THE GENUS *HESPEROYUCCA* (AGAVACEAE) IN THE WESTERN UNITED STATES AND MEXICO: NEW NOMENCLATURAL COMBINATIONS

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ABSTRACT

The genus *Hesperoyucca* (Agavaceae), consisting of three species, is recognized as distinct from *Yucca* based on distinct morphological, phenological and pollinator characteristics, biogeographic considerations and recent DNA analyses. *Hesperoyucca whipplei* is recognized and new combinations for two species are made: *H. newberryi* and *H. peninsularis*. A key that distinguishes *Yucca* from *Hesperoyucca* and the three species of *Hesperoyucca* is included.

RESUMEN

Se reconoce a *Hesperoyucca* (Agavaceae) como género distinto de *Yucca* en base a caracteres morfológicos, fenológicos y del polinizador, a consideraciones biogeográficas y análisis recientes de ADN. *Hesperoyucca* consta de tres especies. Se reconoce *Hesperoyucca whipplei* y se proponen dos combinaciones nuevas para las otras dos especies, *H. newberryi* y *H. peninsularis*. Se presenta una clave para distinguir *Yucca* de *Hesperoyucca* y para identificar las tres especies de *Hesperoyucca*.

KEY WORDS: *Hesperoyucca*, *Yucca whipplei*, Agavaceae, DNA

Within *Yucca* L., as traditionally circumscribed, is a group of species, herein recognized as *Hesperoyucca* (Engelm.) Baker, that has morphological, phenological, and pollinator characteristics markedly different from all others. These characteristics include a loculicidal capsule, a capitate stigma, and glabrous, swollen filaments that are attached to the lower part of the tepals and that draw away from the ovary when the tepals open. These filaments bear bulbous anthers with tufted pubescence that bend toward the stigma and dehisce laterally (Fig. 1). Their pollen is produced in a glutinous mass. The sole pollinator of *Hesperoyucca* is *Tegeticula maculata* Riley, a species of yucca moth (Riley 1892; Trelease 1893, 1902; Powell & Mackey 1966; Davis 1967; Segraves & Pellmyr 2001). The other approximately 47 species of *Yucca* are visited by the remaining species of yucca moth (Pellmyr 1999). In *Yucca*, the pollen is not agglutinated, but produced as single grains, nor are the filaments tufted. Furthermore, the stigmas are not capitate, but divided into three lobes that spread outward. The pubescent filaments are appressed to the ovary and angle outward and when the tepals open.

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Recent analyses of DNA markers, including the internal transcribed spacer region (ITS) of nuclear ribosomal DNA and chloroplast DNA (cpDNA) (Hanson 1993; Bogler 1994; Bogler & Simpson 1995, 1996; Clary 1997) support the recognition of these unique species as members of a separate genus, *Hesperoyucca* (Engelm.) Baker. In the phylogenetic parsimony and maximum likelihood trees from DNA analyses, these species form a branch that is sister to *Hesperaloë* (Agavaceae) and not *Yucca* (Fig. 2). *Hesperaloë* Engelm. includes a group of five species found in the Sonoran and Chihuahuan Deserts allied taxonomically as close relatives to both *Agave* L. and *Yucca* (Correll & Johnston 1979; Gentry 1972; Starr 1997).

The group in question, *Hesperoyucca*, corresponds to Engelmann's (1871) *Yucca* group *Hesperoyucca*, which ranges from California and Arizona to Baja California Norte and Sonora in México. In this paper, *Hesperoyucca* is recognized at the genus level, requiring two new species combinations. A taxonomic treatment of the genus will be published in Flora of North America.

While taxonomists working with *Yucca* have recognized the members of the *Hesperoyucca* group as distinctive from the other *Yucca* species, they have not agreed on infrageneric and infraspecific circumscription. The taxa within *Hesperoyucca* have been classified primarily by growth form (single or multiple rosettes), leaf morphology and whether the plants are monocarpic or polycarpic. Most of the disagreement centers on the significance of morphological variation in *Y. whipplei* Torr. populations in Arizona and California (Trelease 1893, 1902; Haines 1941; McKelvey 1947; Webber 1953; Hochstätter 2000).

