VIOLA CALCICOLA (VIOLACEAE), A NEW ENDEMIC VIOLET FROM THE GUADALUPE MOUNTAINS OF NEW MEXICO AND TEXAS

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ABSTRACT

Viola calcicola is described as growing in limestone located within protected springs and valleys of the Guadalupe Mountains in New Mexico and Texas. This violet is most similar macromorphologically and ecologically to *V. egglestonii* of east-central U.S. limestone cedar glades and micromorphologically to *V. septemloba* of southern Atlantic and Gulf Coast sand pine savannas. However, it diverges from all known heterophyllous-leaved taxa of *Viola* subsection *Boreali-Americanae* in many vegetative and reproductive features. It is removed by hundreds of kilometers from other putatively related heterophyllous-leaved violets, being the first record of lobed-leaved members of the subsection in the western U.S. and the second species of *Viola* found to be endemic to the Guadalupe Mountain region.

RESUMEN

Se describe **Viola calcicola** como una planta que crece en piedra caliza alrededor de manantiales y valles protegidos en la sierra de Guadalupe de Nuevo México y Texas. Esta violeta es muy similar macro morfológica y ecológicamente a *V. egglestonii* de la parte este-central de Estados Unidos en la región conocida como "cedar glades", y micro morfológicamente a *V. septemloba* de la costa sur Atlántica y de las sabanas arenosas de la costa del Golfo, pero difiere de éstas y del resto de las violetas con polimorfismo foliar de la subsección *Boreali-Americanae* en muchos caracteres vegetativos y reproductivos. Espacialmente esta separada por miles de kilómetros de cualquier otra violeta con polimorfismo foliar, siendo este el primer registro de una especie de este tipo en el oeste de Estados Unidos y la segunda especie de *Viola* endémica a la sierra de Guadalupe.

Key Words: *Viola*, Violaceae, Guadalupe Mountains, new species, endemic, *Boreali-Americanae*

INTRODUCTION

Over the last half-century, three taxonomic treatments of North American (primarily U.S. and Canadian) *Viola* (Violaceae) have been proposed by specialists (Russell 1965; McKinney 1992; Gil-ad 1997). These differ substantially in the circumscription, rank, nomenclature and general evolutionary status of several taxa. In these and earlier treatments, specialists have noted two broad groups of taxa with notched, lobed, or divided leaves: homophyllous violets in which all leaf blades are lobed or divided throughout the growing season, and heterophyllous violets which produce undivided blades in the earliest and latest months of the growing season and notched, lobed or dissected leaves during the height of anthesis and into chasmogamous fruit. All three most recent treatments recognize some heterophyllous-leaved taxa, namely *V. egglestonii* Pollard, *V. septemloba* Leconte and *V. triloba* Schwein., at some taxonomic rank. Russell maintained the first three as well as *V. esculenta* Elliott, *V. lovelliana* Brainerd and *V. viarum* Pollard, as distinct species. McKinney synonymized the latter three along with *V. triloba* Schein. within a broadly delimited heterophyllous taxon under the name *V. palmata* L., based on his interpretation that the type of Linnaeus' violet referred to a heterophyllous rather than a homophyllous violet. Gil-ad used the presence of unique or extreme macromorphological characteristics, and micromorphological features in seed coat sculpturing and lateral beard trichomes (Gil-ad 1998), to infer orthospecies status for *V. egglestonii*, *V. septemloba* and *V. triloba* but relegated *V. esculenta*, *V. lovelliana,* and *V. viarum* to hybrid derivatives based on intermediacy of various features. He provided a complete description and illustration of eastern Mexican *V. nuevo-leonensis* W. Becker as a heterophyllous-leaved member of the subsection. Non-specialists have run the gamut in their recognition of these violet taxa in North America. Gleason and Cronquist (1991) took McKinney's broad circumscriptions even further by merging nearly all heterophyllous-leaved and homophyllous-leaved violets into a single taxon as well as synonymizing most homophyllous-

leaved violets. The forthcoming treatment (co-authored by McKinney and R.J. Little) for the *Flora of North America* series will remain largely faithful to McKinney's original revision. The Biota of North America Program website (www.bonap.org, Kartesz 2011) and the USDA Plants Database website (http://plants.usda.gov/java/) follow Gil-ad's taxonomy. Recently published regional and state floras, and checklists, follow either extreme or a middle ground borrowing from both.

Specimens of a *Viola* clearly belonging to subsection *Boreali-Americanae* have been collected occasionally throughout the Guadalupe Mountains, but their identity has engendered taxonomic confusion. Spellenberg et al. (1986) ascribed a series of blue-flowered collections from three canyons in Eddy County, New Mexico by P.J. Knight to *V. viarum* Pollard, noting the large (800 km) range extension eastward to Oklahoma, the westernmost limit of its main range. This interpretation of an apparently disjunct population for an otherwise central U.S. species was proposed in light of other relict species also disjunct in the Guadalupes from their main southeastern hardwood forest ranges, although Spellenberg et al. acknowledged that further study might show the acaulescent blue Guadalupe violet to be unique. Subsequent annotations of specimens by other taxonomists and violet specialists have included *V. lovelliana* E. Brainerd, *V. missouriensis* Greene, and *V. palmata* L. (Worthington 2002).

