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A revised subgeneric classification of *Trillium* (Parideae, Melanthiaceae)

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Abstract

Results of recent molecular phylogenetic analyses have shown that the previous separation of *Trillium* into two subgenera based on pedicellate or sessile flowers is untenable. An updated infrageneric classification is presented recognising four subgenera in the genus, consistent with phylogenetic analyses. The three clades of pedicellate-flowered species are recognised here as subgenera: subgen. *Trillium*, *Delostylis* and newly named *Callipetalon*. The fourth, *Trillium* subgen. *Sessilia*, includes all sessile-flowered species. Orthographic considerations necessitate corrections to two previously published subgeneric names: *Delostylium* and *Sessilium* should be *Delostylis* and *Sessilia*.

Keywords: Asian Flora, North American Flora, *Pseudotrillium*, Trilliaceae, *Trillidium*

Introduction

Trillium Linnaeus (1753: 339) has generally been regarded as comprising two subgenera based on pedicellate or sessile flowers (*e.g.*, Freeman 1975, Case & Case 1997). This simple classification is contradicted by results of molecular studies of the genus showing that the pedicellate trilliums are paraphyletic (Lampley 2021). An updated infrageneric classification is presented here that reflects the phylogenetic results and morphological variation. A phylogenetically informative infrageneric level classification provides a framework for other evolutionary or ecological studies of *Trillium*, *e.g.* seed dispersal studies (Miller *et al*. 2021).

Previous attempts to develop an infrageneric classification for *Trillium* have been unsatisfactory, in part because of the overall morphological unity of the genus. Rafinesque (1830) divided *Trillium* in three subgenera: one for sessile species, another for only *T. catesbaei* Elliott (1817: 429; as *T. stylosum* Nuttall, 1818: 239) and the third for all other pedicellate species. Gleason (1906) subdivided the pedicellate trilliums in three informal groups based on stigma and ovary morphology. His *T. grandiflorum*-type group (with truncate or rounded ovary not deeply angled and uniformly slender stigmas) included *T. grandiflorum* (Michaux 1803: 216) Salisbury (1805: 1), *T. ovatum* Pursh (1813: 245), *T. scouleri* Rydberg in Gleason (1906: 394) (which is currently considered to be a synonym of *T. ovatum* but is under review) and *T. nivale* Riddell (1835: 525). Gleason (1906) also included species in this group that are now considered separate based on molecular studies: *Trillidium* Kunth (1850: 120) (*T. govanianum* (Wallich in Royle 1839: 384) Kunth (1850: 120) and *T. undulatum* (Willdenow 1801: 422) Floden & Schilling in Weakley *et al.* (2018: 477)) and *Pseudotrillium* Farmer (2002: 687) (*P. rivale* (Watson 1885: 378) Farmer (2002: 687)). His *Trillium erectum*-type group (with sharply six-lobed ovary, and sessile, recurved, tapering stigma) included the type species of *Trillium*, *T. cernuum* Linnaeus (1753: 339), as well as *T. erectum* Linnaeus (1753: 340) and other pedicellate species (American and Asian) recognised at the time. Lastly, Gleason recognised a *T. catesbaei*-type group (characterised by uniformly slender stigmas and single, well-defined style), which included *T. catesbaei* and *T. pusillum* Michaux (1803: 215). Barksdale (1938) and Ihara & Ihara (1978, 1982) also developed similar morphological divisions among pedicellate species for which there is some overlap with those of Gleason (Farmer 2007). Takahashi (1982) divided North American *Trillium* species in five main types based on pollen morphology; notably, his spinulate-type, distinguished

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by spinulose exine ornamentation, included three species, *T. nivale, T. ovatum* and *T. grandiflorum*. Asian *Trillium*, *T. apetalon* Makino (1910: 137)*, T. camschatcense* Ker Gawler (1805: t. 855)*, T. smallii* Maximowicz (1884: 217)*, T. tschonoskii* Maximowicz (1884: 218) and interspecific hybrids*,* display granulate-type exine ornamentation most closely resembling that of *T. erectum* (Takahashi 1983).

