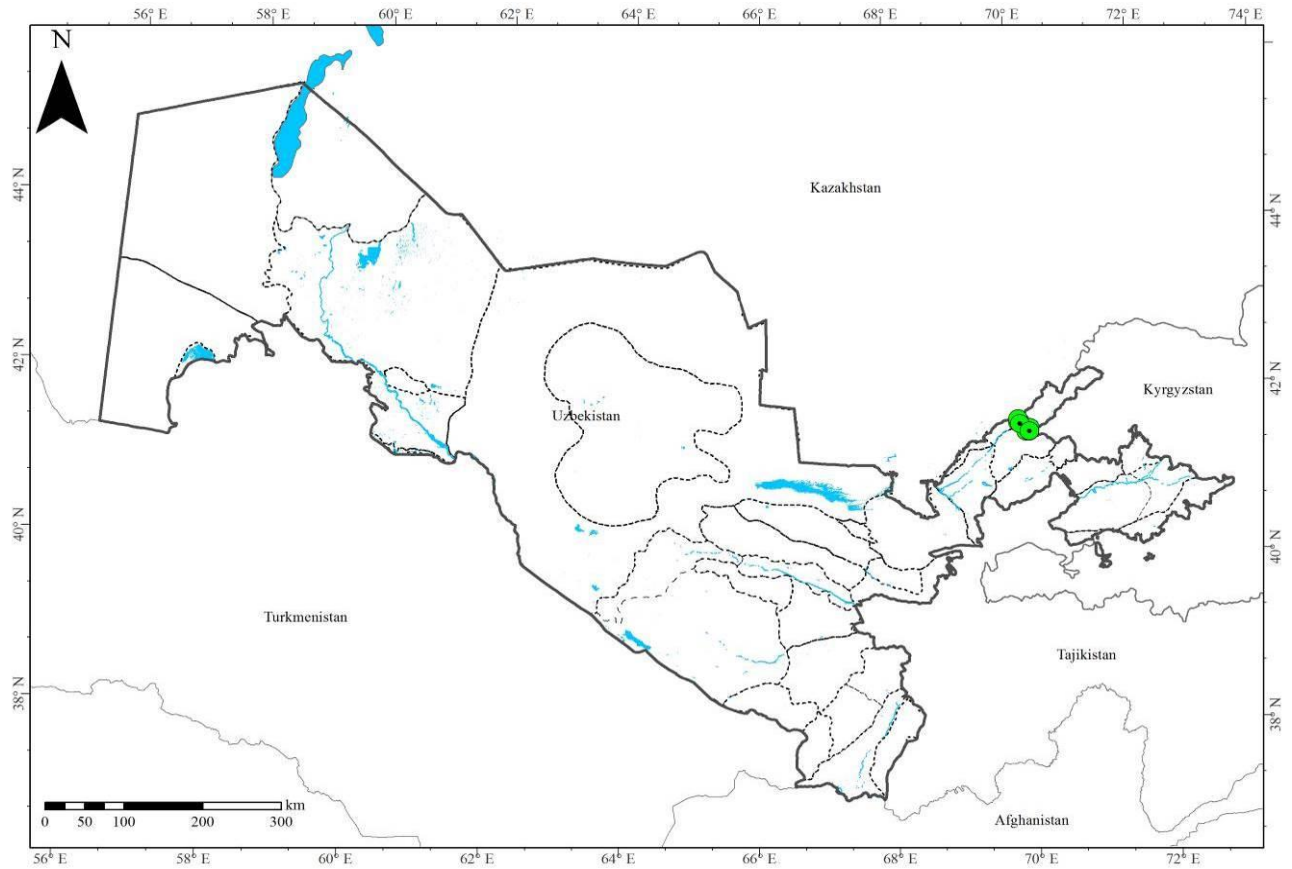


**Fig. 29.** Distribution of *Hedysarum drobovii.*

**Fig. 30.** Distribution area of *Hedysarum drobovii* (as of June 11, 2019).

**Fig. 31.** Distribution area of *Hedysarum drobovii* (as of June 19, 2020).

**12. *Hedysarum mogianicum*** Fedtsch., Rastit. Turkest.: 541 (1915).
≡ *Hedysarum songaricum* var. *mogianicum* B.Fedtsch. in Trudy Imp. S.-Peterburgsk. Bot. Sada 19: 282 (1902)
**Type:**—[Tajikistan]. Mogian, 05.1893, *Komarov* (holotype LE).
**Description:**—Herbs, 70–125 cm tall. Stems many, erect or slightly ascending, glabrous or sparingly pubescent. Stipules lanceolate, white membranous, nerved, glabrous or subglabrous. Leaves 5–10 cm long, short petiolate; leaflets 2–5 pairs, 12–20 × 7–9 mm, elliptic, abaxially without dense short silvery hairs, adaxially glabrous, punctulate. Peduncles (with raceme) distinctly longer than leaves. Racemes rather dense at onset, later elongating, 10- to 25-flowered. Bracts narrowly triangular, 4–5 mm long. Bracteoles subulate, 1.5–2 mm long. Pedicel 2–2.2 mm long. Calyx short campanulate; teeth lanceolate-subulate, lower tooth nearly twice as long as tube, upper teeth as long as or slightly longer than tube. Corolla pinkish lilac; standard oblong, 15–20 × 10–12 mm; wings oblong, 10–13 × 3.5–4 mm; keel narrow, ventrally curved at right angle, 13–17 × 5–6 mm. Ovary hairy. Pods (1- or)2- or 3-jointed, joints elliptic, lower joint often abortive, surface and along sutures with short partly reddish bristles . Seeds reniform, 3–3.2 × 2–2.2 mm (Figs 32–33).
**Flowering time:**—May.
**Fruiting time:**—May-June.
**Habitat:**—On rubbly slopes in fine earth in middle mountain belt, at 1300–2100 m a.s.l. (Fig. 33).


**Fig. 32.** Living plant of *Hedysarum mogianicum*: a, entire plant; b, leaflets (b1, upper part and b2, lower part); c, pod; d, flower; e, calyx; f, standard; g, wings; h, keel. Scale bar 1 cm.

**Distribution:**—Tajikistan and Uzbekistan. Distribution in Uzbekistan: Fig. 34.

**Specimens examined:**—I-4 **Nuratau Region**. I-4-a **Nuratau District**: Nurata ridge (Koytash ridge, Saurak village, 18.07.1937, *Demurina*

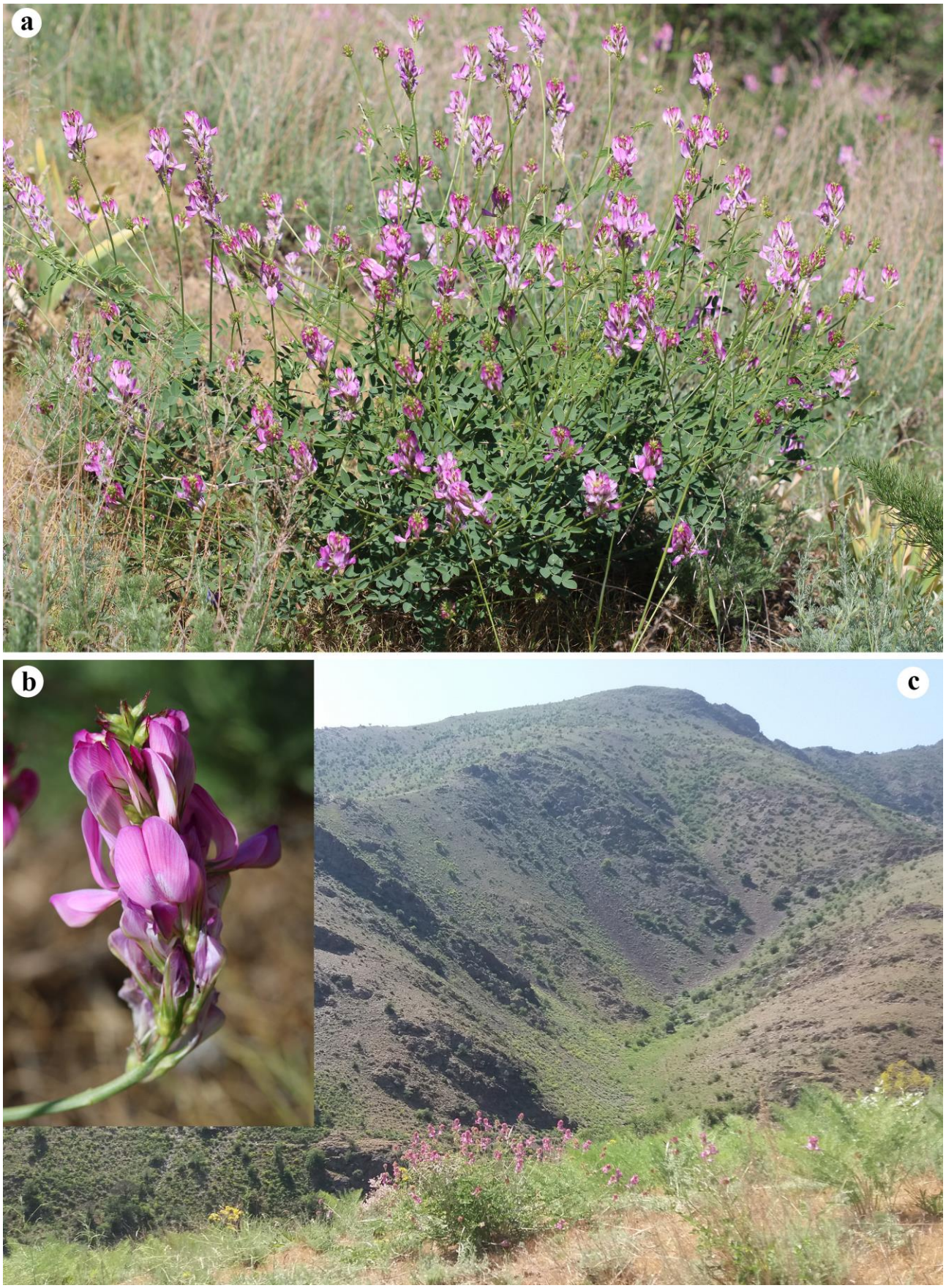


**Fig. 33.** *Hedysarum mogianicum* —a, c: habit of plant, c: raceme.

*609*; upper reaches of the Ukhumsay, 02.06.1964, *Sukervanik 468*; Nurata Reserve, Madzherumsay, tract Fargun, 02.06.2000, *Beshko*; Nurata Reserve, left bank of Khayatsay, 13.05.2019, *Juramurodov 52*; Nurata Reserve, Khayatsay tract, 09.06.2020, *Ortikov, Pulatov, Turdiev, Juramurodov, Makhmudjanov 9062020696, 9062020627, 9062020622, 9062020621, 5052020089*; Northern macro slope of mountain Koytash to the south of the central farmstead of the Kirov collective farm, rocky slopes, 20.06.1971, *Bochantsev, Kamelin 233* (LE)). I-6 **Western Hissar Region**. I-6-a **Kashkadarya District**: Hissar ridge (Kzyldarya River basin, Kunguzlyk tract, 07.07.1941, *Koshurnikova 234*; valley of the Kzyldarya River, in the vicinity of the Tatars, 06.05.1952, *Litvinenko 10*; outskirts of the village of Tamshush, Burichi tract, 10.07.1969, *Mustafaev 151*; Gissar State Reserve, near to the village of Gilan, 29.08.2018, *Turginov, Khujanov 00027* (KUN)). Specimens in TASH unless otherwise specified.

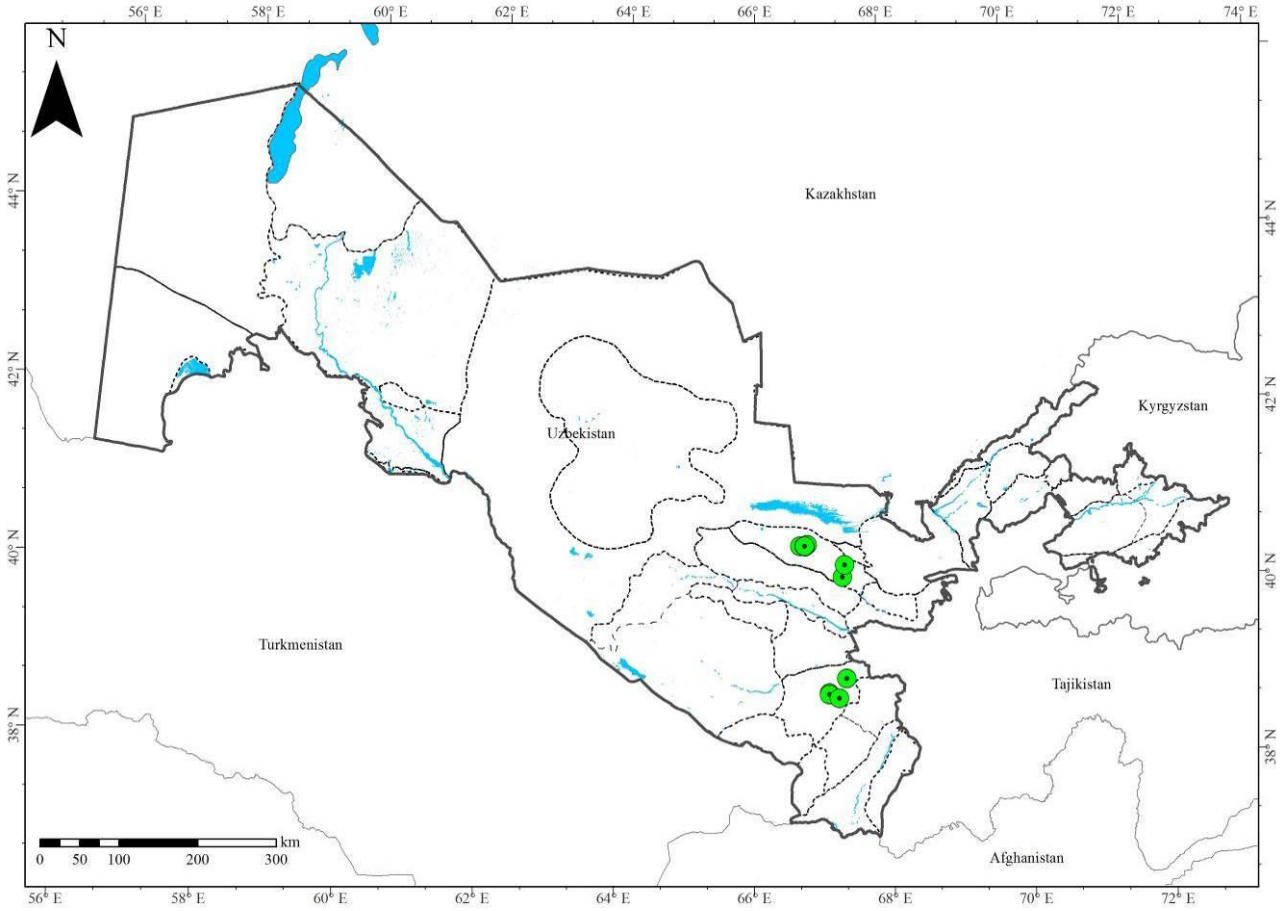


**Fig. 34.** Distribution of *Hedysarum mogianicum.*

**13.** ***Hedysarum amankutanicum*** B.Fedtsch. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 11: 115 (1949).

**Type:**—[Uzbekistan]. Ad pagum Aman-Kutan in montibus ad viam inter Samarkand er Kitab, 04.1913, *A.I. Michelson* (holotype LE; isotype TASH barcode 001947!; Fig. 35).

**Description:**—Herbs, 30–40 cm tall, rootstock deep, branching. Stems numerous, suberect or ascending, 5–8 mm thick, straw-yellow, finely ribbed, subglabrous. Stipules thin coriaceous, brown, connate, sparingly appressed hairy. Leaves 10–12 cm, short petiolate; leaflets 5–8 pairs, oblong, 15–20(25) × 5–7(8) mm.


**Fig. 35.** Holotype specimen of *Hedysarum amankutanicum.*

Peduncles (without raceme) longer than leaves. Racemes dense, elongate; flowers many. Bracts lanceolate, 4–7 mm long. Bracteoles 1.5–3.5 mm long. Pedicel 2–3 mm long. Calyx campanulate, brownish green, subglabrous, teeth linear-subulate, three to four times as long as tube. Corolla light pink; standard oblong, 17–18 (20) × 8–10 mm; wings slightly shorter than keel, 10–13 × 3–4 mm; keel triangular, 13–16 × 5–6 mm. Ovary pubescent. Pods 1- or 2-jointed, joints 8–9 × 5–6 mm, short hairy, gray, with rare short hooks and curved or straight short bristles along edges and sides. Seeds brown, almost reniform.

**Flowering time:**—April.

**Fruiting time:**—Unknown.

**Habitat:**— Mountain slopes among herbs, at ca. 1500 m a.s.l.

**Distribution:**—Uzbekistan (Fig. 36).

**Specimens examined:**—I-5 **Kuhistan Region**. I-5-c **Urgut District**: Zeravshan ridge (Ad pagum Aman-Kutan in montibus ad viam inter Samarkand er Kitab, 25.04.1913, *Michelson* (LE, TASH)).

**Notes:**—Currently, the only known collections of *H. amankutanicum* are the type specimen, which is in LE, and the isotype, which is in TASH, both of which were found in 1913 on the Takhta-Karacha passage. Despite multiple targeted searches for this plant, none have been successful, leading us to believe that *H. amankutanicum* is probably extinct.

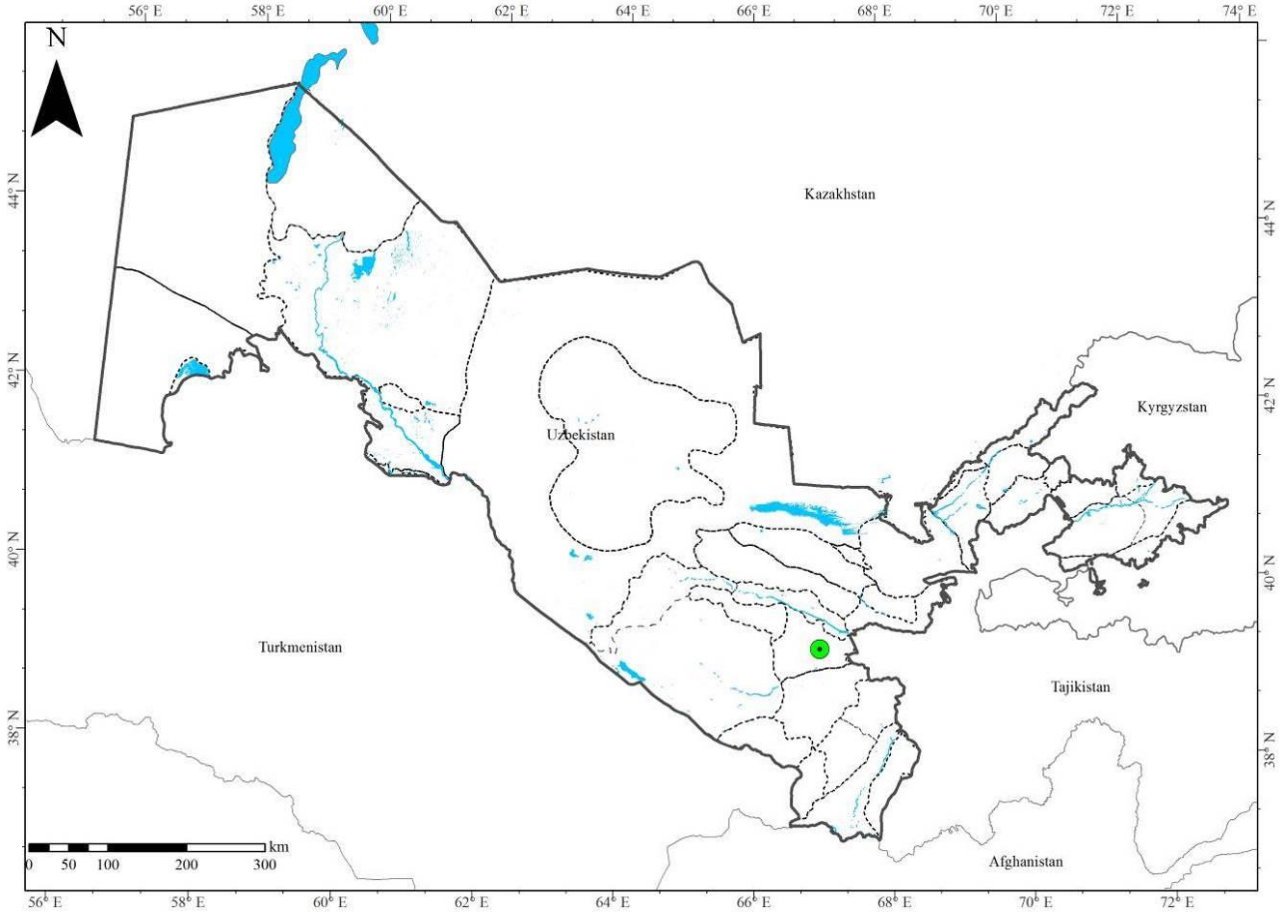


**Fig. 36.** Distribution of *Hedysarum amankutanicum*.

**14. *Hedysarum olgae*** Fedtsch. in Bot. Mater. Gerb. Glavn. Bot. Sada R.S.F.S.R. 1(2): 1 (1919).

**Type:**—[Uzbekistan]. In argillosis declivii meridionalis trajectus Tachta-Karatscha, supra circ. 4000', 26.04.1915, *O.* & *B. Fedtschenko 438* (holotype LE).

**Description:**—Herbs, 25–40 cm tall. Stems numerous, ascending, glabrous, few-branched. Stipules light brown, the lower short, the upper narrowly lanceolate, acuminate. Leaves short

petiolate, appressed sericeous when young, later glabrous or subglabrous, 5–10 cm long; leaflets 9–11 pairs, subsessile, oblong-ovate or rarely suborbicular-elliptic, 10–12 × 4–10 mm. Peduncle elongate, one and half times as long as leaves (without raceme). Racemes dense, many-flowered. Bracts linear-filiform, ca. 5–6 mm long. Bracteoles ca. 0.5–1 mm long. Pedicel 1–1.2 mm long. Calyx campanulate, pubescent, teeth unequal, upper one nearly as long as tube, the lower ones longer, linear-filiform. Corolla purple-violet; standard broadly ovate, apex emarginate, 13–16 × 7–10 mm; wings (3)–4–5 × 1.5–2.5 mm; keel 12–14 × 5–6 mm, curved ventrally at an obtuse angle. Ovary linear, glabrous. Pods flat, joints 1–3, marginal short toothed, appressed short hairy, without bristles and setae, with 8–10 transverse veins. Seeds brown, reniform (Figs 37–38).

