THE EVOLUTION OF CARIBBEAN *JUNIPERUS* (CUPRESSACEAE): TERPENOIDS, RAPDS AND DNA SNPs DATA

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ABSTRACT

SNPs from nrDNA and trnC-trnD cp DNA for the Caribbean junipers have provided additional insight into the evolution of this group of smooth leaf margined junipers. Comparing leaf terpenoids, RAPDS and SNPs from nrDNA and trnC-trnD cp DNA show that each data set reveals different facets of the relationships. In general, the data sets support four major groups: *Juniperus barbadensis* - *lucayana; J. bermudiana*; *J. gracilior* - *ekmanii* - *urbaniana*; *J. saxicola*; *J. virginiana* - *silicicola*. Based on the concordance of these data and morphology, the Caribbean junipers are treated as four species, three of these having varieties: *J. barbadensis, J. barbadensis* var. *lucayana*, *J. bermudiana, J. gracilior, J. gracilior* var. *ekmanii, J. gracilior* var. *urbaniana, J. saxicola, J. virginiana* and *J. virginiana* var. *silicicola*. The evolutionary colonization pathways of the Caribbean junipers are discussed.

KEY WORDS: *Juniperus,* Caribbean, evolution, systematics, terpenoids, RAPDs, nrDNA, trnC-trnD cp DNA, SNPs, Cupressaceae

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The Caribbean junipers have been the focus of our lab in several studies (Adams, 1983, 1986, 1989, 1995, 1997, 2000; Adams et al. 1987; Adams and Hogge, 1983). There are numerous older studies, beginning with Linnaeus (1753) who described only three junipers from the New World (*J. virginiana*, "Virginia and Carolina"; *J. barbadensis*,

"America"; and *J. bermudiana*, "America"). However, Hemsley (1883) equated *J. barbadensis* L. with *J. bermudiana* L., 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* Britt. 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 5 species: *J. saxicola* Britt. & P. 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 and Correll (1982) recognized the juniper of the Bahamas as *J. barbadensis*.

Adams (2000, 2004) recognized: *J. bermudiana* (endemic to Bermuda); *J. barbadensis* (endemic to St. Lucia, extinct on Barbados); *J. lucayana* (Bahamas, Cuba, Jamaica, likely extinct in Haiti), *J. gracilior* (endemic to Hispaniola), *J. gracilior* var. *ekmanii* (Florin) R. P. Adams (endemic to Hispaniola), *J. gracilior* var. *urbaniana* Pilger & Ekman) R. P. Adams (endemic to Haiti), and *J. saxicola* (endemic to Cuba). The juniper of the southeastern United States that occurs on coastal foredunes was recognized as *J. virginiana* var. *silicicola* (Small) E. Murray (Adams, 2004). Farjon (2005) followed Adams (2004) treatment, except he recognized *J. lucayana* as *J. barbadensis* var. *lucayana* (Britt.) R. P. Adams.

Figure 1 shows the populations sampled in this and previous studies. Several taxa are very rare: *J. barbadensis* var. *barbadensis*, known only from Petit Piton, St. Lucia; *J. bermudiana*, endemic to Bermuda; *J. gracilior* var. *ekmanii*, Pic la Selle, Haiti and adjacent mountain in Dominican Republic. *J. gracilior* var. *urbaniana*, Pic le Selle, Haiti, *J. saxicola*, Pico Turquino, Cuba. *Juniperus barbadensis*

has been extinct on Barbados for over 280 years (Adams, 2004) and *J.* lucayana (*J. barbadensis* var. *lucayana*) is presumed extinct in Haiti (and Hispanola) (Adams, 2004).