An infrageneric classification of *Trillium* agreeing with molecular results requires recognition of a minimum of four subgenera if the distinctive sessile-flowered clade is to be recognised at this level. Two clades have been recognised previously as subgenera and the other two only as informal groups. The first, corresponding to the *T. erectum* type of Gleason (1906) agrees with Barksdale (1938) and Ihara & Ihara (1978, 1982) and is sister to the other three. The second pedicellate clade corresponds roughly to the *T. grandiflorum*-type (Gleason 1906) and includes *T. nivale, T. ovatum* and *T. grandiflorum*. Compared to the *T. grandiflorum* group, the *T. erectum* group generally have petals more separated and less overlapping at the base, more open corollas with exposed and prominent ovaries and stigmas that extend beyond the anthers or nearly so at anthesis. This *T. grandiflorum* clade is sister to the last two. The sessile species form a well-supported clade corresponding to *T.* subgen. *Sessilium* Rafinesque (1830: 97), which is sister to the third pedicellate clade, which is consistent with Gleason's *T. catesbaei*-type and *T.* subgen. *Delostylium* Rafinesque (1830: 97) (Farmer 2007, Schilling *et al.* 2017).

Orthographical considerations

The *Trillium erectum* group includes the type species of *Trillium*, *T. cernuum*, and thus becomes *T*. subgen. *Trillium*. The *T. grandiflorum* group has not previously been formally named, and *T.* subgen. *Callipetalon* is erected here. Names have been published for the other two subgenera but require correction as detailed below.

In the process of forming a new subgeneric name for the *Trillium grandiflorum* clade, we noticed two nomenclatural errors. Although *T.* subgen. *Sessilium* received some nomenclatural scrutiny in recent years (Reveal & Gandhi 2014a, Reveal & Gandhi 2014b), one additional correction needs to be made. The subgenus should rather be *T.* subgen. *Sessilia* Rafinesque [as '*Sessilium*']. According to Article 21.2 of the *International code of nomenclature for algae, fungi, and plants* (ICN; Turland *et al.* 2018), the name of a subdivision of a genus must be of the same form as a generic name [i.e., a noun in the nominative singular, as in *Trillium*], a noun in the genitive plural or an adjective in the nominative plural agreeing in gender with the generic name [i.e., neuter in *Trillium*]. The name *Sessilium* is not in any of the permissible forms; it is neither a noun in the nominative singular nor the genitive plural. To be clear, *Sessilium* is an adjective, but not a permissible form. It is the genitive plural, not the nominative plural, of the adjective *sessile*. It is certain that the subgeneric name of *T.* subgen. *Sessilium* is an adjective because Rafinesque explicitly based it on *T. sessile* Linnaeus (1753: 340). Since *Trillium* is a neuter generic name, this subgeneric epithet should then be corrected to *Sessilia*, the neuter nominative plural of *sessilis/sessile.* Under Art. 32.2 of the *Code*, this is a correctable error without change in authorship.

With its connection to the name of a separate genus, however, *Trillium* subgen. *Delostylium* Rafinesque (1830: 97) is a less clear error. When Rafinesque named *T.* subgen. *Delostylium,* he was most likely referring to the genus *Delostylis* Rafinesque (1819a: 102) (now considered a synonym of *Trillium*), which he had named more than a decade before. The only species Rafinesque included in this subgenus was *T. stylosum,* which he had previously treated as *Delostylis stylosum* (Nuttall 1818: 239) Rafinesque (1819b: 192), now considered the type of *Delostylis*. The error lies in the fact that Rafinesque (1830) gave the subgeneric name *Delostylium* the form of an adjective in the neuter nominative plural, but under ICN Article 21.2 it should have been the same form as the other generic name (*Delostylis*, considered a noun in the nominative singular according to ICN Article 20.1). Rafinesque (1840) later referred to the subgeneric epithet as *Delostylis*, perhaps either correcting himself or forgetting the previous epithet, without listing any species. Because at the time of its publication, *T.* subgen. *Delostylium* included only the type species of a previously named genus, it must be considered a new combination at a new rank with the previous genus name as its basionym. It should therefore be correctly cited as *T.* subgen. *Delostylis* (Raf.) Raf. [as '*Delostylium*'].