**Flowering time:**—May.
**Fruiting time:**—May-June.
**Habitat:**—On slate screes, fine earth-stony slopes in juniper forests in middle mountain belt (Fig. 38).
**Distribution:**—Uzbekistan (Fig. 39).
**Specimens examined:**—I-5 **Kuhistan Region**. I-5-c **Urgut District**: Zeravshan ridge (pass Takhtakaracha, 13.05.1916, *Popov 643, 660, 645*; Takhtakaracha pass, 13.05.1916, *Popov 646* (LE); Amankutanskaya forest cottage, 22.05.1933, *Drobov, Sakhabutdinov 21*; village Amankutan, 1941, *Popov* (SAMDU); near the village Amankutan, 1947, *Korotkov 158, 237*; village Amankutan, 09.05.1962, *Markova*; pass Takhtakaracha, 15.05.2019, *Juramurodov 048a, 048b*); I-6 **Western Hissar Region**. I-6-a **Kashkadarya District**: Hissar ridge

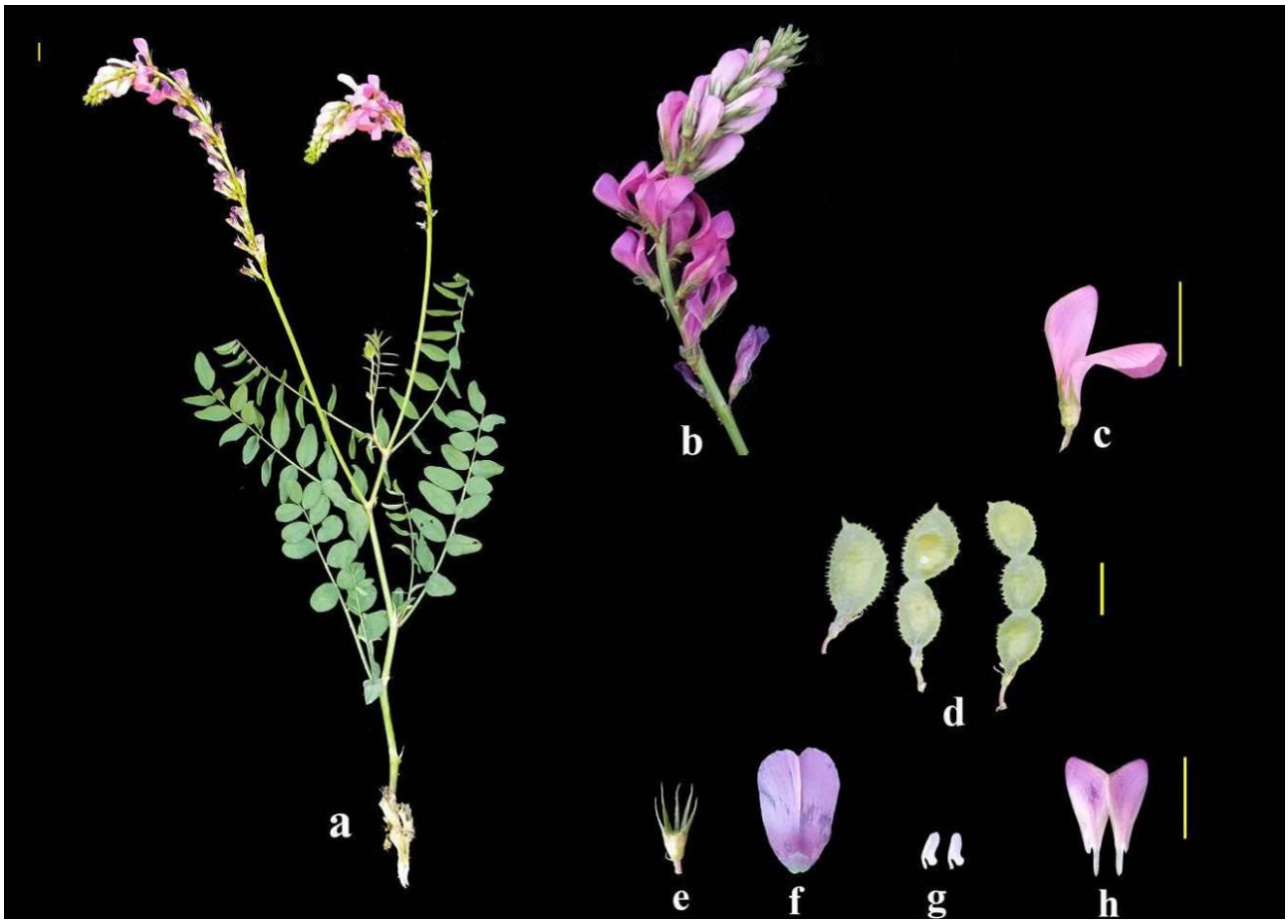


**Fig. 37.** Living plant of *Hedysarum olgae*: a, entire plant; b, raceme; c, flower; d, pod and its joints; e, calyx; f, standard; g, wings; h, keel. Scale bar 1 cm.


**Fig. 38.** *Hedysarum olgae* —a–b: habit of plant.

(Tashkurgan village, 29.05.1916, *Popov, 1044, 1070*; village Tashkurgan, 29.05.1916, *Popov 1047* (LE); Yakkabagdarya River, between Tatars and Chekmenkuydy pass, 22.06.1931, *Granitov 253*; upper Yakkabagdarya River, near Tashkurgan, 21.06.1936, *Botchantsev, Butkov 217*; along the Yakkabag-Kan road, 20.05.1980, *Nabiev, Shermatov, Kazakboev, Levichev 167*; Yakkabag District, Gissar reserve, Kizilsuv area, 13.06.2020, *Khujanov, Kosimov, Akbarov 13062020120, 13062020118*; river valley Langar, between the village Kyzylkishlak and Lyangar, variegated, 01.05.1979, *Pimenov, Klyuykov, Baranova, Vasileva 225* (MW)); I-6-b **Tarkapchigay District:** Hissar ridge (between the upper reaches of the Darya River and Akrabat, 02.06.1976, *Pimenov, Klyuykov, Baranova, Vasilyeva 365* (MW)). I-7 **Hissar-Darvaz Region**. I-7-a **Sangardak-Tupalang District**: Hissar ridge (2 km to the west from the village of Dibaram, ??.05.1966, *Kayumov*). Specimens in TASH unless otherwise specified.

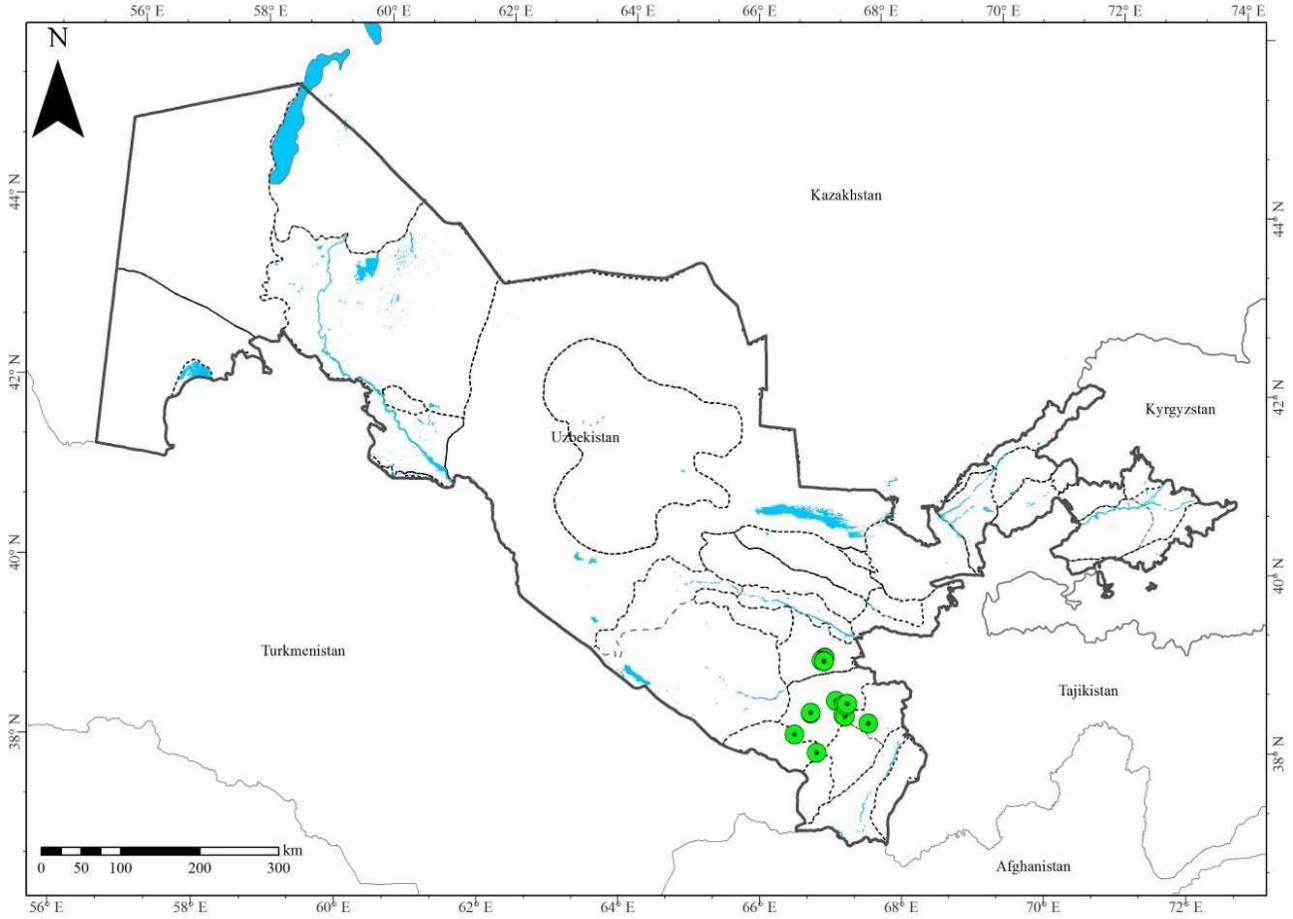


**Fig. 39.** Distribution of *Hedysarum olgae*.

**15. *Hedysarum alaicum*** B. Fedtsch. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 11: 116 (1949).

**Type:**—[Kyrgyzstan]. Northern side of Alay Range, Shakhimardan River basin, Arpa ravine, 32 km south of the town of Skobelev, 22.05.1916, fl., *V. Drobov 1021* (holotype LE barcode 00054329 [photo!]; isotype TASH barcode 001948!; Fig. 40).

**Description:**—Herbs, 30–40 cm tall, rootstock deep, apically slightly thickened, strongly branching and bearing few floriferous stems and many short branches with tufts of leaves. Stems ascending, short, more or less densely appressed hairy as the entire plant (epidermis


**Fig. 40.** Isotype specimen of *Hedysarum alaicum*.

not visible). Stipules light brown, densely appressed hairy, connate. Leaves short petiolate, 6–8 cm long; leaflets 4–6 pairs, oblong-elliptic, 7–14 × 4–7 mm, adaxially densely silvery hairy, abaxially more sparingly so. Peduncle (without raceme) much longer than leaves, slightly curved. Racemes loose, 3- to 8-flowered. Bracts linear-filiform, ca. 4–5 mm long. Bracteoles lanceolate, 1–1.2 mm long. Pedicel ca. 2 mm long. Calyx brownish, appressed white hairy, teeth two to three times as long as tube, lanceolate-subulate. Corolla pink; standard nearly round, 13 × 11 mm, slightly longer than keel, apex broadly notched; wings half as long as keel; keel 11–12 × 5–6 mm. Ovary pubescent. Pods unknown.

**Flowering time:**—May.

**Fruiting time:**—Unknown.

**Habitat:**—On rocky slopes in juniper belt.

**Distribution:**—Kyrgyzstan and Uzbekistan. Distribution in Uzbekistan: Fig. 41.

**Specimens examined:**—I-3 **Fergana-Alay Region**. I-3-b **Eastern Alay District**: Alay ridge (Fergana Province, Skobelevsky District, Ankhorsky section, Arpa ravine, rocky slope in the juniper zone, 22.05.1916, *Drobov 1021* (holotype LE; isotype TASH).

**Notes:**—Only one specimen of *Hedysarum alaicum* is in TASH, which means that all molecular phylogenetic and morphometric analyses were conducted using this single voucher. The species is distributed in an area near the border of Uzbekistan and Kyrgyzstan, which makes it challenging to conduct field research in that region.


**Fig. 41.** Distribution of *Hedysarum alaicum*.

**16.** ***Hedysarum pskemense*** Popov ex B.Fedtsch. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 11: 117 (1949).

**Type:**—[Kyrgyzstan]. Tjan-schan occidentalis, montes Talas Alatau ad fontes rivuli Ispai (holotype LE).

**Description:**—Herbs, 25–30 cm tall, rootstock thickened, deep, strongly branching. Stems

many, ascending, subglabrous or slightly appressed hairy (epidermis visible). Stipules brown, narrowly lanceolate, connate. Leaves short petiolate, 10–15 cm long; leaflets 4–6 pairs, oblong-elliptic, tapering at apex, abaxially densely appressed hairy, adaxially subglabrous, 15–18 × 5–10 mm. Peduncle (without raceme) longer than leaves, sparsely appressed hairy. Racemes dense, 15- to 25-flowered. Bracts linear lanceolate, 2–3 mm long. Bracteoles ca. 1 mm long. Pedicel 1.5–2 mm long. Calyx brownish, teeth three to four times as long as tube. Corolla pinkish lilac; standard ovoid, 14–16 × 7–9 mm; wings ca. 5 mm long; keel slightly shorter than standard. Ovary appressed hairy. Pods 2- to 5-jointed, appressed hairy, joints transversely ribbed, with short thin bristles. Seeds brown, smooth, reniform (Fig. 42).

**Flowering time:**—June-July.

**Fruiting time:**—July-August (-September).

**Habitat:**—On stony and gravelly slopes, in middle and upper mountain belts.

**Distribution:**—Kazakhstan, Kyrgyzstan and Uzbekistan. Distribution in Uzbekistan: Fig. 43.


**Fig. 42.** Living plant of *Hedysarum pskemense*: a, habit; b, raceme; c, pods; d, flower; e, calyx; f, standard; g, wings; h, keel. Scale bar 1 cm. Photo ‘a’ was taken by N. Beshko.

**Specimens examined:**—I-1 **Western Tian-Shan Region**. I-1-a **Ugam-Pskem District**: Pskem ridge (Pskem River valley, 27.07.1957, *Vernik, Kamalov 373*; Oygaing River valley, along the bottom of Tekeshsay, 09.01.1928, *Kultiasov 1015*; valley of the Oygaing River, upper reaches of the Tunduksay gorge, 11.08.2019, *Tojibaev, Juramurodov 1008052, 1008059-1, 1008059-2, 1008060*; Aksarsay, near the village Nanai, 23.06.1948, *Pavlov* (MW); to peaks of Aksarsay, 24.07.1949, *Pavlov 145, 146* (MW); Aksarsay gorge pass, in Koksu gorge, 2900 m, 10.09.1954, *Pavlov 330, 407* (MW)); I-1-b **Western Chatkal**

**District**: Chatkal ridge (right bank of Tashkent, 27.07.1980, *Krasovskaya*). Specimens in TASH unless otherwise specified.

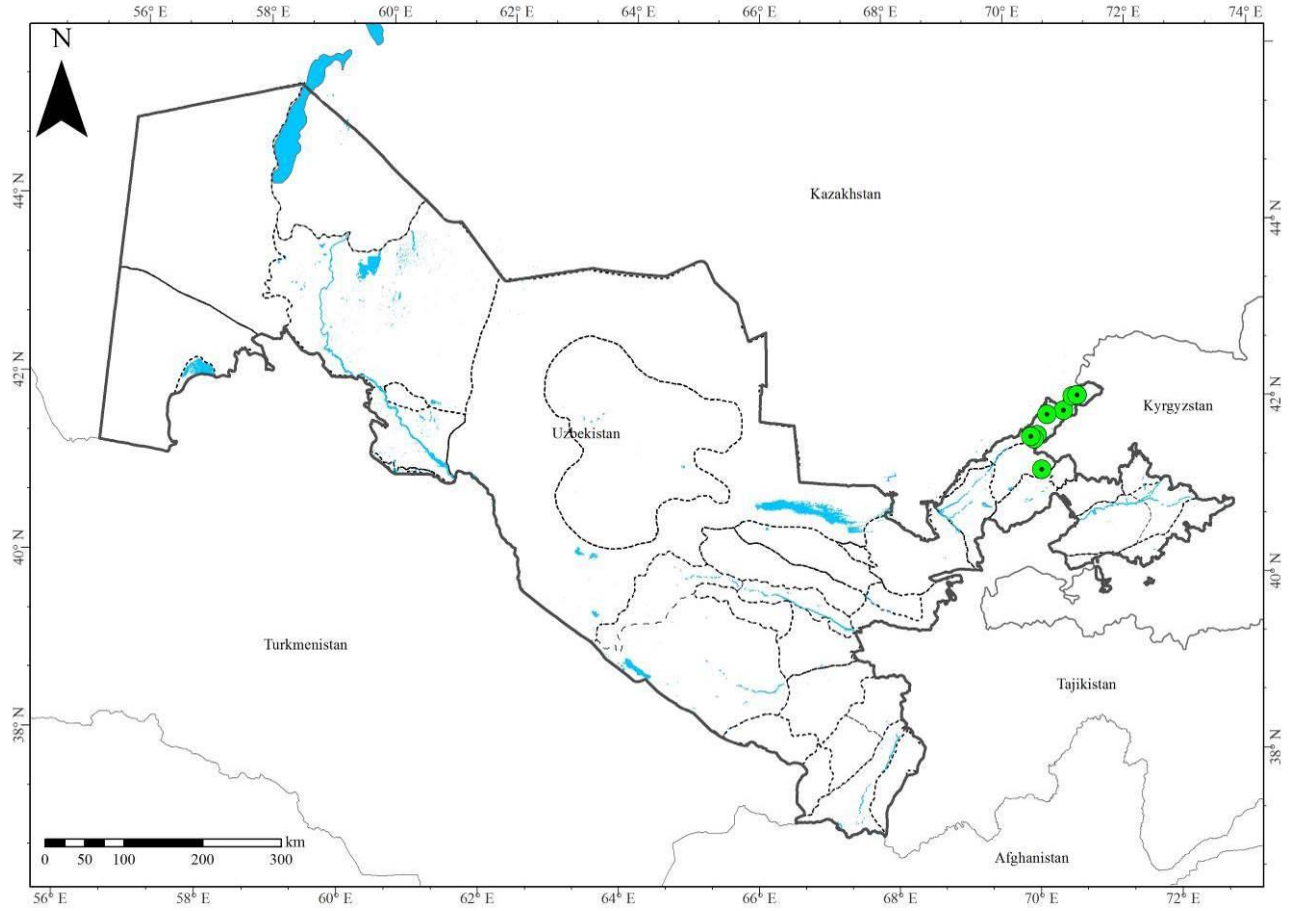


**Fig. 43.** Distribution of *Hedysarum pskemense*.

**17. *Hedysarum baldshuanicum*** B.Fedtsch. in Bull. Herb. Boiss. 7: 258 (1899).
**Type:**—Tajikistan. Baldshuan, 1884, *A. Regel* (syntypes LE).
= *Hedysarum vvedenskyi* Korotkova in Bot. Mater. Gerb. Inst. Bot. Akad. Nauk Uzbeksk. S.S.R. 14: 15 (1954).
**Type:**—[Uzbekistan]. Tupolang River basin, downhill, from Malyand pass, 1½ km to village Krish, dry slopes, red clays, 17.04.1948, fl., fr., *Pyataeva 488* (lectotype TASH barcode 001984!, designated by Juramurodov et al. (2022: 24)).
**Description:**—Herbs, 75 cm tall, completely glabrous. Stems suberect or ascending. Stipules of lower leaves connate, of upper leaves free. Leaves to 20 cm long; leaflets 6–10 pairs, appressed hairy when young, later subglabrous, oblong, 2–3.5(4) × 7–17 mm. Peduncle (with raceme) as long as or longer than leaves. Racemes 5- to 15-flowered. Bracts lanceolate, whitish membranous, loosely hairy, ca. 7–8 mm long, rarely remaining. Bracteoles linear subulate, 0.5–4 mm long. Pedicel 1–3 mm long. Calyx sparingly pubescent, teeth one and half times longer than tube, calyx teeth equal in length. Corolla pinkish lilac; standard oblong-ovate, slightly longer than keel, 12–16 × 6–8 mm; wings 3–3.2 × 1.5–2 mm, with a short auricle at base; keel triangular, curved almost at right angle, 10–14 × 5 mm. Ovary pubescent along upper suture, 3- to 5-ovuled. Pods 1- to 3-jointed, joints glabrous, unequal, round-ovate, convex, sparsely short hairy, transversely ribbed, with thin bristles on ribs, 9–11 × 8 mm. Seeds dark brown, convex, 5 × 4 mm (Figs 44–45).
**Flowering time:**—June-July.
**Fruiting time:**—July-August.
**Habitat:**—On fine earth, cartilaginous slopes, screes and sandstones in lower mountain belt at

1300–1500 m a.s.l. (Fig. 45).

**Distribution:**—Tajikistan and Uzbekistan. Distribution in Uzbekistan: Fig. 46.

**Specimens examined:**—**Western Hissar Region**. I-6-c **Baysun District**: Hissar ridge (surrounding village Shargun on the bank of the river Yaygoklyk, 15.05.1948, *Bondarenko 598*); I-6-e **Surkhan-Sherabad District**: Hissar ridge (Baisuntau, basin of the Machaidarya River, near the village Darband, 18.05.2012, *Turginov*). I-7 **Hissar-Darvaz Region**. I-7-a **Sangardak-Tupalang District**: Hissar ridge (Tupolang River basin, ascent to the Malyand pass, eastern slope, 17.06.1948, *Pyataeva 460*; Divlok tract on the Aigyrkul lakes and from the village to Kshtut, 18.07.1948, *Pyataeva 115*; basin of the Tupolang River, upper reaches of the Shargunsay, on the northern slope among junipers, 31.05.1972, *Nabiev, Shermatov, Kazakbaev 369*; Shargun, 21.04.1977, *Khamidkhodjaev*; Tupolang River basin, upper reaches of Shargunsay, 20.05.1980, *Nabiev, Shermatov, Kazakbaev, Levichev 364*; Boysun Mountains, basin of Khandiza River between Khandiza and Khodjaasmin villages, 01.06.1980, *Nabiev, Shermatov, Kazakbaev, Levichev 539*; Tupolang River basin above village Zevar, 26.06.1986, *Khalilov*; left bank of the Khursandarya, 2190 m a.s.l., 08.06.1984, *Maltsev*; near to village Khufar, at 1600 m a.s.l., 23.05.1995, *Maltsev*; left bank of the Khandiza River, village Khodjaasmin, 30.05.2019, *Juramurodov, Makhmudjanov 005a, 005b*). All specimens are at TASH.

