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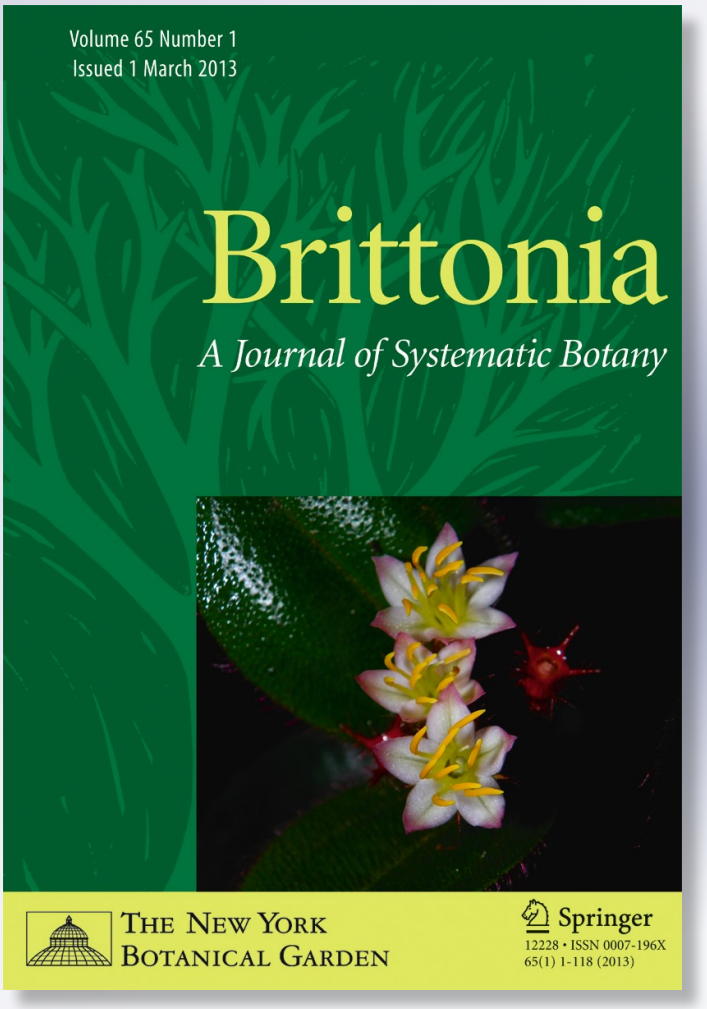

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Two new *Agave* species (Agavaceae) from central Arizona and their putative pre-Columbian domesticated origins

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Abstract. Recent fieldwork in central Arizona resulted in the discovery of two agaves that display low seed set, reproduce mainly by vegetative means, have restricted distributions, and cannot be readily assigned to any existing species. These agaves are closely associated with archaeological structures and features and can be found growing with other previously described pre-Columbian *Agave* domesticates. Herein we describe **Agave verdensis** and **A. yavapaiensis**, two species that can be placed within Gentry's informal Ditepalae *Agave* group, and propose that they are clonal relict domesticates. The two species have affinities with *A. chrysantha*, *A. shrevei*, and *A. delamateri*, the latter also a central Arizona pre-Columbian domesticate. We provide a key to distinguish these species from other agaves in central Arizona and adjacent northern Mexico with which they may be confused. The discovery of these two new species brings the total number of putative Arizona *Agave* domesticates to five species.

Key Words: Agavaceae, *Agave*, Arizona, domesticate, pre-Columbian.