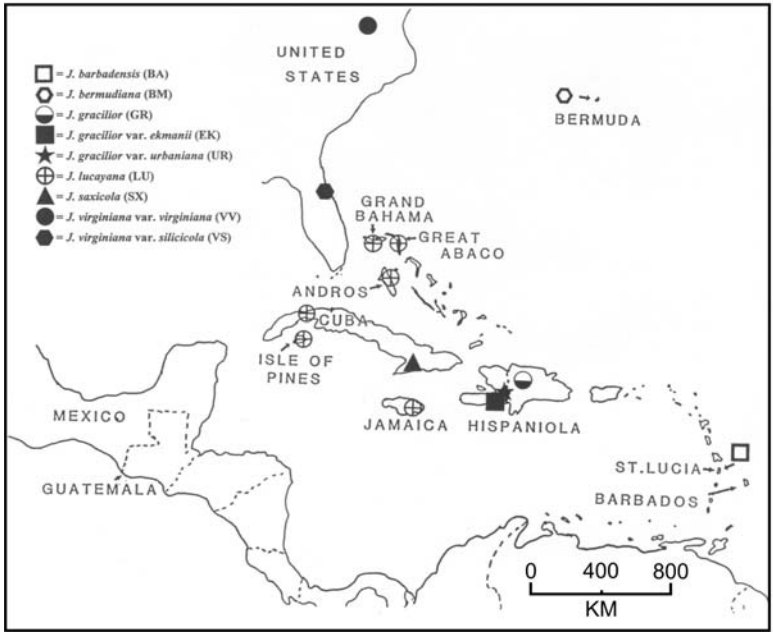

Figure 1. Populations of *Juniperus* sampled in this and previous studies.

Using terpenoid data (based on Adams, 1997), a PCO of the Caribbean junipers (Fig. 2) shows that all of the varieties of *J. gracilior* are very similar in their oils with similarities of 0.85 to 0.88 (eg. 85 - 88%). Their oils are dominated by bornyl acetate (35.7 - 43.9%, vs. less than 4.1% in all other taxa) and all have 0.5 - 0.9% cis-pinene hydrate (found only as a trace in *J. barbadensis*) and 0.8 - 1.2% α-terpineol (found only as a trace in all other taxa). It is interesting to note that the oil of *J. bermudiana* is quite distinct being only 0.77 similar to *J. lucayana* (Fig. 2) and much less similar to *J. virginiana* (0.63, not shown). *Juniperus barbadensis* (St. Lucia) is linked (0.82) to

J. lucayana (Cuba) and provides the linkage between *J. gracilior* (Hispanola) and *J. lucayana* (Cuba).

Juniperus virginiana var. *virginiana* and var. *silicicola* are very similar (0.83) and quite distinct, linking with *J. lucayana* (Bahamas) at 0.72. The *J. lucayana* samples are in two groups: the Bahamas and Cuba-Jamaica. This seems to represent a geographic split within their populations. *Juniperus saxicola* is loosely linked to *J. lucayana* (0.78, Fig. 2).

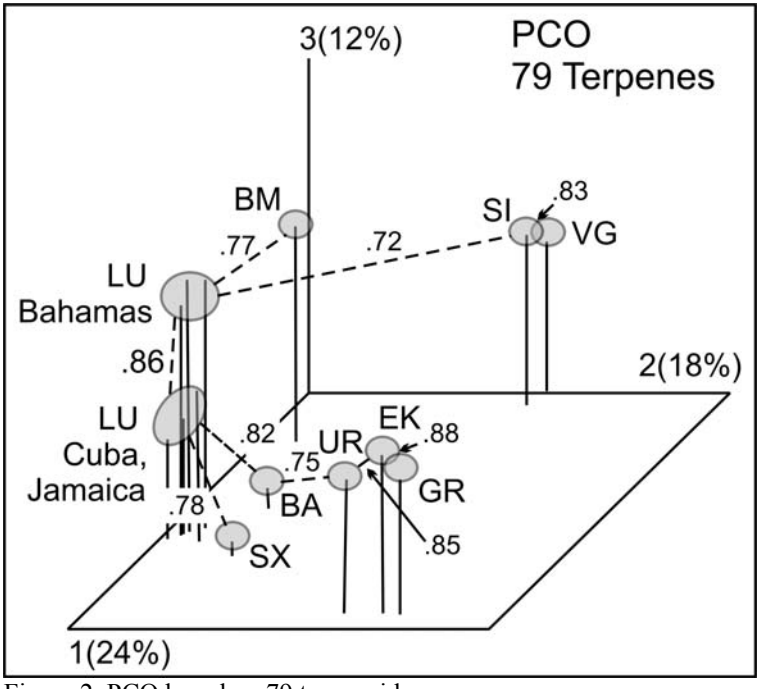

Figure 2. PCO based on 79 terpenoids.

