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# SYSTEMATICS OF *SALVIA PACHYPHYLLA* (LAMIACEAE)

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ABSTRACT

Most populations of *Salvia pachyphylla* occur along mountain ranges adjacent to the Mojave Desert of southern California, southwestern Nevada, and northern Baja California, Mexico. A smaller disjunct group occurs in eastern Arizona near the southern edge of Navajo and Hopi reservation lands near Winslow, AZ. This study was undertaken to determine whether there are morphologically and genetically distinct geographical groups within *S. pachyphylla* and whether these groups form a cohesive unit easily separated from *S. dorrii*. Specimens of *S. pachyphylla* and broadly sympatric taxa in *S. dorrii* were examined in a morphometric analysis of twelve characters. A preliminary molecular analysis using the nuclear ribosomal DNA internal transcribed spacers (ITS-1 and ITS-2) and the embedded 5.8 S subunit was also performed on the same taxa. Morphometric analysis supports the continued recognition of *S. pachyphylla* and *S. dorrii* as distinct species and the recognition of three subspecies within *S. pachyphylla*, requiring two new subspecies, *eremopictus* and *meridionalis*, described here. The molecular data support the recognition of the *S. dorrii* species complex as a whole, but do not support the separation of *S. dorrii* and *S. pachyphylla* as distinct species, although the Mexican populations of *S. pachyphylla* appear genetically distinct.

Key Words: *Salvia pachyphylla*, disjunct distribution, morphometrics, sequence data.

Most *Salvia pachyphylla* Munz populations occur in the Transverse Ranges of the California Floristic Province and the mountain ranges of the Mojave Desert of southern California, southwestern Nevada, and northern Baja California Norte, Mexico. A smaller, disjunct group occurs in eastern Arizona near the southern edge of Navajo and Hopi reservation lands near the city of Winslow, AZ. This interesting disjunct distribution raises questions as to whether the geographical groups are morphologically distinct and whether these groups form a cohesive unit easily separated from *S. dorrii*.

*Salvia pachyphylla* was first collected by the Parish brothers in the San Bernardino Mountains and described as *Audibertia incana* var. *pachystachya* by Gray (1878). Samuel B. Parish (1898) elevated this taxon to *Audibertia pachystachya*. Amos A. Heller (1900) transferred *Audibertia pachystachya* to the genus *Ramona*. Harvey M. Hall (1902) transferred *Ramona pachystachya* to *Salvia* and recognized it as a variety of *S. carnosa* [now known as *S. dorrii*], giving it the name var. *compacta*. Philip A. Munz elevated it to species level (*Salvia compacta*), creating a homonym of *S. compacta* Kuntze (Munz 1927). Finally, Munz (1935) renamed *S. compacta* as *S. pachyphylla* Munz.

*Salvia pachyphylla* is a member of the *Salvia dorrii* (Kellogg) Abrams complex (Strachan 1982), which is comprised of only these two species. Epling (1938) and Strachan (1982) recognized the close relationship between *S. pachyphylla* and *S. dorrii* based upon morphological characters. They are both woody shrubs with peeling bark, opposite leaves in fascicles, and crowded verticils containing pink to magenta-colored bracts. Strachan (1982) used quantitative characters of the leaves and flowers to separate the two species. The leaves of *S. pachyphylla* are usually much larger than those of *S. dorrii* (20–50 mm vs. 4–30 mm). The inflorescence bracts the corollas are also much longer in *S. pachyphylla* (bracts 10–20 mm, corollas 17–28 mm vs. bracts 5–14 mm, corollas 9–18 mm in *S. dorrii*). One of the qualitative differences between the two species is the position of hairs on the corolla. *Salvia pachyphylla* has a ring of hairs within the lower portion of the corolla tube, whereas *S. dorrii* flowers possess hairs on the lower lip of the corolla that extend slightly into the throat. The distance between the base of the tube and the hairs is nearly the same in both species, which suggests that the length of the tube determines the final placement of the hairs (Strachan 1982). *Salvia pachyphylla* has hairs on the adaxial side of the bracts, whereas *S. dorrii* does not. The two species are hypothesized to be reproductively isolated because they are geographically isolated and flower at different times (Strachan 1982). *Salvia pachyphylla* flowers from July to October whereas *S. dorrii* flowers from March to July (September), which Strachan thought would exclude any gene flow. *Salvia pachyphylla* is found on north facing slopes at elevations of 1500–3050 m. The three subspecific taxa of *S. dorrii* found in the southwestern U.S.

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occur at much lower elevations (850–1900 m), even though Strachan (1982) noted higher elevations for the northern part of the range of var. *dorrii*.

Strachan (1982) noted that there may be three morphologically distinct groups within *S. pachyphylla*. The California plants have very large, obovate leaves (23–63 mm) and large bracts (11–20 mm). The Arizona plants have short, spatulate leaves (20–44 mm) and smaller bracts (8–14 mm). The Baja plants have small linear to narrowly spatulate leaves (26–45 mm) and intermediate bracts (10–19 mm). This morphological variation suggests either that the three groups have diverged or that the delimitation of *S. pachyphylla* from *S. dorrii* may have created artificial groups.

Two hypotheses are plausible: 1) *Salvia pachyphylla* once had a more continuous distribution across the Southwest until climate change, and subsequent contraction of pinyon-juniper woodland, split the species into the three groups seen today. If this was the case, one would expect to find some degree of morphological and genetic differentiation among populations across the range of the species; 2) The morphological variation seen in the Arizona populations of *S. pachyphylla* may be a reflection of a closer relationship between the Arizona populations and sympatric subspecies within *S. dorrii*. If this is true, one would expect to see more continuous morphological variation and genetic similiarity between the two species.

To resolve these issues the following questions were asked: 1) Are *Salvia pachyphylla* and *S. dorrii* distinct species? 2) Are there morphologically or genetically distinct geographical subgroups within *S. pachyphylla*? 3) If so, how much variation is found within the Arizona populations? 4) Can morphology or genetic markers be used to suggest an origin for the Arizona plants?

To answer these questions, morphometric analyses were performed on morphological characters and molecular sequence data were gathered from populations of *S. pachyphylla* throughout the geographical range of the species and populations representing the three subspecies of *S. dorrii* found in the Southwest. Morphometric analyses are commonly used to study variation among populations and species (Dodd and Helenurm 2000; Battaglia and Patterson 2001). Recent studies of the internal transcribed spacer region (ITS) (Baldwin et al. 1995; Ballard et al. 1999; Meerow et al. 2000; Urbatsch et al. 2000) have shown that this is a valuable region for phylogenetic studies at the species level and that the ITS region has enough nucleotide sequence variability for resolution of lower-level phylogenetic questions (Baldwin 1995; Soltis et al. 1998).

## Methods

### Morphometric Analysis

One hundred and eighty-two herbarium specimens were used in a morphometric analysis to determine morphological variation within the *Salvia dorrii* species complex. A complete list of the specimens used is included in Taylor (2002) and most are included in the exsiccatae listed in the taxonomic treatment below. Sample sizes are included in the figures below. Two specimens of *S. pachyphylla* from two different populations from Nevada were put into the California group due to similar morphological characters. Both *S. dorrii* subsp. *mearnsii* and *S. dorrii* subsp. *dorrii* were used in the morphometric analysis because populations of each exist in Arizona in close proximity to the populations of *S. pachyphylla*. Other varieties of *S. dorrii* were not used due to their physical distance from the Arizona populations of *S. pachyphylla*.