The Guadalupe violet's unusual short vertical rhizome, sporadically heterophyllous nature, variable near-white to moderately purple corolla, and restriction to limestone substrate in the region initially attracted the attention of the authors. Examinations of specimens in herbaria with substantial Guadalupe Mountain angiosperm collections (NMC, SRSC, TEX/LL, and UNM), coupled with field studies of populations in New Mexico and Texas, have revealed that all collected material with whitish to purplish flowers in the Guadalupe Mountain region belongs to a single taxon, one that is distinct from previously described *Viola guadalupensis* with yellow flowers (belonging to sect. *Chamaemelanium*) in the same region. Plants within a given site encompass a broad range of leaf morphologies, with many plants bearing only unlobed leaves and others producing mid-season leaves with marginal notches or shallowly to moderately lobed blades (rarely, the largest blades are as deeply divided as typical *V. egglestonii*). Furthermore, plants at the lowest elevations in a given site usually possess purple corollas, whereas plants at the top of the same canyon often bear pale violet to nearly white ones.

Scanning electron microscopy was conducted in order to document micromorphological characters found to be taxonomically informative by Gil-ad (1998) in other acaulescent blue violets. Lateral petals and mature seeds were removed from herbarium specimens of *Viola calcicola*. One lateral petal was removed from each of two specimens, *Knight & Fletcher 3419* (UNM) and *Warnock & McVaugh 5418* (SRSC), and cropped to the immediate area around the trichomes before mounting. Two mature seeds from each of two specimens, *Warnock 23336* (SRSC) and *Warnock & Johnston 16536* (SRSC), were prepared following the methods of Gil-ad (1998). Samples were mounted onto carbon tape on separate aluminum stubs and coated with gold palladium at 17 mA for 180 sec. Examinations were performed at The Ohio State University Microscopy and Imaging Facility using an FEI NOVA^{TM} nanoSEM 400 scope. Descriptions and measurements of micromorphological characteristics of petal trichomes and seeds followed Gil-ad's terminology and methods (1998).

Table 1 details distinctions of *V. calcicola* in macromorphological and micromorphological features, in comparison with the four other heterophyllous-leaved species recognized by Gil-ad (1997). The new species diverges from other known species in many macromorphological features: rhizome, foliage, flowers, capsules, and seeds. The combination of these traits is wholly different from any known taxon and expresses a number of extreme features relative to the four previously described species. The main suite of macromorphological features encompasses its typically vertical praemorse rhizome, glabrous foliage, usually broad obtuse to rounded eciliate sepals, beardless spurred petal, sparse lateral petal beard with trichomes (sub)clavate to knob-shaped and cucullate, short green cleistogamous capsules on erect to declining peduncles, and yellow-brown to yellowish olive-brown seeds with darker brown patches. Study of the character states in Table 1 demonstrates that the number of overlapping or shared features between the new violet and other currently recognized heterophyllous-leaved orthospecies is far fewer than the number shared among the other four heterophyllous-leaved species. Its unusual vertical rhizome, sporadically heterophyllous nature, and expanded to

TABLE 1. Comparison of significant morphological features in *Viola calcicola,* sp. nov. and four other North American heterophyllous-leaved species; interpretation or measurement of traits closely follows methods employed by Gil-ad (1997). Bold italic type face in related species indicates a shared feather with *V. calciola.*

Trait	*V. calcicola*	*V. egglestonii*	*V. septemloba*	*V. nuevo-leonensis*	*V. triloba*
Rhizome	**short and erect (rarely elongate and oblique)**	elongate and oblique	elongate and oblique	elongate and oblique	elongate and oblique
Petiole pubescence	**glabrous**	***glabrous*** or sparsely pubescent	***glabrous***	pubescent to sparsely so	pubescent
Leaf blade lobing pattern	**many plants with unlobed leaves, others with some leaves notched or trilobate, middle segment undivided or with 1–2 lobes between it and lateral segments on each side, lateral segments undivided or shallowly lobed**	primary division 3 or 5 segments, secondary division middle w/2–4 segments, lateral undivided or with 2–3 lobes	primary division 3 segments, secondary division middle w/2 lobes, lateral undivided or with 2–4 lobes	(***sub)trilobate,*** middle and lateral segments undivided	***trilobate,*** middle segment undivided or w/1–2 lobes, lateral segments w/1–2 lobes (lower lobe undivided or bilobate)
Lobing depth	**shallowly (rarely deeply) divided**	deeply divided	deeply divided	***shallowly divided***	***shallowly or deeply divided***
Blade pubescence	**±glabrous throughout**	***glabrous throughout***	adaxial glabrous or pubescent, abaxial glabrous, margin ±ciliate	strigose throughout	sparsely pubescent throughout
Sepal shape	**broadly ovate-lanceolate to ovate, (rarely lanceolate)**	lanceolate to ***ovate-lanceolate***	lanceolate	***ovate-lanceolate to ovate***	[shape not described]
Sepal apex	**obtuse to rounded (rarely acute)**	acute to ***rounded***	acute	acute	***obtuse***
Sepal margin	**eciliate**	***eciliate*** or sparsely ciliate	***eciliate***	ciliate	irregularly ciliate
Auricle length (mm)	**0.3–0.5**	0.7–1.5	0.2–2	0.5–1.5	0.5–0.8
Interior corolla color	**whitish to violet w/white center**	violet (#83B/C) w/white center	violet (#83B) w/white center	pale violet (#86D) or violet-blue (#90D) w/white patches on lower ⅓ of each petal	violet (#83B) to purple-violet (#82A) w/white center bordered blue
Spurred petal beard	**absent**	sparse	dense	***absent***	***absent***
Lateral petal beard	**sparse**	dense	dense	***sparse***	dense
Lateral petal trichome shape	**expanded to strongly clavate near apex, the broadest cucullate**	cylindrical or often ***expanded or slightly clavate near apex***	cylindrical	cylindrical	cylindrical
Trichome width (µm)	**42–64**	ca. 100–110	70–80	***60–80***	ca. 90–100
Trichome micromorphology	**visible layer of folds 1, folds below apex curved or twisted, densely packed and overlapping (infrequently linear and somewhat separated)**	***visible layer of folds 1,*** folds below apex ***linear, twisted*** or convoluted, ***densely packed and overlapping***	***visible layer of folds 1,*** folds below apex ***linear or curved, densely packed***	***visible layer of folds 1,*** folds below apex ***linear, densely packed to widely spaced***	visible layer of folds 2, folds below apex ***linear*** or convoluted, ***upper widely spaced, lower densely packed***