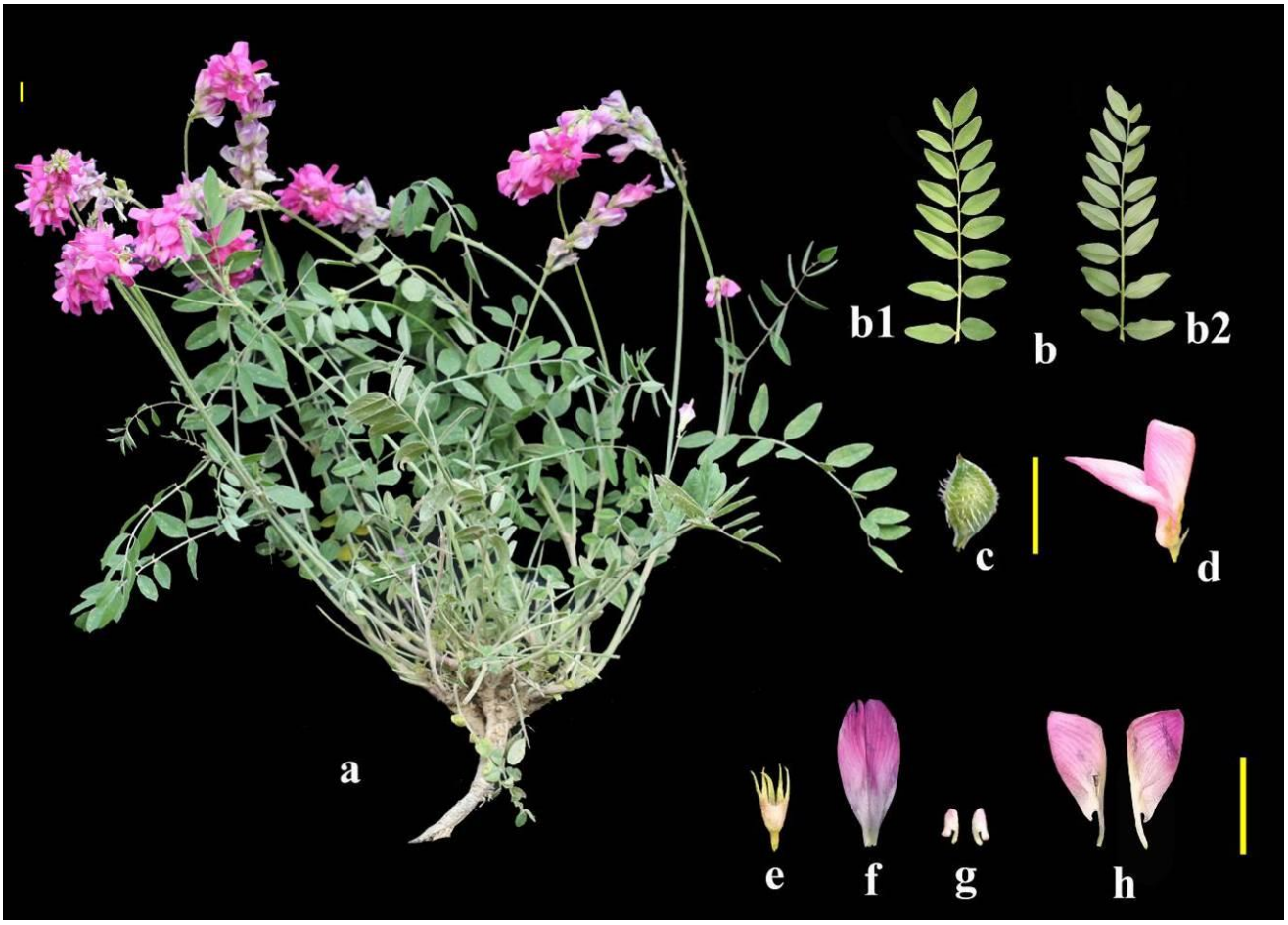


**Fig. 44.** Living plant of *Hedysarum baldshuanicum*: a, entire plant; b, leaflets (b1, upper part and b2, lower part); c, pod; d, flower; e, calyx; f, standard; g, wings; h, keel. Scale bar 1 cm.


**Fig. 45.** *Hedysarum baldshuanicum*—a: raceme, b: pods, c: habit.

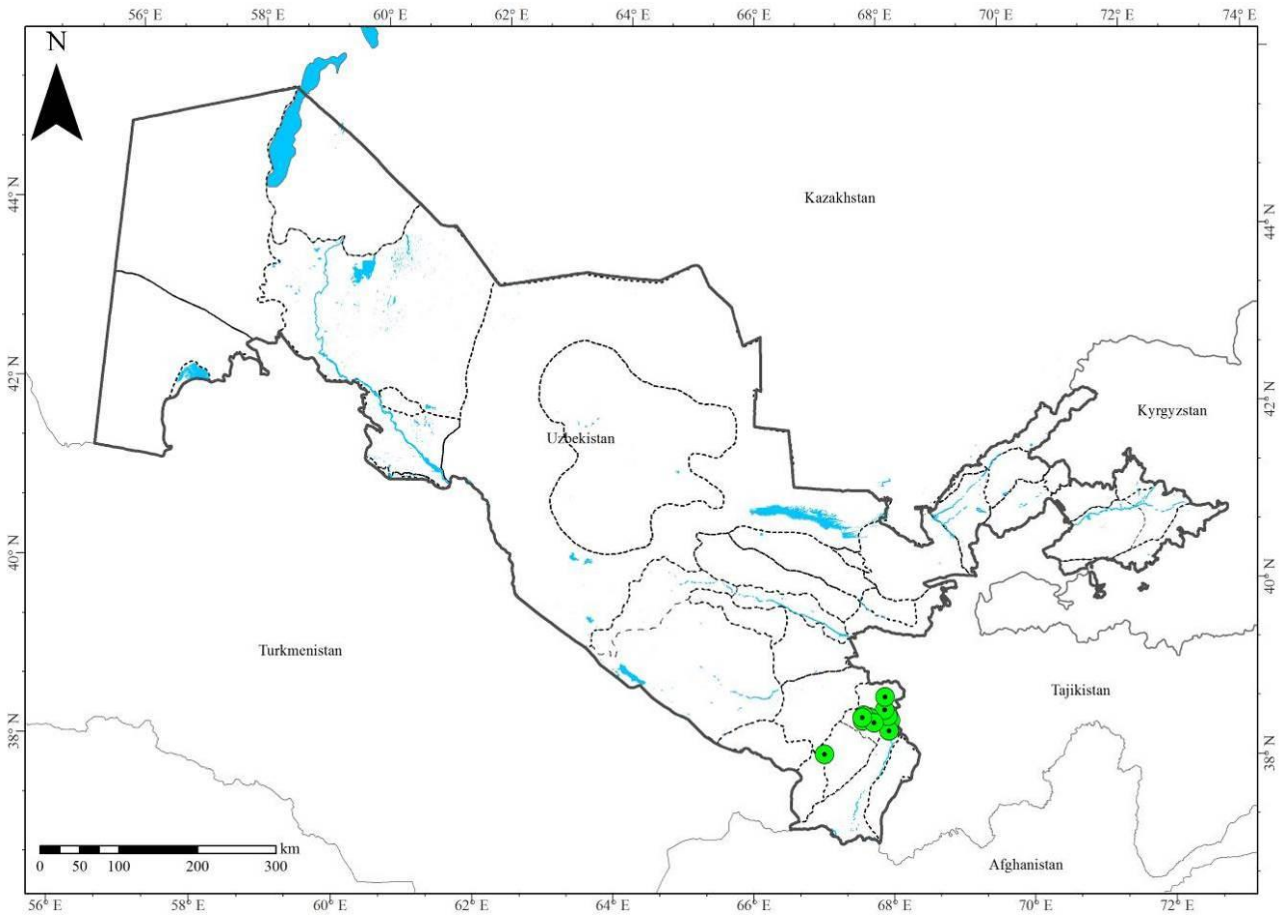


**Fig. 46.** Distribution of *Hedysarum baldshuanicum*.

**18. *Hedysarum montanum*** (B.Fedtsch.) B. Fedtsch. in V.L.Komarov (ed.), Fl. URSS 13: 292 (1948).

≡ *Hedysarum songaricum* var. *montanum* B.Fedtsch. in Trudy Imp. S.-Peterburgsk. Bot. Sada 19: 281 (1902).

**Type:**—Many syntypes from Dzhungarian Alatau, Tian-Schan and Pamir-Alay (LE).

= *Hedysarum issykkulense* Nikitina in Fl. Kirgizsk. SSR 9: 206 (1960).

**Type:**—[Kyrgyzstan]. Depression of Lake Issyk-Kul, Konurlen River valley, among the *Calamagrostis* Adans, on the pebbles, 27.06.1937, *I.V. Vykhodtseva* (holotype FRU).

**Description:**—Herbs, 40–70 cm tall, entirely glabrous, rootstock elongate, thickened, vertical, bearing many stems apically. Stems ascending or suberect, conspicuously ribbed when dry. Stipules triangular-lanceolate, brown, at least lower stipules connate at base. Leaves 10–15 cm long; leaflets 5–10 pairs, pubescent only when young, later glabrous, ovate-elliptic or oblong, rarely lanceolate, 13–20(–28) × (3–)5–8 mm, apex rounded, short mucronate. Peduncle longer than leaves. Raceme at first dense, later elongated, loose. Bracts linear subulate, 3–5 mm long. Bracteoles ca. 0.5–1 mm long. Pedicel 1–2 mm long. Calyx sparingly pubescent, teeth two to three times as long as tube, calyx teeth unequal in length. Corolla pinkish violet; standard longer than keel, limb broadly ovate, apex emarginate, 14–17 × 7–8 mm; wings half as long as keel; lower margin of keel triangular, 12 × 14 mm. Pods 3- to 5-jointed, joints finely pubescent, bristly, bristles on thickened margin longer, incurved. Seeds light or dark brown, smooth, 2–4 × 1.5–3 mm, nearly reniform or ovate (Figs 47–48).

**Flowering time:**—June.

**Fruiting time:**—June-July.

**Habitat:**—Along pebbly riverbeds on clayey and saline ridges, sandy shores of mountain

lakes, on fine earth cameo and gravelly slopes, in forb-cereal groups from high foothills to middle belt of mountains where it occurs among tree-shrub vegetation and in juniper forests. Less common in arable land, along roads (Fig. 48).


**Fig. 47.** Living plant of *Hedysarum montanum*: a, entire plant; b, leaflets (b1, upper part and b2, lower part); c, pods; d, flower; e, calyx; f, standard; g, wings; h, keel. Scale bar 1 cm.

**Distribution:**—Kazakhstan, Kyrgyzstan, Tajikistan, Uzbekistan. Distribution in Uzbekistan: Fig. 49.

**Specimens examined:**—I-3 **Fergana-Alay Region**. I-3-a **Western Alay District**: Alay ridge (valley of Sokh River right bank, 17.06.1962, *Puchkova 28, 33, 38, 40*; Sokh River, foothills, 24.05.1966, *Khalkuziev*); I-3-b **Eastern Alay District**: Alay ridge (in the vicinity of Shakhimardan, 05.06.1947, *Shafeev*; basin of the river Shakhimardan, vicinity of village Jordan, right bank of Dugobasay, 26.06.1961, *Pyataeva, Students*; Mashalang gorge, 08.06.1967, *Khalkuziev, Meliboev*; basin of Shakhimardan River, Mashalang gorge, 16.07.1968, *Khalkuziev*; Shakhimardan River basin, Yardan village, vicinity of Seismological stations, 07.06.2021, *Juramurodov, Jabbarov, Nosirov, Madaminov 7062021155, 7062021156, 7062021157, 7062021158, 7062021160, 7062021161, 7062021162, 7062021163, 7062021164, 7062021165*). I-5 **Kuhistan Region**. I-5-a **Northern Turkestan District**: Turkestan ridge (Zaamin forest cottage, right bank of the Kulsay River, 11.07.1933, *Drobov, Sakhabutdinov 159*; Zaaminsu River basin, Tuyatashsay River valley, 18.07.1935, *Zakrzhevsky 988*; in the lower part of the Kulsay valley, 14.06.1937, *Korotkova 90 185*; upper reaches of the Sanzar, Guralashsay Reserve, in the Kulsu gorge, 22.06.1937, *Korotkova, Vasilkovskaya 420, 433*; upper reaches of the Sanzar, Guralashsay reserve in lateral say on the right side of Guralash, 28.08.1937, *Korotkova, Vasilkovskaya 1200*; in the lower part of the


**Fig. 48.** *Hedysarum montanum*—a: raceme, b–c: habit of plant. Photos ‘a-b’ were taken by N. Beshko.

Kulsay valley, Chertanga, 14.06.1938, *Korotkov 185*; Guralash Nature Reserve, Kuruksay, 16.07.1945, *Nazarenko*; Guralash Nature Reserve, Kulsay, 17.07.1947, *Nazarenko*; Zaaminsu River basin, Kulsay, 28.06.1949, *Korotkova 2246*; Jizzakh forestry around village Kzilmazar, 23.07.1958, *Gorzova*; Guralash Nature Reserve, juniper belt, 31.10.1959, *Pyataeva, Yuldashev 7, 99*; Jizzakh region, Zaamin District, Togterak say, 05.06.1978, *Makhkamova*; Zaamin National Park, near the Zaamin Sanatorium, 21.06.2019, *Juramurodov 51a*, *51b*, *51c*, *51d*). I-7 **Hissar-Darvaz Region**. I-7-a **Sangardak-Tupalang District**: Hissar ridge (around Sangardak, 1.5-2 km to Sakhonkir, 31.05.1968, *Mustafaev 120*; basin of the Sangardak River, village Khandiza, 23.05.1971, *Jumaev*). All specimens are at TASH.

**Notes:**—Most herbarium specimens collected in the North Turkestan District were initially identified by the collectors as *H. songaricum* Bong. As a result, based on these specimens, *H. songaricum* was included in the list of species of *Hedysarum* in Uzbekistan. Our further investigation found hairs on the pods, indicating that these herbarium specimens corresponded to *H. montanum*. Kovalevskaya also identified these specimens as *H. montanum*. Furthermore, our 2019 field research in North Turkestan District revealed that *H. montanum* is extensive in this region. We recommend deleting *H. songaricum* from the flora of Uzbekistan and replacing it with *H. montanum*.

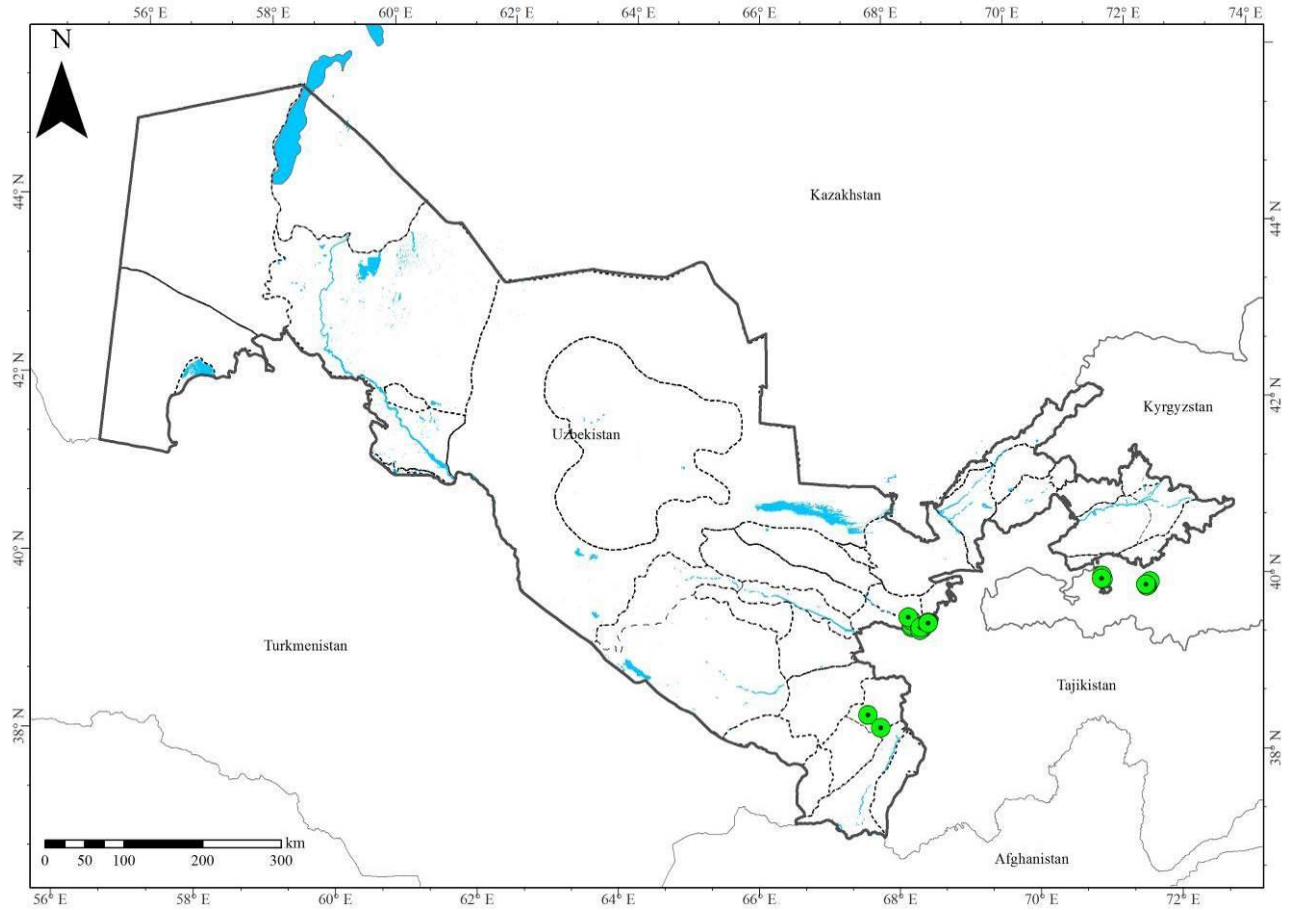


**Fig. 49.** Distribution of *Hedysarum montanum*.

**19. *Hedysarum iomuticum*** B. Fedtsch. in Trudy Imp. S.-Peterburgsk. Bot. Sada 19: 246 (1902).

**Type:**—Tajikistan. Gazy-Mailik Mts., Iomut, *A. Regel*; between Vaxsh and Kafirnigan, 13.05.1883, *A. Regel* (syntypes LE).

= *Hedysarum babatagicum* Korotkova in Bot. Mater. Gerb. Inst. Bot. Zool. Akad. Nauk Uzbeksk. S.S.R. 9: 12 (1947).

**Type:**—[Tajikistan or Uzbekistan]. Southwestern Pamir-Alai, Babatag Mountains, screes of gray clays along 'Babi-Cheka' [Bibi-Cheka] say, 14.07.1936, fr., *S. Lepeshkin & A. Mukhamedzhanov 576* (holotype TASH barcode 001949!).

**Description:**—Herbs, 60–100 cm tall, covered with short appressed silvery hairs. Stems erect or slightly ascending, 3–5(6) mm in diameter. Stipules 10–15 mm long, not connate on upper leaves, falcate. Leaves 10–15 cm long; leaflets 3–5 pairs, 20–40 mm long, 30 mm wide, rather fleshy, orbicular-ovate, apex acute or rounded, densely silvery hairy when young, subglabrous after flowering. Peduncle (with raceme) distinctly longer than leaves. Racemes loose. Bracts before flowering as long as buds, ovate, hairy outside, 7–12 mm long. Bracteoles lanceolate, as long as calyx tube. Pedicel 3.5–4.5 mm long. Calyx campanulate, appressed hairy, teeth lanceolate-subulate, triangular at base, upper teeth shorter than tube, lower teeth nearly as long as tube. Corolla pale violet; standard obovate, apex rounded, abruptly tapering to claw, 17–20 × 10–18 mm; wings lanceolate, 8–12 × 3–5 mm; keel 15–25 × 7–10 mm; ovary linear, hairy; ovules 3 or 4. Pods rounded, joints 2–5, ribbed, densely short hairy, edges and sides with short hard prickles, 7–10 × 6–8 mm; seeds reniform, dark brown, 3–4 × 2–3 mm (Figs 50–51).

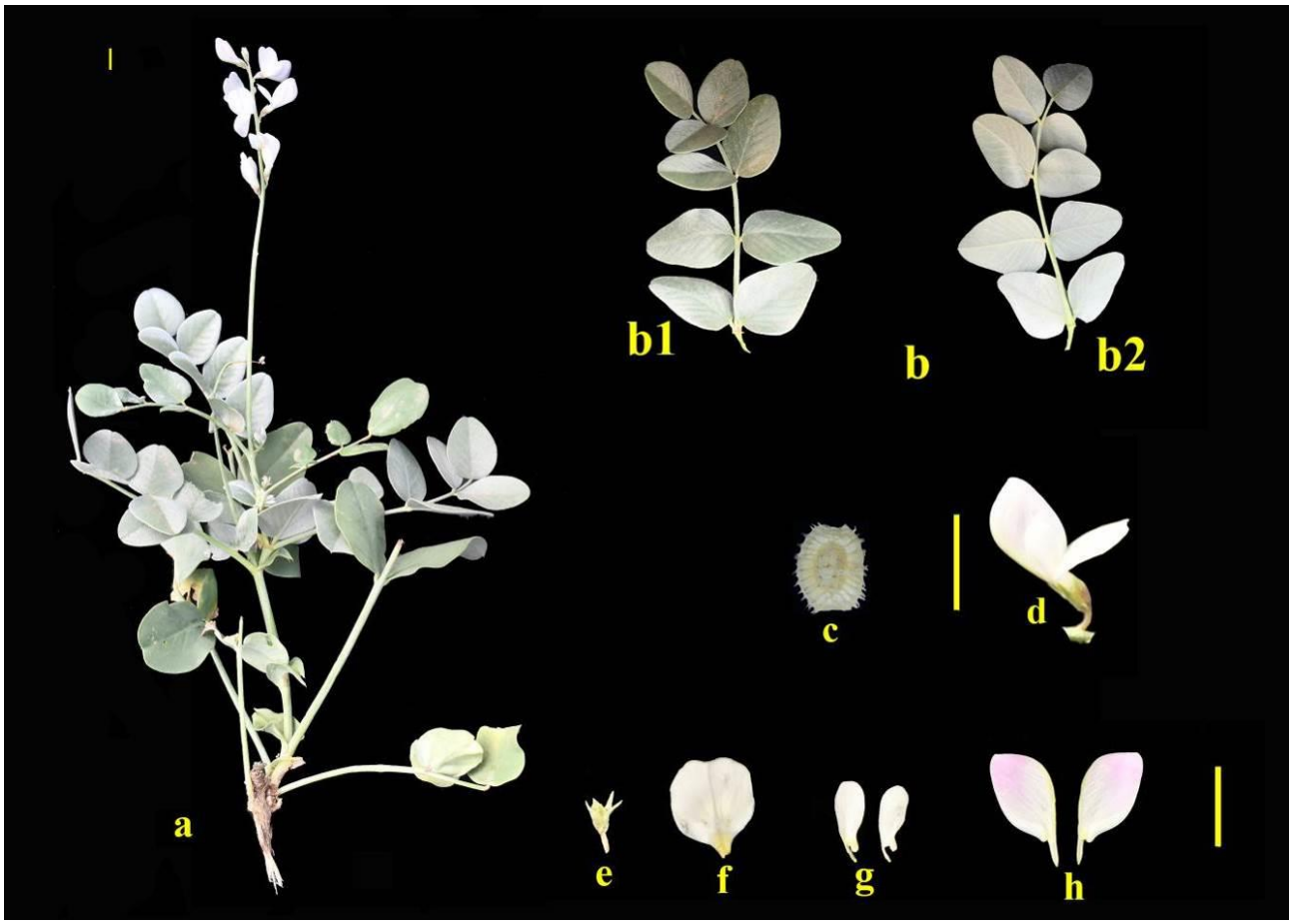


**Fig. 50.** Living plant of *Hedysarum iomuticum*: a, entire plant; b, leaflets (b1, upper part and b2, lower part); c, pod; d, flower; e, calyx; f, standard; g, wings; h, keel. Scale bar 1 cm.

