

PHYTOLOGIA

An international journal to expedite plant systematic, phytogeographical
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A TAXONOMIC CONSPECTUS OF NORTH AMERICAN *DELPHINIUM*

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ABSTRACT

A summary of subsectional groupings in North American *Delphinium* is provided. Nomenclatural adjustments are made so that the names can be used in the upcoming Volume 3 of *The Flora of North America* (Morin *et al.*). Six new taxa are described and three new combinations are made. Also included are a key to subsections of *Delphinium* in North America and keys to species within subsections.

KEY WORDS: *Delphinium*, Ranunculaceae, North America, taxonomy, nomenclature

INTRODUCTION

The forthcoming Volume 3 of *The Flora of North America* (Morin *et al.*) includes the treatment of *Delphinium*. A total of 61 species are recognized in that treatment. These are distributed among ten subsections. With the exception of subsection *Elata* (not native to North America), all of these subsections belong to section *Delphinastrum* of subgenus *Delphinium* (*sensu* Warnock 1993). Six new taxa (two subsections, two species, and two subspecies) are described. In addition, three new combinations are formed. A generic description is included in order to provide context for the subsectional and species descriptions. Several descriptive terms are used in somewhat unusual senses in descriptions. These terms are defined in a brief glossary.

A key to subsections of North American *Delphinium* is presented, as are keys to North American species within subsections, and keys to subspecies for species with newly recognized subspecies. Keys found herein differ somewhat from those to be published in *The Flora of North America*. Differences between the alternate keys are due to inclusion here of some nonmorphological key characteristics (not allowed in the flora format) and reordering of some key characters in multicharacter couplets. Order of characters within multicharacter couplets here is based on effectiveness of separation (most effective character first), while that in the flora is determined by ease of observation (most easily observed first). Since many of the phylogenetically most useful characters are not always observable on all specimens, all keys resort at least in part, to artificial means for separation of taxa.

DELPHINIUM L., *Species Plantarum* 530. 1753.

Perennial herbs, synoecious, protandrous. Roots usually coarsely parted, each with threadlike divisions distally (root sizes in descriptions refer to coarse parts and do not include threadlike extensions). Stems erect, usually unbranched below inflorescences. Leaves cauline and/or basal, alternate, simple, petioled. Blades round to pentagonal or reniform, basal usually larger than cauline; blades palmately lobed \pm to petiole; lobes \pm mucronate, entire except sometimes apically crenate or lacerate, lobes of basal leaves wider and fewer in number than those of cauline leaves; petioles gradually to abruptly shorter upward on stem. Bracts (attached to peduncle) absent or leaflike. Inflorescences dense or open, terminal, 2-100+ flowered racemes, 5-40+ cm long; lateral branches usually absent, if present, then shorter than central; bracteoles (attached to pedicels) subopposite to subalternate. Flowers zygomorphic; sepals 5, usually bluish or purplish, white flowered individuals occur sporadically and usually rarely in most taxa, distinct, 4 \pm ovate to fusiform, upper 1 forms a hollow spur, simple white hairs may occur where sepals are exposed in bud; petals 4, distinct; upper 2 prolonged into spurs, enclosed in upper sepal, mostly white, sometimes colored on exposed surfaces, 12-30 mm long, not clawed, nectar bearing tissues inside narrow cone forming terminus of spurs, nectary scale absent; lower 2 petals clawed, distinct, claws and blades usually \pm perpendicular; claws usually white, \pm strap shaped, 3-8 mm long, sometimes with an enation near the base; blades colored \pm like sepals, \pm ovate, \pm divided from terminus, usually with curled hairs on adaxial blade surface; stamens 25-40, base expanded, staminodia absent; carpels 3(-5), distinct, ovules 8-20 per locule; style narrowly beaked. Fruits follicles, 3(-5), sessile, \pm curved-cylindric, veins prominent or not, styles not greatly modified, glabrous. Seeds dark brown to black although often appearing white because of air in seed coat cells, rectangular to crescent shaped, often \pm rough surfaced; cells usually elongate; cell margins usually smooth. $x=8$.

Ca. 300 species, North Temperate and Arctic, subtropical and Eastern Hemisphere tropical in mountains; 61 species in Western Hemisphere north of México, another eight in México.

Isolating mechanisms in *Delphinium* appear to be primarily ecological, geographic, and/or temporal. Where these distinctions are disrupted, introgression often occurs. Natural hybridization occurs regularly among certain taxa, particularly in areas of disturbance (*i.e.*, roadcuts, drainage ditches, clearcuts, etc.). The more common and easily recognized hybrids are included in the keys.

Unless otherwise noted, descriptions and key leads refer to (and work best with) fresh material. Some features may be significantly altered by pressing, but can usually be determined with a certain amount of effort and experience, even from herbarium sheets.

GLOSSARY TO TERMS AS USED IN KEYS AND DESCRIPTIONS (For those used in a less than typical sense)

arched pubescence—composed of hairs more than 1 mm long, curved to complete more than 180° of arc along length of hair.

ascending pedicels/petioles—diverging from vertical at an angle of less than 40°.

- curled pubescence-composed of hairs more than 1 mm long, curved to complete more than 360° of arc along length of hair; found only on blade of lower petals.
- dense inflorescence-at least some flowers in fresh material touch one another on the same branch (vs. open inflorescence).
- enlarged buds-stem buds at least 3 mm long that form on rootstocks as much as one year before elongation; these are white and easily seen in fresh material, but dark and shriveled when dried.
- glandular pubescence-composed of hairs swollen in lower 1/3 to 1/2.
- leaf lobe-a lobe with defining clefts at least 80% as deep as radius of leaf blade.
- long pubescence-composed of hairs more than 1 mm long, usually perpendicular to surface where attached.
- open inflorescence-flowers on a single branch do not touch one another in fresh material (vs. dense inflorescence).
- seed coat cells elongate-cells having the shape of a tapered cylinder.
- seed coat cells short or blocky-cells having a shape \pm proportional to a brick.
- sepals erect-sepals point forward, \pm extending axis of spur.
- sepals reflexed-sepals fold backward, along axis of spur.
- sepals spreading-sepals oriented \pm perpendicular to spur, each sepal usually \pm cupped, calyx thus forming a bowl shape.
- simple pubescence-composed of hairs less than 1 mm long, often appressed on surface.
- smooth cell margins-long edges of seed coat cells \pm parallel opposite margins of the same cell with no significant curves (vs. undulate cell margins).
- spreading pedicels/petioles-diverging from vertical at an angle of more than 40°.
- undulate cell margins-edges of seed coat cells meander and interlock with margins of adjoining cells (vs. smooth cell margins).

The following key distinguishes subsections of *Delphinium* found in North America. Order of treatment of subsections is based on presumed relationships (artificially linearized) based on morphological and physiological features.

KEY TO SUBSECTIONS OF NORTH AMERICAN *DELPHINIUM*

1. Roots very easily separated from stems, if not extracted with a digging tool, roots typically break cleanly from stems and are completely absent from herbarium specimens; inflorescences usually at least 3 \times wider at base than apex..... 2
2. Primary root segments \pm succulent, usually brittle; roots with a single primary segment (cormlike), or branched from within 1 cm of stem attachment. 10. *Delphinium* subsect. *Grumosa*
2. Primary root segments dry, braided, tough; major root branches usually at least 1 cm from stem attachment. 3
3. Fruits spreading; seeds ringed at chalazal end; inflorescences seldom more than 3 \times longer than wide. 9. *Delphinium* subsect. *Bicoloria*
3. Fruits erect; seeds not ringed at chalazal end; inflorescences seldom less than 3 \times longer than wide. 5. *Delphinium* subsect. *Subscaposa*
1. Roots not easily separable from stems, if not extracted with a digging tool, roots typically break raggedly, leaving a portion attached to the lower stems, \pm intact roots sometimes extracted from the ground simply by pulling the stems;

- inflorescences usually less than 3 × as wide at base than apex. Specimens completely lacking roots should be keyed here..... 4
4. Large (more than 3 mm long) buds present at anthesis on rootcrowns (one or more typically will be found at the base of specimens pulled from the ground); roots more than 20 cm long (often more than 50 cm long), rarely more than fragments of roots associated with herbarium specimens; stems usually 2 or more per root, more than 1 m tall (exceptional plants may be less than 0.5 m tall); basal leaves and lower stem leaves absent at anthesis; midstem leaves 5 or 7 lobed. 5
5. Lower petal blades less than 20% the length of lateral sepals; sepals never red or yellow. 1. *Delphinium* subsect. *Elata*
5. Lower petal blades more than 20% the length of lateral sepals, or sepals red or yellow. 6
6. Lower internodes similar in length to those of midstems; largest leaves found near midstems, gradually reduced upward; bracts (if present) similar to and gradually smaller than leaves. 2. *Delphinium* subsect. *Exaltata*
6. Lower internodes much shorter than those of midstems; largest leaves found near base of stems (sometimes absent at anthesis), often abruptly reduced upward; bracts (if present) markedly smaller and fewer lobed than leaves. 7
7. Inflorescences ± pyramidal; pedicels more than 2 cm long. 3. *Delphinium* subsect. *Wislizenana*
7. Inflorescences cylindric; pedicels less than 2 cm long. 8
8. Seed coat cells more than 3 × as long as wide; pedicels ascending... 4. *Delphinium* subsect. *Multiplex*
8. Seed coat cells less than 3 × as long as wide; pedicels spreading to ascending. 3. *Delphinium* subsect. *Wislizenana*
4. Large buds absent at anthesis from rootcrowns; roots usually less than 20 cm long (or completely absent from specimens), substantial portions of root often present on herbarium specimens; stems 1 per root, less than 1 m tall (exceptional plants may be more than 2 m tall); basal leaves and/or lower stem leaves often present at anthesis; midstem leaves 3 to many lobed. 9
9. Seeds adorned with wavy ridges visible without magnification; pedicels appressed-ascending; inflorescences symmetrical; plants not usually found in damp meadows or on stream banks..... 7. *Delphinium* subsect. *Virescens*
9. Seeds lacking wavy ridges (but may have other protrusions from surface) visible without magnification; if pedicels appressed-ascending (rarely occurs), then inflorescences secund and/or plants found in damp meadows or on stream banks. 10
10. Inflorescence rachis to midpedicel angles less than 30°; spurs often intersect inflorescence rachis. 11
11. Stems less than 60(-80) cm tall; pedicels closely ascending inflorescence rachis (straight); spurs often intersect inflorescence rachis..... 6. *Delphinium* subsect. *Depauperata*
11. Stems rarely less than 60 cm tall, if shorter, then pedicels remotely ascending (sigmoid); spurs sometimes intersect inflorescence rachis... 4. *Delphinium* subsect. *Multiplex*
10. Inflorescence rachis to midpedicel angles more than 30°; spurs rarely intersect inflorescence rachis (except sometimes near tips of spurs)..... 12

12. Lower internodes similar in length to those of midstems; basal rosettes absent; leaves monomorphic; largest leaves found near midstems, gradually reduced upward; bracts (if present) similar to and gradually smaller than leaves. 2. *Delphinium* subsect. *Exaltata*
12. Lower internodes much shorter than those of midstems; basal rosettes (often absent at anthesis) formed 3-28 weeks before stem elongation; leaves \pm dimorphic (rosette leaves with fewer and wider lobes than cauline leaves); largest leaves found near base of stem (sometimes absent at anthesis), often abruptly reduced upward; bracts (if present) markedly smaller and fewer lobed than leaves. 13
13. Roots completely absent from specimens containing stem base. 14
14. Fruits erect; seeds not ringed at chalazal end; inflorescences usually at least 4 \times as long as wide. 5. *Delphinium* subsect. *Subscaposa*
14. Fruits spreading; seeds ringed at chalazal end; inflorescences seldom more than 4 \times as long as wide. 15
15. Sepals red or yellow. 9. *Delphinium* subsect. *Bicoloria*
15. Sepals blue, purple, white, or pink. 16
16. Lowest pedicel less than 1/4 inflorescence length.
..... 10. *Delphinium* subsect. *Grumosa*
16. Lowest pedicel at least 1/4 inflorescence length. 17
17. Seed coat cell surfaces roughened.
..... 10. *Delphinium* subsect. *Grumosa*
17. Seed coat cell surfaces smooth. 18
18. Inflorescences at least 3 \times longer than wide.
..... 10. *Delphinium* subsect. *Grumosa*
18. Inflorescences less than 3 \times longer than wide. 19
19. Lateral sepals usually spreading (reflexed only in *D. antoninum* which has succulent leaves).
..... 9. *Delphinium* subsect. *Bicoloria*
19. Lateral sepals reflexed (succulent leaves never present). 10. *Delphinium* subsect. *Grumosa*
13. Roots (at least a vestige) present on specimens containing stem base or stem base not included in specimen. 20
20. Fruits spreading; seeds ringed at chalazal end. 21
21. Primary root segments \pm succulent, usually brittle; roots with a single primary segment (cornlike), or branched from within 1 cm of stem attachment. 10. *Delphinium* subsect. *Grumosa*
21. Primary root segments usually dry, braided, tough; major root branches usually at least 1 cm from stem attachment.
..... 9. *Delphinium* subsect. *Bicoloria*
20. Fruits erect; seeds not ringed at chalazal end. 22
22. Roots \pm succulent, not braided, usually less than 10 cm long, thin threadlike segments restricted to major segment termini. 23
23. Pedicels appressed-ascending.
..... 7. *Delphinium* subsect. *Virescens*
23. Pedicels spreading to ascending, but never appressed-ascending. 8. *Delphinium* subsect. *Echinata*
22. Roots dry, braided, usually more than 10 cm long, thin threadlike segments apparent nearly entire length, or stem base is not present on specimen. 24
24. Inflorescences \pm pyramidal; pedicels more than 3 cm long. 25

25. Sepals red..... 3. *Delphinium* subsect. *Wislizenana*
 25. Sepals blue, white, or yellow.....
5. *Delphinium* subsect. *Subscaposa*
 24. Inflorescences cylindric; pedicels less than 3 cm long..... 26
 26. Lowest bracts similar to (smaller than) leaves.....
 2. *Delphinium* subsect. *Exaltata*
 26. Lowest bracts distinctly smaller and fewer lobed than
 leaves, or absent. 27
 27. Seed coat cells more than 3 × longer than wide.
 4. *Delphinium* subsect. *Multiplex*
 27. Seed coat cells less than 3 × longer than wide..... 28
 28. Lower portions of stems pubescent with straight
 hairs; glandular hairs absent from pedicels;
 flowering commencing after 1 July (except *D.*
geyeri)..... 3. *Delphinium* subsect. *Wislizenana*
 28. Lower portions of stems glabrous or pubescent
 with arched hairs; glandular hairs present or absent
 on pedicels; flowering completed by 1 July.
5. *Delphinium* subsect. *Subscaposa*

1. *Delphinium* subsect. *Elata* W.T. Wang, Acta Bot. Sinica 10(2):81. 1962. TYPE:
Delphinium elatum L.

Roots 2-5 dm long, twisted fibrous, dry, 5-11 branched; stem buds enlarged, usually present throughout dormant season. Stems 2-8 per root, 7-22 dm tall, usually unbranched, elongation commences within 2 weeks of leaf initiation; base not narrowed, firmly attached to root. Leaves cauline, blade shape and lobing similar throughout, largest at or slightly below middle of stem, gradually reduced into bracts; petioles ascending. Inflorescences narrowly pyramidal to cylindric, 20-100 flowered, usually 3-8 flowers/5 cm, ± dense; pedicels spreading-ascending, usually less than 3 cm long. Bracts ± similar to leaves but smaller. Fruits erect. Seeds rectangular to crescent shaped, 1.5-3.5 mm long × 1.2-2.5 mm wide, not ringed at chalazal end, wing margined; seed coats sometimes with small irregular waves; cells elongate; cell margins smooth. Flowering March to November, more than eight weeks after snowmelt.

As circumscribed by Wang (1962), the subsection includes approximately 30 species. One of these (*Delphinium elatum*) is commonly cultivated in North America. As a perennial, *D. elatum* commonly persists for years near deserted homesites in the cooler parts (Canada, northern United States, Rocky Mountains) of North America, but is less common and normally grown as a garden annual in warmer areas (Florida, Texas).

2. *Delphinium* subsect. *Exaltata* N.I. Malyutin, Bot. Zhurn. (Moscow and Leningrad) 72(5):688. 1987. TYPE: *Delphinium exaltatum* W.T. Aiton.

Roots 1-8 dm long, twisted fibrous, dry, 4-15 branched; stem buds enlarged, usually present throughout dormant season. Stems (1-)3-8(-19) per root, (1-)8-15(-30) dm tall, usually unbranched, elongation commences within 2 weeks of leaf initiation; base not narrowed, firmly attached to root. Leaves cauline, blade shape

and lobing similar throughout, largest at or slightly below middle of stem, gradually reduced into bracts; petioles \pm ascending. Inflorescences cylindric (greatly shortened in some), (15-)25-90(-200+) flowered, usually 5-10 flowers/5 cm, \pm dense; pedicels \pm spreading, usually less than 2 cm long. Bracts \pm similar to leaves but smaller. Fruits erect. Seeds rectangular to crescent shaped, 1.5-3.5 mm long \times 1.2-2.5 mm wide, not ringed at chalazal end, wing margined or not; seed coat cells \pm aggregated into small irregular waves or ripples; cells elongate; cell margins smooth. Flowering in late June-October, more than eight weeks after snowmelt.

Species 14+; twelve species in North America north of México, an additional one in México, and at least one and probably more in Asia. *Delphinium brachycentrum* Ledeb. is found on both sides of the Bering Sea.

Members of *Delphinium* subsect. *Exaltata* are characteristically found in areas of high altitude and/or latitude in which length of growing season is uncertain due to temperature and snowpack conditions. In most plants, growth continues until a killing freeze at the end of summer.

Members of *Delphinium* subsect. *Exaltata* are the typical "tall larkspurs" of poisonous plant literature. Their abundance on some ranges, combined with their large size and toxicity make them significant sources of livestock poisoning. Several of the species (*D. andesicola* Ewan, *D. californicum* Torrey & A. Gray, *D. glaucum* S. Wats., *D. novomexicanum* Wooton, *D. robustum* Rydb., *D. sapellonis* Tidestr., and the Mexican *D. valens* Standl.) in this subsection form a tightly knit group in which the degree of difference between members of the group and patterns of variation within the members appear largely determined by the degree and length of isolation in the various mountain ranges where the plants are found.

KEY TO SPECIES OF DELPHINIUM SUBSECT. EXALTATA

1. Leaves present on lower 20% of stems at anthesis..... 2
 2. Lateral sepals acute at apex; Alaska, Yukon, N.W.T.; elevation under 2000 m. *D. brachycentrum*
 2. Lateral sepals rounded at apex; Colorado, New Mexico; elevation above 2000 m..... 3
 3. Stems less than 30 cm tall; plants of alpine regions..... *D. alpestre* Rydb.
 3. Stems more than (45-)70 cm tall; plants of subalpine and below..... *D. ramosum* Rydb.
1. Leaves absent from lower 20% of stems at anthesis..... 4
 4. Sepals brownish or yellowish..... 5
 5. Buds brownish or yellowish; sepals becoming progressively more brown or yellow with age..... *D. sapellonis*
 5. Buds purple; at least some sepals fading to brown while on the plant. *D. novomexicanum*
 4. Sepals blue or purple (rarely white or pink) not brownish or yellowish..... 6
 6. Hairs in inflorescences glandular..... 7
 7. Inflorescences more than 3 \times longer than broad. *D. barbeyi* \times *D. glaucum* (= *D. occidentale*)
 7. Inflorescences less than 3 \times longer than broad.... *D. barbeyi* (Huth) Huth
 6. Hairs in inflorescences (if present) not glandular..... 8
 8. Midcauline leaf lobes less than 3 \times as long as wide. 9
 9. Sepals bluish to light lavender; 3-7 leaf lobes; east of the Great Plains. *D. exaltatum*

9. Sepals lavender to white; 3-15 leaf lobes; coastal California.
 *D. californicum* Torrey & A. Gray
8. Midcauline leaf lobes more than 3 × as long as wide (neither east of the
 Great Plains nor coastal California)..... 10
10. Leaves laciniate, lobe tips acuminate..... 11
11. Spurs blunt tipped; Arizona. *D. andesicola*
11. Spurs pointed; New Mexico, Colorado..... 12
12. Sepals dark blue; northern New Mexico, southern Colorado...
 *D. robustum*
12. Sepals purple; southern New Mexico..... *D. novomexicanum*
10. Leaves seldom laciniate, lobe tips not acuminate. 13
13. Entire plant finely, evenly puberulent. *D. ramosum*
13. Entire plant glabrous, or if pubescent, then only in inflorescences.
 14
14. Rarely more than 25 flowers per plant; plants of shallow rocky
 soil on steep slopes; sepals blue; Idaho, Montana, Wyoming. .
 *D. glaucescens* Rydb.
14. Rarely fewer than 25 flowers per plant; plants from deeper
 soils on usually gentler slopes; sepals purple, lavender, or
 white; widespread. *D. glaucum*
3. *Delphinium* subsect. *Wisliziana* M.J. Warnock, Madroño 31(4):243. 1984.
 TYPE: *Delphinium wislizeni* Engelm.

Roots (0.5-)1.5-2.4(-8.0) dm long, twisted fibrous, dry to fleshy, 3-8 branched; enlarged stem buds usually absent during dormant season. Stems 1(-4) per root, (3-) 5-9(-12) dm tall, usually unbranched, elongation delayed 2-10 weeks after leaf initiation; base usually not narrowed, firmly attached to root. Leaves basal and cauline, largest near base of stem, usually abruptly smaller on upper stems; basal leaf blades more rounded and with fewer, wider lobes than cauline leaves; lower petioles spreading, cauline ascending. Inflorescences cylindrical to narrowly pyramidal, (4-)6-20(-50) flowered, open to dense, usually 2-9 flowers/5 cm; pedicels spreading to ascending, often more than 2 cm long. Bracts usually smaller and fewer lobed than leaves. Fruits erect. Seeds rectangular to crescent shaped, 2.0-3.5 mm long × 1.3-2.5 mm wide, not ringed on chalazal end, wing margined or not; seed coats ± covered with small irregular waves; cells short, margins usually smooth. Flowering late May to October, more than eight weeks after snowmelt.

Species twelve; five species in North America (north of México), seven more (*Delphinium bicornutum* Hemsl., *D. calcar-equisitis* Gentry, *D. pedatisectum* Hemsl. *D. subscaudens* Ewan, *D. tenuisectum* Greene, *D. viride* Standl., and *D. wislizeni*) in México. *Delphinium cardinale* Hook. and *D. scopulorum* A. Gray grow on both sides of the México/United States border.

Delphinium subsect. *Wisliziana* comprises a group of species found in the mountains of México and mountains of the dry regions of the western United States. Their growth and reproductive success tends to be limited by dependence on summer rains (and stored moisture from snowmelt) rather than controlled by freezing temperatures as in *D.* subsect. *Exaltata*.

KEY TO SPECIES OF *DELPHINIUM* SUBSECT. *WISLIZENANA*

1. Sepals red.....*D. cardinale*
1. Sepals bluish or purplish, not red (rarely white, extremely rarely pink)..... 2
 2. Flowers \pm bright blue, sepals with a lighter median line abaxially; leaves light green, veins obscure; leaf lobe apex gradually tapering to a point..... 3
 3. Flowering in mid to late summer; leaves sparsely pubescent; stems more than (40-)60 cm tall.....*D. stachydeum* (A. Gray) Tidestr.
 3. Flowering early to mid summer; leaves densely pubescent; stems less than 60(-80) cm tall.....*D. geyeri* Greene
 2. Flowers not bright blue (or if bright blue, then lower stems glabrous), sepal color \pm uniform; leaves dark green (at least adaxially), veins prominent; leaf lobe apex abrupt (although usually mucronate)..... 4
 4. Midstems and leaves pubescent; sepals bluish purple.....
.....*D. geraniifolium* Rydb.
 4. Midstems and leaves glabrous to subglabrous; sepals bright blue.....
.....*D. scopulorum*
4. *Delphinium* subsect. *Multiplex* M.J. Warnock, subsect. nov. TYPE: *Delphinium multiplex* (Ewan) C.L. Hitchc. in C.L. Hitchc. et al.

Delphinio subsect. *Exaltatae* N.I. Malyutin similis sed differt foliis amplicissimis prope basim caulium (vs. prope midcaulem) et foliis caulinis abrupte (vs. gradatim) sursum deminutis. *Delphinio* subsect. *Wislizenanae* M.J. Warnock similis sed differt caulibus elongatis 1-3 hebdomades (vs. 2-10 hebdomades) post initio foliorum et gemmis caulinis dormientibus auctis plerumque praesentibus (vs. plerumque absentibus in statu dormienti).

Roots (0.5-)1.0-4.0(-5.0) dm long, twisted fibrous, dry to fleshy, 2-6 branched; stem buds enlarged, sometimes present during dormant season. Stems 1-4(-8) per root, (1-)2-7(-12) dm tall, usually unbranched, elongation delayed 1-3 weeks after leaf initiation; base usually not narrowed, firmly attached to root. Leaves basal and cauline, largest near base of stem, usually abruptly smaller on upper stem; basal leaf blades more rounded and with fewer, wider lobes than cauline leaves; lower petioles \pm spreading, cauline ascending. Inflorescences cylindric, (2-)6-15(-60) flowered, dense to open, usually 3-12 flowers/5 cm; pedicels ascending, usually less than 2 cm long. Bracts usually markedly smaller and fewer lobed than leaves. Fruits erect. Seeds rectangular to crescent shaped, 1.8-3.0 mm long \times 1.3-2.5 mm wide, not ringed at chalazal end, wing margined or not; seed coat cells \pm aggregated into small irregular waves or ripples; cells elongate, margins smooth. Flowering June to August, more than six weeks after snowmelt.

As currently circumscribed, *Delphinium* subsect. *Multiplex* contains four species, all of which are endemic to North America. *Delphinium* subsect. *Multiplex* is most closely related to subsect. *Wislizenana*, but may be distinguished by the shorter time from growth initiation to stem elongation and usual presence of enlarged stem buds during the dormant season. *Delphinium* subsect. *Multiplex* is morphologically similar to subsect. *Exaltata*, but can be separated on the basis of location of largest leaves near base of stem and abrupt reduction in leaf size upward on stems of subsect. *Multiplex*. In subsect. *Exaltata* the largest leaves near midstem and gradually reduced in size upward on stems.

Species of *Delphinium* subsect. *Multiplex* are found in the mountains of the western United States, where they grow and flower in midsummer in sites provided with moisture originating as snowmelt from the previous winter. Their growing season is typically limited more often by reduction in available moisture later in the year than by freezing temperatures.

KEY TO SPECIES OF *DELPHINIUM* SUBSECT. *MULTIPLEX*

1. Sepals yellow or yellowish. *D. viridescens* Leiberg
 1. Sepals bluish or purplish, not yellow or yellowish (sometimes white or lavender)..
..... 2
 2. Green leaves usually absent from lower 20% of stem at anthesis. . . *D. multiplex*
 2. Green leaves present in lower 20% of stem at anthesis. 3
 3. Bracteoles less than 4 mm long; spurs 9-12 mm long; pedicels 0.3-1.5(-2.5)
cm long; sepals white to light blue.
 - *D. inopinum* (Jeps) F.H. Lewis & Epling
 3. Bracteoles more than 4 mm long; spurs 11-22 mm long; pedicels 1-4(-15) cm
long; sepals dark blue..... *D. polycladon* Eastw.
5. *Delphinium* subsect. *Subscaposa* Ewan, Bull. Torrey Bot. Club 63:330. 1936.
LECTOTYPE (here designated): *Delphinium scaposum* Greene.

Ewan (1936) based *Delphinium* subsect. *Subscaposa* on Huth's (1895) description of *Delphinium* tribus *Subscaposa*. Since Huth's combination is invalid (use of tribus as an infrageneric category), Ewan was not required to parenthetically cite Huth. However, since Huth's combination was effectively published and Ewan directly referred to it in his recognition of *D.* subsect. *Subscaposa*, Huth's Latin description of the taxon serves for nomenclatural purposes. Unfortunately, neither Huth nor Ewan designated a type for *Subscaposa*. Nor did Ewan (1942) mention a type in a subsequent treatment of *D.* subsect. *Subscaposa*. The current choice was made from among those taxa included by both previous workers.

