



Podocytisus caramanicus (*Fabaceae*) in the Balkan Peninsula: distribution, habitat and taxonomic notes

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Abstract

Podocytisus caramanicus (*Fabaceae*) is disjunct in southern Anatolia (Turkey) and the Balkan Peninsula, areas representing the entire distribution of the species. It is lectotypified for the first time. A description of the species within its geographical range, and its distribution in the Balkan Peninsula are presented. Habitat, altitudinal and substrate preferences are outlined for each country based on field observations, herbarium and literature data. Recent evaluation by Principal Component Analysis (PCA) confirms that the Anatolian plants and the Balkan plants belong to the same species, a situation paralleling that of *Gonocytisus dirmilensis* (*Fabaceae*), which has a similar disjunct distribution in SW Anatolia and Greece.

Key words

Balkan Peninsula, distribution, *Podocytisus*, taxonomy

Citation

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Introduction

Disjunct distributions of plants occur when populations of the same species are geographically separated due to historical geological events or climatic changes, resulting in fragmented distributions that were once continuous. Such distributions provide valuable insights into biogeographical history, evolutionary processes and species adaptation. The study of these patterns often involves a combination of phylogenetic analysis, fossil evidence and morphological comparisons.

The genus *Podocytisus* Boiss. & Heldr. (*Fabaceae*) is a remarkable case of disjunct distribution, occurring in

two geographically distant regions: southern Anatolia (Turkey) and the Balkan Peninsula. This genus is monotypic and comprises only one species, *Podocytisus caramanicus* Boiss. & Heldr. It is distinguished from similar-looking members of the tribe Genisteae (*Laburnum* Fabr., *Lembotropis* Griseb., *Cytisus* Desf., *Chamaecytisus* Link, *Calicotome* Link, *Genista* L.), by its tardily-dehiscent flattened legumes with a dorsal wing. It was originally described as 'generically distinct by its indehiscent fruit, broadly margined on both sides' (Boissier 1849: 7). This was altered to 'legume flat, stipitate, falcate, sub-indehiscent, with upper suture broadly winged' (Boissier 1872: 35).

Despite the wide but fragmented distribution, little is known about the possible morphological variation between the populations in Turkey and the Balkans. Considering the geographical separation, a crucial question is whether the Balkan and Anatolian populations show significant morphological differences that could indicate incipient speciation or cryptic diversity. In this study, we investigate the morphology, distribution and ecological preferences of *P. caramanicus* throughout its range, incorporating data from herbarium specimens, field observations and historical literature records. We also perform Principal Component Analysis (PCA) to assess morphological variation and determine whether the Anatolian and Balkan populations represent a single taxon. The results are discussed in the broader context of the disjunct distribution of the species in the Balkan and Anatolian regions, drawing comparisons with *Gonocytisus dirmilensis* Hub.-Mor. (*Fabaceae*) which has a similarly fragmented distributional range.

Leaf material has been removed by other researchers for DNA analysis on *Davis* 19848 (K-000556894) from S Anatolia, Turkey, *C. Navarro & al.* 6820 (W-0276253), 6829 (WU-0276253) from N Peloponnese, Greece and on *Karl* s.n. (W-0128642) from Evvia, Greece. No comparative DNA studies have been published so far.

Material and methods

A review and examination of *Podocytisus* specimens from Turkey, Greece, North Macedonia, Albania and Kosovo was carried out. Their distributions based on field notes, herbarium and literature data are illustrated in a map (Fig. 6). The morphological characters were analyzed, recorded and summarized in Table 1. The morphometric measurements for Kosovo and Albanian populations were not included in the table. The data for Kosovo came exclusively from literature, while the Albanian data

Table 1. Morphological characters of *Podocytisus caramanicus* in Greece, Turkey and North Macedonia.

