



The Turkish Endemic *Pseudodelphinium turcicum* (Ranunculaceae): An Unusual Population of *Delphinium* with Peloric Flowers That Has Persisted in the Wild for 20 Years

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THE TURKISH ENDEMIC *PSEUDODELPHINIUM TURCICUM* (RANUNCULACEAE): AN UNUSUAL POPULATION OF *DELPHINIUM* WITH PELORIC FLOWERS THAT HAS PERSISTED IN THE WILD FOR 20 YEARS

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Premise of research. The Turkish endemic *Pseudodelphinium turcicum* (Ranunculaceae) was described by Vural et al. (2012) based on a single population found in the salt lake basin of Tuz Gölü, Konya Province. Although the authors noticed morphological similarities between the plants and *Delphinium* or *Garidella*, they highlighted unusual features, which led them to describe a new genus consisting of a single species, *P. turcicum*. The aim of this study is to investigate the morphological particularities and evolution of *Pseudodelphinium*.

Methodology. We carried out morphological, anatomical, and palynological studies on individuals of *P. turcicum*. We also conducted a molecular phylogenetic analysis to identify the closest relatives of this species.

Pivotal results. This combination of approaches shows that the species belongs in the group of Mediterranean species in *Delphinium* subg. *Delphinium*. Based on our sampling, *P. turcicum* is more precisely sister to the Turkish endemic *Delphinium venulosum*. The perianth of *P. turcicum* flowers consists of tepals that are, anatomically speaking, similar to the sepals of *Delphinium*. A second type of perianth organs was evidenced. They are located between the tepals and the stamens, and their development is arrested at an early stage, therefore being comparable to the ventral petals of *Delphinium* flowers. The pollen of *P. turcicum* is heteromorphic.

Conclusions. We conclude that the population of *P. turcicum* is an unusual population of *Delphinium* presenting peloric flowers (through ventralization) that has been maintained in the wild for at least two decades. We provide hypotheses concerning the identity of the floral organs, as well as an explanation for the origin of the particular floral morphology.

Keywords: anatomy, *Delphinium*, morphology, palynology, peloria, *Pseudodelphinium*.

Online enhancement: appendix figure.

Introduction

The buttercup family (Ranunculaceae), belonging to the order Ranunculales (Wang et al. 2009; APG 2016), arose in the early mid-Cretaceous (c. 108 Ma) and went through a rapid diversifi-

cation during the Campanian between 83 and 74 Ma (Wang et al. 2016b). Currently, the family is divided into five subfamilies and consists of about 43 genera and 2346 species (Christenhusz and Byng 2016) that are mostly herbaceous (Stevens 2001; Wang et al. 2009). Even though the family has a worldwide distribution, most species are restricted to the north temperate regions (Tamura 1993; Stevens 2001). The tribe Delphinieae (subfamily Ranunculoideae) comprises c. 700 species, approximately a quarter of all species diversity within the family, and is mainly distributed from the Mediterranean Basin to Korea, Japan, Siberia, and North America (Jabbour and Renner 2012a; but

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for the tropical African species of *Delphinium*, see Chartier et al. 2016). In Turkey, the family is represented by c. 230 species distributed among more than 19 genera (Güner et al. 2012), *Ranunculus* being the largest genus with 100 taxa, 20 of them endemic for Turkey (Davis et al. 1965). The genus *Delphinium* has 33 taxa, and 17 of them are endemic (Güner et al. 2012). *Delphinium* sensu lato (i.e., including *Consolida* and *Aconitella* sensu Jabbour and Renner 2011) comprises 58 species (Ilarslan 1996; Özçelik and Korkmaztürk 2012), which makes it one of the most species-rich genera of angiosperms in Turkey. Davis et al. (1965) noted that *Delphinium* is a taxonomically difficult genus in Turkey due to the fact that many species are connected by hybrid intermediates.

Recently, Vural et al. (2012) reported the occurrence of a population in central Turkey located in the basin of the large salt lake Tuz Gölü in Konya Province (fig. 1). The lake is one of the largest salt lakes in the world, and the surrounding ecosystems are known for their high levels of plant endemism. Öztürk and Çetin (2013) reported 54 species endemic to the region. According to Vural et al. (2012), the single population of *Pseudodelphinium turcicum* known to date was collected for the first time in 1997 (M. Vural 7793, kept in GAZI and KNYA [herbarium acronyms follow Thiers 2017]) and is composed of short and virgate herbaceous plants with, from the base to the top of the plant, leaves divided into three linear segments and simple linear leaves. The inflorescences are racemose with pubescent bracts and bracteoles similar to the leaves. Flowers are actinomorphic with five free petaloid tepals, numerous free stamens, and three free carpels longitudinally striate (Vural et al. 2012). These plants show features of annual species of *Delphinium* L., but due to significant differences in the floral structure, the authors suggested that plants

from this population could also morphologically relate to *Gari-della* L. However, without any additional argument (e.g., molecular phylogeny) that could have helped them interpret those morphological particularities, Vural et al. (2012) considered that these plants should be attributed to a new genus, *Pseudodelphinium* H.Duman, Vural, Aytaç & Adigüzel (Ranunculaceae), comprising a single species, *P. turcicum* H.Duman, Vural, Aytaç & Adigüzel.