Within *Yucca whipplei*, Trelease (1893) recognized two varieties, Haines (1941) and Munz (1968) each recognized five subspecies and Webber (1953) recognized four varieties. Others argue that growth form is a highly variable character and question the recognition of varieties or subspecies at all (McKelvey 1947; McKinney & Hickman 1993).

McKelvey (1947) described *Yucca newberryi* from Arizona *and Y. peninsularis* from the Vizcaíno Desert region in Baja California Norte. Webber (1953:33) believed leaf, inflorescence and capsule features used by McKelvey to separate *Y. newberryi* from *Y. whipplei* were weak and within the normal variation of *Y. whipplei*. Hochstätter (2000) included *Y. newberryi* as a subspecies of *Y. whipplei*.

Supported by distinctive morphological characteristics, unique species ranges and ITS DNA analyses (Clary 1997), three species of *Hesperoyucca* are here recognized: *H. whipplei*, *H. peninsularis* (McKelvey) Clary, and *H. newberryi* (McKelvey) Clary. A key to the species follows.

The ITS DNA analysis of *Yucca*, *Hesperoyucca*, *Agave* and *Hesperaloë* (Clary 1997) included single individuals from four *Hesperoyucca* populations: *H. whipplei* from Sierra Viejo, Sonora, México (Bogler & Simpson 1996), and from San Diego County, California; *H. peninsularis* from Cataviña, Baja California

Norte, México; and *H. newberryi* from Mohave County, Arizona. The results show each of these samples to be genetically distinct from the others (Clary 1997). The other taxa attributed to *H. whipplei* [*Y. whipplei* subsp. *caespitosa* (M.E.Jones) A.L.Haines, *Y. whipplei* subsp. *percursa* A.L.Haines, *H. whipplei* subsp. *intermedia* A.L.Haines, *Y. whipplei* subsp. *typica* A.L.Haines, and *Y. whipplei* subsp. *parishii* (M.E.Jones) A.L.Haines] were not sampled.

Results of the phylogenetic (parsimony and maximum likelihood) analysis show a tree (Fig. 2) with the *Hesperoyucca* clade split into two branches. One branch contains *H. newberryi*, basal to the lineage, while the other branch contains *H. peninsularis*, which is sister to a branch that contains both *H. whipplei* populations. These data support specific status for *H. peninsularis* and *H. newberryi*, but not the two *H. whipplei* populations since they share unique mutations (Clary 1997).

Recognition of infraspecific taxa within *Hesperoyucca whipplei* is beyond the scope of this paper. Although the taxonomic treatments of *H. whipplei* within the above-cited earlier works give distinctive morphological characters that separate taxa within *H. whipplei*, the treatments, with the exception of McKelvey's (1947), lack sufficient records of specimens seen to evaluate the hypotheses about the proposed nature of variation within *Y. whipplei*. Further systematic study of informative morphological characters and DNA of all taxa of *Hesperoyucca* is warranted to elucidate its entire phylogeny and determine the genetic relationships that underlie the taxonomy of this group.

KEY TO *YUCCA* AND THE THREE RECOGNIZED SPECIES OF *HESPEROYUCCA*

1. Capsules septicidal, the seeds dispersing laterally through openings at the locule tips, or the fruit indehiscent, fleshy or spongy; seeds ultimately dispersed by animals; stigmas 3-lobed, white, the lobes papillose on the inner surface; filaments usually shorter than the pistil, pubescent, distally clavate and eventually turned at a pronounced or negligible angle to the proximal portion; anthers sagittate or hastate; inflorescence bracts on erect, persistent; leaf blades narrowed at junction with spoonlike base, widening above that point before tapering to the tip _____ **Yucca s.l.**