Calipers and a LEICA S6E (0.6–4×) dissecting scope were used to measure the 12 characters discussed below. Four categorical and eight continuous characters were used in the analysis. Measurement of bract length and width were determined by taking the average of three measurements using the lowest bract on the first full flowering verticil. Measurement of the hairs on the abaxial side of the bracts was made by averaging the majority of hair lengths. Hairs along the margin of the bract were calculated by averaging the five longest hairs along the margin. Corolla length was measured on rehydrated flowers at full anthesis. Rehydrated corollas were cut longitudinally to discern whether a ring of hairs was present within the corolla and whether there were hairs on the lip. Leaf length and width were averages based upon the three largest leaves on each specimen. The average of two internode lengths was taken starting at the base of the lowest bract and measuring to the base of the next to the last verticil. The adaxial side of the bracts was observed to determine the presence of hairs. The abaxial side of the bracts was observed to determine whether the glands were sunken into the leaf tissue or raised. Nine of the twelve characters (bract width, bract length, abaxial bract hair length, marginal bract hair length, corolla length, presence of hairs within corolla, leaf length, leaf width, internode length) were analyzed using the computer program SYSTAT version 8.0 (SPSS 1998) to perform a Discriminant Function Analysis (DFA) and Principle Components Analysis (PCA). Six of the 12 characters (bract length, bract width, leaf length, leaf width, internode length, corolla length) were analyzed through Analysis of Variance (ANOVA) using JMP version 4.0.4 (SAS Institute 2001).

TABLE 1. COLLECTION USED IN THE MOLECULAR ANALYSIS. All specimens deposited in the Deaver Herbarium (ASC).

| Taxon | Locality | County/State | Collector/Coll. # | GenBank Accession # |
|---|---|---|---|---|
| Salvia pachyphylla AZ | Meteor Crater | Coconino Co., AZ | R. Taylor 03B | AF538906 |
| | Meteor Crater | Coconino Co., AZ | R. Taylor 03C | AF538907 |
| | N. Winslow | Navajo Co., AZ | R. Taylor 04C | AF538908 |
| | N. Winslow | Navajo Co., AZ | R. Taylor 04E | AF538909 |
| | Dilkon | Navajo Co., AZ | R. Taylor 26A | AF538911 |
| | Dilkon | Navajo Co., AZ | R. Taylor 27 | AF538912 |
| | Petrified Forest | Coconino Co., AZ | R. Taylor 19 | AF538910 |
| Salvia pachyphylla CA | Santa Rosa | Riverside Co., CA | S. Rhodes 9924 | AF538913 |
| | Santa Rosa | Riverside Co., CA | S. Rhodes 9925 | AF538914 |
| | San Bernardino Mtns | San Bernardino Co., CA | S. Rhodes 9926 | AF538915 |
| | San Bernardino Mtns | San Bernardino Co., CA | S. Rhodes 9928 | AF538916 |
| Salvia pachyphylla MX | Sierra San Pedro Martir | Baja, Mexico | S. Rhodes 00124 | AF538917 |
| | Sierra San Pedro Martir | Baja, Mexico | S. Rhodes 00127 | AF538918 |
| Salvia dorrii subsp. Mearnsii | Cottonwood | Yavapai Co., AZ | R. Taylor 14A | AF538900 |
| | Perkinsville | Yavapai Co., AZ | R. Taylor 15A | AF538901 |
| | Sedona | Yavapai Co., AZ | R. Taylor 16D | AF538902 |
| Salvia dorrii var. dorrii | N. Cameron | Coconino Co., AZ | R. Taylor 05C | AF543682 |
| | Cameron | Coconino Co., AZ | R. Taylor 06A | AF538898 |
| | Shadow Mtn | Coconino Co., AZ | R. Taylor 08 | AF538899 |
| Salvia dorrii var. pilosa | San Bernardino Mtns | San Bernardino Co., CA | S. Rhodes 9927 | AF538903 |
| | San Bernardino Mtns | San Bernardino Co., CA | S. Rhodes 9929 | AF538904 |
| | Kingston Mtns | San Bernardino Co., CA | S. Rhodes 9931 | AF538905 |
| Salvia mohovensis | San Bernardino Mtns | San Bernardino Co., CA | R. Taylor 13C | AF538921 |
| | San Bernardino Mtns | San Bernardino Co., CA | R. Taylor 13E | AF53892 |
| | San Bernardino Mtns | San Bernardino Co., CA | R. Taylor 11A | AF538920 |
| Salvia davidsonii | Grand Canyon | Coconino Co., AZ | R. Scott 882 | AF538919 |

## Molecular Analysis

Twenty-six samples were used in the ITS analysis to represent the three geographic groups of *S. pachyphylla* and the three subspecific taxa of *S. dorrii* that are broadly sympatric (Table 1). *Salvia davidsonii* Greenm. and *S. mohavensis* Greene were used as outgroups for this analysis because they are southwestern representatives within the genus *Salvia* but have never been recognized as part of the *Salvia dorrii* species complex. *Salvia mohavensis* is placed within the same section *Audibertia* and sub-section *Jepsonia* as the ingroup (Epling 1938). Samples were taken from populations throughout the Southwest over a four-year period. The two Baja California, Mexico samples were obtained from herbarium sheets in the Deaver Herbarium (ASC).

Genomic DNA was extracted from silica-dried leaf tissue and fresh leaf tissue using a modified CTAB protocol of Doyle and Doyle (1987). Quality and quantity were assessed with gel electrophoresis on a 1% agarose gel. The entire ITS region (ITS 1/5.8 s/ITS 2) was then amplified using primers created with the Oligo program version 6.56; primer sequences are as follows: forward primer: ITSAL22F 5′ GTTTCCGTAGGTGAACCTGC 3′; internal forward primer: ITSAL291F 5′ CTCGGCAACGGATATCTCG 3′; and reverse primer ITSAL693R 5′ TTAAACTCAGCGGGTGATCC 3′. DMSO was added to aid in the reduction of secondary structure (Soltis et al. 1998). Amplification procedures were as follows: four minutes of denaturing at 95°, thirty seconds at 95°, thirty seconds of annealing at 55°, one minute of extension at 72°, thirty two cycles, ten minute extension at 72°, and a holding temperature at 4°.

To assess possible parology, Polymerase Chain Reaction (PCR) products were cloned, due to noise within the sequence and problems with amplification. Cloning was accomplished using an Invitrogen TOPO TA cloning kit (Electroporation protocol) following the manufacturer's recommended procedures. Amplification of the clones were as follows: Five minutes of denaturing at 95°, thirty seconds at 95°, thirty seconds of annealing at 56°, one minute of