The aim of this article is to improve our knowledge of the monotypic genus *Pseudodelphinium* and to better understand its morphological peculiarities and evolution. To do this, we carried out a molecular study to place the genus in the phylogenetic tree of Ranunculaceae. We then undertook a morphological-anatomical study to describe the particular floral organization in the genus. This led us to provide an updated taxonomic treatment for the taxon. In this article, the vocabulary relative to the perianth organs of *Delphinium* follows Rasmussen et al. (2009).

Material and Methods

Taxon Sampling, DNA Sequencing, Alignment, and Phylogenetic Analyses

Plastid and nuclear markers were sequenced from four specimens from the known population of *Pseudodelphinium turcicum*, namely, M. Vural 10643 & O. Tugay (kept at P; barcode [P04021862]: <https://science.mnhn.fr/institution/mnhn/collection/p/item/p04021862>), M. Vural 10650a and M. Vural 10650b (kept at P; [P04021863]; these two individuals are mounted on a single sheet), and M. Vural & O. Tugay 10643.1 (kept at



Fig. 1 Map of Turkey. The zoomed section (scale = 2 km) corresponds to the locality of the single population of *Pseudodelphinium turcicum* currently known: “C4 Konya: Karapınar to Konya road, 30 km, Merdivenli village, 1020 m” (Vural et al. 2012, p. 429). The inferred GPS coordinates are 37.722779, 33.201391. Images from DigitalGlobe. Map data from Google. A color version of this figure is available online.

PE; sequenced by Xiang et al. [2017] for a study focusing on *Delphinium* subg. *Delphinium*). DNA isolation and sequencing relied on the DNeasy 96 Plant kit (Qiagen) and the DNeasy Plant mini kits (Tiangen Biotech, Beijing, China) and relied on the universal primers of Taberlet et al. (1991) for amplifying and sequencing the *trnL* intron and adjacent *trnL-trnF* intergenic spacer. The nuclear ribosomal internal transcribed spacer ITS-1, the 5.8S gene, and ITS-2 were amplified with the external primers of White et al. (1990). PCR products with the expected size were detected by agarose gel electrophoresis before sequencing (Eurofins Genomics MWG/Operon, Les Ulis, France). Sequencing reactions for the *M. Vural* & *O. Tugay* 10643.1 accession were conducted using BigDye Terminator kits (Applied Biosystems, Foster City, CA) with an ABI 3730 DNA automated sequencer (Applied Biosystems).

Sequence assembly of forward and reverse strands was carried out in MEGA v.7 (Kumar et al. 2016), and sequences were subjected to a BLAST search in GenBank. All newly obtained *trnL-F* and ITS sequences of *P. turcicum* were very similar (more than 98% identity) to sequences from species belonging to *D.* subg. *Delphinium*. To clarify the systematic placement of *Pseudodelphinium*, we thus restricted our sampling to the tribe Delphinieae, to which *Delphinium* belongs. Three accessions of *P. turcicum* (*Vural* 10650a was discarded due to an unsuccessful sequencing of the ITS marker) were added to the *trnL-F* + ITS alignment of Wang et al. (2013), which provides the most complete sampling of Delphinieae accessions to date and includes two outgroup accessions from the species *Nigella damascena* and *Megaleranthis saniculifolia*. Sequences were aligned by eye, and the final alignment was 2193 positions long and comprised 290 accessions. The phylogenetic reconstruction relied on maximum likelihood (ML) as implemented in raxmlGUI (Silvestro and Michalak 2012), using the GTR + G + I model (the most general evolutionary model proposed). Statistical support for nodes was assessed by bootstrap resampling of the data under the same model (500 replicates).

Plant Material for the Morphological-Anatomical Study

The morphological-anatomical study was carried out on *P. turcicum* as well as two species of *Delphinium*. We selected *Delphinium venulosum* and *Delphinium virgatum* because *P. turcicum* is sister to *D. venulosum* and is nested within the group of Mediterranean *Delphinium* in *D.* subgenus *Delphinium*, of which *D. virgatum* is a representative. In addition, a phylogenetic analysis focusing on *D.* subgenus *Delphinium* using four markers (*trnK-matK*, *trnS-trnG*, *trnL-F*, and ITS) showed that the accessions of *P. turcicum* (*M. Vural* & *O. Tugay* 10643.1 [PE], also included in this study, and *M. Vural* & *O. Tugay* 10643.2 [PE]) formed a strongly supported clade sister to *D. virgatum* and *D. venulosum* (bootstrap percentage [BP] = 95; posterior probability = 1.0; Xiang et al. 2017). An additional (and geographic) argument is that *D. venulosum* (Turkish endemic) and *D. virgatum* grow in the vicinity of the area where *P. turcicum* was collected (Davis et al. 1965).

