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

· Robert P. Adams

Plant Biotechnology Center, Baylor University, Box 669, Gruver, Texas 79040 U.S.A.

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

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, exserted 2-3 mm from the calyx; stigma erect, barely exserted. 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. tolucensis* 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. tolucensis* 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).

ACKNOWLEDGMENTS

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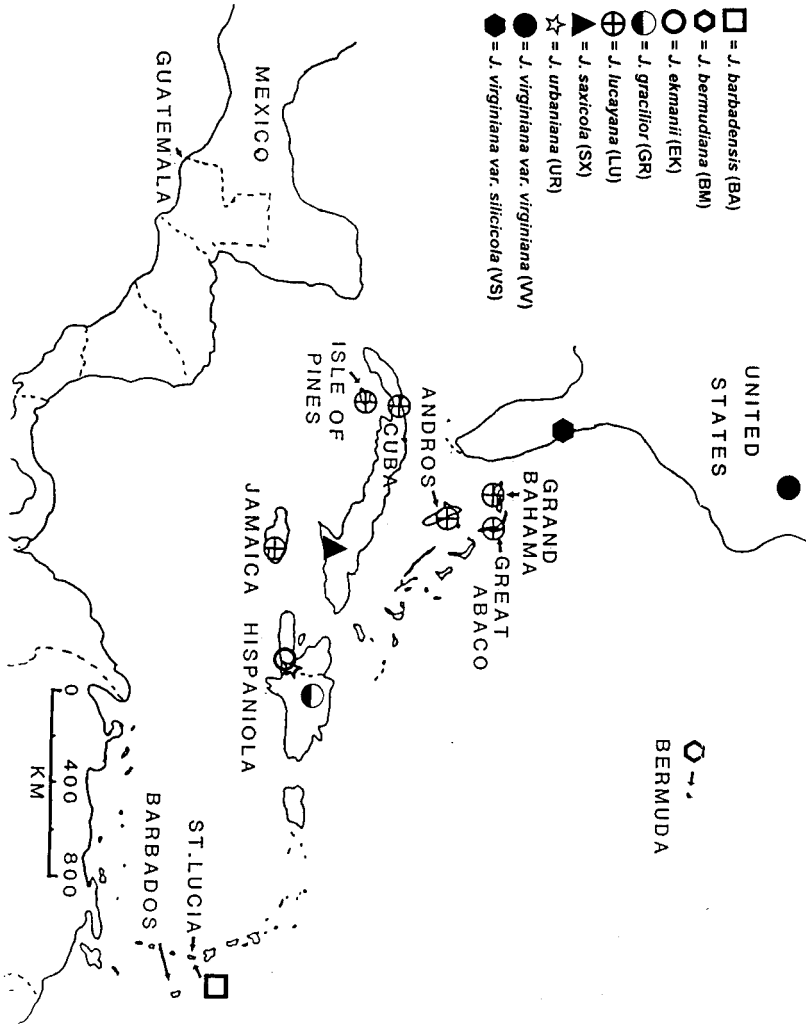
Figure 1. Study area of the Caribbean with population locations. Additional populations of *Juniperus lucayana* (not sampled) occur on a few of the islands of the Bahamas and in eastern Cuba.