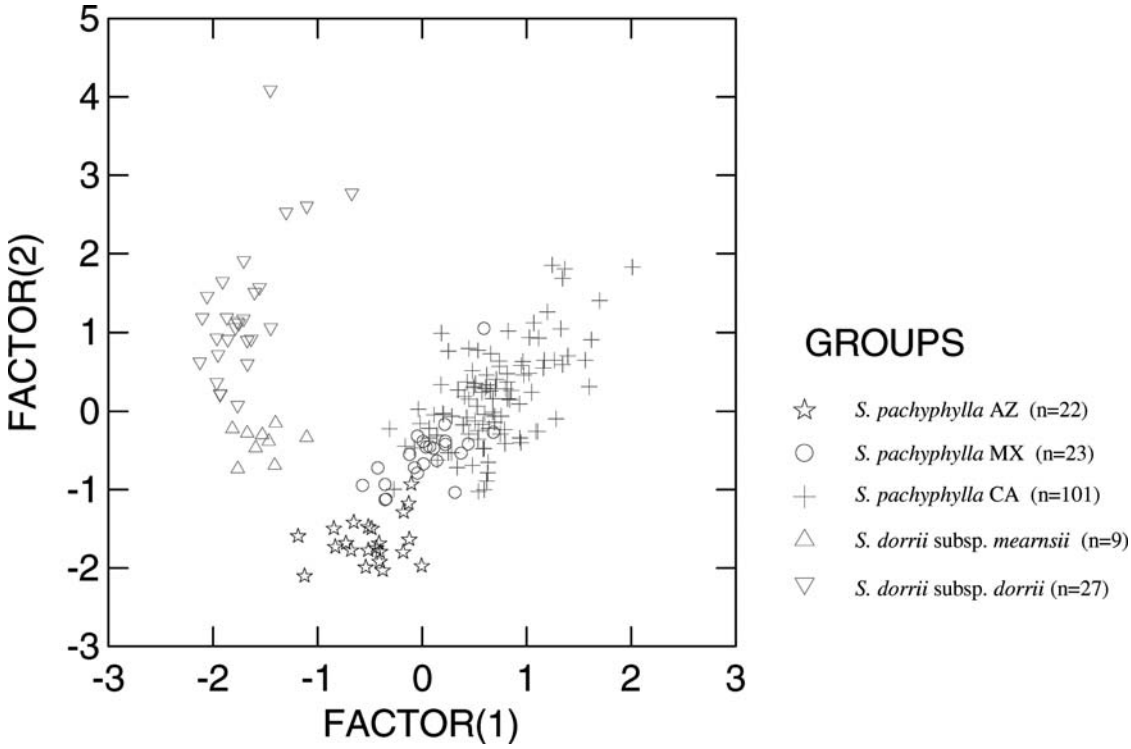


FIG. 1. PCA scatter plot of morphological characters. Factor 1 is the first principal component and Factor 2 is the second principle component. Sample numbers (n) for each taxon in parentheses. See text for discussion of factors.

extension at 72°, thirty five cycles, three minute extension at 72°, and a holding temperature at 4°. PCR concentrations and amplification were assessed electrophoretically on a 1% agarose gel using a low DNA mass ladder. No length mutations were seen in any of the clones. PCR products from three clones were purified using Qiagen's QIAquick PCR purification columns and protocols. Double-stranded PCR products were sequenced on polyacrylamide gels at the Arizona Research Lab in Tucson using a big dye terminator chemistry kit version 2 and an ABI 377 machine.

Forward and reverse sequences and ABI electropherograms were edited in DNA STAR-Seqman II version 5.01 (1989;–2001) after reverse complementation to resolve any ambiguities. Sequences were placed in DNA STAR-Megalign version 5.01 (1993;–2001) and aligned using Clustal W and then aligned visually. All but one of each set of redundant sequences were excluded from the alignments. Sequence alignments were saved as PAUP files and analyzed using PAUP 4.0b10 (Swofford 2002). Heuristic searches were performed with tree bisection and reconnection (TBR) branch swapping and random taxon addition. All searches were run using only informative characters. Gaps were coded as missing data and as a 5th element. One hundred bootstrap replicates were performed using the heuristic search and TBR branch swapping.

## RESULTS

### Morphometric Analysis

Principal component analysis (PCA) of all specimens produced the scatter plot shown in Fig. 1. The factors (i.e., principal components) are linear combinations of characters that best account for variation in the data. The first factor was comprised mostly of bract length, corolla length, ring of hairs, leaf length, and leaf width. Factor two was comprised mainly of one character, bract hair length. The loadings of variables for each factor can be found in Taylor (2002).

The principle components analysis shows clear separation between *S. dorrii* and *S. pachyphylla*. Clear separation is also seen between the Arizona populations and the California populations of *S. pachyphylla* although the Mexico specimens overlap with both the Arizona and California clusters. The PCA results were identical when examining scatter plots containing specimens of *S. pachyphylla* and *S. dorrii* together or just examining scatterplots containing only *S. pachyphylla* specimens (PCA not shown), the trends still remain

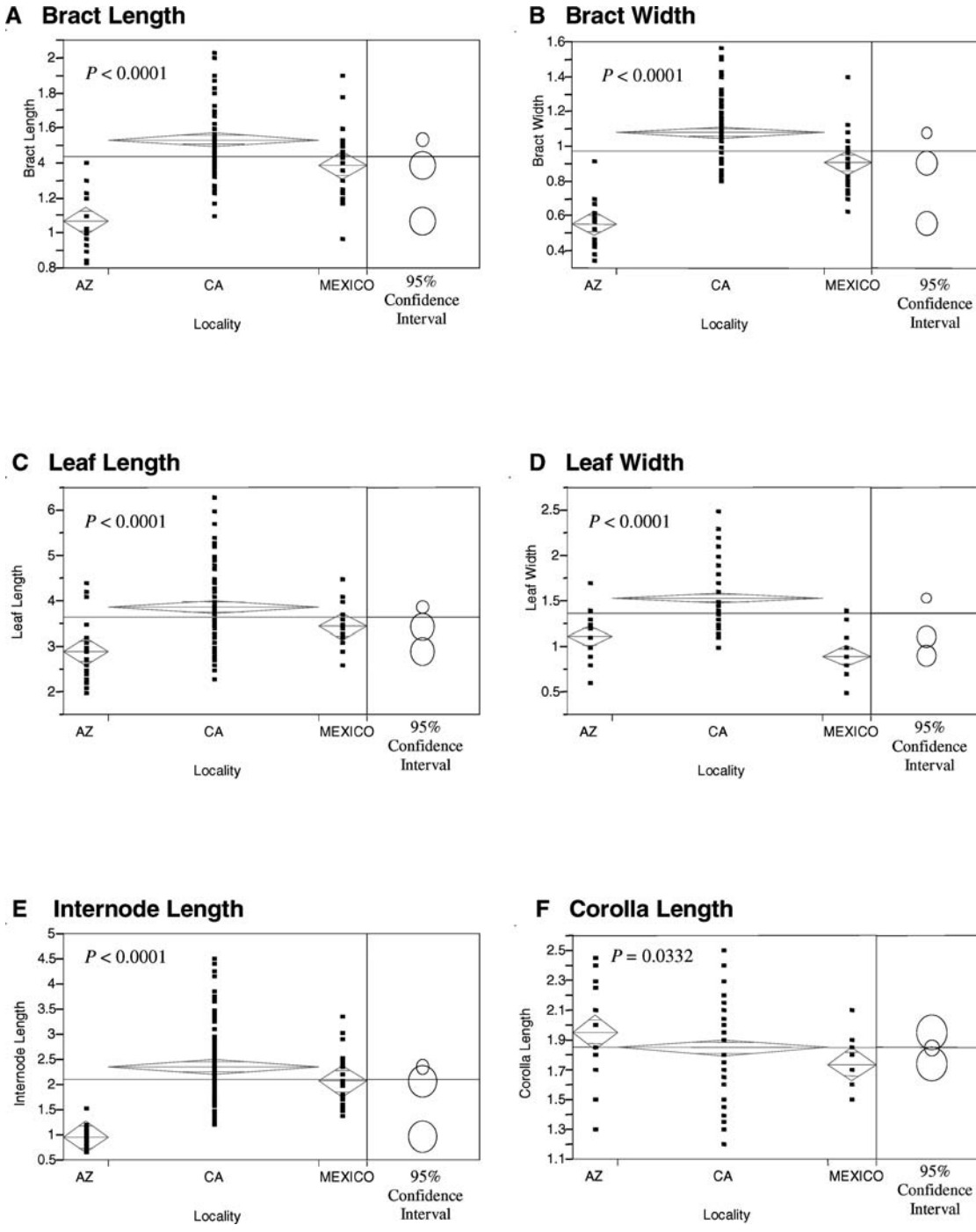


FIG. 2. Distribution and 95% confidence intervals for six morphological characters in *S. pachyphylla* separated by locality. Horizontal line represents overall mean for all groups. Diamonds show means (center line) and the 95% confidence limits (top and bottom lines) for each group. Circles also represent the 95% confidence intervals for each group.

the same between the *S. pachyphylla* geographic groups (Taylor 2002).

