A taxonomic revision of the *Verbascum daenzeri* group (*Scrophulariaceae*)

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Abstract. Taxonomy and distribution of the *Verbascum daenzeri* group has been revised. The group comprises four species, three of them endemic to Greece, and the fourth extending to Bulgaria and Turkey-in-Europe. *Celsia peraffinis* Rech. f., previously sunk into the synonymy of *Verbascum boissieri* (Heldr. & Sartori ex Boiss.) Kuntze, is resurrected as an independent species and recombined as *Verbascum peraffine* (Rech. f.) Zografidis & Strid.

Key words: *Celsia*, Evvia, Greece, taxonomy, *Verbascum*

Introduction

Verbascum is a large genus with center of diversity in an area encompassing the southern Balkans, Anatolia, Transcaucasia, Northwest Iran and the Levant. *Verbascum* and *Celsia* are both Linnaean genera; according to the original definition of Linnaeus, they differ by "filamenta quinque" and "filamenta quatuor", respectively. Members of the *Celsia* group are generally slender, moderately pubescent biennials or short-lived perennials, with solitary flowers in the axil of each bract. Species of *Verbascum* s.str. have flowers mostly in fascicles of 2–7 in the axil of each bract, and are often more robust and densely pubescent or floccose. Monographer Murbeck (1925, 1933) retained *Celsia* and *Verbascum* – albeit with some doubt – as separate genera, whereas in modern Floras they are generally merged, with *Celsia* as a subgenus or section of *Verbascum*. Furthermore, several authors have argued against the taxonomic validity of *Celsia* even within *Verbascum*, and the first assessment of molecular data suggests that *Celsia* and other subdivisions of *Verbascum* are non-natural (Ferguson 1971; Ghahremaninejad & al. 2014, and references therein). Thus defined, *Verbascum* has *ca.* 78 species in Greece, *ca.* 12 of them belonging to the apparently artificial *Celsia* group (Dimopoulos & al. 2013).

In the *Celsia* monograph (Murbeck 1925), the two Greek endemics *Celsia daenzeri* Fauché & Chaub. and *C. boissieri* Heldr. & Sartori ex Boiss., as well as *C. roripifolia* Halácsy, a species occurring in Northeast Greece, South Bulgaria and West European Turkey, constitute a small sub-group within the *Mesantherae* Murb. group – i.e. species having the two anterior stamens with decurrent anthers 1.5–3 mm long – further characterized by "*Segmenta foliorum inferiorum acuta v. acutiuscula*, *lobis dentibusque acutis mucronulatis*. *Capsula indurata*, *rostrata*". As defined by Ferguson (1972), the "*Verbascum daenzeri* group" comprises the three aforementioned species plus *V. rupestre* (Davidof) I. K. Ferguson, a species occurring in NE Greece and Bulgaria, where it is more or less sympatric with *V. roripifolium* (Halácsy) I. K. Ferguson. In our opinion, *V. rupestre* differs in several important characters (cf. below) and should not be regarded as a member of the *V. daenzeri* group. *Celsia peraffinis* Rech. f., a species described from southern Evvia (Rechinger 1956), was

sunk into the synonymy of *V. boissieri* without further comments. Below, we argue that *C. peraffinis* is morphologically and biogeographically distinct and should appropriately be transferred to *Verbascum*. The object of this study is to clarify taxonomy and distribution of members of the *V. daenzeri* group.

Material and methods

We have examined relevant herbarium material mainly at ATH, B, G, LD, W and the private herbarium collection of the senior author (A.S.), and have critically assessed the records (128 in all) in the Flora Hellenica Database; the latter includes herbarium specimens, all published records and a few field notes.

Results

Distinguishing characters of the *Verbascum daenzeri* group are as follows: biennial or perennial herbs; flowers solitary in the axil of each bract; eglandular hairs simple, present only below or absent; stamens 4 with or without a staminode or stamens 5; if stamens 5 then eglandular hairs present; two anterior stamens with decurrent anthers 1.5–3 mm; apical part of the lamina of basal leaves irregularly incised-dentate to pinnatisect with acute segments, basal part pinnatisect with incised-dentate segments; capsule rostrate, indurate, of late dehiscence.