Roots (0.4-)1-3(-4) dm long, fibrous, twisted, dry, 3-8(-12) branched; stem buds minute. Stems 1(-3) per root, (2-)6-11(-17) dm tall, unbranched, elongation delayed 4-10 weeks after leaf initiation; bases often narrowed, firmly attached to root. Leaves basal and cauline, largest near base of stem, often abruptly smaller on upper stem; basal leaf blades more rounded and with fewer, wider lobes than cauline leaves; lower petioles spreading, cauline ascending. Inflorescences cylindrical to narrowly pyramidal, \pm open, (4-)6-25(-90) flowered, usually 4-8 flowers/5 cm; pedicels spreading to ascending, usually less than 2 cm long. Bracts markedly smaller and fewer lobed than leaves. Fruits erect. Seeds rectangular to crescent shaped, 1.3-3.3 mm long \times 1.1-2.3 mm wide, not ringed on chalazal end, \pm wing margined, seed coats usually lacking waves (present only in *Delphinium purpusii* Brandege); cells usually blocky, cell margins undulate or smooth. Flowering March to June, more than six weeks after snowmelt.

Species ten or more; ten in North America including México, possibly others in Asia. *Delphinium parishii* and *D. parryi* range into México in northern Baja California.

Delphinium subsect. *Subscaposa* is comprised of medium sized plants that depend on winter or spring rainfall (snowfall) for growth and reproduction. The

plants often overwinter as a basal rosette, with stem elongation beginning at onset of warm weather in the spring. The growing season for these plants may be cut short by lack of moisture. The plants typically remain dormant throughout the summer and autumn months.

KEY TO SPECIES OF SUBSECTION *SUBSCAPOSA*

1. Pedicels with yellowish glandular hairs (at least apically); sepals reflexed..... 2
 2. Sepals blue (white). *D. lineapetalum* Ewan
 2. Sepals rose to pinkish or yellow..... 3
 3. Flowers rose to pinkish..... *D. purpusii*
 3. Flowers yellow..... *D. xantholeucum* Piper
1. Pedicels lacking yellowish glandular hairs; sepals spreading or reflexed. 4
 4. Cells of seed coats with undulate margins visible at 10 \times ; mature fruits usually less than 3 \times as long as wide; plants of desert, grassland (sometimes with scattered trees) or shrubland..... 5
 5. Sepals rarely reflexed; stems more than (50-)60 cm tall--sepals white to light pink to very light blue, plants from grasslands, open woods..... *D. gypsophilum* Ewan
 5. Sepals (especially laterals) usually reflexed; stems less than 60(-100) cm. . . 6
 6. Plants of very alkaline, fine grained soils; lower petals white (contrasted with blue sepals)--lobe present at junction of blade and claw of lower petals. *D. recurvatum* Greene
 6. Plants of various soils, but not very alkaline, often coarse grained; lower petals concolorous with sepals (blue or white). *D. parishii* A. Gray
 4. Cells of seed coats with smooth margins visible at 10 \times ; mature fruits usually more than 3 \times as long as wide; plants of chaparral, woodlands and forest (rare in shrubland). 7
 7. Sepals strongly reflexed. *D. lineapetalum*
 7. Sepals not strongly reflexed..... 8
 8. Green leaves usually absent from lower 20% of stems at anthesis, if present, then lower stems and/or petioles covered with short, arched hairs. 9
 9. Lower leaf lobes less than 5 mm wide or plants from less than 10 km inland or less than 400 m elevation..... *D. parryi* A. Gray
 9. Lower leaf lobes 5 or more mm wide and plants from more than 10 km inland and more than 400 m elevation. *D. umbracolorum* \times *D. parryi*
 8. Green leaves usually present in lower 20% of stems at anthesis; lower stems and petioles glabrous to subglabrous (straight hairs). 10
 10. Lower leaf lobes less than 4 mm wide..... *D. andersonii* A. Gray
 10. Lower leaf lobes more than 4 mm wide. 11
 11. Cauline leaves gradually smaller and more common than basal leaves..... *D. umbracolorum* F.H. Lewis & Epling
 11. Cauline leaves abruptly smaller and rarer than basal leaves. *D. scaposum*

7. *Delphinium* subsect. *Depauperata* M.J. Warnock, subsect. nov. TYPE: *Delphinium depauperatum* Nutt.

Delphinio subsect. *Virescens* M.J. Warnock similis sed differt radicibus fibrosis (vs. fasciculatis) et paginis seminum exasperatis (vs. undulatis). *Delphinio* subsect. *Multiplex* M.J. Warnock similis sed differt plantis minoribus, radicibus dormientibus auctis absentibus (vs. praesentibus, et caulibus elongatis 2-8 hebdomades (vs. 1-3 hebdomades) post initio foliorum.

Roots 0.2-1.0(-1.5) dm long, twisted fibrous, dry to fleshy, 2-8 branched; stem buds minute. Stems 1(-2) per root, usually unbranched, elongation delayed 2-8 weeks after leaf initiation; base usually not narrowed, firmly attached to root. Leaves basal and cauline, largest near base of stem, usually abruptly smaller on upper stem; basal leaf blades more rounded and with fewer, wider lobes than cauline leaves; lower petioles \pm spreading, cauline ascending. Inflorescences cylindric, dense to open, usually 1-10 flowers/5 cm; pedicels ascending, usually less than 2 cm long. Bracts markedly smaller and fewer lobed than leaves. Fruits erect. Seeds rectangular to crescent shaped, 1.3-2.3 mm long \times 0.8-1.4 mm wide, not ringed on chalazal end, \pm wing margined; seed coats lack waves; cells elongate, margins smooth. Flowering May to July, more than six weeks after snowmelt.

As currently circumscribed, *Delphinium* subsect. *Depauperata* consists of three species, all endemic to North America. Specimens of several Asian species have been seen, and these may fit within *D.* subsect. *Depauperata*, but further study is required to make that determination.

Delphinium subsect. *Depauperata* appears most closely related to *D.* subsect. *Multiplex*. Plants of the former are much smaller and tend to flower earlier than those of the latter. *Delphinium* subsect. *Depauperata* is superficially similar to *D.* subsect. *Virescens*. Several of the more easily seen distinguishing features are enumerated in the diagnosis.

Species of *Delphinium* subsect. *Depauperata* depend on winter rains and melt from winter snows to support their growth and reproduction. Once that moisture is depleted, the plants become dormant until moisture again becomes available during the following growing season. The plants form a rosette early in the growing season, with stem elongation commencing sometime later.

KEY TO SPECIES OF DELPHINIUM SUBSECT. DEPAUPERATA

1. Margins of basal leaf measured less than 1 cm from blade base, demarcate less than 90° of arc when leaf is laid flat; sepal spurs oriented at an angle of 30-45° to the inflorescence axis.....*D. uliginosum* Curran
1. Margins of basal leaf measured less than 1 cm from blade base, demarcate considerably more than 90° of arc when leaf is laid flat; sepal spurs oriented at an angle near 90° to inflorescence axis. 2
2. Cauline leaf blades (at least most of them) exceeding the internodes, basal leaves absent at anthesis, 6 or more cauline leaves present at anthesis.....*D. distichum* Geyer

2. Cauline leaf blades much shorter than internodes, basal leaves usually present at anthesis, 5 or fewer cauline leaves present at anthesis.*D. depauperatum*

7. *Delphinium* subsect. *Virescens* M.J. Warnock, *nom. nov.* Based on: *Delphinium* species group *Caroliniana* Rydb., *Fl. Rocky Mts.* 308. 1917. Non *Delphinium* subsect. *Caroliniana* N.I. Malyutin (*nom. invalid.*--later homonym), Bot. Zhurn. (Moscow and Leningrad) 72(5):691. 1987. LECTOTYPE (here designated): *Delphinium virescens* Nutt.

A summary nomenclatural history of this subsection is appropriate to explain the current interpretation. Rydberg (1917, *in clave*) published *Delphinium* [sp. group]I. *Caroliniana* with neither rank nor type designated. Two species (*D. penardii* Huth and *D. virescens*) were included in the group. According to nomenclatural practice applicable to 1917, this constituted valid publication. Malyutin (1987) described *Delphinium* subsect. *Caroliniana* as a new subsection with *D. carolinianum* Walter (as "*D. carolineanum*") as the type, and included *D. penardii* and *D. virescens* within the subsection (these not treated as components or synonyms of *D. carolinianum* as in the present treatment). Malyutin did not reference Rydberg's earlier combination for *Caroliniana* even though he did use as a basionym for another new combination in the same paper, one of Rydberg's other combinations from the same key in which Rydberg published the *Caroliniana* combination. Since the *International Code of Botanical Nomenclature* ([ICBN] Greuter *et al.* 1994) requires that a lectotype be chosen for Rydberg's combination from among the species explicitly included, and since *D. carolinianum* is not among them, Rydberg's and Malyutin's combinations based on usage of the epithet *Caroliniana* are heterotypic. In such an instance, according to the ICBN (Art. 53.5), Malyutin's *Delphinium* subsect. *Caroliniana* is considered to be a later homonym of Rydberg's *Delphinium* [sp. group]I. *Caroliniana*. In order to minimize future confusion, the new name selected for the currently recognized taxon is derived from the epithet for the lectotype.

Roots, 0.3-0.8(-1.5) dm long, fusiform, fascicled, \pm fleshy, 2-8 branched; stem buds minute. Stems 1(-2) per root, (1.5-)4.0-9.0(-15.0) dm tall, usually unbranched, elongation delayed 4-16 weeks after leaf initiation; base not narrowed, firmly attached to root. Leaves basal and cauline, largest near base of stems, others often abruptly smaller on upper stems; basal petioles spreading, cauline petioles ascending; basal leaf blades more rounded and with fewer, wider lobes than cauline leaves. Inflorescences cylindrical, (4-)6-35(-98) flowered, \pm dense, usually with 3-8 flowers /5 cm; pedicels appressed ascending, usually less than 2 cm long. Bracts markedly smaller and fewer lobed than leaves. Fruits erect. Seeds crescent shaped to obpyramidal, 1.5-2.5 mm long \times 0.8-1.8 mm wide, not ringed at chalazal end, not wing margined; seed coats with prominent multicellular wavy ridges; surface cells \pm blocky, margins straight. Flowering February to July, more than six weeks after snowmelt.

Three species, endemic to North America (including northern México). Each of the three species (only subsp. *vimineum* in *Delphinium carolinianum*) occur on both sides of the México/United States border. No apparent close relatives outside North America.

The nearest relative of *Delphinium* subsect. *Virescens* within North America appears to be *D.* subsect. *Echinata*. While these two subsections are similar in many respects, the seeds of *D.* subsect. *Virescens* are distinctive.

Delphinium subsect. *Virescens* is comprised of medium sized plants that depend on spring rainfall for growth and reproduction. The plants often overwinter as a basal rosette, with stem elongation beginning at onset of warm weather in the spring. The growing season for these plants may be cut short by lack of moisture, or may be extended into summer by greater than normal rainfall. The plants typically remain dormant throughout the summer and autumn months.

KEY TO SPECIES OF *DELPHINIUM* SUBSECT. *VIRESCENS*

1. Sepals light lavender, reflexed; leaves grayish pubescent with short hairs.....
..... *D. wootonii* Rydb.
 1. Sepals white to blue, or if lavender, then not reflexed and leaves not grayish pubescent 2
 2. Plants with a combination of midcauline leaf blades round with at least 7 lobes more than 30% the length of longest lobe; sepals blue; petiole immediately below inflorescence at least 1 cm long.....*D. madrense* S. Wats.
 2. Plants deviating in at least one feature from the combination of midcauline leaf blades round with at least 7 lobes more than 30% the length of longest lobe; sepals blue; petiole immediately below inflorescence at least 1 cm long.....
.....*D. carolinianum*
8. *Delphinium* subsect. *Echinata* (Ewan) N.I. Maljutin, Bot. Zhurn. (Moscow and Leningrad) 72(5):689. 1987. BASIONYM: *Delphinium* series *Echinatae* Ewan, Bull. Torrey Bot. Club 69(2):139. 1942. TYPE: *Delphinium hansenii* (E. Greene) E. Greene.

Roots 0.3-0.8(-3.0) dm long, fascicled, dry to fleshy, 3-9(-20) branched; stem buds minute. Stems 1(-3) per root, (2-)6-11(-17) dm tall, unbranched, elongation delayed 4-10 weeks after leaf initiation; base usually not narrowed, firmly attached to root. Leaves basal and cauline, largest near bases of stems, often abruptly smaller on upper stem; basal leaf blades more rounded and with fewer, wider lobes than cauline leaves. Inflorescences cylindric, (4-)6-25(-90) flowered, dense to open, usually 2-11 flowers/5 cm; pedicels ascending, usually less than 2 cm long. Bracts markedly smaller and fewer lobed than leaves. Fruits erect. Seeds \pm rectangular, 1.5-2.5 mm long \times 0.8-1.5 mm wide, not ringed at chalazal end, \pm wing margined; seed coats not wavelike (may have elongate prism shaped processes); cells \pm blocky, margins smooth or undulate. Flowering March to early July, more than six weeks after snowmelt.

Species four; endemic to western North America. Similar in most features to *Delphinium* subsect. *Virescens*. See discussion under that subsection for differentiating characteristics.

Delphinium subsect. *Echinata* is comprised of medium sized plants that depend on winter rainfall for growth and reproduction. The plants overwinter as a basal rosette, with stem elongation beginning at onset of warm weather in the spring. The growing season for these plants may be cut short by lack of moisture. The plants remain dormant throughout the summer and autumn months.

KEY TO SPECIES OF *DELPHINIUM* SUBSECT. *ECHINATA*

1. Lower petioles glabrous to puberulent with short (less than 0.5 mm long) appressed and/or curved hairs..... 2
 2. Plants atypical in sepal color and/or stem pubescence for the population in which they occur, stem bases puberulent with short curved hairs; stem bases often reddish..... *D. hesperium* subsp. *pallescens* × *D. parryi*
 2. Plants typical in sepal color and stem pubescence for the population in which they occur, stem base glabrous to pubescent with short straight hairs..... *D. hesperium* A. Gray
 1. Lower petioles pubescent with long (more than 0.5 mm long), straight, spreading hairs..... 3
 3. Seeds echinate, appearing fuzzy to the naked eye; lateral sepals 13 mm long or shorter; usually more than 12 flowers on main inflorescence branch..... *D. hansenii* (Greene) Greene
 3. Seeds not echinate, surface appearing ± smooth to the naked eye; lateral sepals 10 mm long or longer; usually fewer than 12 flowers on main inflorescence branch..... 4
 4. Stem bases longitudinally ridged..... *D. hesperium*
 4. Stem bases not longitudinally ridged..... 5
 5. Margins of lower petals glabrous; bracteoles usually 7 mm or more from sepals; sepal spurs often downcurved for more than 3 mm at apex..... *D. hutchinsoniae* Ewan
 5. Margins of lower petals ciliate; bracteoles usually 7 mm or less from sepals; sepal spurs straight or downcurved for less than 3 mm at apex.... *D. variegatum* Torrey & A. Gray
9. *Delphinium* subsect. *Bicoloria* (Rydb.) N.I. Malyutin, Bot. Zhurn. (Moscow and Leningrad) 72(5):687. 1987. BASIONYM: *Delphinium* species group *Bicoloria* Rydb., *Fl. Rocky Mts.* 309. 1917. TYPE: *Delphinium bicolor* Nutt.

In the original publication of *Delphinium* subsect. *Bicoloria*, Malyutin cites the basionym as *D. sect. Bicoloria* Rydb., *Key Rocky Mount. Fl.*: 93. 1919. Even though Malyutin cited the second edition of Rydberg's work and Rydberg designated no taxonomic ranks for his infrageneric categories, these should be considered as bibliographic errors according to the current *ICBN* (Geuter *et al.* 1994).

Roots (0.5-)1.0-3.0(-4.0) dm long, diffuse fibrous, ± braided, dry, 2-9 branched; stem buds minute. Stems 1(-2) per root, (1-)2-4(-9) dm tall, usually unbranched, elongation delayed 2-6(-10) weeks after leaf initiation; base ± narrowed, ± tenuously attached to root. Leaves basal and cauline, round, shape and lobing similar throughout, largest near bases of stems, often abruptly smaller on upper stems; lower petioles spreading, cauline ascending. Inflorescences ± pyramidal, (2-)6-15(-40) flowered, open, usually 2-6 flowers/5 cm; pedicels spreading, usually more than 1.5 cm long. Bracts markedly smaller and fewer lobed than leaves. Fruits spreading. Seeds obpyramidal 1.6-2.9 mm long × 0.7-1.9 mm wide, ± ringed at chalazal end, usually wing margined; seed coats lack waves; cells elongate; cell margins smooth. Flowering May to August or within six weeks after snowmelt.

Species six; six species endemic to North America. *Delphinium* subsect. *Bicoloria* comprises a group of small spring flowering species, several of which are included in the group of "low larkspurs" from poisonous plant literature.

Species of *Delphinium* subsect. *Bicoloria* depend primarily on moisture from winter snows and rains to support their growth and reproduction. Once that moisture is depleted, the plants become dormant until the following growing season when either rains begin to fall or snow begins to melt.

The most consistent feature to differentiate *Delphinium* subsect. *Bicoloria* from *D.* subsect. *Grumosa* is the long fibrous root structure found in species of the former vs. the shorter more fascicled root structure of the latter.

KEY TO SPECIES OF *DELPHINIUM* SUBSECT. *BICOLORIA*

1. Sepals red or yellow. 2
 2. Sepals red, reddish or orange, not bright yellow.
 2. Sepals yellow, not red. *D. luteum* A. Heller
 1. Sepals usually bluish, not red or yellow (sometimes maroon, white, or pink). 3
 3. Flowers with maroon sepals; plants usually distinctly different individuals within populations and often with some degree of infertility. 4
 4. Leaf segments more than 5, 5 mm or less wide.
 4. Leaf segments 5 or fewer, more than 5 mm wide. 5
 5. Lower stems pubescent. *D. nudicaule* × *D. decorum*
 5. Lower stems glabrous. *D. nudicaule* × *D. patens*
 3. Flowers with blue or pink (not maroon) sepals; plants usually similar to other individuals in the population, usually fully fertile. 6
 6. Leaves mostly above lower 1/3 of stem; flowers usually more than 15/main inflorescence axis. *D. trolliifolium* × *D. nudicaule*
 6. Leaves mostly in lower 1/3 of stem; flowers usually fewer than 20/main inflorescence axis. 7
 7. Sepals pinkish; plants usually distinctly different individuals within populations and often with some degree of infertility. 8
 8. Plants in populations with red flowers; usually below 1500 m elevation. *D. nudicaule* × *D. trolliifolium*
 8. Plants in populations with blue flowers; usually above 1500 m elevation. *D. antoninum* × *D. nudicaule*
 7. Sepals blue; plants usually similar to other individuals within populations and fully fertile. 9
 9. Leaves ± succulent; clustered on lower 1/2 of stems. 10
 10. Lateral sepals reflexed. *D. antoninum* Eastw.
 10. Lateral sepals spreading. *D. glareosum* Greene
 9. Leaves not succulent; clustered on lower 1/2 of stem or not. 11
 11. Lower petal blade clefts less than 1/3 blade lengths. *D. bicolor*
 11. Lower petal blade clefts more than 1/3 blade lengths.
 - *D. basalticum* M.J. Warnock

Delphinium bicolor Nutt., J. Acad. Nat. Sci. Philadelphia 7:10. 1834. TYPE: UNITED STATES. Montana: on dry hills, near Flathead or Sailish River,

towards the south sources of the Columbia, 24 Apr 1833, *N.B. Wyeth s.n.* (P!);
Isotypes: K!, NY!, PH!.

Stems 1-4(-7) dm tall; base often anthocyanous, glabrous to puberulent. Leaves mostly in lower 1/3 of stem, round, glabrous to puberulent; basal (0-)2-7 at anthesis, sometimes anthocyanous abaxially, 2-4 cm long × 4-7 cm wide, petioles spreading, 4-8 cm long, glabrous to puberulent, 5-11 lobed, lobes 1-8 mm wide; cauline 3-6 at anthesis, 1-4 cm long × 1.5-7.0 cm wide, petioles ascending, 0.3-5.0 cm long, 3-19 lobed, lobes 1-3 mm wide. Inflorescences 3-12(-22) flowered, 5-17 cm long, open, 2-6 flowers/5 cm, usually unbranched; pedicels 1-4(-8) cm long, ± puberulent. Bracteoles subopposite, 2-7(-17) mm from flowers, 4-6(-8) mm long, green, sometimes white margined, lanceolate, puberulent. Sepals dark blue, puberulent, laterals usually spreading, 16-21 mm long × 6-12 mm wide, spurs straight to gently decurved, elevated 0-40° above horizontal, 13-23 mm long. Lower petal blades covering stamens, 7-12 mm long, clefts 0.1-3.0 mm deep; hairs sparse, short, most numerous on inner lobes below junction of blade and claw, white or yellow. Fruits (12-)16-22 mm long, 4.0-4.5 × as long as wide, usually puberulent. Seeds obpyramidal, 1.8-2.2 mm long × 0.7-1.2 mm wide, ringed at chalazal end, ± wing margined; cells elongate, surfaces ± smooth, shiny; cell margins smooth.

1. Sepals (especially in fresh material) dark blue to purple; plants from nonlimestone derived soils; lower petal clefts 2 mm deep or less. *D. bicolor* subsp. *bicolor*
1. Sepals (especially in fresh material) bright dark blue; plants from limestone derived soil; lower petal clefts at least 2 mm deep. *D. bicolor* subsp. *calcicola*

Delphinium bicolor Nutt. subsp. *bicolor*

Delphinium bicolor Nutt., J. Acad. Sci. Philadelphia 7:10. 1834. TYPE: UNITED STATES. Montana: on dry hills, near Flathead or Sailish River, towards the south sources of the Columbia, 24 Apr 1833, *N.B. Wyeth s.n.* (P!); Isotypes: K!, NY!, PH!. *Plectrornis bicolor* (Nutt.) Lunnell, Amer. Midl. Naturalist 4:362. 1916. - Flathead larkspur

Delphinium bicolor Nutt. var. *montanense* Rydb., Mem. New York Bot. Gard. 1:157. 1900. LECTOTYPE (Ewan 1945, p. 123): UNITED STATES. Montana: Powell Co., Deer Lodge, 1888, *F.W. Traphagen s.n.* (NY!); Isotype: PH!. *Delphinium bicolor* Nutt. forma *montanense* (Rydb.) Ewan, Univ. Colorado Stud., ser. D, Phys. Sci. 2:123. 1945. *Plectrornis bicolor* (Nutt.) Lunnell var. *montanense* (Rydb.) Lunnell, Amer. Midl. Naturalist 4:362. 1916.

Delphinium nuttallianum Pritz. in Walp. var. *pilosa* C.L. Hitchc. in C.L. Hitchc. et al., Vasc. Pl. Pacific NW 2:359. 1964. TYPE: UNITED STATES. Idaho: Lemhi Co., 7 mi E of Tendoy along Lemhi Pass Rd., near old mine tailings, 1 Jul 1957, *C.L. Hitchcock & C.V. Muhlick 21274* (WTU!).

Delphinium bicolor Nutt. forma *devriesii* B. Boivin, Nat. Can. 94:653. 1967. HOLOTYPE: CANADA. Alberta: S of Elkwater Lake Provincial Park, *B. DeVries 3182* (DAO).

Stems 1-4(-7) dm tall; base often anthocyanous, glabrous to puberulent. Leaves mostly in lower 1/3 of stem, round, glabrous to puberulent; basal (0-)2-7 at anthesis, sometimes anthocyanous abaxially, 2-4 cm long × 4-7 cm wide, petioles spreading,

4-8 cm long, glabrous to puberulent, 5-11 lobed, lobes 1-8 mm wide; cauline 3-6 at anthesis, 1-4 cm long \times 1.5-7.0 cm wide, petioles ascending, 0.3-5.0 cm long, 3-19 lobed, lobes 1-3 mm wide. Inflorescences 3-12(-22) flowered, 5-17 cm long, open, 2-6 flowers/5 cm, usually unbranched; pedicels 1-4(-8) cm long, \pm puberulent. Bracteoles subopposite, 2-7(-17) mm from flowers, 4-6(-8) mm long, green, sometimes white margined, lanceolate, puberulent. Sepals dark blue to purplish, puberulent, laterals usually spreading, 16-21 mm long \times 6-11 mm wide, spurs straight to gently decurved, elevated 0-40° above horizontal, 13-18 mm long. Lower petal blades covering stamens, 7-12 mm long, clefts 0.1-2.0 mm deep; hairs sparse, short, most numerous on inner lobes below junction of blade and claw, usually white. Fruits (12-)16-22 mm long, 4.0-4.5 \times as long as wide, usually puberulent.

Flowering late spring to early summer. Dry meadow edges, sage scrub; 600-3100 m elevation; southern Alberta, southeastern British Columbia, southwestern Saskatchewan, Idaho, Montana, northwestern Nebraska, western North Dakota, western South Dakota, and northern Wyoming.

Delphinium bicolor is closely related to *D. glareosum* but differs in its more narrowly lobed cauline leaves, shallower lower petal clefts, narrower fruits, earlier flowering, geographic distribution, and lower mean elevation of populations. Rydberg's *D. bicolor* var. *montanense* tends to have more pubescence and larger flowers, but it is otherwise typical and apparently fully intergradient with *D. bicolor* subsp. *bicolor*. Often referred to as one of the "low larkspurs" in poisonous plant literature, the plant is abundant on some ranges and produces some livestock poisoning.

***Delphinium bicolor* Nutt. subsp. *calicicola* M.J. Warnock & Vanderhorst, subsp. nov. TYPE: UNITED STATES. Montana: Stillwater Co., top of hill, grassland, calcareous soils, 16.5 mi S Jct. Bridger Creek Road and I-90 on Bridger Creek Road, 13 Jun 1983, M.J. Warnock 2819 (SHST!); Isotypes: to be distributed.**

Delphinio bicolori Nutt. subsp. *bicolori* similis sed differt sepalis obscuro-cyaneis (vs. obscuro-indigoticis vel purpurascensibus) 16-21 mm longis \times 9-12 mm lauis (vs. 16-21 mm longis \times 6-11 mm latis), calcaibus sepalorum 15-23 mm longis (vs. 13-18 mm longis), petalis inferi lamina fissa 2 mm vel plus in profunditate (vs. minus quam 2 mm in profunditate), et trichomatibus plerumque flavis (vs. plerumque albis).

Stems 1-3 dm tall; base often anthocyanous, glabrous to subglabrous. Leaves mostly in lower 1/3 of stem, round, glabrous to puberulent; basal 2-5 at anthesis, sometimes anthocyanous abaxially, 1.5-3.5 cm long \times 2.5-4.5 cm wide, petioles spreading, 4-8 cm long, glabrous to puberulent, 5-11 lobed, lobes 1-4 mm wide; cauline 3-6 at anthesis, 1-3 cm long \times 1.5-4.0 cm wide, petioles ascending, 0.3-5.0 cm long, 3-19 lobed, lobes 1-3 mm wide. Inflorescences 3-12 flowered, 5-13 cm long, open, 2-6 flowers/5 cm, usually unbranched; pedicels 1-4 cm long, \pm puberulent. Bracteoles subopposite, 2-5 mm from flowers, 4-6 mm long, green, lanceolate, puberulent. Sepals dark blue, puberulent, laterals usually spreading, 16-21 mm long \times 9-12 mm wide, spurs straight, elevated 10-40° above horizontal, 15-23 mm long. Lower petal blades covering stamens, 7-12 mm long, clefts 2-3 mm deep; hairs sparse, short, most numerous on inner lobes below junction of blade and

claw, usually yellow. Fruits 16-20 mm long, 4.0-4.5 × as long as wide, usually puberulent.

Flowering late spring to early summer (although usually somewhat later than the type subspecies where they are sympatric). Shortgrass prairie and grassy sagebrush on limestone outcrops (typically found in soils containing stones or large rocks at the surface); 1300-2100 m elevation; Montana.

