# THE GENUS *JUNIPERUS* (CUPRESSACEAE) IN MEXICO AND GUATEMALA: NUMERICAL AND MORPHOLOGICAL ANALYSIS

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The genus *Juniperus* (Cupressaceae) consists of approximately 60 species distributed in the Northern Hemisphere, except for *J. procera* Hoch. which extends into the Southern Hemisphere in Africa (Florin, 1963). The delimitation of the species of *Juniperus* is difficult in all of the world; few taxonomic studies have encompassed any large geographical or natural province. Gaussen (1968) lists 99 species in the most recent treatment of the junipers of the world; however, this is an inflated number since many of the species he recognizes had been reduced to synonymy by earlier authors.

*Juniperus* has been divided into three sections: Caryocedrus, Oxycedrus, and Sabina (Endlicher, 1847; Gaussen, 1968). Caryocedrus, a monotypic section, is restricted to the eastern Mediterranean basin; the other two sections are distributed throughout the Northern Hemisphere. Section Oxycedrus is represented in North America by the circumboreal species *J. communis* L. The other junipers (approximately 22 species) in North America belong to the section Sabina, which is characterized by opposite or ternate, scale-like adult leaves, peltate scales in male cones, and female cones terminal on fertile twigs (peduncles). Engelmann (1877) made the first study of the North American (mostly United States) junipers.

The genus *Juniperus* has received considerable attention from North American taxonomists in the past 35 years. Fassett's (1944a, 1944b, 1945a, 1945b, 1945c) and Hall's (1952a, 1952b, 1955, 1962, 1964, 1968) series for morphological studies concerning hybridization in several species of *Juniperus* renewed interest in this genus. More recent studies have used more sophisticated techniques for data collection and analysis. Vasek (1966) and Vasek and Scora (1967) examined three western American species morphologically and chemically. Van Haverbeke (1968), Flake, von Rudloff and Turner (1969, 1973), Adams and Turner (1970), Schurtz (1971), Adams (1969, 1970, 1972, 1973,

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1974a), and Powell and Adams (1973) investigated evolutionary and systematic problems using sophisticated techniques in statistics and numerical taxonomy with several of these studies employing chemical data.

The junipers of North America extend southward into Mexico and Guatemala, the southernmost localities being in the Guatemalan mountains. Standley (1920) presented the first evaluation of the Mexican junipers in this century and recognized four species by studying herbarium specimens. In 1943, Standley and Steyermark (1943) published a previously undescribed species from Mexico and Guatemala. A total of nine species were known from Mexico, and one from Guatemala by 1944. Martínez (1944, 1946) critically examined the Mexican junipers and recognized 21 taxa, several of which had not been previously recognized.

Hall's (1954) review of *Juniperus ashei* Buchholz reaffirmed the citation by Johnston (1943) that the species was in Mexico. Martínez (1946) had rejected Johnston's decision. Standley and Steyermark (1958) documented the presence of two species in Guatemala, which also occur in Mexico. *J. saltillensis* was published as a new species in Mexico by Hall (1971).

Martínez (1946) recognized 12 species, 6 varieties, and 3 forms (Fig. 1) of junipers from Mexico. These taxa were based on field observations, herbarium studies and literature review. It is doubtful that Martínez observed all of the taxa in the field, although he had placed his name and collection numbers on many of the specimens he distributed (McVaugh, 1972). The type specimens of the taxa established by Martínez are distinctly different from one another. Martínez' level of understanding of the variation of the taxa in nature is not known.

The section Sabina junipers of Mexico were divided by Martínez into five subsections of two or more taxa within each subsection. In a diagram (Fig. 1), the subsections were interconnected by lines that appear to indicate relationships; however, the arrangement of the subsections in a pentagon appears to have no phylogenetic implications. Martínez (1946, 1953, 1963) never commented on the interrelationships of the subsections.

The placement of the taxa into the subsections implies relationships of the taxa within subsections as indicated by Martínez (Fig. 1). The subsection Monospermae consists of six taxa. *Juniperus comitana, J. monosperma* var. *monosperma, J. monosperma* var. *gracilis, J. erythrocarpa* var. *coahuilensis* were apparently thought to be closely related to each other as indicated by the lines drawn by Martínez. *J. californica* and *J. gamboana* are related to the other taxa of this subsection, but Martínez did not indicate the afrinities of these two species. Subsection Deppeanae includes four varieties of *J. deppeana* and two forms of *J. patoniana.* Martínez indicates reticulate relationships among these taxa.

The subsection Flaccidae consists of two varieties of *Juniperus flaccida. J. blancoi* and *J. jaliscana* are placed in subsection Jaliscanae. Subsection Monticolae includes *J. durangensis, J. standleyi,* and three forms of *J. monticola.* Reticulate relationships are indicated by Martínez for this subsection.

The separation of the Mexican junipers into subsections was intended to reflect natural groupings. The use of reticulate patterns to show relationships of taxa within subsections suggests that the relationships were not readily apparent to Martínez.

The recently described *Juniperus saltillensis* (Hall, 1971) was not considered by Martínez in his taxonomic treatment of the Mexican junipers. Hall (1971) stated that this species is related to *J. monticola, J. standleyi, J. paliscana,* and *J. blancoi.*

Although the Middle American junipers were recently studied by Martínez (1944, 1946), a reexamination of the morphology is needed for a comprehensive study of these junipers. A second phase of this study will include an examination of the terpenoids of the foliage. In addition, this study will provide information for the evaluation of the relationships of species in the genus *Juniperus* in North America.

## MATERIALS AND METHODS

The specimens were selected to represent the taxa known from Mexico and Guatemala and to represent each taxon from several localities, if possible (Fig. 2). Three to eight branches from female plants were selected from several trees at each locality in 1970 and 1972. Several herbarium specimens of the same collector and collection number were used for *Juniperus blancoi* and *J. patoniana;* few specimens of these two taxa were available.

Twenty-four operational taxonomic units (Sokal and Sneath, 1963) were analyzed. Nineteen of the 24 operational taxonomic units (OTU's) represent the taxa known from Mexico and Guatemala. The five other OTU's represent populations of uncertain affinities.

Female plants selected for analysis included the female cones (megastrobili or galbuli). Studies by Lemoine-Sebastian (1967) indicated that the male cones (microstrobili) were not useful in detecting species differences in *Juniperus* section Sabina.

For various reasons three species were not included in this study. *Juniperus ashei* is not included in this study; this species is known from a few localities and is uncommon in México. Adams and Tuner (1970) studied this species in detail and work is continuing (Adams, 1974a). *Juniperus californica* and *Juniperus scopulorum* were also not included in this study. These species have their centers of distribution in the United States and will be studied at a later phase in The Junipers of North America Project. Distribution information concerning *Juniperus californica* and *Juniperus scopulorum* in Mexico have been recently reviewed by Zanoni and Adams (1973, 1974).

*Morphological characters.* The selection of morphological characters was based on an examination of the literature and specimens. Earlier studies (Hall, 1952a, 1952b, 1955; Hall, McCormick and Fogg, 1962; Hall and Carr, 1964, 1968; van Haverbeke, 1968; Adams and Turner, 1970; Adams, 1972) included up to 29 morphological characters. Sixty-four characters (Table 1) were utilized in this study to provide a broader sampling of characters for analysis.

Peduncles, female cones, seeds, terminal whip leaves, scale leaves, terminal branches and stem bark were examined and scored (Table 1). Ten measurements were taken from each plant or herbarium specimen whenever possible (except as noted in Table 1). Each linear measurement was taken using a reticel in a binocular dissecting microscope. Female cone length and width were measured with a millimeter ruler. Cone and seed colors were determined by comparison to the Munsell Color System charts. The hue, value, and chroma were recorded and analyzed as three separate characters. Cone pulp, cone bloom, seed and leaf shapes, gland shapes, leaf margins, and leaf and gland protrusions were scored by comparison to character states established by a preliminary survey of the specimens studied. Leaf tips were measured for the width at .66 mm from the tip of the whip leaves and at .33 mm from the tip on scale leaves to obtain an estimate of acuteness of the leaf tip. The angle of branching of the ultimate twig was measured with a protractor.