The diagnostic characters for the four species are presented in Table 1. The species can be keyed out as follows:

1. Stamens 4 and staminode present, or stamens 5, the third upper stamen then with a much smaller spherical anther ..... 2.
– Stamens 4 and staminode absent ..... 3.
2. Eglandular hairs filiform; capsule obtuse; biennial monocarpic, rarely with an additional productive year ..... 1. *V. daenzeri*
– Eglandular hairs very short, conical; capsule acute; perennial polycarpic ..... 2. *V. boissieri*
3. Eglandular hairs present; bracts dentate ..... 3. *V. peraffine*
– Eglandular hair absent; bracts entire ..... 4. *V. roripifolium*

1. *Verbascum daenzeri* (Fauché & Chaub.) Kuntze in Revis. Gen. Pl. 2: 469 (1891), Figs 1, 2 (A, B)

Basionym: *C. daenzeri* Fauché & Chaub. in Fauché, Brongn., Chaub. & Bory de St.-Vincent, Expéd. scient. de Morée, Tom. 3, 2 part, Bot.: 342 (1832). Type: "Forêt de Phygalée", Fauché s.n.

At the Paris Natural History Museum (http://www.gbif.org/occurrence/474653080) there is a specimen labelled "*Laconia graeciae*, April 1842. Herb. Boissier", but it was probably collected by Boissier who is known to have traveled in Peloponnisos in 1842. Murbeck (1825: 168) cited Daenzer s.n. (GBOIS), "*ad templum Apollinis*", but this specimen does not appear in the online catalogue of the Boissier Herbarium. Daenzer was a "*pharmacien des armées*", participating in the French scientific and military expedition in Peloponnisos in 1828–1829.

Syn.: *C. daenzeri* var. *lyrata* Boiss. & Heldr. in Boiss. Diagn. pl. nov., Ser. II, No. 3: 151 (1856). Type: "*Laconia prope Mistra*" Boissier s.n., Apr. 1842 (B, G, GBOIS!, K, P); *C. speciosa* Fenzl. in Friedrichsthal, Reise südl. Neu-Griechenl.: 280 (1838). Type: "Alphius, Ufer bei Karithena", Friedrichsthal 919, 1835 (W); *V. friedrichsthalianum* Kuntze in Revis. Gen. Pl. 2: 468 (1891) "*friedrichsthaliana*", nom. nov. for *Celsia speciosa*. [We have not seen the type specimen, but A.Z. recollected *V. daenzeri* in this locality on 02.04.2016].

Biennial monocarpic herb, seldom with an additional productive year. Stem(s) solitary or few, 50–150(–180) cm, simple or sparingly branched above. Lower part of plant with simple, filiform, eglandular hairs present on the stems and on nerves and petioles on the lower surface of leaves. Upper part of plant sparsely glandular-puberulent. Rosette-leaves petiolate, lyrate-pinnatisect, oblong-oblanceolate in outline, with laminas up to 30 × 8 cm; apical part of the lamina irregularly incised-dentate with acute segments, basal part of the lamina pinnatisect with incised-dentate segments. Lower cauline leaves resembling the rosette-leaves but progressively smaller. Middle and upper stem leaves sessile, incised-dentate, frequently well developed and thus stem leafy. Flowers in a long, lax raceme; pedicels 15–30 mm, patent to erecto-patent, ± arcuate, slender; bracts ovate-deltate to lanceolate, dentate. Calyx segments narrowly lanceolate-oblong, acute, 3–5(–7) × 1–1.3 mm. Corolla 25–40 mm diam., yellow; fertile stamens 4 or 5, the fifth (central posterior) either transformed to a staminode or with a much smaller

Table 1. Diagnostic characters of the species of the *Verbascum daenzeri* group.