Table 1. *Continued*

Trait	*V. calcicola*	*V. egglestonii*	*V. septemloba*	*V. nuevo-leonensis*	*V. triloba*
Cleistogamous peduncle final orientation	**declining, arching or erect**	prostrate	***erect***	prostrate, ***occasionally ascending***	prostrate
Cleistogamous capsule color in life	**yellow-green**	***yellow-green***	***yellow-green***	yellow-green to green, sparsely spotted & dotted w/grayed purple	yellow-green to green w/red-purple blotches & spots
Seed length (mm)	**1.50–1.75**	1.8–2.8	2.0–2.3	2.1–2.7	***1.7–2.0***
Seed width (mm)	**1.05–1.25**	1.3–1.7	***1.1–1.6***	1.2–1.7	***1.2–1.5***
Seed color	**background yellow brown (#74) to yellowish olive-brown (#87) with darker brown patches**	btw deep brown (#56) & dark brown (#59)	brown-black (darker than #65), luster shining	deep yellowish brown (#75), comprised of ***brownish black patches*** on moderate to dark orange yellow background	dark orange-yellow (#72)
Seed coat primary sculpture	**cells superficially tetra-, penta- or hexagonal, isodiametric or elongated, cell boundary furrowed, outer periclinal walls unevenly smooth**	***cells superficially pentagonal,*** isodiametric or slightly elongated, cell boundary slightly furrowed, outer periclinal walls unevenly smooth	cells superficially ***tetra-, or pentagonal isodiametric or elongated, cell boundary widely furrowed, outer periclinal walls unevenly smooth*** or finely & irregularly folded	none	none
Seed coat secondary sculpture	**narrowly oblong, pentagonal or rounded, ring-like structures of *spaced, parallel segments***	rosette-like circular plates	large elliptical or ***rounded, structures of spaced, parallel segments***	superficially foveate verrucate structures, with striated or semi-terete folds	aggregates of porous plates, occasionally folded along their margins

clavate or knob-shaped cucullate lateral petal trichomes set the new violet apart from all other lobed-leaved violets. Its sparse lateral petal beards, broader cucullate lateral petal trichomes, seeds with paler ground color and numerous darker patches, and restriction to limestone substrate are highly unusual features in the subsection; it shares sparse lateral petal beards with *V. nuevo-leonensis*, broader cucullate trichomes with *V. cucullata*, mottled seeds with *V. nuevo-leonensis,* and its confinement to limestone with *V. egglestonii*. Following Gil-ad's (1997) key to flowering plants, unlobed-leaved specimens of *Viola calcicola* will key easily to *V. cucullata*, whereas plants with lobed or divided blades will key to *V. triloba* (if one ignores the sparse beards on the lateral petals of the new species). In the Gil-ad key to cleistogamous plants, specimens of *V. calcicola* with unlobed leaf blades will key easily to *V. nephrophylla* if one ignores seed color (comparatively lighter than *V. nephrophylla* in the new species), whereas plants with lobed or divided leaf blades will key generally to *V. septemloba* if the seed color is ignored.

Lateral petal trichomes have the distinctly to strongly clavate shape of *V. cucullata* although they are much smaller than that species and scarcely overlap with *V. nuevo-leonensis* in width. The technical details of the cuticular folds generally match those of *V. septemloba*, but the folds are not as densely packed, and the fine structure of the folds (Fig. 4C–E) does not match any orthospecies or hybrid characterized by Gil-ad. Primary and secondary structures on the seed coat of *V. calcicola* share many details with *V. septemloba* and few with other species. Once again, subtle differences are obvious between the two species, with the ring-like secondary structures in the former having essentially symmetrical and parallel outlines rather than "tear-drop" or pyriform asymmetrical outlines seen in *V. septemloba*. Additionally, the central region within each of the ring-like structures of *V. calcicola* is generally uniformly depressed throughout rather than gradually diminishing in elevation from edge to center as in the structures of *V. septemloba*. Overall, macromorphological traits and preference for limestone ally *V. calcicola* most closely to *V. egglestonii*, whereas micromorphological features of petal trichomes and seeds suggest a close relationship to *V. septemloba* in many details while also highlighting unusual features in the Guadalupe violet.

Short vertical rhizomes in the blue-flowered Guadalupe Mountain violet may be largely genetically fixed but occasionally environmentally influenced, given that one plant growing mostly in deeper soils next to rock exposures has been found with an ascending, elongate rhizome typical of other members of the subsection. The habit of "sporadic heterophylly," in which most Guadalupe Mountain plants within a given population are completely unlobed whereas others produce mid-season leaves with notched or shallowly lobed (rarely deeply dissected) blades, is novel among North American violets. Populations of other heterophyllous-leaved violet species are typically comprised of plants that virtually all produce lobed or dissected blades during mid- or late anthesis and into early fruit. Plants of the new species with variously unlobed or divided leaves are otherwise identical in every other feature and are intermingled throughout a given site.