In the field, *Delphinium bicolor* subsp. *calicicola* is readily distinguished from *D. bicolor* subsp. *bicolor* on the basis of its brighter colored, slightly larger flowers, and its edaphic preference. However, these differences are often not readily apparent from herbarium specimens. Specimens of this taxon misidentified as *D. geyeri* account for most reports of that species from Montana.

Delphinium basalticum M.J. Warnock, *spec. nov.* TYPE: UNITED STATES.

Oregon: Multnomah Co., steep N facing slope, basalt substrate, S of road, 0.1 mi W Oneonta Gorge on Old Columbia Highway, Mt. Hood National Forest, 22 May 1990, M.J. Warnock 8528 (SHST!); Isotypes: to be distributed. - Columbia Gorge larkspur

Delphinio glareoso E. Greene similis sed differt caulibus ac petiolis inferis plusminusve puberulis (vs. glabris vel glaucis), calcaribus sepalorum 14-18 mm longis (vs. 16-20 mm longis), petali inferi lamina fissa 4-5 mm in profunditate (vs. 2-4 mm in profunditate), et fructibus 3.5-4.0 plo longioribus quam latioribus (vs. 2.5-3.0 plo longioribus quam latioribus).

Stems 1 per root, 2.0-5.0(-6.5) dm tall, unbranched, elongation delayed 2-8 weeks after leaf initiation; base often anthocyanous, puberulent. Leaves basal and cauline, round, subglabrous; basal 1-4 at anthesis, green, darker adaxially, 4-6 cm long × 6-9 cm wide, 5-15 lobed, lobes 3-15 mm wide, petioles spreading, 9-15 cm long, subglabrous; cauline 2-5 at anthesis, 2-5 cm long × 5-8 cm wide, 7-19 lobed, lobes 1-12 mm wide, petioles 0-12 cm long, ascending. Inflorescences (2-)-6-16(-26) flowered, pyramidal, 8-22(-35) cm long, open, 2-5 flowers/5 cm, usually branched; pedicels spreading, 2-7 cm long, subglabrous. Bracts trifid to multifid, 1.5-5.0 cm long. Bracteoles subopposite, 4-12 mm from flowers, 3-7 mm long, green, linear, subglabrous. Sepals dark blue, subglabrous, laterals spreading, 15-21 mm long × 7-10 mm wide, spur straight to decurved, elevated 30-45° above horizontal, 14-18 mm long. Lower petal blades slightly elevated, ± exposing stamens, 7-9 mm long, clefts 4-5 mm deep; hairs centered and most common on inner lobe above cleft apex, yellow to white. Fruits spreading, 12-17 mm long, 3.5-4.0 × as long as wide, glabrous. Seeds obpyramidal, 2.2-2.5 mm long × 1.5-1.9 mm wide, ringed at chalazal end, ± wing margined; cells elongate, margins smooth, surfaces smooth, shiny. $n = 8$ (Sutherland 1967 [as *D. trolliiifolium*]).

Flowering in spring (early summer). Basaltic cliff faces, north and east facing slopes at the foot of cliffs; 200-500 m elevation; northwestern Oregon and southwestern Washington.

Most closely related to *Delphinium glareosum*, *D. basalticum* is distinguished by its lack of fleshy leaves, and absence of basal leaves at anthesis. Hybrids with *D. trolliiifolium* A. Gray are known.

10. *Delphinium* subsect. *Grumosa* (N.I. Malyutin) M.J. Warnock, *comb. nov.*
 BASIONYM: *Delphinium* sect. *Grumosa* N.I. Malyutin, Bot. Zhurn. (Moscow
 and Leningrad) 72(5):689. 1987. TYPE: *Delphinium menziesii* DC.

Roots 0.2-0.7(-1.6) dm long, cormlike to fascicled or fibrous, \pm fleshy, 1-5(-9) branched; stem buds minute. Stems 1(-2) per root, (1-)2-4(-9) dm tall, usually unbranched, elongation delayed 2-10 weeks after leaf initiation; base narrowed, tenuously attached to root. Leaves basal and cauline, shape and lobing similar throughout, largest leaves near base of stem, usually gradually smaller on upper stems; lower petioles spreading, cauline ascending. Inflorescences \pm pyramidal, (2-) 6-15(-40) flowered, open, usually 2-6 flowers/5 cm; pedicels spreading, usually more than 1.5 cm long. Bracts markedly smaller and fewer lobed than leaves. Fruits \pm spreading. Seeds obpyramidal, 1.5-2.7 mm long \times 0.7-2.0 mm wide, ringed at chalazal end, wing margined or not; seed coats usually lacking waves; cells elongate, margins smooth. Flowering March to early July, or within six weeks after snowmelt.

Species thirteen or more; thirteen in North America, possibly others in Asia.

Most similar to *Delphinium* subsect. *Bicoloria*, *D.* subsect. *Grumosa* has roots cormlike to fascicled or fibrous (vs. twisted fibrous), 0.2-0.7(-1.6) dm long, (vs. [0.5]1.0-3.0[-4.0] dm long). *Delphinium* subsect. *Grumosa* is an extremely difficult complex, with many variations in a number of morphological traits. Philosophical extremes in taxonomic approach to the complex are represented by the work of Sutherland (1967) in which the species recognized are large agglomerations, and that of Rydberg (1917) in which species epithets are used for some edaphic variants. The complex has been and continues to be a major source of confusion for identification of *Delphinium* in North America. Most of what are referred to as "low larkspurs" in poisonous plant literature refer to members of this subsection.

Delphinium subsect. *Grumosa* comprises a group of small spring flowering species. These species depend primarily on moisture from winter snows and rains to support their growth and reproduction. Once that moisture is depleted, the plants become dormant until the following growing season when either rains begin to fall or snow begins to melt.

KEY TO SPECIES OF *DELPHINIUM* SUBSECT. *GRUMOSA*

1. Sepals ochroleucous or pink, if white then white in most members of the population..... 2
2. Flowers with no trace of pink or lavender..... 3
 3. Spurs less than 12 mm long; sepals spreading to erect; lower petals usually blue or purple..... *D. nuttallii* A. Gray
 3. Spurs more than 11 mm long; sepals widely spreading; lower petals usually yellow..... 4
 4. Stems less than 60 cm tall; widest leaf lobe less than 1 cm wide.....
 *D. menziesii*
 4. Stems more than 60 cm tall; widest leaf lobe more than 1 cm wide.....
 *D. menziesii* \times *D. trolliifolium* = *D.* \times *pavonaceum* Ewan
2. Flowers (especially sepal spur) with some element of pink or lavender..... 5
 5. Stems less than 50(-70) cm tall; plants in population of individuals many of which have similar sepal color..... 6
 6. Seeds with nipple-like hairs on surface; east of the Great Plains.....

-*D. tricorne* Michx.
6. Seeds lacking nipple-like hairs; west of the Great Plains.
*D. nuttallianum* Torrey & A. Gray
5. Stems more than (40-)50 cm tall; plants with sepal color dissimilar from that of most other individuals in the population. 7
7. Plants in populations with red flowers.*D. nudicaule* × *D. trolliiifolium*
7. Plants in populations with blue flowers.*D. trolliiifolium* × *D. nudicaule*
1. Sepals bluish, not ochroleucus, if white, then only as sporadic individuals in a population (sometimes maroon or purple). 8
8. Flowers with maroon sepals; plants usually distinctly different individuals within populations and often with some degree of infertility. 9
9. Lower stems puberulent.*D. nudicaule* × *D. decorum*
9. Lower stems glabrous. *D. nudicaule* × *D. patens*
8. Flowers blue or bluish purple, rarely white or purple sepals; plants usually similar to other individuals in the population, usually fully fertile. 10
10. Leaves mostly above lower 1/3 of stem at anthesis; flowers usually more than 15/main inflorescence axis. 11
11. Inflorescences as wide as long or nearly so; Arkansas.
*D. newtonianum* Dw. Moore
11. Inflorescences at least twice as long as wide; west of the Great Plains. 12
12. Sepals light blue (or pinkish).*D. trolliiifolium* × *D. nudicaule*
12. Sepals dark blue to purplish blue. 13
13. Lobes of midstem leaves more than 6 mm wide; stems more than (40-)60 cm tall. 14
14. Leaf margins crenate. *D. bakeri* Ewan
14. Leaf margins ± incised. *D. trolliiifolium*
13. Lobes of midstem leaves less than 6 mm wide; stems less than 60(-90) cm tall. 15
15. Sepals bluish purple and often fading in press. ... *D. nuttallii*
15. Sepals dark deep blue and retaining color in press. 16
16. Lower petals white, yellowish, or tan; lower petal blade clefts no more than 1/3 blade length.
 *D. sutherlandii* M.J. Warnock
16. Lower petals blue to purple; lower petal blade clefts at least 1/3 blade length.*D. nuttallianum*
10. Leaves mostly in lower 1/3 of stems; flowers often fewer than 20/main inflorescence axis. 17
17. Sepals dark blue-purple (± drab), often partly fading in press (especially veins, giving sepals of dried specimens a mottled appearance), distinctly puberulent externally, usually not reflexed; lower stems pubescent. 18
18. Seeds with nipple-like hairs; at least 2/3 of leaves above lower 1/4 of stems; stems more than (4.5-)6.0 dm tall. *D. alabamicum* Kral
18. Seeds lacking nipple-like hairs; at least 1/3 of leaves above lower 1/4 of stems; stems less than 6.0(-8.5) dm tall. 19
19. Lower petal blade clefts at least 1/3 blade lengths.
*D. decorum* Fisch. & C.A. Mey.
19. Lower petal blade clefts no more than 1/4 blade lengths.
*D. menziesii*

17. Sepals bright blue or purple (not drab blue-purple), usually retaining color in press, usually glabrous, often reflexed; if sepals drab blue-purple, puberulent and not reflexed, then lower stems subglabrous to glabrous.....20
20. Lateral sepals strongly reflexed; leaves with usually 5 or fewer lobes extending 60% to petiole (if more than 5, then pedicels puberulent), lobes often more than 7 mm wide.....21
21. Angle between pedicel and rachis nearly 90°; leaf lobes distinctly wedge shaped, widest in distal 1/3.....*D. gracilentum* Greene
21. Angle between pedicel and rachis usually less than 70°; leaf lobes seldom wedge shaped, widest near midpoint*D. patens* Benth.
20. Lateral sepals not reflexed or only weakly so; leaves with more than 5 lobes extending more than 60% to petiole, lobes less than 7 mm wide.....22
22. Cauline leaves 2 or fewer and less than 1/2 the size of lower leaves; stems glaucous.*D. treleasei* Bush
22. Cauline leaves 3 or more and similar in size to lower leaves; stems often glabrous but not glaucous.23
23. Inflorescences (in normally developed plants) at least 3 × as long as wide; lower petals tan or yellowish, at least 8 mm long.*D. sutherlandii*
23. Inflorescences (in normally developed plants) less than 3 × as long as wide; lower petals blue (except sometimes in white flowered plants), 3-7(-11) mm long.....24
24. Seeds with nipple-like hairs on surface; east of the Great Plains.....*D. tricornis*
24. Seeds lacking nipple-like hairs; west of the Great Plains.*D. nuttallianum*

Delphinium menziesii DC., *Syst. Nat.* 1:355. 1818. TYPE: [UNITED STATES. Washington:] Nova Georgia, A. Menzies s.n. (Banks Herbarium); Isotype: BM!

Roots 0.3-0.6(-1.0) dm long. Stems 1(-3) per root, (1.0-)3.5-7.0(-8.5) dm tall, unbranched, elongation delayed 4-8 weeks after leaf initiation; bases often anthocyanous, puberulent. Leaves basal and cauline, round, puberulent; basal 0-4 at anthesis, sometimes anthocyanous abaxially, (1.5-)2.5-5.0 cm long × 4-9 cm wide, 5-12 lobed, lobes 2-15 mm wide, petioles spreading, 6-11 cm long, puberulent; cauline 3-7(-10) at anthesis, 2-4 cm long × 3-8 cm wide, 7-18 lobed, lobes 1-10 mm wide, petioles ascending, 0.5-9.0 cm long. Inflorescences 3-15(-43) flowered, pyramidal to narrowly pyramidal, 8-20(-41) cm long, open, 1-4 flowers/5 cm, branched or not; pedicels spreading, 1.5-4.0(-7.0) cm long, (glandular) puberulent. Bracts trifid to multifid, 1-4 cm long. Bracteoles subopposite, 8-10(-24) mm from flowers, 4-6(-9) mm long, green to blue, linear, puberulent. Sepals bluish purple or ochroleucous, puberulent, laterals spreading, (11-)13-20 mm long × 5-11 mm wide, spurs straight, elevated less than 30° above horizontal, 11-17 mm long. Lower petal

blades ± covering stamens, 8-12 mm long, clefts 0.2-2.5 mm deep; hairs sparse, well dispersed, but centered and most common near junction of blade and claw above cleft apex, white or blue. Fruits spreading, 11-17 mm long, 3.5-4.0 × as long as wide, puberulent. Seeds obpyramidal, 1.8-2.2 mm long × 1.0-1.3 mm wide, ringed at chalazal end, wing margined, waves lacking; cells elongate, surfaces smooth, shiny, cell margins smooth.

Delphinium menziesii is often confused with *D. nuttallii*, but may be distinguished by consistently larger flowers and usually fewer flowers per plant in the former than the latter. Interestingly, each species produces both blue-purple and ochroleucous flower colors in separate populations.

1. Sepals blue to purple.....*D. menziesii* subsp. *menziesii*
 1. Sepals ochroleucous to white..... *D. menziesii* subsp. *pallidum*

Delphinium menziesii DC. subsp. *menziesii*

Delphinium menziesii DC., *Syst. Nat.* 1:355. 1818. TYPE: [UNITED STATES.

Washington:] Nova Georgia, A. Menzies s.n. (Banks Herbarium); Isotype:

BM!. *Delphinium tricornis* Michx. var. γ *menziesii* (DC.) Huth, *Helios* 10(12):37. 1893. *Delphinium tricornis* Michx. subsp. *menziesii* (DC.) Huth, *Bot. Jahrb. Syst.* 20:343. 1895. *Delphinastrum menziesii* (DC.) Nieuwl., *Amer. Midl. Naturalist* 3:172. 1914.

Delphinium tuberosum Menzies in Hook., *Fl. Bor. Amer.* 1:25. 1840 nomen *invalidum* (not accepted when published). Non *Delphinium tuberosum* Aucher ex Boiss., *Ann. Sci. Nat.*, ser. II 16:370. 1841.

Delphinium pauperculum Greene, *Pittonia* 1:284. 1889. LECTOTYPE (Ewan 1945, p. 106): UNITED STATES. Washington: near the sea coast, Jul 1888, M.A. Knapp s.n. (ND-G!).

Delphinium oreganum Howell, *Fl. NW Amer.* 1:22. 1897. TYPE: UNITED STATES. Oregon: near brooks, Willamette Valley, Jun 1882, T. Howell s.n. (ORE).

Delphinium chilliwacense Greene, *The Ottawa Naturalist* 16:36. 1902. LECTOTYPE (Ewan 1945, p. 105): CANADA. British Columbia: dry rocky banks, Chilliwack Valley, lower Fraser River Valley, 49-49° 10' N, 121° 25' to 122° W, 19 Jun 1901, J.M. Macoun 33573 (ND-G 3277!).

Delphinium menziesii DC. subsp. *pyramidalis* Ewan, *Univ. Colorado Stud.*, ser. D, *Phys. Sci.* 2:107. 1945. TYPE: UNITED STATES. Oregon: Benton Co., Corvallis, 6 May 1916, H.C. Gilbert 1133 (OSC 4151!); Isotypes: NDA, NO!, OSC!. *Delphinium menziesii* DC. var. *pyramidale* (Ewan) C.L. Hitchc. in C.L. Hitchc. et al., *Vasc. Pl. Pacific NW* 2:355. 1964.

Stems 1(-3) per root, (1.0-)3.5-7.0(-8.5) dm tall, unbranched, elongation delayed 4-8 weeks after leaf initiation; bases often anthocyanous, puberulent. Leaves basal and cauline, round, puberulent; basal 0-4 at anthesis, sometimes anthocyanous abaxially, (1.5-)2.5-5.0 cm long × 4-9 cm wide, 5-12 lobed, lobes 2-15 mm wide, petioles spreading, 6-11 cm long, puberulent; cauline 3-7(-10) at anthesis, 2-4 cm long × 3-8 cm wide, 7-18 lobed, lobes 1-10 mm wide, petioles ascending, 0.5-9.0 cm long. Inflorescences 3-15(-43) flowered, pyramidal to narrowly pyramidal, 8-20(-41) cm long, open, 1-4 flowers/5 cm, branched or not; pedicels spreading, 1.5-4.0(-7.0) cm long, (glandular) puberulent. Bracts trifid to multifid, 1-4 cm long.

Bracteoles subopposite, 8-10(-24) mm from flowers, 4-6(-9) mm long, green to blue, linear, puberulent. Sepals bluish purple, puberulent, laterals spreading, (11-) 13-20 mm long \times 5-11 mm wide, spurs straight, elevated less than 30° above horizontal, 11-17 mm long. Lower petal blades \pm covering stamens, 8-12 mm long, clefts 0.2-2.5 mm deep; hairs sparse, well dispersed, but centered and most common near junction of blade and claw above cleft apex, white or blue. Fruits spreading, 11-17 mm long, 3.5-4.0 \times as long as wide, puberulent. Seeds obpyramidal, 1.8-2.2 mm long \times 1.0-1.3 mm wide, ringed at chalazal end, wing margined, waves lacking; cells elongate, surfaces smooth, shiny, cell margins smooth. $2n = 16$ (Lewis *et al.* 1951).

Flowering in spring. Meadows, open woodlands; 0-1000 m elevation; southwestern British Columbia, western Oregon, and western Washington. Hybrids are known with *Delphinium trolliifolium* and *D. nuttallii*.

Delphinium menziesii DC. subsp. *pallidum* M.J. Warnock, *subspec. nov.*

TYPE: UNITED STATES. Oregon: Benton Co., open fields, 12 mi S of Corvallis, 0.5 mi. W of Bruce's Corner, 20 May 1953, A.N. Steward 6351 (US!); Isotypes: ASU!, ISC!, NY(2)!, OSC(3)!, UBC(2)!, UCD!, WS, WTU. - White flowered Menzies' larkspur

Delphinio menziesii DC. subsp. *menziesii* similis sed differt caulibus 5-7 dm longis (vs. 3.5-7.0 dm longis), sepalis albis vel ochroleucis 15-20 mm latis \times 7-11 mm longis (vs. 13-20 mm latis \times 11-17 mm longis), et calcaribus 11-15 mm longis (vs. 11-17 mm longis).

Stems 1 per root, 5-7 dm tall, unbranched, elongation delayed 4-8 weeks after leaf initiation; bases often anthocyanous, puberulent. Leaves basal and cauline, round, puberulent; basal 0-4 at anthesis, sometimes anthocyanous abaxially, (1.5-) 2.5-5.0 cm long \times 4-9 cm wide, 5-12 lobed, lobes 2-15 mm wide, petioles spreading, 6-11 cm long, puberulent; cauline 3-7(-10) at anthesis, 2-4 cm long \times 3-8 cm wide, 7-18 lobed, lobes 1-10 mm wide, petioles ascending, 0.5-9.0 cm long. Inflorescences 3-15(-32) flowered, pyramidal to narrowly pyramidal, 8-20(-34) cm long, open, 1-4 flowers/5 cm, branched or not; pedicels spreading, 1.5-4.0(-6.0) cm long, glandular puberulent. Bracts trifid to multifid, 1-4 cm long. Bracteoles subopposite, 8-12 mm from flowers, 4-6 mm long, green, linear, puberulent. Sepals white to ochroleucous, puberulent, laterals spreading, 15-20 mm long \times 7-11 mm wide, spurs straight, elevated less than 30° above horizontal, 11-15 mm long. Lower petal blades \pm covering stamens, 8-12 mm long, clefts 0.2-2.5 mm deep; hairs sparse, well dispersed, but centered and most common near junction of blade and claw above cleft apex, white or blue. Fruits spreading, 11-17 mm long, 3.5-4.0 \times as long as wide, puberulent. Seeds obpyramidal, 1.8-2.2 mm long \times 1.0-1.3 mm wide, ringed at chalazal end, wing margined, waves lacking; cells elongate, surfaces smooth, shiny, cell margins smooth. $n = 8$ (Sutherland 1967).

Flowering in spring. Meadows, open woodlands; 50-100 m elevation; western Oregon. Hybrids are known with *Delphinium trolliifolium* and have been named *D. \times pavonaceum*.

Delphinium sutherlandii M.J. Warnock, *spec. nov.* TYPE: UNITED STATES. Washington: Pend O'Reille Co., nearly level soil, fencerow, moist grassland, E of road, 1.2 mi N Jct. Rt. 20 and Rt. 211 on Rt. 20, 14 Jun 1984, M.J. Warnock 3525 (SHST); Isotypes: to be distributed.

Delphinio menziesii DC. similis sed differt basibus caulium ac petiolis inferis glabris (vs. puberulis), petali inferi lamina fissa 2-4 mm in profunditate (vs. 0.2-2.5 mm in profunditate), et folliculis 4.5-5.2plo longioribus quam latoribus (vs. 3.5-4.0plo longioribus quam latoribus).

Stems 1 per root, (1.5-)3.0-7.0 dm tall, unbranched, elongation delayed 2-8 weeks after leaf initiation; bases often anthocyanous, glabrous. Leaves basal and cauline, round, subglabrous; basal 0-2 at anthesis, green, darker adaxially, 3-7(-10) cm long × 6-13(-18) cm wide, 5-11(-17) lobed, lobes 3-9(-15) mm wide, petioles spreading to ascending, 8-14 cm long, glabrous; cauline 3-7 at anthesis, 1.5-7.0(-9.0) cm long × 3-13(-16) cm wide, 5-21 lobed, lobes 0.5-6.0(-10.0) mm wide; petioles ascending, 0.4-12.0 cm long. Inflorescences (2-)11-26(-37) flowered, narrowly pyramidal, (4-)12-26(-42) cm long, open, 4-6 flowers/5 cm, branched or not; pedicels spreading, 1-3 cm long, puberulent. Bracts simple to pentafid, 1-4 cm long. Bracteoles subopposite, 2-7 mm from flowers, 3-5 mm long, green to blue, linear lanceolate, puberulent. Sepals dark blue, puberulent, laterals spreading, 14-20 mm long × 5-10 mm wide, spurs gently decurved, elevated 0-20° above horizontal, 14-18 mm long. Lower petal blades slightly elevated, ± covering stamens, 8-12 mm long, clefts 2-4 mm deep; hairs short, sparse, most common just below junction of blade and claw, slightly offset to inner lobes, white. Fruits ± spreading, (13-)18-25 mm long, 4.5-5.2 × as long as wide, puberulent. Seeds obpyramidal, 1.3-1.7 mm long × 0.7-1.0 mm wide, ringed at chalazal end, lacking waves, winged on one margin; cells elongate, surfaces roughened, shiny, cell margins smooth. *n* = 8 (Ornduff 1957 [as *Delphinium nuttallianum*]).

Flowering in spring. Dry meadows, rock outcrops, open conifer woods; 400-800 m elevation; southwestern Alberta, northern Idaho, western Montana, eastern Washington.

Delphinium nuttallii A. Gray, Bot. Gaz. (Crawfordsville) 12(3):54. 1887. TYPE: UNITED STATES. Columbia Plains, *T. Nuttall s.n.* (GH!); Isotypes: BM!,K!,NY!.

Roots 0.3-0.6(-1.0) dm long, ± fleshy. Stems 1 per root, 2-6(-9) dm tall, elongation delayed 2-8 weeks after leaf initiation; bases usually anthocyanous, pubescent. Leaves mostly in lower 1/2 of stem, round to reniform, pubescent; basal 0-2 at anthesis, green on both surfaces, 2.5-8.0 cm long × 5-14 cm wide, 5-12 lobed, lobes 4-7 mm wide, petioles spreading, 6-19 cm long, puberulent; cauline 3-10 at anthesis, 2-6 cm long × 3-8 cm wide, 7-18 lobed, lobes 1-5 mm wide; petioles ascending, 0.3-12.0 cm long. Inflorescences 5-25(-40) flowered, narrowly pyramidal, 9-20(-40) cm long, open, 3-7 flowers/5 cm, unbranched; pedicels spreading, 1.5-4.0(-9.0) cm long, puberulent. Bracts simple to pentafid, 0.5-2.0 cm long. Bracteoles subopposite, 2-3 mm from flowers, 4-6 mm long, green, linear, puberulent. Sepals bluish purple to ochroleucous, puberulent, laterals ± spreading, 8-11 mm long × 3-6 mm wide, spurs straight, slightly elevated, 9-13 mm long.

Lower petal blades \pm covering stamens, 4-6 mm long, clefts 0.5-2.0 mm deep; hairs well dispersed, most common near margins and cleft apex, white to yellow or blue. Fruits \pm spreading, 10-14(-18) mm long, 3.5-4.0 \times as long as wide, pubescent. Seeds obpyramidal, 1.5-2.0 mm long \times 1.0-1.5 mm wide, ringed at chalazal end, lacking waves, wing margined; cells elongate, surfaces smooth, cell margins smooth.

Delphinium nuttallii is often confused with *D. menziesii*, but may be distinguished by consistently smaller flowers and usually more flowers per plant in the former than the latter. Interestingly, each species produces both blue-purple and ochroleucous flowers in separate populations.

1. Sepals blue or bluish purple; spurs 10 mm or more long.
 *D. nuttallii* subsp. *nuttallii*
 1. Sepals white or light yellow; spurs 10 mm or less long.
 *D. nuttallii* subsp. *ochroleucum*

Delphinium nuttallii A. Gray subsp. *nuttallii*

Delphinium nuttallii A. Gray, Bot. Gaz. (Crawfordsville) 12(3):54. 1887. TYPE: UNITED STATES. Columbia Plains, *T. Nuttall s.n.* (GH!); Isotypes: BM!,K!,NY!. *Delphinium exaltatum* W.T. Aiton ϵ *nuttallii* (A. Gray) Huth, Helios 10:36. 1893. *Delphinium bicolor* Nutt. var. *nuttallii* (A. Gray) Huth, Bot. Jahrb. Syst. 20:345. 1895. *Delphinium columbianum* Greene, Erythea 2:193. 1894. *Delphinium columbianum* was published as a *nomen novum* because *Delphinium nuttallii* was interpreted as a later homonym for *Delphinium nuttallianum* Torrey & A. Gray. - Nuttall's larkspur.

Stems 1 per root, 4-7 dm tall, elongation delayed 2-8 weeks after leaf initiation; bases usually anthocyanous, pubescent. Leaves mostly in lower 1/2 of stem, round to reniform, pubescent; basal 0-2 at anthesis, green on both surfaces, 2.5-8.0 cm long \times 5-14 cm wide, 5-12 lobed, lobes 4-7 mm wide, petioles spreading, 6-19 cm long, puberulent; cauline 3-10 at anthesis, 2-6 cm long \times 3-8 cm wide, 7-18 lobed, lobes 1-5 mm wide; petioles ascending, 0.3-12.0 cm long. Inflorescences 5-25(-40) flowered, narrowly pyramidal, 9-20(-40) cm long, open, 3-7 flowers/5 cm, unbranched; pedicels spreading, 1.5-4.0(-9.0) cm long, puberulent. Bracts simple to pentafid, 0.5-2.0 cm long. Bracteoles subopposite, 2-3 mm from flowers, 4-6 mm long, green, linear, puberulent. Sepals bluish purple to ochroleucous, puberulent, laterals \pm spreading, 8-11 mm long \times 3-6 mm wide, spurs straight, slightly elevated, 9-13 mm long. Lower petal blades \pm covering stamens, 4.0-6.5 mm long, clefts 0.5-2.0 mm deep; hairs well dispersed, most common near margins and cleft apex, white to yellow or blue. Fruits \pm spreading, 10-14(-18) mm long, 3.5-4.0 \times as long as wide, pubescent. $n = 8$ (Sutherland 1967).

Flowering in late spring to early summer. Rock outcrops, rocky meadows; 20-300 m elevation; northwestern Oregon and southwestern Washington.