The distributions and 95% confidence intervals for six of the nine morphological characters are shown in Figure 2. All six characters showed significant differences among the three geographical groups of *S. pachyphylla* (ANOVA, $P < 0.05$). For five of the six morphological char-

TABLE 2. CLASSIFICATION MATRIX OF ALL SPECIMENS USED IN THE MORPHOMETRIC ANALYSIS.

| | | A | B | C | D | E | % CORRECT |
|---|---|---|---|---|---|---|---|
| A | *S. pachyphylla* AZ | 21 | 0 | 1 | 0 | 0 | 95 |
| B | *S. pachyphylla* MX | 1 | 21 | 1 | 0 | 0 | 91 |
| C | *S. pachyphylla* CA | 1 | 12 | 88 | 0 | 0 | 87 |
| D | *S. dorrii* ssp. *mearnsii* | 0 | 0 | 0 | 9 | 0 | 100 |
| E | *S. dorrii* ssp. d*orrii* | 0 | 0 | 0 | 0 | 27 | 100 |
| TOTAL | | 23 | 33 | 90 | 9 | 27 | 91 |

acters, P values were less than 0.0001. All pairs of the three geographical groups had significantly different means ($P < 0.05$, Each Pair Student's t-test). The Mexican populations appear intermediate between the California and Arizona populations with respect to bract shape (length and width), and internode length. The California populations appear intermediate in corolla length, while the Arizona populations appear intermediate for leaf width and hair length on the floral bracts.

The classification matrix, derived from a Discriminant Function Analysis (DFA) was used to test group membership based on pre-defined geographic distributions of *S. pachyphylla*. The classification matrix presented in Table 2 had percentages of correct grouping ranging from 87–100%. This matrix indicates complete taxonomic separation between populations of *S. pachyphylla* and *S. dorrii*. No misidentifications were seen. The matrix also provides adequate support for the recognition of all three geographical groups as subspecific taxa within *S. pachyphylla*. Based upon the matrix produced, the Arizona and Mexican specimens will rarely be misidentified (91–95% correct placement), while the morphological variation found in the Californian populations may result in correct placement only 87% of the time. Only a few of the Californian specimens showed extreme variability. Most of the Californian specimens contributed to the limited variability seen in the results discussed above. A jackknife matrix derived from an analysis of all specimens using the same groupings ranged from 85–100% correct grouping (Taylor 2002).

## Molecular Analysis

Sequence characteristics of the ITS region within the *S. dorrii* complex and outgroups are summarized in Table 3. Sequences from cloned DNA showed no variation that would suggest that paralogues were present. Sequences obtained for the ITS 1 region are within the ranges reported by Baldwin et al. (1995), but the size in base pairs (268–277) is larger than all taxa reported, except for the Brassicaceae and Malvaceae. The ITS 2 region is within the reported base pair range. The ITS 1 region also contains 2–7% higher sequence divergence compared to the ITS 2 region. Levels of divergence within the *S. dorrii* species complex, including both ITS regions and the 5.8 S, ranged between 0.1–7.7%. The levels of divergence were much higher when the outgroups were included with ranges between 9.3–28.8%. Rates of divergence are consistent with other studies that compare lower level taxa (Schilling et al. 1998). The G+C content within the ITS 1 and ITS 2 are similar to each other and are much higher than G+C content found in all other families except Rosaceae (Baldwin et al. 1995).

Of the 695 nucleotide positions sequenced during this molecular analysis, 71 were parsimony informative. One hundred equally most parsimonious trees (length 85) were found using 10 random sequence additions with all characters equally weighted and gaps coded as missing data (consistency index (CI) = 0.90, retention index (RI) = 0.94, rescaled consistency (RC) = 0.84) (Fig. 3). One hundred equally parsimonious trees (length 95) were also found using gaps coded as

TABLE 3. SEQUENCE CHARACTERISTICS FOR THE *SALVIA DORRII* COMPLEX AND OUTGROUPS.

| | ITS 1 | ITS 2 | 5.8 S |
|---|---|---|---|
| Aligned Length | 268 | 252 | 162 |
| Un-aligned Length | 268–277 | 243–252 | 162 |
| Sequence Divergence within *S. dorrii* complex (%) | 0.1–7.7 | 0.1–2.5 | 0.1–1.2 |
| Sequence Divergence including outgroups (%) | 13.1–28.8 | 11.0–21.4 | 9.3–10.6 |
| G+C Content (%) | 65–71 | 61–71 | 49–58 |
| Informative Sites within *S. dorrii* complex | 5 | 6 | 1 |
| Informative Sites including Outgroups | 26 | 29 | 16 |
| Informative Sites within *S. dorrii* complex gaps as 5th state | 5 | 8 | n/a |
| Informative Sites including Outgroups gaps as 5th state | 93 | 34 | n/a |

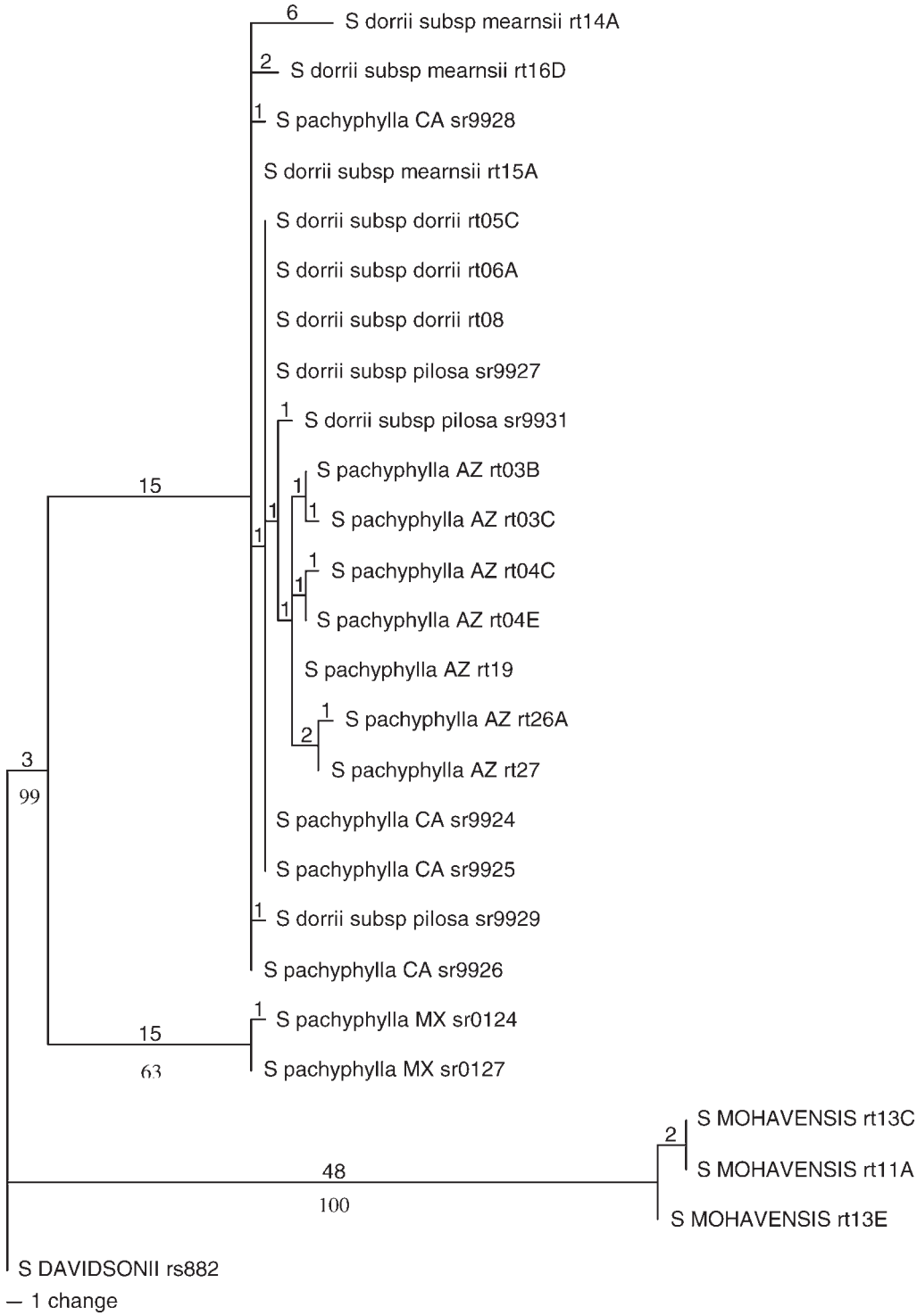


FIG. 3. Phylogram of ITS sequence data; one of one hundred equally most parsimonious trees showing branch lengths above the nodes and bootstrap support for selected nodes; initials after taxon names refer to collector/collection numbers: rt = R. Taylor collections; sr = S. Rhodes collections; rs = R. Scott collections.

a 5th state (CI = 0.90; RI = 0.94). No major changes in topology were evident by coding gaps as missing or as a 5th state. There is little resolution between *S. pachyphylla* and the taxa sampled from the *S. dorrii* complex with one notable exception, the *S. pachyphylla* specimens from Mexico. The *S. pachyphylla* populations from Mexico appear genetically distinct from all of the rest of the *S. dorrii* complex. The *S. pachyphylla* populations from the Arizona group form a weak clade. There is no support for a group representing the *S. pachyphylla* populations that occur in California. The *S. dorrii* complex as a whole formed a strong clade (bootstrap = 99%).