A de novo or recent hybrid origin for the violet under consideration is untenable, given that no other heterophyllous-leaved species inhabit the south-central U.S. within hundreds of kilometers of the region in question. Two other, strictly unlobed-leaved members of the subsection, *Viola missouriensis* and *V. nephrophylla*, have been recorded in nearby counties, although neither approaches the Guadalupe violet in any but a few disparate traits. The available macromorphological and micromorphological evidence supports recognition of the acaulescent blue violet in the Guadalupe Mountains as a divergent new orthospecies with an unusual restriction to limestone substrates. Characteristics and their measurements presented below follow Gil-ad (1997), and are organized generally to allow direct comparison with his descriptions of accepted orthospecies.

TAXONOMY

Viola calcicola R.A. McCauley & H.E. Ballard, sp. nov. (**Figs. 1–3**). TYPE: U.S.A. TEXAS. CULBERSON CO.: Smith Canyon, above Frijole, E of Guadalupe Mountains, 1800 m, abundant about spring, in crevices of limestone rocks, flowers nearly white, the lower petal with prominent blue lines, 3 May 1947 (fl, fr), *R. McVaugh 8149* (HOLOTYPE: TEX!; ISOTYPES: MICH, TEX!).

Acaulescent, heterophyllous, perennial herb in crevices of limestone, 3–9(–14) cm tall; rhizome vertical and praemorse, rarely oblique and somewhat elongated, typically to 2.5 cm long, 5–7 mm diam., bearing stout fi-

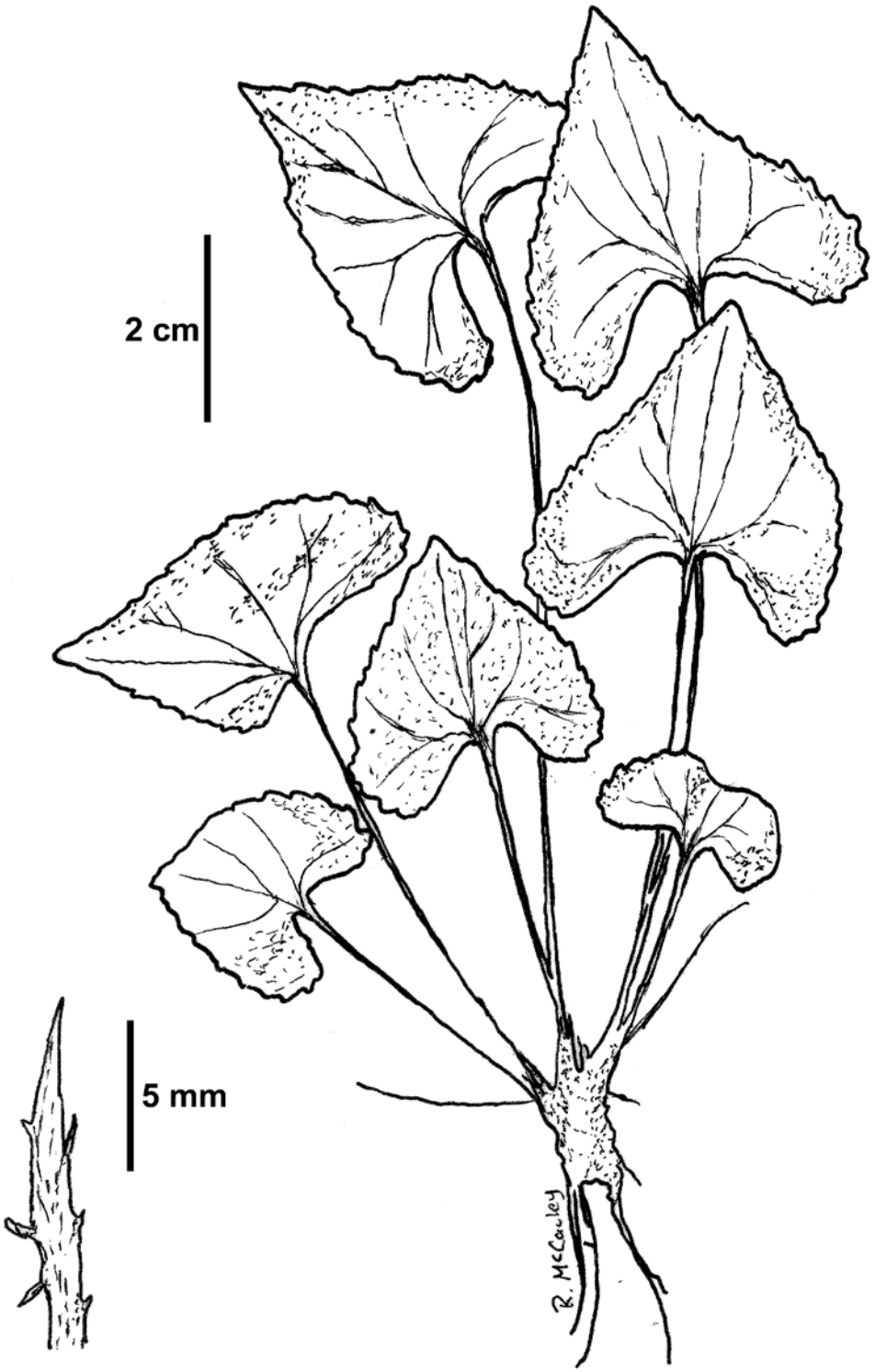

Fig. 1. *Viola calcicola* sp. nov. **A.** Habit. **B.** Stipule. Drawn from *R.A. McCauley 649* (FLD) and the holotype *R. McVaugh 8149* (TEX).