Resumen. Trabajo de campo reciente en el centro de Arizona, ha resultado en el descubrimiento de dos agaves que presentan una baja producción de semillas, se reproducen principalmente por medios vegetativos, tienen distribución restringida y no pueden asignarse a ninguna de las especies existentes. Estos agaves están asociados con estructuras arqueológicas y pueden encontrarse creciendo con otros agaves pre-Colombinos domesticados y anteriormente descritos. Se describe a continuación, **Agave verdensis** y **A. yavapaiensis**, dos especies que pueden ubicarse entre el grupo Ditepalae de agaves propuesto informalmente por Gentry. Las dos especies tienen afinidades con *A. chrysantha*, *A. shrevei* y *A. delamateri*. El último también es un *Agave* pre-Colombino domesticado del centro de Arizona. Proveemos una clave para distinguir estas especies de otros agaves en el centro de Arizona y el noroeste de México con los cuales pueden ser confundidos. El descubrimiento de estas dos nuevas especies eleva el número total de agaves domesticados en Arizona a cinco especies.

The genus *Agave* (Agavaceae) is a taxonomically complex group composed of over 200 species native primarily to arid and semiarid regions of the Americas with a center of diversity in central Mexico (García-Mendoza, 2002). Agaves were important Native American foods, fibers, beverages and medicines (Castetter et al. 1938; Callen, 1965; Gentry, 1982; Bruman, 2000; Hodgson, 2001a) and have been cultivated in Mexico from at least the Late Preclassic through the Postclassic Period (400 BC–AD 1500) (Zizumbo-Villarreal et al., 2009). The ease with which humans can cultivate agaves led Gentry (1982) to believe that agaves were seminal to early agricultural developments in Mexico, calling the human-agave relationship a "symbiosis" because people benefitted from the various *Agave* products and in return tended and dispersed *Agave* propagules.

Minnis and Plog (1976) first proposed that live agaves may have been transported by humans in Arizona (though not purposefully for cultivation), based on the close associa-

tion of *Agave parryi* Engelm. with archaeological sites outside of its normal range in eastern Arizona (Minnis & Plog, 1976). Later, Miksicek (1984) and Fish et al. (1985) found the first archaeological evidence that agaves were extensively cultivated outside Mexico. North of Tucson, Arizona, they documented agricultural structures and features associated with roasting pits containing charred *Agave* macrobotanical specimens dating from AD 700 with expanding production through the Hohokam Classic Period AD 1150-1450. Subsequently, similar structures and macrobotanical remains were identified throughout southern and central Arizona, often beyond the distribution of native agaves (Bohrer, 1987; Gasser & Kwiatkowski, 1991). Because these archaeological sites lacked preserved taxonomically informative characters such as leaves or flowers, it was presumed that *Agave murpheyi* Gibson and perhaps another cultivar of ultimate Mexican origin were grown (Fish et al., 1992).

While archaeological studies left little doubt about extensive *Agave* cultivation in Arizona, little attention was given to the natural history and evolutionary affinities of *Agave murpheyi* and *A. parryi* and how man may have manipulated them. Research programs implemented at the Desert Botanical Garden and the University of Georgia combined floristic, ethnobotanical, systematic, and population genetic studies to reveal population genetic structures indicating complex and active cultivation of *A. delamateri* Hodgson & Slauson, *A. murpheyi,* and *A. parryi* (Parker et al., 2007, 2010). These support earlier arguments for the "pre-Columbian domesticate" vs. "wild" species status of *A. murpheyi*, *A. delamateri*, and *A. phillipsiana* Hodgson, the latter a recently described species from Arizona (Hodgson & Slauson, 1995; Hodgson, 2001a, 2001b; Reveal & Hodgson, 2002; Hodgson & Salywon, 2009).

The evidence supporting domestication of these agaves is that they 1) are always found associated with archaeological sites and/or features; 2) produce very little or no fertile seed; 3) reproduce readily by vegetative means, mostly by offsets (*A. murpheyi* also produces bulbils on the flower stalk), making them easier to propagate; 4) have leaves that are more easily cut than other wild species, hence they are somewhat easier to harvest; 5) have relatively uniform intra- and inter-population morphology; 6) yield large "cabezas" or "heads" (the leaf base/caudex biomass) that are cooked for consumption; 7) have synchronous flowering within each taxon; and 8) have roasted "heads" that taste sweeter and are less fibrous than other wild species.