Characters	Greece	Turkey	North Macedonia
Habit/height	erect shrub, 1-2(2.5) m	erect shrub, 1-2(2.5) m	erect shrub, 1-2 m
Young twigs	glabrous	glabrous	glabrous
Leaflets	obovate, glabrous above	obovate, glabrous	obovate, glabrous
Terminal leaflets	(3)5-17(20) × 3-12 mm	10-20 × 5-13 mm	5-13(16) × 2.5-9.0 mm
Inflorescence	lax raceme 5-30 cm long	lax raceme 10-30 cm long	lax raceme 5-25 cm long
Raceme	5-15-flowered	5-10-flowered	(3)5-10-flowered
Pedice length	5-10 mm, elongating to 15 mm in fruit	4-12 mm	4.0-8.3 mm
Pedice indumentum	glabrous	glabrous	glabrous
Calyx upper lip (with 2 teeth)	3.0-4.5 mm long	4.0-5.5 mm long	3.2-3.6 mm long
Calyx lower lip (with 3 teeth)	4.5-6.0 mm long	5-6 mm long	3.5-4.2 mm long
Corolla colour	bright yellow	bright yellow	bright yellow
Standard length	10-15(18) mm, glabrous	12-15 mm, glabrous	9.0-13.2 mm, glabrous
Wing petal length	10-15(18) mm, glabrous	12-15 mm, glabrous	7.6-10.2 mm, glabrous
Keel length	10-15(18) mm, ventrally pilose in proximal third	10-15 mm, glabrous	8.0-11.1 mm, glabrous
Standard to keel length	standard as long as keel	standard as long as keel	slightly longer or equalling keel
Stamens	monadelphous	monadelphous	monadelphous
Anthers	glabrous	glabrous	glabrous
Style length	5-6 mm, reflexed, glabrous	5-6 mm, reflexed, glabrous	8.4-11.4 mm, reflexed, glabrous
Legume	25-35(40) × 10-18 mm	30-35(50) × 8-12 mm	23-42 × 10-11 mm
Dorsal wing	2-3 mm broad	2.0-2.5 mm broad	2.0-2.5 mm broad
Ovule number	3-9	5-9	5-9
Number of seeds in legume	3-6	3-6	5-6(9)
Seed	4.5- 5.0 × 3.5 mm	4-5 × 3.0-3.5 mm	5.0-5.5 × 3.5 mm
Seed shape	oblong-subreniform	oblong-subreniform	oblong-subreniform
Seed colour	pale brown turning black	pale brown turning black	pale brown turning black

set contained only four specimens, one from each of the four known localities. The measurements obtained in Table 1 were used to create a PCA diagram to assess morphological variation across populations.

Results and discussion

Typification

Podocytisus caramanicus Boiss. & Heldr. in Boiss., Diagn. Pl. Orient. ser. 1, 9: 7 (1849).

Protologue: [Turkey C4 Konya] 'in collibus apricis Tauri Isaurici in valle fluvii Djoksu [Göksu] inter Karaman et Ermenek', Fl. Junio (Heldreich).

Lectotype designated here by Kit Tan & al.: [Turkey C4 Konya] Taurus Isauricus inter Karaman et Ermenek, Jul. 1845, Heldreich s.n. (G00331323-SIB 402660/1 in G-Boiss.); isolectotypes E! G-Boiss. (00634210-SIB 497609/1! 00634220-SIB 497609/3!), GOET! K!

≡ *Laburnum caramanicum* (Boiss. & Heldr.) Benth. & Hook.f., Gen. Pl. 1: 481 (1865).

≡ *Cytisus caramanicus* (Boiss. & Heldr.) Nyman, Consp. Fl. Eur.: 155 (1878).

= *C. nigricans* var. *kindlii* Adamović in Denkschr. Kaiserl. Akad. Wiss. Wien, Math-Naturwiss. Kl. 74(1): 128 (1904). – Type: [NC Greece, Nomos Pellis, Eparchia Edessis] 'in fruticetis et in nemoribus regionis inferioris ad Voden [Edessa]', June 1902, Kindl (holo. BEOU!).

= *Podocytisus americanus* G. Nicholson, Hand-list Trees Shrubs 1 [Polypet.]: 107 (1894), not validly publ.

The protologue published in 1849 does not indicate that two syntypes exist: one with flowering material collected by Heldreich in June 1845 (in valle Djok-sou Tauri Caramanici, alt. 3500'), and another with fruiting material collected one month later in July 1845 (Taurus Isauricus inter Karaman et Ermenek). Although the protologue cited 'June', this notation refers only to the flowering period rather than to a specific specimen.

We designate the specimen from July 1845 as a lectotype, as Boissier (1849) emphasized that the morphology of the fruits is the key distinguishing feature of the genus. Moreover, the specimen from June 1845 was absent in G-Boiss. whereas several specimens from July 1845 were available, which Boissier had received from Heldreich.

The specimens from the June 1845 gathering seem to be rare or at least, not widely distributed. They were found



Fig. 3. *Podocytisus caramanicus*: habit and part of inflorescence in June, N Peloponnese, Greece.