1. Capsules loculicidal, the seeds dispersing laterally through fringed or rudimentary false placental septa; seeds initially wind dispersed; stigmas capitate, bright green, densely long papillate; filaments usually longer than pistil, finely papillate, and more or less swollen the entire length, stoutest at or near the middle, erect or spreading outwardly from point of attachment at anthesis, bearing tufts of papillae at the apex; anthers cordate; inflorescence bracts becoming reflexed above the base, easily detached; leaf blades widest just above basal spoon and tapering to tip _____ **Hesperoyucca**
   2. Mature leaf blades usually long and slender, to 0.7–2.0(–2.5) cm wide above the base, to 45–60(–100+) cm long, flexible, or if rigid, then distinctly thickened.
      3. Mature capsules with conspicuous placental wings; plants with single or multiple rosettes; western southern California and adjacent northern Baja California and Sonora _____ **H. whipplei**
      3. Mature capsules with rudimentary placental wings; rosettes solitary; Mojave County, Arizona and vicinity _____ **H. newberryi**

2. Mature leaf-blades rather short and broad, to (2.5–)3.2–4.0 cm wide, straight and rigid, or falcate, tapering from above basal spoon to the tip; plants forming clustered rosettes; Vizcaíno region, Baja California Norte, México _____ **H. peninsularis**

Hesperoyucca (Engelm.) Baker, Bull. Misc. Inform. Kew 1892(61):8. 1892. *Yucca* subgen. *Hesperoyucca* (Engelm.) Baker. Gard. Chron. n.s. 6:196. 1876. Based on *Yucca* (without rank) *Hesperoyucca* Engelm. in S. Wats. et al., Botany [fortieth parallel]: 497. 1871 as group 2: HESPERO-YUCCA. *Yucca* Sect. *Hesperoyucca* (Engelm.) in McKelvey, Yuccas Southw. U.S. 2:14. 1947. TYPE: *Yucca whipplei* Torr. in Ives.

There is disagreement regarding authorship of the genus *Hesperoyucca*. Engelmann (1871) divided *Yucca* into two major groups: EU-YUCCA and HESPERO-YUCCA, the former with three subgroups: Sarcocarpa, Clistocarpa and Chaenocarpa. His group *Hesperoyucca* contained only *Yucca whipplei*. Engelmann (1873) provided a similar summary classification, but within his Euyucca, changed the names to Sarcoyucca, Clistoyucca, Chaenoyucca (note change from "-carpa" to "-yucca"). In 1875 Engelmann retained four equal groups under *Yucca*: Sarcoyucca, Clistoyucca, Chaenoyucca and Hesperoyucca. But at no time did Engelmann indicate ranks for his groups within *Yucca*. Baker (1876) gave the rank subgenus to Engelmann's *Hesperoyucca* recognizing within it a single species, *Yucca whipplei*. Greuter et al. (1993) and Greenhouse and Strother (in press) accept this as legitimizing Engelmann's *Hesperoyucca* as a subgenus. In 1892, Baker noted that *Y. whipplei*, "had better be kept as a genus distinct from *Yucca*, under Engelmann's name *Hesperoyucca*" but he still listed the species as *Yucca whippleii* (sic.) Torrey. Greuter et al. (1993) accept this as having erected the genus *Hesperoyucca*. (Engelm.) Baker in 1892. Greenhouse and Strother (in press) following ICBN Art. 34.1 (Greuter et al. 2000), do not accept this as creating a new genus as Baker listed the species as *Yucca whipplei* and thus did not accept the new combination. Trelease (1893:208) accepted Baker's (1892) suggestion of the genus rank for *Hesperoyucca*, formally recognizing *Hesperoyucca* at the same rank as, and separate from *Yucca*, and distinguishing *Hesperoyucca* from the "true Yuccas." The combination *Hesperoyucca whipplei* appears in the list of illustrations, in the Explanation of Plates (Trelease 1893:215) and as the generic name of variety *graminifolia* (Trelease 1893:215, tt. 17 & 23). This is considered by Greenhouse and Strother (in press) to be the first legitimate use of the name of the genus *Hesperoyucca*. However, Baker's (1892) mere suggestion in print of generic rank for *Hesperoyucca* is accepted by Names in Current Use (Grueter et al. 1993) and by Flora North America (FNA) to be the first valid use of *Hesperoyucca* as a genus, not Trelease's (1893) taxonomic description.

Distribution.—U.S.A. California, Arizona. México. Baja California Norte, Sonora.