Recent fieldwork in central Arizona has resulted in the discovery of two additional *Agave* species that display these domestication traits. Moreover, they are sometimes found together or with other *Agave* domesticates (*Agave delamateri* and *A. phillipsiana*). The newly discovered agaves have leathery, erect flowers, dimorphic tepals with the outer whorl larger than the inner, and the outer tepal tips cucullate with a dark, corneous and pubescent cap, warranting placement in Gentry's informal group Ditepalae (Gentry, 1982). Yet, they are morphologically distinct from any existing species based upon both vegetative and reproductive characters. They show affinities to *A. delamateri* and *A. chrysantha* Peebles, from central Arizona, and *A. shrevei* Gentry, native to Chihuahua and Sonora, Mexico, all in the Ditepalae.

Sequence data from the chloroplast *psbA-trnH* intergenic spacer region and the *rpoC1* intron support both a close relationship of these new agaves to *A. delamateri* and their distinctiveness from other wild agaves in Arizona and Mexico, without clearly identifying a putative wild ancestor (Salywon et al., unpubl. data).

Here we describe two new species to accommodate these putative domesticates, and we provide a key to distinguish them from other similar agaves in central Arizona and adjacent northern Mexico with which they may be confused.

Agave verdensis Hodgson & Salywon, **sp. nov.** Type: U.S.A. Arizona. Yavapai Co.: Hill north of Sacred Mountain archaeological site, south of Wet Beaver Creek and [U.S. Forest Service] Ranger Station, 4033 ft, 23 Jun 2010, *W. C. Hodgson & A. Salywon 25495* (holotype: DES [4 sheets]; isotypes: ASC, ASU, MO, NY). (Figs. 1, 2)