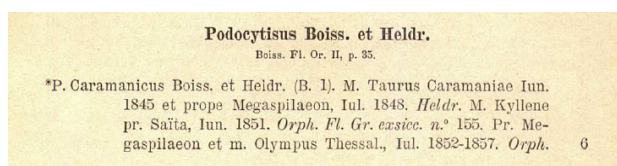


Fig. 1. Extract from Heldreich (1877:12) listing *Podocytisus* specimens in the Orphanides herbarium.

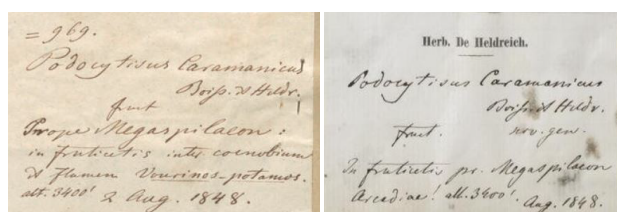


Fig. 2. Labels of first collection of *Podocytisus caramanicus* from Greece by Heldreich.



Fig. 4. *Podocytisus caramanicus*: inflorescences in July, Katlanovska Brezica, North Macedonia.

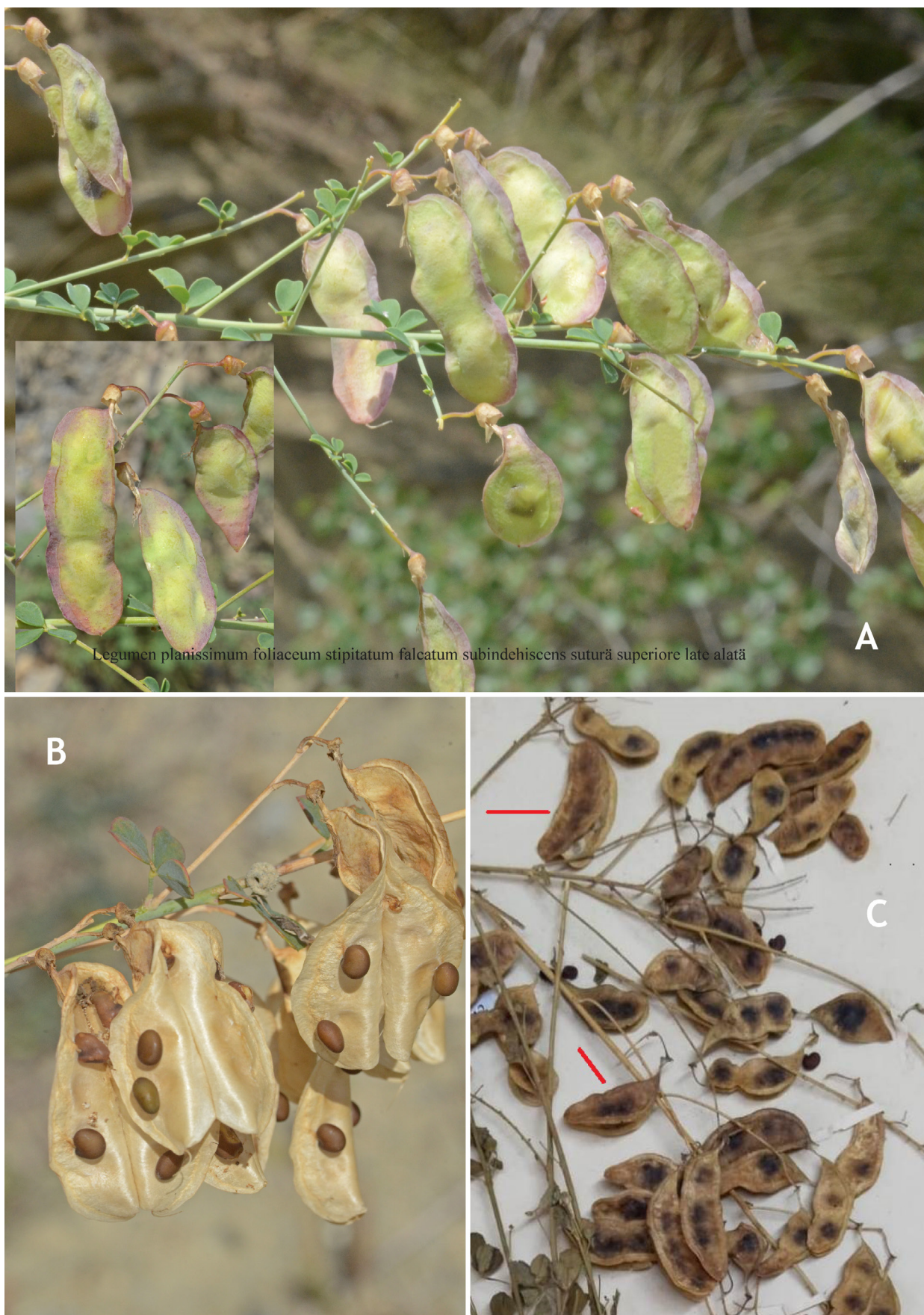


Fig. 5. *Podocytisus caramanicus*: **A**, nearly mature fruits showing broad dorsal wing in August, Sarandaporos River, Greece; **B**, dehiscent fruits with ripe seeds in October, Kastoria, Greece; **C**, herbarium specimen in September, S Albania, X. Qosja s.n. (TIR), dehiscent fruits indicated by red lines.

in the Natural History Museum, London (BM001217376) and in Herbarium E (E00334012), in the latter herbarium one was mounted on the same sheet as a July 1845 specimen (E00334013). However, it appears that the corresponding labels had been erroneously exchanged. The BM specimen is clearly labelled and its features match those of E00334012, confirming that both belong to the same collection of June 1845 from the original provenance.

There is some evidence that a specimen dated June 1845 also exists in ATHU. Heldreich (1877) published a catalogue of the *Leguminosae* existing in the herbarium of Theodoros Orphanides, professor of botany at the University of Athens. On page 12 of this publication a specimen of *P. caramanicus* from the Taurus mountains was listed as collected by himself in June 1845 (Fig. 1). We have requested information on this specimen from the hosting herbarium (ATHU) but so far have received no response so we do not know for certain if the specimen is extant or had been destroyed after 180 years.

It is interesting to note that *P. caramanicus* was first collected in Greece by Heldreich in 1848 from the northern Peloponnese, near Megaspileo (*prope Megaspilaeon, alt. 3400', 2 Aug. 1848*), Heldreich (ATHU, G! K!), see Fig. 2.