**Flowering time:**—May.

**Fruiting time:**—May-June.

**Habitat:**—On outcrops of variegated rocks, outcrops of red clays and sandstones, less often on fine earth-rubbly terraces, screes, in pistachio, ephemeral-sagebrush associations in the foothills.

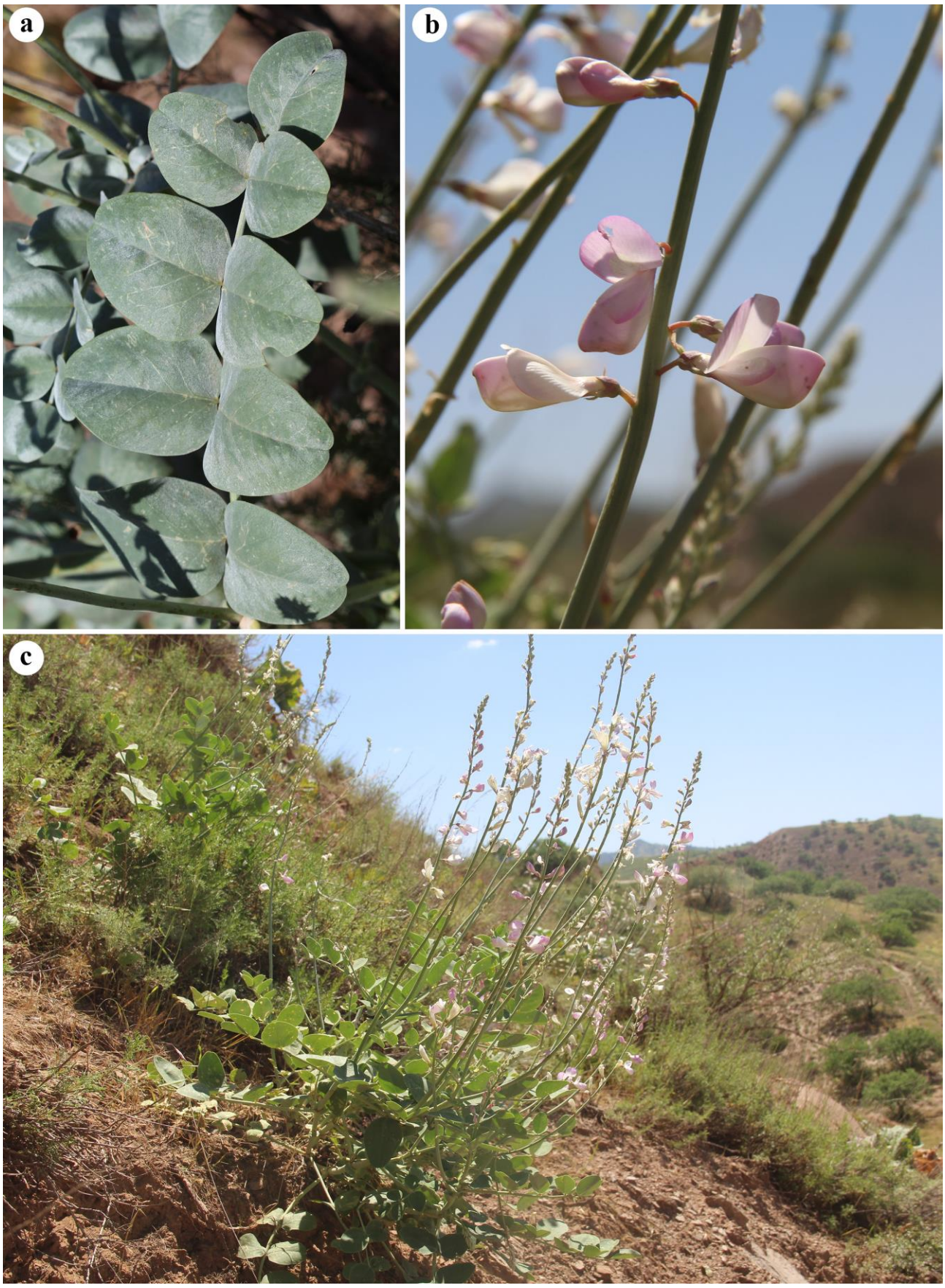


**Fig. 51.** *Hedysarum iomuticum*—a: leaf, b: raceme, c: habit of plant.

**Distribution:**—Tajikistan and Uzbekistan. Distribution in Uzbekistan: Fig. 52.

**Specimens examined:**—I-6 **Western Hissar Region**. I-6-c **Baysun District**: Hissar ridge (Baysun, on outcrops of variegated rocks near the Tashkak village, 08.05.1930, *Botchantsev, Vvedensky* (TASH, MW); Byuryutakht Mountains, plastered slopes of cliffs to the south of Bitau, 13.05.1930, *Lepeshkin* (TASH, MW); Khodzhaipak in the foothills of the Chulbair Mountains, 15.05.1930, *Botchantsev*; on rocky-fine-grained gypsum slopes near the Khodjaipak spring in the foothills of the Chulbair Mountains, 15.05.1930, *Botschantsev, Vvedensky* (MW); fine-grained gypsum slopes of the Surkhi gorge near the village of Sina and the foothills of the Chulbair Mountains, 03.06.1930, *Nikiforova, Popov* (MW); Gadzhirkaya Mountains, gypsum outcrops on the slopes, 05.06.1930, *Lepeshkin*; Byuryutakht Mountains, 04.19.1941, *Popova 218*; on the way from winter Bishtau to Byuryutakht, 05.05.1941, *Popova 323, 343*; Byuryutakht Mountains, northern slopes, 04.06.1941, *Popova 625* (TASH); the foothills of the Chulbair Mountain, near the village of Khodjaipak, 26.05.1977, *Bochantsev 417* (LE); Chulbair Mountain, near the village of Sina, 30.05.1978, *Bochantsev 156* (LE)). I-7 **Hissar-Darvaz Region**. I-7-a **Sangardak-Tupalang District**: Hissar ridge (valley of the Sangardak River between the Bakhcha village and the spring of Sharakat sloped the mountains, 31.05.1948, *Bondarenko 846*; right bank of the Tupolang River, Gazarak village, 15.06.1948, *Pyataeva*; basin of the Tupolang River, middle course of the Malyandarya River, 15.06.1948, *Pyataeva 427*). I-8 **Panj Region**. I-8-a **Babatag District**: Babatag ridge (outcrops of red and gray sandstones and clays with gypsum after Bibichek sago, 15.07.1936, *Lepeshkin, Mukhamedzhanov 580*; Biyasimas, 04.05.1940,

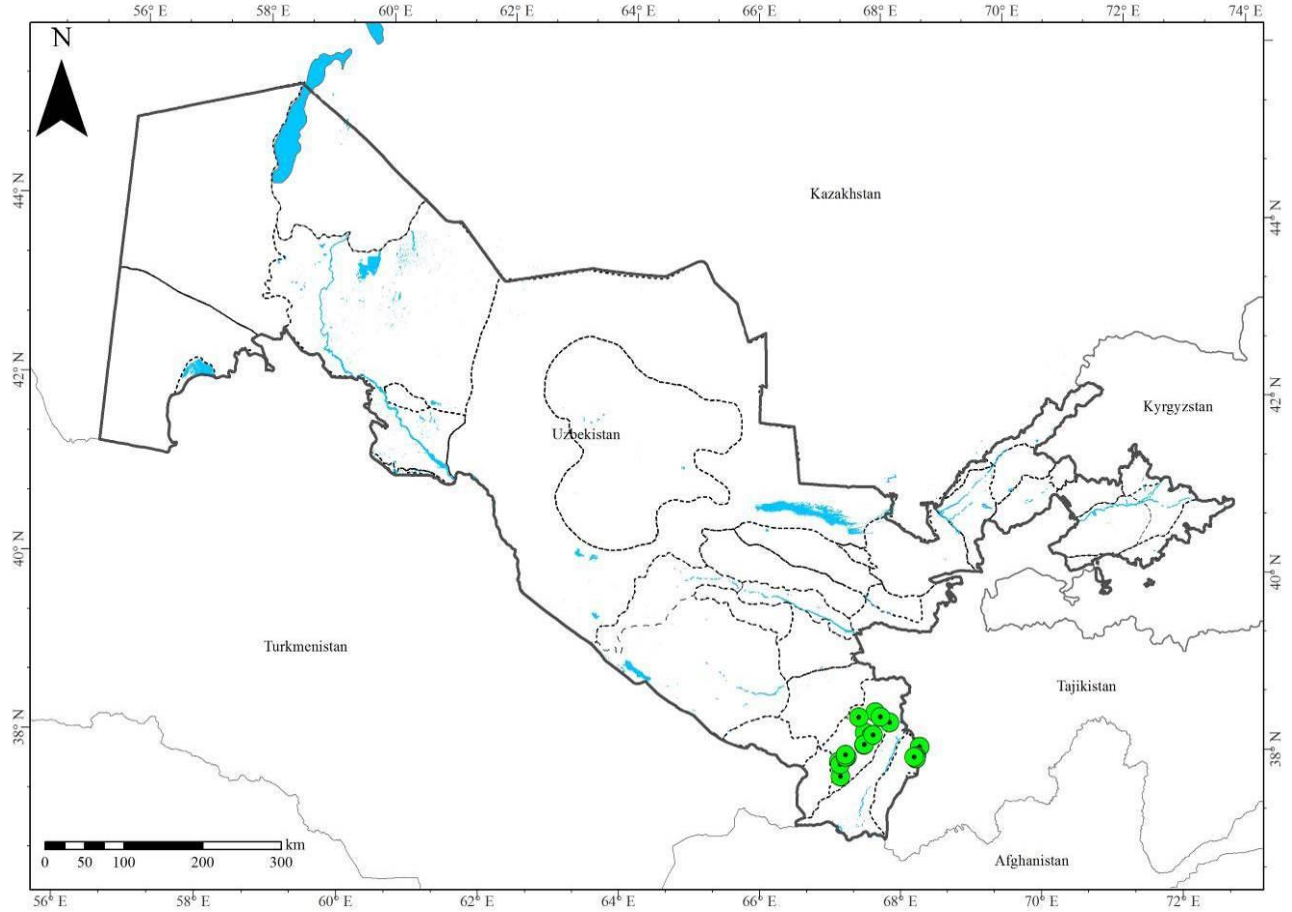


**Fig. 52.** Distribution of *Hedysarum iomuticum*.

*Bukasov 21*; between village *Hodzhakulsun* and village Naubad, 17.05.1941, *Lopott, Pinkhasov 282*; in the vicinity of village Chagam, 26.05.2019, *Pulatov, Jabborov*; vicinity village Chagam, 23.05.2020, *Pulatov, Juramurodov, Jabborov, Rakhmatov, Makhmudjanov, Madaminov, Habibullaev, 23052020373, 23052020375, 23052020378, 23052020379, 23052020384, 23052020396*). Specimens in TASH unless otherwise specified.

**20. *Hedysarum santalaschi*** B. Fedtsch. in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 11: 116 (1949).

**Type:**—[Kyrgyzstan]. In jugo Bischttir et Atschiktasch in valle Santalasch, 14.07.1938, *O. Neustrujeva-Knorring* (holotype LE).

**Description:**—Herbs, not more than 15 cm tall, rootstock firm, 7–8 mm thick, strongly branching apically, branches brown, leafless, 5–6 mm long, bearing at apex short annotinous, shoots 3–5 cm long at onset of anthesis, green, sparingly appressed hairy, consisting of 2–4 short internodes. Stipules brown, oblong-lanceolate, sparingly pubescent, free or nearly so at one side (opposite petiole). Leaves 3–5 cm long, lower leaves with longer petiole, sparsely appressed hairy; leaflets 5–8 pairs, linear-lanceolate, acuminate, 6–10 × 1–3 mm. Peduncle (without raceme) about as long as leaves. Racemes loose. Bracts ca 2 mm long. Bracteoles ca. 0.5–0.7 mm long. Pedicel ca. 1–3 mm long. Calyx campanulate, brown, teeth slightly longer than tube. Corolla pinkish lilac; standard wide, orbicular-ovate, apex truncate, 10–11 mm long; wings 4–5 mm long, subrectangular, apex somewhat rounded, with short tooth at base; keel as long as standard, lower margin of limb rounded-obtuse angular, apex somewhat attenuate. Pods 2- to 4-jointed, joints orbicular-ovate, 7 × 6 mm wide, finely appressed hairy, marginal third of joint surface with about 10 smooth inconspicuous ribs, middle part with reddish bristles less than l mm long. Seeds light brown, reniform, 3–3.5 × 2.5 mm (Fig. 53)

**Flowering time:**—July-August.

**Fruiting time:**—August.

**Habitat:**—On gravelly screes, fine earth-gravelly slopes in upper mountain belt.

**Distribution:**—Kyrgyzstan and Uzbekistan. Distribution in Uzbekistan: Fig. 54.

**Specimens examined:**—I-1 **Western Tian-Shan Region**. I-1-b **Western Chatkal District**: Chatkal ridge (the Chatkal River valley, basin of the Akbulak River, upper reaches of Sargardonsay, Mingbulak tract, 01.07.1957, *Nabiev 1095* (TASH)).

**Notes:**—Because only one specimen of *Hedysarum santalaschi* is in TASH, all molecular phylogenetic and morphometric analyses were based on this single sample (Fig. 53). The species occurs in an area near the border of Uzbekistan and Kyrgyzstan, which makes it challenging to conduct field research in that region.


**Fig. 53.** Herbarium specimen of *Hedysarum santalaschi*.

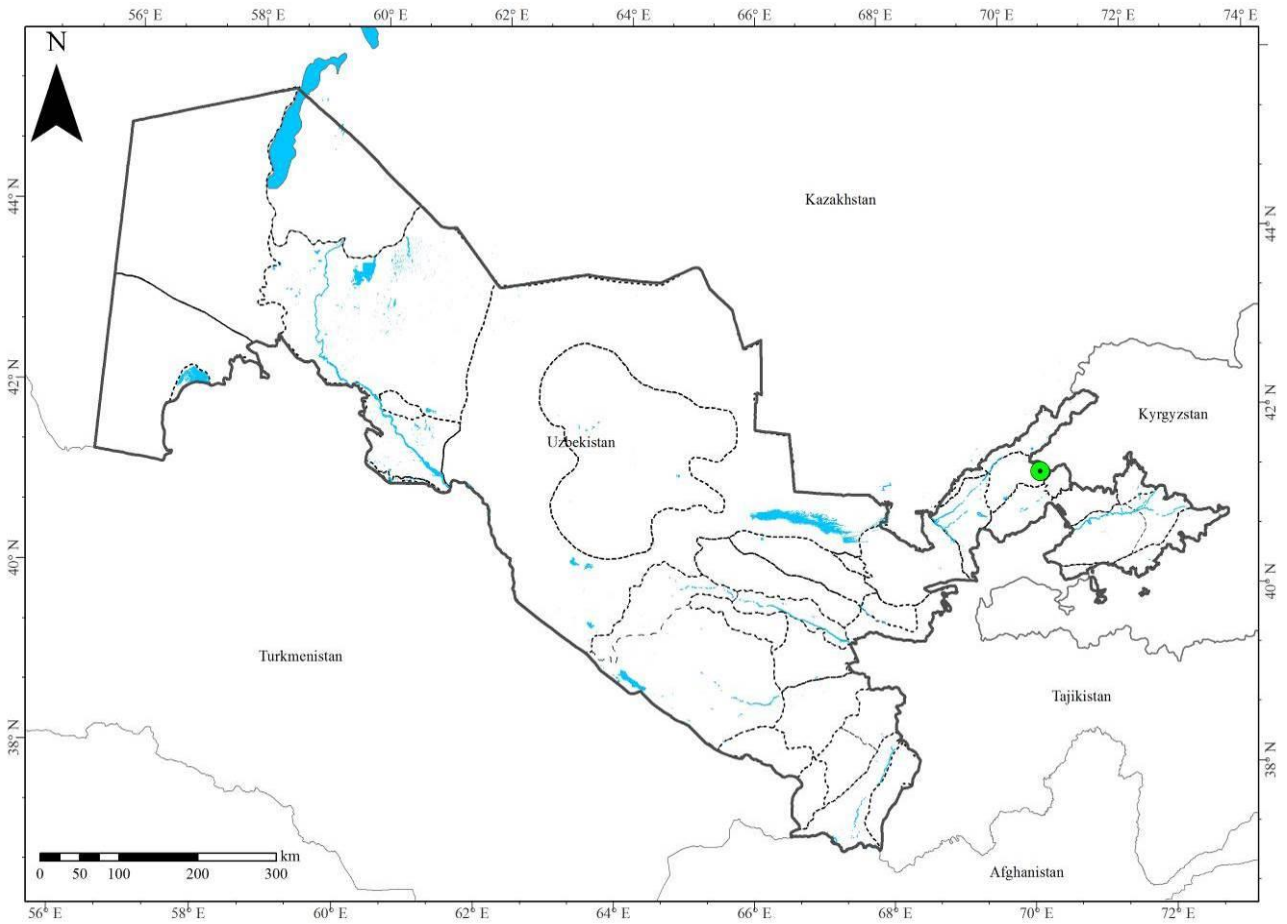


**Fig. 54.** Distribution of *Hedysarum santalaschi*.

**21.** ***Hedysarum bucharicum*** B. Fedtsch. in Trudy Imp. S.-Peterburgsk. Bot. Sada 19: 322 (1902).

**Type:**—[Uzbekistan]. Bukhara, Jakkabag: Darwasa-kam, 17.06.1896, *Lipsky* (holotype LE).

= *Hedysarum pamiralaicum* Korotkova in Bot. Mater. Gerb. Inst. Bot. Zool. Akad. Nauk Uzbeksk. S.S.R. 9: 7 (1947).

**Type:**—Uzbekistan. Xoja-Gurgur-Ata Mts., upper reaches of Kyzylnaursay, 19.07.1934, *A. Butkov* (holotype TASH barcode 001977!).

= *Hedysarum purpureopilosum* Kitam. in Acta Phytotax. Geobot. 17: 137 (1958).

**Type:**—Afghanistan. Shishigar, 11.06.1955, *S.Kitamura* (holotype KYO).

**Description:**—Herbs, 15–20 cm tall. Stems thin, ascending, whole plant sparingly appressed hairy. Stipules pale, connate at base, triangular-lanceolate. Leaves 4–10 cm long; leaflets 5–8 pairs, oblong-lanceolate, 14–18 × 2–8 mm. Peduncle longer than leaves. Racemes 12- to 25-flowered, loose post anthesis. Bracts persistent, hairy, ca. 3 mm long. Bracteoles 2.5–3 mm long. Pedicel ca. 1 mm long. Calyx pubescent, teeth lanceolate, one and half to two times as long as tube. Corolla bright violet; standard 9–12 × 7–8 mm, obovoid; wings (2.5–)3–4 × 1.5–2 mm; keel 9–11 × 3.5–4 mm, almost triangular. Ovary pubescent. Pods 1- to 3-jointed; joints 5–8, gray, rounded, 8–10 × 7 mm, with transverse ribs with few reddish prickles on each. Seeds nearly rounded, brown, 3.5–4 × 2.5–3 mm (Fig. 55).

**Flowering time:**—April-May

**Fruiting time:**—June-July.

**Habitat:**—On outcrops of variegated rocks, fine earth-rubbly slopes, in almond groves, rose gardens and juniper forests (Fig. 55a).

**Distribution:**—Uzbekistan, Afghanistan and Iran. Distribution in Uzbekistan: Fig. 56.

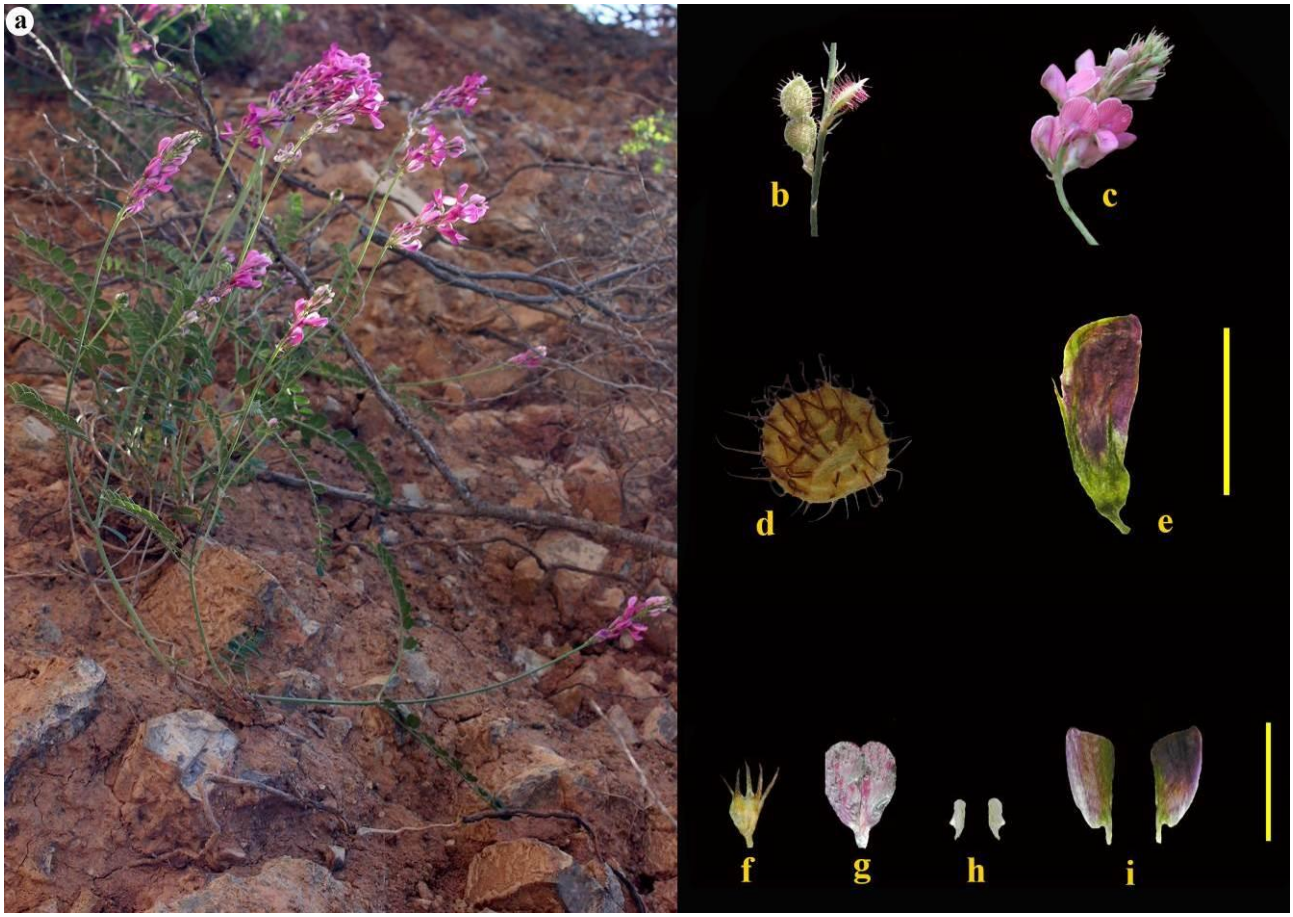


**Fig. 55.** Living plant of *Hedysarum bucharicum*: a, habit of plant; b, pods; c, raceme; d, pod; e, flower; f, calyx; g, standard; h, wings; i, keel. Scale to 1 cm. Photo 'a' was taken by N. Beshko.