Figure 3 shows the PCO based on 132 RAPDs (re-drawn from Adams, 2000). Again, one sees that all of the varieties of *J. gracilior* are very similar in their RAPDs with similarities of 0.83. *Juniperus bermudiana* is less distinct, and similar to *J. lucayana* (Fig. 3). Again, *J. bermudiana* is much more similar to *J. lucayana* (0.83) than to *J. virginiana* (0.70, not shown). This suggests that *J. bermudiana* did not arise from *J. virginiana* (directly) but from *J. lucayana* (or an ancestor).

With the RAPDs, *J. saxicola* links to *J. barbadensis*, but it has essentially the same linkage to *J. gracilior var. ekmanii* (not shown).

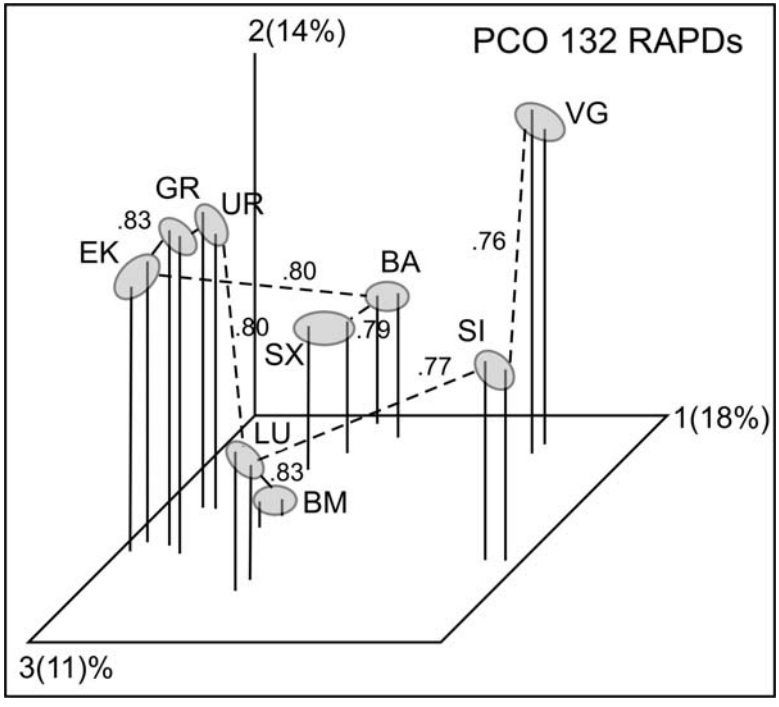

Figure 3. PCO based on 132 RAPDs.

Juniperus virginiana and *J. v.* var. *silicicola* are well separated (Fig. 3).

The purpose of this study was to utilize additional data sets (Single Nucleotide Polymorphisms, SNPs) of nr DNA and trnC-trnD, cp DNA to gain additional insight on the relationships among the *Juniperus* taxa in the Caribbean.

MATERIALS AND METHODS

Specimens collected: taxon, acronym, collector number, location: *J. barbadensis* (BA), *Adams 5367-5371;* Petit Piton, St.

Lucia, BWI; *J. bermudiana* (BM), *Adams 11080-11082*, Bermuda; *J. gracilior* var. *ekmanii* (EK), *Adams 7653-7654*, 3-4 km ne Mare Rouge, Pic la Selle, Haiti; *J. gracilior* var. *gracilior* (GR), *Adams 7664-7667,* w of Constanza, Dominican Republic; *J. gracilior* var. *urbaniana* (UR) *Adams 7656-7658,* 4-5 km ne Mare Rouge, Pic la Selle, Haiti; *J. lucayana: Adams 5259-5280*, Havana Botanical Garden (seed from Sierra de Nipe), Cuba; *Adams 5281-5282*, Havana Botanical Garden (seed from Isle de Pinos), Cuba; *J. saxicola* (SX) *Adams 5284-5285,* w slope of Pico Turquino, Prov. Granma/ Santiago de Cuba boundary, Cuba; *J. virginiana* var. *virginiana* (VG) *Adams 6753-6755*; on I35, Hewitt, TX; *J. virginiana* var. *silicicola* (SI) *Adams 9186-9188,* Ft. Desoto Park, Mullet Key, Florida. Herbarium vouchers for all of the aforementioned collections are deposited at BAYLU.