Hesperoyucca whipplei (Torr.) Baker ex Trel., Ann. Rep. Missouri Bot. Gard. 4:208. 1893. (**Fig. 1**). Basionym: *Yucca whipplei* Torr. in J.C. Ives. Rep. Colorado R. 4 (Bot.):29. 1861. TYPE: U.S.A. CALIFORNIA. SAN DIEGO CO.: San Pasqual, *A. Schott s.n.* (LECTOTYPE: NY!). The

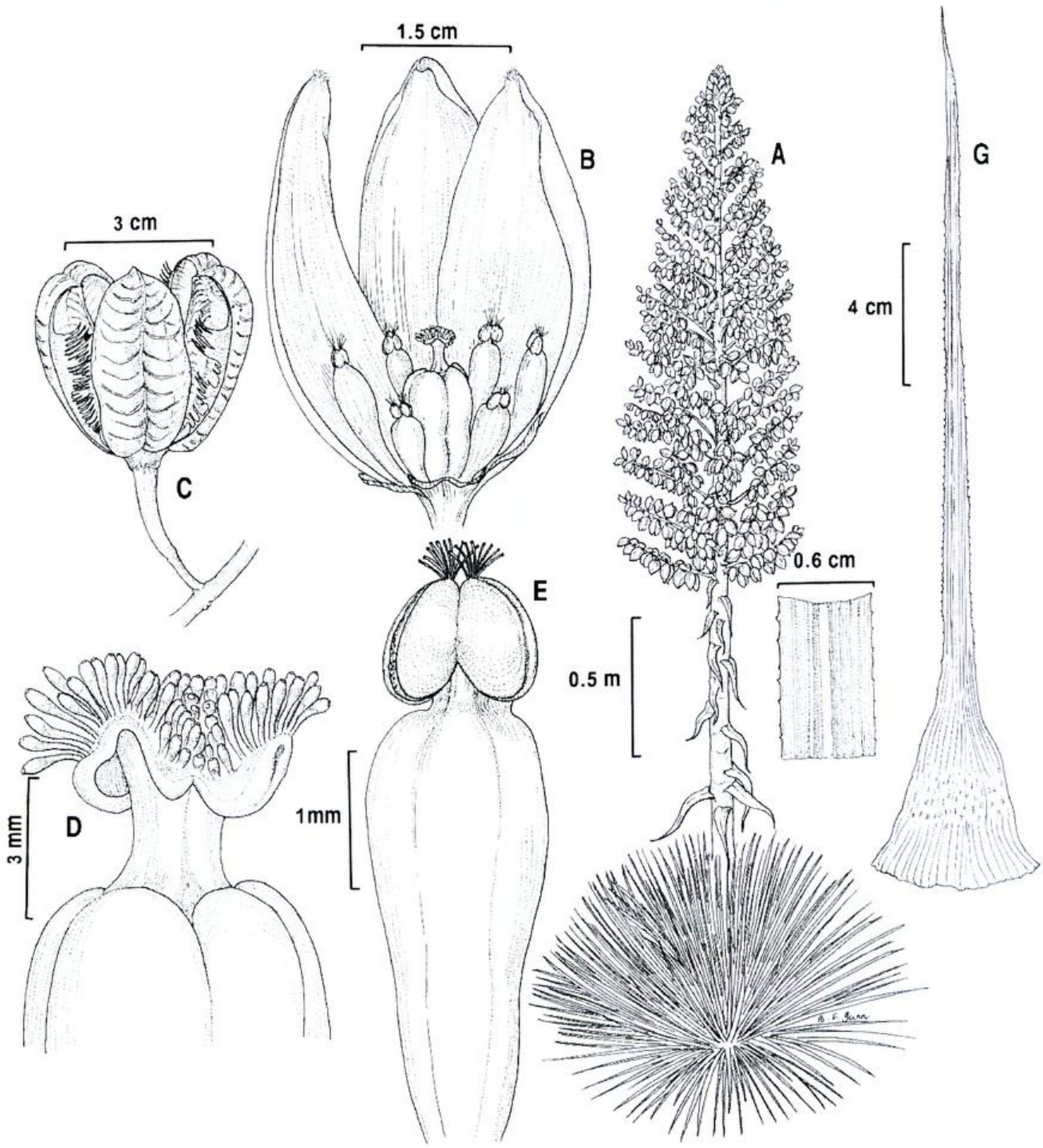

FIG. 1. Illustration of *Hesperoyucca whipplei*: A. Growth habit, showing basal leaf rosette and inflorescence [from photo voucher 148731 (MO)]; B. Flower, showing tepals, filaments and central ovary [from Nichols B-4-21-92 (TEX), and photo by Constance & Morrison 2269, 1150192 (MO)]; C. Capsule, showing fringed placenta septa margins and loculicidal dehiscence [135741 (MO)]; D. Capitate stigma, showing papillae on stigma surface [from Nichols B-4-21-92 (TEX) and photo by Constance & Morrison 2269, 1150192 (MO)]; E. Stamens showing cordate anthers and tufted pubescence [from Nichols B-4-21-92 (TEX)]; F–G. Leaf blade (F) detail showing minutely serrated leaf margin and (G) with expanded basal spoon [from photo by Constance & Morrison 2269, 1150192 (MO)].

citation in *Yucca* is often given as: *Yucca whipplei* Torr. in Emory, Rep. U.S. & Mex. Bound. 2:222. 1859. Torrey noted "if it prove to be a distinct species it may be called *Y. whipplei*." Greenhouse and Strother (in press) consider Torrey's name as provisional and not validly published as of 1859, but validly published in Ives' "Report upon the Colorado River of the west" (Torrey 1861). Baker (1892) suggested that the species should be recognized within *Hesperoyucca*. Trelease (1893) formally recognized *Hesperoyucca* as a genus, and *Hesperoyucca whipplei* as a

