TAXONOMY OF THE MULTI-SEEDED, ENTIRE LEAF TAXA OF JUNIPERUS, SECTION SABINA: SEQUENCE ANALYSIS OF nrDNA AND FOUR cpDNA REGIONS

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ABSTRACT

An analysis of the multi-seeded, entire leaf margined taxa of Juniperus sect. Sabina is presented based on nrDNA and four cpDNA regions. These DNA data revealed several previously unknown affinities with J. sabina and J. chinensis, better resolution of the J. excelsa - polycarpos complex and the Caribbean junipers, including the recognition of Juniperus gracilior var. saxicola, comb. nov. and Juniperus semiglobosa var. jarkendensis, comb. nov. Juniperus sabina var. davurica (Mongolia) was found to be clearly separated from J. sabina (Europe), supporting the recognition of J. davurica Pall., J. d. var. arenaria, comb. nov. and J. d. var. mongolensis, comb. nov. The taxonomy of the entire group is reviewed and necessary changes made in several taxa. Phytologia 94(3): 350-366 (December 1, 2012).

KEY WORDS: Taxonomy, Juniperus, section Sabina, nrDNA, petN-psbM, trnS-trnG, trnD-trnT, trnL-trnF, Juniperus gracilior var. saxicola com. nov., J. semiglobosa var. jarkendensis comb. nov., J. davurica var. arenaria, comb. nov. and J. davurica var. mongolensis, comb. nov.

Recently, Mao et al. (2010) presented an abbreviated phylogeny of *Juniperus* as part of a study focused on intercontinental dispersal. As such, that report was incomplete as it did not include all taxa in the three sections, nor did it include taxonomically difficult infra-specific taxa.

To remedy these shortcomings, we have presented analyses of the serrate leaf taxa of *Juniperus*, sect. *Sabina* (Adams and Schwarzbach, 2011) and all taxa of *Juniperus* sect. *Juniperus* (Adams and Schwarzbach, 2012). The purpose of the current study is to continue this work by analyzing all the multi-seeded, entire leaf margined taxa of section *Sabina* using the most informative nuclear (nrDNA- ITS) and cpDNA regions (petN-psbM, trnS-trnG, trnD-trnT, trnL-trnF). The pseudo-denticulate species, *J. phoenicea* (Adams, 2011) is included, as its placement is uncertain (Mao et al. 2010).

MATERIALS AND METHODS

Specimens used in this study: J. blancoi, El Oro, Mex., Adams 6849, J. b. var. mucronata, Maicoba, Mex., Adams 8702, J. b. var. huehuentensis, w. Durango, Mex. Adams 10247, J. barbadensis, Petit Peton, St. Lucia, BWI, Adams 5368, J. b. var. lucayana, Isle de Pinos, Cuba, Adams 5281, J. bermudiana, Bermuda, Adams 11083, J. chinensis, Shizuoka Prefecture, Japan, Adams 8535, J. c. var. sargentii, Hokkaido, Japan (ex N. Yoshida) Adams 8688, J. communis L. var. communis, Adams 7846, 7847, Stockholm, Sweden (outgroup), J. erectopatens, s of Songpan, Sichuan, China, Adams 8532, J. excelsa, w of Lemos, Greece, Adams 8785, 9433, J. foetidissima, Mt. Parnassus, Greece, Adams 5645, J. gracilior, Dominican Republic, Adams 7664, J. g. var. ekmanii, Haiti, Adams 7653, J. g. var. urbaniana, Haiti, Adams 7656, J. horizontalis, Montana, USA, Adams 7096, J. jarkendensis, Kunlun Mtns., Xinjiang, China, Adams 7820, J. maritima, Brentwood Bay, VI, BC, Canada, Adams 11056, J. phoenicea, El Penon, Spain, Adams 7077, J. p. var. turbinata, w Setubal, Portugal, Adams 7077, Tarifa sand dunes, Spain, Adams 7302, J. polycarpos, Lake Sevan, Armenia, Adams 8761, J. p. var. seravschanica, s of Dzhabagly, Kazakhstan, Adams 8224, J. p. var. seravschanica, Quetta, Pakistan (ex A. Hafeez Buzdar) Adams 8483, J. p. var. turcomanica, Kopet Mtns., Turkmenistan, Adams 8757, J. procera, 6184, w of Addis Ababa,