Therefore, the updated subgeneric orthography in *Trillium* is as formally treated below (Fig. 1):
Trillium L. subgen. *Trillium*
Trillium L. subgen. *Callipetalon* Lampley & E.E.Schill.
Trillium L. subgen. *Delostylis* (Raf.) Raf. [as '*Delostylium*']
Trillium L. subgen. *Sessilia* Raf. [as '*Sessilium*']

Key to the subgenera of *Trillium*

1 Flowers usually pedicellate; leaf uniformly green, usually not mottled **2**
- Flowers sessile; leaf green usually with darker shades of green and silver mottling scattered over the surface4. *T.* subgen. *Sessilia*
2 Stigmas uniform (not tapered), united in a common style or at least basally connate; ovary at anthesis somewhat obscured by corolla and stamens and relatively less exserted, 3- or 6-angled, typically white, greenish white or green; petal with margins undulate, basally overlapping, pink or white aging to various pink shades or remaining white (*T. nivale*); adaxial petal venation not engraved; flower funnelform or at least with basally erect petals shallowly encircling ovary; leaf ovate, elliptic-ovate, ovate-rhombic, ovate-lanceolate or oblong **3**
- Stigmas thicker basally and tapered above, separate; ovary at anthesis exposed, exserted or only slightly obscured, typically strongly 6-angled or ridged, generally dark red, to creamy white or white with red markings; petal with margins entire, separate or only slightly overlapping, if white, aging to brown; adaxial petal venation typically engraved; flower open, or widely agape, not funnelform; leaf shape rhombic, broadly elliptic, rhombic-ovate or lanceolate-elliptic (*T. hibbersonii*) .....1. *T.* subgen. *Trillium*
3 Stigmas connate; leaf elliptic-ovate, ovate-lanceolate or oblong ..... 3. *T.* subgen. *Delostylis*
- Stigmas only basally connate; leaf ovate, elliptic-ovate or ovate-rhombic ..... 2. *T.* subgen. *Callipetalon*

Taxonomic Synopsis

(References: Case 2003, Case & Case 1997, Freeman 1975, Fukuda *et al.* 1996, Gaddy 2008, Liang & Soukup 2000, O'Neill *et al*. 2020, Patrick 1984, Samejima & Samejima 1987, Schilling *et al.* 2013, Schilling *et al.* 2017, Schilling *et al*. 2019, Weakley 2020).

Trillium Linnaeus (1753: 339), *nom. cons.*
Type:—*Trillium cernuum* L. (1753: 339)

Trillium L. subgen. ***Trillium***
Heterotypic synonym: *Trillium* subgen. *Anthopium* Rafinesque (1830: 97). Type:—*Trillium acuminatum* Raf. [= *T. erectum* L.; Freeman (1975).]

Included species:—14 (–15). *Trillium apetalon*; *T. camschatcense*; *T. cernuum*; *T. channellii* Fukuda, Freeman & Itou (1996: 164); *T. erectum*; *T. flexipes* Rafinesque (1840: 133); *T. ×hagae* Miyabe & Tatewaki (1936: 189); *T. hibbersonii* (Taylor & Szczawinski 1975: 250) O'Neill & Farmer (2020: 193)*; T. rugelii* Rendle (1901: 331); *T. simile* Gleason (1906: 391)*; T. smallii*; *T. sulcatum* Patrick (1984: 27); *T. tschonoskii*; *T. vaseyi* Harbison (1901: 24).

Distribution:—North America and Asia. Up to eight species occur in eastern and north-central North America. Inclusion of an additional species in this group, *Trillium hibbersonii*, adds a disjunct western component to the North American distribution. At least six species inhabit East Asia, especially Japan, eastern China and eastern Russia, although the precise number is debatable. *Trillium tschonoskii* and *T. camschatcense* are the most widespread Asian species; however, *T. tschonoskii* reaches the furthest west, stretching even to the Himalayas up to 3200 m.

Habitat:—Typically rich mesic forests, deciduous or mixed, or coves, often on slopes, sometimes near riverbanks. Some species may inhabit somewhat acidic soils, e.g., *Rhododendron* thickets (*Trillium erectum, T. simile, T. vaseyi*). *Trillium hibbersonii* grows on rocky sea cliffs in scant, acidic soils. *Trillium channellii* is exceptional in inhabiting volcanic plains near lakes.