Delphinium nuttallii A. Gray subsp. *ochroleucum* (Nutt.) M.J. Warnock, *comb. nov.* BASIONYM: *Delphinium menziesii* DC. [var.] β *ochroleucum* Nutt. in Torrey & A. Gray, *Fl. N. Amer.* 1:31. 1838. TYPE: UNITED STATES. Oregon: open prairies and along the banks of the Wahlamet [sic], [1834], *T. Nuttall s.n.* (GH!); Isotypes: BM!,K(2)!,NY!. - light yellow flowered larkspur.

- Delphinium leucophaeum* Greene, Erythea 3:118. 1895. TYPE: UNITED STATES. Oregon: 1882, T.S. Brandegee s.n. (CAS!); Isotype: BM!.
Delphinium nuttallii A. Gray var. *leucophaeum* (Greene) K.C. Davis, Minnesota Bot. Stud. 2:450. 1900. *Delphinastrum leucophaeum* (Greene) Nieuwl., Amer. Midl. Naturalist 3:1172. 1914.
Delphinium willametense Suksd., Deutsch. Bot. Monatsch. 16:210. 1898. LECTOTYPE (Ewan 1945, p. 110): UNITED STATES. Oregon: Clackamas Co., auf feuchten Platzen, oft im Gebusch, bei Milwaukie am Willamette Flusse, 16 Jul 1893, W.N. Suksdorf 2225 (WS); Isolectotypes: F!,MIN!,MO!,ND-G!,NY!,P(2)!,UC(2)!,US!.

Stems 1 per root, 3-6 dm tall, unbranched; base anthocyanous, ± long puberulent. Leaves mostly in lower 1/2 of stems, round to reniform, puberulent especially abaxially; basal 0-2 at anthesis, green, 2.5-6.0 cm long × 5-11 cm wide, petioles spreading, 6-13 cm long, long puberulent, 5-12 lobed, lobes 4-7 mm wide; cauline 3-9 at anthesis, 2-5 cm long × 3-8 cm wide, 7-18 lobed, lobes 1.5-5.0 mm wide, petioles 0.3-7.0 cm long, ascending. Inflorescences 5-12(-33) flowered, narrow pyramidal, 9-20(-29) cm long, open, 3-7 flowers/5 cm, unbranched; pedicels spreading to ascending, 1.5-4.0(-6.0) cm long, puberulent. Bracts simple to pentafid, 0.5-2.0 cm long. Bracteoles subopposite, 2-8(-14) mm from flowers, 3-5 mm long, green, lanceolate to linear, puberulent. Sepals ochroleucous to white, puberulent, laterals ± spreading, 10-16 mm long × 5-7 mm wide, spurs straight, 9-11 mm long. Lower petal blades ± covering stamens, 4-6 mm long, clefts 1-2 mm deep; hairs sparse or common, centered and most dense below junction of blade and claw, yellow or white. Fruits ± spreading, 5-14(-18) mm long, puberulent, 3.5-4.0 × as long as wide. *n* = 8 (Sutherland 1967).

Flowering in late spring. Rock outcrops, rocky meadows; 50-100 m elevation; northwestern Oregon.

The range of morphological features of *Delphinium nuttallii* subsp. *ochroleucum* is almost completely encompassed within *D. nuttallii* subsp. *nuttallii*. Sepal color is the only feature consistently separating the two subspecies. Were it not for the fact that a given population typically contains plants of only one flower color, a rank of forma would be more appropriate.

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DOCUMENTED CHROMOSOME REPORTS AND SUPPLEMENTARY
INFORMATION ON PREVIOUSLY REPORTED CHROMOSOME COUNTS OF
NORTH AMERICAN *DELPHINIUM*

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ABSTRACT

Chromosome numbers are reported from new documented counts of 21 *Delphinium* species from North America. In addition, clarifications and comments are provided for previously reported chromosome counts of North American *Delphinium*. This information is provided to support inclusion of the chromosome data in the forthcoming volume of *Flora of North America* that will contain the treatment for *Delphinium*. Two of the newly documented counts are from species not previously reported, an additional twelve include documentation for counts previously reported.

KEY WORDS: *Delphinium*, Ranunculaceae, chromosome counts, North America

Chromosome counts are documented for 85 collections of *Delphinium* from North America. These reports represent 23 taxa from 21 species. Counts for two species are reported where no previous chromosome counts are known. Counts for another twelve species are documented here, for which counts had previously been reported by Warnock but not documented. Vouchers are housed in the herbaria cited (by acronyms listed in Holmgren *et al.* [1990]) with each report. Discussion on sources of material and likelihood of accurate identifications for another 51 taxa are included. Chromosome counts for 63 taxa are summarized.

Delphinium alabamicum R. Kral

UNITED STATES. Alabama: Franklin Co., 0.8 mi. NW Jct. County Road 24 and County Road 99 on 24, NW facing slope, overgrown *Juniperus* glade on limestone, 30 May 1981, M.J. Warnock 2263 (ILL,MO,NO,PAC,SHST,TEX); $n=8$ (1 plant counted).

With the exception of Warnock (1982 [$n=8$ --based on the counts reported here]), no previous report of chromosome numbers for *Delphinium alabamicum* has been located.

Delphinium andersonii A. Gray

Reported by Lewis *et al.* (1951) as $2n=16$ based on three specimens from California. All of these seem to be accurately identified.

Delphinium andesicola Ewan

UNITED STATES. Arizona: Cochise Co., Rustler Park Campground, Coronado National Forest, W end of meadow, E facing slope, T17S R30E Sec. 33 SW 1/4 SE 1/4, 14 Aug 1978, *M.J. Warnock 1644* (ILL,SHST,TEX); $n=8$ (12 plants counted).

Reported as $n=8$ by Warnock (1987) without further elaboration, but that report based on this count. No other reports on chromosome numbers of *Delphinium andesicola* have been located.

Delphinium barbeyi (Huth) Huth

UNITED STATES. Wyoming: Albany Co., Rt. 130, 0.2 mi. W of University of Wyoming Science Research Station Road, N of road, S facing slope along stream, 19 Jul 1978, *M.J. Warnock 1299* (ILL); $n=8$ (29 plants counted).

Chromosome counts for *Delphinium barbeyi* have been previously reported by Crawford & Gardener (1974) as $2n=16$ based on a specimen from Carbon Co., Wyoming. This specimen appears to be accurately identified.

Delphinium bicornutum Hemsl. subsp. *bicornutum*

MEXICO. Oaxaca: 7.6 mi. NE turnoff to Ixtlán de Juárez on Rt. 175, roadcut S of road, edge of mixed *Pinus*-hardwood forest, 19 October 1981, *M.J. Warnock 2539* (ENCB,ILL,MEXU,MO,SHST,TEX); $n=8$ (3 plants counted).

MEXICO. Oaxaca: 6.5 mi. NE turnoff to Ixtlán de Juárez on Rt. 175, roadcut S of road, edge of mixed *Pinus*-hardwood forest, 19 October 1981, *M.J. Warnock 2540* (ENCB,ILL,MEXU,MO,NO,PAC,SHST,TEX,WIS); $n=8$ (3 plants counted).

Reported as $n=8$ by Warnock (1987) based on this count, but not further documented in that publication. No additional chromosome counts for *Delphinium bicornutum* subsp. *bicornutum* have been located.

Delphinium bicornutum Hemsl. subsp. *oaxacanum* M.J. Warnock

MEXICO. Oaxaca: ca. 11.5 mi. S Miahuatlán on Puerto Angel road, steep NE facing slope, *Pinus-Quercus* woods, 19 October 1981, *M.J. Warnock 2536* (ENCB,ILL,MEXU,MO,PAC,SHST,TEX,WIS); $n=8$ (3 plants counted).

Chromosome number of *Delphinium bicornutum* subsp. *oaxacanum* reported without additional information, as $n=8$ (Warnock 1984) based on this count. No further chromosome counts of *Delphinium bicornutum* subsp. *oaxacanum* have been located.

Delphinium brachycentrum Ledeb.

Langlet (1932) reported *Delphinium brachycentrum* as $n=8$ based on a specimen cultivated at the Bergen Botanic Garden. The source of the cultivated specimen was not cited and I have not seen a voucher specimen. This report has not been included in the *Flora of North America* manuscript.

Delphinium calcar-equitis Standl.

MEXICO. Chihuahua: 7.8 mi. N of La Bufa turnoff on road between Creel and Guachochic, E of road, N facing slope in ravine, *Pinus-Quercus* woods, 23 Aug 1980, M.J. Warnock, J.A. Norris, & S.P. McCormick 2145 (ILL,TEX); $n=8$ (2 plants counted).

MEXICO. Chihuahua: 15.7 mi. W San Juanito Road on road to Yepachic, S of road, steep moist N facing slope, *Pinus-Quercus* forest, 25 Sep 1981, M.J. Warnock 2372 (ENCB,ILL,MEXU,MO,PAC,SHST,TEX); $n=8$ (3 plants counted).

Reported as $n=8$ by Warnock (1987) without further documentation. That report based on the counts documented here. No additional counts for *Delphinium calcar-equitis* have been found.

Delphinium californicum Torrey & A. Gray subsp. *californicum*

Reported by Lewis *et al.* (1951) as $2n=16$ based on two specimens from California. Both specimens represent *Delphinium californicum* subsp. *californicum*. Al-Kelidar & Richards (1981) cite *D. californicum* as a name on source material they grew and identified as *D. elatum*, and for which they report a chromosome number of $2n=32$. No voucher specimen has been seen.

Delphinium cardinale Hook.

Propach (1940) reported *Delphinium cardinale* as $2n=16$ based on seeds received from a commercial source. Voucher specimens have not been seen, nor were they mentioned in Propach's paper. Reported by Lewis *et al.* (1951) as $2n=16$ based on six collections from California. Specimens of the two collections from Santa Barbara Co. have not been examined, however, the other four are accurately identified. Mehlquist *et al.* (1943) report *D. cardinale* as naturally $n=8$, but that they were able to produce fertile $n=16$ plants by treatment with colchicine. No seed source nor voucher specimen was cited. The latter count was not included in the *Flora of North America* manuscript.

Delphinium carolinianum Walter subsp. *carolinianum*

UNITED STATES. Illinois: Henderson Co., rest area ca. 2 mi. NE Dallas City on Rt. 96, T8N R6W Sec. 30 SE 1/4, hill prairie, S facing slope, 23 May 1978, M.J. Warnock 460 (ILL); $n=8$ (22 plants counted).

UNITED STATES. Missouri: Carroll Co., 1.1 mi. W Jct. Rt. C and Rt. Z on C, N side of road, clayey shale soil, S facing slope, 23 May 1978, M.J. Warnock 464 (ILL); $n=8$ (1 plant counted).

UNITED STATES. Illinois: Pike Co., ca. 5 mi. SE of Kinderhook on Rt. 96, E of road, bluff prairie, SW facing slope, 23 May 1978, M.J. Warnock 478 (ILL); $n=8$ (9 plants counted)

- UNITED STATES. Missouri: Ozark Co., 4.8 mi. E Jct. US 160 and Rt. PP on 160, N side of road, shallow loose rocky soil on edge of deciduous woods, 27 May 1978, *M.J. Warnock 493* (ILL,TEX); $n=8$ (3 plants counted).
- UNITED STATES. Missouri: Barry Co., 1.7 mi. N Jct. Rt. M and Rt. E on M, T22N R26W, SE of road above roadcut, rocky soil, 28 May 1978, *M.J. Warnock 528* (ILL,PAC,SHST,TEX); $n=8$ (22 plants counted).
- UNITED STATES. Arkansas: Madison Co., 6.5 mi. W Jct. Rt. 68 and Rt. 21S on 68, roadside, N of road, SW facing rocky slope, 29 May 1978, *M.J. Warnock 544* (ILL,PAC,SHST,TEX); $n=8$ (4 plants counted).
- UNITED STATES. Arkansas: Carroll Co., 5.1 mi. W Jct. Rt. 68 and US 62 on 68, T18N R22W, W side of road, SE facing slope, 29 May 1978, *M.J. Warnock 545* (ILL,TEX); $n=8$ (1 plant counted).
- UNITED STATES. Arkansas: Marion Co., 7.4 mi. W Jct. US 62 and Rt. 202 on 62, T19N R17W, W side of road on roadcut and above, E facing slope, rocky soil, 29 May 1978, *M.J. Warnock 550* (ILL,MO,PAC,SHST,TEX); $n=8$ (23 plants counted).
- UNITED STATES. Arkansas: White Co., 3.5 mi. N Jct. US 167 and US 67 on 167, T9N R5W, E side of road, gravelly soil, 30 May 1978, *M.J. Warnock 558* (ILL, PAC,TEX); $n=8$ (2 plants counted).
- UNITED STATES. Arkansas: Prairie Co., 1.1 mi. E Jct. US 70 and Rt. 11S on 70, T2N R5W, between highway and railroad, low prairie, 30 May 1978, *M.J. Warnock 573* (ILL,PAC,TEX); $n=8$ (1 plant counted).
- UNITED STATES. Oklahoma: McCurtain Co., 6.6 mi. E Jct. Rt. 70 and Rt. 209S on 70, T6S R21E, between highway and railroad, grassy area near edge of brush, 5 Jun 1978, *M.J. Warnock 677* (ILL,PAC,SHST,TEX); $n=8$ (3 plants counted).
- UNITED STATES. Arkansas: Sebastian Co., ca. 0.5 mi. W Jct. Rt. 22 and Rt. 292 on 22, T8N R31W, S side of road, clay soil, little slope, 5 Jun 1978, *M.J. Warnock 679* (ILL,MO,PAC,SHST,TEX); $n=8$ (3 plants counted).
- UNITED STATES. Missouri: Morgan Co., 0.3 mi. E Jct. US 50 and Rt. 5 on 50, T45N R18W, between highway and railroad, prairie, clay soil, 6 Jun 1978, *M.J. Warnock 680* (ILL,PAC,SHST,TEX); $n=8$ (6 plants counted).
- UNITED STATES. Illinois: Henderson Co., rest area ca. 2 mi. NE of Dallas City on Rt. 96, T8N R6W Sec. 30 SE 1/4, S of road, hill prairie, loess soil, W facing slope, 19 Jun 1978, *M.J. Warnock 912* (ILL,MO,PAC,SHST,TEX); $n=8$ (11 plants counted).
- UNITED STATES. Illinois: Henderson Co., rest area ca. 2 mi. NE of Dallas City on Rt. 96, T8N R6W Sec. 30 SE 1/4, S of road, hill prairie, loess soil, W facing slope, 19 Jun 1978, *M.J. Warnock 912* (ILL,MO,PAC,SHST,TEX); $n=16$ (3 plants counted).

Previously reported by Lewitsky (1931 [as *Delphinium azureum*]) as $2n=32$, Gregory (1941) as $2n=32$, Keener (1976) as $2n=16$ or 32, and Warnock (1981) as $n=8,16$. Source of material was not mentioned for Lewitsky's count. Gregory's count was performed on plants grown from seed at the Blandly Experimental Farm at the University of Virginia. Gregory does not mention whether or not voucher specimens were made, nor where they might have been deposited. Keener's (1976) report is without further documentation, as is that of Warnock (1981), although the latter is based in part on the counts reported here.

- Delphinium carolinianum* Walter subsp. *vimineum* (D. Don) M.J. Warnock
UNITED STATES. Louisiana: Bienville Par., 2.4 mi. E Jct. Rt. 4 and Rt. 9 on 4, T15N R6W, S side of road, roadside ditch, E facing slope, 31 May 1978, *M.J. Warnock 588* (ILL,PAC,TEX); $n=8$; (24 plants counted).
- UNITED STATES. Louisiana: Bienville Par., 0.2 mi. E Jct. Rt. 4 and Rt. 9 on 4, T15N R6W, S side of road, roadside ditch, E facing slope, 31 May 1978, *M.J. Warnock 598* (ILL,PAC,TEX); $n=8$; (2 plants counted).
- UNITED STATES. Louisiana: Caddo Par., 4.8 mi. E of state line on US 79, T16N R16W, W side of road, fine grained sand soil, W facing slope, 31 May 1978, *M.J. Warnock 600* (ILL,MO,PAC,SHST,TEX); $n=8$; (2 plants counted).
- UNITED STATES. Louisiana: Caddo Par., 4.8 mi. E of state line on US 79, T16N R16W, W side of road, fine grained sand soil, W facing slope, 31 May 1978, *M.J. Warnock 600* (ILL,MO,PAC,SHST,TEX); $n=16$; (1 plant counted).
- UNITED STATES. Texas: Panola Co., 2.0 mi. S Jct. Rt. 31 and US 79 on 31, E of road, above ditch and in pasture, W facing slope, 31 May 1978, *M.J. Warnock 601* (ILL,SHST,TEX); $n=8$; (4 plants counted).
- UNITED STATES. Texas: Panola Co., 2.0 mi. S Jct. Rt. 31 and US 79 on 31, E of road, above ditch and in pasture, W facing slope, 31 May 1978, *M.J. Warnock 601* (ILL,SHST,TEX); $n=16$; (1 plant counted).
- UNITED STATES. Texas: Nacogdoches Co., 0.3 mi. N Jct. US 259 and FM 1087 on 259, E of road, NW facing slope, sandy soil, 31 May 1978, *M.J. Warnock 603* (ILL,PAC,SHST,TEX); $n=8$; (4 plants counted).
- UNITED STATES. Texas: Nacogdoches Co., 0.3 mi. N Jct. US 259 and FM 1087 on 259, E of road, NW facing slope, sandy soil, 31 May 1978, *M.J. Warnock 603* (ILL,PAC,SHST,TEX); $n=16$; (1 plant counted).
- UNITED STATES. Texas: Nacogdoches Co., 1.0 mi. N Jct. US 259 and FM 1087 on 259, E of road, W facing slope, sandy soil, 31 May 1978, *M.J. Warnock 605* (ILL,PAC,SHST,TEX); $n=8$; (29 plants counted).
- UNITED STATES. Texas: Leon Co., 1.6 mi. E Jct. Rt. 7 and FM 1511 on 7, S side of road, sandy gravel soil, 31 May 1978, *M.J. Warnock 609* (ILL,TEX); $n=8$; (17 plants counted).
- UNITED STATES. Texas: Leon Co., 1.6 mi. E Jct. Rt. 7 and FM 1511 on 7, S side of road, sandy gravel soil, 31 May 1978, *M.J. Warnock 609* (ILL,TEX); $n=16$; (1 plant counted).
- UNITED STATES. Texas: Grimes Co., 2.4 mi. W Jct. FM 149 and Rt. 90 on 149, N of road, slight W facing slope, grassland, 7 Apr 1990, *M.J. Warnock 8198* (SHST); $n=8$; (22 plants counted).
- UNITED STATES. Texas: San Augustine Co., Weches Outcrop, Halley Property, ca. 2 mi. SE San Augustine, $94^{\circ} 05' 06''$ W $31^{\circ} 31' 30''$ N, level to slight N facing slope, thin soil, 350 ft. elevation, 9 Apr 1990, *M.J. Warnock 8237* (SHST); $n=8$; (11 plants counted).
- UNITED STATES. Texas: Trinity Co., 5.4 mi. W Jct. Rt. 94 and US 287 on Rt. 94, N of road, nearly level soil, 4 May 1990, *M.J. Warnock 8381* (SHST); $n=8$; (12 plants counted).
- UNITED STATES. Texas: Trinity Co., 5.4 mi. W Jct. Rt. 94 and US 287 on Rt. 94, N of road, nearly level soil, 4 May 1990, *M.J. Warnock 8381* (SHST); $n=16$; (2 plants counted).
- UNITED STATES. Texas: San Augustine Co., 1.3 mi. N Jct. Rt. 147 and FM 1279E on 147, Sabine National Forest, sandy soil, S facing slope, 5 May 1990, *M.J. Warnock 8399* (SHST); $n=8$; (14 plants counted).

- UNITED STATES. Texas: Harrison Co., 3.7 mi. SE Jct. Rt. 31 and I-20 on Rt. 31, N of road, nearly level soil, 5 May 1990, *M.J. Warnock 8403* (SHST); $n=8$; (22 plants counted).
- UNITED STATES. Texas: Harrison Co., 3.7 mi. SE Jct. Rt. 31 and I-20 on Rt. 31, N of road, nearly level soil, 5 May 1990, *M.J. Warnock 8403* (SHST); $n=16$; (2 plants counted).
- UNITED STATES. Texas: Van Zandt Co., NW area of interchange of I-20 and FM 1255, nearly level soil, 5 May 1990, *M.J. Warnock 8404* (SHST); $n=8$; (24 plants counted).
- UNITED STATES. Texas: Bastrop Co., 5.3 mi. SW Jct. Rt. 21 and US 290 on Rt. 21, E of road, sandy soil, slight S facing slope, 6 May 1990, *M.J. Warnock 8415* (SHST); $n=8$; (19 plants counted).
- UNITED STATES. Texas: Bastrop Co., 5.3 mi. SW Jct. Rt. 21 and US 290 on Rt. 21, E of road, sandy soil, slight S facing slope, 6 May 1990, *M.J. Warnock 8415* (SHST); $n=16$; (1 plant counted).
- UNITED STATES. Texas: Walker Co., 0.4 mi. E Jct. FM 1696 and I-45 on 1696 extension, S of road, NW facing slope, sandy soil, 8 May 1990, *M.J. Warnock 8417* (SHST); $n=8$; (3 plants counted).
- UNITED STATES. Texas: Walker Co., 0.4 mi. E Jct. FM 1696 and I-45 on 1696 extension, S of road, NW facing slope, sandy soil, 8 May 1990, *M.J. Warnock 8417* (SHST); $n=16$; (1 plant counted).
- UNITED STATES. Texas: Madison Co., 0.3 mi. S Jct. Terdanway Rd. and FM 2548 on Terdanway Rd., E of road, sandy soil, nearly level ground, 8 May 1990, *M.J. Warnock 8418* (SHST); $n=8$; (24 plants counted).
- UNITED STATES. Texas: Cherokee Co., Old Palestine Cemetery, 1.1 mi. W Jct. Rt. 21 and FM 241 on 21, S of road, slight S facing slope, sandy soil, 8 May 1990, *M.J. Warnock 8419* (SHST); $n=8$; (23 plants counted).
- UNITED STATES. Texas: Panola Co., SW of Jct. US 79 and Panola Co. 108, N facing slope, sandy soil, 8 May 1990, *M.J. Warnock 8420* (SHST); $n=8$; (26 plants counted).
- UNITED STATES. Texas: Panola Co., SW of Jct. US 79 and Panola Co. 108, N facing slope, sandy soil, 8 May 1990, *M.J. Warnock 8420* (SHST); $n=16$; (2 plants counted).
- UNITED STATES. Louisiana: Caddo Par., 2.7 mi. S Jct. US 79 and I-20 on 79, W of road, SE facing slope, sandy soil, 8 May 1990, *M.J. Warnock 8421* (SHST); $n=8$; (17 plants counted).
- UNITED STATES. Louisiana: Caddo Par., 2.7 mi. S Jct. US 79 and I-20 on 79, W of road, SE facing slope, sandy soil, 8 May 1990, *M.J. Warnock 8421* (SHST); $n=16$; (1 plant counted).
- UNITED STATES. Louisiana: Bienville Par., 0.1 mi. E Jct. Rt. 4 and Rt. 9, N of road, sandy soil, slight E facing slope, 8 May 1990, *M.J. Warnock 8422* (SHST); $n=8$; (20 plants counted).
- UNITED STATES. Texas: Cass Co., 1.9 mi. E Jct. FM 3129 and US 59 on 3129, N of road, sandy soil, S facing slope, 11 May 1990, *M.J. Warnock 8445* (SHST); $n=8$; (23 plants counted).

Reported as $n=8,16$ by Warnock (1981) without further documentation. That report based on those collections reported above and made before 1979. No other reports for *Delphinium carolinianum* subsp. *vimineum* have been seen.

Delphinium carolinianum Walter subsp. *virescens* (Nutt.) R.E. Brooks

UNITED STATES. Oklahoma: Ellis Co., 20.7 mi. E Jct. US 60 and Rt. 283 on 60, just W of rest area, T19N R21W, S of road, low area in prairie hills, sandy soil, 8 Jun 1978, *M.J. Warnock 711* (ILL,SHST,TEX); $n=8$; (16 plants counted).

UNITED STATES. Colorado: Larimer Co., 1.5 mi. W Jct. County Road 19 and County Road 38E on 38E, W side of road, steep E facing slope, sandstone, 15 Jun 1978, *M.J. Warnock 857* (ILL,SHST,TEX); $n=8$; (17 plants counted).

UNITED STATES. Iowa: Monona Co., hill prairie just NE of Turin, T83N R44W, loess soil, SW facing slope, 18 Jun 1978, *M.J. Warnock 904* (ILL,SHST,TEX); $n=8$; (3 plants counted).

UNITED STATES. Texas: Tom Green Co., 3.1 mi. W Jct. FM 388 and FM 1692 on 388, N of road, slight N facing slope on limestone, *Prosopis* woods, 18 Apr 1979, *M.J. Warnock, P.P. Lowry, & A.G. Jones 1788* (ILL); $n=8$; (3 plants counted).

Reported by Gregory (1941) with a count of $n=8$ (as *Delphinium penardii* Huth), Keener (1976) as $2n=16$ (as *D. virescens* Nutt.), Warnock (1981) with a count of $n=8$ (as *Delphinium carolinianum* subsp. *penardii* [Huth] Warnock), and by Löve & Löve (1982) as $2n=16$ (as *D. virescens*). Gregory's count was performed on plants grown from seed at the Blandy Experimental Farm at the University of Virginia. Gregory does not mention whether or not voucher specimens were made and deposited, nor what the source of seeds was. Keener's (1976) report is without further documentation, as is that of Warnock (1981), although the latter is based on the counts reported here. The count by Löve & Löve is based on a specimen from Manitoba and represents *D. carolinianum* subsp. *virescens*.

Delphinium decorum Fisch. & C.A. Meyer subsp. *tracyi* Ewan

Reported by Lewis *et al.* (1951) as $2n=16$ based on two collections from California. Both Lewis *et al.* collections come from an area that suggests the specimens are accurately identified. Kurita (1956) reported *Delphinium decorum* as $2n=32$. The source of Kurita's material is not clear, nor does the collection appear to be vouchered. Therefore, Kurita's report was not included in the *Flora of North America* manuscript.

Delphinium depauperatum Torrey & A. Gray

Ornduff (1958) reported *Delphinium depauperatum* (as *D. cyanoreis*) as $n=8$ based on three specimens from Idaho. These specimens are accurately identified as *D. depauperatum*. Sutherland (1967) reported a count of $n=8$ based on a specimen from Idaho. Sutherland's collection is also *D. depauperatum*.

Delphinium distichum Geyer *ex* Hook.

Sutherland (1967) reported *Delphinium distichum* as $n=8$ based on "repeated estimate" of chromosome number in a collection from Yakima Co., Washington. Sutherland's specimen is accurately identified as *D. distichum*.

Delphinium elatum L.

Lewitsky (1931) reported *Delphinium elatum* as $2n=32$, but did not cite a source for material. Propach (1940) reported *D. elatum* as $2n=32$ based on a specimen collected in the wild. It is not clear whether or not this collection was vouchered. Karatshova *et al.* (1974) reported *D. elatum* as $2n=32$ based on a collection from the Ob Region of Russia. I have not seen a voucher of this collection and neither of the two previous reports was included in the *Flora of North America* manuscript because the source of material was not North American. Al-Kelidar & Richards (1981) also reported $2n=32$, but cite source material having been received under several different binomials (some under names of North American species), and I have not seen voucher specimens for any of them.

Delphinium exaltatum W.T. Aiton

Al-Kelidar & Richards (1981) cite *Delphinium exaltatum* as a name on source material they grew and identified as *D. elatum*, and for which they report a chromosome number of $2n=32$. No voucher specimen has been seen, nor is a source of the material given. Due to uncertainties associated with it, this report is not included in the *Flora of North America* manuscript.

Delphinium geraniifolium Rydb.