Stem bark exfoliation patterns were scored in the field when the specimens were collected. The bark descriptions of Martínez (1963) were used for the specimens distributed by Martínez.

All characters that were not present or not determinable from the specimens examined were scored with -1.0, indicating that no comparison was to be made for that character on that tree in the data analysis.

*Data analyses.* Analysis of variance (ANOVA) was performed on each of the 64 characters to detect (by use of the F ratio of the variance among OTU's/variance within OTU's) which characters exhibited statistically significant differences among OTU's. A modified Student-Newman-Keuls (SNK) multiple range test (Adams, 1970) for unequal OTU samples was used to analyze each character to detect which OTU means were significantly different at the .05 level.

A weighted mean character difference (M. C. D.) similarity measure (Adams, 1970; Adams, 1974b) was used to determine the similarities among the 24 OTU's. Three separate analyses were made with the data derived from the ANOVA and SNK multiple range tests. The first analysis consisted of 63 characters and used $\sqrt{F - 1}$ as the weight of each character comparison; the second used 45 characters and $\sqrt{F - 1}$ character weighting; the third used 45 characters and $F - 1$ character weighting. The 45 characters were selected from the list of the 63 characters to eliminate many characters that were thought to be easily influenced by environmental differences or characters thought to be subjectively scored during data collection.

The single linkage method of Sneath (1957) was used for clustering.

RESULTS. Analysis of variance revealed that fifty-eight of the 64 characters had significant F ratios ($P = .05$). Two characters, branch flaccidness (FLC) and scale leaf tip divergence (LFD) had infinite F ratios because these characters had no variation within OTU's. Female cone surface texture (FRS), hilum scars per seed (HNO), scale leaves per 3.33 mm (RLO), and scale leaf rupture (RRP) had non-significant F ratios. The SNK tests were run on the 62 characters (excluding FLC) and (LFD) to determine which OTU means were significantly different. Fifty-eight of these 62 characters (excluding FLC and LFD) had significant SNK tests. The characters FRS, HNO, RLO, and RRP did not have significant SNK tests.

The characters of branch flaccidness (FLC) and scale leaf tip divergence (LFD) were assigned F ratios equivalent to the F ratio of cone pulp (RFP) for inclusion of these characters in the computation of similarity measures. The F ratio of cone pulp was selected because the meristic characters branch flaccidness (FLC) and scale leaf tip divergence (LFD) exhibited variance within and among OTU's similar to that exhibited in cone pulp (FRP). Although no SNK tests were computed for FLC and LFD, these characters separate the flaccidan complex from all other OTU's examined in this study.

Before computation of the similarity measures, one character, hilum scars per seed (HNO) with a F ratio less than 1.0, was discarded from the analysis.

Clustering (Fig. 3), using 63 characters and $\sqrt{F - 1}$ character weights, illustrates several groupings of OTU's. The flaccidan complex, *Juniperus flaccida* var. *flaccida* (FL) and *J. flaccida* var. *poblana* (FP), forms a quite distinct group. The monticolan complex of *J. monticola* f. *monticola* (MM), *J. monticola* f. *compacta* (MC), and *J. monticola* f. *orizabensis* (MO) is well defined. The deppeanan complex of *J. deppeana* var. *deppeana* (DD), *J. deppeana* var. *robusta* (DR), *J. deppeana* var. *zacatecensis* (DZ), the OTU DZA, and *J. patoniana* (DP) is also fairly distinct. The one-seeded complex of *J. gamboana* (GA) *J. saltillensis* (SL), *J. comitana* (CO), *J. erythrocarpa* var. *coahuilensis* (ERW and EW), *J. monosperma* var. *gracilis* (MG), and the OTU's LLR, MLB and MLT is apparent. The *J. monosperma* var. *monosperma* from USA (MS), *J. durangensis* (DU), *J. standleyi* (ST), *J.jaliscana* (JA), and *J. blancoi* (BL) cluster rather loosely and do not enter into these complexes.

Three of the OTU's that were of uncertain identities were quite similar to other OTU's. DZA, *Juniperus deppeana* from El Alamo, Zacatecas, is most similar to *J. deppeana* var. *robusta.* This OTU (DZA) was collected near *J. deppeana* var. *zacatecensis* which indicates that these taxa are sympatric in the state of Zacatecas.

Several incongruities exist between the expected clustering pattern based on the SNK tests interpretations and field observations, and the clustering patterns using 63 characters with $\sqrt{F-1}$ character weights. *Juniperus durangensis* (DU) and *J. standleyi* (ST) were expected to show greater similarity to the monticolan complex of the *J. monticola* forms. *J. monosperma* var. *monosperma* from USA (MS) was expected to be more similar to the one-seeded complex. *J. erythrocarpa* var. *coahuilensis* from western Mexico (EW) was expected to be more similar to the OTU of the same taxon from eastern Mexico (ERW).

The character list was examined and 18 characters were recognized as possibly being variable due to environmental influences or being subjectively scored. Fifteen of these 18 characters were removed because they were likely to be easily influenced by the environment. These characters include: seed length X width (SEV), hilum scar length (HIL), whip leaf length (WLL), whip leaf width (WLW), whip leaf length X width (WLV), number of whip leaves per 6.6 mm. (WLO), whip leaf gland length X width (WGV), length from whip leaf gland center to leaf tip (WCT), scale leaf length (RLL), scale leaf width (RLW), scale leaf length X width (RLV), number of scale leaves per 3.3 mm (RLO), scale leaf gland length X width (RGV), length from scale leaf gland center to leaf tip (RCT), and diameter of the ultimate twig (DIA). The following three characters were removed from the data analysis because they were believed to be subjectively scored: cone surface texture (FRS), number of scale leaves per node (RLN), and stem bark exfoliation pattern (BRK). Although the number of scale leaves per node has frequently been used to characterize species of junipers, it appears that the selection of certain twigs can bias the results in that binate and ternate leaf arrangements can often be observed on the same twig as well as different twigs.

Figure 4 illustrates the similarities of OTU's based on the remaining 45 characters with $\sqrt{F-1}$ character weights. This recomputation of similarity measures and the phenogram resulted in resolution of few of the incogruities observed in the similarity measures based on 63 characters and $\sqrt{F-1}$ character weights. The *Juniperus monosperma* var. *monosperma* from USA (MS) has a greater similarity to the one-seeded OTU's. The positions of *J. standleyi* (ST) and *J. durangensis* (DU) are not similar to those expected from the SNK tests or from observations of specimens.

A heavier weighting (F – 1) was used as suggested by the recent work of Adam (1975). Figure 5 illustrates the similarities of OTU's based on 45 characters with F – 1 character weights. The flaccidan, deppeanan, monticolan and monosperman complexes are still apparent as seen in Figures 3 and 4. In contrast to Figures 3 and 4, *Juniperus durangensis* (DU) is more similar to the monticolan complex but the clustering with *J. monticola* f. *orizabensis* (MO) was not expected. *J. standleyi* (ST) is also more similar to the monticolan complex. *J. monosperma* var. *monosperma* from USA (MS) shows close affinities with the one-seeded complex. *J. erythrocarpa* var. *coahuilensis* from eastern Mexico (ERW) is most similar to the plants of the same taxon in western Mexico (EW), although EW is most similar to LLR and *J. monosperma* var. *gracilis* (MG)!

Several groups are apparent in each of the three phenograms. The flaccidan complex of *Juniperus flaccida* var. *flaccida* (FL) and *J. flaccida* var. *poblana* (FP) is quite distinct from the other OTU's. The deppeana complex of *J. deppeana* var. *deppeana* (DD), *J. deppeana var. robusta* (DR), and *J. deppeana* var. *zacatecensis* (DZ) remains a distinct group. The OTU DZA is most similar to *J. deppeana* var. *robusta* (DR). *J. patoniana* (DP) is most similar to *J. deppeana* var. *robusta* (DR) and clusters with the *J. deppeana* varieties.