Flowers, buds, and pollen grains of *D. venulosum* and *D. virgatum* were taken from dried specimens at the P herbarium (National Museum of Natural History, Paris). The flowers of *D. venulosum* were obtained from the Turkish specimen *P.E.E. Sintenis* 4627 (P00201219). Flowers of *D. virgatum* were taken

from the Croatian specimen (P02681093; Unio Itineraria, 1829). Flowering individuals of *P. turcicum* were sent by *M. Vural* (*M. Vural* 10643 & *O. Tugay*, *M. Vural* 10650a, and *M. Vural* 10650b) and are now kept at P. Floral buds for the anatomical study were sampled from the specimen *M. Vural* 10643 & *O. Tugay*, and young floral buds and pollen grains for the morphological analysis were sampled from the specimens *M. Vural* 10650a and *M. Vural* 10650b (fig. 2A).

Restoration of the Flowers

The dried flowers sampled from herbarium specimens were restored in an ammoniacal 10% aqueous solution at 60°C for 24 h, fixed with FAA (90% ethanol 70%, 5% formalin, 5% acetic acid) for 24 h, and finally stored in a mixture of water, ethanol, and glycerol in equal volumes.

Dissection and Observation of Adult Flowers

Three adult flowers of *P. turcicum* were dissected using a stereomicroscope (Nikon SMZ 745T). Two of the flowers were dissected without being restored, and one was restored as detailed above. The dried flowers were mounted and put in an envelope pasted on the sheet (P04021863). The restored flower was mounted on a glass slide, which is kept at P.

SEM Observations

Fourteen restored buds (four for *D. venulosum*, four for *D. virgatum*, and six for *P. turcicum*) were sampled. Buds were dissected using a stereomicroscope (Nikon SMZ 745T). They were dehydrated in an ethanol series (70%, 80%, absolute alcohol) and dried using an Emitech K850 critical-point dryer (Quorum Technologies) and then mounted on aluminum stubs with colloidal graphite, sputter-coated with gold (60 s of metallization) using a JFC-1200 fine coater (JEOL), and observed using an SU3500 SEM (Hitachi). Pollen grains were fixed directly on aluminum stubs with colloidal graphite and observed using the same SEM. Samples are kept at P slide library.

Anatomical Sections

Three preanthetic floral buds were sampled for each of the species *D. venulosum*, *D. virgatum*, and *P. turcicum* and were restored. Buds were dehydrated through a t-butyl series and embedded in paraffin (melting point: 58°–60°C; Gerlach 1984). Serial transverse sections were cut at a thickness of 12 µm using a rotary microtome (Leitz 1512) and then stained with AstraBlue 0.5% aqueous (Chroma 1B 163) and Ziehl's fuchsine (RAL 320490-1000) 10% aqueous and mounted in the mounting medium Eukitt (O. Kindler E0214). Mounted buds were observed using a Nikon Eclipse Ci microscope. Floral vascularization was reconstructed by drawing selected serial cross sections of the anthetic flowers using a camera lucida and superimposing tracing papers. Because restoration of the bud of *D. venulosum* was problematic due to the poor tissue preservation, a second bud from the same specimen (*P.E.E. Sintenis* 4627) was dissected to check organ arrangement. Samples are kept at P slide library.