Ethiopia, Adams 6184, J. procumbens, 8683, Hokkaido, Japan (ex N. Yoshida) Adams 8683, J. sabina, Baltschieder, Switzerland, Adams 7611, J. s. var. arenaria, Lake Qinghai sand dunes, Qinghai, China, Adams 10347, J. s. var. davurica, 15 km se Ulan Batar, Mongolia, Adams 7353, J. s. var. mongolensis, on sand dunes, 80 km sw Ulan Bator, Mongolia, Adams 7354, J. scopulorum, Kamas, UT, USA, Adams 10895, J. semiglobosa, Kyrgyz range, 60 km sw Bishket, Kyrgystan, Adams 8210, J. saxicola, Pico Turquino, Cuba, Adams 5284, J. thurifera, 2 km e Ruidera, Spain, Adams 7083, J. t. var. africana, 60 km e Marrakech, Morocco, Adams 9420, J. tsukusiensis, Yakushima Island, Japan (ex Jin Murata), Adams 8806, J. tsukusiensis var. taiwanensis, Mt Chingshui, Taiwan, Adams 9061, J. virginiana, Waco, TX USA, Adams 6754, 32 km e Knoxville, TN, USA, Adams 10234, J. v. var. silicicola, Ft. DeSoto Park, Mullet Key, FL, USA, Adams 9186-88. Voucher specimens are deposited in the herbarium, BAYLU, Baylor University.

One gram (fresh weight) of the foliage was placed in 20 g of activated silica gel and transported to the lab, thence stored at -20° C until the DNA was extracted by use of a Qiagen mini-plant kit (Qiagen, Valencia, CA) as per manufacturer's instructions.

PCR amplification, sequencing and data analyses - see Adams and Schwarzbach (2012).

RESULTS AND DISCUSSION

The multi-seeded, smooth leaf margined junipers are very diverse (Fig. 1) having several distinct groups: the eastern hemisphere excelsa-polycarpos, chinensis, sabina and the western hemisphere virginiana and Caribbean clades. Juniperus erectopatens exhibits an isolated position (Fig. 1); J. phoenicea was included, although it is loosely associated with this group (Fig. 1). Despite the large amount of data, the extremely closely related taxa of the Caribbean are not resolved, awaiting more detailed analyses (Fig. 1). The classical taxon, J. polycarpos var. seravschanica (Kazakhstan, Pakistan) is placed in a different clade from that of J. polycarpos - excelsa (Fig. 1).

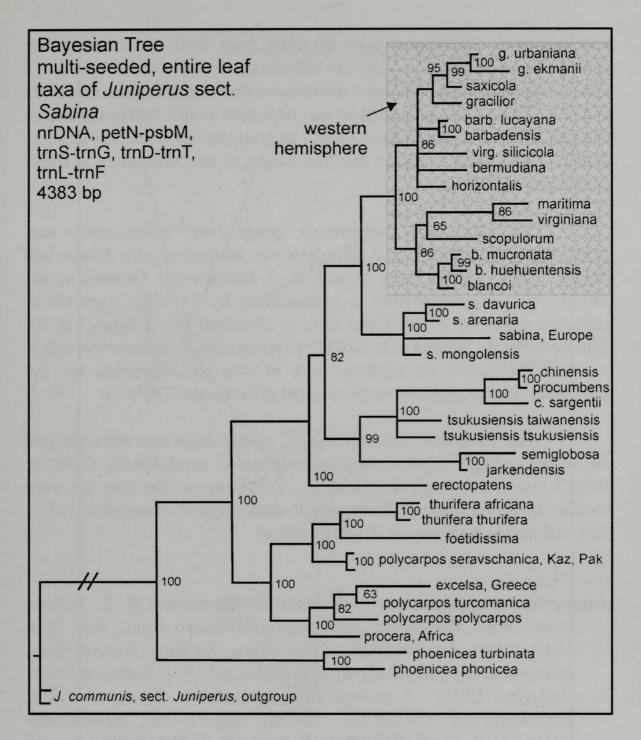


Figure 1. Bayesian tree for multi-seeded, entire leaf taxa, sect. *Sabina*. Numbers at the branch points are posterior probabilities (as percent).