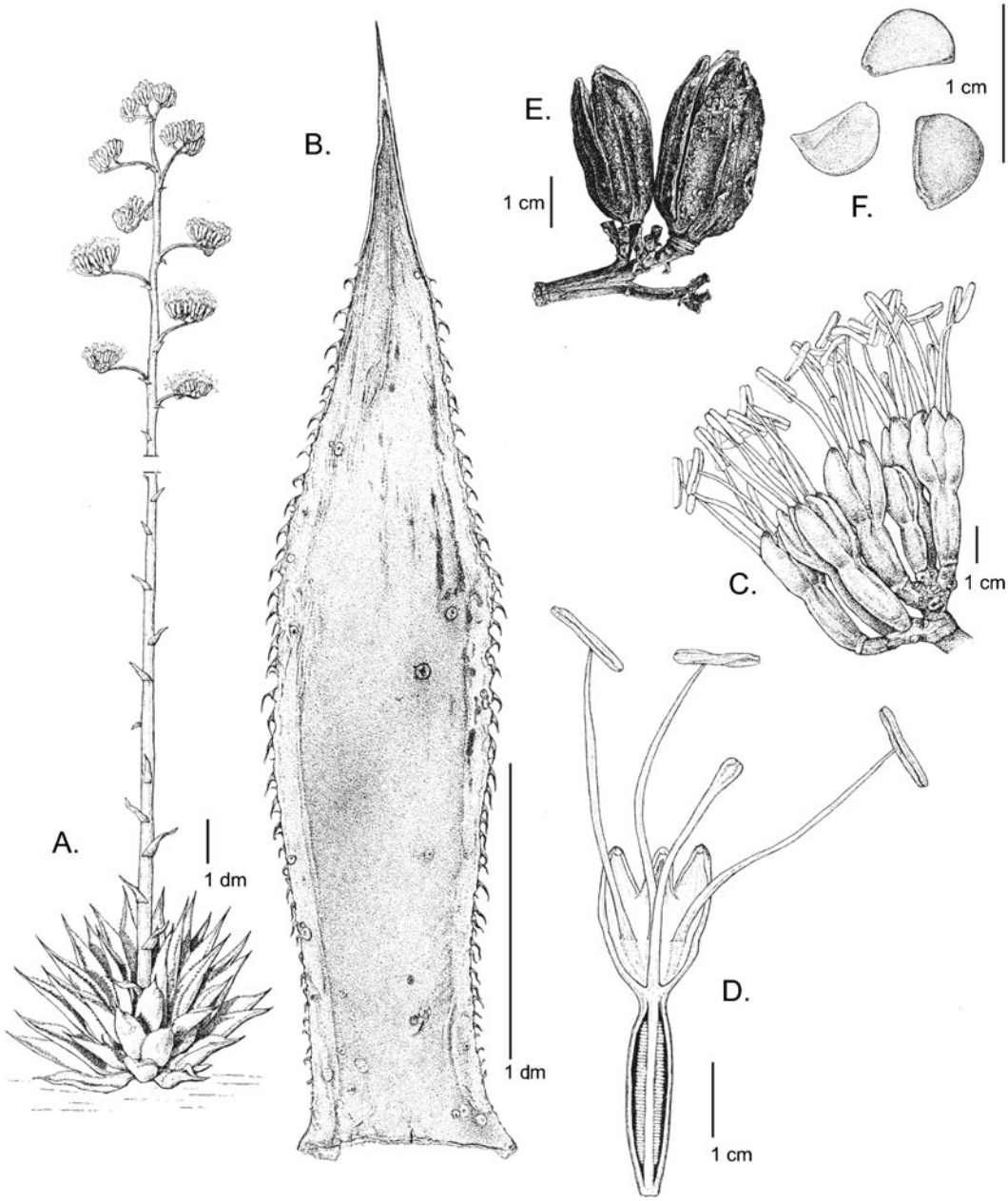

Fig. 1. *Agave verdensis*. **A**. Habit. **B**. Leaf. **C**. Flower cluster. **D**. Flower, longitudinal section. **E**. Capsules. **F**. Seeds (A–D from *Hodgson & Salywon 25495,* DES; E, F, *Hodgson et al. 25898,* DES.)

Planta acaulescens, surculosa, 50–60×50–60 cm lata, foliis 28–42(–47)×5.5–10(–13) cm, bevi-lanceolatis vel brevi-oblanceolatis, acuminatis; dentibus marginalibus valde deflexis, elevatis vel recurvis, subinde porrectus, spina terminali 1.8–3.4 cm longa, scapus inflorescentiam includens 4.5–6 m altus, inflorescentia paniculata, 18–20 ramos laterales, gerens; flores 42–57 mm longi; tepalis, filamentis et stylis cremeis vel cremeo-luteis; ovario 18–28×4–7.5(–10) mm, pallide viridi; capsulae linearioblongae vel obovoideae, (26–)32–39×14–22 mm, valvulis (10-)11-18 mm latis, stipitatae, stipitibus 1–4.5 mm longis, seminibus 6.5×5 mm, nigris.

Fig. 2. *Agave verdensis* (A, B) and *A. yavapaiensis* (C, D). **A**. Rosette (type locality). **B**. Flower cluster (*Hodgson 22112*). **C.** Rosette (type locality). **D.** Flower cluster (type locality).

Plants 50–60 cm high and broad, rosettes open, freely offsetting via rhizomes, forming clones of few to many plants. Leaves numerous, short-lanceolate to short-oblanceolate, 28–42(–47) cm×5.5–10(–13) cm, broadest at, just below, or just above middle, firm, acuminate, erect-spreading, guttered, easily cut with knife, glaucous-gray, flushed with maroon distally; marginal teeth firmly attached, strongly deflexed, occasionally porrect, recurved, or upturned, especially along distal 1/3 of leaf margin, close-set, gray, brown, dark mahogany to brown-black; interstitial teeth (0–)2–8 along distal 2/3 of leaf margin; terminal spine 1.8–3.4 cm, gray to dark gray-mahogany brown. Inflorescence narrowly paniculate, stalk 4.5–6 m tall, maroon-green glaucous, with 18–20 lateral, perpendicular to ascending maroon-glaucous branches in upper 2/5 of stalk, these 13.5–17 cm long at widest point of inflorescence. Flowers 15–49 in individual clusters, 42–57 mm long, with a sweet-musky fragrance at anthesis; tepal lobes persistently erect, clasping filaments, becoming leathery with age, in two series, slightly unequal to subequal, the outer series 7.8–11.5 mm long, light cream, with conspicuous brown, papillose, cucullate tips, those of inner series 7–10.2 mm long, light cream with less cucullate and lighter tip, white ciliate hairs within apices, strongly keeled; floral tube 13–15×12–15 mm, light green, thick, bulging at base of tepal lobes; filaments cream to cream-yellow, 31–49 mm