	V. daenzeri	*V. boissieri*	*V. peraffine*	*V. roripifolium*
Life cycle (typically)	Biennial monocarpic	Perennial polycarpic	Short-lived perennial bicarpic	Biennial monocarpic
Eglandular hairs	filiform, numerous	very short, conical, sparse	filiform, sparse	absent
Lamina of larger rosette leaves (cm)	to 25 × 8, apical part ± shallowly incised	to 15 × 4, apical part ± deeply incised, rachis thick	to 15 × 4, apical part ± deeply incised, rachis thin	to 15 × 4, apical part ± deeply incised, rachis thin
Height of stem (cm)	50–150(–180)	30–80(–110)	40–100	50–180
Stem leaves	± gradually reduced	abruptly reduced	± gradually reduced	gradually reduced
Inflorescence	frequently branched (50 %)	less frequently branched (20 %)	frequently branched (50 %)	typically branched
Bracts	dentate	entire or shortly dentate	dentate	entire
Calyx segments Mm	lanceolate-oblong, entire 3–5(–7) × 1–1.3	lanceolate-oblong, entire 2–4 × *ca.* 1	ovate-lanceolate ± dentate 2–7 × 1–3.5	lanceolate-oblong, entire 2–4 × *ca.* 1
Diameter of corolla (mm)	25–40	20–30	25–40	20–35
Staminode or 5th stamen	present	present	absent	absent
Capsule shape and dimensions (excl. rostrum) (mm)	ovoid-oblong or subglobose, obtuse 4.5–6 × 4–5	ovoid-lanceolate, acute 5–7.5 × 3–5	ovoid, obtuse to subacute 3.5–6 × 3–4.5	globose, obtuse 3.5–5 × 3–4.5
Seed dimensions (mm)	0.7 × 0.5	1–1.2 × 0.6–0.7	0.7 × 0.5	0.6 × 0.4

rounded anther; two anterior stamens with decurrent anthers 1.5–3 mm; stamen filaments with purple and white hairs. Capsule 4.5–6 × 4–5 mm (excl. rostrum) ovoid, indurate, obtuse, with a rostrum 1–3 mm. Seeds dark-brown, obpyramidal to ovoid-oblong, faveolate, *ca.* 0.7 × 0.5 mm.

Described from the vicinity of the temple of Apollo Epikourios in Peloponnisos (Nomos Messinias) and distributed almost exclusively in the floristic region of Pe. A single record exists from Zakinthos. A specimen from Eparchia Parnassidos (StE) (Panoutsopoulou 2322, ATH), previously identified as *V. daenzeri*, matches *V. boissieri* in all characters except for the obtuse capsules (Fig. 3).

The species inhabits lowland to montane dry and mesic, non-ruderal, ± open sites such as forest and scrub edges, verges and rock outcrops, and grows on various substrates. Reported from near sea level to 1700 m. Flowering April to June and fruiting May to July.

2. *Verbascum boissieri* (Heldr. & Sartori ex Boiss.) Kuntze in Revis. Gen. Pl. 2: 469 (1891) (Fig. 1)

Basionym: *Celsia boissieri* Heldr. & Sartori ex Boiss. in Fl. Orient. vol. 4: 353 (1879) [excl. *V. daenzeri* var. *lyrata* Boiss. & Heldr. (emend. Murb.)]. Type material: "*In regione media montis Parnethis Atticae, 2000 ft*", Heldreich 317, 08.06.1855 (M, MPU, P!).