Fig. 2. Variation in leaf blade morphology in *Viola calcicola* sp. nov.

brous roots to 1 mm diam. Leaves all unlobed or with some leaves shallowly (rarely deeply) trilobate; stipules scarious to semi-herbaceous, pale or often flushed and streaked with purple, free, narrowly triangular to linear-lanceolate, 6–10 mm long, apex acuminate, margins irregularly to remotely glandular-fimbriate, eciliate; petioles on largest leaves 3–7(–9.5) cm long, green, glabrous; blades cordate or triangular-cordate to deltoid, deeply to shallowly cordate at base, margins rounded-serrate most of their length but low-serrate to subentire near apex, apex sharply acute to acuminate (larger blades) or obtuse to broadly rounded (smaller blades), medium green to darker blue-green (or drying gray-green) sometimes lightly to moderately flushed with purple abaxially, 1–3(–4.5) cm long and 0.8–3(–4.5) cm wide, largest blades at chasmogamous anthesis with length:width ratio 1.2–1.6, apical angle 31–60(–86)°, all blades either unlobed, narrowly ovate, deeply cordate at base, the larger narrowly acute to subacuminate at apex, or the larger blades on some plants notched or weakly to moderately (rarely deeply) trilobate, the middle primary division with the terminal lobe triangular to broadly oblong-ovate, broadly obtuse to (more commonly) narrowly and sharply acute at apex (rarely narrowly linear-lanceolate in the most deeply dissected blades), bearing 1–2 slender lanceolate to oblong lobes on each side near the base between the middle and lateral primary divisions, the lateral divisions obtriangular and incised or shallowly lobed (rarely deeply divided), margins remotely to uniformly serrate but less pronouncedly so nearest the apex, glabrous throughout or with occasional hairs at the base of serrations. Chasmogamous flowers on glabrous peduncles generally borne at or slightly to well above the leaf blades, peduncles elongating in fruit, 3–6(–11) cm long, green and sometimes flushed or finely dotted with purple, two bractlets inserted at variable positions on peduncle, proximal or remote, 2–3 mm long, lanceolate, green, acute at apex, margins scarious, entire, eciliate; sepals variable, ovate to broadly ovate-lanceolate in some plants, lanceolate in others, distinctly 3-veined, the midvein often pronounced and elevated near the auricles, green or flushed to suffused with purple, the lowest 3–5 mm long and 1–2 mm wide, sepal length:capsule length ratio ca. 0.6, glabrous adaxially, margins scarious and eciliate, apex commonly obtuse to broadly rounded (rarely more or less sharply acute); auricles 0.3–0.5 mm long, quadrate to broadly rounded or subtruncate, glabrous; spur 1.0–1.5 mm long; corolla 0.8–1.5 cm long, petals on different plants varying from nearly white (faintly flushed with violet) to medium purple, lateral petals having few inconspicuous purple veins, spurred petal with prominent and extensive nectar guides, lateral and upper petals narrowly obovate, spurred petal obovate with long-tapering base, 10–13(–15) mm long including spur, 3–5 mm wide, broadly obtuse to rounded at apex; spurred and upper petals glabrous within, lower lateral petal beard sparse with few to several trichomes of variable length, medial on interior surface, trichomes noticeably expanded to (more commonly) clavate or knob-shaped distally, the broadest rounded and cucullate at apex, 42–64 µm wide, with 1 layer of visible cuticular folds, folds below the apex commonly curved or twisted and densely packed, less often linear and somewhat separated, overlapping; stamens 2–2.5 mm long; style ca. 2 mm long, apex expanded into two prominent wing-like appendages, terminating in an erect stigmatic surface. Chasmogamous capsules ellipsoid, green in life (straw-

Fig. 3. *Viola calcicola* sp. nov. **A.** Photo of typical plant at type locality. **B.** Plant showing short erect rhizome and the subglobose capsule. **C.** Type locality, Smith Springs, Guadalupe Mts., May 2011.

colored when dry), sometimes finely spotted with red-purple, smooth, glabrous, (6.5–)7–9 mm long. Cleistogamous peduncles erect or arching to declining, distinctly shorter than the leaves, slender, glabrous, green, sometimes flushed or finely spotted with red-purple. Cleistogamous flower buds to 3 mm long; capsules broadly obovoid to subglobose, green in life (straw-colored when dry), smooth, glabrous, 4.5–6 mm long. Seeds from chasmogamous capsules yellow-brown (ISCC-NBS #74) with numerous slightly darkened patches, broadly obovoid, ca. 1.75 mm long, 1.25 mm wide, with a small lateral caruncle 0.30–0.5 mm long extending ⅓–⅖ the length of the seed from the funiculus; seeds from cleistogamous capsules slightly narrower and paler than chasmogamous ones, yellowish olive-brown (ISCC-NBS #87) with somewhat more contrasting darker patches giving a conspicuous mottled appearance, particularly toward the basal end, obovoid, 1.50–1.75 mm long, 1.05–1.15 mm wide, the caruncle identical to that in chasmogamous seeds. Seeds of both types under magnification displaying primary coat structure with cells superficially tetra-, penta- or hexagonal, isodiametric or elongated, the cell boundary furrowed, outer periclinal walls unevenly smooth; secondary coat structure represented by symmetrically narrowly oblong, pentagonal or rounded, ring-like structures of spaced parallel segments, the "basin" within the ring-like structures more or less uniform in elevation and mostly depressed well below the top of the structures.