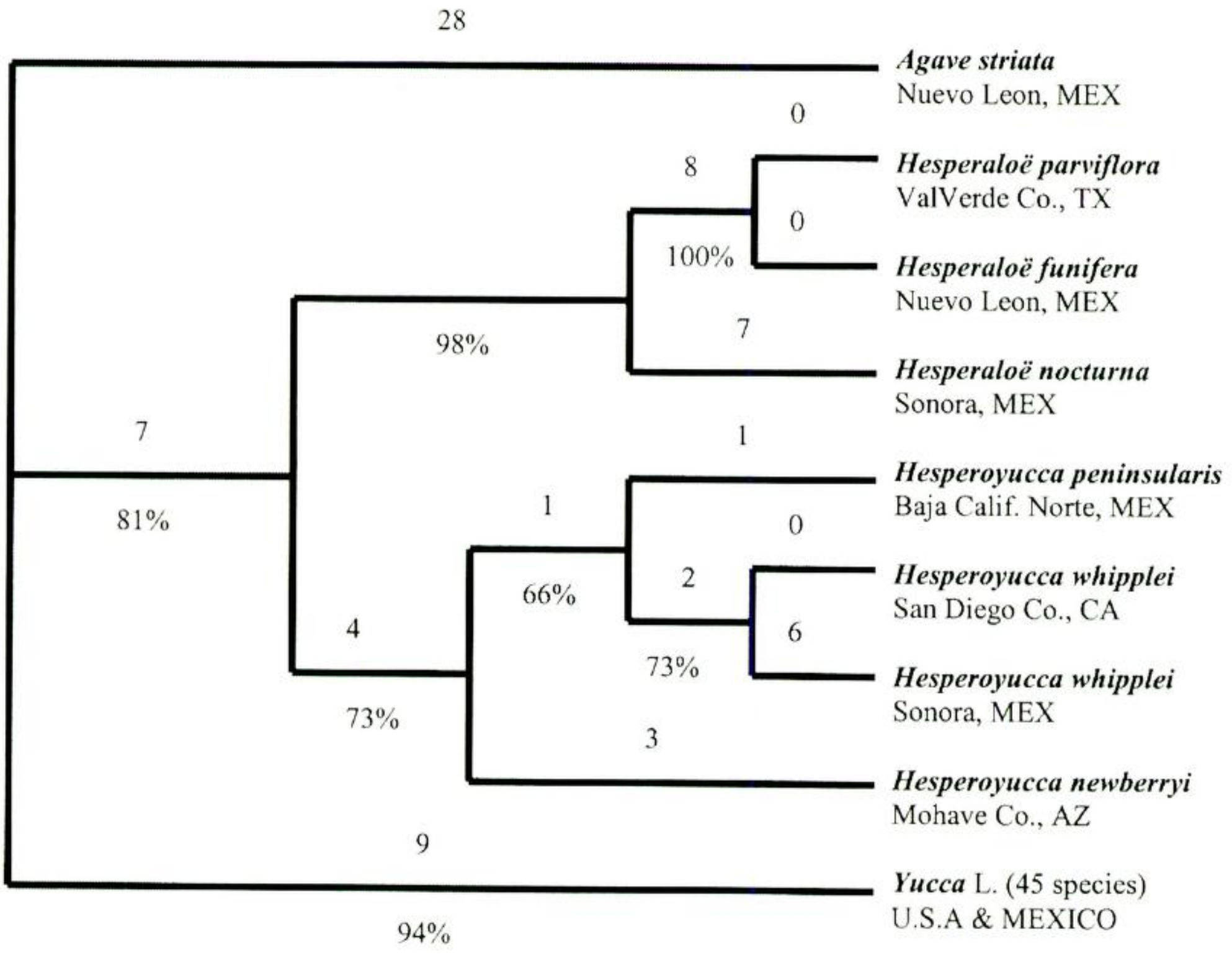

FIG. 2. ITS 1 & 2 strict consensus tree of the 10,777 most parsimonious 467 step trees found by PAUP (CI=0.89, HI=0.527, RI=0.846). Step changes are written above branches, with bootstrap percentages > 50 % written below (Clary 1997). Samples of *Agave striata*, *Hesperaloë parviflora*, *Hesperaloë funifera*, *Hesperoyucca whipplei* (Sonora, Mexico) are from Bogler (1994, 1996); samples of *Hesperaloë nocturna*, *Hesperoyucca peninsularis*, *Hesperoyucca whipplei* (San Diego, California), *Hesperoyucca newberryi* and *Yucca* L. are from Clary (1997).

species. The combination listed above, can be shortened to *Hesperoyucca whipplei* (Torr.) Trel. following ICBN Art. 46.4 (Greuter et al. 2000). Torrey's (1859) paper cited a single specimen, "a yucca found by Mr. Schott on rocks near San Pasqual, southern California." Torrey (1861) in the Ives Report cited three collections, "Mouth of Diamond River, 3 April, growing in tufts, on rocks," another by Dr. Bigelow in Cajon Pass (California) in the Whipple expedition and by Mr. Schott near San Pasqual. The latter is here designated as lectotype.