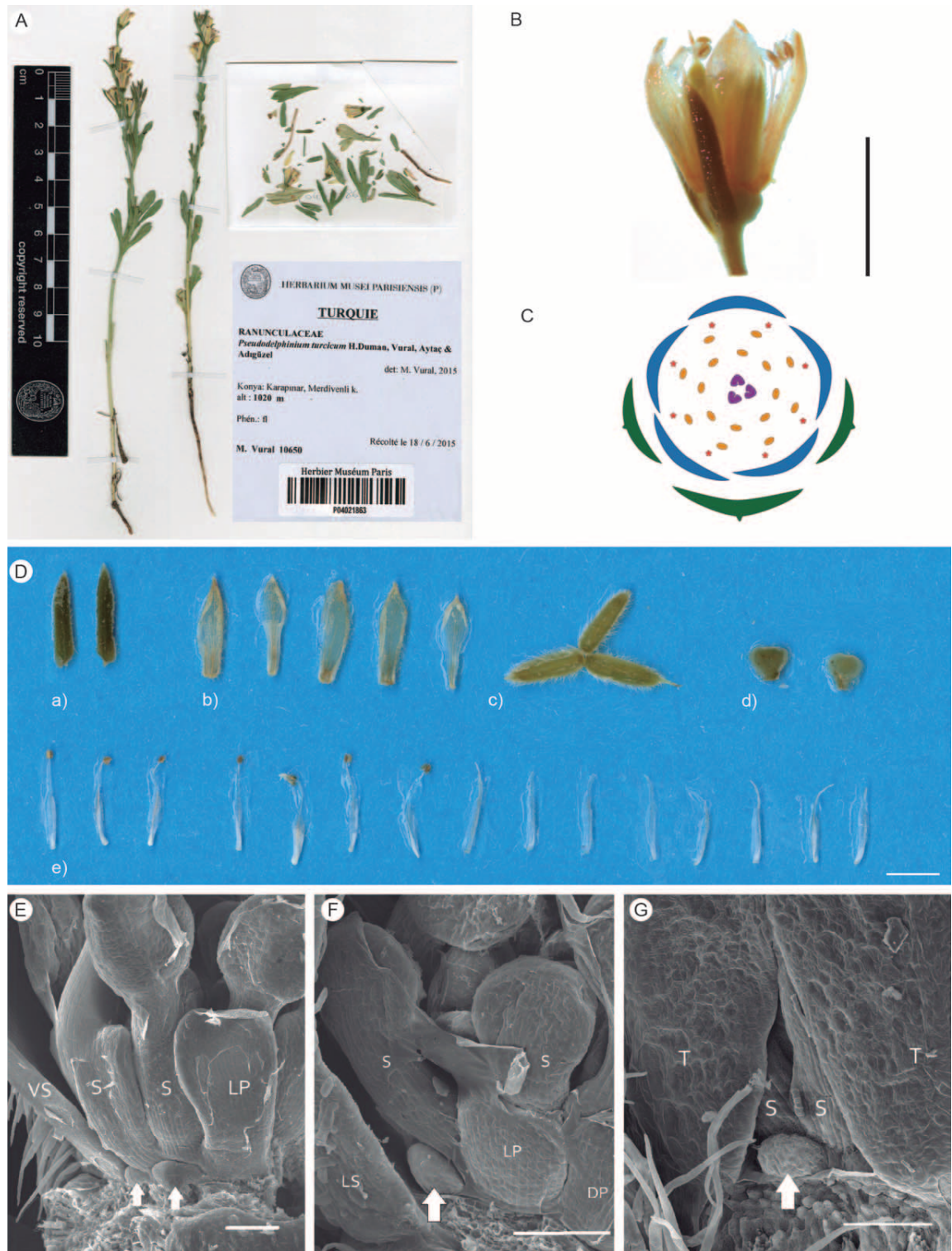


Fig. 2 A–D, *Pseudodelphinium turcicum* flower morphology. A, Sheet of *M. Vural 10650a* (right specimen) and *M. Vural 10650b* (left specimen) [P04021863] housed at P herbarium. B, Detail of a restored flower; scale = 0.5 cm. C, Floral diagram: bract and bracteoles are in green, perianth is in blue, stamens are in orange, carpels are in magenta, and red stars indicate the hypothetical position of young perianth organs with an arrested development. D, Floral dissection of the restored flower; scale = 1 cm. a = bracteoles; b = tepals; c = carpels; d = receptacle; e = stamens (stamens at the right lost their anthers during dissection). E–G, SEM micrographs of floral buds. E, *Delphinium venulosum*; scale = 1 mm. Arrows show young ventral petal organs (one lateral and one ventral sepal were removed). F, *Delphinium virgatum*; scale = 1 mm. The arrow points to a young ventral petal (the dorsal sepal was removed). G, *P. turcicum*; scale = 1 mm. The arrow points to a young dorsal organ with an arrested development (the dorsal tepal was removed). DP = dorsal petal; LP = lateral petal; LS = lateral sepal; S = stamen; T = tepal; VS = ventral sepal.

Results

Pseudodelphinium turcicum Belongs in
Delphinium Subg. *Delphinium*

The GenBank accession numbers for the *trnL-F* marker for *M. Vural 10643* & *O. Tugay* and *M. Vural 10650a* and *10650b* are KY596027, KY596028, KY596029, respectively. The GenBank accession numbers for the ITS marker for *M. Vural 10643* & *O. Tugay* and *M. Vural 10650b* are KY596030, KY596031, respectively (the sequencing of this marker for *Vural 10650a* was unsuccessful). The reconstructed ML tree is shown in figure 3. The topology and phylogenetic relationships among accessions of *Delphinieae* are identical to those shown by Wang et al. (2013). For this reason, each of the *Staphisagria* lineage, the clades composing the genus *Aconitum*, and the sister group of *D. subg. Delphinium* were collapsed in figure 3. All three accessions of *P. turcicum* form a clade (BP = 85%) sister to *D. venulosum* (BP = 70%). *Pseudodelphinium turcicum* belongs to the clade of Mediterranean species of *Delphinium* within subgenus *Delphinium* (BP = 100%).

Morphology

Pseudodelphinium turcicum exhibits a short virgate stem (c. 20 cm high) with a simple taproot, glaucous vegetative parts, and alternate leaves (2–2.5 cm long × 1.2–1.8 cm wide) with palmate venation at the base of the plant and simple leaves at the top (1.3–1.7 cm long × 0.3 cm wide). The inflorescence is a raceme (sometimes panicle) with actinomorphic bisexual flowers (fig. 2A). The flower is enclosed by one bract and two lateral bracteoles. It consists of three whorls: perianth, androecium, and gynoecium (fig. 2B, 2C). The tepals of the uniseriate and pentamerous perianth are quincuncially overlapping (fig. 2B–2D). In the three analyzed flowers, tepals are 6–7 mm long × 1–2 mm wide, oblong to oblanceolate, with acuminate apex, truncate base (fig. 2D), cream to primrose sensu Beentje (2012; fig. 2B), and pubescent, especially on the abaxial side. The androecium is composed of 11–16 stamens with basifixed anthers and a glabrous filament winged on the lower half. The wing is 0.5–0.7 mm wide. The gynoecium consists of three hypogynous and pubescent carpels (fig. 2D) with greenish styles (0.1–0.2 mm long) and bilobed greenish stigmas (0.29–0.35 mm long). In