Description of species across its geographical range (Figs. 3-5)

Erect, non-spiny shrub 1-2 (2.5) m tall. Young twigs and branches slender, virgate, terete, weakly striate, glaucous, glabrous. Stipules absent. Leaves 3-foliolate. Petioles 3-15 mm, glabrous to sparsely hairy; upper leaves subsessile. Leaflets shortly petiolulate, obovate, (3)5-17 (20) × 2.5-13.0 mm, obtuse or mucronulate, glaucous, glabrous above, sparsely hairy along midvein beneath. Flowers in lax, erect, terminal racemes 5-30 cm long, each raceme (3)5-15-flowered. Bract single, lanceolate, ca. 2 mm, pilose-pubescent, at middle or lower 1/3 of pedicel, persistent. Bracteoles 2-3, minute, at base of calyx or at middle of pedicel, sericeous-pubescent. Pedicels 4-12 mm, elongating to 15 mm in fruit, glabrous. Calyx cupular-campanulate, shallowly bilabiate, ciliolate, persistent; upper lip 3.0-5.5 mm, with 2 teeth; lower 3.5-6.0 mm, with 3 teeth; teeth ± equal, less than 0.5 mm. Corolla bright yellow. Standard subreflexed, orbicular-ovate, 9-15 (18) mm, ± equalling wings and keel, glabrous. Wings (7.6)10-15 (18) mm, corrugate-plicate in proximal third, glabrous. Keel beaked, (8)10-15 (18) mm, glabrous or ventrally pilose in proximal third. Stamens monadelphous; anthers linear-oblong, glabrous. Ovary linear, glabrous, 3-9-ovulate; style reflexed or perpendicular, 5-8 (11.4) mm, glabrous, persistent; stigma terminal, capitate-discoid, papillose-ciliate. Infructescence pyramidal, to 35 cm long. Legume with 4-7 mm stipe partially ensheathed when young by persistent filament bases, pendent, laterally compressed, ovate to oblong or falcate-subpanduriform, 25-35(-50) × (8)10-15 (18) mm, with 2-3 mm broad dorsal wing, late dehiscent; valves thin, chartaceous, pale green suffused

purplish or brownish, glabrous or sparsely hairy. Seeds 3-6 (9), oblong-subreniform, 4.0-5.5 × 3.0-3.5 mm, pale brown turning black, smooth, without strophiole. $2n = 48$ (Greece, Cusma-Velari & Feoli-Chiapella 2009).