Conservation:—Most Asian and a few North American species may be considered narrow endemics: *Trillium apetalon, T. channellii, T. ×hagae, T. hibbersonii, T. simile, T. smallii,* and *T. vaseyi.* Widespread *T. tschonoskii* is currently classified as EN (Endangered) by the IUCN Red List due to past and projected future population reduction, rarity across a fragmented distribution, high ethnobotanical demand and extensive habitat loss (Chauhan 2021).

Notes:—Hybridization is thought to be common in this subgenus and may be a cause of taxonomic uncertainty (Barksdale 1938, Kurabayashi 1958, Haga *et al.* 1974, Case & Case 1997, Kubota *et al.* 2006, Millam 2006, Stoehrel 2010). Notably, *Trillium ×hagae* is the hybrid between *T. camschatcense* and *T. tschonoskii* and typically occurs sporadically in populations alongside both parents (Haga *et al.* 1974, Samejima & Samejima 1987). It is reported to be a sterile, reoccurring triploid; however, it has given rise to a fertile, true-breeding hexaploid (Haga 1956). The hexaploid occurs after spontaneous chromosome doubling after hybridization and may be found in a few pure populations in eastern Hokkaido (Haga *et al.* 1974, Samejima & Samejima 1987, Case & Case 1997). The hexaploid is recognised as a species (referred to as *T. hagae*) by Case & Case (1997) and Samejima & Samejima (1962, 1987). The triploid may be distinguished from the hexaploid because it is more widespread with *gigas* features and a conical

ovary. Based on these traits, it is likely that the *T. hagae* originally described by Miyabe & Tatewaki (1936) was the triploid hybrid rather than the hexaploid. Further studies of the status of the hexaploid might warrant its description as a separate taxon. Other hybrids have been formally described from Japan: *T. apetalon* hybridizes with *T. tschonoskii* and *T. camschatcense* to form two sterile hybrids, *T.* ×*miyabeanum* Tatewaki and *T.* ×*yezoense* Tatewaki, respectively (Case & Case 1997). In addition, numerous varieties and forms have been described in this subgenus, some of which are likely the result of hybridization (Case & Case 1997).

Whereas North American *Trillium* species are diploid, Asian *Trillium* species are polyploid except for *T. camschatcense* (Haga & Channell 1982). Experimental crosses between *T. camschatcense* and North American *T. erectum* group species produced viable seeds; however, crosses between *T. camschatcense* and American species outside this group, including *T. grandiflorum* and sessile-flowered species, produced only abortive ovules (Haga & Channell 1982). This compatibility among species, similar morphology and the pollen exine structure of Asian species showing a close relationship to *T. erectum* (Takahashi 1983) provide additional support for the inclusion of Asian *Trillium* species in this subgenus.

An undescribed taxon from the mountains of northern Georgia and South Carolina (*Trillium* sp. 2 or "Amicalola Trillium" in Weakley (2020)), is under study by AF. *Trillium taiwanense* Ying (1989: 154) is not recognised here based on DNA evidence and morphological similarities to *Paris* (Farmer & Schilling 2002, Ying 1989). *Trillium tschonoskii* is likely the only *Trillium* present in Taiwan.

2. ***Trillium*** L. subgen. ***Callipetalon*** Lampley & E.E.Schill., *subgen. nov.*

Type:—*Trillium grandiflorum* (Michx.) Salisb.

This subgenus has solid green (not mottled) leaves, pedicellate flowers, and delicate petals aging pink that are erect and somewhat imbricate at the base, partly obscuring the ovary. The stigmas are typically less than or nearly equal to the stamens in height, and the anthers are longer than the filaments. It is similar to *Trillium* subgen. *Delostylis* Raf. but distinguished from it by the stigmas connate only at the base rather than united.

Included species: 3 (–6), *T. grandiflorum*, *T. nivale*, *T. ovatum*.

Etymology:—Greek *calli-* (beautiful) and *petalon* (petal), for the famously beautiful flowers with snow-white petals found in this *Trillium* clade.