## Discussion

The morphometric data not only suggest continued recognition of *S. dorrii* and *S. pachyphylla* as separate species, but the data also support recognition of three distinct groups within *S. pachyphylla*. The molecular data do not fully reflect the amount of morphological divergence seen in the *S. dorrii* species complex. The molecular data show strong support for the *S. dorrii* complex as a whole but provide little else, except that the Mexican populations of *S. pachyphylla* appear to be genetically distinct from the rest of the *S. dorrii* complex. Lack of molecular divergence has been documented in the Asteraceae where morphology evolves faster than DNA sequences even in rapidly evolving gene regions (Baldwin et al. 1998; Baldwin 2000). ITS sequences in woody plants evolve much more slowly than ITS sequences in herbaceous annuals of recent origin (Baldwin et al. 1995). Some populations of *S. pachyphylla* and *S. dorrii* subsp. *mearnsii* have large, gnarled trunks with peeling bark, which suggests that they may be very long-lived shrubs. A small pilot study looking at the 3′ end of *mat*K and its adjacent spacer region of the chloroplast DNA of four taxa within the *S. dorrii* complex corroborates the ITS results and suggests that *S. pachyphylla* may be paraphyletic (Taylor 2002).

Many different Native American tribes have used both species within the *Salvia dorrii* complex for medicinal or ceremonial purposes in the past and some continue to use it today (Zigmond 1981; Huisinga 2001). *Salvia pachyphylla* currently is wild-harvested by the Navajo and Hopi as ceremonial tobacco and medicine (Phyllis Hogan personal communication). Trade can function as a mode of transportation to a new locality, which can help organisms overcome geographical barriers enabling genetic and morphological differentiation (Brooks and Johannes 1990). Most populations of *S. pachyphylla* occurring within Arizona are found in close proximity to ruins, suggesting that they might be products of prehistoric introduction. If the Arizona populations had shown little or no morphological or genetic variation and had nested within one of the other geographical groups, this mode of introduction, although untestable, might have been more plausible.

The results of the PCA and ANOVAs show that there has been significant morphological differentiation of all *S. pachyphylla* populations in Arizona when compared to the California and Mexico populations. These results thus refute the possibility that the Arizona populations were remnants of trade between groups of indigenous peoples. In addition, there is evidence that the presence of the species predated human migration into northern Arizona. Plant macrofossils from packrat middens are an ideal method for reconstructing past plant species distributions and ages (Cole 1990). The Cricetid rodent, *Neotoma stephensi* (the packrat), has been known to collect plant material within a 30–100 meter radius from the nest for nest building materials (Van Devender et al. 1987). Packrat urine contains high amounts of calcium oxalate, which aids in solidifying the midden into rock-like deposits (Wells 1976). The crystallized urine envelops and protects the plant macrofossil from decay, preserving it for years to come (Cole 1990). It has been shown that midden deposits are preserved for over 50,000 years in optimal conditions (Wells 1976; Cole 1990).

Material from packrat middens show species within the *S. dorrii* complex to be at least 39,900 years old based on carbon dating of leaves (K. Cole unpublished data). Leaves of *S. pachyphylla* found in Nevada have been dated to between 10,060–11,940 years old (K. Cole unpublished data), which predates Archaic Cultural Groups of PaleoIndians (Fish and Fish 1984). Samples of *S. dorrii* subsp. *dorrii* from packrat middens found in Arizona have been dated between 12,015–17,400 years old (K. Cole unpublished data). There are no known specimens of *S. pachyphylla* from middens in Arizona to date, but, based upon the midden data presented above, it is plausible that *S. pachyphylla* occurred in Arizona well before settlement by PaleoIndian groups. The present day distribution of the three extremely small populations of *S. pachyphylla* in Arizona adjacent to ruins may be the result of past wild-harvesting or natural remnant populations that are soon to become extinct. The fourth Arizona population of *S. pachyphylla* is extensive and has very large individuals, seedlings, and many different intermediate age classes indicating that the occurrence of *S. pachyphylla* in Arizona is probably not a remnant of past use by Paleoindians.

The research presented here is not definitive but suggests that the distribution of *S. pachyphylla* was once more continuous, with vicariant

events causing the contraction of the populations to the geographically distinct groups seen today. This vicariance might have been caused by climate changes such as rising temperatures and decreasing moisture during the formation of the Mojave Desert (Raven and Axelrod 1978; Stott 1981; Axelrod 1983; Schaffer 1993). The contraction to the current disjunct distribution in Arizona might also have occurred as late as the Holocene, when pinyon-juniper woodland again dominated the landscape until warmer, drier climate resembling present day conditions occurred at the end of the Pleistocene (Martin and Mehringer 1965). Examples of disjuct distributions from northern Baja California, Mexico and northeastern Arizona are known from other taxa such as *Errazurizia* Phil. and phylogenetic studies of these groups might lead to a better understanding of southwestern biogeography.

Results of the morphological data support the recognition of subspecific taxa within *S. pachyphylla*, as presented below. Due to the size of most of the Arizona populations and the importance of this plant to tribes in the Southwest, monitoring of populations and of annual harvesting is recommended. Future research within the *S. dorrii* complex should include larger sample sizes, additional molecular markers, and ecological observations to understand whether the recognition of one or two distinct species within the *Salvia dorrii* species complex is warranted.

## Taxonomic Treatment

### *Salvia pachyphylla* Munz Rose Sage

Aromatic, branching perennial shrub with gray peeling bark 35–100 cm tall 40–150 cm wide, generally much wider than tall. LEAVES opposite, fascicled, glandular, 2.0–6.3 cm long and 0.5–2.5 cm in wide, fleshy, obovate to rhombic, attenuate at the base of the leaf, tip acute to obtuse, abaxial and adaxial sides covered in appressed white hairs. INFLORESCENCE of 1-many verticils subtended by many bracts; bracts green to magenta in color, glandular, ciliate, scarious, rotund to orbicular, pubescent. FLOWERS several per verticil; calyx connate, lobed at the top, green to purple, pubescent; corolla connate, blue to violet, limb comprised of an upper lip and two bilateral lobes, tube containing a ring of hairs; stamens 4, exerted from corolla. FRUIT 1–4 nutlets. SEEDS tan to black. Found on north facing slopes in conifer forests, 1219–2830 m (4000–9284 ft). Three subspecies distributed in southwestern North America (Fig. 4). Uses: smoke or tea to calm the mind, and used in the treatment of epilepsy (Whiting 1939; Zigmond 1981).