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^{o} C until the DNA was extracted. DNA was extracted using the Qiagen DNeasy mini kit (Qiagen Inc., Valencia CA).

SNPs obtained from DNA sequencing

ITS (nrDNA) and trnC-trnD amplifications were performed in 50 µl reactions using 10 ng of genomic DNA, 3 units Qiagen Taq polymerase, 5 µl 10x buffer (final concentration: 50 mM KCl, 10 mM Tris-HCl (pH 9), 0.01% gelatin and 0.1% Triton X-100), 1.75 mM $MgCl_2$, 20 µl Q solution (2X final), 400 µM each dNTP, 1.8 µM each primer and 4%(by vol.) DMSO.

Primers (5'-3'):

ITS: ITSA = GGA AGG AGA AGT CGT AAC AAG G;
ITSB = CTT TTC CTC CGC TTA TTG ATA TG.
ITSA and ITSB primers from Blattner (1999).

trnC-trnD: CDFor: CCA GTT CAA ATC TGG GTG TC
CDRev: GGG ATT GTA GTT CAA TTG GT
CDFor, CDRev primers from Demesure et al. (1995).
CD10F: AAA GAG AGG GAT TCG TAT GGA
CD3R: AAC GAA GCG AAA ATC AAT CA
CD10F and CD3R primers from Andrea Schwarzbach (pers. comm.).

The following PCR conditions were used: MJ Research Programmable Thermal Cycler, 30 cycles, 94°C (1 min.), 50°C (2 min.), 72°C (2 min.), with a final step of 72°C (5 min.). The PCR reaction was subjected to purification by agarose gel electrophoresis (1.5% agarose, 70 v, 55 min.). The nrDNA primers (ITSA, ITSB) produced a band of approx. 1120 bp. The internal trnC-trnD primers, CD10F-CD3R produced a band of approx. 800 bp. In each case the band was excised and purified using a Qiagen QIAquick gel extraction kit.

The gel purified DNA band with the appropriate primer was sent to McLab Inc. for sequencing. Sequences for both strands were edited and a consensus sequence was produced using Chromas, version 2.31 (Technelysium Pty Ltd.). Alignments were made using Clustal W and then manually corrected. Indels were coded with a "-" for the first nucleotide and "I" for succeeding nucleotides such that an indel was treated as a single mutation event. Overall sequences have been deposited in GenBank (Schwarzbach et al., in prep.).

SNPs analyses

Aligned data sets (nrDNA and trnC-trnD) were analyzed by CLEANDNA (Fortran, R. P. Adams) to remove invariant data. Mutational differences were computed by comparing all SNPs, divided by the number of comparisons over all taxa (= Gower metric, Gower, 1971; Adams, 1975). Principal coordinate analysis was performed by factoring the associational matrix using the formulation of Gower (1966) and Veldman (1967). A minimum spanning network was constructed by selecting the nearest neighbor for each taxon from the pair-wise similarity matrix, then connecting those nearest neighbors as nodes in the network (Adams, 2004).

RESULTS AND DISCUSSION

Analyses of 1119 bp of nrDNA (ITS) sequences revealed 27 SNPs among the taxa including a 3 bp deletion in both samples of *J. g.* var. *ekmanii* and a 1 bp insertion in all six samples of *J. v.* var. *virginiana* and *J. v.* var. *silicicola*. PCO of the SNPs resulted in 5 eigenroots that were larger than the average diagonal value. These 5 eigenroots accounted for 42.49, 20.48, 12.98, 8.54 and 5.80% of the variation among the OTUs or a total of 90.21%. From this factor

analysis there appear to be 4 major and 2 minor groups. Ordination (Fig. 4) shows four major groups: (SI, VG, *J. virginiana*) , (BA, LU, *J. barbadensis* - *lucayana*), (BM, *J. bermudiana*), and (SX, UR, GR, EK,