Resembling *V. daenzeri* but perennial polycarpic, with sparse, very short, conical eglandular hairs, acute to subacute capsules 5–7.5 × 3–5 mm and larger seeds 1–1.2 × 0.6–0.7 mm. *Verbascum boissieri* is also generally a less robust species, with more incised basal leaves – but this trait is mostly noticeable when comparing well-grown individuals; see also "*Discussion*" below – laminas up to 15 × 4 cm, less frequently branched stems 30–80(–110) cm in height, middle and upper cauline leaves always very small and thus stems never appearing leafy, bracts smaller and mostly entire and ± smaller calyx segments (2–4 × *ca.* 1 mm). The corollas are also smaller (20–30 mm diam.). The leaves of *V. boissieri* have a relatively thick rachis, are more rigid and often turn dark upon drying, unlike the leaves of the other members of the group.

Described from Mt Parnitha (occurrence confirmed by several recent collections) and distributed in Sterea Ellas, just extending to the Isthmus of Corinth area of NE Peloponnisos (Fig. 3).

Habitat and phenology as for *V. daenzeri*. Frequently found on bare limestone on Mt Parnitha. Reported from sea level to 1100 m.

3. *Verbascum peraffine* (Rech. f.) Zografidis & Strid, **comb. nov.** (Fig. 1)

Basionym: *C. peraffinis* Rech. f. in Anz. Österr. Akad. Wiss. Wien, Math.-Naturwiss Kl. 93: 100 (1956). Type: "*Montes Ocha, in valle umbrosa in querceto-castanetis declivium boriealis-orientalium versus Kallianou, 300–900 m*", Rechinger 16339, 22.05.1955 (G!, M, W!).