Key to the Subspecies of *S. pachyphylla*

1. Internode length between verticils (6.5-) 8.5–10 (-15.5) mm, bract width (3.5-) 5.5–5.9 (9.2) mm, endemic to northeastern Arizona . . . . . *S. pachyphylla* subsp. *eremopictus*
1. Internode length between verticils (14.5-) 18.5–25 (-45) mm, bract width (6.5-) 9–13 (-15.7) mm.
2. Shrubs with a well-defined woody trunk, leaf length (2.6-) 3–3.6 (-4.4) mm, leaf width (5-) 7–11 (-14) mm, endemic to Baja California, Mexico . . . . . .*S. pachyphylla* subsp. *meridionalis*
2. Subshrubs mostly branching below the ground, leaf length (2.3-) 3.7–4.2 (-6.3) mm, leaf width (10-) 13–17 (-25) mm, southern California and Nevada . . . . . *S. pachyphylla* subsp. *pachyphylla*

*Salvia pachyphylla* P. A. Munz subsp. *pachyphylla* Rose Sage Illustration: Brittonia 34(2): 167. 1982.

*Audibertia incana* var. *pachystachya* A. Gray, Syn. Fl. N. Amer., ed. 2. 2(1): 461. 1886. *A. pachystachya* Parish, Erythea 6:91. 1898; not *Salvia pachystachya* Trautv. *Ramona pachystachya* A. A. Heller, Muhlenbergia 1:4. 1900. *Salvia carnosa* var. *compacta* H. M. Hall, Univ. Calif. Publ. Bot. 1:111. 1902, nom. superfl. *S. compacta* Munz, Bull. S. Calif. Acad. Sci. 26:22. 1927; not *S. compacta* Kuntze, 1891. *S. pachyphyulla* Epling ex Munz, Man. S. Calif. Bot. 445. 1935. Type: UNITED STATES. California: San Bernardino Co.: Bear Valley, San Bernardino Mts., Aug 1882, *Parish & Parish 330* (lectotype, GH; isolectotypes A, DS, F).

Subshrubs extensively branching below the ground, 30–45.5 cm tall, 61–120 cm wide. INTERNODES 1.2–4.5 cm. LEAVES obovate, 2.3–6.3 cm long, 1.0–2.5 cm wide. FLOWERS 1.2–2.5 cm long. BRACTS many; 1.1–2.03 cm long; 0.8–1.57 cm wide; hairs on bracts 0.01–0.02 mm long; hairs on bract margins 0.01–0.055 mm. SEEDS 3 mm long, 2 mm wide.

*Paratypes.* U.S.A., California. Inyo Co., Panamint Mtns, Death Valley National Monuemnt, Aguereberry Point, 1961 m, 02 July 1983, *R.F. Thorne 56130.1* (RSA); Jail Canyon, 2438 m, 11 July 1977, *A.P. Romspert 13* (RSA); Rogers Peak, 2591 m, 10 July 1974, *L. DeBuhr 44818* (RSA); Wildrose Canyon, 1920 m, 3 July 1974, *L. DeBuhr 44793* (RSA); T19S R45E sect. 27, 1951 m, 15 August 1968, *J.L. Reveal 1786* (RSA); Dolomitic Rocky Ridge, UTM 497130E, 4023510N, 1951 m, 2 July 1983, *P.M. Peterson 1183* (RSA); Narrow Canyon above Townes Pass, 17 June 1937, *C. Epling* (RSA); Thorndike's Ranch, 2286 m, 7 July 1937, *C. Epling* (RSA);Wild Rose Canyon to Telescope Peak, 2682 m, 8 July 1937, *P.A. Munz 14793* (RSA); 2133 m, 16 May 1931, *R. Hoffmann 459* (RSA); Kern Co., Scodie Mtns, Walker Pass Trailhead on Pacific Crest Trail, T26S R37E sect. 19, 1707 m, 6 August 1988, *B.*

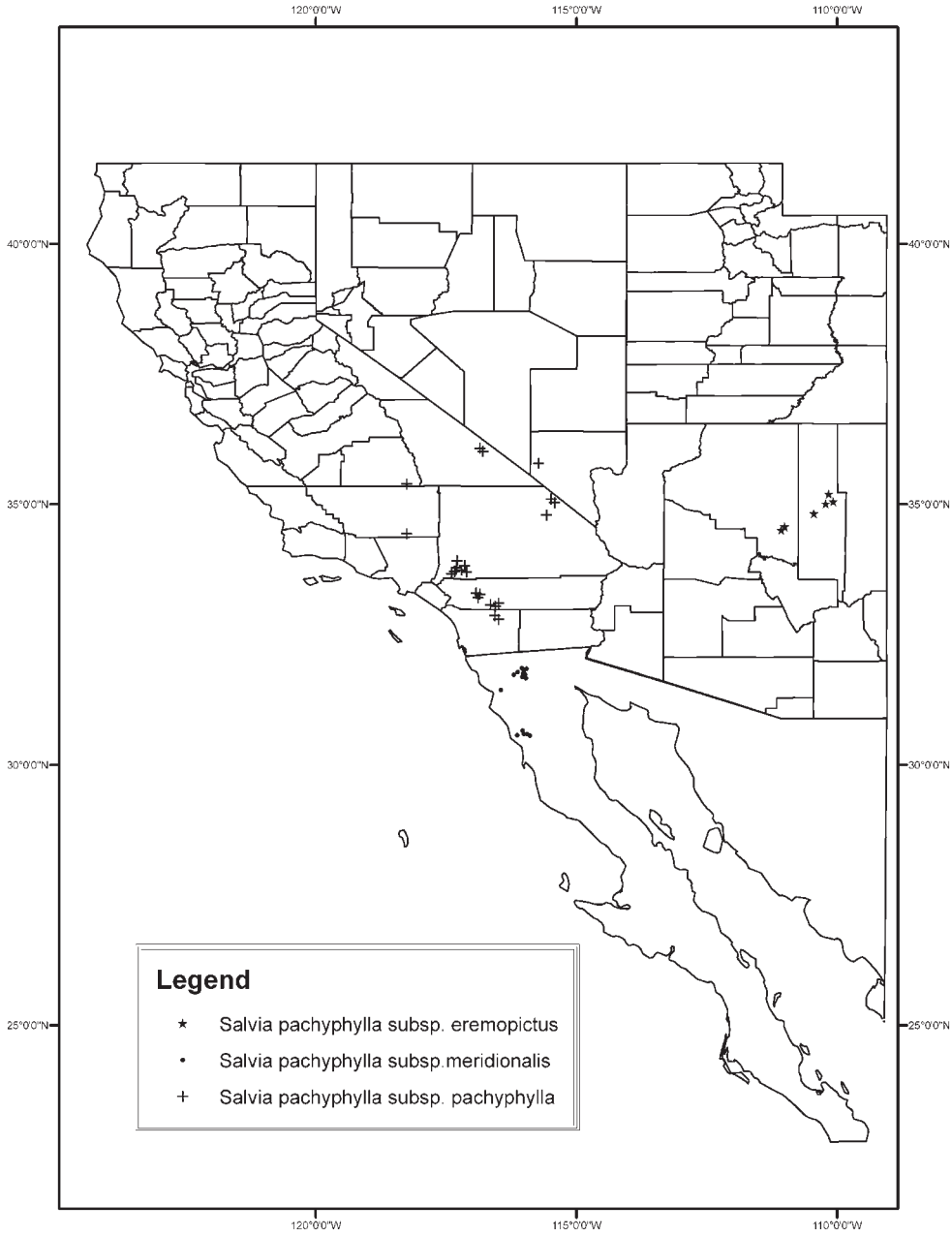


FIG. 4. Distribution of the three subspecies of *Salvia pachyphylla*.