**Specimens examined:**—I-6 **Western Hissar Region**. I-6-a **Kashkadarya District.** Hissar ridge (tract Kara and Shiran near Tashkurgan, 30.05.1916, *Popov 1094*; low mountains to the south-east from the Guzar city, Kattauru River, gypsum outcrops along Kyzylsay, 09.06.1935, *Lepeshkin 11*; upper reaches of the river Yakkabagdarya, around village Tashkurgan, outcrops of variegated rocks in Turk at the lane, Kizylgaz, 21.06.1936, *Botchantsev* and *Butkov 177*; Ishkent, 20.07.1942, *Arnolds*; Kyzylmazar, 25.07.1942, *Arnoldy*; Kichikuradarya River valley 62 km east of village Derab, 16.05.1959, *Lee, Niyazov 403*; Langar River basin, river valley Aksu, between villages Kyzyl and Kyzylmechat, 14.05.1972, *Nabiev, Shermatov, Kazakboev 59*; Suykbulak pass, 16.06.1913, *Vasilevskaya 707* (LE); Yakkabag Daria, near to village Tashkurgan, 21.06.1936, *Bochantsev, Butkov 177* (LE)); I-6-b **Tarkapchigay District:** Hissar ridge (around village Akrabat, 27.05.1941, *Popova 538*; Dekhkanabad District, village Chakchak, 25.05.2019, *Abduraimov c-5*; above village Tarkapchigay, 31.05.????, *Kamelin et al. 657* (LE)); I-6-c **Baysun District:** Hissar ridge (Khodjagurgurat Mountains, upper reaches of Chakmaksay, 16.08.1934, *Demurina 751, 753*; Khoja-Gur-Gur-Ata Mountains, left bank, Chakmaksay Rivers, 01.07.2020, *Ortikov, Turdiev, Juramurodov 1072020072, 1072020073, 1072020074*). Specimens in TASH unless otherwise specified.

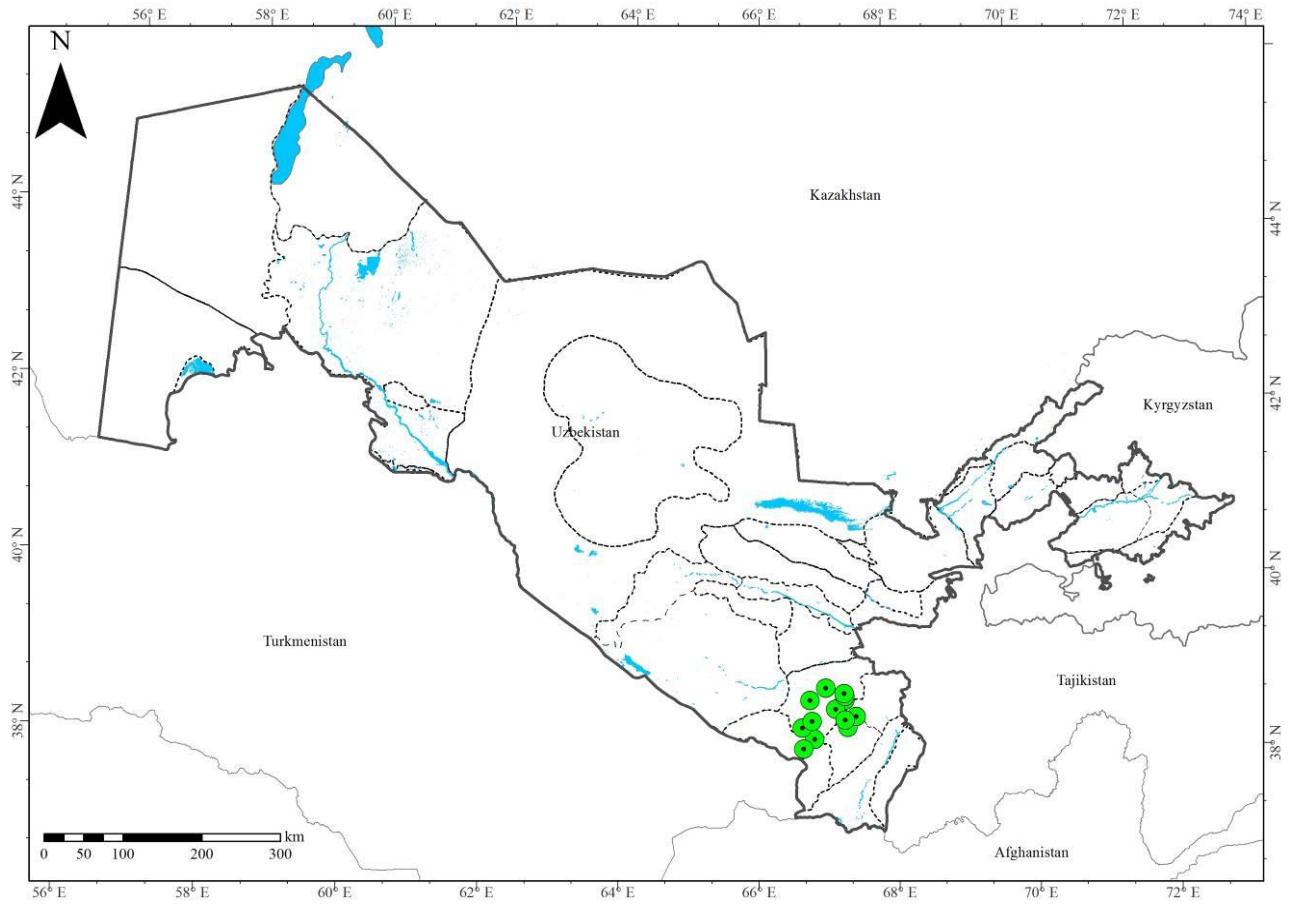


**Fig. 56.** Distribution of *Hedysarum bucharicum*.

**22.** ***Hedysarum turkestanicum*** Regel & Schmalh. in Izv. Imp. Obshch. Lyubit. Estestv. Moskovsk. Univ. 34(2): 21 (1882).

**Type:**—[Kyrgyzstan]. Described from Mount Daigor in Fergana (holotype LE).

= *Hedysarum alabukense* Nikitina in Fl. Kirgiz. SSR, Suppl. 1: 114 (1967).

**Type:**—In declivibus argillosis jugi Czatkalensis, regio praemontana in vicinitate pagi Ala-Buka, 29.06.1960, *A.Ubukeeva* (holotype FRU).

**Description:**—Herbs, 20–40 cm tall, appressed hairy. Stems suberect or ascending, thin, cylindrical, hardly angular, sparsely pubescent (epidermis visible). Stipules long connate, deciduous. Leaves 3–8 cm long; leaflets 4–6 pairs, flat, oblong or elliptic, 12–25 × 3–6 mm. Peduncle (without raceme) longer than leaves. Racemes rather dense, many-flowered. Bracts shorter than pedicels. Bracteoles 1.2–1.4 mm long. Pedicel 1.5–1.8 mm long. Calyx appressed hairy, teeth subulate, twice as long as tube. Corolla pink; standard 11–12 mm long, post anthesis distinctly shorter, limb oblong-elliptic; wings one-third to one-half as long as keel, 5–6 mm long; keel 13–14 mm long. Pods 3- to 5-jointed, joints ca. 5 mm long, ribbed, with sparse white hairs and prickles elongating into long reddish bristles. Seeds brown, 2.5–3 × 2 mm (Figs 57–58).

**Flowering time:**—May-June.

**Fruiting time:**—June.

**Habitat:**—On fine earth slopes in grass-forb groups and outcrops of variegated rocks in foothills (Fig. 57).

**Distribution:**—Kyrgyzstan and Uzbekistan. Distribution in Uzbekistan: Fig. 59.

**Specimens examined:**—I-2 **Fergana Region**. I-2-a **Southern Chatkal District**: Chatkal ridge (Nanai, 19.07.1951, *Galkina*; Namangan region, Yangikurgan District, Nanai villages, 17.05.2020, *Ortikov 67*; Nanai villages, 29.05.2021, *Juramurodov, Gulomov 2905202110, 2905202106, 2905202107, 2905202108, 2905202106*). All specimens are at TASH.


**Fig. 58.** *Hedysarum turkestanicum*—a, c: habit of plant, b: pods.


**Fig. 57.** Living plant of *Hedysarum turkestanicum*: a, entire plant; b, flower; c, pods; d, calyx; e, standard; f, wings; g, keel. Scale bar 1 cm.

**Fig. 59.** Distribution of *Hedysarum turkestanicum*.

**23. *Hedysarum taschkendicum*** Popov in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 7: 15 (1937).

**Type:**—[Kazakhstan]. Tian-schan occidentalis, ad declivia collium argillosa pr. st. v. f. Sary-Agatach, 29.05.1928, fl. et fr., *Granitov 636* (holotype TASH barcode 001981!).

**Description:**—Herbs, 20–45 cm tall. Stems nodose, elongate, sparsely pubescent (epidermis visible). Stipules submembranous, linear-subulate, elongate, hardly connate. Leaves 10–15 cm long; leaflets 4–7 pairs, oblong or linear-oblong, sometimes narrowly so, acute or obtuse, nerves prominent, 10–45 × 2.5–8–12 mm. Peduncle terminal, straight or slightly curved, distinctly longer than leaves. Racemes rather dense, oblong, 3–7 cm long, 25- to 40-flowered. Bracts lanceolate, 4–5 mm long. Bracteoles 1.5–2 mm long. Pedicel erect or declinate, shorter than calyx, 1–4 mm long. Calyx teeth unequal, grayish, teeth subulate, pointed upwards, as long as or 1–3 times longer than tube. Corolla pinkish lilac or whitish pink; standard half to two-thirds as long as keel, limb oblong-ovate, dilated distally, apex emarginate, 8–13 × 8–11 mm; wings one fourth as long as keel, 4–7 × 2–2.5 mm; keel narrowly oblong, hardly dilated distally, lower margin nearly triangularly curved, 13–16 × 5–7 mm. Ovary pubescent. Pods 2- to 4-jointed, joints suborbicular, 7–10 × 6–8 mm, densely pubescent, with large rough bristles on thick nerves; bristles of mixed length, not hairlike, shorter ones red, longer ones not red. Seeds dark brown, ovate or reniform, flat, 3–3.5 × 2.5–3 mm (Figs 60–61).

**Flowering time:**—May-July.

**Fruiting time:**—June-August.

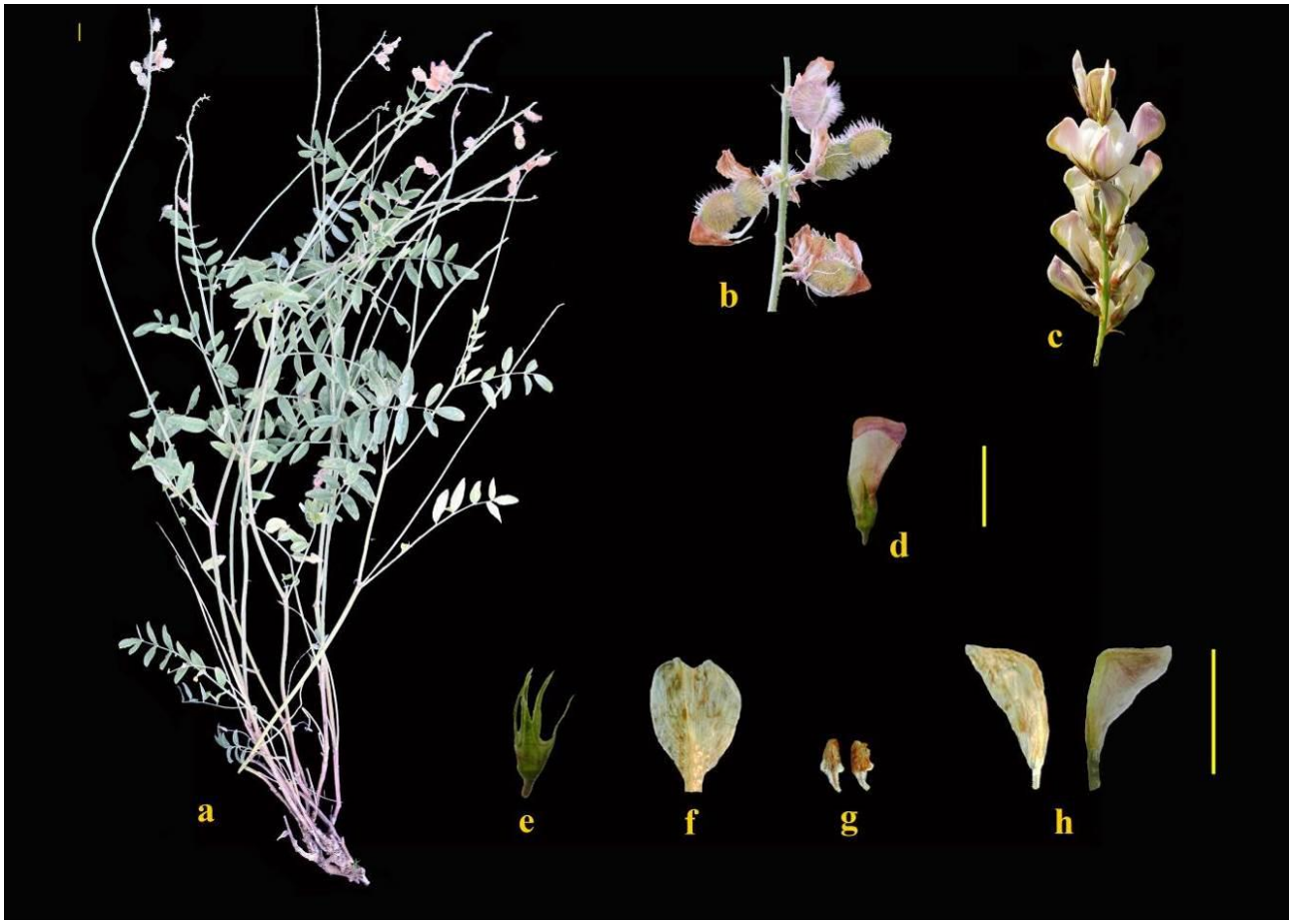


**Fig. 60.** Living plant of *Hedysarum taschkendicum*. a, entire plant; b, pods; c, raceme; d, flower; e, calyx; f, standard; g, wings; h, keel. Scale bar 1 cm.

**Habitat:**—On loess cliffs and slopes, dry stony and rubbly slopes, red clay outcrops, on deposits in foothills, up to lower (rarely middle) belt of mountains where it occurs on fine earth-stony slopes among trees and shrubs (Fig. 61).
**Distribution:**—Kazakhstan and Uzbekistan. Distribution in Uzbekistan: Fig. 62.
**Specimens examined:**—I-1 **Western Tian-Shan Region**. I-1-b **Western Chatkal District**: Chatkal ridge (Chimgan tract, 27.07.1919, Ambrak, right bank of the Kangli River, 28.05.1922, *Korovin 1209*; Chimgan tract, 07.07.1926, *Popov 21*; near the Chimgan Botanical Station, Melovoy pass, 20.07.1926, *Mokeeva*; Chimgan, 27.06.1934, *Alekseeva 283*; near the village Nevich, 19.06.1936, *Korotkova, Titov 368, 370*; Nurekata valley, 25.07.1936, *Korotkova, Titov 1679*; tract river Bashkyzylsay, 27.07.1936, *Korotkova, Titov 1756, 1785*; Sokaksay River basin, northwest slope of the left side of Kattasay, 1938, *Saranskaya, Klima 417*; Sokaksay River basin, northern slope of Bumardak, 21.06.1938, *Saranskaya, Klima 134, 135, 161*; Sokaksay River basin, watershed of Tashkesken and Kuduksay, 16.07.1938, *Saranskaya, Klima 313*; large Chimgan, *Pyataeva 184*; around Nevich village, 26.06.1947, *Pyataeva, Students 10, 75*; village Nevich, 27.06.1947, *Botchantsev, Vvedensky*; around Zarkent, 27.06.1949, *Students 36*; Tashkent Alatau mountains, basin of Aksakatasay, near Altynbel pass, 29.07.1953, *Maylun, Nabiev, Zuckerwanik 970*; Aktash tract, 28.06.1956, *Granitov, Zuckerwanik 386*; Aktash tract, right bank of Akbulaksay, 28.06.1956, *Granitov, Zuckerwanik 314*; upper reaches of Galvasaya, Melovoy pass, 08.07.1956, *Granitov, Zuckerwanik 768*; Melevoy pass, 08.07.1956, *Granitov, Zuckerwanik 751*; upper reaches of the Chimgan River, 01.06.1961, *Adylov 1667*; southern slope of Bashkyzylsay, 28.06.1961, *Melimuradov, Nazarov*; Bashkyzylsay, Adyr zone, 28.06.1961, *Absusalamov, Baikabulov*; Bashkizilsay River, Chatkal Mountain forest reserve southern slope, 24.06.1971, *Adylov*; upper reaches of Kaznakoksay, left tributary of Bashkizilsay, 06.07.1972, *Adylov 14*; tracts Kukar, 20.07.1972, *Adylov 90*; river floodplain Aksakata, 20.06.1973, *Pratov, Kazakboev*; Tashkent Alatau, Parkent District, left bank of Karamansay, 08.06.2019, *Juramurodov 88, 89*; Big Chimgan, 01.07.2019, *Juramurodov*; Big Chimgan, 19.06.2020, *Dekhkanov, Ortikov, Turdiev, Juramurodov 19062020086, 19062020087*; upper reaches of Beldersay, near the Meteorological station, 18.06.2020, *Dekhkanov, Ortikov, Turdiev, Juramurodov 18062020046, 18062020047*; clay cliffs to the riverbed of the tributary of the Chirchik River near the Barrage station, 01.06.1952, *Uvelev* (LE); Bashkyzylsay, Parkent District, 19.06.1960, *Salikhova, Amiraev* (LE)); I-1-d **Kurama District**: Kurama ridge (between the Angren and Inklob state farms, 1934, *Lavrenov*; left bank of the Angren River, middle course of the Koshrabat River, 22.06.1924, *Korovin 398*; left bank of the Angren River, against Ablyk, 22.06.1924, *Korovin 348, 352*; right bank Iertashsay River, 21.07.1938, *Pyataeva, Momotov 83*; Saukbulak River basin, near Sardzhailak village, 19.06.1939, *Kudryashev 133*; say Nishbash with its tributary Lashkerek, 09.07.1939, *Demurina 50*; village Gulbak, 03.08.1939, *Mironov 511, 510, 518*; Almalyk, 20.05.1940, *Vasilkovskaya 141*; 8-10 km south of Almalyk low Karabel Mountains, 25.05.1940, *Vasilkovskaya 169*; Lyashkaraksay, on northern slopes, 09.06.1940, *Korotkova 146;* Nishbashsay, around Tugai, 10.06.1940, *Usmanov 866*; village Baksuk, 11.06.1954, *Li, Mailun 124*; 15 km south of Angren city, 20.07.1960, *Vasiliev*; Gushsay, right bank 7-8 km southeast from its confluence with Angren, 13.06.1963, *Bulgakov 36907*; Kamchik pass, 12.08.1969, *Baikabilov, Ashurmetov, Normatov*; Almalyk, in ephemeral vegetation on slopes, 20.05.1940, *Vashlkovshaya 141* (LE); Yangaklksay (small) valley of the Angren River, left bank, on slopes, 06.07.1954, *Knorring 84* (LE); Angren River valley, 16 km below the city of Angren, 17.05.1965, *Pavlov 116* (LE); Angren River valley, 16 km below the city of Angren, 17.05.1965, *Pavlov 116* (MW)), Chatkal ridge (village Karakhtai, 02.07.1939, *Mironov 184*; village Karakhtai, 16.07.1939, *Kuznetsova*; Irtashsay, eastern slope, 17.08.1939, *Kudryashev 1191*;

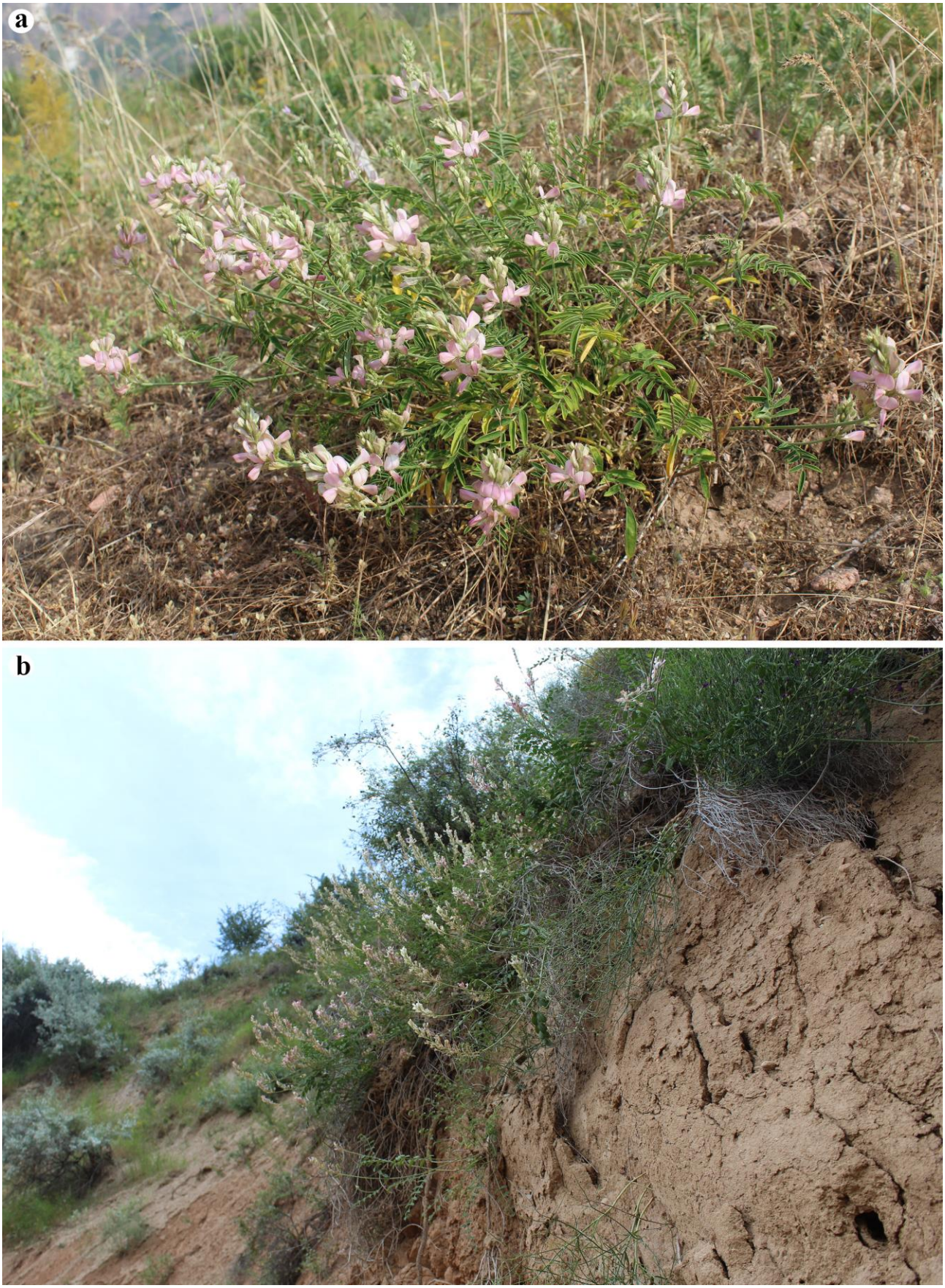


**Fig. 61.** *Hedysarum taschkendicum* —a–b: habit of plant.

Shavazikolonsaya, western slope, 09.08.1952, *Gubaidulina*; upper reaches of Shavazikolonsaya, 16.07.1953, *Gubaidulina*; upper reaches of Shavazikolsay, 09.08.1953, *Maylun, Nabiev, Zuckerwanik 1194*; Angren-Kokand road 2 km from the village Akhmedabad, 13.08.1969, *Baikabilov, Ashurmetov, Normatov*; Mountain Forest Reserve, Iransay, 25.07.1956, *Sochkov* (LE)); I-1-f **near-Tashkent District** (village Akkovaka, 29.05.1922, *Korovin 1257*). Specimens in TASH unless otherwise specified.