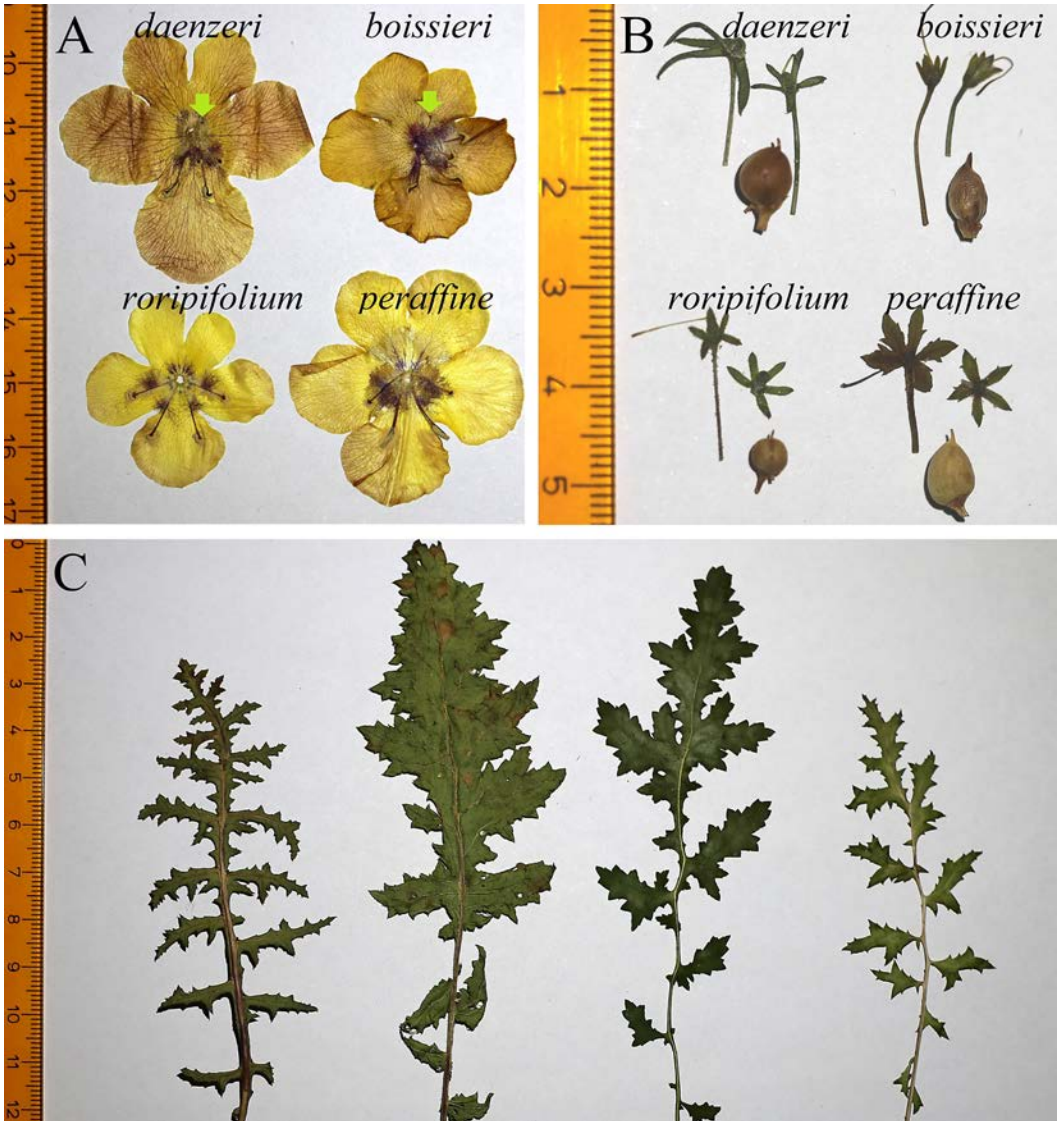

Fig. 1. Illustration of diagnostic characters of the *V. daenzeri* group. A: Corolla; green arrows indicate the presence of a fifth stamen with a small rounded anther in *V. daenzeri* and *V. boissieri*. **B:** Calyx and capsule. **C:** Upper rosette-leaves of well developed plants; numbers indicate the ratio of the length of the particular leaf-lamina illustrated to the length of the largest leaf-lamina observed for the respective species.

Fig. 2. Stems and partial inflorescences of *Verbascum daenzeri* (**A, B**) and *V. roripifolium* (C, D).