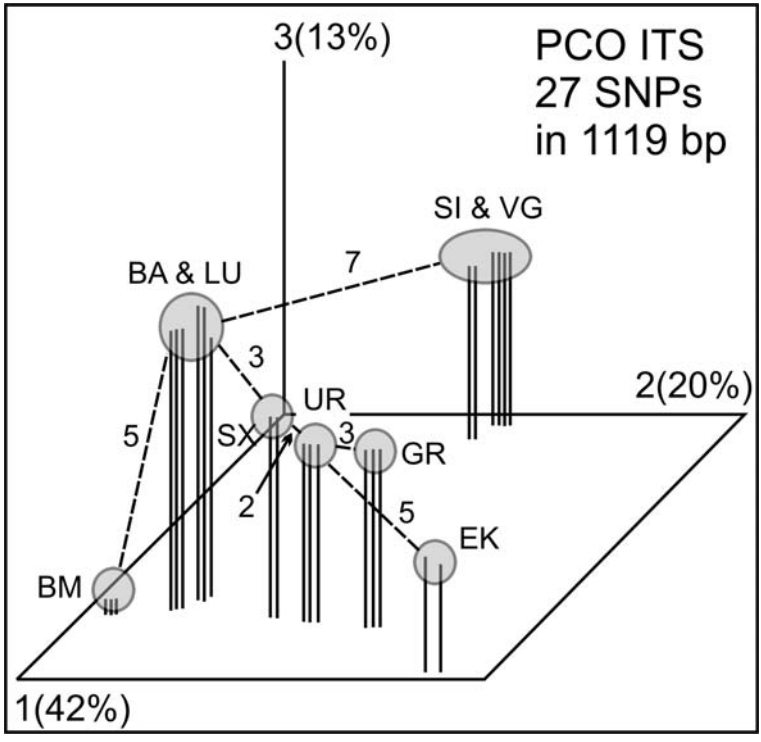

Figure 4. PCO based on 27 SNPs of nr DNA.

J. saxicola - *J. gracilior*). The most surprising facet is the 5 SNPs differentiating EK (*J. gracilior* var. *ekmanii*), from *J. gracilior* var. *urbaniana* (UR). Another interesting point is the very close linkage of *J. saxicola* with *J. gracilior* var. *urbaniana* and *J. barbadensis*. Because *J. saxicola* is frozen in neoteny and thus, has only juvenile leaves, it appears morphologically very distinct from all other Caribbean junipers. However, this may be misleading, as the SNPs indicate. *Juniperus bermudiana* is quite distinct.

Another aspect shown is that *J. barbadensis* (St. Lucia) and *J. lucayana* (Cuba) differed by only a single SNP. All samples of *J. barbadensis* were identical. The lack of variation is indicated in figure 4 in which identical sequences are denoted by vertical bars that are closely spaced. In fact, the only other polymorphisms were found in *J. g*. var. *ekmanii* (1 bp difference), and *J. v*. var. *silicicola* (2 bp). One *J. v.* var. *silicicola* was identical to *J. v*. var. *virginiana* (Fig. 4).

Sequencing of the trnC-trnD region of cp DNA with the CD10F - CD3R primers resulted in a partial sequence of 798 bp in *J. v.* var. *virginiana*. However, all the other taxa in this study had a 245 bp deletion resulting in 553 bp. Analyses of these sequences revealed 6 SNPs plus the deletion (coded as a single event or SNP). PCO of these data resulted in two eigenroots accounting for 100% of the variance among taxa with roots of 83 and 17%. Two eigenroots imply n+1 groups, or 3 groups of taxa. This is shown in figure 5. There was no variation found within groups (VG), (BA, BM, GR, LU, SI) and (EK, SX, UR). *Juniperus virginiana* (VG) from the mainland (and thought to be an ancient species, Adams, 2004), yielded 798 bp with this set of trnC-trnD primers and this size is consistent with the other smooth leaf margined junipers of the western hemisphere (Schwarzbach, et al., in prep.). However, *J. v.* var. *silicicola* shares the 245 bp deletion with all the junipers of the Caribbean. This seems to provide evidence that the Caribbean (plus Bermudian) junipers were derived from *J. v.* var. *silicicola* or a common ancestor or perhaps that *J. v.* var. *silicicola* was of hybrid origin between *J. lucayana* and *J. v.* var. *virginiana*.