UNITED STATES. Arizona: Coconino Co., 0.1 mi. N US 180 on Snow Bowl Road, W of road, Coconino National Forest, silty soil at edge of large meadow, 16 Aug 1978, *M.J. Warnock 1692* (ILL,SHST,TEX); $n=8$; (4 plants counted).

No previous reports for *Delphinium geraniifolium* have been located.

Delphinium geyeri Greene

UNITED STATES. Colorado: Larimer Co., near high point of road to N, just N of Dixon Canyon Dam at Horsetooth Reservoir, T7N R69W, steep W facing slope, rocky, many shrubs, 15 Jun 1978, *M.J. Warnock 859* (ILL,SHST,TEX); $n=8$; (32 plants counted).

UNITED STATES. Wyoming: Carbon Co., 3.2 mi. N Jct. Carbon County 351 and US 30 on 351, T21N R86W, E of road, slightly rolling sage prairie, gravelly sand soil, 16 Jun 1978, *M.J. Warnock 874* (ILL,SHST,TEX); $n=8$; (26 plants counted).

UNITED STATES. Wyoming: Natrona Co., ca. 5 mi. S Jct. Rt. 220 and Kortess Dam Road, T30N R82W, W of road, E facing slope above roadcut, sagebrush prairie, sandy soil, 16 Jun 1978, *M.J. Warnock 880* (ILL,SHST,TEX); $n=8$; (7 plants counted).

UNITED STATES. Colorado: Larimer Co., ca. 0.2 mi. S of Livermore on US 287, E side of road, NW facing slope, sandy soil, 18 Jul 1978, *M.J. Warnock 1270* (ILL,TEX); $n=8$; (9 plants counted).

UNITED STATES. Wyoming: Albany Co., Rt. 130 at stream ca. 0.5 mi. E of Centennial, S of road, S facing slope, rocky sand stream sediments, grassland, 19 Jul 1978, *M.J. Warnock 1278* (ILL,SHST,TEX); $n=8$; (2 plants counted).

Previously reported by Al-Kelidar & Richards (1981) as $2n=32$. However, the material they counted and reported was sent to them as seeds under the name

Delphinium decorum Fisch. & C.A. Meyer, and since I have not seen their voucher specimen (NCE) I cannot confirm their identification. Crawford & Gardener (1974) reported *D. geyeri* as $2n=16$ based on three collections from Colorado and Wyoming.

Delphinium glaucum (S. Wats.) S. Wats.

UNITED STATES. Wyoming: Carbon Co., Rt. 130, ca. 1 mi. S Medicine Bow National Forest Boundary, 0.9 mi. S Brush Creek Campground entrance, Medicine Bow National Forest, W of road, in willows along stream, 19 Jul 1978, *M.J. Warnock 1314* (ILL,SHST); $n=8$; (5 plants counted).

Previously reported as $2n=16$ by Lewis *et al.* (1951 [based on a specimen from San Bernardino Co., California]) and Crawford & Gardener (1974 [as *Delphinium occidentale* based on two collections from Wyoming]), and $2n=32$ by Al-Kelidar & Richards (1981). The Al-Kelidar & Richards (1981) report is somewhat dubious since they listed this as a taxon where "it has not been possible to verify source names." Ward & Spellenberg (1982 [as *D. occidentale*]) report *D. glaucum* as $n=8$ based on a specimen from Park Co., Wyoming. The specimens of Lewis *et al.*, Crawford & Gardener, and Ward & Spellenberg appear to be accurately placed as *D. glaucum*.

Delphinium gypsophilum Ewan subsp. *gypsophilum*

Lewis *et al.* (1951) reported as $2n=16$ (based on a collection [*Lewis & Epling 531*] from Kern Co., California and $2n=32$ (based on collections [*Lewis & Epling 530, 537, 713, 715, Lewis & Mehlquist 441, 451, 454*] from California). Each of these are *Delphinium gypsophilum* subsp. *gypsophilum*. Additional collections (beyond those listed above) cited in Lewis *et al.* under *D. gypsophilum* either represent *D. gypsophilum* subsp. *parviflorum*, or the specimens have not been examined.

Delphinium gypsophilum Ewan subsp. *parviflorum* F.H. Lewis & Epling

Lewis *et al.* (1951) reported as $2n=16$ based on collections (*Epling 735, Lewis & Epling 657, 661, 664, 689, 692, 694, 697, 698, 699, 782*) from California and listed as *Delphinium gypsophilum* subsp. *gypsophilum*. I have examined all of these with the exception of *Epling 735* and *Lewis & Epling 692, 694*, and find them to be *D. gypsophilum* subsp. *parviflorum*.

Delphinium hansenii Greene subsp. *ewanianum* M.J. Warnock

UNITED STATES. California: Madera Co., N of Jct. Co. Rd. 415 and Co. Rd. 400, SW facing slope, open oak woods, 23 Mar 1990, *M.J. Warnock 8179* (SHST) $n=16$; (3 plants counted)

Lewis *et al.* (1951 [as *Delphinium hansenii*]) cited several specimens from California indicating that *D. hansenii* subsp. *ewanianum* is $2n=32$. From among these, identifications of *Epling 564*, and *569*, have been examined and their identifications confirmed as *D. hansenii* subsp. *ewanianum*.

Delphinium hansenii Greene subsp. *hansenii*

Lewis *et al.* (1951) cited numerous specimens from California indicating that *Delphinium hansenii* subsp. *hansenii* is $2n=16$ or $2n=32$. From among these, identifications of Epling 561, 563, Epling & Mehlquist 470, and Lewis & Epling 606 (all $2n=16$) and Epling 582 and Epling 578 (both $2n=32$) have been examined and their identifications confirmed as *D. hansenii* subsp. *hansenii*.

Delphinium hansenii Greene subsp. *kernense* (Davidson) Ewan

Lewis *et al.* (1951 [as *Delphinium hansenii*]) cited numerous specimens from California indicating that *D. hansenii* subsp. *kernense* is $2n=16$. From among these, identifications of Lewis, Epling, & Mehlquist (24 May 1943, 12.5 mi. S of Bodfish) and Lewis, Epling, & Mehlquist (24 May 1943, near Fairview) have been examined and their identifications confirmed as *D. hansenii* subsp. *kernense*.

Delphinium hesperium A. Gray subsp. *cuyamaca* (Abrams) F.H. Lewis & Epling

Lewis *et al.* (1951 [as *Delphinium hesperium* var. *cuyamaca*]) reported as $2n=16$ based on two specimens from San Diego Co., California. These specimens appear to be accurately identified.

Delphinium hesperium A. Gray subsp. *hesperium*

Lewis *et al.* (1951) reported *Delphinium hesperium* as $2n=16$ based upon numerous specimens from California. These specimens appear to be accurately identified.

Delphinium hesperium A. Gray subsp. *pallescens* (Ewan) F.H. Lewis & Epling

Lewis *et al.* (1951 [as *Delphinium hesperium* f. *pallescens*]) reported as $2n=16$ based upon numerous specimens from California. Lewis & Epling 709 and Lewis & Epling (6 May 1944, Beck Rd.) have been examined and confirmed as *D. hesperium* subsp. *pallescens*. Additional specimens cited also appear to be accurately identified.

Delphinium luteum A. Heller

Guerrant (1978) reported *Delphinium luteum* as $n=8$. This count was not vouchered.

Delphinium menziesii DC. subsp. *menziesii*

Reported by Sutherland (1967 [as *Delphinium menziesii* var. *menziesii*]) as $n=8$ based on a specimen from Skagit Co., Washington. This specimen is included within the current circumscription of *D. menziesii* subsp. *menziesii*.

Delphinium menziesii DC. subsp. *pallidum* M.J. Warnock

Reported by Sutherland (1967 [as *Delphinium menziesii* var. *pavonaceum* ined.]) as $n=8$ based on a specimen from Benton Co., Oregon. This specimen is included within the current circumscription of *D. menziesii* subsp. *pallidum*.

Delphinium multiplex (Ewan) C.L. Hitchc.

Reported by Ornduff (1957 [as *Delphinium cyanoreios* f. *multiplex*]) as $n=8$ based on a specimen from Kittitas Co., Washington. This specimen appears to be *D. multiplex*.

Delphinium novomexicanum Wooton

UNITED STATES. New Mexico: Lincoln Co., 2.3 mi. W Jct. Rt. 532 and Rt. 37 on 532, T11S R12E Sec. 31 SE 1/4, Lincoln National Forest, S of road, S facing slope, meadow, silty soil with scattered rocks, 13 Aug 1978, *M.J. Warnock 1600* (ILL,TEX); $n=8$; (2 plants counted).

Reported by Spellenberg (1979) as $n=8$ based on a specimen from Lincoln Co., New Mexico. This specimen is accurately identified as *Delphinium novomexicanum*.

Delphinium nudicaule Torrey & A. Gray

Tjebbes (1927) and Lawrence (1936) both reported *Delphinium nudicaule* as $2n=16$, but neither cited a source for material. Propach (1940) reported *D. nudicaule* as $2n=16$ based on seeds received from a commercial source. Voucher specimens have not been seen, nor were they mentioned in Propach's paper. Lewis *et al.* (1951) reported *D. nudicaule* as $2n=16$ based on several collections from California. These specimens appear to be accurately identified.

Delphinium nuttallianum Pritz.

UNITED STATES. Colorado: Larimer Co., N lateral moraine at Moraine Park, Rocky Mountain National Park, T5N R73W Sec. 31, NW 1/4, 8250-8600 ft., S facing slope, rocky soil, 15 Jun 1978, *M.J. Warnock 827* (ILL); $n=8$; (1 plant counted).

Previously reported by Lewis *et al.* (1951 [based on a specimen from Nevada Co., California]), Ornduff (1957 [as *Delphinium bicolor* f. *helleri* based on a specimen from Crook Co., Oregon]), Wiens & Halleck (1962 [as *D. nelsonii* E. Greene based on a specimen from Boulder Co., Colorado]), Sutherland (1967 [as *D. menziesii* var. *levicaule* *ined.* based on a specimen from Kittitas Co., Washington]), Hartman & Crawford (1971 [as *D. nelsonii* based on a specimen from Wyoming]), and Crawford & Gardener (1974 [as *Delphinium nelsonii* based on specimens from Wyoming]) as $2n=16$.

Delphinium nuttallii A. Gray subsp. *nuttallii*

Reported by Sutherland (1967) as $n=8$ based on a specimen from Cowlitz Co., Washington. This specimen is accurately identified.

Delphinium nuttallii A. Gray subsp. *ochroleucum* M.J. Warnock

Reported by Sutherland (1967 [as *Delphinium nuttallii* var. *ochroleucum* *ined.*]) as $n=8$ based on a specimen from Clackamas Co., Oregon. This specimen falls within the current circumscription of *D. nuttallii* subsp. *ochroleucum*.

Delphinium parishii A. Gray subsp. *pallidum* (Munz) M.J. Warnock

Lewis *et al.* (1951 [as *Delphinium inopinum*]) reported as $2n=16$ based on three specimens from Ventura Co., California. These specimens have been examined and represent what is currently recognized as *D. parishii* subsp. *pallidum*.

Delphinium parishii A. Gray subsp. *parishii*

Lewis *et al.* (1952) reported *Delphinium parishii* as $2n=16$ based on numerous collections from California. The Lewis *et al.* collections appear to be accurately identified.

Delphinium parryi A. Gray subsp. *blochmaniae* (Greene) F.H. Lewis & Epling

Lewis *et al.* (1951 [as *Delphinium parryi* var. *blochmanae*]) reported as $2n=16$ based on four specimens from San Luis Obispo Co., California. These specimens appear to be accurately identified.

Delphinium parryi A. Gray subsp. *maritimum* (Davidson) M.J. Warnock

Lewis *et al.* (1951 [as *Delphinium parryi*]) reported as $2n=16$ based on *Lewis 631* from Los Angeles Co., California. This specimen falls within the current circumscription of *D. parryi* subsp. *maritimum*.

Delphinium parryi A. Gray subsp. *parryi*

Lewis *et al.* (1951 [as *Delphinium parryi* and *D. parryi* subsp. *seidiosum*]) reported as $2n=16$. Included among the Lewis *et al.* citations are specimens of *D. parryi* subsp. *maritimum* and *D. parryi* subsp. *purpureum*, but most of the collections represent *D. parryi* subsp. *parryi*.

Delphinium parryi A. Gray subsp. *purpureum* (F.H. Lewis & Epling) M.J. Warnock

Lewis *et al.* (1951 [as *Delphinium parryi*]) reported as $2n=16$ based on *Lewis & Epling 754* from Ventura Co., California. This specimen represents what is currently recognized as *D. parryi* subsp. *purpureum*.

Delphinium patens Benth. subsp. *hepaticoideum* Ewan

Lewis *et al.* (1951 [as *Delphinium patens*]) reported as $2n=16$ based on *Mehlquist 390* from Santa Barbara Co., California. This specimen appears accurately identified as *D. patens* subsp. *hepaticoideum*.

Delphinium patens Benth. subsp. *patens*

Lewis *et al.* (1951) report (as *Delphinium gracilentum* based on a collection from Butte Co., California) as $2n=16$. Specimens of this collection in the herbarium at LA have been identified as *D. patens* subsp. *patens*. Lewis *et al.* (1951) also report (as *D. patens*) *Mehlquist 316A* as $2n=16$. This latter collection is *D. patens* subsp. *patens*.

Delphinium pedatisectum Hemsl.

MEXICO. Hidalgo: Llano Grande, ca. km 8 on road to El Chico, *Abies* forest and edges, N facing slope, 29 Aug 1980, M.J. Warnock, J.A. Norris, & S.P.

McCormick 2204 (ENCB,ILL,MEXU,MO,NO,PAC,SHST,TEX); $n=8$ (3 plants counted).

MEXICO. Querétaro: km 143 on Rt. 120, ca. 2 mi. E Pinal de Amoles, S of road, N facing roadcut, metamorphic rock face, 24 Nov 1980, *M.J. Warnock 2228* (ENCB,ILL,MEXU,MO,NO,PAC,SHST,TEX); $n=8$ (2 plants counted).

MEXICO. Querétaro: km 136 on Rt. 120, ca. 2 mi. W Pinal de Amoles, S of road, W facing slope, *Pinus-Quercus* woods, 12 Oct 1981, *M.J. Warnock 2459* (ENCB,ILL,MEXU,PAC,TEX); $n=8$ (3 plants counted).

MEXICO. Querétaro: km 143 on Rt. 120, ca. 2 mi. E Pinal de Amoles, S of road, N facing roadcut, metamorphic rock face, 12 Oct 1981, *M.J. Warnock 2462* (ENCB,ILL,MEXU,TEX); $n=8$ (3 plants counted).

Reported as $n=8$ by Warnock (1987) without further documentation, but that report based on the counts cited here. No additional counts for *Delphinium pedatisectum* have been located.

Delphinium polycladon Eastw.

Lewis *et al.* (1951) reported *Delphinium polycladon* as $2n=16$ based on a specimen from Mariposa Co., California. This specimen appears to be accurately identified. Snow (1959) reported *D. polycladon* as $2n=16$ based on *Snow 284* from Tuolumne Co., California. This specimen has been seen and its identification confirmed.

Delphinium purpusii Brandegee

Lewis *et al.* (1951) report *Delphinium purpusii* as $2n=16$ based on three collections from Kern Co., California. Specimens cited in Lewis *et al.* appear to be accurately identified.

Delphinium ramosum Rydb.

UNITED STATES. Colorado: Mineral Co., 13.6 mi. N Jct. Rt. 149 and US 160 on 149, E of road, steep SW facing rocky slope, scattered shrubs, 23 Jul 1979, *M.J. Warnock & R.W. Sterner 1935* (ILL,SHST); $n=8$; (1 plant counted).

Delphinium ramosum has been previously reported as $2n=16$ by Crawford & Gardener (1974) based on a collection from Las Animas Co., Colorado. This specimen has not been examined.

Delphinium recurvatum Greene

Lewis *et al.* (1951) report *Delphinium recurvatum* as $2n=16$ based on three specimens from central California. One of these (*Epling & Miles 542*) has been examined and its identification confirmed as *D. recurvatum*.

Delphinium scaposum Greene

Spellenberg (1979) reported *Delphinium scaposum* as $n=8$. Identification of the voucher specimen appears to be correct.

Delphinium scopulorum A. Gray

UNITED STATES. Arizona: Apache Co., 5.4 mi. S Jct. US 666 and US 180 on 666, Apache National Forest, E of road, silty soil in meadow, T5N R30E, 15 Aug 1978, *M.J. Warnock 1672* (ILL,SHST,TEX); $n=8$; (2 plants counted).

A count for *Delphinium scopulorum* was reported by Gregory (1941) as $n=8$. Gregory's count was performed on plants grown from seed at the Blandy Experimental Farm at the University of Virginia. Gregory does not mention whether or not voucher specimens were made and deposited, nor what the source of seeds was. The report had no further documentation, and given the common misapplication of the name *D. scopulorum* among specimens of many *Delphinium* species in western North America, it is not at all clear without a voucher, whether Gregory's plant was this or another.

Delphinium subscandens Ewan

MEXICO. Jalisco: ca. 9 mi. S of Rt. 15 on road to Tequila Microwave Station, N slope of Cerro Tequila, *Quercus* woods, N facing slope, rocky soil, 30 October 1981, *M.J. Warnock 2600* (ENCB,ILL,MEXU,MO,PAC,SHST,TEX,WIS); $n=8$ (5 plants counted).

Reported by Warnock (1987) as $n=8$ without further elaboration, but that report based on this count. No other reports for *Delphinium subscandens* have been located.

Delphinium sutherlandii M.J. Warnock

Ornduff (1957) reported *Delphinium sutherlandii* (as *D. nuttallianum*) as $n=8$ based on a collection from Sanders Co., Montana. This specimen represents what is currently recognized as *D. sutherlandii*.

Delphinium treleasei Bush

UNITED STATES. Arkansas: Marion Co., 0.8 mi. W Jct. US 62 and Rt. 178 on 62, S of road above roadcut, thin soil on limestone, nearly level, *Juniperus* glade, 4 Jun 1981, *M.J. Warnock 2274* (ILL,MO,PAC,SHST,TEX); $n=8$ (3 plants counted).

UNITED STATES. Arkansas: Carroll Co., 1.7 mi. S Jct. Rt. 187 and US 62 on 187, N of road, WSW facing slope, thin soil on limestone, *Juniperus* glade, 5 Jun 1981, *M.J. Warnock 2285* (ILL,MO,PAC,SHST,TEX); $n=8$ (3 plants counted).

UNITED STATES. Missouri: Dade Co., 1.5 mi. E Jct. Rt. Y and Rt. H on Y, S of road, W facing slope, *Juniperus* glade, thin soil on limestone, 6 Jun 1981, *M.J. Warnock 2289* (ILL,MO,PAC,SHST,TEX); $n=8$ (3 plants counted).

Warnock (1982) reported $n=8$ based on the counts reported here. Smith *et al.* (1992) also reported $n=8$ based on a specimen from Baxter Co., Arkansas. The specimen of Smith *et al.* has not been examined.

Delphinium tricornes Michx.

UNITED STATES. Illinois: McDonough Co., Bethel Twp., N side of Camp Creek, S facing slope, deciduous woods, gravelly soil, 10 May 1978, *M.J. Warnock* 415 (ILL); $n=8$; (4 plants counted).

Previously reported by Keener (1976) as $2n=16$, Gregory (1941) as $n=8$ (as *Delphinium tricornes*) and as $2n=16$ (as *D. flexuosum* Raf.), and Kurita (1956) as $2n=32$ (as *D. flexuosum* Raf.). Gregory's counts were performed on plants grown from seed at the Blandy Experimental Farm at the University of Virginia. Gregory does not mention whether or not voucher specimens were made and deposited, nor what the source of seeds was. Keener's (1976) report is without further documentation. Source of material for Kurita's count is unknown.

Delphinium trolliifolium A. Gray

Reported by Lewis *et al.* (1951 [based on specimens from Humboldt Co., California]) as $2n=16$ and by Sutherland (1967 [based on a specimen from Multnomah Co., Oregon]) as $n=8$. These collections appear accurately identified as *Delphinium trolliifolium*. A report by Zhukova (1961) lists *D. trolliifolium* as $2n=32$, but does not appear to be vouchered, nor is a source of material cited.

Delphinium umbraculorum F.H. Lewis & Epling

Lewis *et al.* (1951) reported *Delphinium umbraculorum* as $2n=16$ based on numerous collections from San Luis Obispo and Santa Barbara counties, California. From among these, specimens of Lewis & Epling 691 have been examined and confirmed as *D. umbraculorum*. The UC collection of Lewis & Epling 701 appears to be intermediate between *D. umbraculorum* and *D. parryi* subsp. *parryi*.

Delphinium variegatum (Torrey & A. Gray) subsp. *variegatum*

Lewis *et al.* (1951) reported *Delphinium variegatum* as $2n=16$ and $2n=32$. This report was based on numerous collections from California. Among the collections cited, the tetraploid reports originate from the borders of the Central Valley, while the diploid reports come from throughout the range of *D. variegatum* subsp. *variegatum*. All of their cited specimens examined to date have been accurately identified as *D. variegatum*.

Delphinium wislizeni Engelm.

MEXICO. Chihuahua: 4.7 mi. E Mesa del Huracán on road to Las Varas, S of road, steep N facing slope, rhyolite rock outcrop, *Pinus* woods, 21 Aug 1980, *M.J. Warnock, J.A. Norris, & S.P. McCormick* 2116 (ENCB,ILL,MEXU,MO,PAC,SHST,TEX); $n=8$ (4 plants counted).

MEXICO. Chihuahua: km 45 W of La Junta on road to Tomochic, S of road, steep N facing slope, rhyolite, open *Pinus* woods, 22 August 1980, *M.J. Warnock, J.A. Norris, & S.P. McCormick* 2128 (ENCB,ILL,MEXU,MO,PAC,SHST,TEX); $n=8$ (20 plants counted).

MEXICO. Chihuahua: km 45 W of La Junta on road to Tomochic, S of road, steep N facing slope, rhyolite, open *Pinus* woods, 22 August 1980, *M.J. Warnock,*

- J.A. Norris, & S.P. McCormick 2128 (ENCB,ILL,MEXU,MO,PAC,SHST,TEX); $n=16$ (1 plant counted).
- MEXICO. Durango: km 32 on Rt. 40 W of Ciudad Durango, steep E facing slope, E of road, open *Pinus-Juniperus* woods, rhyolitic rock outcrop, 25 Aug 1980, M.J. Warnock, J.A. Norris, & S.P. McCormick 2165 (ILL,TEX); $n=8$ (7 plants counted).
- MEXICO. Chihuahua: N slope of La Bufa, above Cusihuirachi, steep N facing rhyolitic slope, *Quercus* woods, 23 Sep 1981, M.J. Warnock 2351 (ENCB,ILL,MEXU,MO,PAC,SHST,TEX); $n=8$ (3 plants counted).

Reported but not otherwise documented by Warnock (1987) as $n=8,16$, based on the counts reported here. No other reports for *Delphinium wislizeni* have been located.

Delphinium wootonii Rydb.

- UNITED STATES. New Mexico: Doña Ana Co., 0.4 mi. after beginning of one way road to campground of Aguirre Springs Recreation Area, just SE of road on S facing slope, large granite boulders, desert scrub, 16 Apr 1979, M.J. Warnock, P.P. Lowry, & A.G. Jones 1787 (ILL,PAC,SHST,TEX); $n=8$; (2 plants counted).

Previously reported without further documentation as $n=8$ by Warnock (1981). That report based on the count documented here. No additional counts for *Delphinium wootonii* have been located.

Delphinium xantholeucum Piper

- Reported by Sutherland (1967) as $n=8$ based on a specimen from Chelan Co., Washington. This collection is accurately identified.

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ADDENDUM TO "THE RESURRECTION OF *ALCANTAREA* AND *WERAUHIA*,
A NEW GENUS" (BROMELIACEAE: TILLANDSIOIDEAE)

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ABSTRACT

An addendum to a recently published paper, "The resurrection of *Alcantarea* and *Werauhia*, a new genus" (Grant 1995) is presented. Taxonomic amendments include: accepting new synonymy proposed by Utley (1994) including *Vriesea breedloveana* L.B. Smith = *Werauhia werckleana* (Mez) J.R. Grant, *V. chiapensis* Matuda = *W. pectinata* (L.B. Smith) J.R. Grant, *V. cornus-cervi* Rohweder = *W. werckleana* (Mez) J.R. Grant, *V. ovandensis* Matuda = *W. pycnantha* (L.B. Smith) J.R. Grant, *comb. nov.*, and *V. patzeltii* Rauh subsp. *panamaensis* Rauh = *W. greenbergii* (Utley) J.R. Grant, and the transfer of *Vriesea burgeri* L.B. Smith and *V. macrantha* Mez & Wercklé to *Werauhia* as *W. burgeri* (L.B. Smith) J.R. Grant, *comb. nov.*, and *W. macrantha* (Mez & Wercklé) J.R. Grant, *comb. nov.* While a translation of the *Alcantarea* abstract into Spanish was published, its translation into Portuguese and the translations of the *Werauhia* text into both Portuguese and Spanish were omitted by the publisher. They are printed here in their entirety. Several errors in the text are also corrected.

KEY WORDS: Bromeliaceae, Tillandsioideae, *Alcantarea*, *Werauhia*, *Vriesea*

INTRODUCTION

This addendum accounts for taxonomic changes and errors in the text of the paper "The resurrection of *Alcantarea* and *Werauhia*, a new genus" (Grant 1995). While an updated manuscript containing these revisions was sent to the publisher of that paper, the computer diskette containing the file became corrupted during international mail transport, and the corrections were not made. Therefore, the original manuscript was printed without the amendments. This paper summarizes the changes that should have been made.

ALCANTAREA

Sumário. Este é o primeiro de uma série de artigos que irão revisar os limites genéricos na Tillandsioideae. O objectivo é delimitar os limites de gênero individuais a fim de desenvolver um sistema natural e filgênico de classificação de nível genérico

dentro da sub-família. Aqui, *Alcantarea* (Morren ex Mez) Harms é reclassificada de sua prévia posição sub-genérica a uma categoria genérica. Ela se distingue de *Vriesea* por suas espectaculares pétalas espirais, longilíneas, fusiformes, distintamente flácidas, e por sementes com comas basais e ápices. A história, nomenclatura, taxonomia e relacionamento genérico do gênero são discutidas. Dez espécies formam o gênero, oito das quais são novos acréscimos: *Alcantarea brasiliana* (L.B. Smith) J.R. Grant, *comb. nov.*, *A. duarteana* (L.B. Smith) J.R. Grant, *comb. nov.*, *A. extensa* (L.B. Smith) J.R. Grant, *comb. nov.*, *A. farneyi* (Martínelli & Costa) J.R. Grant, *comb. nov.*, *A. geniculata* (Wawra) J.R. Grant, *comb. nov.*, *A. imperialis* (Carrière) Harms, *A. nahoumii* (Leme) J.R. Grant, *comb. nov.*, *A. odorata* (Leme) J.R. Grant, *comb. nov.*, *A. regina* (Vellozo) Harms, e *A. vinicolor* (Pereira & Reitz) J.R. Grant, *comb. nov.* *Alcantarea* está limitada aos estados brasileiros de Rio de Janeiro, Espírito Santo, Minas Gerais e Bahia, a área de núcleo de diversidade de *Vriesea*.

WERAUHIA

Sumário. Um nove gênero de Bromeliaceae representado por sessenta e seis espécies e uma espécie previamente atribuída a *Vriesea* Lindley subgênero *Vriesea* divisão *Xiphion* (E. Morren) E. Morren ex Mez. Em homenagem ao Professor Dr. Werner Rauh, é denominada *Werauhia* J.R. Grant gen. nov. O mesmo é caracterizado por plantas de floração noturna, e em geral por uma falta de coloração brilhante, sobretudo brácteas e flores, principalmente carnosas, de simetria bilateral, frequentemente com corolas zigomórficas, androcoo e gynoocoo, as duas últimas consideravelmente dentro da corola, apêndices de pétalas dactilóides com um a cinco dedos de tamanhos variados, estigmas com morfologia de tipo cúpula, faltando papellae e com cúpulas escuras resistentes. Dentro de *Werauhia*, duas divisões são descritas: *Werauhia* para trinta espécies representando elementos "aliados thecophylloid" de Utley, e *Juleya* J.R. Grant sect. nov. em homenagem ao Dr. John F. Utley por trinta e seis espécies e uma subespécie representando "thecophylloid vrieseas". O gênero se estende do sul do México, através da América Central às Índias Ocidentais, Perú e nordeste do Brasil. Seu núcleo de diversidade é a cadeia de montanhas que incluem a Cordilheira de Guanacaste, Cordilheira de Tilaran, Cordilheira Central e Cordilheira de Talamanca em Costa Rica e oeste do Panamá.