Hesperoyucca whipplei var. *graminifolia* Trel., Ann. Rep. Missouri Bot. Gard. 4:215. 1893, based on: *Yucca graminifolia* A.W. Wood, Proc. Acad. Nat. Sci. Philadelphia 20:167. 1868, *non* Zucc. 1837. TYPE: U.S.A. CALIFORNIA. LOS ANGELES CO.: Mountains 12 mi E of Los Angeles, 3 Mar 1866, *A. Wood s.n.* McKelvey (1947:32) notes a specimen at GH. Greenhouse and Strother (in press) note that Wood's initial combination was superfluous due to the existence of *Y. graminifolia* Zucc. The name was legitimized by Trelease's reference in 1893.

Yucca whipplei var. *parishii* M.E. Jones, Contr. W. Bot. 15:59. 1929. *Yucca whipplei* subsp. *parishii* (M.E. Jones) A.L. Haines, Madroño 6:44. 1941. TYPE: No specimens were cited by Jones (1929). Jones (p. 59) described this taxon as "the common form at low elevations on the Pacific slope, seldom if ever found on the desert side." Haines (1941) gave the location of the type (California: San Bernardino Co.: above Cajon Pass, *M.E. Jones s.n.*) but selected no lectotype. Jones collected several specimens from the Cajon Pass (POM, photocopy!), but none have been designated as a type. With further study, a type may be designated for this taxon.