Distribution:—North America. Two species occur in the eastern US: *Trillium nivale,* from the mid-Atlantic states westward to the central Great Plains states, and *T. grandiflorum,* which overlaps with much of the distribution of *T. nivale*, Minnesota to Nova Scotia south to northern Alabama. *Trillium ovatum* inhabits western US states north to southern Canada.

Habitat:—Rich deciduous or mixed woods, fields and floodplains (*Trillium grandiflorum*); limestone substrates, rocky areas and floodplain with gravel-sand soils (*T. nivale*); coniferous and mixed forests and along mountain streams (*T. ovatum*).

Conservation:—The three species are widespread; however, certain infraspecific taxa are not (*Trillium ovatum* var. *oettingeri* (Munz & Thorne 1973: 15) Case in Kiger *et al.* (2001: 201) occurs in the Salmon and Siskiyou Mts.; *T. ovatum* f. *maculosum* Case & Case (1997: 118) occurs in at least one county in California, although more populations have been informally reported).

Notes:—The members of this subgenus were all included in Gleason's (1906) *Trillium grandiflorum*-type morphological group, although he also included *Trillidium* and *Pseudotrillium*. *Trillium* subgen. *Callipetalon* is also distinguished by a unique exine ornamentation (Takahashi 1982).

Trillium crassifolium Piper (1899: 104), *T. scouleri, T. ovatum* var. *oettingeri*, *T. ovatum* var. *stenosepalum* Gates (1917: 61), and *T. ovatum* f. *maculosum* are widely considered to be synonyms of *T. ovatum,* although this is under review by ES (Case & Case 1997, Meredith *et al*. 2020a, NatureServe 2021).

3. ***Trillium*** subgen. ***Delostylis*** (Raf.) Rafinesque [as '*Delostylium*'] (1830: 97).

Type:—*Trillium stylosum* Nuttall (1818: 239) (≡*D. stylosum* (Nutt.) Rafinesque (1819b: 192), =*T. cernuum* Michaux (1803: 216), =*T. catesbaei* Elliott (1817: 429))

Homotypic synonym: *Delostylis* Rafinesque (1819a: 102). Type:—*D. cernuum* Rafinesque (1819a: 102)), *nom. illeg.* superfl. *Trillium stylosum* Nuttall (1818: 239). *Delostylis stylosum* (Nutt.) Rafinesque (1819b: 192)

Included species: 7 (–12), *Trillium catesbaei*; *T. georgianum* Farmer (2017: 287); *T. ozarkanum* Palmer & Steyermark (1935: 504); *T. persistens* Duncan (1971: 244); *T. pusillum*; *T. texanum* Buckley (1861: 443); *T. virginianum* (Fernald 1943: 397) Reed (1982: 279)

Geography:—South-eastern and south-central North America, from Maryland westward to Texas.

Habitat:—Acidic soils and rhododendron thickets, mixed woodland or mountain coves, flats along small streams (*Trillium catesbaei* and *T. persistens*). Low swampy woods, floodplain swamps, acidic soil (*T. pusillum* and *T. texanum*). Flatwoods over seasonally wet calcareous substrate (*T. georgianum*). Rocky, calcareous upland and occasionally floodplains (*T. ozarkanum*).

Conservation:—Federally listed as endangered, *Trillium persistens* is rare and occurs in four counties in northern Georgia and South Carolina (Meredith & Trillium Working Group 2019 2020b). The recently described *T. georgianum* is known from only one county in Georgia (Schilling *et al.* 2017).

Notes:—Stigmas 3, uniformly thin, united in a common style; petals somewhat thin-textured, margins undulate, venation not engraved, pink, or white aging to various pink shades; leaf shape trends toward more narrow (blade longer than wide; elliptic-ovate, ovate-lanceolate, or oblong) than those of species from the other pedicellate-flowered subgenera; ovary 6-angled.

Trillium georgianum, T. texanum, *T. ozarkanum*, and *T. virginianum* are considered by some as varieties of *T. pusillum*. Farmer (2007) proposed that five species in addition to these be elevated from varieties of the *T. pusillum* complex. *Trillium virginianum* is probably the most notable of this complex and the only member of the pedicellate clades with sessile to subsessile flowers.