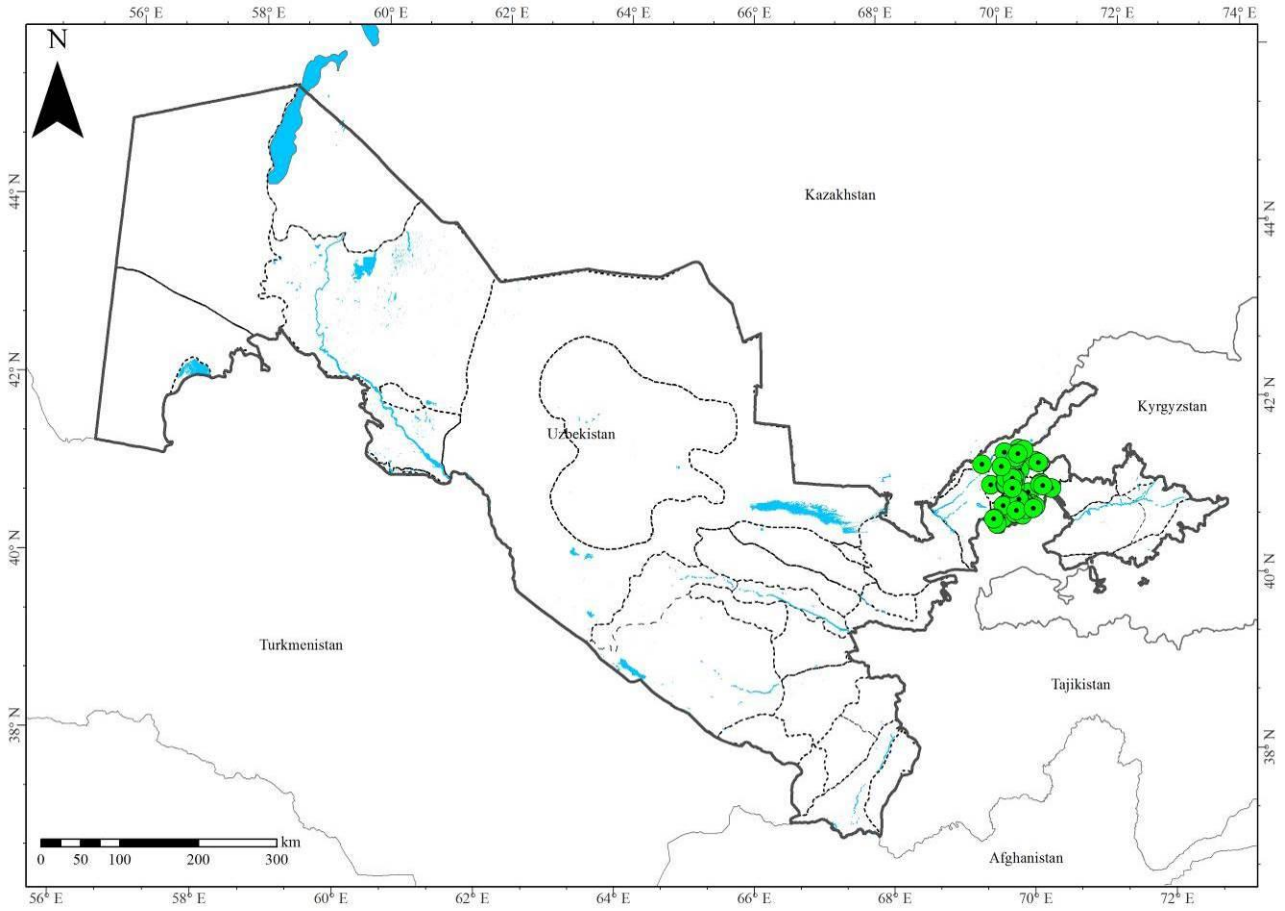


**Fig. 62.** Distribution of *Hedysarum taschkendicum.*

**24.** ***Hedysarum nuratense*** Popov in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 7: 16 (1937).

**Type:**—[Uzbekistan] In montibus Nuratau prope Dzhizak, *Spiridonov* (holotype LE).

**Description:**—Herbs, 20–40 cm tall. Stems elongate, sparsely pubescent (epidermis visible). Stipules submembranous, linear-subulate, elongate, hardly connate. Leaves 6–13 cm long; leaflets 4 or 5 pairs, flat, oblong or oblong-linear, 15–20 × 4–13 mm, obtuse or acute, abaxially more densely white hairy, with prominent lateral nerves. Peduncle terminal, hardly longer than leaves (excluding raceme). Racemes short at first, later elongating, narrow. Bracts 8–10 mm long, lanceolate, densely hairy. Bracteoles 1.5–2 mm long. Pedicel 1–1.2 mm long. Calyx teeth linear-subulate, three to four times as long as tube, nearly as long as corolla. Corolla pinkish lilac; standard nearly as long as keel at anthesis, with limb oblong-ovate, 12–15 × 8–10(12) mm; wings half as long as standard, 5–8 × 2.5–3 mm; keel triangular, 11–16 × 5–7 mm. Ovary hairy. Pods 1- to 3-jointed, joints suborbicular, 6–8 × 6–8 mm, transversely nerved, pubescent along nerves, with numerous hairs elongated at tip into long red bristles. Seeds dark brown, nearly round, 3.5–4 × 3–4 mm (Fig. 63).

**Flowering time:**—May-June.

**Fruiting time:**—June-July.

**Habitat:**—On herbaceous grassy or fine earth-gravelly slopes, outcrops of gypsum rocks,

along gravelly river banks, very rarely in rain-fed cropland, from lower to middle mountain belt, where it enters juniper forests (Fig. 64).

**Distribution:**—Uzbekistan (Fig. 65).


**Fig. 63.** Living plant of *Hedysarum nuratense*. a, entire plant; b, raceme; c, pods; d, flower; e, calyx; f, standard; g, wings; h, keel. Scale bar 1 cm.

**Specimens examined:**—I-4 **Nuratau Region**. I-4-a **Nuratau District**: Nurata ridge (near to Jizzakh, the steep slope of the mountain near to village Iran, 11.04.1915, *O.* and *B.A. Fedtschenko 189* (LE); foothills of the Nurata ridge on the line of the city of Jizzakh, 16.05.1928, *Sovetkina 213*; mountains Koytash, village Karatash, 14.06.1937, *Korotkov*; village Gudjum, 23.07.1937, *Demurina 725, 728*; Koytash Mountains, village Tutly, 29.05.1940, *Gomolitsky, Dolgikh 76*; Koitash Mountains, northeast from the Kuvakia village, 24.04.1941, *Momotov 15, 43*; Ustyugsay, northeast fine earth slope, 02.06.1954, *Burygin 343*; 15 km east of Farizh, 12.05.1955, *Zaprometova*; sowing slopes of Arsafsay, 30.04.1956, *Zaprometova;* 1 km northeast of village Karabagdan, 19.06.1956, *Zakirov 293*; Ustoksay, 13.07.1956, *Vvedensky 115*; state farm Kyzylcha, 3 km from village Kovcha, 13.06.1963, *Ivanova 58*; upper reaches of the Ustuksay, around Faselman lake, 28.05.1964, *Zuckerwanik 341*; sovkh. Karlamarx, Jilandysay River basin, 23.05.1967, *Perelygina;* Hayatsay, 09.05.2014, *Sun, Deng, Volis, Zhou, Tojibaev 17256* (KUN); upper reaches of the Ustuksay, 08.06.2014, *Beshko*; right bank of Hayatsay, near to village Khayat, 11.05.2019, *Juramurodov 51*; Nurata Reserve, Khayatsay tract, 05.05.2020, *Akbarov, Turdiev, Juramurodov 5052020087, 5052020088, 5052020086, 7052020166*); I-4-b **Aktau District**: Aktau ridge (Malguzar Mountain Aktash, 04.06.1931, *Kasimenko 799*; upper reaches of Tutaksay, 4 km upstream of the waterfall, southwest slope at base, 07.06.1951, *Neustrueva-Knorring, Uvetkova 176*; From the upper reaches of the Tutaksay, Northern slope,

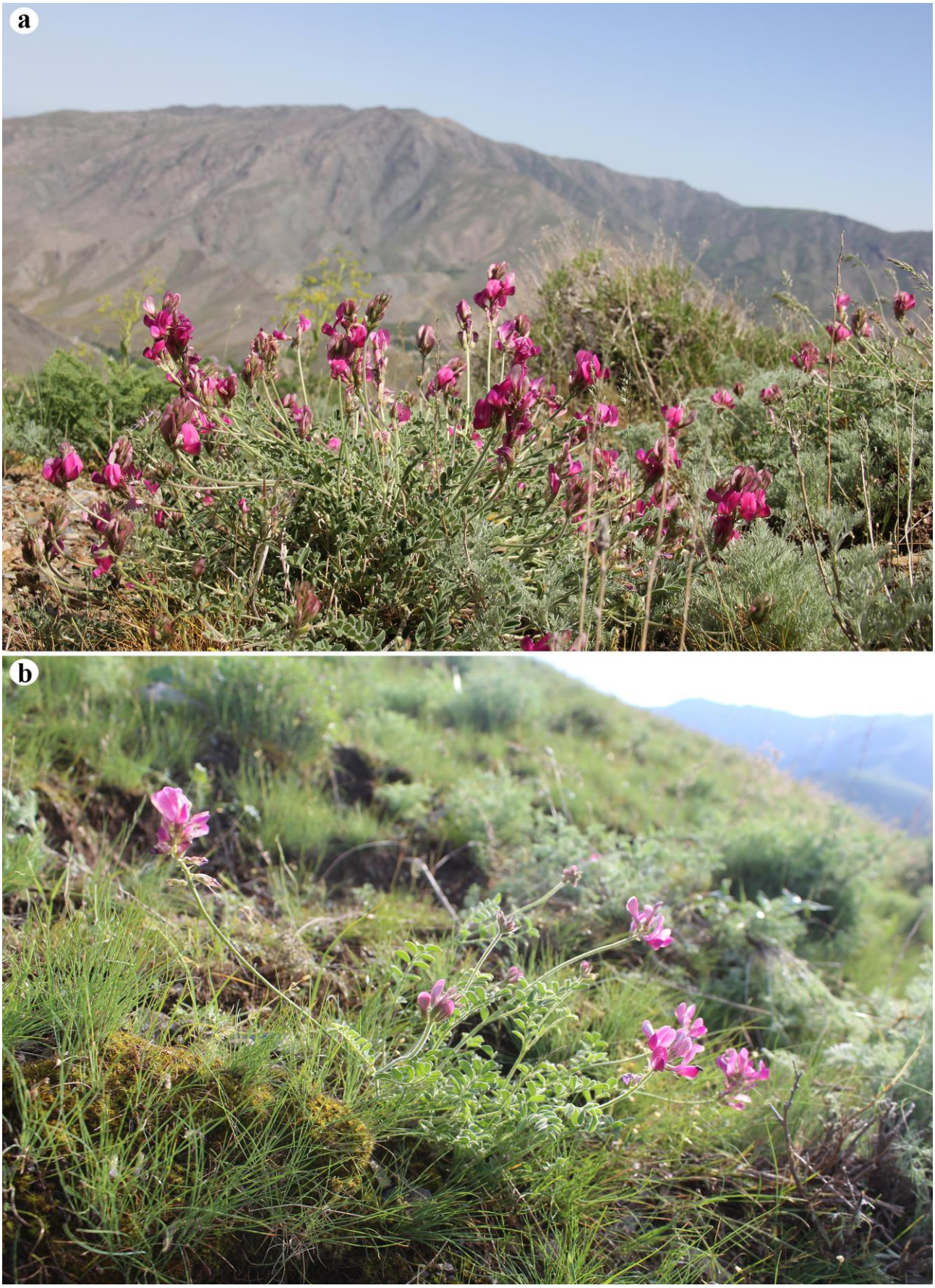


**Fig. 64.** *Hedysarum nuratense* —a–b: habit of plant. (photo ‘a’ was taken by N. Beshko).

07.061951, *Neustrueva-Knorring* (MW); from the upper reaches of the Tutaksay, 1.5–2 km to the north-west slope, 07.06.1952, *Neustrueva*, *Uvetkova 185* (LE); 1 km west of the village of Gum, 01.06.1956, *Zakirov 273*; Pitov village, 18.04.1963, *Khaidarov 853, 869*; Bukhara region, Navoi District, high adyrs east of the Sarmych River, 26.04.1965, *Pryakhin*). **I-5 Kuhistan Region.** I-5-a **Northern Turkestan District**: Turkestan ridge (Basin of the Sanzar River, Zaamin forest cottage, ancient river terrace west of the Aldashman River, 11.07.1934, *Gomolitsky*, *Protopov 72*; Basin of the Sanzar River, Zaamin forest dacha, wet gravel bank of the Aldashman River, 12.07.1934, *Gomolitsky*, *Protopov 99*; basin of the Sanzar River, Zaamin forest cottage, river valley Baikungur, 22.09.1934, *Gomolitsky 406*; basin River Guralash, around village Karakshakshak, 26.06.1935, *Zakrzhevsky 602*; village Beshbulak, 08.06.1937, *Demurina 129*; northwest slope of Almasay, 23.05.1938, *Demurina 16*); I-5-b **Malguzar District**: Malguzar ridge (basin of the Sanzar River, Malguzar ridge, Djinichke pass, 21.05.1935, *Zakrzhevsky 72*; Beshkubu vil. towards the Zaamin Mountains, 22.05.1937, *Korotkova*, *Vasilkovskaya 109*; Sabystlansay, a tributary of the Djenichkesay, 27.06.1952, *Mironova 68*; 8 km southeast from Zaamin, 20.05.1954, *Krasnopolin*; Malguzar Mountains on the way to Shpigar village, northern slope, 06.06.1914, *Mikhelson* (LE). I-6 **Western Hissar Region**. I-6-c **Baysun District**: Hissar ridge (Saryshato pass, near village Derbent, 30.05.1941, *Popova 574*; above the village of Machay, 08.06.1947, *Korotkova 809*). Specimens in TASH unless otherwise specified.

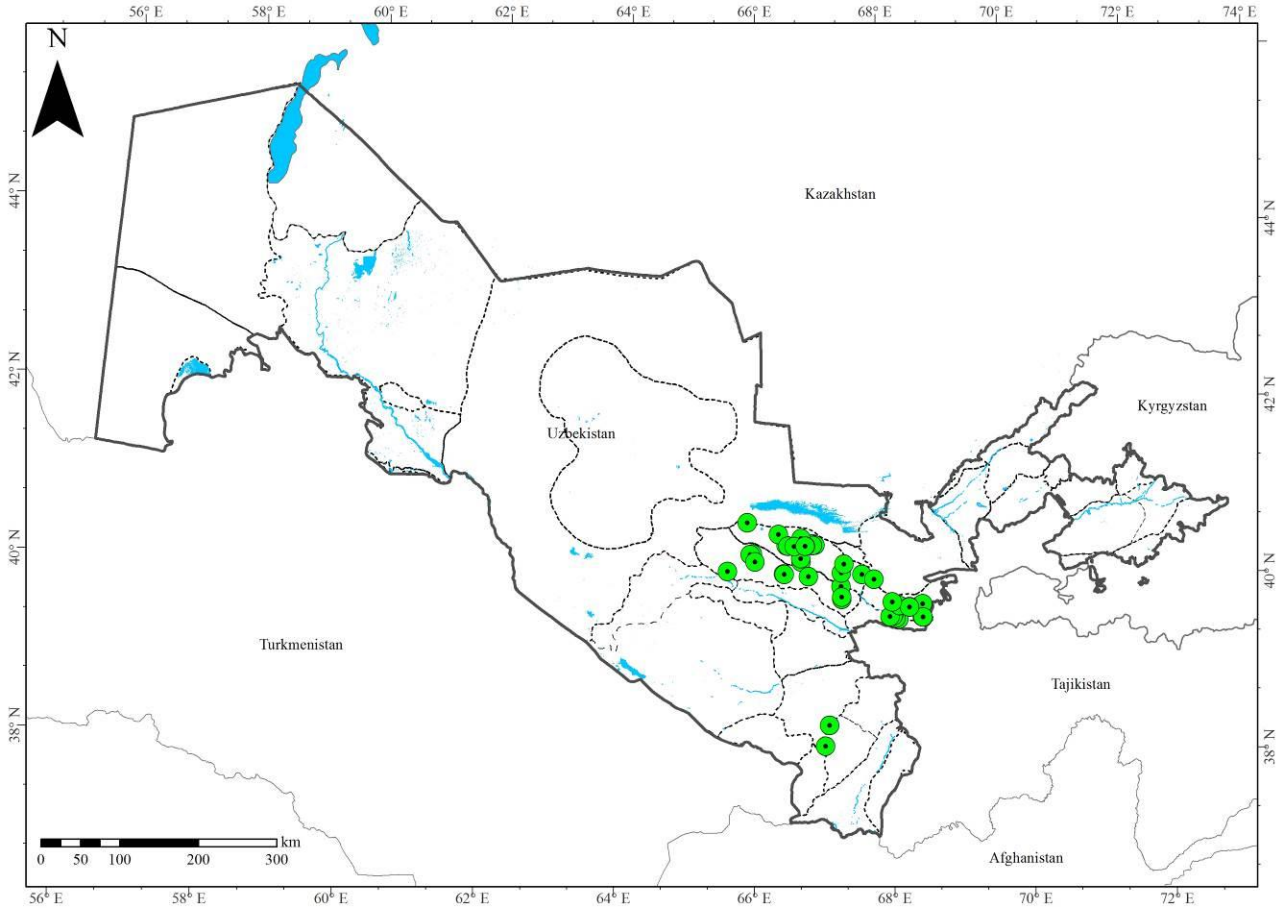


**Fig. 65.** Distribution of *Hedysarum nuratense*.

**25. *Hedysarum sunhangii*** Juram. & Tojibaev in Phytotaxa 524 (1): 4 (2021).

**Type:**—[Uzbekistan]. Surkhandarya Province, Babatag Ridge, Khodja kulsunsay tract, 1050 m, 38.328024°N, 68.218302°E, 24.05.2019,

*N.Beshko, A.Makhmudov 2405201907* (holotype TASH barcode 058995!).

**Description:**—Herbs, 25–40 cm tall. Stem densely pubescent (epidermis not visible). Stipules triangular, hairy outside, inside glabrous, submembranous, linear-subulate, elongate, 6–8 mm long, hardly connate. Leaves imparipinnate, 6–13 cm long, with 2–4 pairs of leaflets. Leaflets flat, ovate or broadly ovate, 16–30 × 12–20 mm, obtuse, abaxially more densely white hairy, with prominent lateral nerves. Peduncle terminal, hardly longer than leaves (excluding raceme); racemes condensed when flowering, elongating when fruiting, narrow, with 7–20 flowers. Bracts linear-lanceolate, 4.5–5.5 mm long, hairy, caducous. Bracteoles 1.2–1.7 mm long. Pedicels 1–2 mm long. Calyx campanulate, 7–9 mm long, calyx teeth linear-subulate, teeth of different lengths, 2.5 to 3 times as long as tube, shorter than corolla (not nearly as long as corolla). Corolla dark or light pink, 13–16 mm long; standard shorter than keel, limb oblong-ovate, 11–13 mm long; wings 4–5 mm long; keel 14–16 mm long, limb obliquely triangular; ovary hairy. Pods 2- to 4-jointed, joints suborbicular, 5–7 mm long, ribbed, transversely nerved, pubescent, densely so along nerves with numerous prickles elongating into long reddish bristles to 4 mm long. Seeds ca. 3 × 2.5 mm, convex, light brown, smooth (Fig. 66).