Juniperus barbadensis (BA), *J. bermudiana* (BM), *J. gracilior* (GR), *J. lucayana* (LU), and *J. virginiana* var. *silicicola* (SI) share no SNPs (Fig. 5). It is notable that *J. saxicola* (SX) is grouped with *J. gracilior* var. *ekmanii* (EK) and *J. gracilior* var. *urbaniana* (UR) (Fig. 5). All members of the (EK, SX, UR) group share the single SNP that separates it from the (BA, BM, GR, LU, SI) group. The grouping of *J. saxicola* with *J. gracilior* var. *urbaniana* was also supported by the ITS SNPs (Fig. 4).

There is no doubt that the Caribbean junipers are extremely similar and very difficult to separate into species in the herbarium.

Figure 6 shows a diagram based on the gross morphology. *Juniperus bermudiana* and *J. saxicola* are the only taxa that are easy to key out.

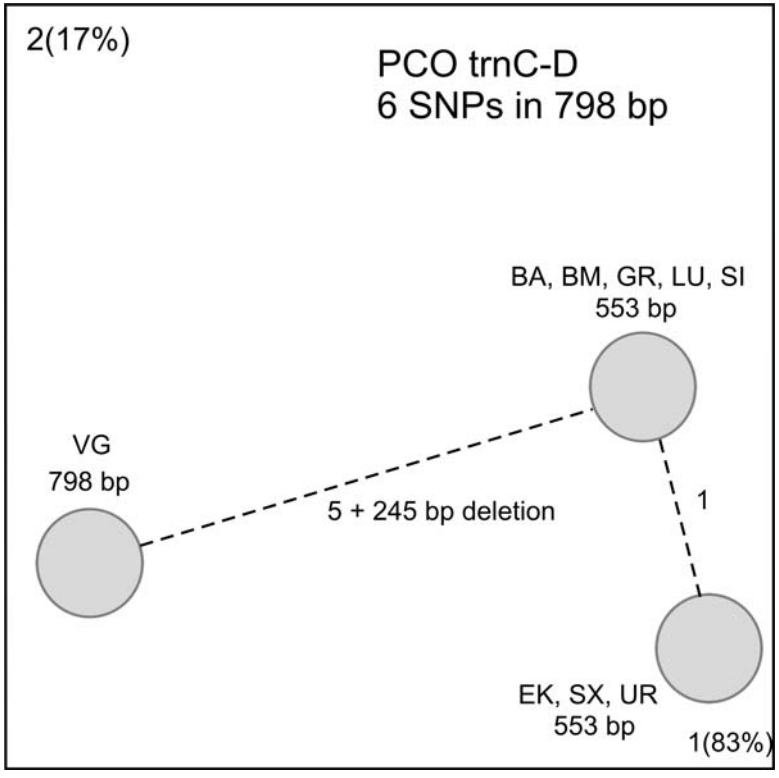

Figure 5. PCO of trnC-trnD SNPs based on 789 bp of sequence data. Note that there was no variation found in groups (VG), (BA, BM, GR, LU, SI) and (EK, SX, UR).

Juniperus bermudiana has opposite leaves that result in square leafy branchlets and *J. saxicola* has only awl shaped leaves due to the taxon being fixed in neoteny. However, examination of individuals at the summit of Petit Piton, St. Lucia revealed a few adult plants with only juvenile foliage (this is not uncommon in *Juniperus*), so the separation of *J. saxicola* from *J. barbadensis* with juvenile leaves, might not be

possible in the herbarium in this instance. *Juniperus virginiana* var. *virginiana* and *J. v.* var. *silicicola* are extremely similar in their morphology.