Taxonomic considerations

To examine taxonomic ranks at the terminus of the tree, a minimum spanning network was constructed to include both SNPs and indels (termed Mutational Events, MEs). *Juniperus phoenicea* and *J. p.*

var. *turbinata* are separated by 66 MEs from their nearest neighbor (*chinensis* group, Fig. 2). The 23 MEs between var. *phoenicea* and var. *turbinata* is comparable to differences between recognized species Fig. 2). These data suggest that var. *turbinata* might be recognized at the specific level (*J. turbinata* Guss.) as proposed by LeBreton and Paz (2001). Additional research into the nature of this difference is under investigation (RPA).

The Juniperus tsukusiensis group (var. tsukusiensis, var. taiwanensis) was treated as J. chinensis var. tsukusiensis by Adams and Farjon (Table 1), but later treated as J. tsukusiensis (Adams et al., 2011). It is separated from J. jarkendensis by 24 MEs, from the J. davurica group by 24 MEs and from J. chinensis by 32 MEs (Fig. 2). The decision by Adams et al. (2011) to recognize J. tsukusiensis and J. t. var. taiwanensis as separate taxa is strongly supported by our molecular data as well as morphological differences (Table 1).

The *Juniperus jarkendensis | J. semiglobosa* taxa are separated by 24 MEs (Fig. 2), but *J. jarkendensis* and *J. semiglobosa* differ by only 7 out of the total of 354 MEs. Furthermore, the taxa are very similar in morphology. The present data support recognition of *J. jarkendensis* as a variety of *J. semiglobosa*:

Juniperus semiglobosa var. jarkendensis (Komarov) R. P. Adams, comb. nov. Basionym: Juniperus jarkendensis Kom., Not. Syst. Herb. Petrop. 4: 181 (1923). Type: China, Xinjiang, Kunlun Shan, Yarkant River, mtns. near Shache (Yarkant), V. I. Robarovski 409 (holotype LE!). J. sabina var. jarkendensis (Kom.) J. Silba, Phytologia 68: 33 (1990). Sabina vulgaris var. jarkendensis (Kom.) C. Y. Yang in Fl. Reipub. Pop. Sin. 7: 360 (1978).

Juniperus sabina (Europe and central Asia) is separated by 24 MEs from the davurica group (J. s. var. davurica, var. arenaria, var. mongolensis) (Fig. 2).

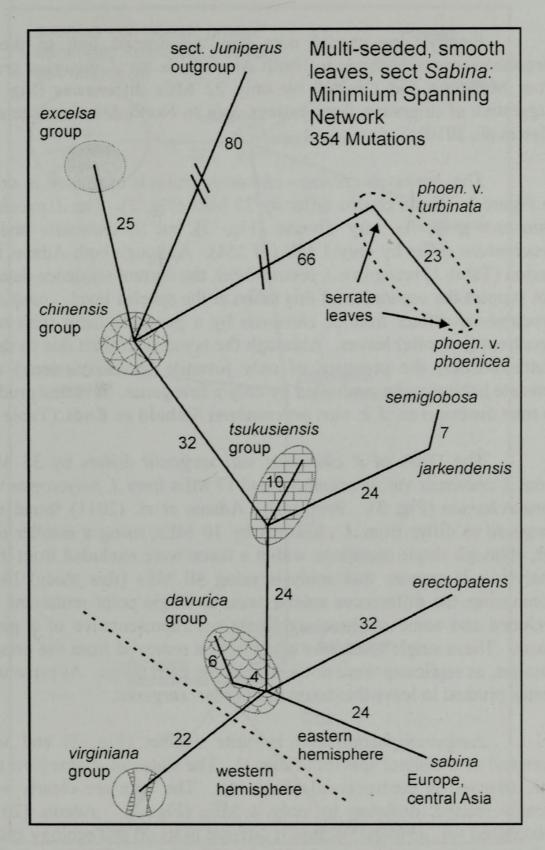


Figure 2. Minimum spanning network of the multi-seeded, smooth leaf junipers of sect. *Sabina*. Numbers next to links are the number of Mutational Events (MEs = #SNPs + # indels).