*Ertter 7891* (NY, RSA); Riverside Co., San Jacinto Mtns, 1402 m, June 1901, *H.M. Hall 2160* (NY, RSA); north slope, 1829 m, 20 August 1922, *E.C. Jaeger 1010* (RSA); Tahquitz Peak, 22 August 1933, *L. Crutcher 3* (RSA); Tahquitz Valley, 2652 m, 31 August 1930, *J. Ewan 2149* (RSA); Santa Rosa Mtns, 1981 m, 21 August 1952, *P.A. Munz 17995* (NY, RSA); 2 September 1970, *C.W. Tilforth 297* (RSA); dry slopes, 2134 m, 29 June 1922, *P.A. Munz 5888* (RSA); near Santa Rosa Springs campground, 2088 m, 15 June 1978, *C. Davidson 7382* (RSA); 2138 m, 21 August 1971, *N.R. Zabriskie 438* (RSA); near Vendeventer Flat, 1676 m, 1 July 1933, *V. Duran 3490* (NY,RSA); stony slopes near creek, 1524 m, 25 June 1922, *P.A. Munz 5813* (RSA); Toro Peak, 2438 m, 14 August 1938, *P.A. Munz 15363* (RSA); Vandeventer Flat, 2073 m, 21 August 1952, *P.A. Munz 17981* (NY, RSA); Cultivated, 2 September 1954, *E.K. Balls 19778* (NY, RSA); virgin spring, 2652 m, 14 August 1938, *P.A. Munz 15346* (RSA); Toro Mtn, July 1901, *E.E. Schel-*

*lenger* (RSA); San Bernardino Co., Blk. Hawk Mine, near Victorville, 4 July 1926, *M.E. Jones* (RSA); Clark Mtns 4.2 miles NNW of Mountain Pass, 2134 m, 6 July 1972, *B. Prigge 2* (RSA); 4 miles NW of mountain pass, 2250 m, 6 July 1973, *B. Prigge 1197* (NY, RSA); Pachalka Spring, 1981 m, 6 October 1935, *C.B. Wolf* (RSA); Hanna Flats, near Fawnskin, 1829 m, 23 July 1941, *G.T. Hastings* (NY); Keystone Mine, 45(air)miles E of Baker, 5.5 (air)miles S of Ivanpah at Jct. Roads to Keystone Mine and Keyston Springs, 1680 m, 29 August 1973, *J. Henrickson 12620* (RSA); Kingston Mtns, 2 miles from peak, 1676 m, 23 October 1977, *J. Henrickson 16297* (RSA); Kingston VABM, 2136 m, 18 September 1980, *S. Castagnoli 228* (RSA); Mid-Shut-Up canyon, 1524–1676 m, 23 October 1977, *J. Henrickson 16305* (NY); on a rocky ridge, 2134 m, 27 July 1949, *J. Roos 4507* (RSA); Porcupine Canyon, 2134 m, 21 September 1980, *R.F. Thorne 54790* (RSA); New York Mtns, Keystone Canyon, 1580 m, 7 July 1973, *J. Henrickson 11056* (RSA); 1737 m, 29 October 1976, *R.F. Thorne 47965* (RSA); 29 July 1952, P.C. Everett 17299 (RSA); Keystone Spring, 1707 m, 13 October 1935, *P.A. Munz 13874* (RSA); San Bernardino Mtns, 8.7 miles SE of Lucerne Valley, 1398 m, 18 June 1978, *C. Davidson 7300* (RSA); Barton Flats, 1981 m, 30 October 1955, *L. Benson 15607* (RSA); Bear Lake, 2000 m, 7 July 1931, *E.W. Clokey 5292* (NY); Bear Valley, 1 August 1901, *L.R. Abrams 2077* (RSA); 1895, *A. Davidson* (RSA); Big Bear Lake, 22 August 1935, *C.L. Hitchock 2825* (RSA); 6 July 1924, *J.M.J.* (RSA); 8 August 1964, *B. C. Templeton 10191* (RSA); Big Meadows, 1990 m, 27 July 1925, *J.B. Feudge 1242* (RSA); 2134 m, *N.C. Cooper 2886* (RSA); Cactus Flat, 1829 m, 25 June 1926, *P.A. Munz 10501* (RSA); Cactus Flat, August 1915, *F. Grinnell* (RSA); Camp Osceola, on the upper Santa Ana River, 1829 m, 21 July 1936, *E.R. Johnson* (NY); Coon Creek, Heart Bar State Park, 34°10′N, 116°45′W, 2286 m, 9 August 1992 , *S.D. White 599* (RSA); Cushenbury canyon, 1450 m, 5 May 1978, *R.F. Thorne 51874* (NY); 23 September 1927, *M. Jones* (RSA); Cushenbury Grade, 1219 m 9 July 1927, *J.T. Howell 318* (RSA); Fish Creek, 2743 m, 14 July 1924, *P.A. Munz 8497* (RSA); Santa Ana River, 1966 m, 22 October 1931, *C.B. Wolf* (NY); Foxesee Creek, 2438 m, 22 August 1920, *F.W. Peirson 1060* (NY); from Bear Lake to Holcomb Valley, 2134 m, 5 July 1930, *F.W. Peirson 9011* (RSA); Heart Bar campground, 34°10′N, 116°43′W, 2438 m, 17 July 1989, *B. Wagner* (RSA); Holcomb Valley, 3N10, 3N16, 7390 m, 12 & 13 July 1979, *R.F. Thorne 53493* (NY); Green Lead Mine road, 2195 m, 7 August 1931, *J. Ewan 4867* (NY); , T3N R1W sect. 34/26, 2134, 27 June 1979, *J. Strachan 2994* (NY); Johnson Grade, 1981 m, 5 July 1935, *M.B. Dunkle 4015* (NY); Baldwin Lake, 1951 m, 22 August 1932, *P.A. Munz 12707* (RSA); Lucerne Valley, OMYA's Crystal Creek Haul road, 34°20.5′N, 116°56.5 W, 1770 m, 27 August 1998, *S.D. White 7092* (NY); Marble Canyon, 34°20.5′N, 116°52.5′W, 1585 m, 26 August 1998, *S.D. White 7094, 7097* (RSA); near Bear Valley, September 1893, *T. Minthorn* (RSA); Nelson Ridge, south of Smarts Ranch, 34°16′.1″N, 116°45′37.1″W, 1951 m, 29 July 1998 , *S. Boyd 10259* (NY); Old Rose Mine, 2134 m, 9 October 1937, *P.A. Munz 14955* (NY); Onyx summit, 2450 m 30 August 1975, *C. Davidson 3234* (RSA); 34°11′13″N, 116°42′53″W, 2551 m, 27 March 1999, *S. Rhodes 9928* (RSA); Rose Mine, 2134 m, 21 October 1945, *H. Crooks 93* (NY); Santa Ana Canyon, 24 July 1906, *H.M. Hall 7549* (NY, RSA); Santa Ana River, 1920 m, 21 August 1922, *P.A. Munz 6147* (RSA); SE Terrace Springs and W of Arrastre Creek, 34°19′44″N, 116°45′58″W, 1463 m, 25 June 1998, *V. Soza 308* (RSA); Seven Oaks, July 1902, *C. Wilder 395* (NY); South Fork Public campground, 1981 m, 24 July 1947, *P.A. Munz 12053* (NY, RSA); South Fork, 1890 m, 26 July 1906, *J. Grimmell 307* NY; Sugarloaf Mountain, 2591 m, 22 July 1926, *P.A. Munz 10779* (RSA); 3 August 1932, *F.R. Fosberg 8617* (RSA);Warrens Well, 1280 m, 30 June 1938, *E.C. Jaeger* (NY); San Diego Co., Tantillas Mtns, 1875, *E. Palmer 304* (NY, RSA); Tulare Co., Chimney Creek Campground, opposite Lamont bench mark, 3 miles S of the BLM Chimney Creek Campground, 29 June 1985, *D.W. Mc Neil 3110* (NY); Kern Plateau, east of Long Valley, 1676–1859 m, 8 August 1967, *J.T. Howell* (NY); Kernville, head of Sand Canyon, T24S R36E sec29Se, 1981 m, 10 June 1986, *B. Ertter 6382* (NY).