4. ***Trillium*** subgen. ***Sessilia*** Rafinesque [as '*Sessilium*'] (1830: 97).

Type:—*Trillium longiflorum* Rafinesque (1830: 97), here designated (=*T. sessile* Linnaeus (1753: 340))

Homotypic synonyms: *Esdra* Salisbury (1866: 60). Type:—*Trillium sessile* Linnaeus (1753: 340)

Phyllantherum (Rafinesque in Schultes & Schultes 1830: 1497) Nieuwland (1913: 112), nom superfl. illeg. Type:—*Phyllantherum sessile* (L.) Nieuwland (1913: 112) (≡*T. sessile* Linnaeus)

Trillium subgen. *Phyllantherum* Rafinesque (1820: 72), nom. inval.

Trillium [unranked] *Phyllantherum* Rafinesque in Schultes & Schultes (1830: 1497). Type:—*T. sessile* Linnaeus.

Trillium subgen. *Phyllantherum* (Raf. in Schult. & Schult. f.) Freeman (1975: 2). Type:—*T. sessile* Linnaeus, lectotype designated by Freeman (1975).

Included species: 26 (–28), *Trillium albidum* Freeman (1975: 48); *T. angustipetalum* (Torrey 1857: 151) Freeman (1975: 55); *T. chloropetalum* (Torrey) Howell (1902: 661); *T. cuneatum* Rafinesque (1840: 133); *T. decipiens* Freeman (1975: 17); *T. decumbens* Harbison (1902: 158); *T. delicatum* Floden & Schilling (2019: 110); *T. discolor* Wray in Hooker (1831: t. 3097).; *T. foetidissimum* Freeman (1975: 31); *T. gracile* Freeman (1969: 289); *T. kurabayashii* Freeman (1975: 56); *T. lancifolium* Rafinesque (1840: 132); *T. ludovicianum* Harbison (1901: 23); *T. luteum* (Muhlenberg 1813: 38) Harbison (1901: 21); *T. maculatum* Rafinesque (1830: 103); *T. oostingii* Gaddy (2008: 383); *T. parviflorum* Soukup (1980: 330); *T. petiolatum* Pursh (1813: 244); *T. recurvatum* Beck (1826: 178); *T. reliquum* Freeman (1975: 21); *T. sessile* Linnaeus; *T. stamineum* Harbison (1901: 23); *T. tennesseense* Schilling & Floden (2013: 145); *T. underwoodii* Small (1897: 172); *T. viride* Beck (1826: 178); *T. viridescens* Nuttall (1835: 155).

Geography:—Disjunct in eastern and western North America.

Habitat:—Diverse, but mostly in sloping mixed woodlands on mesic, limestone soils, many in wooded intermittent floodplains.

Conservation:—Several species with restricted ranges: *Trillium delicatum, T. discolor, T. tennesseense, T. kurabayashii, T. oostingii* and *T. parviflorum*. Still others in this group have somewhat wider distributions but may be restricted to a single watershed. *Trillium lancifolium* is rare and endangered in its wide but scattered distribution. *Trillium reliquum* is a federally listed species; however, it is abundant enough to be classified NT (near threatened) and stable (Meredith *&* *Trillium* Working Group 2019 2020c).

Notes:—Sessile flowers, leaf variously mottled, petals mostly erect, margins entire, ovary 3- or 6-angled or -winged, stigmas 3, separate, linear or subulate.

Freeman refined our understanding of *Trillium* subgen. *Sessilia* (as *T.* subgen. *Phyllantherum*) in his significant taxonomic revisions, describing or elevating in rank seven species and naming eight colour forms (Freeman 1969, Freeman 1975, Freeman & Heineke 1987). He conceptualized three species groups within the subgenus based on morphology. Subsequently, Murray (1983, 1984) devised a lengthy classification scheme of the subgenus complete with a host of sections, subsections, series and subseries names. *Trillium cuneatum* and *T. lancifolium* appear to be species complexes (under study by JL).