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-oplopenone; Acetate II = 8-α-acetoxyelemol; (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-cubenol. 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
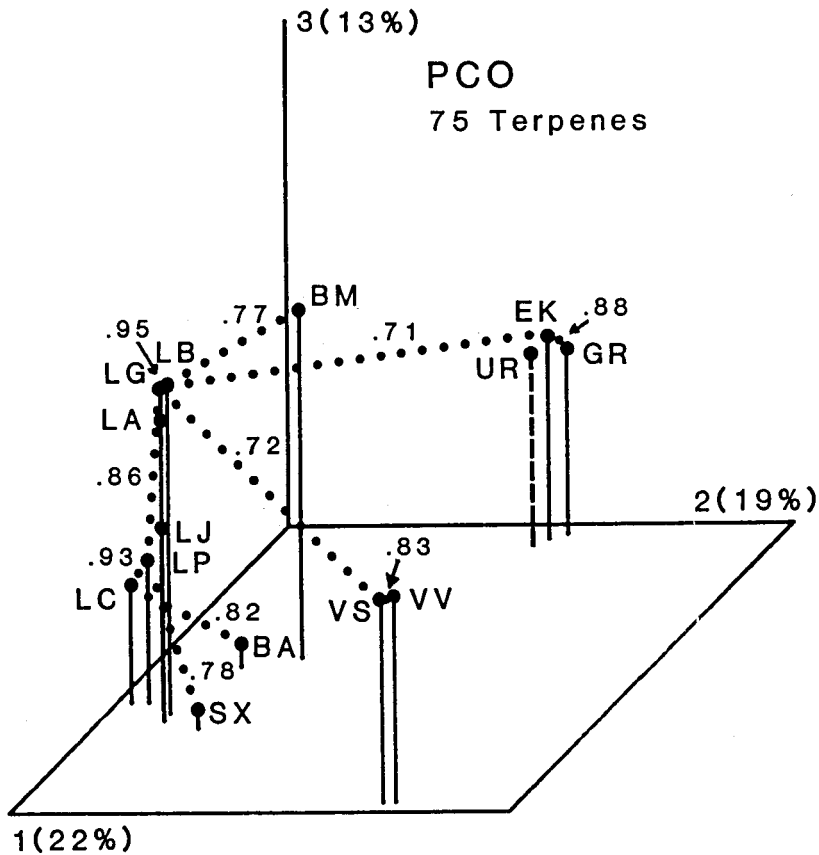
Figure 2. Principal coordinate analysis using 75 terpenoids from the volatile leaf oils. The individual components were weighted by F-1 (F from ANOVA of the fifteen OTUs) in the similarity measure. The minimum spanning network (dashed line) distances are the similarities. The OTU codes are: BA = *Juniperus 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
Safrole	-	T	-	-	0.5	-	-	-	-	13.7	6.7
cis-Sabinyl 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-Oplopenone	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-leafed (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 (Gaussen 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* in 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
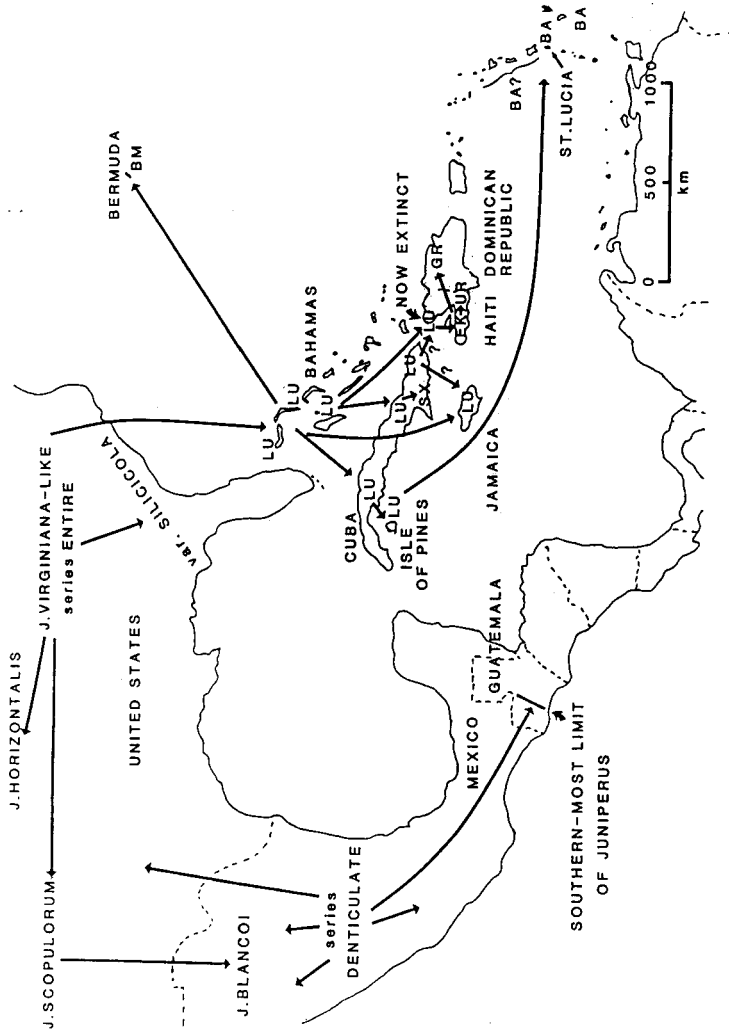
Figure 3. Proposed speciation of *Juniperus* into the Caribbean. Note especially that the junipers from the southern México/northern Guatemala area are in denticulate-series, whereas all the junipers of the Caribbean, Bermuda and eastern United States are in entire-series. BA = *J. barbadensis*; BM = *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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