Distribution and Habitat.—*Viola calcicola* occurs in scattered locations principally along the eastern flank of the Guadalupe Mountains and occasionally in the upper reaches of the larger mountain canyons. It is confined to cracks of Permian Age limestone in sheltered canyons and springs. The species is commonly found beneath an overstory association of *Acer grandidentatum* Nutt., *Arbutus xalapensis* Kunth, and *Quercus muehlenbergii* Engelm. At the type locality *V. calcicola*, while common, is highly localized to rocks in close proximity to water (e.g., rocky stream terraces or canyon walls flanking streams). The geographic distribution of the species is hundreds of kilometers distant from the nearest population of other North American heterophyllous-leaved species.

Phenology.—Blooming April to May. Fruits present May to October.

Etymology.—*Viola calcicola* is named in recognition of its obligate limestone substrate.

Taxonomic distinctions and affinities.—Other currently recognized heterophyllous-leaved orthospecies in subsection *Boreali-Americanae* are *Viola egglestonii* Pollard, found in limestone cedar glades of the east-central U.S.; *V. septemloba* Leconte, located in sandy open pine savannas in the southeastern U.S.; *V. nuevo-leonensis* W. Becker of sandy open oak-pine forests in northeastern Mexico; and *V. triloba* Schwein., found in sandy loam or clay soils in dry-mesic forests of the eastern U.S. and Canada (Gil-ad 1997). The new violet shares a restriction to limestone substrate with *V. egglestonii*, although the local floras of the two violets are dramatically different. *Viola calcicola* resembles *V. egglestonii* and *V. septemloba* in its glabrous foliage and eciliate sepals but diverges in its peculiar sporadically heterophyllous nature. However, blades on lobed-leaved plants are similar to those of *V. triloba* var. *triloba* and *V. nuevo-leonensis* as they are usually shallowly divided, with the sinuses of the lobes reaching less than halfway to the petiole summit, and the terminal lobe triangular or oblong-ovate. In *V. calcicola* occasional plants with deeply divided leaf blades closely resemble typical *V. egglestonii*. Corolla color in plants of certain sites often varies from nearly white to medium violet, and this appears to be at least partly related to topographic position (for instance, plants with moderately purple or bluish-purple corollas are generally found at or near the bottom of a canyon or escarpment, while plants with nearly white corollas grow principally in exposed microsites at or near the top of the canyon). Its sparse and localized lateral petal beard is similar to that of *V. nuevo-leonensis* and unlike other North American members of the subsection. Specimens with unlobed leaves have been misidentified frequently as *V. missouriensis*, whereas plants with conspicuously lobed leaves have been misidentified most often as *Viola* (×) *viarum*. A misidentification of specimens assigned to the latter may represent the basis for the disjunct county record of that taxon in the BONAP distribution map. The Guadalupe violet shares most of its micromorphological features in petal trichomes and seed coat with *V. septemloba*.

Paratypes: **U.S.A. NEW MEXICO. Eddy Co.:** 38 mi SW of Carlsbad, BLM Lonesome Ridge ACEC, perennial, growing in narrow cracks in limestone, N-facing cliffs, 5–15 ft above canyon bottom, T26S R22E Sec 19 N ½ of SE ¼, 5040 ft, 29 Mar 1989 (fl), *W.W. Dunmire 1091* (UNM); Guadalupe Mts., In tiny cracks in solid limestone, 7 Apr 1937 (fl), *L.N. Goodding 2323* (NMC); Guadalupe Mts., Rocky cliffs around springs,