Another distinct group is the monticolan complex, which is composed of *Juniperus monticola* f. *monticola* (MM), *J. monticola* f. *compacta* (MC), *J. monticola* f. *orizabensis* (MO). *J. durangensis* (DU) and *J. standleyi* (ST) have affinities to the monticolan complex, but these affinities are not consistent in the phenograms. The one-seeded complex of *J. gamboana* (GA), *J. comitana* (CO), *J. saltillensis* (SL), *J. erythrocarpa* var. *coahuilensis* (ERW and EW), *J. monosperma* var. *gracilis* (MG) form a group. The affinities of *J. jaliscana* (JA) and *J. blancoi* (BL) are not clear from any of the data analyses. The complexes of taxa recognized in these data analyses are similar to those of Martínez (Fig. 1) with various distinguishing characteristics shown in Table 2.

## DISCUSSION AND CONCLUSIONS

This study of the Mexican and Guatemalan junipers revealed several new relationships not apparent in the studies by Martínez. *Juniperus flaccida* (var. *flaccida* and var. *poblana*) has large, many-seeded cones, large scale leaves with divergent leaf tips, and pendulant branches (see Table 2). The origin and affinities of this species are not known. *J. flaccida* is most common in the hills and low mountains (800 - 2 900 m.) of southern Mexico, where it apparently evolved into the two varieties. The species is not found at the Isthmus of Tehuantepec or in localities southeast of the isthmus. This arid, low-altitude (250 m) region has been a barrier to the southern extension of the ranges of many plants since the late-Tertiary (Steyermark, 1950), as has been the case in the junipers. The northernmost locality is in northeastern Sonora.

*Juniperus deppeana*, another species with large, several-seeded cones, bears superficial resemblance to *J. flaccida.* Martínez recognized four varieties of *J. deppeana*. Three of these varieties; *J. deppeana* var. *deppeana, J. deppeana* var. *robusta*, and *J. deppeana* var. *zacatecensis*, were examined in this study. These varieties are distinct from one another. The similarities of the OTU DZA and *J. patoniana* (DP) to the varieties of *J. deppeana* are of special interest. DZA represents a population collected at El Alamo, Zacatecas. The identity of this OTU was in question because the population was located within the distribution range of *J. deppeana* var. *zacatecensis*, but the morphology appeared to be different from members of that variety. The similarity measures computed for DZA indicate that it is most similar to *J. deppeana* var. *robusta*. This evidence and evidence from the examination of other specimens indicate that DZA is *J. deppeana* var. *robusta* and that *J. deppeana* var. *robusta* and *J. deppeana* var. *zacatecensis* are sympatric in the state of Zacatecas, near the state of Durango.

The OTU DP consisted of specimens identified as *Juniperus patoniana* by Martínez. This OTU is most similar to *J. deppeana* var. *robusta* and is similar to the other varieties of *J. deppeana*. Martínez (1946) indicated that it was not conspecific with that taxon or with any other known taxon.. The descriptions (Martínez, 1946) of *J. patoniana* and *J. deppeana* var. *robusta* are similar, except for the bark exfoliation patterns. *J. patoniana* has bark that is divided into long rectangular strips, that are sometimes interlaced. *J. deppeana* var. *robusta* has bark that is divided into small, rectangular plates that are almost square. A variant of *J. patoniana, J. patoniana* f. *obscura*, has bark with square plates near the ground and lacerated or rent bark above. Adams (1973) reported a form of *J. deppeana, J. deppeana* f. *sperryi* (Correll) Adams, which is chemically and morphologically very similar to typical *J. deppeana* in the Davis

Mountains of west Texas, except for the furrowed bark! He concluded that perhaps only a difference of a few genes is responsible for this form. Thus it seems reasonable that *J. patoniana* may represent only a few gene differences from *J. deppeana* var. *robusta.* The other character states of *J. patoniana* are within the range of character states for *J. deppeana* var. *robusta.* The taxon is also within the geographic range of *J. deppeana* var. *robusta.* The data analyses in this study suggest that *J. patoniana* should be recognized as a subspecific category of *J. deppeana,* i.e., *J. deppeana* var. *patoniana* (Martínez) Zanoni (Zanoni and Adams, 1976).

The varieties of *Juniperus deppeana* are generally widely distributed in Mexico (Fig. 2). *J. deppeana* var. *deppeana* occurs in the Sierra Madre Oriental from the State of Mexico northward to Coahuila. *J. deppeana* var. *robusta* is found in the Sierra Madre Occidental in the states of Zacatecas, Durango and Chihuahua. The range of *J. deppeana* var. *zacatecensis* is limited to the state of Zacatecas.

*Juniperus durangensis, J. monticola,* and *J. standleyi* form a loose species group, although the similarities of these species to *J. blancoi, J. jaliscana,* and *J. saltillensis* obscure these relationships in the phenograms. This group is characterized by small, many-seeded cones and ultimate branches that have a beaded appearance due to the shape and arrangement of scale leaves (Table 2). The similarities of these three species suggest common ancestry and divergence into three different geographic regions. *J. durangensis* is found in isolated populations in the pine-oak forests at 2 100 to 2 700 m in the Sierra Madre Occidental. The most widespread species, *J. monticola,* is scattered on the higher volcanoes of the Neovolcanic Axis across southern Mexico and on peaks in the folded and faulted Sierra Madre Oriental at elevations generally over 3 000 m (except at El Chico, Hidalgo, where *J. monticola* f. *monticola* is growing at 2 450 m). *J. monticola* was divided into three subspecific taxa (Martínez, 1946): *J. monticola* f. *compacta; J. monticola* f. *monticola;* and *J. monticola* f. *orizabensis.* These taxa were found to be distinct from one another in this study. Examination of herbarium specimens indicated that *J. monticola* f. *compacta* and *J. monticola* f. *monticola* intergrade and are commonly sympatric in the Neovolcanic Axis. *J. monticola* f. *compacta* and *J. monticola* f. *orizabensis* are sympatric in the eastern Neovolcanic Axis and in the Sierra Madre Oriental.

*Juniperus standleyi* is known from the Sierra de los Cuchumatanes, Guatemala and from Volcán Tacaná, Mexico, at elevations over 3 000 m. This species is located on a land mass that has been open to colonization of plants since the early Tertiary (Steyermark, 1950). *J. standleyi* apparently has been geographically separated from *J. monticola* and *J. durangensis* for a considerable period of time.

The one-seeded junipers form the largest and most widespread group of junipers in North America. These taxa are very abundant in northern Mexico and adjacent southwestern United States. Two taxa are known from Chiapas, Mexico and Guatemala. The Mexican and Guatemalan junipers: *Juniperus comitana, J. erythrocarpa* var. *coahuilensis, J. gamboana,* and *J. monosperma* var. *gracilis* are very similar to each other.

Analysis of the OTU's LLR and MLB indicates that they are most similar to *J. monosperma* var. *gracilis.* These OTU's probably represent variation of *J. monosperma* var. *gracilis* at the periphery of its distribution. MLT is most similar to *J. monosperma* var. *gracilis,* but the identity of this OTU is not clear from the phenograms. The OTU consisted of samples from very old, single-stemmed trees at La Trinidad, Nuevo León. It is possible that MLT is *J. monosperma* var. *gracilis*; the differences being related to the ages of the trees. The junipers sampled for *J. monosperma* var. *gracilis* were shrubs and not as old as the trees at La Trinidad, Nuevo León.

Interestingly, *Juniperus monosperma* var. *gracilis* is more similar to *J. erythrocarpa* var. *coahuilensis, J. comitana,* and *J. gamboana* than it is to *J. monosperma* from the U.S.A. If this analysis is correct, *J. monosperma* var. *gracilis* should probably be allied to a different species.

*Juniperus erythrocarpa* var. *coahuilensis* from western Mexico (EW) is very similar to the plants from eastern Mexico (ERW) of the same taxon, and to *J. monosperma* var. *gracilis. J. gamboana* and *J. comitana* are most similar to each other and then to *J. monosperma* var. *gracilis. J. saltillensis* is most similar to *J. monosperma* var. *gracilis.*

Although the affinities of the one-seeded junipers are not clear from this study nor from Martínez (1946), several observations may be made concerning these taxa. Hall (1971) stated that the *J. saltillensis* was related to *J. blancoi, J. durangensis, J. jaliscana,* and *J. monticola.* Analysis of *J. saltillensis* (mean number of seeds per cone = 1.43) in this study indicates that it is more similar to the one-seeded junipers. The distribution and habitats of *J. saltillensis* are also similar to the one-seeded junipers, with which it is often found in the same locations in eastern Mexico.