long, subequally inserted 5.7–8.7 mm above base of tube; anthers 11–20 mm long; ovary 18–28×4–7.5(–10) mm, light green, neck 4.5–7 mm long, light green-cream; style cream, 32–47 mm long. Capsules only produced in upper 2/5 of inflorescence, linear-oblong to obovoid, with short beak, (26–)32–39×14 –22 mm, the valves 10–18 mm wide, short-stipitate, the stipe 1–4.5 mm long; viable seed few, dull black, crescentic, rugose, with narrow marginal wing, 6.5×5 mm. $2n=60$ (*Baker 11854*, DES, meiotic cell complements, count by Marc Baker; *Hodgson 20109* (DES), meiotic cell complements, Andrew Salywon; root tip mitosis, plant in clone of *Hodgson 20109* (DES), Kathleen Parker, Univ. of Georgia, pers. comm., June 2007).

Distribution and ecology.—*Agave verdensis* is only known from 43 populations occurring near habitation and agricultural archaeological sites associated with pre-Columbian cultures from ca A.D. 1100–1400, at elevations between 3465 and 4455 ft (1050–1350 m). It grows on rocky, limestone, sandstone or clayey-loamy igneous derived soils in semi-arid desert grassland to pinyon-juniper woodland. Associated species include *Vachellia constricta* Bentham, *Senegalia greggii* (A. Gray) Britton & Rose, *Agave chrysantha* Peebles, *A. delamateri* Hodgson & Slauson, *A. phillipsiana* Hodgson, *Berberis haematocarpa* Woot., *Canotia holacantha* Torr., *Cylindropuntia acanthocarpa* (Engelm. & J. M. Bigelow), *C. leptocaulis* (DC.) F. M. Knuth, *Hilaria jamesii* (Torr.) Benth., *Ephedra torreyana* S. Wats. var. *torreyana, Fouquieria splendens* Engelm., *Gutierrezia sarothrae* (Pursh) Britton & Rusby, *Juniperus osteosperma* (Torr.) Little, *Krameria erecta* Willd. ex J. A. Schultes, *Larrea tridentata* (DC.) Coville, *Nolina microcarpa* S. Wats., *Opuntia engelmannii* Salm Dyck ex Engelm., *O. phaeacantha* Engelm., *Pinus monopylla* Torr. & Frém., *Prosopis velutina* Woot., *Quercus turbinella* Greene, *Rhus trilobata* Nutt., *Yucca baccata* Torr., and *Y. elata* (Engelm.) Engelm. var. *verdensis* (McKelvey) Reveal.

Phenology.—Flowering late June through mid July; flowering is synchronous. i.e., all of the plants that are flowering in a given year are at a similar stage of flowering. Fruiting in late summer to fall.

Etymology and common names.—The epithet refers to Verde Valley, where it occurs. Because of its proximity and regional importance to the Sacred Mountain settlement, it bears the common name, "Sacred Mountain agave."

Conservation status.—*Agave verdensis* is a rare taxon, and for this reason, detailed locality data is omitted here.