**Flowering time:**—May.

**Fruiting time:**—May-June.

**Habitat:**—On red clay soils at 900–1100 m a.s.l. (Fig. 67).

**Distribution:**—Uzbekistan (Fig. 68).

**Specimens examined:**—I-8 **Panj Region**. I-8-a **Babatag District**: Babatag Ridge (Khodja kulsunsay tract, 1050 m, 24.05.2019, *Beshko, Makhmudov, 2405201907*; vicinity of the tract

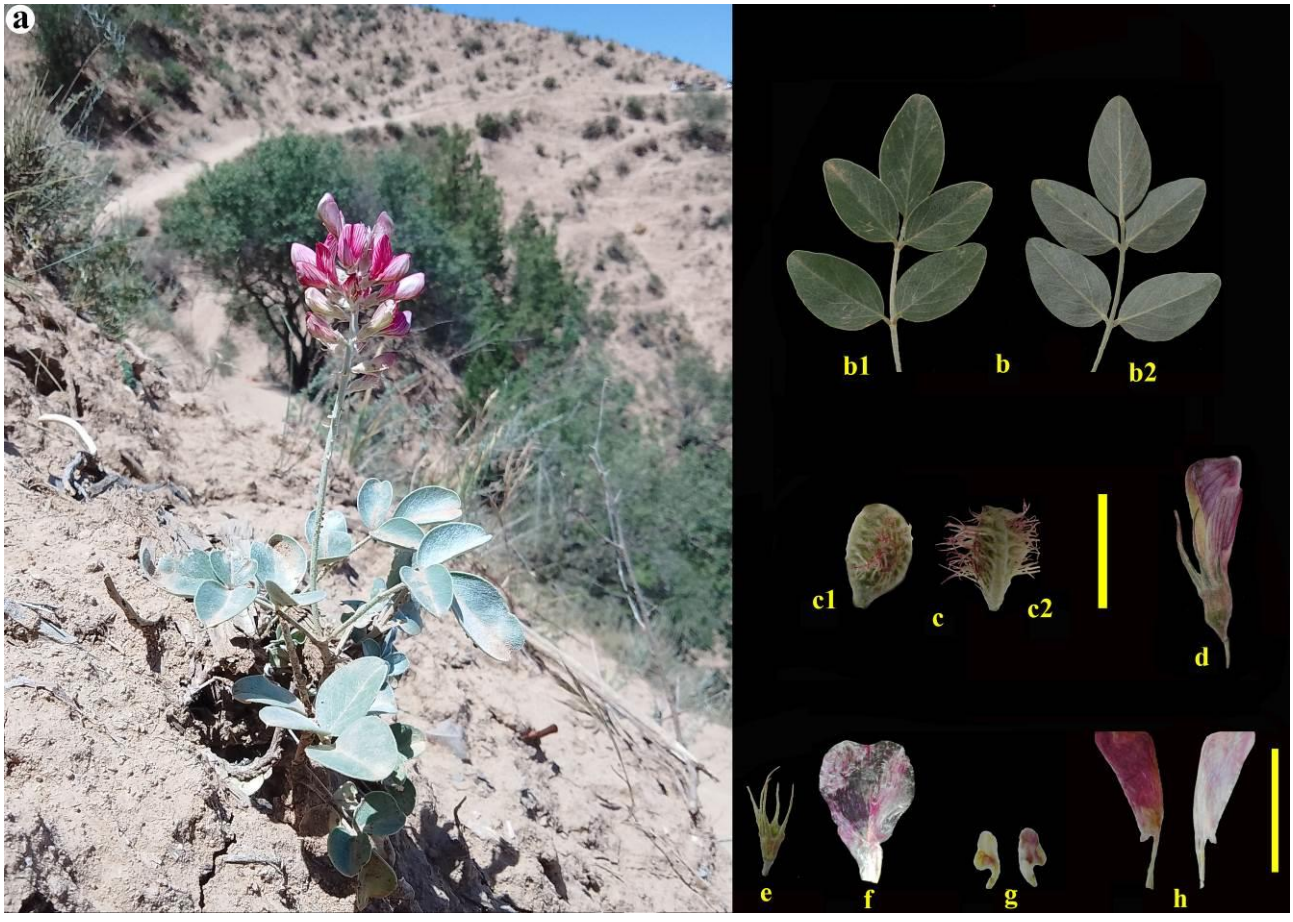


**Fig. 66.** Living plant of *Hedysarum sunhangii*: a, habit; b, leaflets (b1, upper part and b2, lower part); c, pod (c1, front side, and c2, lateral side); d, flower; e, calyx; f, standard; g, wings; h, keel. Scale bar 1 cm.


**Fig. 67.** *Hedysarum sunhangii* —a: raceme, b–c: habit of plant. (photo ‘c’ was taken by N. Beshko).

Khojakulsun, 1025 m. a.s.l., 22.05.2020, *Juramurodov, Makhmudjanov, Pulatov, Jabborov, Rahmatov, Madaminov, Habibullaev, 2205202094, 22052020106, 2205202092, 2205202091*; near village Allamjan, 06.06.2022, *Tojibaev, Juramurodov*). All specimens are at TASH.

**Notes:**—We recently discovered *Hedysarum sunhangii* based on the type specimen collected by Beshko and Makhmudov in 2019 in the Bobotog Range in the southwestern Pamir-Aloy region of Uzbekistan, as well as from the paratype specimens collected by Juramurodov et al. in 2020 in the same area (Juramurodov et al. 2021). Initially, *H. sunhangii* was known only from the type locality on Babatag Ridge in the southeast Surkhandarya Province, Uzbekistan. However, during field research on the Bobotog Ridge in 2022, we discovered an additional population approximately 35–40 km south of the type locality (Fig. 68).

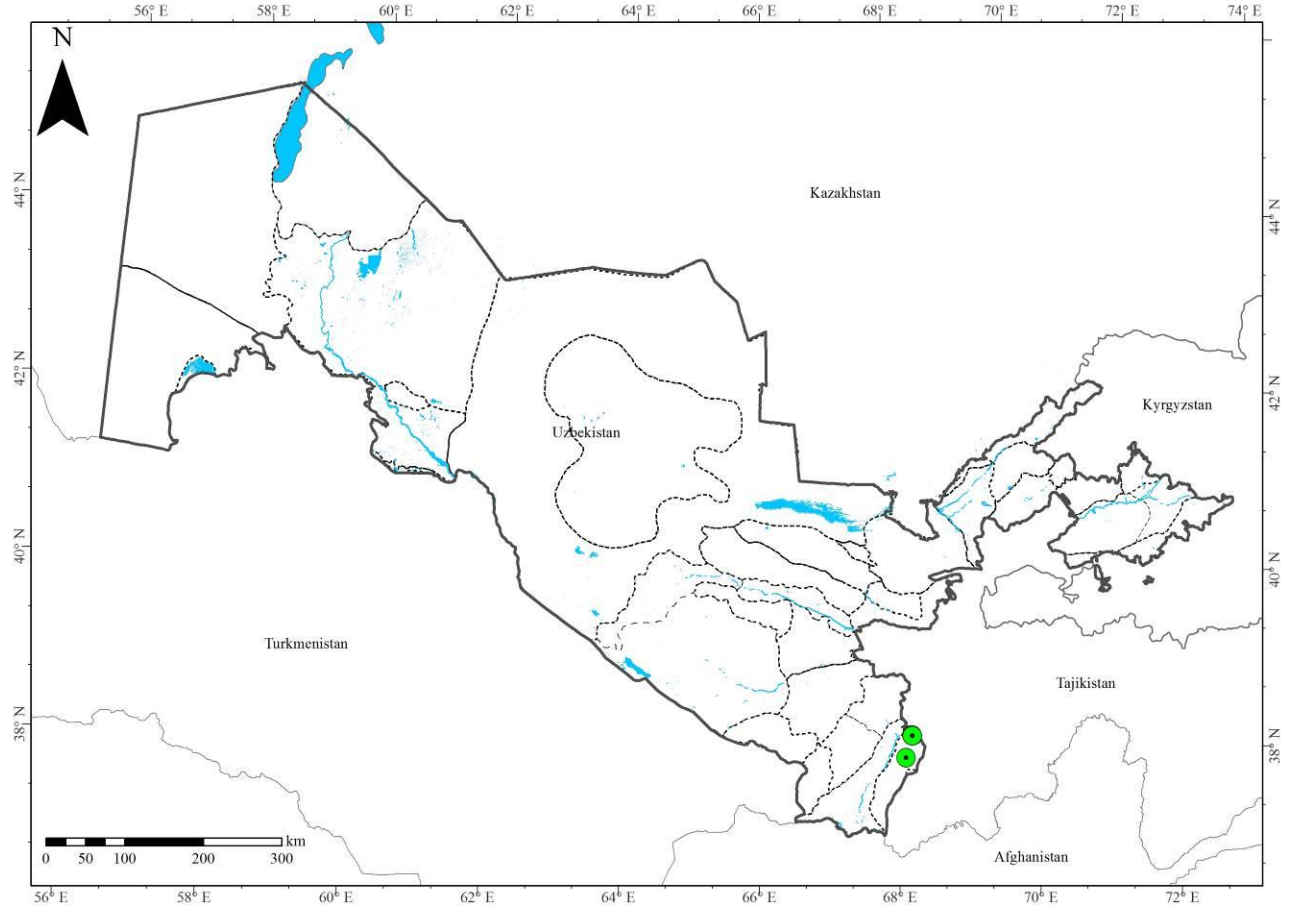


**Fig. 68.** Distribution of *Hedysarum sunhangii*.

**26. *Hedysarum kudrjaschevii*** Korotkova in Bot. Mater. Gerb. Inst. Bot. Zool. Akad. Nauk Uzbeksk. S.S.R. 9: 10 (1947).

**Type:**—[Uzbekistan]. Western Pamir-Alai, upper reaches of Yakkobag-Darya River, near Tash-Kurgan village, Kapyr-Sai tract, gypsum slopes, 04.07.1936, fr., *V. Botschantsev & A. Butkov 653* (holotype TASH barcode 001958!; Fig. 69).

**Description:**—Herbs, 30–35 cm tall, angular, suberect, densely appressed silvery hairy. Leaves 5–12 cm long. Stipules triangular-ovate, apex gradually acuminate, entire, nearly free, rigid, ca. 10 mm long. Leaves imparipinnate, 5–9 cm long, with 2–4 pairs of leaflets. Leaflets lanceolate or elliptic, 13–30 × 7–15 mm, base rounded or broadly cuneate, apex abruptly tapering and mucronate, abaxially with sharply protruding nerves. Peduncle axillary, longer than leaves, together with inflorescence 10–15 cm long; racemes many-flowered, dense. Bracts linear-lanceolate, nearly as long as calyx, 6–7


**Fig. 69.** Holotype specimen of *Hedysarum kudrjaschevii*.

mm long. Bracteoles 1.5–2 mm long. Pedicels 2 mm long. Calyx tube 2–3 mm long; calyx teeth lanceolate, teeth of equal length, 5–6 mm long, nearly three times as long as tube. Corolla 10–12 mm long, persistent in fruit; standard orbicular-oblong, 10–12 mm long, nearly as long as keel; wings 4–5 × 2–3 mm, oblong-obovate, apex rounded, base short auriculate, claw ca. 2 mm long; keel 11–14 × 4 mm, apex attenuate and short beaked. Pods 1- to 3-jointed, joints orbicular, 6–8 mm long, covered with short appressed hairs and long spreading purple or reddish bristles. Seeds ca. 3–4 × 3–3.5 mm, orbicular, blackish brown, smooth.

**Flowering time:**—May-June.

**Fruiting time:**—June-July.

**Habitat:**—Gypsiferous slopes.

**Distribution:**—Uzbekistan (Fig. 70).

**Specimens examined:**—I-6 **Western Hissar Region**. I-6 **Western Hissar Region**. I-6-a **Kashkadarya District**: Hissar ridge (upper reaches of the Yakkobag-darya River, surroundings of Tash-Kurgan village, Kapyr-Sai tract, gypsum slopes, 04.07.1936, *Bochantsev*, *Butkov 653* (holotype, TASH)).

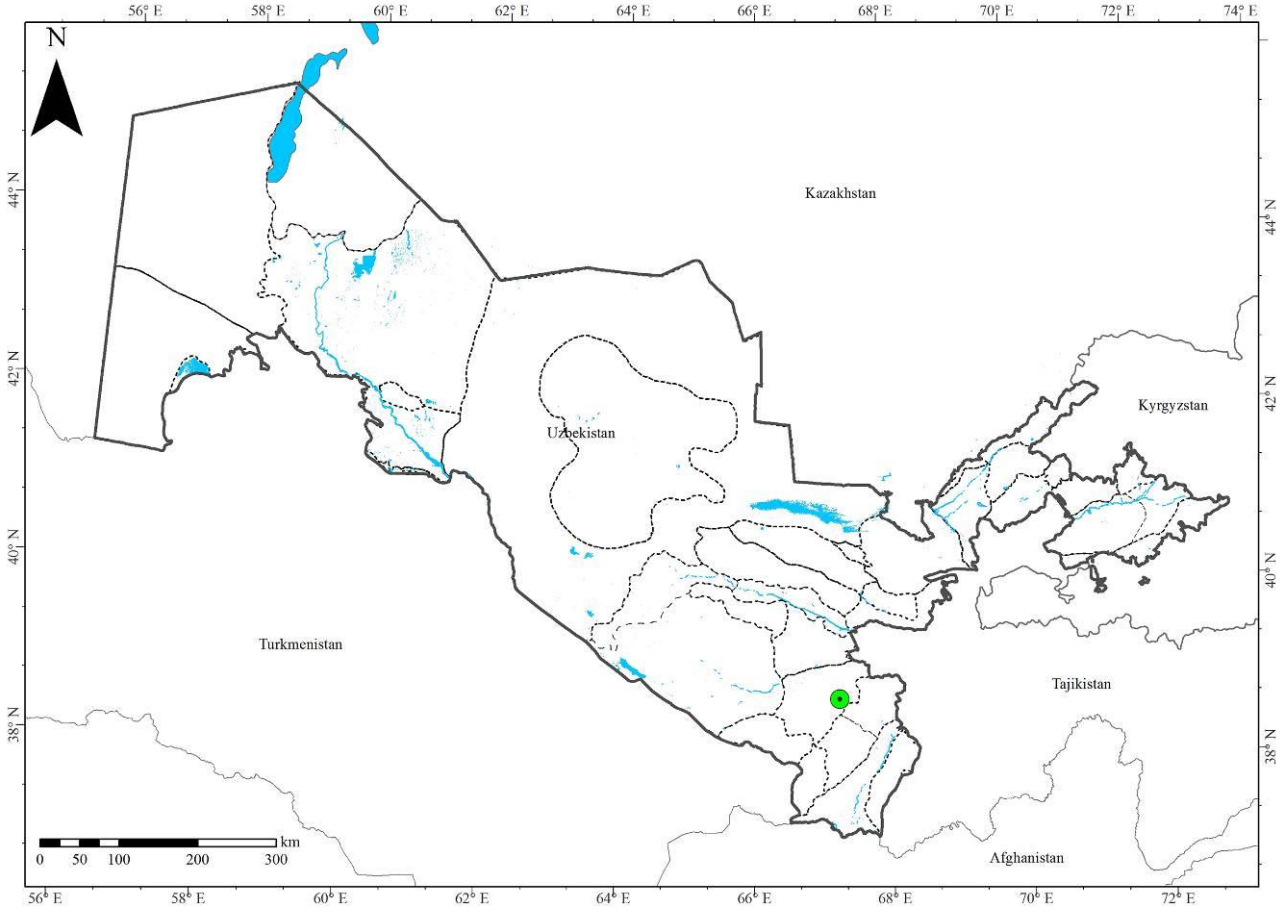


**Fig. 70**. Distribution of *Hedysarum kudrjaschevii*.

**Notes:**—Kovalevskaya (1981) considered *Hedysarum kudrjaschevii* to be a synonym of *Hedysarum nuratense*. We also found that these two species share several similarities, such as having long purple or reddish hairs on the pods, standard and keel of almost the same length, long bracteoles, and other similar features. However, after re-examining the type specimen of *H. kudrjaschevii*, we identified features that distinguish it from *H. nuratense*, including being covered with dense hairs, 2–4 pairs of leaflets and large leaves. Consequently, we determined *H. kudrjaschevii* to be more similar to *H. sunhangii* in having 2–4 pairs of leaflets, pod structure, leaflet size, and wing length. Nevertheless, the elliptic or lanceolate leaves of *H. kudrjaschevii* are thickly hairy on both surfaces, the bracts are longer (6–7 mm long),

and the standard and keel are relatively short and nearly equal tin size, making it easily distinguishable from *H. sunhangii*. Additionally, our phylogenetic analysis confirmed that *H. kudrjaschevii* is a distinct species and differs from *H. nuratense* and *H. sunhangii*.

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## Disclosure statement

No potential conflict of interest was reported by the authors.

## References

Amirahmadi A, Osaloo SK, Moein F, Kaveh A, Maassoumi AA (2014) Molecular systematics of the tribe *Hedysareae* (Fabaceae) based on nrDNA ITS and plastid *trnL-F* and *matK* sequences. *Plant Systematics and Evolution* 300(4): 729–747.

Aytaç Z, Ertuğrul T, Erst A, Fişne A (2022) A new *Hedysarum* L. species (Fabaceae) from Türkiye, *Hedysarum dazkiriense*. *Phytotaxa* 574(4): 273–281.

Baitenov MS (1956) New species of the genus *Hedysarum* L. *Bulletin Acad. Science Kazakh. SSR*. 3: 100–105. (in Russian).

Baitenov MS (1961) *Hedysarum* L. Flora Kazakhstana. The Academy of Sciences of the Kazakh SSR Press, Alma-Ata, vol. 5: 420–440. (In Russian).

Baitenov MS (1964) The *Hedysarum* species in Kazakhstan. PhD Thesis, Tomsk, Russia

Choi BH, Ohashi H (2003) Generic criteria and an infrageneric system for *Hedysarum* and related genera (Papilionoideae-Leguminosae). *Taxon* 52(3): 567–576.

Choi BH, Ohashi H (1996) Pollen morphology and taxonomy of *Hedysarum* and its related genera of the tribe *Hedysareae* (Leguminosae-Papilionoideae). *Journal of Japanese Botany* 71: 191-213.

Dehshiri MM, Goodarzi M (2016) Taxonomic notes on *Hedysarum* sect. *Crinifera* (Fabaceae) in Iran, with the description of a new species. *In Annales Botanici Fennici*. Finnish Zoological and Botanical Publishing Board 53:1–2, 21–26.

Duan L, Wen J, Yang X, Liu PL, Arslan E, Ertuğrul K, Chang ZY (2015) Phylogeny of *Hedysarum* and tribe Hedysareae (Leguminosae: Papilionoideae) inferred from sequence data of ITS, *matK*, *trnL-F* and *psbA-trnH*. *Taxon* 64(1): 49–64.

Doyle JJ, Doyle JL (1987) A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemical Bulletin* 19: 11–15.

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32(5): 1792–1797.

Fedtschenko BA (1902) The genus *Hedysarum*. *Acta Horti Petrop* 19: 185–342. (In Russian)

Fedtschenko BA (1919) *Hedysarum olgae* p. sp. *Botanicheskie Materialy Gerbariya Glavnogo Botanicheskogo Sada R.S.F.S.R* 2(1): 1. (In Russian).

Fedtschenko BA (1948) *Hedysarum*. In: Komarov VL, Shishkin BK, Bobrov EG (eds.), *Flora of URSS*, vol. 13. Academy of Sciences of the USSR, Moscow & Leningrad, pp. 259–319. (In Russian).

Fedtschenko BA (1949) New species of the genus *Hedysarum* L. *Not. Syst. Herb. Inst. Bot. Komarovii Acad. Sci. URSS*, 11: 114–118. (In Russian).

Hassanov FO (Ed.) (2019) *The Red Data Book of the Republic of Uzbekistan*. 'Chinor ENK' Press, Tashkent, vol. 1: 62–67.

International Plant Names Index. Available online: http://www.ipni.org (Accessed September 15, 2023).

Juramuradov IJ, Byalt VV, Mirzalieva DU, Tojibaev KSh (2022) Type specimens of names of taxa of genus *Hedysarum* L. (Fabaceae) from Central Asia in the National Herbarium of Uzbekistan (TASH). *Vestnik Tomskogo gosudarstvennogo universiteta. Biologiya = Tomsk State University Journal of Biology* 57: 6–27.

Juramurodov I, Makhmudjanov D, Yusupov Z, Tojibaev K (2023a) First Comparative Analysis of Complete Chloroplast Genomes Among Six *Hedysarum* (Fabaceae) Species. *Frontiers in Plant Science* 14:1211247.

Juramurodov I, Makhmudjanov D, Nikitina E, Liu PL, Yusupov Z, Deng T, Tojibaev K, Sun H (2023b). Phylogenetic relationships and biogeography in *Hedysarum* L. (Hedysareae, Fabaceae) with a focus on Central Asian taxa. *Taxon* 72(6): 1262–1284.

Juramurodov I, Tojibaev K, Nikitina E, Makhmudjanov D, Yusupov Z, Deng T, Dehkanov D (2021) *Hedysarum sunhangii* (Fabaceae, Hedysareae), a new species from Pamir-Alay (Babatag Ridge-Uzbekistan). *Phytotaxa* 524(1): 1–13.

Karimova VV (1978) *Hedysarum* L. In: Ovchinnikov P.N. (ed.), *Flora of Tajikistan SSR*, 2nd ed., vol. 5. Science Press, Leningrad, pp. 505–527 and 636–637. (In Russian).

Korotkova EE (1947) New species of the genus *Hedysarum* L. *Not. Syst. Herb. Inst. Bot. et Zool. Acad. Sci. Uzbek*, 9: 6–14. (In Russian).

Korotkova EE (1954) New species of the genus *Hedysarum* L. from Central Asia. *Not. Syst. Herb. Inst. Bot. et Zool. Acad. Sci. Uzbek* 14: 13–16. (In Russian).

Korotkova EE (1955) *Hedysarum* L. In: Korovin EP, Vvedenskiy AI (eds.), *Flora of Uzbekistan*, vol. 3. The Academy of Sciences of the Uzbek SSR Press, Tashkent, pp. 723–736. (In Russian).

Kovalevskaya SS (1981) Genus 561 (33) *Hedysarum* L. In: Vvedenskiy AI, Kamelin RV, Kovalevskaya SS, Nabiev MM (eds.), *Conspectus Florae Asiae Mediae. Critical checklist of flora*, vol 6. The Uzbek SSR 'Fan' Press, Tashkent, pp. 286–311. (In Russian).

Kudryashev SN (1940) New plant species from Pamir-Alai and Hindukush. *Not. Syst. Herb. Inst. Bot. et Zool. Acad. Sci. Uzbek* 1: 3–6. (In Russian).

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution* 35(6): 1547–1549.

Lazkov GA (2008) A new species of the genus *Hedysarum* (Fabaceae) from Kyrghyzia. *Botanical Journal* (St. Petersburg) 93(2): 343–346.

Liu PL, Chen XL, Lu Y, Chang ZY, Yue M (2019) New species discovered from old collections, the case of *Hedysarum wangii sp. nov.* (Fabaceae, Hedysareae). *Phytotaxa* 413(1): 27–38.

Liu PL, Wen J, Duan L, Arslan E, Ertuðrul K, Chang ZY (2017) *Hedysarum* L. (Fabaceae: *Hedysareae*) is not monophyletic – evidence from phylogenetic analyses based on five nuclear and five plastid sequences. *PLoS ONE* 12: e0170596.

Lock JM (2005) *Hedysareae*. In: Lewis, G., Schrire, B., Mackinder, B. & Lock, M. (eds.), *Legumes of the World*. Richmond: Royal Botanic Gardens, Kew, pp. 489–495.