The subspecific epithet *Juniperus erythrocarpa* var. *coahuilensis* was applied to the Mexican plants of *J. erythrocarpa* by Martínez (1946). The type specimen, other specimens, and living material of *J. erythrocarpa* from Texas has been examined. The Texas plants appear to be the same taxon as the Mexican plants. Therefore, recognition of the Mexican plants as a different taxon is unwarranted.

Adams (1972) included trees referable to *J. erythrocarpa* in a stduy of *J. pinchotii* populations from Texas. His results indicate that these trees (*J. erythrocarpa* )are very similar chemically to *J. pinchotii* and rather unsimilar to *J. nonosperma, athlough* these trees (*J. erythrocarpa*) were about equally similar to *J. monosperma* and *J. pinchotti* when similarities were computed with 17 morphological characters. *Juniperus erythrocarpa* was considered to be synonymous with *J. pinchotii* in the flora of Texas (Correll and Johnson, 1970). The status of *J. erythrocarpa* will be reevaluated later when the terpenoid data have been analyzed.

Differences among the one-seeded junipers were acknowledged by botanists by the recognition of many species within this group. It appears that the differences within this group have been overemphasized and that many of the taxa should be reduced to subspecific categories. No changes are proposed in this study, other thant the recognition of *Juniperus erythrocarpa* var. *coahuilensis* as *J. erythrocarpa*. Further work with these junipers and the one-seeded junipers from the United States is planned to properly evaluate the affinities of these taxa.

The affinities of the species *Juniperus jaliscana* and *J. blancoi* to the other junipers are not clear in this study. Martínez (1946) indicated that these species constituted a subsection in his taxonomic treatment; this study did not substantiate his conclusion. These species exist in small, widely separated populations. *J. jaliscana* is known from El Salto, Durango and from two localities in the region of Río de Bavispe, Sonora.

Except for *Juniperus scopulorum* (Zanoni and Adams, ~~1974~~ 1975b), *J. blancoi* is the only Middle American juniper with smooth or entire leaf margins. Engelmann (1877) and Hall (1952) were among the first to recognize the importance of leaf margins in the identification and taxonomy of the junipers. Formal taxonomic recognition of subdivisions of the sabinoid junipers on the basis of leaf margin was given by Gaussen (1967). Section Sabina (class Sabina in Gaussen, 1968) was divided into the subsections (sections in Gaussen, 1967 and 1968): Denticulatae (toothed leaf margins) and Integrae (smooth leaf margins). The classification of the junipers of the world with subdivisions based on leaf margins was presented by Gaussen (1967 and 1968). It is not surprising that *J. blancoi* did not show close affinities to the other Mexican and Guatemalan junipers, if the leaf margin really indicate two lines of evolution in the sabinoid junipers. *J. blancoi* would be even more dissimilar if this character were weighted as heavily as inferred from Gaussen's treatment.

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## SUMMARY

The relationships of 18 taxa of Mexican and Guatemalan *Juniperus* were examined by use of 64 morphological characters in analysis of variance, multiple range tests and numerical taxonomic methods. Four species complexes were apparent. The flaccidan complex consisted of two varietis of *J. flaccida.* The deppeanan complex includes four varieties of *J. deppeana. Juniperus patoniana* Martínez is closely associated with varieties of *J. deppeana* and is treated as a variety of *J. deppeana. Juniperus durangensis, J. standleyi,* and the three forms of *J. monticola* comprised the monticolan complex. The one-seeded complex included *J. comitana, J. erythrocarpa, J. gamboana, J. monosperma* var. *gracilis,* and *J. saltillensis. Juniperus erythrocarpa* var. *coahuilensis* was not distinct from *J. erythrocarpa.* Two species, *J. blancoi* and *J. jaliscana,* did not appear to be closely related to the other Middle American junipers.

## RESUMEN

Las relaciones de los 18 taxa del género *Juniperus* en México y Guatemala fueron examinadas usando el análisis de varianza, pruebas de intervalo múltiple y los métodos taxonómicos numéricos en los 64 caracteres morfológicos usados. Cuatro complejos de especies fueron aparentes. El complejo "flaccidan" que consta de dos variedades de *J. deppeana. Juniperus patoniana* Martínez la cual, está cercanamente asociada con las variedades de *J. deppeana* y se trata como una variedad de *J. deppeana. Juniperus durangensis, J. standleyi,* y las tres formas de *J. monticola* comprenden el complejo "monticolan". El complejo de una semilla incluye a *J. comitana, J. erythrocarpa, J. gamboana, J. monosperma* var. *gracilis,* y *J. saltillensis. Juniperus erythrocarpa* var. *coahuilensis* no fue diferente a *J. erythrocarpa.* Dos especies, *J. blancoi* y *J. jaliscana,* no parecen estar relacionadas a los otros cedros de México y Guatemala.

## BIBLIOGRAPHY


ADAMS, R. P. 1972. Chemosystematic and numerical studies of natural populations of *Juniperus pinchotii* Sudw. *Taxon 21*: 407-427.

——. 1973. Reevaluation of the biological status of *Juniperus deppeana* var. *sperryi* Cornell. *Brittonia 25*: 284-289.

——. 1975. Population differentiation and relict disjunctions in *Juniperus ashei* (Cupressaceae) based on terpenoid data. *J. Molec. Evol.* (in press).

——. 1975. Statistical character weighting and similarity stability. *Brittonia* (in press).

ADAMS, R. P. and B. L. TURNER. 1970. Chemosystematics and numerical studies of natural population of *Juniperus ashei* Buch. *Taxon 19*: 728-751.

CORRELL, D. S. and M. C. JOHNSTON. 1970. *Manual of the vascular plants of Texas.* Renner: Texas Research Foundation.

ENDLICHER, I. L. 1847. *Synopsis coniferarum.* Sangalli: Scheitlin and Zolikofer.

ENGELMANN, G. 1877. The American junipers of the section Sabina. *Trans. Acad. Sci. St. Louis 3*: 583-592.

FASSETT, N. C. 1944a. *Juniperus virginiana, J. horizontalis,* and *J. scopulorum* -I. The specific characters. *Bull. Torrey Bot. Club 71*: 410-418.

——. 1944b. *Juniperus virginiana, J. horizontalis* and *J. scopulorum* II. Hybrid swarms. *Bull. Torrey Bot. Club 71*: 475-783.

——. 1945a. *Juniperus virginiana, J. horizontalis,* and *J. scopulorum* III. Possible hybridization of *J. horizontalis* and *J. scopulorum. Bull. Torrey Bot. Club 72*: 42-46.

——. 1945b. *Juniperus virginiana, J. horizontalis,* and *J. scopulorum* - IV. Hybrid swarms of *J. virginiana* and *J. horizontalis. Bull. Torrey Bot. Club 72*: 379-384.

——. 1945c. *Juniperus virginiana, J. horizontalis* and *J. scopulorum* - V. Taxonomic treatment. *Bulll. Torrey Bot. Club 72*: 480-482.

FLAKE, R. H., E. VON RUDLOFF, and B. L. TURNER. 1969. Quantitative study of clinal variation in *Juniperus virginiana* using terpenoid data. *Proc. Natl. Acad. U.S.A. 64*: 487-494.

——. 1973. Confirmation of a clinal pattern of chemical differentiation in *Juniperus virginiana* from terpenoid data obtained in successive years, p. 215-228, *In* V. C. Runeckles and T. J. Mabry (ed.), *Recent advances in Phytochemistry,* Vol. 6. New York: Academic Press.

FLORIN, R. 1963. The distribution of conifer and taxad genera in time and space. *Acta Horti Berg. 20*: 121-312.

GAUSSEN, H. 1967. La classification des genévriers (*Juniperus*). *Compt. Rend. Hebd. Seances Acad. Sci. 265*: 954-957.

——. 1968. Les gymnospermes actuelles et fossiles. Les cupressacees. *Trav. Lab. Forest. Toulouse Tome II,* Sect. I, Vol. 1, partie II 2, Fasc. 10. 1-326.

HALL, M. T. 1952a. A hybrid swarm in *Juniperus* L. *Evolution 6*: 347-357.

——. 1952b. Variation and hybridization in *Juniperus. Ann. Missouri Bot. Garden 39*: 1-64.