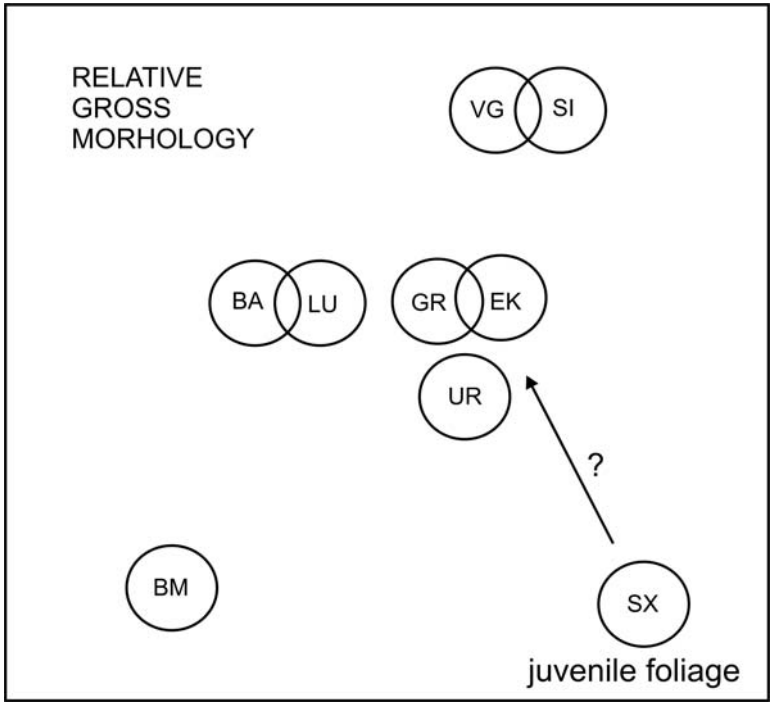

Figure 6. Relative gross morphology for the Caribbean junipers. Because *J. saxicola* (SX) has only juvenile leaves, it is appears very distinct, but it may relate to the typical morphology.

The data sets examined in this study agree in several facets: *J. bermudiana* (BM) is distinct; *J. v.* var. *virginiana* is distinct from the Caribbean junipers; all the other taxa are very similar. *Juniperus virginiana* var. *virginiana* and var. *silicicola* are very similar in all the analyses except the RAPDs and trnC-trnD SNPs. *Juniperus barbadensis* (BA) and *J. lucayana* (LU) are either identical or nearly identical in most analyses. This supports the recognition of *J.*

barbadensis var. *lucayana* (Adams, 1995, Farjon, 2005). Generally, the recognition of *J. gracilior* with two varieties (var. *ekmanii*, var. *urbaniana*) is supported by terpenoids, RAPDs and SNPs of nr DNA. The placement of *J. saxicola* is problematical. The terpenoids show it to be distinct (Fig. 2), somewhat similar to *J. lucayana* in Cuba, and the RAPDs show (Fig. 3) its affinity about equally to *J. barbadensis* and *J. lucayana*. The ITS SNPs place it (Fig. 4) intermediate between *J. gracilior* var. *urbaniana* and *J. barbadensis* - *lucayana* and the trnC-trnD SNPs place it with *J. g.* vars. *ekmanii* and *urbaniana*.

SPECIATION IN THE WEST INDIES

All of the junipers of the Caribbean 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 Mexico 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 (Fig. 7). The clearest evidence presented in this study is the trnC-trnD, 245 bp deletion in cp DNA that is shared by all Caribbean junipers, as well as *J. v*. var. *silicicola* and *J. bermudiana* (Fig. 6).

Colonization of *Juniperus* into the West Indies is postulated to have occurred by long distance bird dispersal of *J. virginiana* (or its ancestor) to Cuba or the Bahama Islands and then to Bermuda, Jamaica, and Hispaniola (Adams, 2004). *Juniperus saxicola* may have evolved from ancestral *J. gracilior*-like plants or from *J. barbadensis* var. *lucayana* plants of eastern Cuba from seeds carried into the Pico Turquino region. Either by a chance founder's 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. barbadensis* var. *lucayana*. The large distance from Cuba to St. Lucia and the lesser Antilles render this hypothesis somewhat tentative. The alternative mode, island-hopping from Hispaniola may be a more attractive option, but at present, the lack of suitable habitat on many of the intervening islands makes this scenario unlikely.