Finally, one should note that the nearest link to the *J. virginiana* group, endemic to North America, is the *J. davurica* group from Mongolia and Qinghai by only 22 MEs differences (Fig. 2), suggestive of migration from eastern Asia to North America (see also Mao et al., 2010).

The Juniperus excelsa - chinensis group is examined in detail in Figure 3. These groups differ by 25 MEs (Fig. 2). The J. excelsa - chinensis group is very diverse (Fig. 3) but J. chinensis and J. procumbens differ by only 1 ME (of 354). Although both Adams and Farjon (Table 1) recognize J. procumbens, the current sequence data do not support the separation of this taxon at the species level. Juniperus procumbens differs from J. chinensis by a prostrate habit with only decurrent (juvenile) leaves. Although the taxon is distinct due to these characteristics, the presence of only juvenile leaves (neoteny) and prostate habit may be controlled by only a few genes. It seems prudent to treat the taxon as J. c. var. procumbens Siebold ex Endl. (Table 1).

The DNA of *J. chinensis* var. *sargentii* differs by 35 MEs from *J. chinensis* var. *procumbens* and 17 MEs from *J. polycarpos* var. *seravschanica* (Fig. 3). Previously, Adams et al. (2011) found var. *sargentii* to differ from *J. chinensis* by 10 MEs, using a smaller data set, although single mutations within a taxon were excluded from their analysis. It appears that analysis using all MEs (this study) likely accentuates the differences among taxa, as single point mutations are included and some of these are likely not representative of a given taxon. These single mutations could not be removed from the present data set, as replicates were not analyzed for each taxon. At present, it seems prudent to leave this taxon as *J. c.* var. *sargentii*.

Juniperus foetidissima is quite distinct (Fig. 3) and well accepted as a distinct species (Table 1). The status of J. thurifera and var. africana is controversial (Table 1). The taxa are clearly very closely related, differing by only 4 MEs (Fig. 3). Adams (2011) recognized var. africana because it differed in its oil and ecology and to call attention to its conservation in the Atlas Mtns. The present data offer little support for the recognition of var. africana.

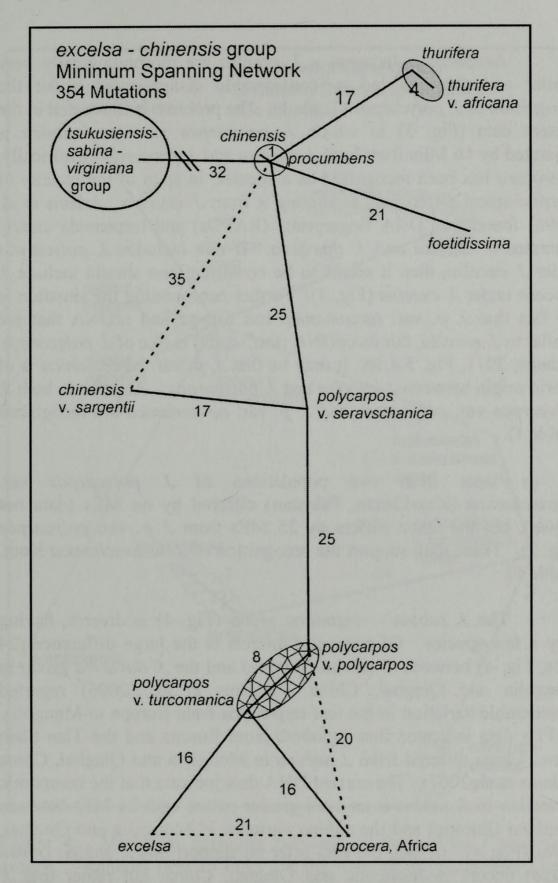


Figure 3. Minimum spanning network of the *excelsa* - *chinensis* group. Numbers next to links are the number of Mutational Events (MEs). Dashed lines are second nearest links.