——. 1954. Nomencaltural notes concerning *Juniperus. Rhodora 56*: 169-177.

——. 1955. Comparison of juniper population of an Ozark glade and old fields. *Ann. Missouri Bot. Garden 42*: 171-194.

——. 1971. A new species of *Juniperus* from Mexico. *Fieldiana, Bot. 34*: 45-53.

HALL, M. T. and C. J. CARR. 1964. Differential selection in juniper population from the Baum limestone and Trinity sand of southern Oklahoma. *Butler Univ. Bot. Stud. 14*: 21-40.

——. 1968. Variability in *Juniperus* in the Palo Duro Canyon of western Texas. *Southw. Naturalist 13*: 75-98.

HALL, M. T., J. F. MCCORMICK, and G. G. FOGG. 1962. Hybridization between *Juniperus ashei* Buchholz and *Juniperus pinchotii* Sudworth in southwestern Texas. *Butler Univ. Bot. Stud. 14*: 9-28.

JOHNSTON, I. M. 1943. Plants of Coahuila, eastern Chihuahua and adjoining Zacatecas and Durango. *J. Arnold Arbor. 24*: 306-339.

LEMOINE-SEBASTIAN, C. 1967. Appareil reproducteur male des *Juniperus. Trav. Lab. Forest. Toulouse Tome I.* Vol. VI. art. XXV. 1-35.

Martínez, M. 1944. Nuevas especies de *Juniperus*. *Anal. Inst. Biol.* México 15: 7-15

——. 1946. *Los Juniperus mexicanos Anal. Inst. Biol. México* 17: 3-128.

——. 1953. *Las pináceas mexicanas* México. Secr. Agric. Ganad. Subsecr. Recurs. Forest. Caza.

——. 1963. *Las pináceas mexicanas.* Tercera edición. México: Universidad Nacional Autónoma de México.

McVaugh, R. 1972. Botanical exploration in Nueva Galicia, Mexico. *Contr. Univ. Michigan Herb. 9*: 205-357.

Powell, R. A. and R. P. Adams. 1973. Seasonal variation in the volatile terpenoids of *Juniperus scopulorum* (Cupressaceae). *Amer. J. Bot. 60*: 1041-1050.

Schurtz, R. H. 1971. *A taxonomic analysis of a triparental hybrid swarm in Juniperus L.* Ph. D. dissertation, Univ. Nebraska.

Sneath, P. H. A. 1957. The application of computers to taxonomy. *J. Gen. Microbiol. 17*: 201-226.

Sokal, R. R. and P. H. A. Sneath. 1963. *Principles of numerical taxonomy.* San Francisco: W. H. Freeman and Company.

Standley, P. C. 1920. Trees and shrubs of Mexico. *Contr. U.S. Natl. Herb. 23*: 1-170.

Standley, P. C. and J. A. Steyermark. 1943. Studies of Central American plants - III. *Field. Mus. Nat. Hist., Bot. Ser. 23*: 1-28

——. 1958. Flora of Guatemala. *Fieldiana, Bot. 24*: 1-478.

Steyermark, J. A. 1950. Flora of Guatemala. *Ecology 31*: 368-372.

Van Haverbeke, D. F. 1968. A populational analysis of *Juniperus* in the Missouri River Basin. *Univ. Nebraska Stud. n.s. 38*: 1-82.

Vasek, F. C. 1966. The distribution and taxonomy of three western junipers. *Brittonia* 18: 350-372.

Vasek, F. C. and R. W. Scora. 1967. Analysis of the oils of western North American junipers by gas-liquid chromatography. *Amer. J. Bot. 54*: 781-789.

Zanoni, T. A. and R. P. Adams. 1973. Distribution and synonymy of *Juniperus californica* Carr. (Cupressaceae) in Baja California, Mexico. *Bull. Torrey Bot. Club 100*: 364-367.

Zanoni, T. A. and R. P. Adams. 1975. Southern range extension of *Juniperus scopulorum* Sarg. (Cupressaceae) into Mexico. *Southw. Naturalist* 20 (in press).

——. 1976. Distribution and synonymy of the Mexican and Guatemalan *Juniperus* (Cupressaceae). *Bull. Torrey Bot. Club* (~~in press~~).

TABLE 1

Morphological characters and the states used. Superscrits (a) and (b) indicate that the character was used in computation of similarity matrices based on 63 and 45 morphological characters, respectively.

| Characters | States (if applicable) |
|---|---|
| *Peduncles* | |
| PED[ab] | LENGTH: average of up to 10 measurements and not less than 5 (in mm.). |
| PEK[ab] | PEDUNCLES CURVED: per cent curved, up to 10 measurements and not less than 5. |
| *Cones* | |
| FRV[ab] | LENGTH X WIDTH: average of 10 measurements and not less than 4 (in $mm^2$.). |
| FRR[ab] | LENGTH/WIDTH: average ratio of up to 10 measurements and not less than 4. |
| FRS[a] | SURFACE TEXTURE: 1. = smooth; 2. = bumpy; 3. = scale sutures obvious; 4. = horny. |
| FHU[ab] | COLOR HUE: average hue of up to 10 cones and not less than 4. |
| FVA[ab] | COLOR VALUE: average value of up to 10 cones and not less than 4. |
| FCH[ab] | COLOR CHROMA: average chroma of up to 10 cones and not less than 4. |
| BLM[ab] | BLOOM: 1. = very light; 2. = light 3. = medium; 4. = heavy; 5. = obscures cone color. |
| FRP[ab] | PULP: 1. = soft fleshy; 2. = fleshy to fibrous; 3. = soft fibrous; 4. = hard fibrous. |
| *Seeds* | |
| SEV[a] | LENGTH X WIDTH: average of up to 10 measurements and not less than 4 (in $mm^2$.). |
| SER[ab] | LENGTH/WIDTH: average ratio of up to 10 measurements and not less than 4. |
| SSH[ab] | SHAPE: 1. = widest at basal half; 2. = widest at middle; 3. = widest at distal half. |
| SHU[ab] | COLOR HUE: average hue of up to 10 seeds and not less than 4. |
| SVA[ab] | COLOR VALUE: average value of up to 10 seeds and not less than 4 seeds. |
| SCH[ab] | COLOR CHROMA: average chroma of up to 10 seeds and not less than 4 seeds. |

TABLE 1. (Continued)

| Characters | States (if applicable) |
|---|---|
| SEG[ab] | GROOVES: average number of grooves per seed of up to 10 seeds and not less than 4. |
| SPF[ab] | SEEDS PER CONE: average of up to 10 cones and not less than 4. |
| SSZ[ab] | RELATIVE SEED SIZE: = 1 (% large seeds) + 2 (% medium seeds) + 3 (% small seeds). |
| HIL[a] | HILUM SCAR LENGTH: average of up to 10 measurements and not less than 4. |
| HNO | HILUM SCARS PER SEED: average of up to 10 measurements and not less than 4. (in mm). |
| H/S[ab] | HILUM LENGTH/SEED LENGTH: average of up to 10 measurements and not less than 4 |
| *Whip Leaves* | |
| WLL[a] | LENGTH: average of up to 10 measurements and not less than 4 (in mm.). |
| WLW[a] | WIDTH: average of up to 10 measurements and not less than 4 (in mm.). |
| WLV[a] | LENGTH X WIDTH: average of up to 10 measurements and not less than 4 (in $mm^2$.). |
| WLR[ab] | LENGTH/WIDTH: average of up to 10 measurements and not less than 4. |
| WLS[ab] | SHAPE: 1. = widest at basal half; 2. = widest at middle; 3. = widest at distal half. |
| WLM[ab] | MARGIN: 1. = smooth; 2. = emarginate; 3. = light serration, small teeth; 4. = heavy serration, large teeth. |
| WLT[ab] | TIP: width of leaf tip. 66 mm. from tip, average of up to 10 measurements and not less than 4. |
| WLD[ab] | DORSAL SURFACE: 1. = sunken; 2. = smooth; 3. = lightly keeled; 4. = strongly keeled. |
| WLN[ab] | LEAVES PER NODE: 2. = two; 3. = three. |
| WLO[a] | LEAVES PER 6.6 mm.: average of up to 10 measurements and not less than 4. |
| WGV[a] | GLAND LENGTH X WIDTH: average of up to 10 measurements and not less than 4 (in $mm^2$.). |
| WGR[ab] | GLAND LENGTH/WIDTH: average of up to 10 measurements and not less than 4. |