Additional specimens examined. U.S.A. Arizona. Coconino County: overlooking and east of Interstate 17, 1217 m, 17 Nov 2006, *Hodgson 21312* (DES), 1220 m, 21 Nov 2006, *Hodgson 21319* (DES); Verde Valley, east of Highway 89, north of Page Springs, 1230 m, 12 Mar 2007, *Hodgson 21539* (DES), 1257 m, 12 Mar 2007, *Hodgson 21542* (DES); Verde Valley, Sacred Mountain area, 1235 m., 13 Mar 2007, *Hodgson 21543* (DES), 1210 m, 13 Mar 2007, *Hodgson 21544* (DES), 1199 m, 13 Mar 2007, *Hodgson 21547* (DES). **Yavapai County**: west of Montezuma Castle National Monument, 3370 ft, 27 May 1995, *Baker et al. 11854* (DES 2 sheets); west of Interstate 17 and Highway 179, 1260 m, 25 Mar 1995, *Hodgson 8889* (ASU, DES); near highway 279, 1112 m, 10 Jul 2003, *Hodgson 17248* (ASU, DES 2 sheets), 1227 m, 17 Oct 2003, *Hodgson 17470* (DES), *17472* (DES 4 sheets), *17473* (DES), 1246 m, 22 Jun 2004, *Hodgson 18008* (ASU, DES 2 sheets), *18010* (ASU, DES 3 sheets), 21 Jun 2004, *Hodgson 18009* (ASU, DES 3 sheets); near Oak Creek, 1243 m, 3 Jun 2004, *Hodgson 18012* (DES 2 sheets), *18016* (DES 3 sheets), 3 Jun 2004, *Hodgson 18017* (DES 2 sheets), 1166 m, 16 Aug 2004, *Hodgson 18304* (DES); north of Verde River, 1006 m, 14 Jun 2005, *Hodgson 20105* (DES 3 sheets), 1157 m, 16 Jun 2005, *Hodgson 20108* (ASU, DES), 16 Jun 2005, *Hodgson 20109* (DES), 1204 m, 16 Jun 2005, *Hodgson 20111,* (ASU, DES), *20112* (ASU, DES 2 sheets), 1214 m, 16 Jun 2005, *Hodgson 20113* (DES 2 sheets), 1322 m, 12 Jul 2005, *Hodgson 20410* (DES 2 sheets); Page Springs area, 1140 m, 13 Mar 2007, *Hodgson 21544* (DES); south of Sacred Mountain, 1288 m, 21 Jun 2007, *Hodgson 22112* (ASC, DES); 1452 m, *Hodgson & Puente 20416* (DES), 1457 m, 14 Jul 2005, *Hodgson & Puente 20417* (DES), 1451 m, 14 Jul 2005, *Hodgson & Puente 20418* (DES); west of Page Springs, 1094 m, 5 Sep 2003, *Hodgson et al. 17424* (DES); near Montezuma Castle, 1012 m, 27 Sep 2003, *Hodgson et al. 17447* (DES); near Montezuma Well, 1082 m, 27 Sep 2003, *Hodgson et al. 17448* (DES); south of Sacred Mountain, 1187, 27 Sep 2003, *Hodgson et al. 17449* (DES), 1232 m, 21 Jun 2004, *Hodgson et al. 18235* (ASU, DES); Sacred Mountain area, 1451 m, 14 Jul 2005, *Hodgson et al. 20414* (DES); southeast of Sedona, 1226 m, 21 Nov 2006, *Hodgson et al. 21316* (DES).

This species was first collected from near Sedona in 1995 and tentatively determined as "*A.* aff. *delamateri* with influence from *A. chrysantha*" (*Hodgson 8889*, DES). Additional populations and collections were not identified until eight years later, when populations near