Resumen. Un nuevo género de Bromeliaceae es descrito por sesenta y seis especies e una subespecie atribuidas previamente a *Vriesea* Lindley subgênero *Vriesea* sección *Xiphion* (E. Morren) E. Morren ex Mez. En honor al Prof. Dr. Werner Rauh se ha llamado *Werauhia* J.R. Grant, gen. nov. El mismo se caracteriza por plantas con florecimiento generalmente nocturno, una ausencia general de coloración brillante, brácteas y flores principalmente carnosas y frecuentemente unilaterales, simetría bilateral, corolas, androecios y ginoecios frecuentemente cigomórficos, donde los dos últimos se encuentran incluidos dentro de la corola, apêndices dactilares en los pétalos con uno a cinco dedos de longitud variada, estigmas con morfología tipo cúpula, con ausencia de papilas, y cápsulas resistentes y de color oscuro. Dentro de *Werauhia*, se describen dos secciones: *Werauhia* para treinta especies representando elementos de los "thecophylloid allies" de Utley, y *Juleya* J.R. Grant sect. nov. en honor del Dr. John F. Utley, para treinta y seis especies e una subespecie representando los "thecophylloid vrieseas" de Utley. El género se extiende desde el sur de México, a través de América Central y las Antillas Occidentales, al Perú y el nordeste brasileño. Su centro de diversidad y de mayor concentración de especies es en la cadena de

montañas que incluyen la Cordillera de Guanacaste, la Cordillera de Tilaran, la Cordillera Central y la Cordillera de Talamanca en Costa Rica y en el oeste de Panamá.

Based on the work of Utey (1994), the following changes are noted: *Vriesea breedloveana* L.B. Smith = *Werauhia werckleana* (Mez) J.R. Grant, *V. chiapensis* Matuda = *W. pectinata* (L.B. Smith) J.R. Grant, *V. cornus-cervi* Rohweder = *W. werckleana* (Mez) J.R. Grant, *V. ovandensis* Matuda = *W. pycnantha* (L.B. Smith) J.R. Grant, and *V. patzeltii* Rauh subsp. *panamaensis* Rauh = *W. greenbergii* (Utey) J.R. Grant. Additionally, some of the taxa reduced to synonymy in Grant (1995) were recognized as distinct in Utey (1994) including: *Vriesea burgeri* L.B. Smith, *V. dodsonii* L.B. Smith, *V. macrantha* Mez & Wercklé, *V. macrochlamys* Mez & Wercklé, *V. nutans* L.B. Smith, and *V. rugosa* Mez & Wercklé. After reexamination of type material, I will recognize *V. burgeri* and *V. macrantha* as distinct taxa and here make the appropriate changes. It is best to keep the remaining taxa in synonymy until such time as they can be confirmed as distinct. After these adjustments, *Werauhia* is recognized to contain 64 species.

Werauhia burgeri (L.B. Smith) J.R. Grant, *comb. nov.* BASIONYM: *Vriesea burgeri* L.B. Smith, *Phytologia* 28(4):326. 1974. TYPE: COSTA RICA. Puntarenas: between Río Coton and Río Negro (about 15 km from Sabalito) near Las Alturas lumber camp, *Burger & Matta U. 4583* (HOLOTYPE: US; Isotypes: CR, F not seen).

Werauhia greenbergii (Utey) J.R. Grant, *Abh. Akad. Wiss. Lit. Mainz. Math.-Naturwiss. Klasse, Trop. Subtrop. Pflanzenwelt* 91:42. 1995. BASIONYM: *Vriesea greenbergii* Utey, *Tulane Stud. Zool. Bot.* 30. 1983. TYPE: COSTA RICA. Alajuela: north of San Ramón, *Utey & Utey 3741* (HOLOTYPE: DUKE not seen; Isotypes: CR, DUKE not seen, F not seen, US).

= *Vriesea patzeltii* Rauh var. *panamaensis* Rauh in *Abh. Akad. Wiss. Lit. Mainz, Math.-Naturwiss. Klasse, Trop. Subtrop. Pflanzenwelt* 60:86. 1987.

Werauhia patzeltii (Rauh) J.R. Grant subsp. *panamaensis* (Rauh) J.R. Grant, *Abh. Akad. Wiss. Lit. Mainz. Math.-Naturwiss. Klasse, Trop. Subtrop. Pflanzenwelt* 91:47. 1995. Placed in synonymy under *Vriesea greenbergii* by Utey (1994:127.). TYPE: PANAMA. Colón: Smithsonian Tropical Research Institute, *Dressler s.n.* (HOLOTYPE: HEID not seen).

Werauhia macrantha (Mez & Wercklé) J.R. Grant, *comb. nov.* BASIONYM: *Vriesea macrantha* Mez & Wercklé in *Mez, Bull. Herb. Boissier ser. 2, 4(9):867*. 1904. TYPE: COSTA RICA. Without locality, *Wercklé s.n.* (HOLOTYPE: B not seen [photo US]).

Werauhia pectinata (L.B. Smith) J.R. Grant, *Abh. Akad. Wiss. Lit. Mainz. Math.-Naturwiss. Klasse, Trop. Subtrop. Pflanzenwelt* 91:33. 1995. BASIONYM: *Vriesea pectinata* L.B. Smith, *Lilloa* 6:387. 1941. TYPE: GUATEMALA. Alta Verapaz: Cobán, *Standley 69055* (HOLOTYPE: F not seen).

= *Vriesea chiapensis* Matuda, *Anales Inst. Biol. Univ. Nac. México* 23:130. 1952. ***Werauhia chiapensis*** (Matuda) J.R. Grant, *Abh. Akad. Wiss. Lit. Mainz. Math.-Naturwiss. Klasse, Trop. Subtrop. Pflanzenwelt* 91:31. 1995. Placed in synonymy under *Vriesea pectinata* by Utey (1994:131.). TYPE: MEXICO. Chiapas: Monte Bello, near Comitan, *Ramírez 178* (HOLOTYPE: MEXU not seen).

- Werauhia pycnantha* (L.B. Smith) J.R. Grant, *comb. nov.* BASIONYM: *Vriesea pycnantha* L.B. Smith, Contr. Gray Herb. 154:31. 1945. TYPE: GUATEMALA. Quezaltenango: along Río Samalá, Santa María de Jesús to Calahuaché, *Steyermark 33903* (HOLOTYPE: F, not seen [photo US]).
 = *Vriesea ovandensis* Matuda, Cact. Suc. Mex. 2(4):78. 1957. *Werauhia ovandensis* (Matuda) J.R. Grant, Abh. Akad. Wiss. Lit. Mainz. Math.-Naturwiss. Klasse, Trop. Subtrop. Pflanzenwelt 91:33. 1995. Placed in synonymy under *Vriesea pycnantha* by Utley (1994:131.). TYPE: MEXICO. Chiapas: Monte Ovando, northeast of Escuintla, *Matuda 32634* (HOLOTYPE: MEXU not seen; Isotype: US).
- Werauhia werckleana* (Mez) J.R. Grant, Abh. Akad. Wiss. Lit. Mainz. Math.-Naturwiss. Klasse, Trop. Subtrop. Pflanzenwelt 91:38. 1995. BASIONYM: *Vriesea werckleana* Mez, Bull. Herb. Boissier ser. 2, 3(2):136. 1903, not *Thecophyllum werckleanum* Mez (1903:139.) [= *Werauhia nephrolepis*]. TYPE: COSTA RICA. Cartago: Vicinity of Cartago, *Wercklé 16210* (HOLOTYPE: B not seen [photo US]; Isotype: US).
 = *Vriesea breedloveana* L.B. Smith, Phytologia 28(4):326. 1974. *Werauhia breedloveana* (L.B. Smith) J.R. Grant, Abh. Akad. Wiss. Lit. Mainz. Math. - Naturwiss. Klasse, Trop. Subtrop. Pflanzenwelt 91:31. 1995. Placed in synonymy under *Vriesea werckleana* by Utley (1994:134.). TYPE: MEXICO. Chiapas: Mun. Zinacantan, along Hwy. 190 in the Zinacantan paraje of Navenchauk, *Breedlove 15438* (HOLOTYPE: US).
 = *Vriesea cornus-cervi* Rohweder, Abh. Auslandsk., Band 61, Reihe C, Naturwiss. 18:82. 1956. *Werauhia cornus-cervi* (Rohweder) J.R. Grant, Abh. Akad. Wiss. Lit. Mainz. Math.-Naturwiss. Klasse, Trop. Subtrop. Pflanzenwelt 91:31. 1995. Placed in synonymy under *Vriesea werckleana* by Utley (1994:134.). TYPE: EL SALVADOR. Sonsoñate: Laguna de las Ranas, *Rohweder 436* (HOLOTYPE: HBG not seen).

ERRATA

- p. 15, line 26, replace: "Wawra, H.R. & H.R. von Fernsee" with "Wawra, H., Ritter von Fernsee".
- p. 19, lines 16-17, replace: "*Vriesea* sect. *Xiphion* (E. Morren) J.R. Grant, *comb. ined.*, (Grant in prep.)" with "*Vriesea* sect. *Xiphion* (E. Morren) E. Morren, *Belgique Hort.* 28:257. 1878." Since *Vriesea* sect. *Xiphion* already exists, the implied need for a change in rank is incorrect.
- p. 27, line 16, replace: "apically" with "basally".
- p. 27, line 31, replace: "basally" with "apically". The words "basally" and "apically" were inadvertently reversed in the key. Their use throughout the remainder of the text is correct.

The "Index to Names Cited" at the end of the *Werauhia* text refers only to the taxa listed in the *Werauhia* portion of the paper. It does not include the taxa mentioned in the *Alcantarea* text.

MAP: The title of the map was omitted. It should read: "Approximate Distributions of *Alcantarea*, *Vriesea*, and *Werauhia*".

ACKNOWLEDGMENTS

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GENERIC LIMITS IN THE ALOMIINAE (EUPATORIEAE - ASTERACEAE),
AND NEW COMBINATIONS IN *BRICKELLIASTRUM* AND *BARROETEA*

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ABSTRACT

Broadened concepts of the genera *Brickellia* and *Steviopsis* in the subtribe Alomiinae are rejected, and new combinations are provided in *Barroetea* for *Brickellia sonorana* B.L. Turner and in *Brickelliastrum* for *Steviopsis nesomii* B.L. Turner.

KEY WORDS: *Barroetea*, *Brickellia*, *Brickelliastrum*, *Flyriella*, *Phanerostylus*, *Steviopsis*, Asteraceae, taxonomy, nomenclature

Recent alternative generic concepts in the subtribe Alomiinae of the Eupatorieae have been presented by Turner (1988, 1990, 1991, 1994) and Turner *et al.* (1991). These concepts are not accepted here for reasons already presented by King & Robinson (1987) in their summary of the Eupatorieae. Still, two new combinations are necessary, and a few comments seem in order.

The tendency to broaden the concept of *Brickellia* Elliot to include species with only five ribs on the achene, once placed in *Eupatorium* L., was initiated by Harcombe & Beaman (1967). The group involved was later recognized by King & Robinson (1987) as a separate genus *Phanerostylus* (A. Gray) R.M. King & H. Rob. Since then, the concept of *Brickellia* has been extended further by Turner (1991) and Turner *et al.* (1991) to include both *Phanerostylus* and the related but previously distinct *Barroetea* A. Gray. The unified concept of Turner seems to be defined only by having a chromosome number of $x = 9$. The closely related *Flyriella* R.M. King & H. Rob., that has similar pubescence on the style base but has a base number of $x = 10$, is excluded. The concept of *Brickellia* accepted here and by King & Robinson (1987) continues to rely on characteristics other than chromosome number and exclude species without 10-ribbed achenes from the genus. *Barroetea* is defined by its obcompressed achenes combined with distinctive prickles on the points of the leaves. *Phanerostylus* is distinguished by its unique type of dense papillosity on the large corolla lobes and style branches. Turner *et al.* (1991) and Turner (1991) consider *Barroetea glutinosa* Brandegees (*Phanerostylus glutinosa* [Brandegee] R.M. King & H. Rob. = *Brickellia problematica* B.L. Turner, *nom. nov.*) as intermediate between *Barroetea* and *Phanerostylus*. It has somewhat obcompressed achenes as in *Barroetea*, but lacks the leaf form or the aspect of the plants. The species has the papillosity of *Phanerostylus* to which it seems closely related, and in which it is best placed, in spite of the branching inflorescence.

Turner (1991), in his recent review of *Barroetea* (as part of *Brickellia* subg. *Phanerostylus*), reduced two traditional species to synonymy. *Barroetea brevipes*

B.L. Rob. was placed in *B. laxiflora* Brandegee and *B. setosa* A. Gray was placed in *B. subuligera* (Schauer) A. Gray. These have not been fully reevaluated here, but the new species of *Barroetia*, described by Turner (1991) as a *Brickellia*, is in need of a new combination.

Barroetia sonorana (B.L. Turner) R.M. King & H. Rob., *comb. nov.*
 BASIONYM: *Brickellia sonorana* B.L. Turner, *Phytologia* 71:51. 1991.

A second area of the Alomiinae that has suffered alteration involves the genus *Steviopsis* R.M. King & H. Rob. The genus was originally proposed (King & Robinson 1971) for a few narrow-leaved species from west-central México that have weakly subimbricate involucre and sometimes whorled leaves. *Steviopsis* is one of a group of the Alomiinae in México lacking hairs on the style base. The concept was broadened by Turner (1988) to include the related *Dyscritogyne* R.M. King & H. Rob. and *Asanthus* R.M. King & H. Rob. which have more strongly subimbricate involucral bracts. *Dyscritogyne* differs also by the distinctive glandular pubescence of its achenes. The *Steviopsis* and *Dyscritogyne* grouping was traditionally placed in *Eupatorium* rather than the related *Brickellia*, while species of *Asanthus* have been placed in *Brickellia*. Members of the broader concept may have 5-7 or even 10 ribs on the achenes. *Brickelliastrum* R.M. King & H. Rob. then including only *B. fendleri* (A. Gray) R.M. King & H. Rob., and at that time known only from the United States, was not included in *Steviopsis* by Turner (1988). However, one species later named as *Steviopsis nesomii* B.L. Turner by Turner (1990) was later renamed as a new species, *Brickelliastrum villarrealii* R.M. King & H. Rob. by King & Robinson (1994). A new combination for the older Turner name of the second species of *Brickelliastrum* is needed. Unfortunately, the combination provided by Turner (1994) for *B. fendleri* in *Steviopsis* was the wrong combination, reducing all of *Brickelliastrum* to synonymy under *Steviopsis*. The relationship between the latter two genera seems particularly tenuous, with *Brickelliastrum* having the flattened outer surfaces of the pappus bristles, a characteristic of closer relatives of *Brickellia* in the Alomiinae. It remains necessary to make the appropriate new combination for the second species of *Brickelliastrum*.

Brickelliastrum nesomii (B.L. Turner) R.M. King & H. Rob., *comb. nov.*
 BASIONYM: *Steviopsis nesomii* B.L. Turner, *Phytologia* 68:410. 1990.
Brickelliastrum villarrealii R.M. King & H. Rob., *Phytologia* 76:17. 1994.

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**PRINOSCIADIUM TURNERI, A NEW SPECIES FROM COLIMA, MEXICO
(APIACEAE, APIOIDEAE)**

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ABSTRACT

The current status and brief history of the genus *Prinosciadium* S. Wats. is summarized, and an additional taxon, *P. turneri* Constance & Affolter, *spec. nov.*, from Colima, México, is described and illustrated.

KEY WORDS: Apiaceae, Colima, gypsum, México, *Prinosciadium*

The endemic Mesoamerican genus *Prinosciadium* was proposed by Sereno Watson in 1888 on the basis of the three taxa *P. pringlei* S. Wats. and *P. madrese* S. Wats., both described from Pringle collections, and *P. mexicanum* (L.) S. Wats., transferred from *Angelica* L. and eventually synonymized under *P. thapsoides* (DC.) Mathias. The root of the generic name, *prion* [a saw], derives from the sierran habitat of the Pringle collections rather than from the characteristic serration of leaf blades and winged rachises.

Two years later, Coulter & Rose (1900, p. 148) noted that, "Recent collections have remarkably increased it [*Prinosciadium*], no less than twelve additional species being described and with indications of still others." In the following decade, Rose (1905, 1906, 1909) added seven species.

Mathias & Constance reduced several described species to synonymy and added a new one to achieve a total of sixteen species and one variety in *North American Flora* (1945). Nearly 30 years later, the same authors proposed two additional taxa (1973). Number of species has remained static for the past 20 years.

The first attempted arrangement, or "synopsis of specific groups" (Coulter & Rose 1900), divided the constituent taxa then known into two major categories, depending upon whether or not the main rachis and its primary branches are conspicuously winged with serrate wings. That primary division of the key remains in place today, and serves to explain why lower leaves are so essential in identifying the species. Since the plants often reach a height of several meters, these leaves are frequently unrepresented in herbarium specimens. Lack of lower leaves, or the lack of attention to them, is responsible for this belated recognition of the following taxon.

PRIONOSCIADIUM TURNERI Constance & Affolter, Figure 1.

Prionosciadium turneri Constance & Affolter, *spec. nov.* TYPE: MEXICO. Colima: shaded northern slopes on low mountain ridge, ca. 20 km SSW of Colima, gypsum outcrops with begonias, ca. 400 m, spring 1978, *Billie L. Turner s.n.* (HOLOTYPE: UC!; Isotypes: MEXU!, TEX). (From garden-grown material, C-2053).

Plantae graciles leviter succulentae glaucae inflorescentia foliisque minute papilloso; folia basalia triangulo-ovata 1-2-pinnata divisionibus lanceolatis vel ovatis acuminatis serratis labatisve, petiolo rhachidive exalatis; folia caulina opposita petiolis gracilibus vagina breve angusta inconspicua; involucrem plerumque deficiens bracteolis involucellorum filiformibus; radii subaequales, pedicellis fertilibus paucis; flores flavescens disco prominenti ovario plus minusve scaberulo; fructus late ovalis, costis dorsalibus prominentibus lateralibus anguste alatis; vittae pleures.

Plants slender, slightly succulent and glaucous, 6-15 dm tall from a massive odorless white caudex, the inflorescence and foliage minutely papillose (Figure 1d); basal leaves triangular-ovate, 1-2 dm long and broad, 1-2-pinnate, the leaf divisions lanceolate to ovate, acuminate, 1.5-6.0 cm long, 0.5-2.5 cm broad, mucronulate-serrate and often lobed toward base; petiole slender, unwinged above the short oblong sheath, 6-12 cm long; cauline leaves opposite, like the basal, slender-petiolate, the sheaths short, narrow, inconspicuous; inflorescence of terminal compound umbels; involucre of 1 or 2 filiform bracts or lacking; rays 7-12, spreading-ascending, subequal, 2.0-4.5 cm long; umbellets 10-20-flowered; involucre of 2-6 filiform bractlets 3-5 mm long; fertile pedicels 2-5, 2-3 mm long; flowers pale yellow, the styles 1.5 mm long, the disk prominent, the ovary papillose; fruit broadly oval, 4.0-4.5 mm long, 3 mm broad, rounded to truncate at apex and base, \pm papillose, the dorsal ribs prominent, the lateral broadly winged, the wings nearly as broad as the body; vittae 1-3 in intervals, 4-6 on commissure; seed dorsally compressed in transection, the face broadly sulcate; cotyledons ovate, obtuse, 15-25 mm long, 8-10 mm broad; chromosome number, $n = 22$.

PARATYPES: MEXICO. Colima: mountain summits near pass ca. 11 mi SSW of Colima on Manzanillo road, occasional on rocks in ravine, deciduous woodland, 500 m, 19 Jul 1957, *McVaugh et al.* 15,566 (MICH,UC); abundant on open grassy summits and bluffs, 10 Aug 1957, 16,057 (MICH,UC).

The complete lack of any winged rachis, the slender-petiolate cauline leaves, the papillose ovaries, and the small fruit appear to separate this from any other species in the genus. It was grown at Berkeley from seed generously supplied by Dr. Turner in 1978, and it is still growing (if rarely fruiting) seventeen years later. It was first thought it might be *Prionosciadium acuminatum* B.L. Rob., which has also been in cultivation in the same period (C-1871), but it lacks the strongly winged leaf rachises, the reddish-brown petals, and the milky juice of that species.

The figure was prepared by Charlotte Mentges Hannan. The chromosome count was obtained by the late Dr. Tsanlang ["T. I."] and FeiMei Chuang.

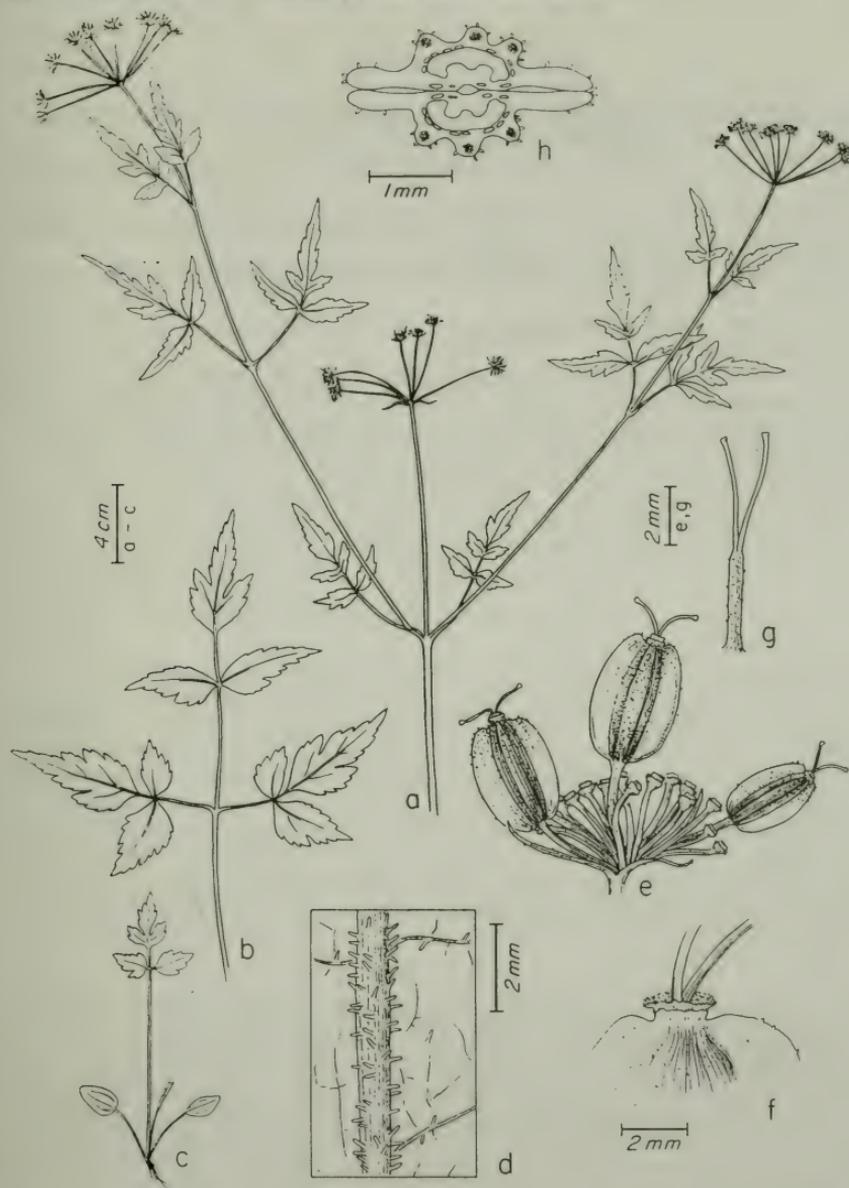


Figure 1. *Prinosciadium turneri*, a. partial inflorescence; b. lower cauline leaf; c. seedling; d. detail of lower leaf surface, showing papillae; e. fruiting umbellet; f. apex of fruit; g. carpopore; h. fruit transection. (a-d from type collection, e-h from McVaugh et al. 16,057).

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TWO NEW SPECIES OF *CASTILLEJA* (SCROPHULARIACEAE) FROM
SOUTHERN OAXACA, MEXICO

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ABSTRACT

Two new species of *Castilleja* are described from Cerro Quiexobra in southern Oaxaca, México, where they apparently are narrowly endemic. Both are members of sect. *Euchroma* but their relationships lie within different species groups. *Castilleja quiexobrensis* apparently is related to the widespread, primarily Mexican species *C. scorzonrifolia* and *C. nervata*; *C. nivibractea* may be most closely allied with *C. tolucensis* and *C. zempoaltepetlensis*, both of which are relatively restricted in geographic distribution, occurring in high-elevation habitats of southern México.

KEY WORDS: *Castilleja*, Scrophulariaceae, México

It is remarkable to note the discovery of two new species of *Castilleja* apparently growing closely adjacent to one another. These join a group of recently described taxa collected by Andrew McDonald on Cerro Quiexobra in southern Oaxaca, presently included among the following genera: *Ageratina*, *Aphanactis*, *Archibaccharis*, *Erigeron*, *Gnaphaliothamnus*, *Hieracium*, *Nama*, *Sabazia*, *Senecio*, and *Verbesina*. It is likely that these new paintbrushes will also prove to be narrow endemics, but they are as distinctive in morphology as most others in the genus. McDonald collected one other species of *Castilleja* on Cerro Quiexobra, *C. integriflora* L.f., but this species is a member of sect. *Castilleja* (Nesom 1992c) and is distantly related to the two new ones, both of which are members of *Castilleja* sect. *Euchroma* (Nutt.) Benth. (*sensu* Eastwood 1909).

CASTILLEJA QUIEXOBRENSIS Nesom, *spec. nov.* TYPE: MEXICO. Oaxaca, Mpio. Miahuatlán, 35 km ESE of Miahuatlán, 5 km NE of Santo Domingo Ozolotepec, Cerro Quiexobra and vicinity, timberline vegetation in open glades along ridges and mountain saddles; dominated below by pine forest; 3650-3800 meters; 16° 10' N, 96° 15' W; 10 Dec 1989, A. McDonald 2928 (HOLOTYPE: TEX!; Isotype: TEX!).

Castillejae scorzonrifoliae Kunth ac *C. nervatae* Eastwood similis sed ab ambobus differt combinatione characterum: caulibus rectis, foliis amplectentibus lobis lineari-lanceolatis, bracteis floralibus flabellati-lobatis, calycibus viridibus annulo distali albo, et corollis exsertis.

Annual herbs from a simple caudex and shallow fibrous roots, stems and herbage with a mixture of eglandular and stipitate-glandular hairs. Stems erect, mostly single from the base, ca. 15-45 cm tall, villous with vitreous hairs 0.8-1.5 mm long, the stipitate-glandular hairs somewhat shorter. Leaves 3-nerved, lanceolate to oblanceolate, 2.5-3.5 cm long, relatively even-sized upward, the lower distinctly clasping but not auriculate, with 1-2 pairs of ascending-divergent, linear-lanceolate lobes or merely toothed near the apex, pilose-hirsute and glandular, stiffly hirsute along the veins, especially on the lower surface. Inflorescence congested, rapidly lengthening at maturity and fruiting; floral bracts 15-20 mm long, about equal or slightly shorter than the calyx, the lower bracts similar to the upper cauline leaves, green, the upper bracts with orange-red, obovate lobes. Calyx 16-20 mm long, constricted below the middle and widening distally, the primary lobes 7-9 mm long, equal in length, green with a white rim ca. 1 mm wide, with truncate-rounded to slightly undulate apices. Corollas 18-25 mm long, galea 10-12 mm long, ca. half the length of the corolla, exerted 3-7 mm, green dorsally with red sides, the dorsal surface sparsely pilose, lower lip of 3, narrow, thick, green teeth 1 mm long; stigma strongly recurved, slightly exerted. Infructescence 15-28 cm long; fruits ovoid, 11-15 mm long, spaced 10-15 mm apart at maturity. Known only from the type collection.