TABLE 1. (Continued)

| Characters | States (if applicable) |
|---|---|
| WGS[ab] | GLAND SHAPE: 1. = widest at basal half; 2. = widest at middle; 3. = widest at distal half. |
| WGP[ab] | GLAND PROTRUSION: 1. = sunken; 2. = smooth; 3. = protrudes. |
| WRP[ab] | GLAND RUTURE: 1. = no; 2. = yes. |
| WCT[a] | LENGTH FROM WHIP LEAF GLAND CENTER TO LEAF TIP: average of up to 10 measurements and not less than 4 (in mm.) |
| WGM[ab] | RATIO OF WLL/WCT: average of up to 10 measurements and not less than 4 measurements. |
| *Scale Leaves* | |
| RLL[a] | LENGTH: average of 10 measurements (in mm.). |
| RLW[a] | WIDTH: average of 10 measurements (in mm.). |
| RLV[a] | LENGTH X WIDTH: average of 10 measurements (in $mm^2$.). |
| RLR[ab] | LENGTH/WIDTH: average of 10 measurements. |
| RLS[ab] | SHAPE: 1. = widest at basal half; 2. = widest at middle; 3. = widest at distal half. |
| RLM[ab] | MARGIN: 1. = smooth; 2. = emarginate; 3. = light serration, small teeth; 4. = heavy serration, large teeth. |
| RLT[ab] | TIP: width of leaf tip .33 mm. from tip, average of 10 measurements. |
| RLD[ab] | DORSAL SURFACE: 1. = sunken; 2. = smooth; 3. = lightly keeled; 4. = heavily keeled. |
| RLN[a] | LEAVES PER NODE: 2. = two; 3. = three. |
| RLO[a] | LEAVES PER 3.3 mm.: average of 10 measurements. |
| RGV[a] | GLAND LENGTH X WIDTH: average of up to 10 measurements (in $mm^2$.). |
| RGR[ab] | GLAND LENGTH/WIDTH: average of up to 10 measurements. |
| RGS[ab] | GLAND SHAPE: 1. = widest at basal half; 2. = widest at middle; 3. = widest a distal half. |
| RGP[ab] | GLAND PROTRUSION: 1. = sunken; 2. = smooth; 3. = protrudes. |
| RRP[ab] | GLAND RUPTURE: 1. = no; 2. = yes. |
| RCT[a] | LENGTH FROM SCALE LEAF GLAND CENTER TO LEAF TIP: average of 10 measurements (in mm.). |
| RGM[ab] | RATIO OF RLL/RCT: average of up to 10 measurements. |
| LFD[ab] | LEAF TIP DIVERGENCE: 1. = not divergent; 2. = divergent. |

TABLE 1. (Continued)

| Characters | States (if applicable) |
|---|---|
| *Branches* | |
| FLC[ab] | BRANCH FLACCIDNESS: 1. = not flaccid; 2. = flaccid. |
| BTC[ab] | TERMINAL WHIP CURVATURE: 1. = straight; 2. = curved; average of up to 5 measurements. |
| BDG[ab] | DEGREE OF BRANCHING ON TERMINAL WHIP BRANCH: average of up to 5 measurements. |
| BDS[ab] | DISTICHOUS BRANCHING ON LATERAL BRANCHES: 1. = yes; 2. = no. |
| BAN[ab] | ANGLE OF BRANCHING OF ULTIMATE TWIG: average of up to 10 measurements to nearest 5 degrees). |
| DIA[a] | DIAMETER OF ULTIMATE TWIG: average of 10 measurements (in mm.). |
| BRK[a] | STEM BARK EXFOLIATING PATTERN: 1. = long strips; 2. = fibrous strips; 3. = quadrangular plates; 4. = long plates; 5. = interlaced; 6. = papery-scaley. |

TABLE 2.

Characterization of the complexes of Middle American *Juniperus*.

| *Character* | *deppeanan* | *flaccidan* | *one-seeded* | *monticolan* |
|---|---|---|---|---|
| Cone length X width (FRV) | large | large | small | intermediate |
| Cone pulp (FRP) | fibrous | fibrous | soft, fibrous to fleshy | soft, fibrous |
| Seeds per cone (SPF) | several | many | one | several |
| Seed length X width (SEV) | large | large | intermediate | small |
| Hilum scar length (HIL) | long | long | intermediate | short |
| Angle of branching of ultimate twig (BAN) | narrow | narrow | medium to wide | wide |
| Cone color (FHU, FVA) | dark, reddish brown | dark, reddish brown | variable | variable |
| Peduncle length (PED) | intermediate | intermediate | short | long |
| Peduncle curvature (PEK) | straight | straight | straight | curved |
| Leaves per node (WLN, RLN) | 2 or 3 | mostly 2 | mostly 3 | 2 |
| Terminal whip (BTC) | straight | straig or curved | straight (curved in *J. saltillensis*) | curved |
| Scale leaf width (RLW) | wide | variable | variable | variable |
| Scale leaf tip divergence (LFD) | appressed | divergent | appressed | appressed |
| Branch flaccidness (FLC) | not flaccid | flaccid | not flaccid | not flaccid |

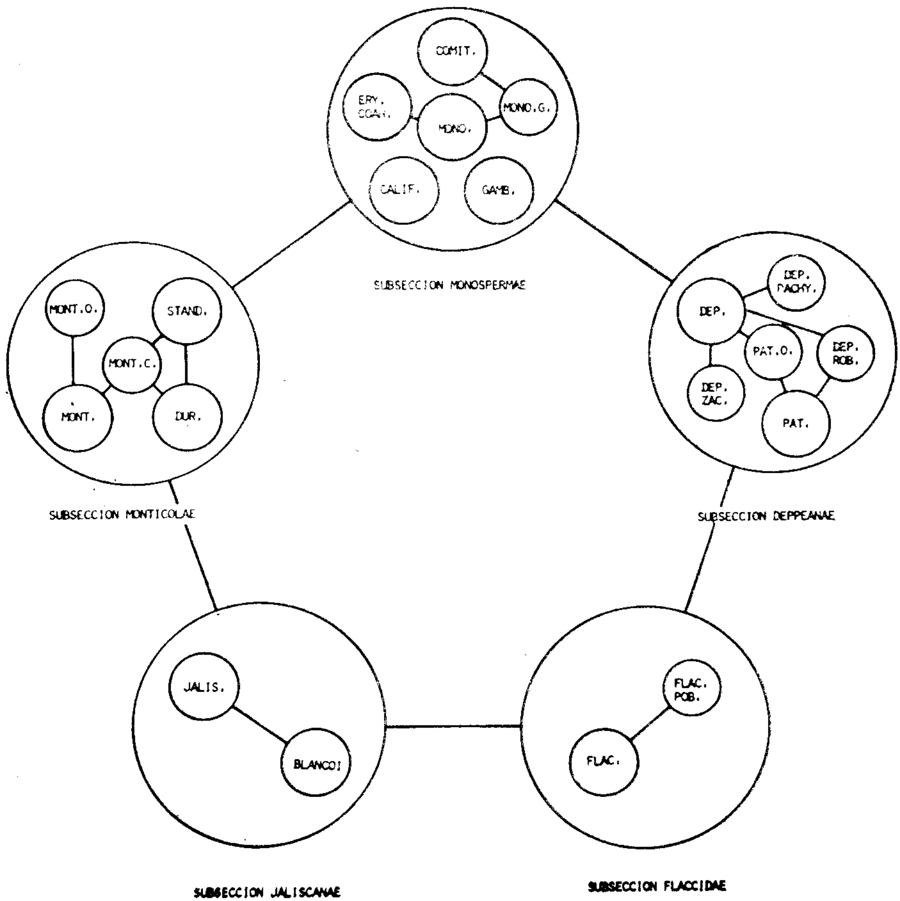
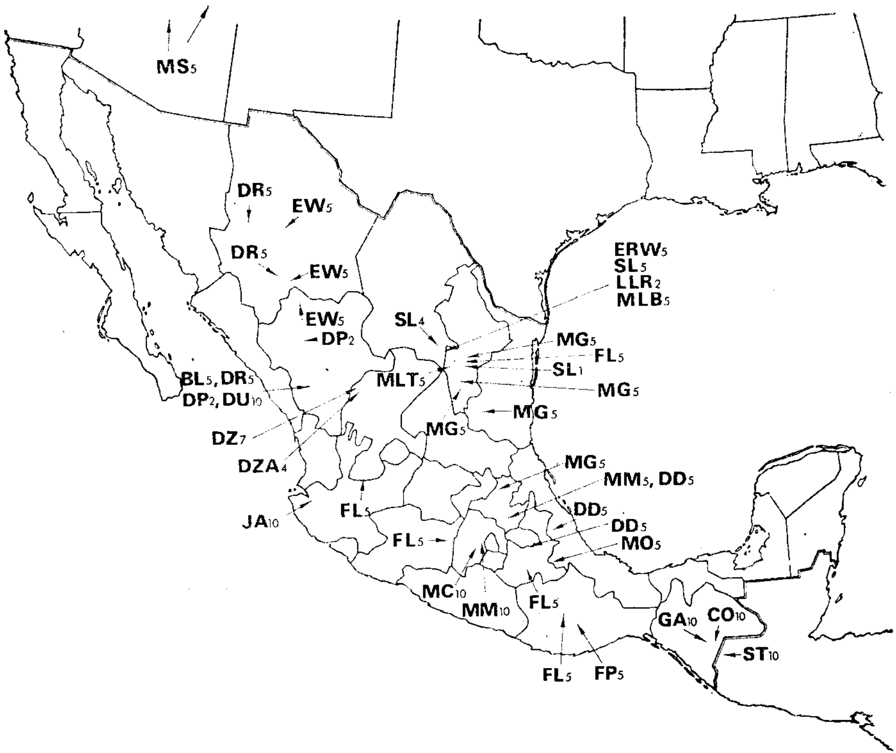