Almost mature legumes may provide the impression that the marginal wing surrounds the fruit as Boissier stated in 1849. Examination of herbarium material shows that the wing is restricted only to the dorsal suture, along which the legume dehisces. The carpel is flattened towards the ventral margin which develops the same reddish-purple colour as the dorsal margin, and thus simulates a wing (Fig. 5A).

Habitat, ecology and distribution in the Balkan peninsula

Mainly western part of Balkan Peninsula (North Macedonia along the Vardar Valley reaching southeastern Kosovo), South Albania and Greece (Fig. 6); disjunct in river gorges of south-central Anatolia.

Greece: open pine and mixed deciduous forest, rocky and stony slopes, phrygana, shady gravelly road embankments, abandoned vineyards, etc., on limestone, conglomerate, eroded flysch or serpentine, 200-1500 m. Flowering May to July; fruiting till late September.

Central Peloponnese northwards to N Pindos and North Central, rare in the northeast, absent from all islands except the West Aegean island of Evvia.

North Macedonia: hornbeam and oak forests, grazed scrubland, edge of fields, cultivated and abandoned vineyards, roadsides, on limestone, silicate, paleogene marl, etc., 200-800 m. Flowering June to July; fruiting mid-August to September.

In catchment area of Vardar River, north of Udovo-Demir Kapija to the Skopje and Tetovo valleys, mainly within the association *Hippocrepido emeroides-Carpinetum orientalis* (shibljak formation - degraded oak forest).

Podocytisus was found in 1917 for the first time in North Macedonia in the area of the Vardar River by Bornmüller (1925). Em (1953, 1967) provided a distribution map based on information from Bornmüller (1927, 1937), Košanin (1927) and Soška (1938, 1939a, 1939b) as well as from his own findings in the foothills of Šar Planina and Skopska Crna Gora. A complete list of localities is now provided.

Skopje: Vodno, v. Drachevo, v. Oreshani, between v. Jabolce and v. Patishka Reka, v. Dolno Kolichani, Skopska Crna Gora, Žeden Gorge, Treska Gorge, Pčinja Gorge, Taorska Gorge (Micevski 2001); Kapina (Soška 1938); Dobri Dol, between v. Gradovci and v. Gumalevo, v. Ržaničino, Venec-Gradmanska River between v. Orašec and Pčinja, 550 m (Em 1953); Osoj (Matvejeva 1968); Lepenec River, Markova River (Browicz 1978); Katlanovska Brezica (*Quercus* forest margins, 41°51'47" N, 21°43'09" E, 520 m, 10.07.2014, V. Matevski (MKNH)); Katlanovo, between v. Vetersko and v. Rudnik, 41°49'31" N, 21°44'00" E, 449 m, 21.08.2014, V. Matevski (MKNH)). The last two records from V. Matevski are published here