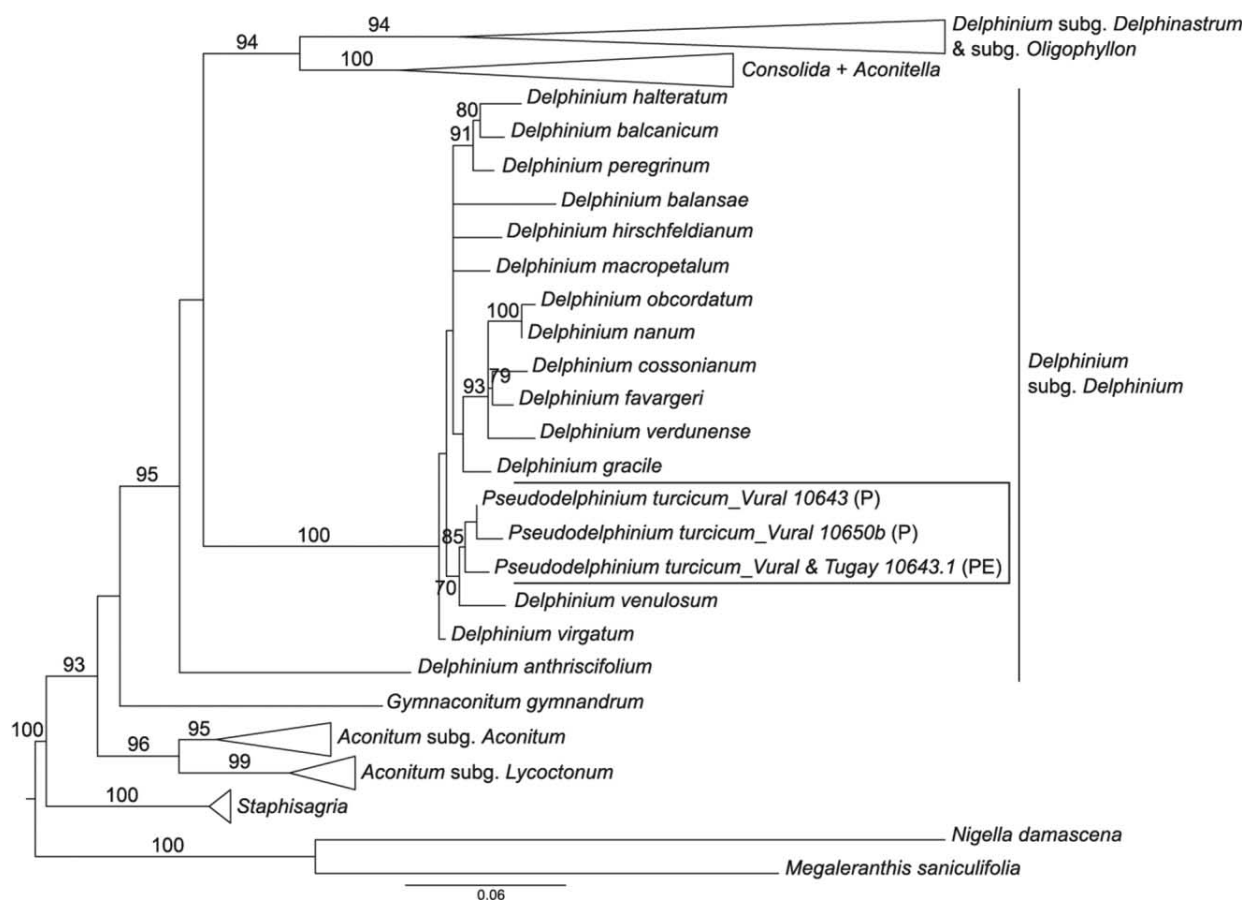


Fig. 3 Maximum likelihood tree of Delphinieae based on the combined *trnL-F* and ITS data set. The focus is put on the clade of Mediterranean *Delphinium* species belonging to the subgenus *Delphinium* that includes the three *Pseudodelphinium turcicum* accessions. Bootstrap percentages ≥ 70 are indicated.

the floral bud of *P. turcicum*, young perianth organs with an arrested development were found between the developing tepals and the filaments (fig. 2G) and were not visible in the anthetic flower.

Delphinium venulosum and *D. virgatum* flowers have a similar general organization, with two differentiated and zygomorphic whorls. The calyx consists of five quincuncially overlapping petaloid sepals: two ventral, two lateral, and one dorsal spurred sepal. The corolla consists of four dorsal organs (the two dorsalmost being spurred). Each petal is located at the base of each stamen parastichy. They vary in size, depending on whether they are located in the dorsal or ventral half of the flower (fig. 2E, 2F).

Delphinium venulosum and *D. virgatum* have spheroidal tricolpate pollen grains with a length of 22–31 μm , a microechinate exine, and an ornamented aperture membrane (fig. 4A, 4B; shape differences are due to the desiccation of the grains). The pollen grains of *P. turcicum* are heteromorphic; they vary in the number and distribution of apertures and in length (22–31 μm). Both di- and tricolpate pollen grains are observed. Their

exine is microechinate as well, with an ornamented aperture membrane (fig. 4C, 4D).