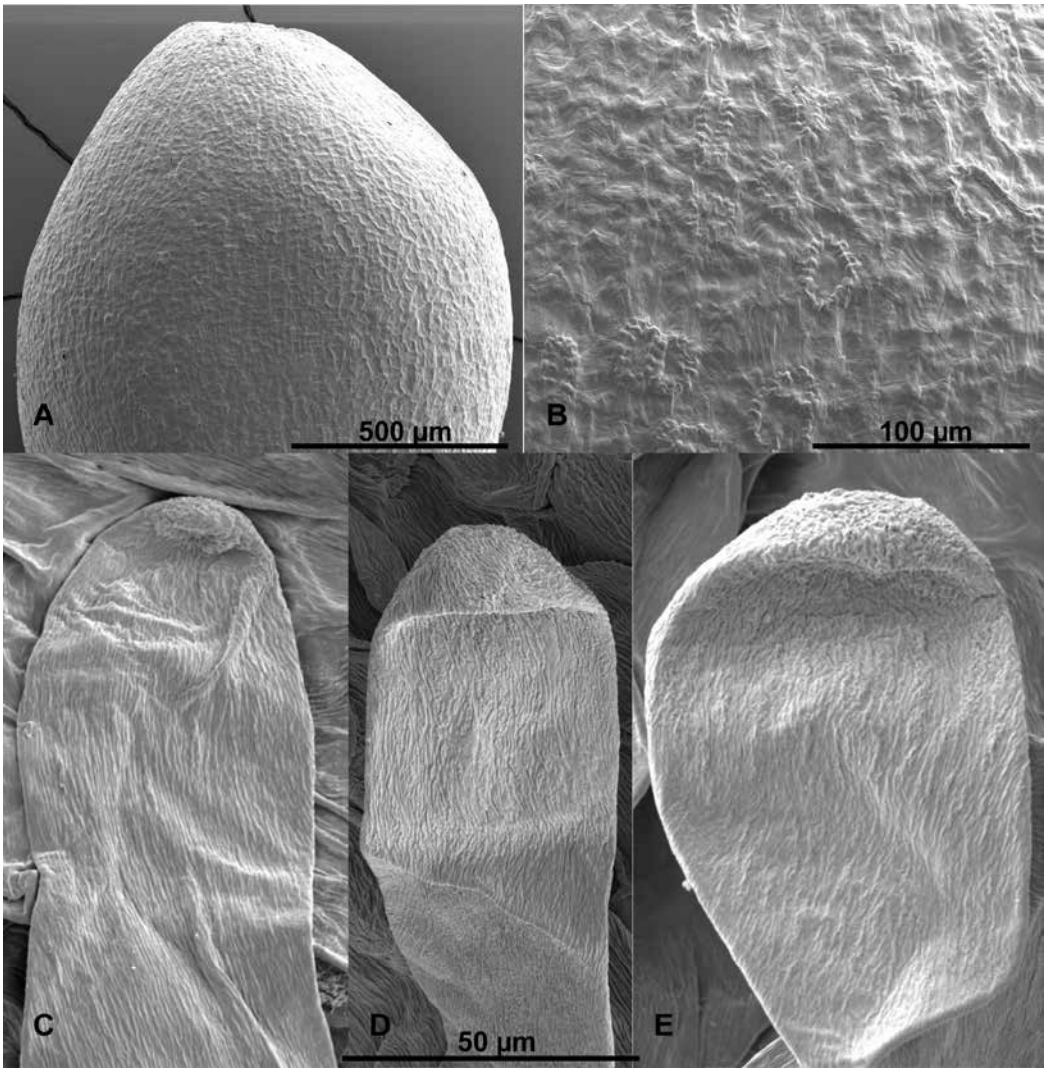

Fig. 4. ***Viola calcicola*** **sp. nov. A–B. SEM micrographs of mature chasmogamous seed, *Warnock & Johnston 16536* (SRSC). C–E. SEM micrographs of lower lateral petal trichomes, *Warnock & McVaugh 5418* (SRSC).**

27 Jun 1942 (fr), *Hershey 2639* (NMC); Guadalupe Mountains, Big Canyon, old ranch tract 2 hrs drive from Carlsbad, frequent in cracks of limestone, losing corollas and going into full fruit, mostly unlobed leaf blades but occasional plants with coarsely toothed or pedately lobed blades, 29 Apr 1995 (fl, fr), *P. Knight, H.E. Ballard, P. Meloche, T. Lowrey, B. Sivinsky, L. Paul, M. Parker s.n.* (BHO, UNM); mouth of Black Canyon on E side of Guadalupe Mts., ca 30 mi S of Carlsbad, on limestone, 5000 ft, 26 Mar 1982 (fl), *P.J. Knight 1822* (UNM); on limestone, mouth of Black Canyon on E side of Guadalupe Mts., ca 30 mi S of Carlsbad, 24 May 1982 (fl), *P.J. Knight 1981* (UNM); Big Canyon just N of Black Canyon, on E side of Guadalupe Mts. ca 30 mi S of Carlsbad, on limestone, 5000 ft, 24 May 1982 (fl, fr), *P.J. Knight 1983* (NY, UNM); collected in Big Canyon of the Guadalupe Mountains, T26S R21E Sec 24 NE ¼ of the SE ¼, 14 Apr 1987, (fl), *Knight and Fletcher 3419* (UNM). **Otero Co.:** N. McKittrick Canyon, At first crossing of Texas-New Mexico boundary, on the New Mexico side, Collected in gravels and boulders of stream bottom, In Riparian type habitat and below protected cliffs, Big tooth maple, Ponderosa Pine, Madrone, Hop-Horn beam, *Q. muehlenbergia* [sic!], 18 Oct 1973 (fl, fr), *T. F. Patterson 500–549 501* (LL). **TEXAS. Culberson Co.:** McKittrick Canyon, Riparian litter in limestone gravels, 5400 ft, 27 Apr 2002, (fr), *Blaxland s.n.* (GUMO); McKittrick Canyon, confluence of North & Middle canyons, Riparian litter in limestone gravels, 5680 ft, 27 Apr 2002, (fl), *Blaxland s.n.* (GUMO); North McKittrick canyon near state line, Riparian leaf litter in