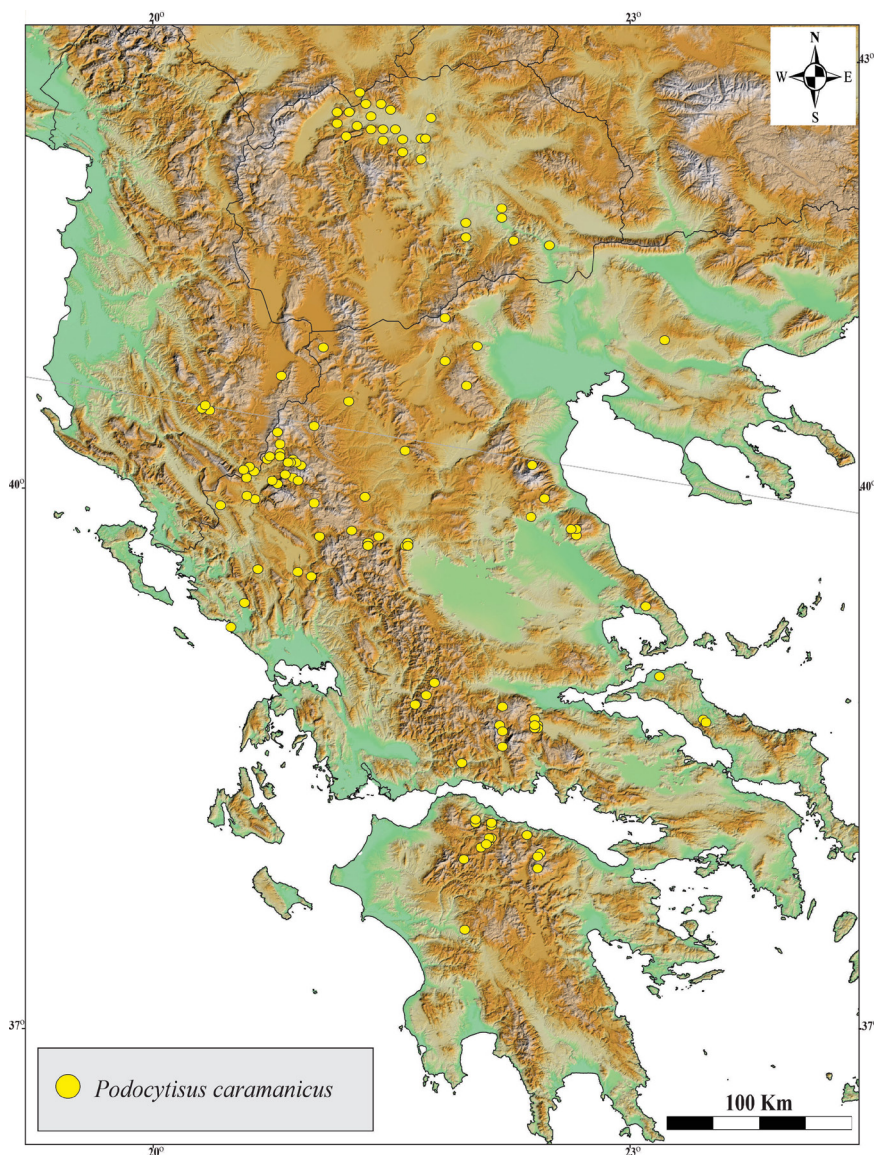


Fig. 6. Distribution of *Podocytisus caramanicus* in the Balkan Peninsula based on field notes, herbarium and literature data.

for the first time [MKNH refers to the Macedonian National Herbarium].

Tetovo: Dobraski Žeden (Teofilovski 2011).

Kumanovo: Kozjak, v. Sushevo (Matvejeva 1973).

Veles (Bornmüller 1927; Em 1953).

Negotino: Serta Mt (Micevski 2001).

Kavadarci: between Crna River and v. Pravednik; Ljubash, v. Begnishte, v. Resava, v. Vatasha (Jurišić 1923; Em 1953).

Demir Kapija Gorge (Micevski 2001).

Valandovo: Udovo (Em 1953).

Kosovo: stony and rocky calcareous slopes in gorge-like valley, 200–400 m. Flowering end of June.

Only in southeastern Kosovo near border with North Macedonia. Along the valley of Lepenc River, especially between the towns of Hani i Elezit and Kačanik.

The discovery in Kosovo (at that time in Serbian territory) was made by E and M. Mayer who reported numerous flowering populations along the Lepenc Valley on

29 June 1979, between the town of Djeneral Janković to below Kačanik (Mayer 1981). Further field work is needed to confirm specific plant communities, microhabitat preferences and associated species.

Albania: openings of degraded slopes with mixed macchie dominated by evergreen shrubs such as *Arbutus andrachne*, *Arbutus unedo*, *Phillyrea latifolia*, *Quercus ilex*, *Pistacia terebinthus*, *Rhus coriaria*, *Juniperus oxycedrus* subsp. *deltoides*, *Spartium junceum*, *Asparagus acutifolius* and deciduous shrubs such as *Paliurus spina-christi*, *Rosa canina*, *Pyrus amygdaliformis*, *Rubus sanctus*, *Cistus creticus* and *Staelhelia uniflosculosa* (Shuka & Tan 2024), mainly on flysch, rarely on limestone, 300–750 m. Flowering June to early August; fruiting mid-August to September.

South Albania (Mediterranean climate areas). Upper part of Vjosa Valley from Draçova to Çarshova, vicinity of thermal waters in Vromonero, Leskoviku vineyards and along Osumi River near Çorovoda (Baldacci 1899, Mitrushi 1966, Barina 2017, D. Shuka obs.).