Anatomy

Bracts and bracteoles of the three species are supplied by five vascular bundles. In bracts, these bundles originate from three independent traces: one median nondivided and two lateral ones. Lateral bundles bifurcate after entering the organ. Bracteole bundles originate from a single trace, which gets divided at first into three (one median and two lateral), and then the two lateral traces bifurcate again (fig. 5).

The sepals of *D. venulosum* and *D. virgatum* and the perianth organs of *P. turcicum* are composed of three independent and nonramified traces, one median and two lateral (fig. 5). Petals of *D. venulosum* and *D. virgatum* are vascularized by a single trace. In the two spurred petals, this trace bifurcates before entering the organ. Stamen vascularization in the three species is established by a single trace, and carpel vascularization is composed of three independent and nonramified traces, one median and two lateral (fig. 5).

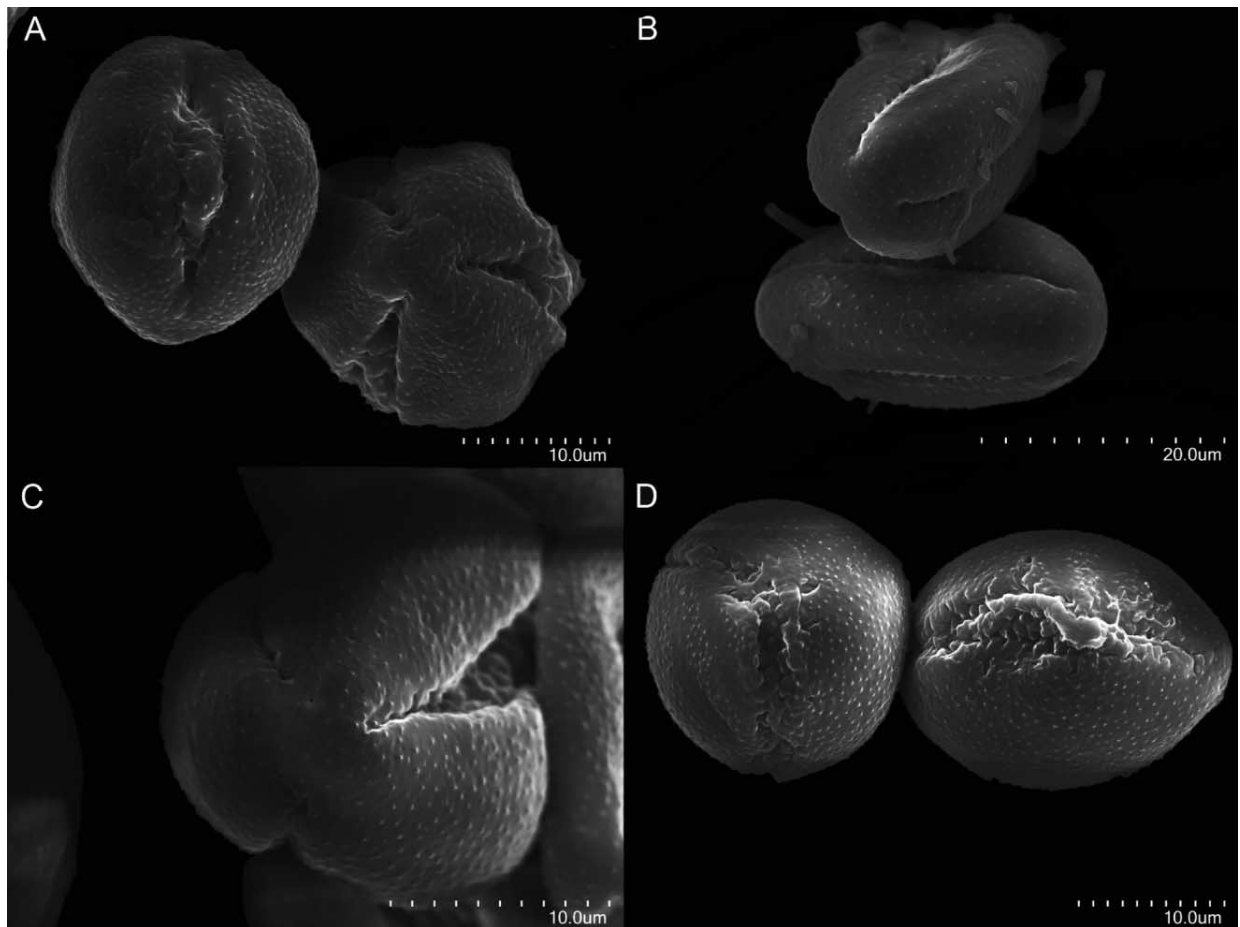


Fig. 4 SEM micrographs of pollen grains of *Delphinium venulosum* (A; left: equatorial view, right: polar view), *Delphinium virgatum* (B), *Pseudodelphinium turcicum* (C; polar view), and *P. turcicum* (D; left: polar view, right: equatorial view).