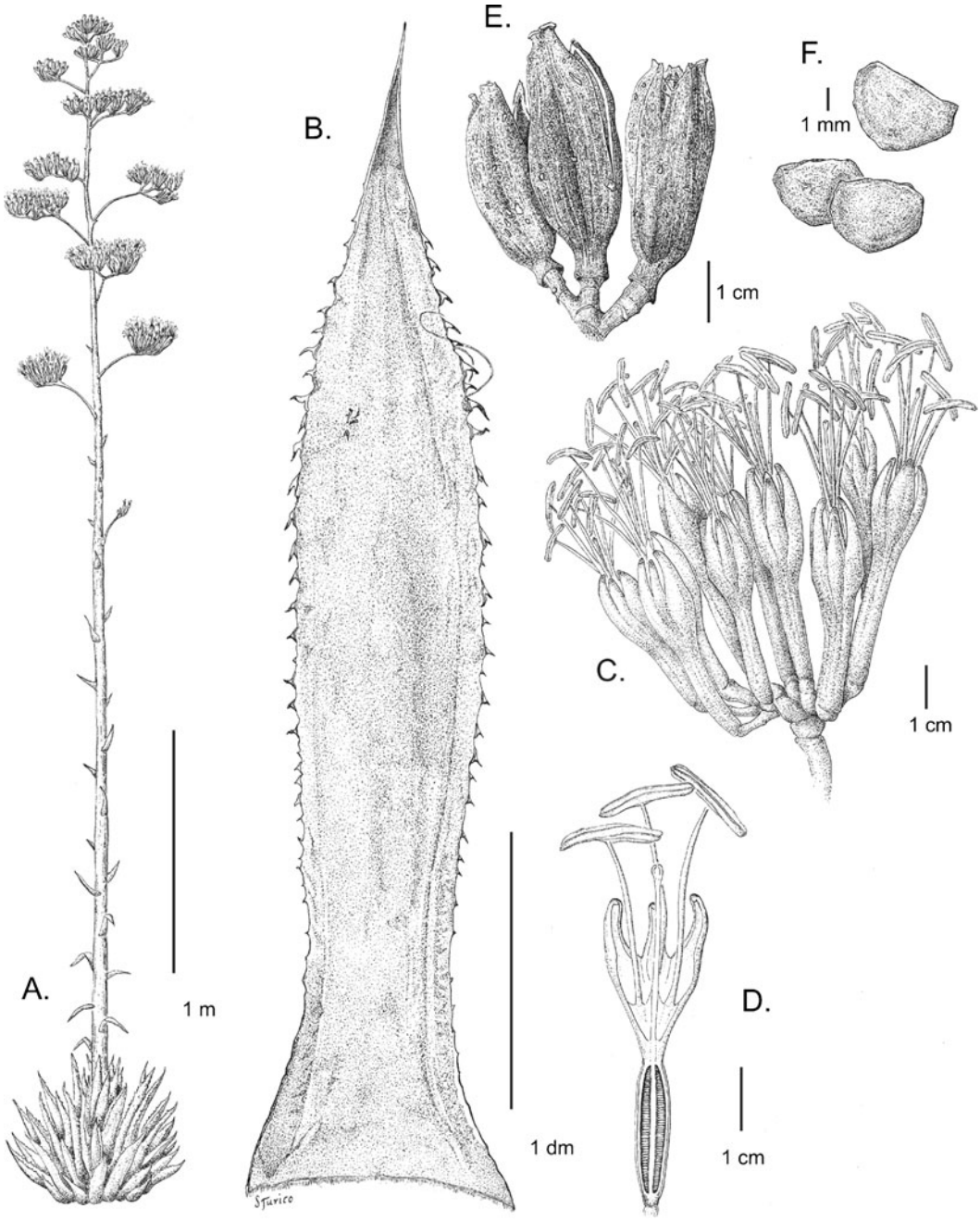

Fig. 3. *Agave yavapaiensis*. **A**. Habit. **B**. Leaf. **C**. Flower cluster. **D**. Flower longitudinal section. **E**. Capsules. **F**. Seeds (A–D, *Hodgson & Salywon 25496,* DES; E–F, *Hodgson et al. 25900*, DES.)

the Sacred Mountain archaeological site were found. With these additional collections, the cohesive nature of this taxon and the traits indicative of domestication became apparent.