limestone gravels, 5520 ft, 27 Apr 2002, *Blaxland s.n.* (GUMO); Bear Canyon, Pocket depression in shaded limestone boulders, hardwood overstory, 6720 ft, 28 Apr 2002, (fl), *Blaxland s.n.* (GUMO); North McKittrick Canyon, 28 Apr 1975, (fl), *J.K. & T.B. s.n.* (GUMO); Guadalupe Mts., Guadalupe Mountains National Park, Smith Spring, common in small cracks of limestone, 1829 m, 10 May 2011, *R.A. McCauley 649* (FLD); North McKittrick Canyon, GMNP, fairly common on limestone boulders of the inner canyons of GMNP, according to collector of this specimen, Brent Wauer, 15 Apr 1988 (fl), *A.M. Powell 5496* (SRSC); frequent in rock crevices along Smith Spring, Guadalupe Mts., 6000 ft, 10 Jul 1949 (fr), *B.L. Turner 1249* (SRSC); frequent in damp crevices and boulders of Smith Canyon, limestone soil, Guadalupe Mountains, 6000 ft, 15 Sep 1948, (fr), *B.L. Turner and B. H. Warnock 93* (SRSC); infrequent in crevices of limestone boulders in Upper Pine Spring Canyon, Guadalupe Canyon, 7000 ft, 3 May 1947 (fl), *B.H. Warnock 5418* (SRSC); fruiting, limestone bluffs above Hunter Lodge in south McKittrick Canyon, Guadalupe Mountains, 5500 ft, 31 Aug 1950 (fr), *B.H. Warnock 9512* (SRSC); infrequent perennial, limestone soil, at lodge in South McKittrick canyon, Guadalupe Mountains, J.C. Hunter ranch, 5800 ft, 20 Oct 1957, (fr), *B.H. Warnock 15952* (SRSC); sparse perennial, South McKittrick Canyon, Guadalupe Mts., limestone soil, 6200 ft, 30 April 1961 (fl, fr), *B.H. Warnock 18234* (SRSC); rare perennial, limestone soil in South McKittrick Canyon above Hunter's Lodge, Guadalupe Mountains, 6800 ft, 27 May 1968, (fr), *B.H. Warnock 23180* (SRSC); infrequent perennial in mid South McKittrick Canyon, Guadalupe Mountains National Park, 6500 ft., 25 Sep 1971 (fr), *B.H. Warnock 23336* (SRSC); infrequent perennial, flowers lavender, limestone soil, south McKittrick Canyon of Guadalupe Mountains, 6500 ft, 18 May 1958 (fl), *B.H. Warnock and M.C. Johnston 16479* (SRSC); infrequent perennial, limestone soil, lower south McKittrick Canyon, Guadalupe Mountains, 6000 ft, 18 May 1958 (fr), *B.H. Warnock and M.C. Johnston 16536* (SRSC); infrequent perennial, lavender flowers, in lower South McKittrick Canyon, Guadalupe Mountains, 6000 ft., 18 May 1958 (fl), *B.H. Warnock and M.C. Johnston 16556* (SRSC); infrequent perennial herb, Smith Spring, Guadalupe Mts. National Park, 26 July 1971 (fr), *T. Weston 147* (SRSC).

DISCUSSION

Recognition of *V. calcicola* adds a second endemic *Viola* to the Guadalupe Mountain flora, and the first heterophyllous-leaved member of the *Boreali-Americanae* group to the western U.S. The yellow-flowered *V. guadalupensis* Powell and Wauer of sect. *Chamaemelanium* also occurs in limestone along the eastern flank of Frijole Ridge and is known from approximately 4 reported populations along the eastern escarpment of the mountains (Powell & Wauer 1990; Mullet et al. 2008; Marcussen et al. 2011; F. Armstrong, pers. comm.). Anomalous specimens of a third violet, referred to by others as *Viola purpurea* Kellogg, represent a different yellow-flowered species of Sect. *Chamaemelanium* that has been rarely collected in upland areas of the Davis Mountains and in the Texas portion of the Guadalupes. Specimens assigned to this latter violet do not closely match described taxa in subsect *Purpureae* and might represent yet another new taxon. Further investigation would shed light on the status of this third *Viola*, which is disjunct by more than 500 km from the next nearest populations of the *Purpureae* to the west in Arizona.

The origin and evolutionary relationships of *Viola calcicola* are as yet unclear, although the new species is clearly related to other heterophyllous-leaved eastern species. However, the new species diverges from these others in many vegetative and reproductive traits as well as the fine micromorphological details of petal trichomes and seed coat. It shares fewer features with the other heterophyllous-leaved species than the currently recognized species share amongst each other, suggesting long-term divergence from a common ancestor. Generally, *V. calcicola* shares the most macromorphological features and also its restriction to limestone substrate with *V. egglestonii*, but most micromorphological features with *V. septemloba*. It is unique in its short vertical rhizomes and its sporadic nature of leaf blade lobing. It shares the sparse lateral petal beards with *V. nuevo-leonensis* and generally clavate to knob-shaped cucullate trichomes of the lateral petals with eastern North American *V. cucullata*. Its unusually broad range of corolla color pigmentation, even within sites, appears to correlate with elevation or ecological exposure (or both), with plants at the bottom of escarpments or canyons producing deeply pigmented corollas and plants near or at the top producing whitish corollas. One explanation is that less pigmented (more reflective) corollas at higher topographic positions aid in reducing the deleterious effects of ultraviolet radiation on reproductive structures in more exposed, sunny microsites.

Unlobed-leaved plants of *V. calcicola* could be mistaken morphologically for *Viola missouriensis* or *V. nephrophylla*, both of which are reported from southeastern New Mexico, where they reach their southern range limit. However, the new species is easily distinguished from both by its short vertical rhizome; sparse lateral petal beards composed of generally clavate to knob-shaped, cucullate lateral petal trichomes; and yellowish brown seeds with numerous darker brown patches. Its living green cleistogamous capsule differentiates it further from *V. missouriensis* and its glabrous spurred petal distinguishes it from *V. nephrophylla*.

The inferred close relationship of *Viola calcicola* with *V. egglestonii* and its broader affinities to other central U.S. and Mexican heterophyllous-leaved species are based on available morphological traits and ecological observations. Nevertheless, *V. calcicola* diverges in many features from other heterophyllous-leaved violets and possesses a few characteristics that are highly unusual or unique in the subsection. The proposed relationship hypotheses are testable using appropriate molecular markers. The authors are currently isolating and evaluating the efficacy of potentially informative microsatellite loci as well as several nuclear and chloroplast gene regions with sufficient polymorphisms to test such hypotheses. Future genetic studies on *Viola calcicola* and its *Boreali-Americanae* kin will potentially illuminate phylogenetic relationships, biogeographic affinities, and evolutionary origins of the new Guadalupe Mountain endemic and other North American species in this taxonomically challenging but evolutionarily intriguing group of violets.

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