*Distribution.* Inyo, Kern, Riverside, San Bernardino, San Diego, Cos., California and Clark and Tulare Cos., Nevada. 1219–2682 m (4000–8800 ft). Flowering from June–October.

*Habitat.* North facing slopes. Loose sand, limestone, or granitic soil. Found among pines and junipers.

*Epithet etymology.* The epithet refers to the thick leaves.

**Salvia pachyphylla subsp. eremopictus** R. Taylor subsp. nov. (Fig. 5) Arizona Rose Sage—TYPE: USA, Arizona: Navajo Co., 16.5 mi N of Interstate 40 on Hwy 87, just past mile marker 362; 2.5 mi N of Little Painted Desert State Park. UTM Zone 12 S, 550587E, 3893128N, 1676 m elev., 28 October 1999, *R. Taylor 04* (holotype, RSA; isotypes, ARIZ, ASC, ASU, NY).

Similis subsp. *pachyphylla*, sed differt floris internodis brevis, 6.5–15.5 mm longi, bracteae 3.5–9.2 mm lata.


FIG. 5. Illustration of *Salvia pachyphylla* subsp. *eremopictus*: A—flowering branch; B—longitudinal view of flower; scale bars = 1 cm.

Shrubs with well defined woody trunk, 35–50 cm tall, 40–150 cm wide. LEAVES spatulate, 2.0–4.4 cm long, 0.6–1.7 cm wide. INFLORESCENCE internodes 0.65–1.55 cm. FLOWERS 1.3–2.45 cm long. BRACTS many; 0.83–1.4 cm long; 0.35–0.92 cm wide; hairs on bracts 0.01 mm long; hairs on bract margins 0.01–0.03 mm. SEEDS 2.5–4 mm long, 1.5–2.5 mm wide.

*Paratypes.* U.S.A., Arizona. Apache Co., Petrified Forest National Monument, Chinde Mesa, 12 S 603424E 3892175N, 1804 m elev., 17 July 1998, *M. Hansen s.n.* (ASC); 2 September 2000, *R. Taylor 19* (ASC); Coconino Co., Meteor Crater, N-facing slope of crater, 35°01.923′N, 111°01.520′W, 1646 m elev., 28 October 1999, *R. Taylor 03* (ASC); 18 October 1998, *M. Hansen s.n.* (ASC); 26 May 1994, *J. Beasley s.n.* (ASC); 21 September 1998, *S. Hill 31025* (ASC); Navajo Co., Navajo Reservation, NW of Dilkon, 35°28′N, 110°19′W, 1937 m, 7 October 2001, *R. Taylor 26* (ASC, NY, RSA).

*Distribution. Salvia pachyphylla* subsp. *eremopictus* is known only from the southern Colorado Plateau in Apache, Coconino and Navajo Counties on Navajo reservation, National Park Service, State land, and private land at 1539–1937 m (5500–6356 ft) (Fig. 4). Flowering from (May) July–October usually after summer monsoon rains begin.

*Habitat. Salvia pachyphylla* subsp. *eremopictus* is found on barren north-facing slopes and washes on basalt and painted desert soils derived from Chinle shale. Found among juniper and salt bush.

*Epithet etymology.* The subspecific epithet refers to the "Painted-Desert" substrates derived from Chinle shale where historical populations of this taxon had been found. During this study three new populations were found on volcanic substrates adjacent to "Painted-Desert" formations.

**Salvia pachyphylla subsp. meridionalis** R. Taylor subsp. nov. Baja Rose Sage Illustration: Brittonia 34(2): 167. 1982.—TYPE: MEXICO, Baja California Norte, Sierra San Pedro Martir, La Encantada, rock hillsides about margin of meadow, 2100 m elev., 18 September 1930, *I. L. Wiggins and D. Demaree 48872* (holotype, RSA; isotypes, NY).

Similis subsp. *pachyphylla*, sed differt folia anguste, 5–14 mm lata.

Shrubs with well defined woody trunk, 30–45.5 cm tall, 61–120 cm wide. INTERNODES 1.4–3.35 cm. LEAVES linear to spatulate, 2.6–4.5 cm long, 0.5–1.4 cm wide. FLOWERS 1.5–2.1 cm long. BRACTS many; 0.97–1.9 cm long; 0.63–1.4 cm wide; hairs on bracts 0.01–0.015 mm long; hairs on bract margins 0.03–0.06 mm. SEEDS 3.0–4.0 mm long, 2.0–3.0 mm wide.

*Paratypes.* MEXICO, Baja California Norte. Observatoria UNAM, San Pedro Martir, 2830 m, 13 October 1985, *A. Gonzalez* (ASC); La Grulla, San Pedro Martir, 2286 m, 1926, *C.G. Abbott* (NY); UNAM Observatory, San Pedro Martir Mtns National Park, 1372 m, 5 August 1995, *H.D. Hammond 10844* (NY); UNAM Observatory, San Pedro Martir Mtns National Park, Vallecitos, 2590–2743 m, 1 September 1985, *J. Donahue 96055* (NY); Cerro Verado Blanco, San Pedro Martir, north-north west of the observatory, 31°3′N,115°9′W, 2345 m, 16 September 1998, *J. Rebman 5610* (RSA); Laguna Hanson, 9 July 1938, *M.B. Dunkle 5416* (RSA); Yerba Buena, Sierra San Pedro Martir, 31°00′N, 115°27′W, 16 August 1967, *Moran/ Thorne 14200* (RSA); La Corona, Sierra San Pedro Martir, 30°58′N, 115°35′W, 2000 m, 30 August 1963, *R. Moran 11272* (RSA); Rancho Mezquite, Sierra Juares, 32°18′N, 116°00′W, 1450 m, 3 September 1966, *R. Moran 13446* (RSA); Arroyo Copal, Sierra San Pedro Martir, 31°04′N, 115°28′W, 2550 m, 24 August 1968 , *R. Moran 15436* (RSA); Laguna Hanson, Sierra de Juares, Constitucion National Park, 32°02.5′N, 115°55′W, 1610 m, 15 September 1983, *R.F. Thorne 57116* (RSA); Sierra Juarez, Estado de Baja California,

3 miles east of Laguna Hanson, 32°02′N, 115°52′W, 26 July 1994, *J. Rebman 2839* (NY);14 miles south of La Rumerosa, 32°21′N, 116°00′W, 29 June 1962, *R. Moran 9805* (RSA); La Corona de Abajo, Parque Nacional Sierra San Pedro Martir, 2080 m, 27 August 1988, *R. Noyes 638* (RSA); Cerro Botella Azul, Sierra San Pedro Martir, 19 July 1988, *S. Boyd 2643* (RSA); Vallecitos, Sierra San Pedro Martir, 1 mile S of La Tasajera, 20 July 1988 , *S. Boyd 2725* (RSA); Vallecitos, Sierra San Pedro Martir, 2456 m, 21 September 1930 , *Wiggins & Demaree 4971*(NY, RSA); La Encantada, Sierra San Pedro Martir, 30°55′N, 115°24′W, 2200 m, 19 August 1967, *Moran & Thorne 14370* (RSA); La Encantada, *Wiggins & Demaree 4887* (NY, RSA); La Encantada, Sierra San Pedro Martir, 2200, 18 September 1930, *Wiggins & Demaree 4892* (NY, RSA); Yellow pine belt, between Ojos Negros and Neji Rancho, 16 September 1929, *Wiggins & Gillespie 4137* (NY, RSA).

*Distribution. Salvia pachyphylla* subsp. *meridionalis* is distributed in the Sierra San Pedro Martir and Sierra Juarez from 32°00′N, 116°00′W to 30°25′N, 115°30′W at 1372–2830 m (4500–9284 ft) (Strachan 1982, Fig. 2). Flowering from June–August.

*Habitat. Salvia pachyphylla* subsp. *meridionalis* is found on north-facing rocky slopes derived from coarse sand and granitic soil. Found among pines.

*Epithet etymology.* The subspecific epithet refers to the southern-most distribution of this taxon.

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