Castilleja quiexobrensis is similar and presumably closely related to *C. scorzonifolia* Kunth and *C. nervata* Eastw. (Nesom 1992a) in its stipitate-glandular vestiture, linear-lanceolate leaves, and submedially constricted calyx with equal-length lobes with blunt-rounded apices. It is more similar to *C. nervata* in foliar vestiture but more similar to *C. scorzonifolia* in its straight stems, clasping leaves, and exerted corollas. The new species differs from both in its lobed leaves and bracts. All three species can be distinguished by the following contrasts:

1. Stems slightly zig-zag at the nodes; leaves nonclasping; calyx completely green; corolla not exerted from the calyx. *C. nervata*
1. Stems straight; leaves clasping; calyx red or white at the apex; corolla exerted from the calyx. (2)
2. Leaves and floral bracts entire; calyx red-tipped; taprooted. *C. scorzonifolia*
2. Leaves and floral bracts lobed; calyx green with a narrow white, apical rim; shallowly fibrous-rooted. *C. quiexobrensis*

CASTILLEJA NIVIBRACTEA Nesom, *spec. nov.* TYPE: MEXICO. Oaxaca, Mpio. Miahuatlán, 35 km ESE of Miahuatlán, 5 km NE of Santo Domingo Ozolotepec, Cerro Quiexobra, Subalpine glades surrounded by pine forest on ridgetops and mountain saddles; usually dominated by *Lupinus*, *Penstemon*, and miscellaneous forbs; "occasional in glades, common in [the] open pine forest." 3500-3700 meters; 16°10'N, 96°15'W; 3 Oct 1990, A. McDonald 3002 (HOLOTYPE: TEX!).

Castillejæ konzattii Fernald *ex* Eastw. similis sed differt vestimento eglanduloso, foliis caulinis lobis lateralibus longioribus, bracteis floralibus plerumque lorum lateralium 2-binorum alborum, et calycibus roseis annulo distali albo, sine constrictione submediali.

Perennial herbs from a branching, strongly woody caudex and root; stems and herbage stiffly pilose with vitreous, conspicuously jointed hairs mostly 0.8-1.5 mm long, eglandular. Stems erect, basally ascending, 25-40 cm tall, with few or no branches. Leaves linear-lanceolate, not clasping, 3-veined, the lower 3-5 cm long, 2-3 mm wide, relatively even-sized upward, entire or with a pair of widely divergent, linear lobes on the distal half, the upper with 2-3 pairs of divergent, linear-lanceolate lobes, the basal lobes 10-22 cm long, the distal lobes 4-10 mm long. Inflorescence congested, ca. 3-5 cm long, rapidly lengthening at maturity and fruiting; floral bracts 15-20 mm long, with distinctly white, obovate lobes ("distally white and basally pink during anthesis, pink after anthesis," according to the collection data), scabrous-hispidulous, about equal the calyx length. Calyx 12-14 mm long, even in width from base to tip (not submedially constricted), the primary lobes 6-7 mm long, equal in length, 3 mm wide, truncate-rounded apically, pink with a distal, creamy-white rim 1 mm wide. Corolla 15-17 mm long, the galea green, ca. 7 mm long, ca. half the length of the corolla, densely pilose on the dorsal surface, exerted 2-3 mm from the calyx; stigma erect, barely exerted. Fruits broadly oblong-lanceolate, 8-10 mm long, spaced ca. 1 cm apart in the mature infructescence. Known only from the type collection.

Castilleja nivibractea apparently is most closely related to *C. toluensis* Kunth and *C. zempoaltepetlensis* Nesom, a pair of species from high elevation habitats in southern México (Nesom 1992b). All three produce calyces of even width from base to apex (without the prominent medial or submedial constriction characteristic of the numerous species of the *C. scorzonerifolia* group) and all produce strongly lobed to dissected leaves and bracts. In contrast to the new species, *C. toluensis* and *C. zempoaltepetlensis* arise from thin rhizomes, produce stipitate glands on stems and leaves, and neither has white-lobed floral bracts, although the latter is distinctive in its white calyx. Among the Mexican species of *Castilleja*, *C. nivibractea* is the only one with white-lobed bracts.

In the Latin diagnosis, *Castilleja nivibractea* is compared to *C. conzattii* (of the *C. scorzonerifolia* group), to which it might run in the artificial key to species of sect. *Euchroma* with lobed leaves and/or floral bracts (Nesom 1992b).

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REVISIONARY STUDY OF CARIBBEAN SPECIES OF *JUNIPERUS*
(CUPRESSACEAE)

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ABSTRACT

Analyses of the junipers in the Caribbean (including Bermuda and Florida), based on 75 leaf terpenoids, revealed that the Caribbean junipers appear to have arisen from the ancient Appalachian region (*Juniperus virginiana* L. of the entire leaf-margined-series or its ancestor) and not from the junipers of southern México and Guatemala, which belong in the denticulate-series. This revision now recognizes: *J. barbadensis* L. (St. Lucia); *J. barbadensis* var. *lucayana* (Britton) R.P. Adams, *comb. nov.* (Bahamas, Cuba, Jamaica, Hispaniola); *J. gracilior* Pilger (Hispaniola); *J. gracilior* var. *ekmanii* (Florin) R.P. Adams, *comb. nov.* (Hispaniola); *J. gracilior* var. *urbaniana* (Pilger & Ekman) R.P. Adams, *comb. nov.* (Haiti); and *J. saxicola* Britton & Wilson (Cuba). In addition, *J. bermudiana* L. is maintained for the name of the Bermuda juniper. The identity of several previously unidentified terpenoids is also reported.

KEY WORDS: Cupressaceae, *Juniperus*, evolution, taxonomy, terpenes, Caribbean

The genus *Juniperus* is divided into three sections: *Caryocedrus*, *Juniperus*, and *Sabina* (Adams & Demeke 1993). The Caribbean junipers have been the focus of numerous studies, beginning with Linnaeus (1753) who described only three junipers from the New World (*J. virginiana* L., "Virginia and Carolina"; *J. barbadensis* L., "America"; and *J. bermudiana* L., "America"). However, Hemsley (1883) equated *J. barbadensis* with *J. bermudiana*, adopting *J. bermudiana* as the name for all of the Caribbean junipers. Sargent (1902) recognized *J. barbadensis* and said it occurred along the Atlantic coast of Georgia and Florida as well as "on the Bahamas, San Domingo (Dominican Republic), mountains of Jamaica and on Antigua." Britton (1908) recognized *J. lucayana* Britton in the Bahamas and reserved *J. barbadensis* for the plants of southern Georgia, Florida, and the rest of the Caribbean. Pilger (1913) equated *J. bermudiana* and *J. barbadensis*, but used *J. barbadensis* for the name of the common juniper of the Caribbean on the grounds that it was listed first by Linnaeus (1753). Florin (1933) reviewed the junipers of the Caribbean and recognized five species: *J. saxicola* Britton & Wilson from Cuba; *J. lucayana* from Cuba, Haiti, Jamaica, and the Bahamas; *J. gracilior* Pilger from Haiti and Dominican Republic; *J. ekmanii* Florin from Haiti; and *J. urbaniana* Pilger & Ekman from Haiti. Carabia (1941) recognized *J. barbadensis* throughout the Caribbean, *J. bermudiana* on Bermuda, and *J. virginiana* in the United States. Gillis (1974) treated the Bahamian

junipers as *J. bermudiana*. Correll & Correll (1982) recognized the juniper of the Bahamas as *J. barbadensis*.

Morphologically all the Caribbean species of *Juniperus*, except *J. bermudiana* and *J. saxicola*, are very similar and difficult to distinguish. All the Caribbean junipers are in section *Sabina* and are also in the entire leaf-margin-series. Based on DNA fingerprinting, the entire leaf margin and denticulate-series appear to represent monophyletic groups (Adams & Demeke 1993). The variable nature of leaves, even on a single branch, has resulted in confusion in the taxonomy of the Caribbean junipers. It is unlikely that the systematic relationships could ever be determined based solely on morphology. However, they each possess quite different patterns of volatile leaf oils and the taxa are readily separated using such data (Adams 1983a; Adams & Hogge 1983; Adams *et al.* 1987b; Adams 1989). Examination of both the volatile leaf oils and morphology of natural populations of *J. virginiana* and *J. silicicola* Small indicated (Adams 1986) that these taxa are conspecific and the juniper of the coastal foredunes of the southeastern United States (*J. silicicola*) was therefore maintained as a variety of *J. virginiana* (i.e., *J. v.* var. *silicicola* (Small) E. Murray. In previous studies of the Caribbean junipers, the volatile oil compositions of *Juniperus barbadensis*, *J. bermudiana*, *J. ekmanii*, *J. gracilior*, *J. lucayana*, *J. saxicola*, *J. virginiana*, and *J. virginiana* var. *silicicola* have been reported and the systematic relationships examined among the taxa (Adams 1983a; Adams & Hogge 1983; Adams *et al.* 1987a,b; Adams 1989).

I have made several attempts to collect materials from *Juniperus urbaniana* without success. However, Walter Judd collected this prostrate shrub in 1984 and provided a duplicate specimen to the author. A recent analysis of the oil from individual leaf glands of herbarium specimens of *J. urbaniana* (dried eight years) and *J. ekmanii* (dried eleven years) gave such remarkable results that it now appears feasible to address the systematics of the Caribbean junipers.

MATERIALS AND METHODS

Figure 1 shows the populations sampled. Taxon, acronym, collector number, location: *Juniperus barbadensis* (BA), Adams 5367-5371; Petit Piton, St. Lucia, BWI; *J. bermudiana* (BM), Adams 2553-2567, Bermuda; *J. ekmanii* (EK), Adams 3106-3107, Pic la Selle, Haiti; *J. gracilior* (GR), Adams 2785-2794, W of Constanza, Dominican Republic; *J. lucayana* (LG), Adams 2686-2695, 55 km S of Marsh Harbour, Great Abaco, Bahamas; (LA), Adams 2696-2705, 5 km S of Andros Town, Andros Island, Bahamas; (LB), Adams 2706-2715, 3 km N of Freeport, Grand Bahama Island, Bahamas; (LC), Adams 5259-5280, Havana Botanical Garden (seed from Sierra de Nipe), Cuba; (LP), Adams 5281-5282, Havana Botanical Garden (seed from Isla de Pinos), Cuba; (LJ), Adams 2875-2884, Hardware Gap, Blue Mtns., St. Andrew Parish, Jamaica; *J. saxicola* (SX), Adams 5284-5285, W slope of Pico Turquino, Prov. Granma/ Santiago de Cuba boundary, Cuba; *J. urbaniana* (UR), Walter Judd 4935, Pic la Selle, Haiti (specimens at FLAS and BAYLU); *J. virginiana* (VV), Adams 2409-2423; 16 km E of Dulles Airport on highway I-495, Fairfax Co., Virginia; *J. virginiana* var. *silicicola* (VS), Adams 2775-2784, 1.6 km E of the jct. of US highway 1 and E. Halifax St., Oak Hill, Volusia Co., Florida). Herbarium vouchers for all of the aforementioned collections are deposited at BAYLU.

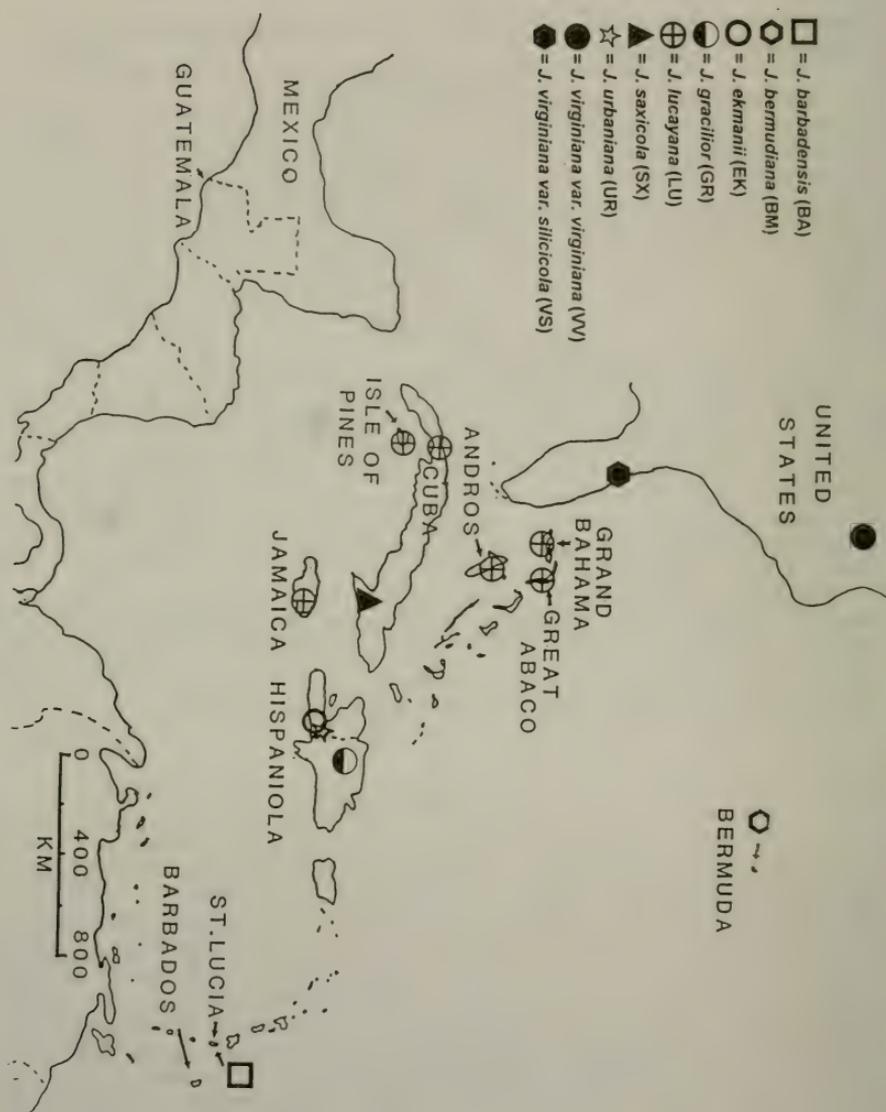


Figure 1. Study area of the Caribbean with population locations. Additional populations of *Juniperus lucayana* (not sampled) occur on a few of the islands of the Bahamas and in eastern Cuba.

Analyses of the volatile leaf oils and principal coordinate analysis follows Adams (1989).

RESULTS AND DISCUSSION

Several of the compounds previously unidentified or tentatively identified (Adams 1989) are now identified. These are (terms relative to Adams 1989): RRT 0.337 = β -thujone; RRT 0.658 = epi-cubebol; RRT 0.715 = germacrene D-4-ol; RRT 0.732 = β -oplophenone; Acetate II = 8- α -acetoxylemol; (Kaur-16-ene) = abietadiene; RRT 1.099 = cis-abietal. A complete listing of compounds in this study is given in Table 1.

Analyses of the *Juniperus urbaniana* herbarium specimen (eight years old) was accomplished by directly puncturing leaf glands with a fine syringe needle, then directly injecting its contents into a GC/MS. The same procedure was performed on a specimen of *J. ekmanii* (eleven years old). The results can be seen in the highlighted columns in Table 1 (UR, EG). Notice that the oils are practically identical. Both are dominated by bornyl acetate (as are the fresh leaf oils of *J. ekmanii*, EK, and *J. gracilior*, GR). In addition, both UR and EG have large amounts of borneol and moderate quantities of cubebol and 1-epi-cubebol. The few compounds that differ between the dried herbarium gland oils of *J. urbaniana* (UR) and *J. ekmanii* (EG) are β -cubebene, elemicin, elemol, cedrol, β -eudesmol, and α -eudesmol (Table 1). In spite of the changes in oil composition in the dried leaf of *J. ekmanii* over eleven years, it is still quite similar to that obtained from fresh leaves, taking into consideration the loss of the most volatile monoterpenes such as α -pinene, sabinene, etc.

Several compounds from the herbarium leaf glands are probably rearrangement and free-radical products. For example, cis-sabinene hydrate, borneol, germacrene D, and epi-cubebol are greatly increased in both the *Juniperus ekmanii* (EG) and *J. urbaniana* (UR) oil gland samples over their amounts in the fresh oil of *J. ekmanii* (EK, Table 1). The increased concentrations of sesquiterpenes are likely due to two factors: loss of the monoterpenes by volatilization automatically increased the relative concentration of the less volatile sesquiterpenes, and direct analysis of the oil glands resulted in more higher boiling compounds than steam distillation produces.

In any case, both herbarium specimens had been stored in the same storage conditions for approximately the same period, so the high similarity between the gland oils is indicative of a high similarity between the original oils. The converse would not necessarily be true. That is, if the composition of the dried oil gland oils were different, this could be due to either differences in the original fresh oils or differences in the manner in which the oils changed. Based on the fact that the morphologies of *Juniperus ekmanii* and *J. urbaniana* are practically identical, it is not surprising that the essential oils are practically identical. However, due to changes in the oils in the herbarium specimens over time, and in the method of analysis, it is not proper to include *J. urbaniana* in the following numerical analyses.

In order to assess the relationships among the junipers of the West Indies, weighted Gower metric similarities were computed among the thirteen OTUs using F-1 weights (F ratio from ANOVA) for 75 terpenoids. The resulting similarity matrix was then factored using principal coordinate analysis (PCO). The first eight eigenroots (coordinates) accounted for 22.2, 19.1, 13.3, 10.4, 7.8, 6.9, 5.7, and

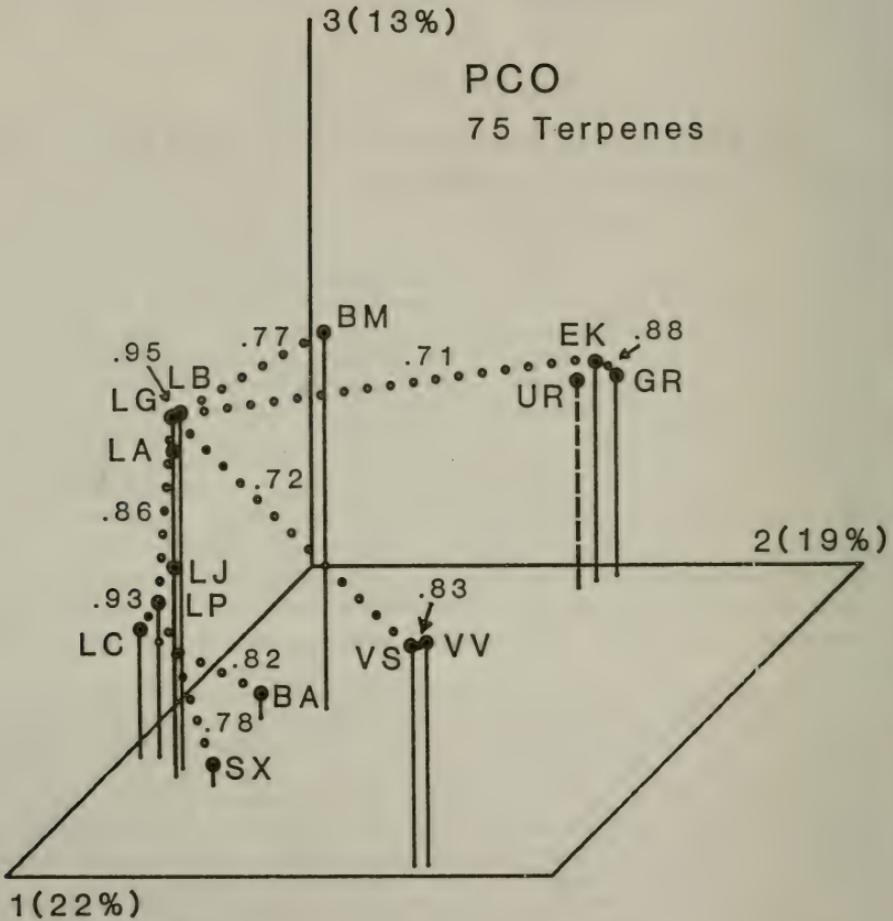


Figure 2. Principal coordinate analysis using 75 terpenoids from the volatile leaf oils. The individual components were weighted by F-1 (F from ANOVA of the fifteen OTUs) in the similarity measure. The minimum spanning network (dashed line) distances are the similarities. The OTU codes are: BA = *Juniperus barbadensis*, St. Lucia; BM = *J. bermudiana*, Bermuda; EK = *J. ekmanii*, Haiti; GR = *J. gracilior*, Dominican Republic; LA, LB, LC, LG, LJ, and LP = *J. lucayana*, from, respectively, Andros Island, Grand Bahama Island, Cuba (mainland), Jamaica, and Isle of Pines; SX = *J. saxicola*, Cuba; VV = *J. virginiana*, Washington, D.C.; and VS = *J. virginiana* var. *silicicola*, Florida, USA. The percentage number on each axis is the percent of the total variation among the OTUs accounted for by that axis. The numbers on the dotted lines are the similarities between OTUs. The dashed line (UR) shows the estimated position of *J. urbaniana* based on oil gland analysis.

Table 1. Composition of the Volatile Leaf Oils of Bermuda and Caribbean junipers compared with oil from glands on herbarium specimens of *Juniperus ekmanii* (EG) and *J. urbaniana* (UR). Data incorporated from previous reports (Adams 1983; Adams 1989; Adams & Hogge 1983; Adams, *et. al.* 1987a). Compounds are listed in order of their elution from a DB1 column. BA = *J. barbadensis*, St. Lucia, BWI; LJ = *J. lucayana*, Jamaica; LB = *J. lucayana*, Bahama Islands; BM = *J. bermudiana*, Bermuda; EG = *J. ekmanii*, oil gland, EK = *J. ekmanii*, Haiti; GR = *J. gracilior*, Dominican Republic; SX = *J. saxicola*, Cuba; UR = *J. urbaniana*, oil gland, Haiti; VS = *J. virginiana* var. *silicicola*, Florida, USA; and VV = *J. virginiana* var. *virginiana*, Washington, D.C. USA. Compound names in parenthesis are tentatively identified. T = trace amount (less than 0.5%). Note particularly the highlighted columns for UR and EG.

Compound	% total oil										
	BA	LJ	LB	SX	BM	UR	EG	EK	GR	VS	VV
Percent Yield	0.6	0.6	0.2	0.3	0.3	NA	NA	1.4	0.8	0.4	0.2
RRT = 0.143	-	-	T	-	-	-	-	-	0.8	-	-
RRT = 0.151	-	-	T	-	-	-	-	-	0.8	-	T
Tricyclene+ α -Thujene	0.9	0.6	0.5	1.1	T	0.3	T	1.9	1.4	T	T
α -Pinene	7.4	49.1	33.0	24.4	22.3	0.4	T	1.3	1.8	2.4	1.4
Camphene	T	T	T	T	0.7	0.4	T	1.9	1.2	T	T
Sabinene	31.0	9.7	8.3	25.2	2.8	1.3	0.8	5.0	10.1	T	6.7
β -Pinene	T	1.1	1.2	T	0.6	-	-	T	T	T	T
1-Octen-3-ol	-	T	T	-	1.0	-	-	T	T	0.9	-
Myrcene	3.8	3.2	4.0	2.7	2.9	0.9	0.4	2.5	1.9	0.9	0.9
2-Carene	-	T	T	-	-	T	T	T	-	T	T
α -Phellandrene	T	-	-	T	T	T	-	-	T	-	-
3-Carene	-	-	-	T	T	-	-	-	-	T	T
α -Terpinene	1.7	T	T	2.4	T	T	T	0.9	1.7	T	T
p-Cymene	T	T	T	0.8	0.5	0.3	T	0.5	1.4	T	-
β -Phellandrene	T	-	-	T	-	-	-	-	-	-	T
Limonene	34.2	25.9	18.0	2.6	35.3	3.2	1.0	9.6	7.3	33.3	8.9
(E)-Ocimene	0.7	T	-	T	T	-	-	-	-	-	T
γ -Terpinene	2.7	0.8	0.7	3.7	0.7	0.6	0.4	1.7	3.5	T	T
trans-Sabinene hydrate	0.9	-	T	0.7	-	1.0	0.7	0.9	1.1	-	T
Terpinolene	1.2	1.0	0.8	1.2	0.8	T	T	0.6	0.9	T	0.5
4-Terpinenyl acetate	T	T	-	-	-	-	-	-	-	-	T
Linalool	-	-	T	-	1.1	-	T	0.6	2.6	1.5	4.4
β -Thujone	-	-	-	-	T	-	-	1.6	2.0	-	-
cis-Sabinene hydrate	0.7	T	T	T	T	0.5	0.3	-	T	-	T
cis-Pinene hydrate	T	-	-	-	-	T	T	0.5	0.8	-	-
Camphor	-	T	T	2.8	6.5	T	T	5.8	1.1	T	3.7
trans-Pinocarveol	-	-	T	-	1.1	-	-	-	-	-	-
trans-Pinene hydrate	T	T	T	-	-	-	-	T	0.7	-	-

Table 1 (continued).

Compound	% total oil										
	BA	LJ	LB	SX	BM	UR	EG	EK	GR	VS	VV
Camphene hydrate	-	-	T	-	1.4	0.4	0.8	2.2	1.4	T	T
Borneol	T	T	T	-	2.1	13.3	26.7	5.1	2.0	-	0.8
4-Terpineol	6.5	1.6	2.5	5.9	1.4	0.4	0.5	6.3	11.6	T	1.5
Myrtenal	-	-	T	-	0.7	-	-	-	-	T	T
α -Terpineol	T	T	T	T	T	1.5	T	0.8	0.9	-	T
Estragole	-	-	-	-	-	-	-	-	-	0.5	T
p-Cymen-8-ol	-	T	T	T	T	T	-	-	-	T	T
cis-Piperitol	T	-	-	T	-	-	-	T	T	-	-
trans-Piperitol	T	-	-	-	-	-	-	-	-	-	-
RRT = 0.426	-	-	-	-	-	-	-	-	1.2	-	-
Carvone	T	T	T	-	1.0	-	-	T	T	T	T
Citronellol	T	T	0.9	T	T	-	T	0.6	0.6	T	2.3
Piperitone	-	-	0.6	-	-	-	-	-	T	T	T
Bornyl acetate	T	0.6	4.1	T	3.7	41.5	44.7	43.9	35.7	T	2.1
Safrrole	-	T	-	-	0.5	-	-	-	-	13.7	6.7
cis-Sabinyol acetate	T	-	T	-	0.8	-	-	-	T	-	-
Methyl eugenol	-	T	-	-	T	-	-	-	T	8.2	2.9
Caryophyllene	T	T	T	T	T	0.5	T	T	T	T	T
Thujopsene	T	-	T	T	2.1	-	-	T	T	-	-
α -Cadinene	-	-	T	-	-	-	-	T	T	-	T
(β -Cadinene)	-	-	T	-	-	T	1.0	T	T	T	T
Germacrene D	T	0.6	T	2.5	T	0.3	0.2	-	-	T	T
Cuparene	T	-	-	-	-	-	-	-	-	-	-
β -Cubebene	-	-	0.8	-	-	0.5	-	T	T	-	-
epi-Cubebol	-	-	0.9	-	-	0.9	0.3	-	-	-	-
α -Muurolene	T	T	-	T	T	0.5	0.3	T	T	T	T
γ -Cadinene	T	-	0.8	T	-	-	-	T	-	T	T
Cubebol	-	T	2.0	T	-	9.4	5.6	T	T	T	-
δ -Cadinene	T	T	0.7	T	T	0.8	0.9	T	T	0.7	0.8
RRT = 0.0692	-	-	0.6	-	-	-	-	-	-	T	T
Elemicin	-	-	-	-	-	0.2	-	T	T	-	T
Elemol	T	T	T	1.8	T	1.3	-	-	-	2.1	8.2
Cadinol isomer 1	T	T	-	-	-	-	-	-	-	-	-
Germacrene D-4-ol	T	-	1.9	-	-	-	-	-	-	0.9	T
Cadinol isomer 2	-	T	0.9	-	-	-	-	-	-	0.8	0.7
β -Oplophenone	T	T	2.2	T	T	-	-	-	-	0.7	2.0
Widdrol	T	-	-	-	-	-	-	-	-	-	-
Cedrol	T	-	-	-	-	-	0.2	-	-	-	-
1-epi-Cubenol	-	-	1.2	-	T	3.9	2.4	T	T	0.7	0.9
γ -Eudesmol	-	-	-	0.8	-	-	-	-	-	3.4	2.8

Table 1 (continued).