Maddison WP, Maddison DR (2019) Mesquite: a modular system for evolutionary analysis, Version 3.61. Available at: www.mesquiteproject.org. (Accessed September 15, 2023)

Makhmudjanov D, Juramurodov I, Kurbonaliyeva M, Yusupov Z, Dekhkonov D, Deng T, Tojibaev K, Sun H, (2022) Genus *Eremurus* (Asphodelaceae) in the flora of Uzbekistan. *Plant Diversity of Central Asia* 2: 82–127.

Minh BQ, Lanfear R, Trifinopoulos J, Schrempf D, Schmidt HA (2021) IQ-TREE version 2.1.2: Tutorials and Manual Phylogenomic software by maximum likelihood.

Nafisi HA, Kazempour-Osaloo Sh, Mozaffarian V, Schneeweiss GM (2019) Molecular phylogeny and divergence times of the genus *Hedysarum* (Fabaceae) with special reference to section *Multicaulia* in Southwest Asia. *Plant Systematics and Evolution* 305(10): 1001–1017.

Nafisi HA, Kazempour-Osaloo Sh, Kaveh AK, Mahmoodi MO (2021) A taxonomic revision of the genus *Hedysarum* L. (Fabaceae-Hedysareae) in Iran. *Phytotaxa* 511(2):79–110.

Nikitin VV (1949) Genus (33) *Hedysarum* L. In: Shishkin BK, Nikitin BB (eds.), *Flora of Turkmenistan*, vol. 4. The Turkmen branch of the academy of sciences of the USSR Press, Ashgabat, pp. 306–312. (In Russian).

Nikitina EV (1957) Genus (29) *Hedysarum* L. In: Vvedensky AI (ed.), Flora of Kirghiz SSR, vol. 7. The Academy of sciences of the Kyrgyz SSR Press, Frunze, pp. 398–413. (In Russian).

Podlech D (2012) *Checklist of the flowering plants of Afghanistan*. München: Ludwig-Maximilians Universität Press.

Popov MG (1937) New species of Legumes from Central Asia. *Not. Syst. Herb. Inst. Bot. et Zool. Acad. Sci. Uzbek* 7: 13–16.

POWO Plants of the World Online. (2023) Facilitated by the Royal Botanic Gardens, Kew. Available from: http://www.plantsoftheworldonline.org (Accessed September 15, 2023)

Rambaut A (2012) FigTree v1. 4.0. University of Oxford, Oxford, UK. http://tree.bio.ed.ac.uk/software/figtree

Ranjbar M, Karamian R, Johartchi MR (2006) Notes on the taxonomy of *Hedysarum* (Fabaceae) in Iran. *Annales Botanici Fennici* 43: 152–155.

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient bayesian phylogenetic inference and model choice across a large model space. *Systematic biology* 61(3): 539–542.

Sang T, Crawford DJ, Stuessy TF (1997) Chloroplast DNA phylogeny, reticulate evolution and biogeography of *Paeonia* (Paeoniaceae). *American Journal of Botany* 84(4): 1120–1136.41.

Sennikov AN (Ed.) (2016) Flora of Uzbekistan, vol. 1. 'Navroʻz' Press, Tashkent, xxviii + 173 pp. (In Russian).

Sennikov AN (Ed.) (2017) Flora of Uzbekistan, vol. 2. 'Navroʻz' Press, Tashkent, xii + 200 pp. (In Russian).

Sennikov AN (Ed.) (2019) Flora of Uzbekistan, vol. 3. 'Ma'naviat' Press, Tashkent, xii + 201 pp. (In Russian).

Sennikov AN (Ed.) (2022) Flora of Uzbekistan, vol. 4. 'Fan' Press, Tashkent, xviii + 238 pp. (In Russian).

Sennikov A, Khassanov F, Ortikov E, Kurbonaliyeva M, Tojibaev KSh (2023) The genus *Iris* L. sl (Iridaceae) in the Mountains of Central Asia biodiversity hotspot. *Plant Diversity of Central Asia* 2(1): 1–104.

Sultanova BA (1970) Diagnosis of new species of *Hedysarum* L. Flora of the Kirghiz SSR. Addition 2, vol. 2. pp. 31–37. (In Latin and Russian).

Sultanova BA (1971) The genus *Hedysarum* L. in Kyrgyzstan. PhD Thesis, Frunze. (In Russian).

Sultanova BA (1973) Addition to the flora of Kyrgyzstan. Materials on the flora of Kyrgyzstan pp. 43–44. (In Latin and Russian).

Taberlet P, Gielly L, Pautou G, Bouvet J (1991) Universal primers for amplification of three non-coding regions of chloroplast

DNA. *Plant molecular biology* 17(5): 1105–1109.

Tate JA, Simpson BB (2003) Paraphyly of *Tarasa* (Malvaceae) and diverse origins of the polyploidy species. *Systematic Botany* 28: 723–737.

Thiers B. (continuously updated). Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden. Available from http://sweetgum.nybg.org/science/ih/. (Accessed September 15, 2023).

Tojibaev K, Beshko N, Turginov O, Mirzalieva D (2014) New records for Fabaceae in the flora of Uzbekistan. *Flora Mediterranea* 24: 25–35.

Tojibaev KSh, Beshko NY, Popov VA (2016) Botanical-geographical regionalization of Uzbekistan. *Botanicheskiĭ Zhurnal* 101(10): 1105–1132.

Tojibaev KSh, Dekhkonov D, Ergashov I, Sun H, Deng T, Yusupov Z (2022) The synopsis of the genus *Tulipa* (Liliaceae) in Uzbekistan. *Phytotaxa* 573(2): 163–214.

Tojibaev KSh, Juramurodov IJ, Sun H (2021) *Hedysarum talassicum* Nikitina & Sultanova. In Findings to the flora of Russia and adjacent countries: New national and regional vascular plant records, 3 (A.V. Verkhozina, ed.). *Botanica Pacifica* 10(1): 91–92.

Turakulov I, Safarov N, Tojibaev K, Suyunkulov H, Park M, Na N, Usmonov M, Chang KS, Oh SH, Jang CG (2021) The flora of the Western Tian-Shan: Tajikistan part. *Journal of Asia-Pacific Biodiversity* 14(2): 221–227.

Turdiboev OA, Shormanova AA, Sheludyakova MB, Akbarov F, Drew BT, Celep F (2022) Synopsis of the Central Asian *Salvia* species with identification key. *Phytotaxa* 543(1): 1–20.

Vaidya G, Lohman DJ, Meier R (2011) SequenceMatrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information. *Cladistics* 27(2): 171–180.

White TJ, Bruns T, Lee S, Taylor J (1990) *Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics*. In Donald O. Natvig (ed.). PCR protocols: a guide to methods and applications 18(1): 315–322.

Xu LR, Choi BH (2010) *Hedysarum* L. In: Wu ZY, Raven PH, Hong DY (eds). *Flora of China*, vol. 10. Beijing: Science Press, St. Louis: Missouri Botanical Garden Press. pp. 514–525.

**Appendix.** Voucher information and GenBank accession numbers of species used in this study. New sequences generated in this study are indicated by an asterisk (*).

| No | Scientific Name | Collection date | Collection site (in Uzbekistan) | GPS source | Collector | Voucher number | nrDNA ITS | trnL-F | matK | psbA-trnH |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | *Hedysarum alaicum* B.Fedtsch. | 22/05/1916 | Ferghana Province | N. 39.995854 E. 71.790385 | Drobov V.P. | 1021a | OM458868 | OM585613 | | |
| 2 | *H. amankutanicum* B.Fedtsch. | 25.04.1913 | Samarkand Province, Urgut District | N. 39.31481 E. 66.940661 | Mikhelson A.I. | 1071a | OM458870 | OM585616 | | |
| 3 | *H. angrenicum* Korotkova | 27/07/1931 | Tashkent Province, Oxongaron District | N. 41.20000 E. 70.3942 | Maskevich A.A. | 203a | OM458872 | OM585617 | | |
| 4 | *H. baldshuanicum* B.Fedtsch. | 30/05/2019 | Surkhandarya Province, Sariosiyo District | N. 38.622451 E. 67.580378 | Juramurodov I.J. Maxmudjanov D.I. | 005a | OM458843 | OM585601 | OM898910 | OM898878 |
| 5 | *H. bucharicum* B.Fedtsch. | 20/05/2019 | Surkhandarya Province, Boysun District | N. 38.385551 E. 67.130115 | Juramurodov I.J. | 067a | OM030218 | OM585621 | OM898916 | OM898898 |
| 6 | *H. drobovii* Korotkova | 11/06/2019 | Tashkent Province, Bustonlik District | N. 41.560828 E. 70.106407 | Juramurodov I.J. | 1106a | OM030219 | OM585622 | OM898918 | OM898892 |
| 7 | *H. flavescens* Regel & Schmalh. | 10/08/2019 | Tashkent Province, Bustonlik District | N. 42.15705 E. 70.876473 | Tojibaev K.Sh. Juramurodov I.J. | 1008006 | OM458845 | OM585602 | OM898899 | OM898879 |
| 8 | *H. gypsaceum* Korotkova | 23/05/2019 | Namangan Province, Chartak District | N. 41.266541 E. 71.887084 | Juramurodov I.J. Gulamov R.K. | 045-1 | OM030221 | ON147182 | OM898908 | |
| 9 | *H. iomuticum* B.Fedtsch. | 26/05/2019 | Surkhandarya Province, Uzun District | N. 38.113833 E. 68.237942 | Pulatov S.O., Jabborov A.M. | 003a | OM458847 | OM585603 | OM898912 | OM898881 |
| 10 | *H. jaxarticum* Popov. | 16/06/1953 | Tashkent Province, Parkent District | N. 41.38045 E. 69.77491 | Maylun Z. & al. | 782 | OM458875 | OM585618 | OM898919 | |
| 11 | *H. kudrjaschevii* Korotkova | 04/07/1936 | Kashkadarya Province, Dekhkanabad District | N. 38.762901 E. 67.243734 | V. Bochantsev | 653 | OR041883* | OR047642* | | OR047643* |
| 12 | *H. lehmannianum* Bunge | 06/06/2012 | Surkhandarya Province, Boysun District | N. 38.337148 E. 67.163574 | Turginov O.T. | 0490-1 | OM458851 | OM585605 | OM898902 | OM898883 |
| 13 | *H. magnificum* Kudr. | 20/05/2019 | Surkhandarya Province, Boysun District | N. 38.406537 E. 67.167624 | Juramurodov I.J. | 066a | OM458849 | OM585604 | OM898901 | OM898882 |
| 14 | *H. minjanense* Rech.f. | 30/06/1961 | Surkhandarya Province, Boysun District | N. 38.531337 E. 67.359572 | Pryakhin M.M. | 1961 | OM458874 | | | OM898896 |
| 15 | *H. mogianicum* B.Fedtsch. | 13/05/2019 | Jizzakh Province, Forish District | N. 40.519616 E. 66.750403 | Juramurodov I.J. | 052a | OM458853 | OM585606 | OM898913 | OM898884 |

| No | Scientific Name | Collection date | Collection site (in Uzbekistan) | GPS source | Collector | Voucher | nrDNA ITS | trnL-F | matK | psbA-trnH |
|---|---|---|---|---|---|---|---|---|---|---|
| 16 | *H. montanum* (B.Fedtsch.) B.Fedtsch. | 21/06/2019 | Jizzakh Province, Zaamin District | N. 39.628815 E. 68.492429 | Juramurodov I.J. | 051a | OM458855 | OM585607 | OM898903 | OM898885 |
| 17 | *H. nuratense* Popov | 05/05/2020 | Jizzakh Province, Forish District | N. 40.522187 E. 66.763718 | Akbarov F.I., Turdiev D.E., Juramurodov I.J. | 5052020086 | OR041881* | | | |
| | | 11/05/2019 | Jizzakh Province, Forish District | N. 40.522241 E. 66.763648 | Juramurodov I.J. | 051 | | MZ647715 | MZ647713 | ON147184 |
| 18 | *H. olgae* B.Fedtsch. | 15/05/2019 | Samarkand Province, Urgut District | N. 39.275159 E. 66.942306 | Juramurodov I.J. | 048a | OM030220 | OM585623 | OM898909 | OM898886 |
| 19 | *H. plumosum* Boiss. & Hausskn. ex Boiss. | 22/06/2019 | Jizzakh Province, Zaamin District | N. 39.620829 E. 68.393334 | Juramurodov I.J. | 004a | OM458857 | OM585608 | OM898905 | OM898888 |
| 20 | *H. popovii* Korotkova | 14/08/1924 | Namangan Province, Pop District | N. 41.31029 E. 70.565617 | Korovin E.P. | 661 | OR041882* | OM585624 | | OM898890 |
| 21 | *H. pskemense* Popov ex B.Fedtsch. | 10/08/2019 | Tashkent Province, Bustonlik District | N. 42.149812 E. 70.87378 | Tojibaev K.Sh. Juramurodov I.J. | 1008059 | OM458861 | OM585609 | OM898906 | OM898891 |
| 22 | *H. taschkendicum* Popov | 08/06/2019 | Tashkent Province, Parkent District | N. 41.380257 E. 69.75585 | Juramurodov I.J. | 088 | OM458863 | OM585610 | OM898914 | OM898893 |
| 23 | *H. turkestanicum* Regel & Schmalh. | 23/05/2019 | Namangan Province, Yangikurgan District | N. 41.532550 E. 71.706354 | Juramurodov I.J. Gulomov R.K. | 011 | OM458866 | OM585611 | OM898915 | OM898894 |
| 24 | *H. talassicum* Nikitina&Sultanova | 11/08/2019 | Tashkent Province, Bustonlik District | N. 42.173586 E. 70.956551 | Tojibaev K.Sh., Juramurodov I.J. | 1108149 | OM458867 | OM585612 | OM898907 | OM898895 |
| 25 | *H. santalaschi* B.Fedtsch. | 01/07/1957 | Tashkent Province, Bustonlik District | N. 41.40457 E. 70.336868 | Nabiev M.M. | 1095a | OM458876 | OM58562 | | OM898897 |
| 26 | *H. sunhangii* Juramurodov & Tojibaev | 05/22/2020 | Surkhandarya Province, Uzun District | N. 38.320062 E. 68.225442 | Pulatov et al. | 22052020106 | OR041880* | | | |
| | | 24/05/2019 | Surkhandarya Province, Uzun District | N. 38.328013 E. 68.21836 | Beshko N.Yu., Makhmudov A. | TASH058995 | | MZ647714 | MZ647712 | ON147183 |
| 27 | *Onobrychis chorassanica* Bunge ex Boiss. | – | – | – | – | – | KP338196 | KP338315 | KP338573 | KP338448 |
| 28 | *Caragana grandiflora* DC. | – | – | – | – | – | AB051905 | AB287412 | AB854564 | |
| 29 | Eversmannia subspinosa (Fisch. ex DC.) B.Fedtsch. | – | – | – | – | – | KP338144 | AB854527 | AB854573 | KP338394 |

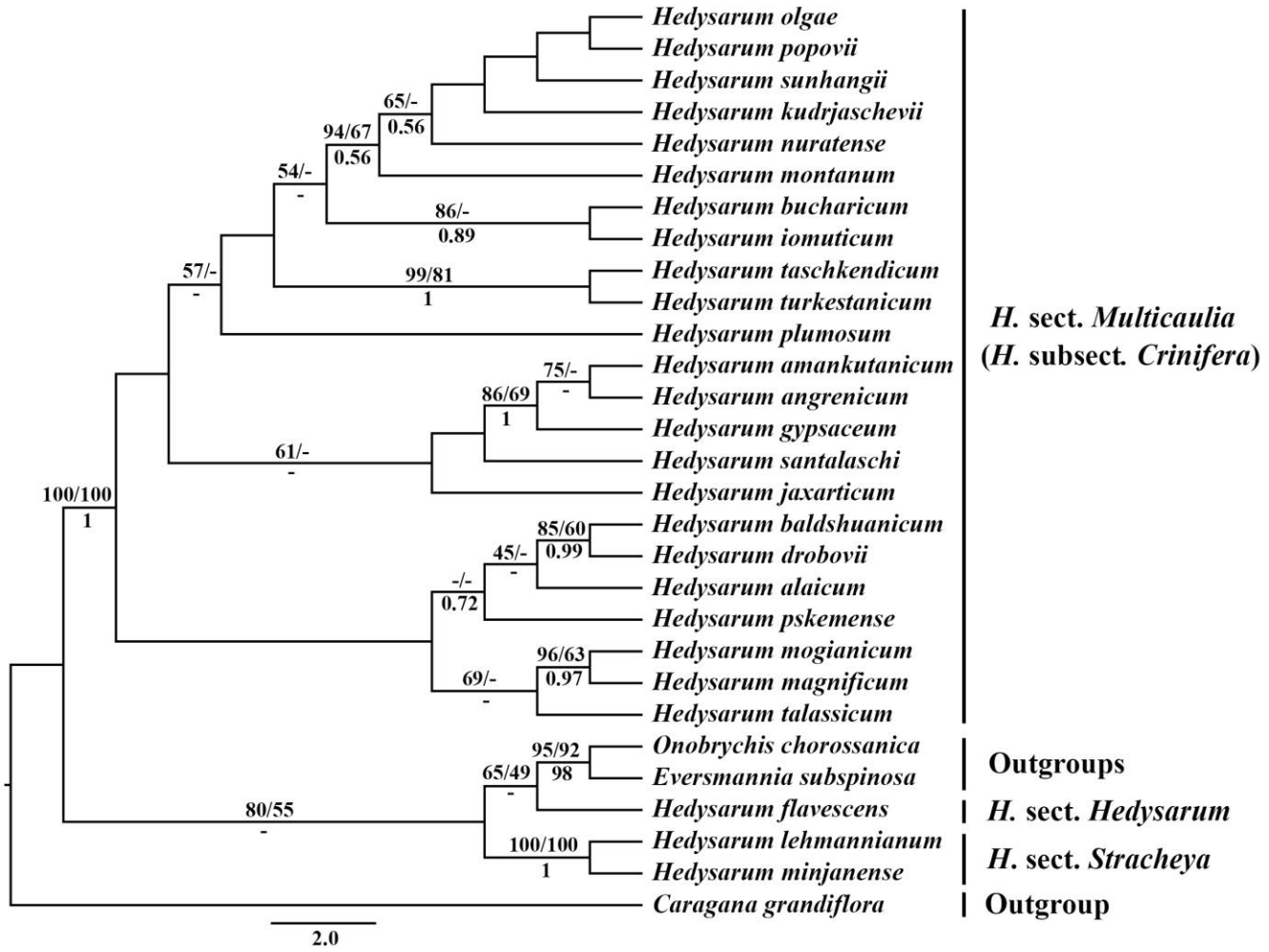


**Fig. S1.** Maximum likelihood tree inferred from nrDNA ITS sequences. Bootstrap values of maximum likelihood (ML) / maximum parsimony (MP) are given on each branch; Bayesian posterior probability (PP) is below branches. Only bootstrap values >45% are shown.

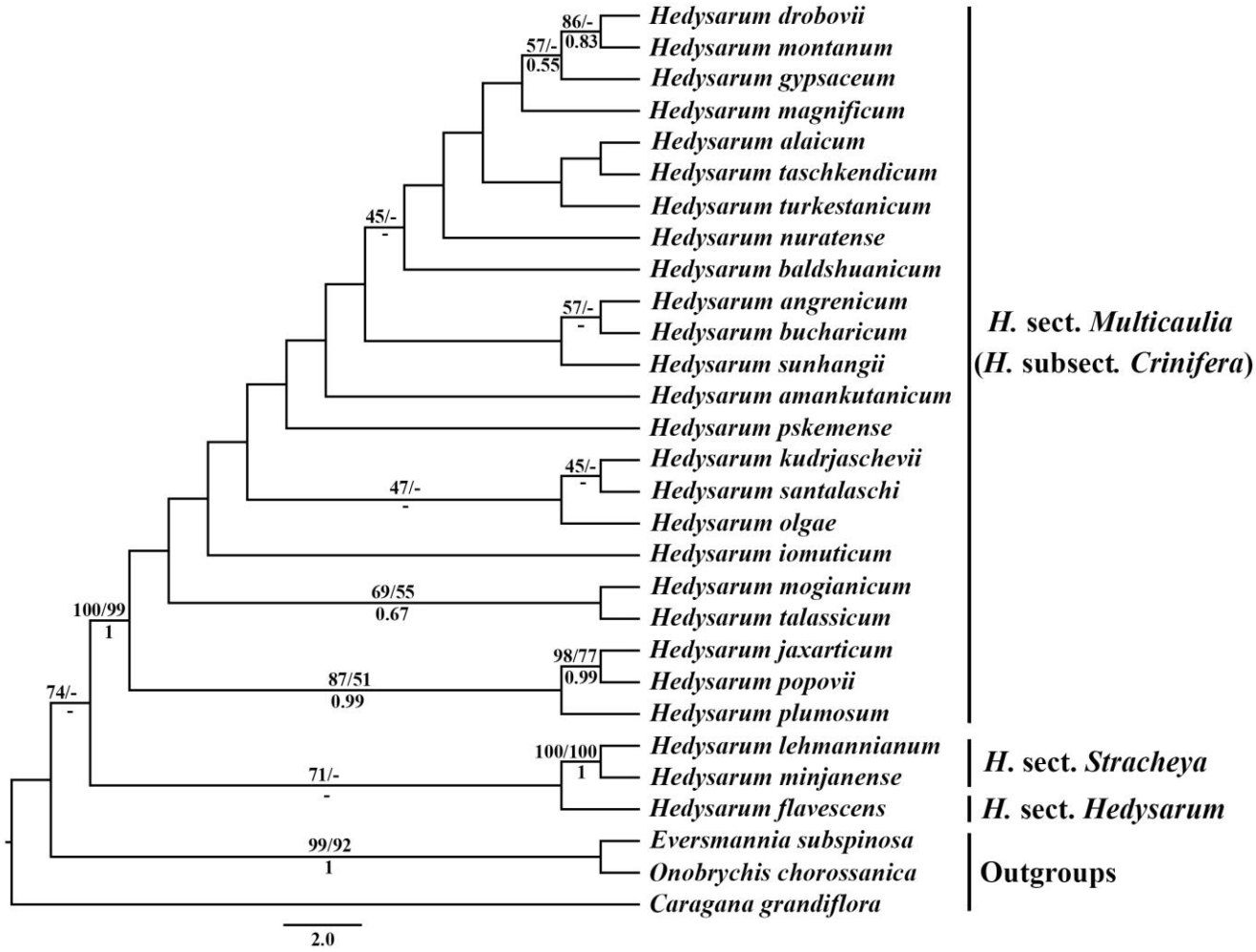


**Fig. S2.** Maximum likelihood tree inferred from combined plastid (*trnL-trnF*, *matK* and *psbA-trnH*) sequences. Bootstrap values of maximum likelihood (ML) / maximum parsimony (MP) are given on each branch; Bayesian posterior probability (PP) is below branches. Only bootstrap values >45% are shown.