Juniperus polycarpos - J. excelsa are morphologically very similar and this has led to considerable disagreement about the recognition of J. polycarpos (Table 1). The problem is illustrated in the present data (Fig. 3) in which J. polycarpos var. turcomanica is separated by 16 MEs from both J. excelsa and J. procera. Historically, J. procera has been recognized as a species, in spite of the paucity of morphological differences separating it from J. excelsa. Adams et al. (1993) found that DNA fingerprints (RAPDs) and terpenoids clearly separated J. excelsa and J. thurifera. If one includes J. polycarpos under J. excelsa, then it seems to be consistent one should include J. procera under J. excelsa (Fig. 3). Further confounding the situation is the fact that J. p. var. turcomanica has foliage and nrDNA that are similar to J. excelsa, but its cpDNA (tnrC-trnD) is like of J. polycarpos. (Adams, 2011, Fig. 5.4.1). It may be that J. p. var. turcomanica is of hybrid origin between J. excelsa and J. polycarpos. At present, both J. polycarpos var. polycarpos and J. p. var. turcomanica are recognized (Table 1).

Plants from two populations of *J. polycarpos* var. *seravschanica* (Kazakhstan, Pakistan) differed by no MEs (data not shown), but the taxon differs by 25 MEs from *J. p.* var. *polycarpos* (Fig. 3). These data support the recognition of *J. seravschanica* Kom. (Table 1).

The *J. sabina - virginiana* group (Fig. 4) is diverse, having only a few species. Of particular interest is the large difference (24 MEs, Fig. 4) between *J. sabina* (Europe) and the *J. davurica* group in Mongolia and Qinghai, China. Adams et al. (2006) reported considerable variation in the leaf terpenoids from Europe to Mongolia. RAPDs data indicated that *J. sabina* from Europe and the Tian Shan Mtns., China differed from *J. sabina* in Mongolia and Qinghai, China (Adams et al. 2007). The current DNA data indicate that the taxonomic separation in *J. sabina* is an even greater extent with 24 MEs between *J. sabina* (Europe) and the *sabina* varieties in Mongolia and Qinghai, China (Fig. 4). In fact, the data offer no support that *J. sabina* (*sensu stricto*) occurs in Mongolia and Qinghai, China, but rather that *J. davurica* Pall. should be recognized in this region (Table 1). It is apparent that *J. sabina* var. *arenaria* and *J. s.* var. *mongolensis* are not

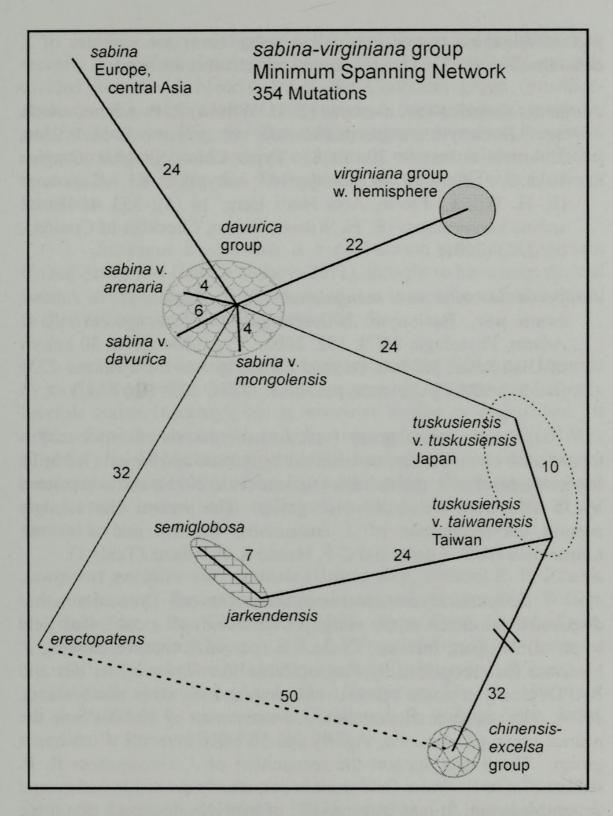


Figure 4. Minimum spanning network of the *sabina - virginiana* groups. Numbers next to links are the number of Mutational Events (MEs). Dashed line is second nearest link.