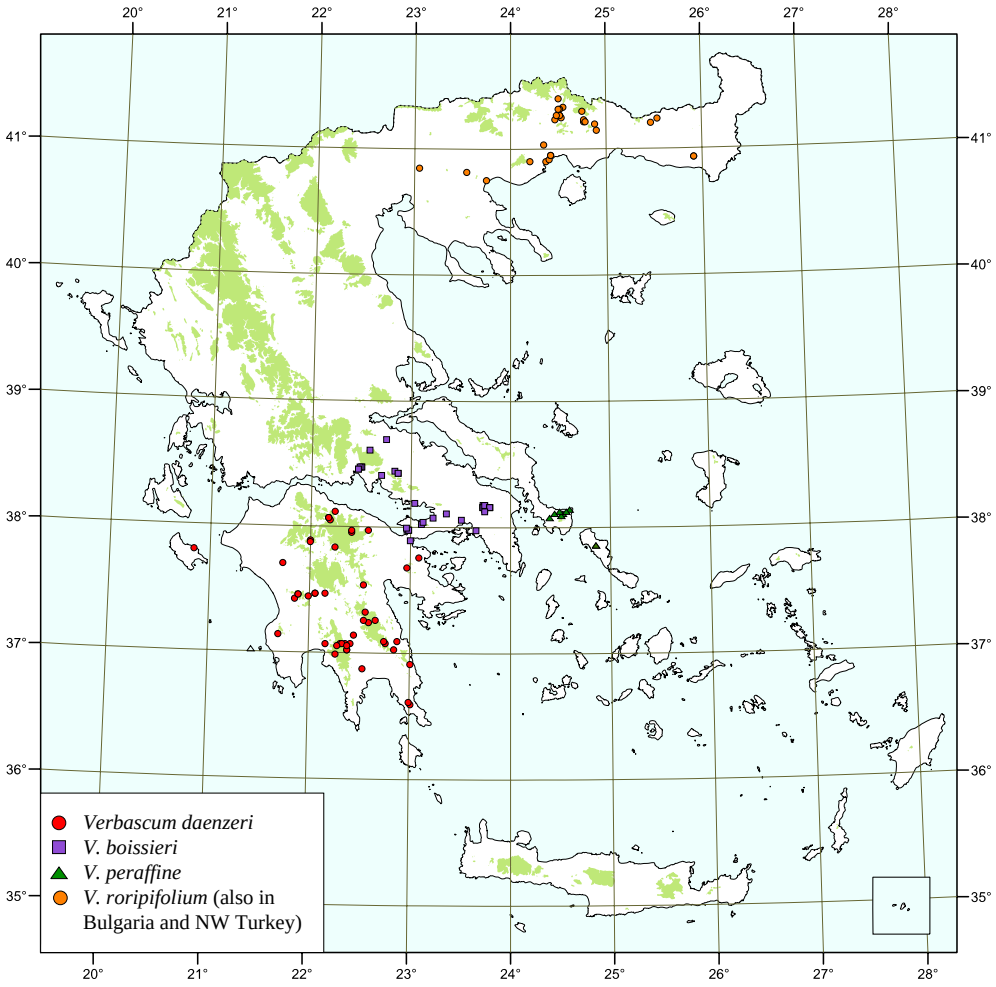

Fig. 3. Greek distribution of the four species in the *Verbascum daenzeri* group, according to records in the Flora Hellenica Database.

Syn.: *V. boissieri* sensu I. K. Ferguson in Tutin & al., Fl. Europ., vol. 3: 209 & 351 (1972), non Kuntze.

Resembling *V. daenzeri* but short-lived perennial, usually with two productive years, with ovate to lanceolate, ± dentate calyx segments 2–7 × 1–3.5 mm and corollas lacking the 5th stamen or the staminode. *Verbascum peraffine* is also less robust (stems 40–100 cm), with more slender and incised rosette leaves, leaf-laminas up to 15 × 4 cm and with sparser eglandular hairs than *V. daenzeri*. The capsules are mostly subacute. The species was considered as synonymous with *V. boissieri*, but is clearly distinct by its filiform eglandular hairs, absence of the staminode or the 5th stamen, smaller seeds, ± leafy stems, slender leaves (the rachis of the leaf is relatively thin), dentate bracts and bigger, ± dentate sepals. Typically the corollas are also larger. With respect to life cycle, *V. peraffine* approaches *V. boissieri* but seldom has more than two productive years, whereas the latter is typically polycarpic.

Described from southern Evvia (Mt Ochi). Material from northern Andros (Snogerup 9111, LD; Stamatiadou 18289, ATH), previously identified as *V. daenzeri*, matches plants from Evvia [T. Tyler, curator of Herbarium LD, kindly examined the Snogerup collection, confirming its identity as *V. peraffine*]. (Fig. 3).

Habitat and phenology as for *V. daenzeri*. Reported from 100 to 900 m.

4. *Verbascum roripifolium* (Halácsy) I. K. Ferguson in Heywood, Bot. J. Linn. Soc. 64: 230 (1971), (Figs 1, 2C, 2D)

Basionym: *Celsia roripifolia* Halácsy in Oesterr. Bot. Z. 40: 405 (1890). Type: [Bulgaria]: "*In saxosis apricis prope Bachkovo, M. Rhodope*", Pichler s.n., Jun. 1890 (BEI, B, BP, G, LD, P!, PAL, S, WU).

Syn.: *C. daenzeri* sensu Velenovský in Fl. bulg., p. 418 (1891), non Fauché & Chaub.

This species differs from other members of the group in being glabrous below (eglandular hairs absent), typically with sparsely branched stems and smaller, globose capsules 3.5–5 × 3–4.5 mm. From *V. daenzeri* it

additionally differs in lacking the staminode or the 5th stamen, in the more incised leaves, the entire bracts and the ± smaller corollas (20–35 mm of diam.) and calyx segments (2–4 × *ca.* 1 mm). Compared to *V. boissieri*, it also lacks the 5th stamen or staminode, is always leafy above and generally taller (up to 180 cm or more in height), has smaller seeds and is biennial. From *V. peraffine* it further differs in being biennial, larger, with smaller and entire bracts and calyx segments and with usually smaller corollas.