Figure 1. Subsections and taxa of *Juniperus* in Mexico as recognized by Martínez (adapted from Martínez, 1963). Subsection Monospermae: *J. comitana* Martínez (COMIT.); *J. monosperma* (Engelm.) Sarg. var. *monosperma* (MONO.); *J. monosperma* var. *gracilis* Martínez (MONO. G.); *J. gamboana* Martínez (GAMB.); *J. californica* Carriere (CALIF.); *J. erythrocarpa* var. *coahuilensis* Martínez (ERY. COAH). Subsection Deppeanae: *J. deppeana* Steudel var. *deppeana* (DEP.); *J. deppeana* var. *pachyphlaea* (Torrey) Martínez (DEP. PACHY.); *J. deppeana* var. *robusta* Martínez (DEP. ROB.); *J. deppeana* var. *zacatecensis* Martínez (DEP. ZAC.); *J. patoniana* Martínez f. *patoniana* (PAT.); *J. patoniana* f. *obscura* Martínez (PAT. O.). Subsection Flaccidae: *J. flaccida* Schlecht. var. *flaccida* (FLAC.); *J. flaccida* var. *poblana* Martínez (FLAC. POB.). Subsection Jaliscanae: *J. blancoi* Martínez (BLANCOI); *J. jaliscana* Martínez (JALIS.). Subsection Monticolae: *J. standley* Steyermark (STAND.); *J. durangensis* Martínez (DUR); *J. monticola* Martínez f. *monticola* (MONT.); *J. monticola* f. *compacta* Martínez (MONT. C.); *J. monticola* f. *orizabensis Martínez* (MONT. O.).




| OTU | Taxon | Source |
|---|---|---|
| BL | *J. blancoi* | El Salto, Dgo. |
| CO | *J. comitana* | La Trinitaria, Chis. |
| DD | *J. deppeana* | Apizaco, Pue. |
| | var. *deppeana* | El Chico, Hgo. |
| | | Llanos de Perote, V. C. |
| DP | *J. patoniana* | Dgo. |
| DR | *J. deppeana* | Cd. Guerrero, Chih. |
| | var. *robusta* | Huejotitan, Chih. |
| | | Hacienda Coyotes, Chih. |
| DZ | *J. deppeana* | Mina Dolores, Zac. |
| | var. *zacatensis* | Jimenez del Teul, Zac. |
| DZA | *J. deppeana* | El Alamo, Zac. |
| | var. ? | |
| ERW | *J. erythrocarpa* | Saltillo, Coah. |
| | var. *coahuilensis* | |
| EW | *J. erythrocarpa* | Chihuahua, Chih. |
| | var. *coahuilensis* | San Francisco del Oro, Chih. |
| | | Las Nieves, Dgo. |
| FL | *J. flaccida* | El Limon, Zac. |
| | var. *flaccida* | Puerto del Gato, Mich. |
| | | Tehuacan, Pue. |
| | | Morelos, Oax. |
| | | San Marcos, N. L. |
| FP | *J. flaccida* | Ocotepec, Oax. |
| | var. *poblana* | |
| GA | *J. gamboana* | Comitan, Chis. |
| JA | *J. jaliscana* | Cuale, Jal. |
| MG | *J. monosperma* | Trancas, Hgo. |
| | var. *gracilis* | Palmillas, Tamps. |
| | | Dr. Arroyo, N. L. |
| | | Pto. de Pastores, N. L. |
| | | Cerro Potosi, N. L. |
| MS | *J. monosperma* | Arizona and Colorado, USA |
| | var. *monosperma* | |
| MC | *J. monticola* | Nevado de Toluca, Mex. |
| | f. *compacta* | |
| MM | *J. monticola* | El Chico, Hgo. |
| | f. *monticola* | Tantoco, Mex. |
| MO | *J. monticola* | Pico de Orizaba, V. C. |
| | f. *orizabensis* | |
| SL | *J. saltillensis* | Tokio, N. L. |
| | | Saltillo, Coah. |
| | | Encantada, Coah. |
| ST | *J. standleyi* | Mexico and Guatemala |
| LLR | *J. monosperma* | Saltillo, Coah. |
| | var. *gracilis* ? | |
| MLB | *J. monosperma* | Saltillo, Coah. |
| | var. *gracilis*? | |
| MLT | *J. monosperma* | La Trinidad, N. L. |
| | var. *gracilis*? | |