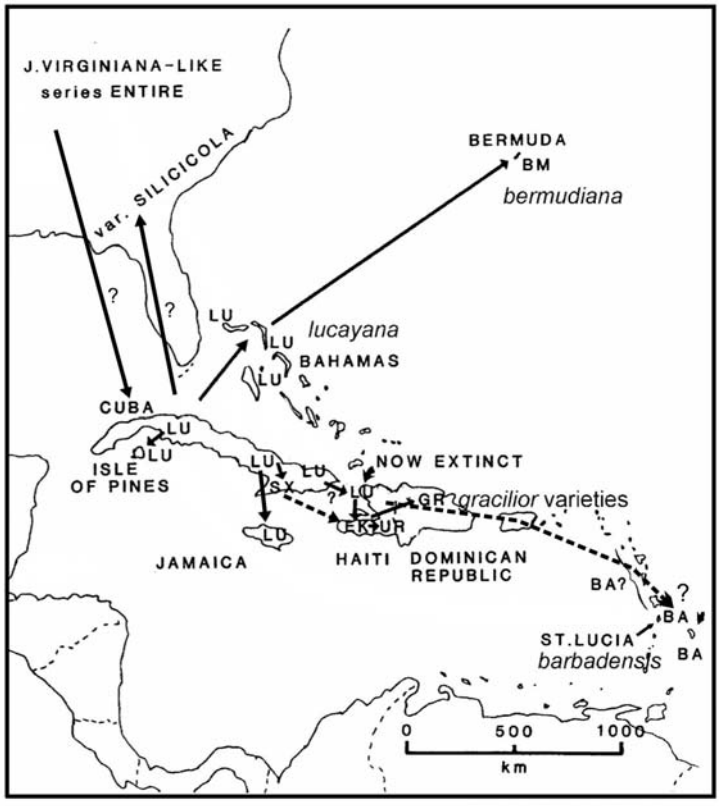

Figure 7. Postulated speciation of the smooth-leaf margined *Juniperus* of the Caribbean.

It seems plausible that the 245 bp deletion occurred in junipers in Cuba or Hispaniola and then this cpDNA type was introduced into *J. virginiana* in se USA to produce *J. v.* var. *silicicola*.

The junipers of Hispaniola appear to have arisen from *J. barbadensis* var. *lucayana* or its ancestor. Although *J. b.* var. *lucayana* seems now to be extinct in Hispaniola, specimens collected earlier in the twentieth century in northern Haiti appear to be *J. b.* var. *lucayana*. The junipers in the *J. gracilior* complex were likely derived from

ancestral *J. b.* var. *lucayana*. *Juniperus gracilior* var. *urbaniana* probably arose from *J. g.* var. *ekmanii* or its ancestor.

The introduction of *J. bermudiana* into Bermuda must have been relatively recent because Bermuda's soil was reportedly formed only during the first inter-glacial period of the Pleistocene (Bryan and Cady, 1934; Cox, 1959). Herwitz (1992) recently estimated the ages of the highest eolianite dunes on Bermuda (Southampton, 73 m elev.) at 85,000 yr bp and the oldest hill, Walsingham (29 m elev.) at greater than 880,000 yr bp.

Juniperus bermudiana, endemic to Bermuda, 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 and 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.

Considering the genetic bottleneck that the Bermuda junipers must have gone through in arriving at their current reduced state (Bennett and Hughes, 1959), we cannot be certain that extant trees fairly represent the gene pool that evolved on Bermuda. This may account in part, for the divergence of *J. bermudiana* from the Caribbean junipers.

The differentiation of these island populations has been affected both by selection and founders effects. Genetic drift may have also 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 yr bp, with another drop in sea level of 146 m at 40,000 yr bp. 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. lucayana* often occurs at 1 to 2 m above sea level. Broecker (1965) reported evidence for higher levels about 80,000 yr bp 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 Caribbean junipers.

Based on the data presented, the recognition of the taxa as shown in table 1 is prudent. Additional kinds of data may provide more insight into these relationships, but it seems likely that a new data set may not completely resolve these complex patterns.

Table 1. *Juniperus* of the Caribbean.

Taxon	Distribution, status
J. barbadensis var. *barbadensis*	St. Lucia, BWI, endemic, endangered
J. barbadensis var. *lucayana*	Cuba, Jamaica, Bahamas, threatened
J. bermudiana	Bermuda, endemic, endangered Threatened by hybridization with introduced *J. virginiana*.
J. gracilior var. *gracilior*	Dominican Republic, threatened?
J. gracilior var. *ekmanii*	Haiti, Dom. Rep., endangered
J. gracilior var. *urbaniana*	Haiti, endangered
J. saxicola	Cuba, Pico Turquino, endangered?
J. virginiana var. *virginiana*	e US, weedy, expanding its range
J. virginiana var. *silicicola*	coastal fore dunes, se US, may be threatened by beach development

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