part of *J. sabina* (*sensu stricto*) but rather these are varieties of *J. davurica* (Fig. 4). Two nomenclatural adjustments are needed:

Juniperus davurica var. arenaria (E. H. Wilson) R. P. Adams, comb. nov. Basionym: Juniperus chinensis var. arenaria E. H. Wilson, J. Arnold Arbor. 9: 20. 1928. Type: China, Qinghai, Qinghai Lake, J. F. Rock 13346 (holotype A!; isotypes E, K). J. arenaria (E. H. Wilson) Florin, Acta Horti Berg. 14 (8): 353. 1948. J. sabina var. arenaria (E. H. Wilson) Farjon, Checklist of Conifers, ed. 2, 73 (2001).

Juniperus davurica var. mongolensis (R. P. Adams) R. P. Adams, comb. nov. Basionym: Juniperus sabina var. mongolensis R. P. Adams, Phytologia 88(2): 182. 2006. Type: Mongolia, 80 km sw of Ulan Batar, 1230 m, on sand dunes, 16 Jun 1994, Adams 7255 (holotype BAYLU); topotypes Adams 7254, 7256 (BAYLU).

The *J. tsukusiensis* group (var. *tsukusiensis var. taiwanensis*) is treated as *J. chinensis* var. *tsukusiensis* by Adams and Farjon (Table 1), but later treated as *J. tsukusiensis* (Adams et al., 2011), and is separated by 32 MEs from the *J. chinensis* group. The present data strongly support the recognition of *J. tsukusiensis* Masam. and *J. t.* var. *taiwanensis* (R. P. Adams and C-F. Hsieh) R. P. Adams (Table 1).

Juniperus erectopatens is an unusual taxon. The senior author discovered the taxon at the margins (wasteland) of a cultivated field south of Songpan, Sichuan, China. It is a small tree, resembling J. chinensis (as recognized by Farjon, Table 1). However, its oils and RAPDs clearly separate it from J. chinensis and any other taxa (Adams, 1999). The sequence data separate J. erectopatens by 32 MEs from the nearest taxon (J. davurica, Fig. 4) and 50 MEs from the J. chinensis group. These data support the recognition of J. erectopatens R. P. Adams (Table 1). More field work is desperately needed to understand better this taxon. It may be a product of hybridization, such that these 'apparent mutations' are actually DNA from another species.

The *J. virginiana* group is the least diverse and probably most recently diversified of the major groups (Fig. 5). Overall, the group is divided into the *J. blancoi* group, the Caribbean group (*gracilior-barbadensis*) and outliers, *J. virginiana*, *J. horizontalis*, *J. maritima* and *J. scopulorum* (Fig. 5). The *J. blancoi* group is located in western and central Mexico and consists of 3 closely related varieties, differing by only 3-4 MEs (Fig. 5). Both Adams and Farjon (Table 1) accept these taxa.

Juniperus horizontalis is a cool-season species of northern United States and Canada (Adams 2011), thought to have been derived from *J. scopulorum* or *J. virginiana*, so it is surprising to find it linked to the Caribbean and *blancoi* groups (Fig. 5).