**Figure 2.** Collection localities and number of specimens used in the data analyses.

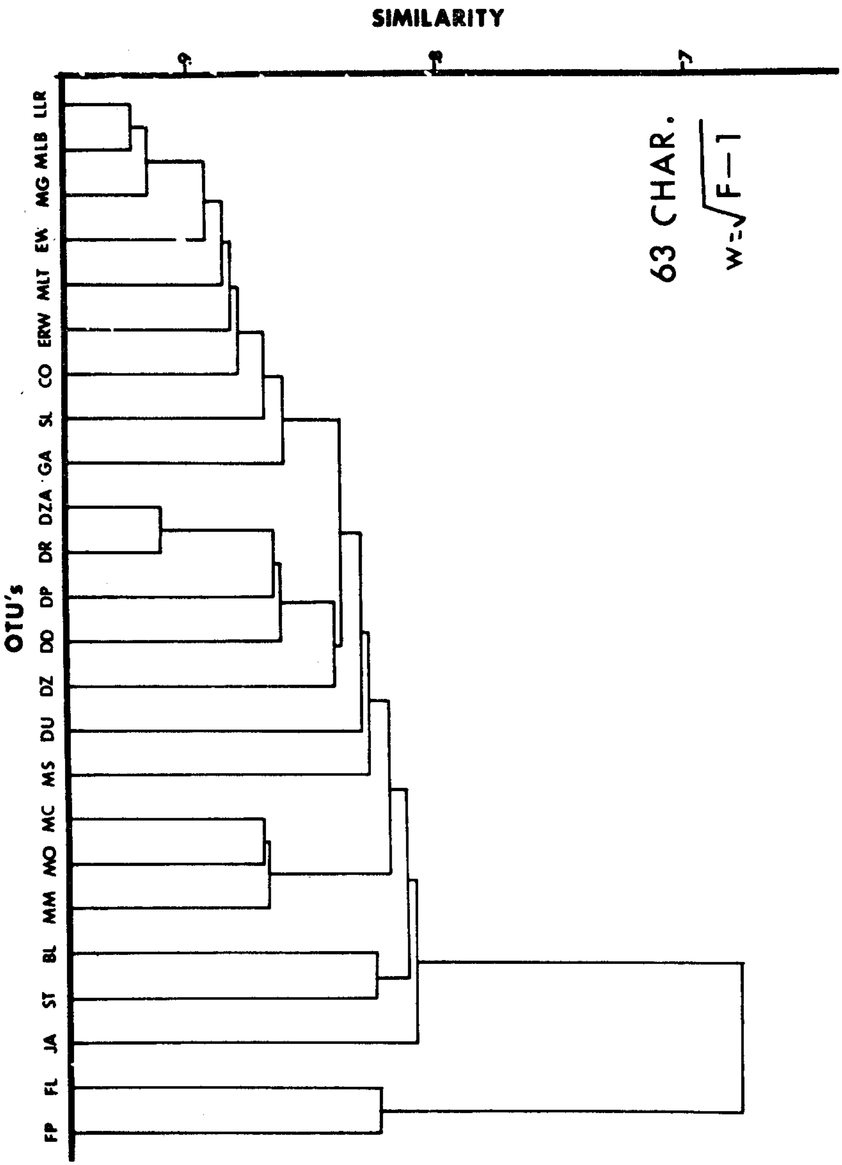



Figure 3. Single linkage clustering of 24 OTU's using 63 morphological characters. Character weights were $\sqrt{F-1}$.

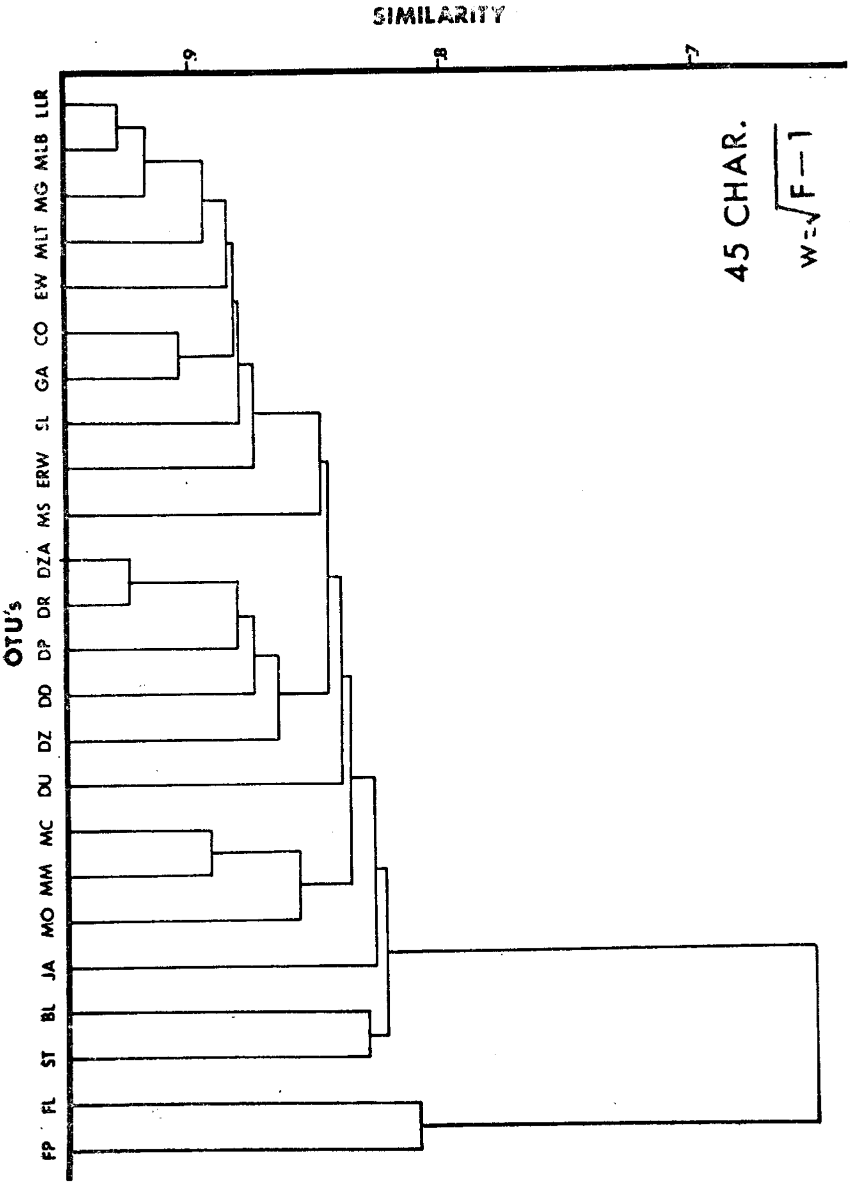



Figure 4. Single linkage clustering of 24 OTU's using 45 morphological characters. Character weights were $\sqrt{F-1}$.

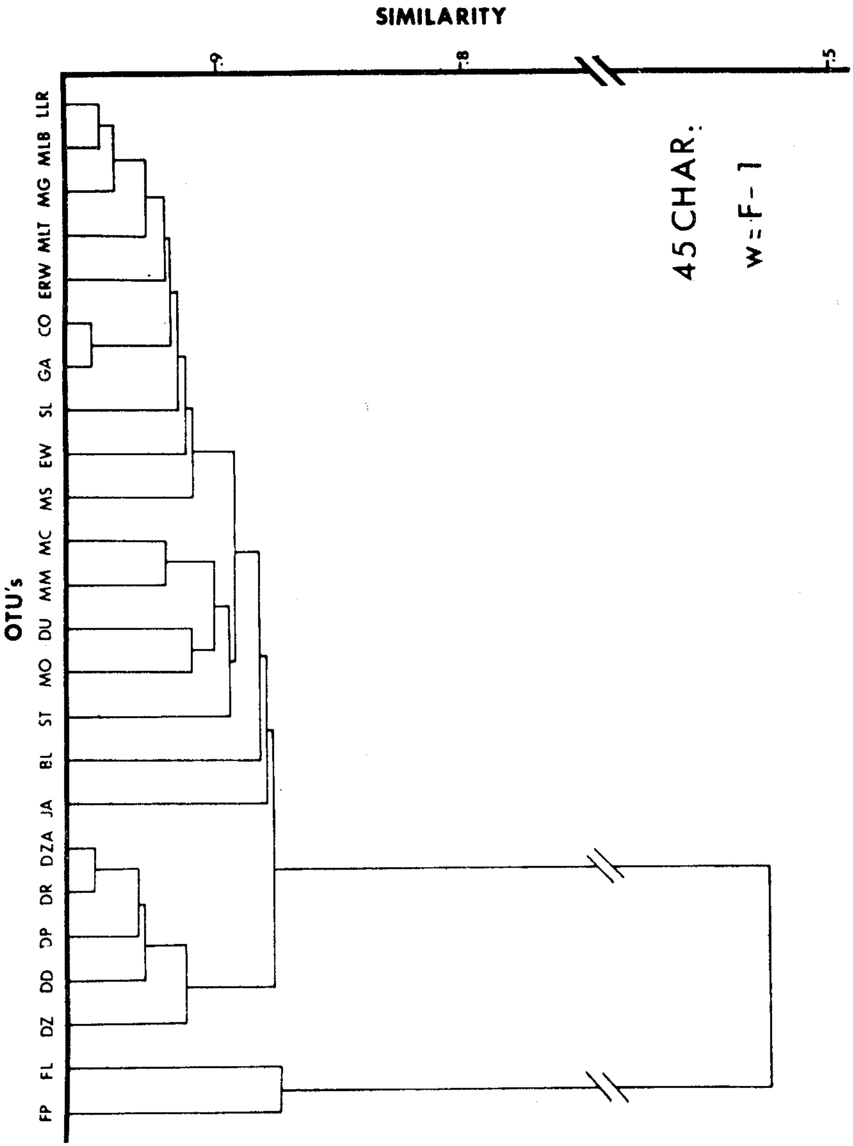



Figure 5. Single linkage clustering of 24 OTU's using 45 morphological characters. Character weights were F — 1.