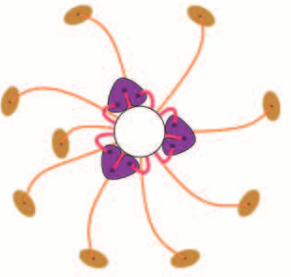
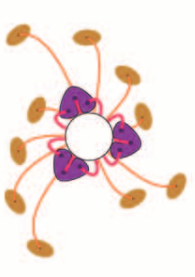
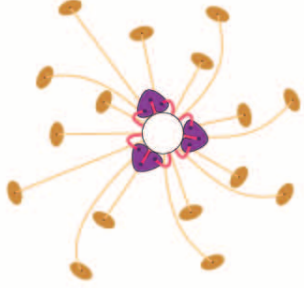



	<i>Delphinium virgatum</i>	<i>Delphinium venulosum</i>	<i>Pseudodelphinium turcicum</i>
Bract and bracteoles			
Sepals or tepals			
Petals			
Stamens and carpels			
Perianth and reproductive organs			

Fig. 5 Floral vascularization of each floral whorl (bract and bracteoles, sepals or tepals, petals, stamens and carpels) and of the whole flower (perianth and reproductive organs) of *Delphinium virgatum*, *Delphinium venulosum*, and *Pseudodelphinium turcicum*.

Discussion

Phylogenetic Placement of Pseudodelphinium in the Tribe Delphinieae

The topology and the well-supported nodes (BP > 70%) of the inferred ML tree are consistent with the ML trees presented by Jabbour and Renner (2012a) and Wang et al. (2013; fig. 3). The three accessions of *Pseudodelphinium turcicum* formed a well-supported clade sister to *Delphinium venulosum* and nested within *D.* subg. *Delphinium*. A study focusing on the molecular phylogeny and biogeography of the subgenus *Delphinium* found that the two accessions of *P. turcicum* (M. Vural & O. Tugay 10643.1, included in this study, and M. Vural & O. Tugay 10643.2) formed a clade sister to *D. venulosum* + *D. virgatum* (BP = 95%; PP = 1.0; Xiang et al. 2017). The results of Xiang et al. (2017), based on more phylogenetic markers and a different set of accessions, are in accordance with ours (fig. 3). Following this molecular evidence, *P. turcicum* should be considered as a species of *Delphinium*.

Morphological Similarities of Pseudodelphinium with Delphinium

The specimens of *P. turcicum* we investigated showed typical ranunculaceous features, namely, herbaceous habit, palmate venation, free and numerous stamens, numerous ovules, and beaked fruits (fig. 2A–2D; Vural et al. 2012; Wang et al. 2016a). Similar to the annual species of *Delphinium*, *P. turcicum* exhibits glaucous vegetative parts and a simple taproot, alternate palmately lobed leaves, and a terminal raceme or panicle (fig. 2A; Pawłowski 1964; Davis et al. 1965; Zohary 1966; Townsend 1980; Blanché 1990; Iranshahr 1992; Vural et al. 2012). Although *Pseudodelphinium* seems to differ from *Delphinium* by its spurless actinomorphic flowers and uniseriate perianth (fig. 2A–2D), some floral characteristics of *Delphinium* could be found in *Pseudodelphinium*: (i) bisexual flowers whose perianth is composed of five free, pilose, and quincuncially overlapping petaloid organs; (ii) numerous stamens with basally winged filaments; (iii) superior ovaries; (iv) three dehiscent follicles containing numerous ovules (fig. 2B–2D; Pawłowski 1964; Davis et al. 1965; Zohary 1966; Townsend 1980; Blanché 1990; Iranshahr 1992; Vural et al. 2012); (v) black spheroidal seeds with five to eight transversal rings of concentric scales and an umbilical orifice occupying one-half to one-third of the total seed volume (Blanché 1990; Vural et al. 2012); and (vi) a proportion of the pollen grains being tricolpate with microechinate exine and an ornamented aperture membrane (fig. 4C, 4D; Saidabadi 1968; Bursali and Dogan 2005; Sharifnia et al. 2013).

Pollen heteromorphism was already reported in the Ranunculaceae (Humphrey 2016; Wang et al. 2017). To understand the origin of pollen heteromorphism in *Pseudodelphinium* and the implications for its fitness, it would be necessary to investigate microsporogenesis and test the viability of the pollen, as well as conduct an ecological study about the fertilization success of individual pollen grains. To our knowledge, pollen heteromorphism has thus far never been reported in *Delphinium*.

The perianth of *P. turcicum* is composed of a single pentamerous whorl of petaloid organs considered here as tepals

(fig. 2B–2D; Vural et al. 2012). Vural et al. (2012) interpreted this whorl as the corolla. However, comparing the arrangement and the morphological characteristics of the tepals in *P. turcicum* with the sepals in *Delphinium*, we consider instead that *P. turcicum* tepals are equivalent to *Delphinium* sepals and that adult flowers lack a fully developed corolla. Additionally, *P. turcicum* organs with an arrested development are found between tepals and stamens (fig. 2E–2G). These young organs are similar to the ventral petals with an arrested development in *Delphinium* flowers (Payer 1857; Kosuge 1994; Jabbour et al. 2009; Jabbour and Renner 2012b). Based on the organization of the androecium in *P. turcicum* (fig. 5) and the appendix (available online), we hypothesize that there are eight petals with an arrested development in this species, each one being initiated at the base of each stamen parastichy. They develop until they reach a size and shape similar to the young ventral petals of *Delphinium* flowers at the stage of the establishment of zygomorphy (see fig. 2 in Jabbour et al. 2009).