The Caribbean group is closely related and difficult to separate by morphology. The Cuban *Juniperus saxicola* is a tree that has only juvenile leaves (neoteny), but is otherwise similar to *J. gracilior*. It differs from the shrubby *J. gracilior* var. *urbaniana* by only 3 MEs (Fig. 5). The DNA data suggest that *J. saxicola* and *J. g.* var. *ekmanii* are conspecific members of the *J. gracilior* group. However, tree habit and juvenile leaves seem sufficient to recognize *J. saxicola* at the varietal level:

Juniperus gracilior var. saxicola (Britton & P. Wilson) R. P. Adams, comb. nov. Basionym: Juniperus saxicola Britton & P. Wilson, Bull. Torrey Bot. Club 50: 35. 1923. Type: Cuba, Granma Prov., Sierra Maestra, Oriente, J. S. S. (Frere) Leon 10798 (holotype NY!). J. barbadensis L. subsp. saxicola (Brittion & P. Wilson) Borhidi, Acta Bot. Acad. Sci. Hungarica 37: 90. 1992. J. barbadensis L. var. saxicola (Brittion & P. Wilson) Silba, J. Int. Conifer Preserv. Soc. 7(1): 25. 2000.

Juniperus barbadensis (sensu stricto) is known only from Petit Piton, St. Lucia, BWI (Adams, 2011), whereas J. b. var. lucayana is widespread growing on Hispanola, Jamaica, Cuba and the Bahama Islands. The taxa are nearly indistinguishable, differing only by glands conspicuous on old whip leaves (Adams 2012). The DNA data show these taxa differ by only 1 ME (of 354), providing no support to the continued recognition of J. b. var. lucayana (Table 1).

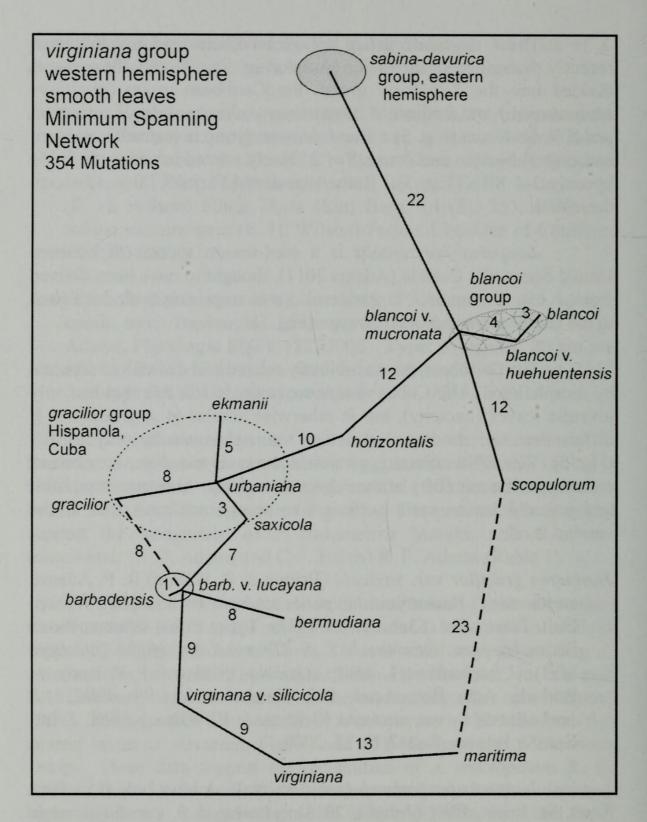


Figure 5. Minimum spanning network of the *virginiana* group. Numbers next to links are the number of MEs. Dashed lines are second nearest link.

Juniperus bermudiana is obviously closely related to J. barbadensis (Fig. 5), but growing in an isolated habitat has evolved shorter scales leaves appearing as a string of beads, not to mention differences in its leaf essential oils (Adams 2000; Adams and Wingate 2008; Adams 2008). Although its DNA differences are only 8 MEs, it seems prudent to retain it at the specific level (Table 1).

Juniperus virginiana var. silicicola is a curious taxon with affinities to both the Caribbean junipers and the mainland, J. virginiana. Adams et al. (2008) found that its nuclear nrDNA was identical to J. virginiana, but its cpDNA (trnC-trnD) was identical to the Caribbean species including, a 245 bp indel. That data was suggestive that J. v. var. silicicola may be of hybrid origin between J. virginiana and Caribbean J. barbadensis (or an ancestor). The present DNA data show the taxon to occupy an intermediate position between J. virginiana and J. barbadensis (Fig. 5).