Yucca whipplei var. *caespitosa* M.E. Jones, Contr. W. Bot. 15:59. 1929. *Yucca whipplei* subsp. *caespitosa* (M.E.Jones) A.L. Haines, Madroño 6:43. 1941. TYPE: U.S.A. CALIFORNIA. SAN BERNARDINO CO.: Cactus Flat in Cushenbury Canyon, 12 May 1926, *Jones s.n.* (HOLOTYPE: POM!; ISOTYPE: CAS).

Yucca whipplei subsp. *intermedia* A.L. Haines, Madroño 6:43. 1941. *Yucca whipplei* var. *intermedia* (A.L. Haines) J.M.Webber. Yuccas Southw. 34. 1953. TYPE: U.S.A. CALIFORNIA. LOS ANGELES CO.: Malibu Lake, Santa Monica Mountains, 1 Jun 1940, *Haines s.n.* [HOLOTYPE: LA (photocopy!)].

Yucca whipplei subsp. *percursa* A.L.Haines. Madroño 6:43:1941. *Yucca whipplei* var. *percursa* (A.L. Haines) J.M. Webber. Yuccas Southw. 35. 1953. TYPE: U.S.A. CALIFORNIA. SANTA BARBARA CO.: Cachuma Mountain in San Rafael Mountains, *Haines s.n.* (not found). A search at LA has found no authentic material. A neotype may be designated after further study.

Distribution.—U.S.A. California: San Diego, Orange, Riverside, San Bernardino, Los Angeles, Ventura, Santa Barbara, Kern, San Luis Obispo, Tulare, Monterey, San Benito counties; México. Baja California Norte: Municipio Ensenada, Mexicali; Sonora.

Hesperoyucca newberryi (McKelvey) Clary, comb. nov. BASIONYM: *Yucca newberryi* McKelvey, Yuccas Southw. U.S. 2:49. 1947. *Yucca whipplei* subsp. *newberryi* (McKelvey) Hochstätter, Succulenta (Netherlands) 79:39. 2000. TYPE: U.S.A. ARIZONA. MOHAVE CO.: Below rim of S wall of Colorado River, at New Water Point, 29 Apr 1934, *McKelvey 4087* (HOLOTYPE: A!).

Distribution.—U.S.A. Arizona: Mohave County.

Hesperoyucca peninsularis (McKelvey) Clary, comb. nov. BASIONYM: *Yucca peninsularis* McKelvey, Yuccas Southw. U.S. 2:52. 1947. TYPE: MÉXICO. BAJA CALIFORNIA NORTE: Canyon 10 mi E of El Rosario, 8 Feb 1935, *I.L. Wiggins 7559* (HOLOTYPE: DS!).

Yucca whipplei subsp. *eremica* Epling & A.L.Haines, Brittonia 9:172. 1957. TYPE: Epling and Haines designated a type collection from Baja California Norte, from 13 mi SE of Rosario in cirio-cardon community, 15 Apr 1957, *A.L. Haines 5759* (not found). A search at LA has found no authentic material. A neotype will be designated after further study.

Distribution.—México. Baja California Norte.

Matuda and Piña-Lujan (1980) consider *Yucca whipplei* subsp. *eremica* Epling & A.L.Haines to be a synonym of *Y. peninsularis*. The original collections of each species are from the same area, 10 E of, and 13 miles SE of El Rosario. Comparisons of habit and leaf morphology in the original descriptions (McKelvey 1947; Epling & Haines 1957; Matuda & Piña-Lujan 1980) and of both live and vouchered specimens at TEX indicate that both belong to the same species.

ACKNOWLEDGMENTS

I thank James Zarucchi (MO), Victoria Hollowell (MO), William Hess (MOR), Beryl Simpson, James Henrickson and Tom Wendt (TEX), John Strother (UC) for helpful comments on the manuscript. Photocopies of specimens were provided by Lee Lenz (POM) and Barry Prigge (LA). I thank the curators of UC, POM, DS, GH for specimen loans. David Bogler (MO) provided photographs and was an advisor for the illustration (Fig. 1) drawn by Bee Gunn (MO) and Yevonn

Wilson Ramsey (MO). Molecular and morphological research was supported by the National Science Foundation Doctoral Dissertation Improvement Award #9410882.

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