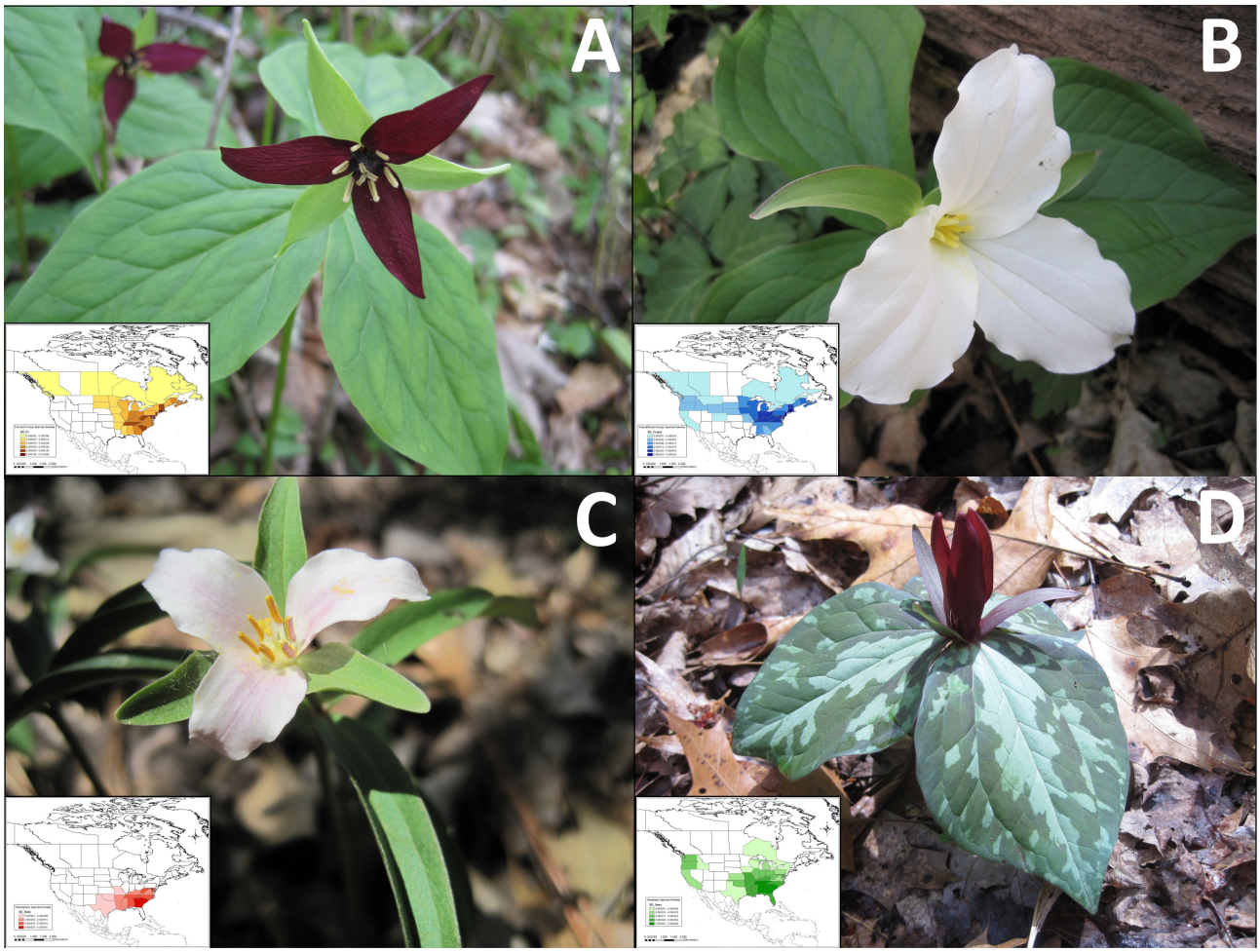

FIGURE 1. Representative species of the four *Trillium* subgenera. A. *Trillium erectum* (*T.* subgen. *Trillium*). B. *Trillium grandiflorum* (*T.* subgen. *Callipetalon*). C. *Trillium georgianum* (*T.* subgen. *Delostylis*). D. *Trillium cuneatum* (*T.* subgen. *Sessilia*). Inset maps show the North American distribution of each subgenus. Darker colours represent higher *Trillium* species density per state/province (species/area km^2). Photographs and maps by JL.

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