Anatomical Similarities of Pseudodelphinium with Delphinium

The perianth organs (tepals) of *P. turcicum* have a trilacunar three-traced vascularization, which is a feature of the outermost perianth organs of Ranunculales (fig. 5; Hieppo 1965; Stevens 2001; Wang et al. 2009). As in the other Delphinieae investigated so far (Novikoff and Jabbour 2014), *P. turcicum* stamens have a unilacunar one-traced vascularization, and the vascularization of the ovary is equivalent to the vascularization in other *Delphinium* species (fig. 5). Based on the floral anatomy of *D. virgatum* and *D. venulosum* and the findings of Novikoff and Jabbour (2014), the vascularization of the tepals in *P. turcicum* is identical to the vascularization of the sepals in *Delphinium*. However, none of the perianth organs of *P. turcicum* shows a typical *Delphinium* petal-like venation (fig. 5). This is an additional argument to hypothesize that *P. turcicum* adult flowers lack a fully developed corolla. A way to determine the identity of the perianth organs in *P. turcicum* would be to investigate the expression of A- and B-function genes (Coen and Meyerowitz 1991) in dissected flowers.

During the last 200 years, numerous plants showing abnormal flowers in Ranunculaceae have been described (e.g., De Candolle 1827; Payer 1857; reviewed in Jabbour et al. 2015), some of them explaining changes in floral symmetry from zygomorphy to actinomorphy (e.g., Clusius 1601; Linnaeus 1744; Masters 1904). In most cases, changes in floral symmetry correspond to peloria (e.g., Masters 1904), i.e., a radialization of a usually zygomorphic floral ground plan. In addition, in the case of *P. turcicum*, flowers did not show any nectariferous organs, indicating a particular case of peloria, namely, *peloria anectararia* (Linnaeus 1744; Rudall and Bateman 2003). The dorsal perianth organs of the flower show ventral characteristics. The floral phenotype in *P. turcicum* would then be the result of a ventralization of the flower (see Luo et al. 1996). Numerous studies demonstrated that zygomorphy depends on the expression of the TCP family genes *CYCLOIDEA* (*CYC*) and *CYC*-like genes. Some *CYC* copies act as repressors of development of the primordia in the floral meristem or repress the development of dorsal floral organs in zygomorphic flowers (Luo et al. 1996; Citerne et al. 2000, 2006). In the flowers of *P. turcicum*, the expression of

CYC-like genes could affect all the organs of the perianth by repressing the development of the perianth organs located between the tepals and the stamens, hence resulting in actinomorphic flowers without fully developed petals.

Nevertheless, even if genetic causes could underlie this unusual floral phenotype in a taxon that is, molecularly speaking, a *Delphinium* representative, and knowing that the single population of *P. turcicum* is found in a very particular ecosystem (basin of a salt lake), floral morphological-anatomical abnormalities could also be due to extrinsic causes. More studies about the distribution of the population enriched by more material and ecological data are needed at this stage to test these alternative hypotheses. We highlight that our study relied on three specimens of *P. turcicum* only. More material is needed for future morphological and evo-devo studies to understand the bases of this unusual floral phenotype.

Based on the array of evidence of molecular and morphological-anatomical data presented, the generic name *Pseudodelphinium* H.Duman, Vural, Aytaç & Adigüzel should be sunk into synonymy with *Delphinium*. The taxonomic treatment follows.

Delphinium L.

= *Pseudodelphinium* H.Duman, Vural, Aytaç & Adigüzel in Turk. J. Bot. 36(5):428. 2012

Type—*Pseudodelphinium turcicum* H.Duman, Vural, Aytaç & Adigüzel.

Delphinium turcicum (H.Duman, Vural, Aytaç & Adigüzel) Espinosa, *comb. nov.*

= *Pseudodelphinium turcicum* H.Duman, Vural, Aytaç & Adigüzel in Turk. J. Bot. 36(5):428. 2012

Type—Turkey. C4 Konya: Karapınar to Konya road, 30 km, Merdivenli village, 1020 m, dry plain steppes, 28 July 1998, *H.Duman 6824 & Z.Aytaç* (holotype: GAZI, isotypes: ANK, HUB)

Conclusions

The molecular phylogenetic evidence shows that the Turkish endemic *Pseudodelphinium turcicum* belongs in *Delphinium* and should not be considered as a distinct genus. The morphology and anatomy of the vegetative and reproductive organs of *P. turcicum* flowers lead us to conclude that the single population of the monospecific genus *Pseudodelphinium* corresponds to a population of *Delphinium* with peloric flowers and a corolla with an arrested development. The formal perianth organs in *P. turcicum* are interpreted as equivalents to sepals in a *Delphinium* typical flower. Interestingly, specimens from this population of annual plants were collected already 20 years ago. The conditions of the maintenance in the wild of these plants with an unusual floral phenotype need to be investigated. Future research may address the molecular or environmental causes of this unusual phenotype, investigate the role of pollen dimorphism in the ecology of these plants and their mating system(s), and study the genetic relationships of this population with neighboring populations of *Delphinium*.

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