Juniperus scopulorum is separated by 12 MEs from *J. blancoi* var. *mucronata* and 23 MEs from *J. maritima* (Fig. 5). The close relationship of *J. scopulorum* and *J. blancoi* is shown in their morphology, and by likely hybridization in the Colonia Pacheco area of northern Mexico in the Pleistocene with nearby populations of *J. b.* var. *mucronata* (Adams 2011b).

Juniperus maritima is separated by 13 MEs from J. virginiana, and 23 MEs from J. scopulorum. Several characters support the close relationship of J. maritima and J. virginiana: slender foliage, strong central axis, fruit maturing in one year, and growth in mesic habitats. If J. maritima were to be treated as a variety, it would have to be a variety of J. virginiana, not J. scopulorum. However, DNA data give strong support to the continued recognition of J. maritima at the specific level (Table 1).

Table 1. Comparison of Adams and Farjon taxonomic treatment of taxa in this study. Taxa with support for a modified taxonomic status are in bold.

| Adams (2011) | Farjon (2005, 2010) | Supported, this study |
|-------------------------|-------------------------|--------------------------|
| J. barbadensis | J. barbadensis | J. barbadensis |
| J. b. var. lucayana | J. b. var. lucayana | J. barbadensis |
| J. bermudiana | J. bermudiana | J. bermudiana |
| J. blancoi | J. blancoi | J. blancoi |
| J. b. v. huehuentensis | J. blancoi | J. b. var. huehuentensis |
| J. b. var. mucronata | J. b. var. mucronata | J. b. var. mucronata |
| J. chinensis | J. chinensis | J. chinensis |
| J. c. var. sargentii | J. c. var. sargentii | J. c. var. sargentii |
| J. c. var. tsukusiensis | J. c. var. tsukusiensis | J. tsukusiensis |
| J. c. var. taiwanensis | J. c. var. tsukusiensis | J. t. var. taiwanensis |
| J. erectopatens | J. chinensis | J. erectopatens |
| J. excelsa | J. excelsa (in part) | J. excelsa |
| J. foetidissima | J. foetidissima | J. foetidissima |
| J. gracilior | J. gracilior | J. gracilior |
| J. g. var. ekmanii | J. g. var. ekmanii | J. g. var. ekmanii |
| J. g. var. urbaniana | J. g. var. urbaniana | J. g. var. urbaniana |
| J. horizontalis | J. horizontalis | J. horizontalis |
| J. jarkendensis | J. semiglobosa | J. semiglobosa |
| | | var. jarkendensis |
| J. maritima | J. scopulorum | J. maritima |
| J. phoenicea | J. phoenicea | J. phoenicea |
| J. p. v. turbinata | J. p. subsp. turbinata | J. turbinata |
| J. procera | J. procera | J. procera |
| J. procumbens | J. procumbens | J. chinensis var. |
| | | procumbens |
| J. polycarpos | J. excelsa subsp. | |
| | polycarpos | J. polycarpos |
| J. p. v. seravschanica | J. e. subsp. polycarpos | J. seravschanica |
| J. p. v. turcomanica | J. e. subsp. polycarpos | |
| J. sabina | J. sabina | J. sabina |
| J. s. var. arenaria | J. s. var. arenaria | J. davurica var. |
| | | arenaria |
| J. s. var. davurica | J. s. var. davurica | J. davurica var. |
| | | davurica |
| | | |

| J. s. var. mongolensis | J. s. var. arenaria | J. davurica var. mongolensis |
|------------------------|-----------------------|---------------------------------|
| J. scopulorum | J. scopulorum | J. scopulorum |
| J. semiglobosa | J. semiglobosa | J. semiglobosa |
| J. saxicola | J. saxicola | J. gracilior var. saxicola |
| J. thurifera | J. thurifera | J. thurifera |
| J. t. var. africana | J. thurifera | J. thurifera |
| J. virginiana | J. virginiana | J. virginiana |
| J. v. var. silicicola | J. v. var. silicicola | J. v. var. silicicola |

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