PCA analysis of the morphometric characteristics of *Podocytisus caramanicus* (Fig. 7)

The PCA diagram presents a visual overview of the morphometric differences in three geographical populations — Greece (circles), Turkey (triangles) and North Macedonia (asterisks).

Features and their significance

Principal Component 1 (PC1) explains 90.75% of the variance, capturing the most differentiation and indicating the dominance of a single morphometric character which determines the most variation; it is probably related to leaflet size, habit or inflorescence.

Turkish population (triangles) — mainly clustered to the right side of PC1 axis. This indicates a uniform set of morphometric characters with little variation within the population as compared to Greece. Some individuals are slightly more dispersed along PC2 but the overall differentiation is determined by PC1. Environmental conditions or genetic divergence may account for the uniformity.

Greek population (circles) — showing a high degree of variation. Widely distributed across PC1, indicating considerable morphometric diversity probably due to greater genetic diversity or phenotypic plasticity. Some individuals show negative PC1 values, thus clearly separating them from the Turkish and North Macedonian populations. There is little dispersion along the PC2 axis but this axis plays only a minor role in population differentiation.

North Macedonian population (asterisks) — positioned at the centre of PC1 axis, reflecting an intermediate morphology between Greece and Turkey. There is moderate variation, less dispersion (variation) than in Greece but higher than in Turkey. Its relatively compact grouping indicates greater morphometric stability than Greek populations, probably influenced both by gene flow and environmental factors.

Principal Component 2 (PC2) accounts for 9.04% of the variance, indicating a minor role in separating populations due to small morphological differences. However, some Turkish individuals show variation along this axis.

Conclusion

The PCA analysis shows clear morphological differentiation among the three studied populations of *P. caramanicus*, with the Turkish population showing the least variation. The Greek population shows the most variation and North Macedonian population represents an intermediate group. Most of the morphological differentiation is captured by Principal Component 1 (PC1). The higher variation noted in Greek plants may also result from the broader sample of material examined (more than 70 specimens), whereas for Turkey and North Macedonia they are less than 25 each. Data from Kosovo is represented by literature reports and from Albania, one specimen from each of the four known localities. These specimens exhibited morphological features that were largely consistent with those from North Macedonia and northern Greece. The analysis shows the conspecific position of the three studied populations. The general facies of the species remains constant and recognizable and these morphological differences are probably shaped by climatic, ecological or genetic factors over 25 million years when the species once occupied a continuous land mass from Turkey to Greece. Further research including genetic analysis or ecological modelling may provide some information for the underlying causes of this diversity. It was not a surprise to find that Heldreich had collected *P. caramanicus* in Greece, Nomos & Eparchia Evritanias, near the village of Mikrochorio on 12 August 1879 (G!) and *G. dirmilensis* occurs in the same area, just 2 km from Mikrochorio (G!). Thus the situation of *P. caramanicus* parallels that of *G. dirmilensis* which has a similar disjunct distribution in SW Anatolia and Greece (Tan & al. 2025).

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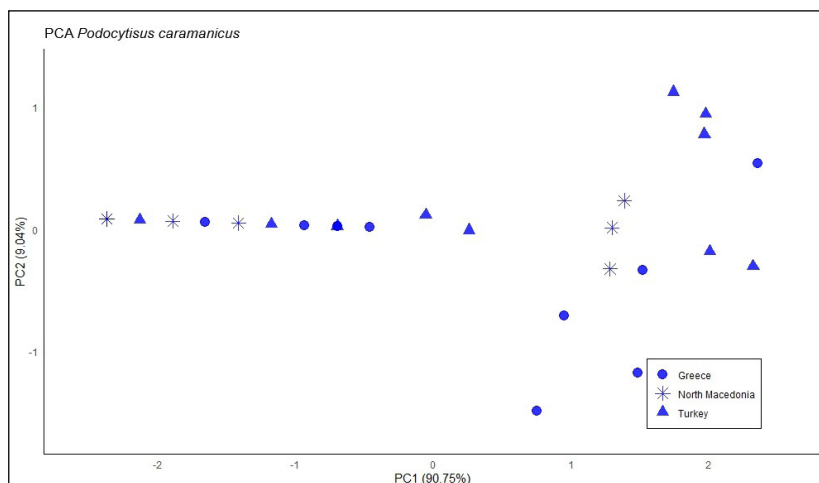


Fig. 7. Principal Component Analysis (PCA) diagram for *Podocytisus caramanicus*.

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