Compound	% total oil										
	BA	LJ	LB	SX	BM	UR	EG	EK	GR	VS	VV
τ -Cadinol	-	T.	-	-	-	-	-	T	T	2.0	T
τ -Muurolol	-	T	1.6	-	T	0.3	0.1	T	-	-	2.4
β -Eudesmol	-	-	-	1.2	-	0.3	-	-	-	2.8	1.7
Cadinol isomer 4	-	0.5	-	-	-	-	-	-	-	-	-
α -Cadinol	T	-	-	T	-	-	-	-	-	-	-
α -Eudesmol	-	-	-	1.6	-	0.5	-	-	-	3.4	3.1
RRT=0.769	T	-	2.3	1.3	T	T	T	T	T	-	-
Oplopanone	T	T	T	-	-	0.6	0.2	T	-	-	-
RRT = 0.791	T	T	0.9	1.6	T	-	-	T	T	T	T
8- α -Acetoxyelemol	-	-	-	T	-	-	-	-	-	1.8	3.5
Abietatriene	T	-	T	T	T	-	-	-	T	T	-
Manool	-	-	T	0.9	-	-	-	-	-	T	T
Abietadiene	T	-	T	T	0.7	-	-	-	T	-	-
cis-Abietal	0.6	T	T	T	-	-	-	-	-	-	-

4.9% (total of 90.3%) of the variation among the thirteen OTUs. Note that the dotted line for *Juniperus urbaniana* (Figure 2) is placed to denote that, if it were possible to include this taxon, its oil is almost identical to that of *J. ekmanii* (see discussion above). The first coordinate (22%) separates the junipers of Hispaniola (EK, GR) from all the other taxa in the study (Figure 2). The second coordinate (19%) separates the two varieties of *J. virginiana* (VV, VS) from all the other taxa (Figure 2). The third coordinate (13%) separates *J. barbadensis* (BA) and *J. saxicola* (SX) from the other taxa. Coordinate 4 (not shown) separated *J. bermudiana* from *J. saxicola* and coordinate 5 separated various populations of *J. lucayana*. The two varieties of *J. virginiana* were separated on coordinate 6 (not shown).

The minimum spanning network that is superimposed (Figure 2) is based on the similarity measures and, thus, is useful in sensing the distortion of viewing these thirteen OTUs in a 3-dimensional ordination.

Several patterns are apparent from the chemical data. The island populations of *Juniperus lucayana* are very similar to each other (similarities range from 0.95 to 0.86, Figure 2). *Juniperus ekmanii* is quite similar to *J. gracilior* (0.88), and both are quite dissimilar to the other junipers (Figure 2) in their volatile leaf oils. The *J. virginiana* varieties are also very similar to each other but quite distinct from other Caribbean taxa. *Juniperus bermudiana* is distinct but most similar to the *J. lucayana* populations. *Juniperus barbadensis* is similar to *J. lucayana* (0.82), but somewhat distinct. And finally, *J. saxicola*, although morphologically quite distinct in having only decurrent leaves, is clearly similar to the *J. barbadensis* - *J. lucayana* group.

In summary, both chemical (this paper) and morphological (Adams 1983a) data, support the following systematic treatment for the Caribbean junipers.

Key to Caribbean species of *Juniperus*

1. Plants with all leaves decurrent. 1. *J. saxicola*
1. Plants with both scale-like and decurrent (at least on juvenile growth) leaves. 2
 2. Ultimate leafy branchlets 1.3-1.6 mm wide, and 2-4 cm long, scale leaves overlapping by almost 1/2 their length. 2. *J. bermudiana*
 2. Ultimate leafy branchlets 0.7-1.0 mm wide and 0.5-2.0 cm long, scale leaves overlapping by about 1/4 their length. 3
 3. Scale leaf tips acuminate to mucronate; 1-2 seeds per female cone, single-seeded cones globose, but 2-seeded cones nearly reniform. 4
 4. Branchlets drooping, ultimate leafy branching angle 20-30°; glands on old brown persistent whip leaves not conspicuous. 3. *J. gracilior*
 4. Branchlets not drooping, ultimate leafy branching angle 35-40°; glands on old, brown, persistent whip leaves conspicuous. 5
 5. Erect trees; whip leaf glands oval (to twice as long as wide). 4. *J. gracilior* var. *ekmanii*
 5. Prostrate shrubs; whip leaf glands elongated (3-4 times as long as wide). 5. *J. gracilior* var. *urbaniana*
 3. Scale leaf tips obtuse to acute; 2-4 seeds per female cone, female cones reniform (rarely globose). 6
 6. Glands on old brown persistent whip leaves conspicuous, sunken and extending almost to the whip leaf tip. 6. *J. barbadensis* var. *barbadensis*
 6. Glands on old brown persistent whip leaves scarcely conspicuous, if visible then neither sunken nor extending almost to the whip leaf tip. 7. *J. barbadensis* var. *lucayana*

1. *Juniperus saxicola* Britton & Wilson, Bull. Torrey Bot. Club 50:35. 1923. TYPE: CUBA. Sierra Maestra, Oriente, León 10798 (HOLOTYPE: NY)

Small tree, 3-8 m tall. Leaves all decurrent, spreading, 5-7 mm long and ca. 1 mm wide, scale leaves never present on adult trees. Seed cones dark blue with bloom, subglobose to reniform, ca. 5 mm long, 3-4 mm diam., 2 seeds/cone. Pollen shed in winter (?).

The species has apparently been fixed by neoteny in the juvenile-leaved (decurrent) growth stage, because even in the adult, reproductive individuals have only juvenile leaves (an awn-shaped blade that diverges from the stem at 45 to 60° and a sheath portion that clasps the stem). Generally, in *Juniperus* section *Sabina*, only young (up to 4 or 5 years old) junipers have the awn-shaped (decurrent) leaves. The scale (adult) leaves are then produced throughout the life span, except that juvenile (decurrent) leaves are produced at the tips of branches during a rapid growth period or on damaged branches. Having only juvenile leaves on adult trees is very rare in the Western Hemisphere where field examination of thousands of junipers has resulted in finding only three or four plants that have only juvenile foliage on otherwise mature trees (personal observation). However, at least two species in the Eastern Hemisphere (*J. davurica* Pallas and *J. squamata* D. Don in Lamb.) are also fixed in the juvenile state and some cultivars of *J. chinensis* L. have almost all juvenile (decurrent) leaves.

All the specimens examined of *Juniperus saxicola* have decurrent leaves and no other juniper species has been found from the Pico Turquino region. Thus, it appears

that this small region has a reproductive population in which the genes for juvenile leaf form have become fixed.

Distribution: Endemic to Cuba. On rocks, crest of Sierra Maestra and Pico Turquino, Granma Prov. (previously Oriente Prov.), Cuba.

Representative Specimens: CUBA: Sierra Maestra, Cueva del Aura, Roig & Bucher 6692 (NY!); Pico Turquino, 1600 m, Ekman 11024 (NY!); Sierra Maestra, steep rocks of Loma Regino (N spur of Pico Turquino), 1700 m, Ekman 14607 (NY!); Estribo del Pico Turquino, Bisse, Dietrich, Kohler, Leper, Gutiérrez, & Duany 40486 (HAJB!); Loma Regiono, Sierra Maestra, Acuna 15050 (HAJB!); Sierra Maestra, cima del Pico Turquino, Acuna 9492 (HAJB!), Pico Turquino, Adams 5284, 5285 (BAYLU).

2. *Juniperus bermudiana* L., *Sp. Pl.* 1039. 1753. TYPE: BERMUDA. *Linnaeus* 1198.2 (HOLOTYPE: LINN!). *Juniperus virginiana* L. var. *bermudiana* (L.) Vasey, Rpt. (U.S.) Comm. Agric. 1875:185. 1876. *Sabina bermudiana* (L.) Antoine, *Cupress.* -*Gatt.* 65. 1857.
Juniperus oppositifolia Moench, *Meth. Pl.* 698. 1794.

Trees to 15 m tall. Thin bark exfoliating in strips. Leafy branchlets 2-4 cm long, and 1.3-1.6 mm wide, branching angle 30-35°. Scale leaves opposite, thus branchlets strongly quadriform (four sided), overlapping by about 0.4-0.5 times their length, green, decurrent on young plants and on rapidly growing shoots but otherwise scale-like, about 1 mm long, with obtuse to acute tips, rounded on the back and tightly appressed. Glands on scale-like leaves inconspicuous, elongated and sunken, extending almost to the tip of the whip leaf. Seed cones dark blue with bloom, subglobose to reniform, 4-5 mm long, 6-8 mm wide when reniform, 1-2(-3) seeds/cone. Pollen shed in spring(?).

Juniperus bermudiana has been subject to attack by two scale insects, *Lepidosaphes newsteadi* and *Carulaspis minima*, that were apparently introduced from the U.S. mainland prior to 1942 (Bennett & Hughes 1959; Groves 1955). These insects cause defoliation and death. Groves (1955) estimated that 90% of the trees were dead by 1955. In 1978, William E. Sterrer, Bermuda Biological Station, (pers. comm.) estimated that perhaps 99% of the original trees were dead.

Distribution: Endemic to Bermuda Island.

Representative specimens: *R.P. Adams* 2553-2567 (BAYLU).

3. *Juniperus gracilior* Pilger var. *gracilior*, *Symbol. Antill.* 7:481. 1913. TYPE: DOMINICAN REPUBLIC. Azua Prov.: near Las Canitas, 1300 m, *M. Fuertes* 1939 (LECTOTYPE [here designated]: NY; Isolectotype: US; Syntypes: *Tuerckheim* 2981, *Eggers* 2320).

Tree to 10 m tall. Branches lax and branchlets thin, branching angle 25°. Foliage light green. Scale leaves 1.0-1.5 mm long with acuminate to mucronate tips, opposite, with some branchlets appearing quadriform. Glands on scale leaves not conspicuous, if visible then oval and often sunken. Seed cones globose (if with one seed) or reniform (if with 2 seeds), with bloom, reddish-blue, mature in 1 year, 1-2 seeds/cone, borne on short, straight peduncle (2 mm). Pollen shed in winter(?).

Pilger also cited *W. Buch 313 p. p.* from near St. Michel, Haiti as *Juniperus gracilior* but this should be referred to *J. barbadensis* var. *lucayana*.

Distribution: *Juniperus gracilior* is endemic to Hispaniola occurring at elev. of 1000 - 1700 m.

Representative Specimens: DOMINICAN REPUBLIC. La Vega Prov.: Constanza, 1200 m, *José de js. Jiménez 4043* (US); 16 km W of Constanza, 1400 m, *Adams 2785-2794* (BAYLU). Azua Prov., Valle del Yaque, ca. 1700 m, *Ekman H13709* (US).

4. *Juniperus gracilior* Pilger var. *ekmanii* (Florin) R.P. Adams, *comb. nov.* BASIONYM: *Juniperus ekmanii* Florin, Ark. Bot. 25A(5):14-15. 1933. TYPE: HAITI. Ouest Dept., Massif de la Selle, above Croix-des-Bouquets, 2100 m, *Ekman H3140* (HOLOTYPE: S; Isotypes: GH,IJ!,K!,US).

Trees to 15 m tall, subglobose crown. Bark on main branches exfoliates in irregular plates. Foliage rigid, grayish-green, ultimate leafy branching angle large (37-42°). Glands on old brown persistent whip leaves conspicuous, dark brown; scale leaves mostly opposite but ternate on some branchlets, leaf tips acuminate to mucronate. Glands ovate but not very conspicuous. Seed cones reddish-brown underneath the bluish bloom, 1 and 2 seeds per cone [Seed cones have not been found on the type or any other specimens examined]. Pollen shed in winter (?).

Distribution: Haiti: Massif de la Selle, probably now close to extinction.

Representative Specimens: HAITI. Mare Rouge, 1770 m, *Adams 3106, 3107* (BAYLU); above Marigot, *Ekman 10056* (EHH).

5. *Juniperus gracilior* Pilger var. *urbaniana* (Pilger & Ekman) R.P. Adams, *comb. nov.* BASIONYM: *Juniperus urbaniana* Pilger & Ekman, Ark. Bot. 20A(15):9. 1926. TYPE: HAITI. Ouest Dept., Morne de la Selle, limestone area, 2500-2600 m, *Ekman H3157* (HOLOTYPE: B, destroyed; LECTOTYPE (here designated): *Ekman H3157* [K!]; Isolectotypes: IJ!,MICH,NY,S,US). *Juniperus barbadensis* L. var. *urbaniana* (Pilger & Ekman) Silba, *Phytologia* 56:340. 1984.

Prostrate shrub. Scale leaves opposite with leaf tips acuminate to mucronate. Branchlets mostly quadriform. Glands on old, brown, persistent whip leaves elongated (3-4 × as long as wide), conspicuous, dark brown, glands on scale leaves ovate. Seed cones with bloom, reddish-blue, 5-7 mm in diam., one and sometimes 2 seeds/cone. Fruit mature in one year. Pollen shed in winter (?).

Distribution: Endemic to Pic la Selle, Massif de la Selle, Haiti on peculiar limestone region near the top at ca. 2300-2550 m.

Representative Specimens: HAITI. Massif de la Selle: ca. 2550 m, *Judd 4935* (FLAS,BAYLU).

6. *Juniperus barbadensis* L. var. *barbadensis*, *Sp. Pl.* 1039. 1753. TYPE: BARBADOS. *Linnaeus 1198.1* (HOLOTYPE: LINN!). *Juniperus virginiana* L. var. *barbadensis* (L.) Gordon, *Pinetum* 114. 1858. *Sabina barbadensis* (L.) Small, *Fl. Southeastern U.S.* 33,1326. 1903.

Juniperus virginiana L. *humilis* Lodd., *Cat.* 1836.

Trees to 10 m tall. Bark thin, and bark separating in strips. Branchlets slender, leaves usually opposite, thus branchlets quadriform. Leaves light green, decurrent on young plants and on rapidly growing shoots but otherwise scale-like, about 1 mm long, with obtuse to acute tips, rounded on the back and tightly appressed. Glands on scale-like leaves inconspicuous, but oval to ovate, glands on old, brown persistent whip leaves conspicuous, sunken and elongated extending almost to the whip leaf tip. Seed cones reddish-blue with bloom, reniform (occasionally subglobose) and somewhat flattened, 4-5 mm long, 6-8 mm wide when reniform, 2-3 seeds/cone. Pollen shed January-March.

Distribution: Now known only from the island of St. Lucia, BWI, summit of Petit Piton, 700-730 m. The taxon is now extinct on Barbados, having been cut out before 1700 (Adams *et al.* 1987a,b; Adams 1989). A visit to Barbados revealed that the habitat was converted to sugar cane fields over 280 years ago.

Representative Specimens: ST. LUCIA. Petit Piton, April 1922, *Watts s.n.* (NY); Petit Piton, 730 m, *Adams 5367-5371* (BAYLU).

7. *Juniperus barbadensis* L. var. *lucayana* (Britton) R.P. Adams, *comb. nov.* BASIONYM: *Juniperus lucayana* Britton, *North Amer. Trees* 121. 1908. TYPE: NEW PROVIDENCE. Southwest Bay, coast coppice, *Britton & Brace 497* (Holotype not published, lectotype [here designated]: *Britton & Brace 497* [NY]).

Juniperus australis Pilger in Urban, *Symbol. Antill.* VII:479. 1913.

Juniperus virginiana L. var. *australis* Endl., *Syn. Conif.* 28. 1847.

Trees to 12 m tall. Bark thin and separating in strips. Branchlets slender, 0.5-2.0 cm long, width 0.8-0.9 mm, leaves usually opposite, thus branches quadriform. Leaves decurrent on young plants and on rapidly growing shoots but otherwise scale-like, about 1 mm long, with obtuse to acute tips, rounded on the back and tightly appressed. Glands on scale-like leaves inconspicuous, but oval to ovate, glands on old, brown persistent whip leaves not conspicuous, but if visible, then not sunken and extending almost to the whip leaf tip. Seed cones dark blue with bloom, usually reniform (occasionally subglobose) and somewhat flattened, 4-5 mm long by 5-7 mm wide when reniform, 2-4 seeds/cone. Pollen shed in January-February.

Britton did not cite any specimens in his publication of *Juniperus lucayana* (*North Amer. Trees* 121. 1908.). However, he did annotate the *Britton & Brace 497* specimen in the NY collection as "type." Thus, one can take this to be the intended type collection.

Reports of *Juniperus lucayana* on New Providence could not be confirmed in 1980. The taxon is also reported from Cat Cay. Specimens have been examined from Haiti (St. Michel de l'Atalaye; Gros Morne near Pendu; Bassin Bleu; and Crete-Sale), but field trips to the areas failed to discover any plants in recent years. *Juniperus lucayana* is now presumed to be extinct on Hispaniola.

Distribution: On limestone coppices near sea level, up to 1,600 m in dry hills. Cuba: Sierra de Nipe region, Holguin Province, swamps in the south-central portion of the Isle of Pines (= Isla de Pinos). Jamaica: 1,100-1,200 m near Clydesdale in St. Andrew Parish. Bahamas: On coppice limestone near sea level on Andros, Grand Bahama, and Great Abaco Islands.

Representative Specimens: CUBA. Holguin: 700-1,000 m, *Bisse 15775* (HAJB!); *Bisse, Myer, Bassler, Alvarez, & Gutiérrez 35818* (HAJB!). Guantanamo: *Bisse & Lippold 10222* (HAJB!). Isle of Pines: *Roig & Cremata 1846* (HAJB!).

JAMAICA. St. Andrew Parish: Cinchona, 1,500 m, *Harris 11928* (IJ!); near Cinchona, 1,500 m, *Maxon & Killip 1341* (IJ!); Clydesdale, 1,200 m, *Adams 2875-2884* (BAYLU).

Evolution of Bermudan, Caribbean, and other entire-leafed junipers

The junipers of the Western Hemisphere are found in two sections: section *Juniperus* with only one circumboreal species, *Juniperus communis* L. in North America; and section *Sabina* with 39 taxa in North America. Section *Sabina* has been divided into two informal series (Gausson 1968) based on the leaf margins (as seen at 40× magnification): entire (series) and denticulate (series). Recently, Adams & Demeke (1993), using DNA (RAPD's), have shown that the denticulate leafed junipers are confined to Guatemala, México, and the western United States. One should note that *J. phoenicea* L. (Mediterranean) has hyaline leaf margins that split into segments that appear to be denticulate. These are actually "pseudodenticulate" as the DNA clearly indicated (Adams & Demeke 1993). The denticulate-series likely originated in the highlands of México as a part of the Madro-Tertiary geoflora and radiated into the arid and semi-arid regions of the southwestern United States and throughout the highlands of México as far south as Guatemala (Figure 3). The southernmost species in continental North America (*J. comitana* Martínez, *J. gamboana* Martínez, and *J. standleyi* Steyermark) are now found in the highlands of Chiapas, México and Guatemala (Figure 3) at elevations ranging from 1,300 to over 3,000 m (Zanoni & Adams 1979; Adams *et al.* 1985). These species appear to have arisen out of the adaptive radiate complex of ancestral denticulate junipers (Figure 3). In the Western Hemisphere the entire-leafed-series is composed of *J. blancoi* Martínez, *J. horizontalis* Moench, *J. scopulorum* Sarg., *J. virginiana*, and *J. virginiana* var. *silicicola* on continental North America plus all the junipers of the West Indies and Bermuda (Figure 3). The entire-series on continental North America appears to have arisen from *J. virginiana* (or a common ancestor) from the ancient land mass of Appalachia (Anderson 1953; Flake *et al.* 1969). Elements of the eastern North American flora are thought to be closely related to species of the Old World (Fernald 1931) and this is certainly true of *J. virginiana* of the eastern United States and *J. sabina* L. of southern Europe.

Juniperus scopulorum, a sibling species of *J. virginiana*, has been treated as a variety of *J. virginiana* (var. *scopulorum* [Sarg.] Lemmon; and var. *montana* Vasey [Zanoni 1978]). Several studies have confirmed hybridization between these taxa (see Adams 1989). *Juniperus scopulorum* is postulated (Adams 1983b) to have arisen from *J. virginiana* (Figure 3). *Juniperus horizontalis* is closely related to both *J. scopulorum* and *J. virginiana* and has been treated as a variety, *J. virginiana* var. *prostrata* (Persoon) Torrey. *Juniperus horizontalis* hybridizes in several areas with *J. virginiana* and with *J. scopulorum* (see Adams 1989). *Juniperus horizontalis* is postulated to have been derived from *J. virginiana* or its ancestor (Figure 3). *Juniperus blancoi* is very closely related to *J. scopulorum* (Adams 1983b) and is confined to a few locations in central and northern México along flowing streams in high mountains. It is postulated to have been derived from *J. scopulorum* (it may be

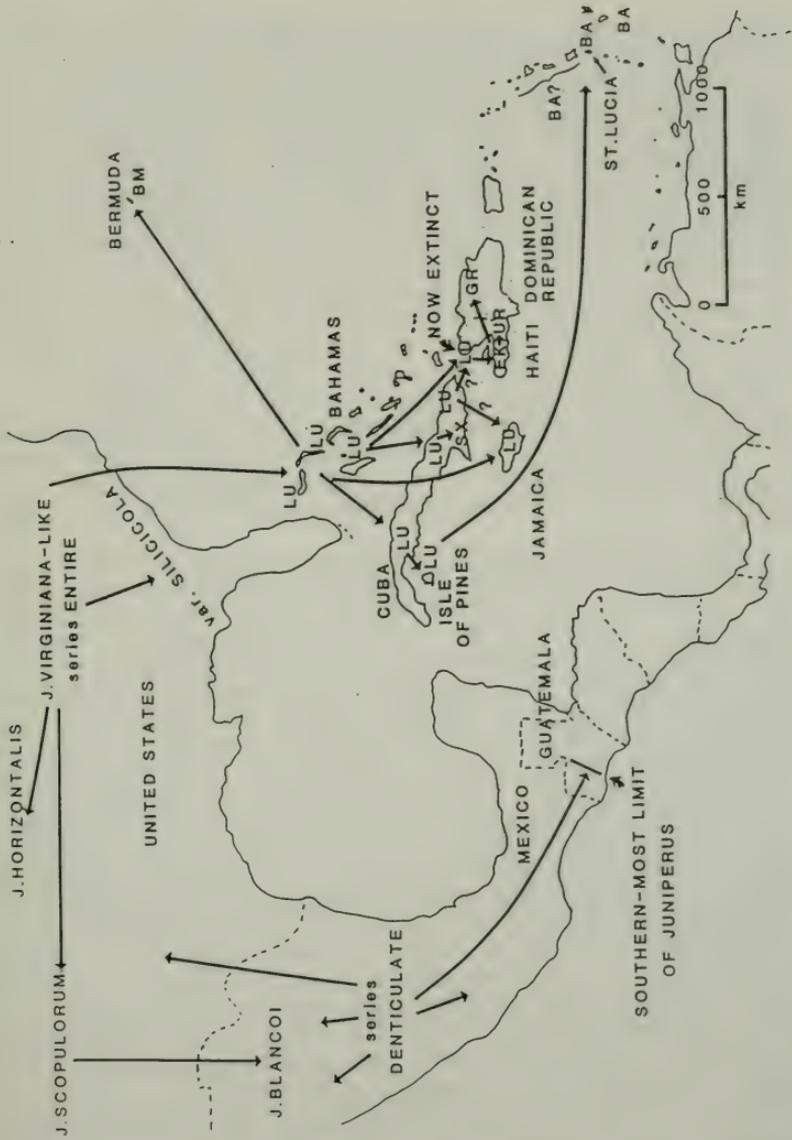


Figure 3. Proposed speciation of *Juniperus* into the Caribbean. Note especially that the junipers from the southern México/northern Guatemala area are in denticulate-series, whereas all the junipers of the Caribbean, Bermuda and eastern United States are in entire-series. BA = *J. barbadensis*; BM = *J. bermudiana*; EK = *J. gracilior* var. *ekmanii*; GR = *J. gracilior* var. *gracilior*; LU = *J. barbadensis* var. *lucayana*; SX = *J. saxicola*; UR = *J. gracilior* var. *urbaniana*.

conspecific; see Adams 1983b). The only other member of the entire-series, *J. virginiana* var. *silicicola*, is weakly differentiated from *J. virginiana* (Adams 1986) and may have been derived as recently as the Pleistocene (Figure 3).

Speciation of *Juniperus* into the West Indies is postulated to have occurred by long distance bird dispersal of *J. virginiana* (or its ancestor) to the Bahama Islands, and then to Bermuda, Cuba, Jamaica, and Hispaniola. *Juniperus saxicola* most likely evolved from ancestral *J. lucayana* in eastern Cuba from seeds carried into the Pico Turquino region. Either by a chance founder effect or by genetic drift, the gene(s) for controlling the conversion from juvenile (awn-like) to adult (scale-like) leaves became fixed such that all adults now have only juvenile leaves. *Juniperus barbadensis* appears to have arisen from *J. lucayana*, possibly from Cuba. The large distance from Cuba to St. Lucia and the Lesser Antilles render this hypothesis somewhat tentative. The alternative mode, island-hopping from Hispaniola is less attractive because suitable habitat would seem unlikely on many of the intervening islands.

The junipers of Hispaniola appear to have arisen from *Juniperus lucayana* or its ancestor. Although *J. lucayana* seems now to be extinct in Hispaniola, specimens collected earlier this century in northern Haiti appear to be *J. lucayana*. The junipers in the *J. gracilior* complex were most likely derived from ancestral *J. lucayana*. *Juniperus gracilior* var. *urbaniana* probably arose from *J. g.* var. *ekmanii* or its ancestor.

The evolutionary divergence of an ancestral juniper to become the present day *Juniperus bermudiana* in Bermuda must have been relatively recent because Bermuda's soil was formed only during the first interglacial period of the Pleistocene (Bryan & Cady 1934; Cox 1959). Herwitz (1992) recently estimated the ages of the highest eolianite dunes on Bermuda (Southampton, 73 m elev.) at 85,000 years before present (ybp) and the oldest hill, Walsingham (29 m elev.) at greater than 880,000 ybp.

Considering the genetic bottleneck that the Bermuda junipers must have gone through in arriving at their current reduced state, I cannot be certain that extant trees fairly represent the gene pool that evolved on Bermuda. This may account in part, for the rapid and large divergence of *Juniperus bermudiana* from the Bahama junipers.

All of the junipers of the Caribbean Islands have smooth leaf margins (entire-series), and no junipers from the denticulate (serrate) leaf-margined junipers (denticulate-series) are present in the Caribbean. In contrast, the junipers found in southern México and Guatemala are only in series-denticulate (the southernmost range of *Juniperus* in the continental Western Hemisphere). The affinities of the Caribbean junipers are clearly not with the junipers of Central America. The spread of the junipers across the Caribbean Islands has most likely been by birds from eastern North America. The differentiation of these island populations has been affected both by selection and founder effects. Genetic drift may also have played a part in their diversification because of the expansion and contraction of their ranges during the Tertiary and Pleistocene. According to Curray (1965), the Caribbean Sea level dropped approximately 122 m, about 19,000 ybp with another drop in sea level of 146 m at 40,000 ybp. Rosen (1978) showed that these drops in sea level would unite several of the Bahamian Islands. Conversely, a rise in the ocean level of only a few meters would inundate many juniper sites in the Bahamas where *J. barbadensis* var. *lucayana* often occurs at 1 to 2 m above sea level. Broecker (1965) reported evidence for higher levels about 80,000 ybp in the Bahamas. Thus, there is ample evidence of changes in available juniper habitat, which in turn has probably led to local extinctions as well as range expansions. This, coupled with limited gene flow between the islands, has led to the considerable amount of diversity and differentiation in the leaf oils of the Caribbean junipers.

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