Described from Rhodope Mts, South Bulgaria. Several records from NE Greece. Also reported from West European Turkey (Fig. 3).

Habitat as for *V. daenzeri*. In flower from May to July and fruits appear from June to August. In Greece reported from 120 to 600 m.

Discussion

As indicated from morphology and phytogeography, the members of the *V. daenzeri* group are schizoendemic species and, furthermore, because all species inhabit more or less the same habitats, the principal force of evolution in this group is likely to be geographical isolation between the populations. The species are mostly characterized by differential combinations and gradients of the same qualitative and quantitative traits, but unique characters are also represented, e.g., the distinct eglandular hairs of *V. boissieri* and the dentate calyx segments of *V. peraffine*. It is interesting to note that *V. peraffine* appears intermediate to all three species and through its association with *V. roripifolium* (owing to the absence of the staminode and the slender, deeply incised leaves) the latter species is more rigorously linked with the group. This hypothesis is also supported by the fact that the Balkan element is significantly represented in the flora of Evvia as noted by Trigas (2003).

Verbascum rupestre, native to South Bulgaria, northeastern mainland Greece and the islands of Thasos and Samothraki, was included in the *daenzeri* group by Ferguson, but the species is strikingly different from all members of this group. In fact, this is an isolated species as already suggested by both Davidof and Murbeck (Murbeck 1925). The most obvious differences between *V. rupestre* and members of the *daenzeri* group are (1) the soft capsule lacking a rostrum and opening soon after the maturation of the seeds, (2) the very different shape of the rosette leaves (lyrate-pinnatisect with a distinct, rounded, crenate terminal lobe) and (3) the distinctly smaller corolla. It should be noted that the ontogeny of leaves in *Verbascum* is a gradual process and the first rosette leaves are much less developed. This is especially apparent for those species with deeply dissected leaf laminas, where the first rosette leaves are only dentate or pinnatifid. Also, it is not uncommon that small individuals may not have developed the representative dissection of basal leaves but still flower and complete their life cycle. Thus, only well-grown individuals should be assessed for this trait – which may be a problem since smaller plants are generally preferred by the collectors to better fit the herbarium sheet.

The *daenzeri* group is a compelling example for demonstrating the taxonomic unsoundness of *Celsia*; the group includes *V. daenzeri* and *V. boissieri*, two species that frequently have a functional 3rd central posterior stamen and these species are, in turn, clearly related to the "pure *Celsiae*" *V. peraffine* and *V. roripifolium*. Further, we hypothesize that the group may be related to the "pure *Verbasca*" *V. blattaria* L. and *V. meincheanum* Murb., the former widely distributed in Eurasia and North Africa – and highly invasive in North America – and the latter endemic to South Turkey. *Verbascum blattaria* lacks the eglandular hairs and typically has only shortly petiolate rosette leaves with crenate or pinnatifid laminas with ± obtuse lobes. However, this species is highly polymorphic in Greece and approaches the *V. daenzeri* group through its variety *carduifolium* Murb. *Verbascum meincheanum* approaches *V. daenzeri* even more but it is densely hirsute, with long hairs that cover the plant up to the pedicels and itself is closely similar to 2–3 other Anatolian endemics in which all 5 anthers are reniform-medifixed, thus possibly indicating a different lineage. In conclusion, the absence of a functional 5th stamen is an important character for species delimitation – where additional characters should also be addressed – but its sole use in higher rank circumscriptions within *Verbascum* is potentially misleading and should be avoided. The *V. daenzeri* group may actually prove to include *V. blattaria*, and/or *V. meincheanum*, which are excluded from this provisional treatment in the absence of molecular data and very strong morphological or phytogeographical support.

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