Clones occur near major archaeological sites/features atop ridges with permanent or seasonal water sources. Its namesake, Sacred Mountain, is one of several archeo-

logical sites stretching along Beaver Creek (Pilles, 1981) that contained an unusually high frequency of Pre-Columbian agricultural features (Fish & Fish, 1984). Sacred Mountain agave grows with *A. delamateri*, *A. phillipsiana*, *A. parryi* and *A. chrysantha* Peebles, on the more arid, nutrient-poor slopes and ridgelines near these fields. The Sacred Mountain agave may represent a specialized, signature regional plant developed by prehistoric Verde Valley farmers.

Agave yavapaiensis Hodgson & Salywon, **sp. nov.** Type: U.S.A. Arizona. Yavapai Co.: Near Page Springs, 3904 ft, 23 Jun 2010, *W. C. Hodgson & A. Salywon 25496* (holotype, DES [5 sheets]; isotypes: ASC [2 sheets], ASU [2 sheets], MO [2 sheets], NY [2 sheets]). (Figs. 2, 3)

Planta acaulescens, surculosa, 60–70×60–70 cm lata, foliis 33.5–50×4.2–8 cm, anguste ellipticis vel linearioblanceolatis, abrupte acuminatis; dentibus marginalibus porrectis, recurvis vel deflexis, spina terminali 1.6–3.1 cm longa; scapus inflorescentiam includens 4–6 m altus; inflorescentia paniculata, 16–18 ramos laterales gerens; flores 42–57 mm longi; tepalis, filamentis et stylis cremeis vel cremeis vel cremeo-luteis; ovario 20–26×5–8.5 mm, viridi vel atroviridi; capsulae lineares vel lineari-oblongae, 34–42×11–17, valvulis 8–12 mm latis, stipitatae, stipitibus 4–6 mm longis, seminibus 5×4 mm, nigris.

Plants ca. 60–70 cm high and broad, rosettes open, freely offsetting via rhizomes, forming clones of few to several plants. Leaves numerous, narrowly elliptic to linear-oblanceolate, abruptly acuminate, 33.5–50×4.2–8 cm, broadest at or just above or below middle, firm, abrupt-acuminate, erect-spreading, easily cut with knife, blue- green, usually without maroon flush distally, deeply guttered; marginal teeth porrect, upturned or recurved, close-set, firmly attached, gray, red-brown to dark mahogany; interstitial teeth 3–7 along distal 2/3 of leaf; terminal spine 1.6–3.1 cm long, gray to dark brown-gray. Inflorescence narrowly paniculate; stalk to 4–6 m tall, dark green-maroon, glaucous, with 16–18 lateral, slightly ascending branches in upper 2/5 of stalk, these 13–18 cm long at widest point. Flowers 42–57 mm long, with a sweet-musky fragrance at anthesis; tepals persistently erect, clasping filaments, becoming leathery with age, in two series, unequal, those in outer series 11–12 mm long, cream to cream-yellow, with brown papillose-pubescent cucullate tips, those of inner series 9–10.5 mm long, cream to cream-yellow, strongly keeled, with white ciliate hairs within apices; floral tube 13–16×11–15.5 mm, thickish, bulging at base of tepal lobes, dark chartreuse-green; filaments cream-yellow, 33–43 mm long, subequally inserted, 5–10.5 mm above base of tube; anthers 10–18 mm long; ovary 20–26×5–8.5 mm, green to dark chartreuse green, neck chartreuse-green, 2–4 mm long; style light cream, 28–39 mm long. Capsules only produced in upper 1/4 of stalk, linear to linear-oblong, apiculate, 34–42×11–17 mm, the valves 8–12 mm wide, stipitate, the stipe 4–6 mm long; viable seed few, dull black, 5×4 mm. $2n=60$, a diploid (root tip mitosis, plant in clone of *Hodgson 17363* (DES), Kathleen Parker, Univ. of Georgia, pers. comm., June 2007).

Distribution and ecology.—*Agave yavapaiensis* is only known from ten populations occurring near habitation and agricultural archaeological sites associated with pre-Columbian cultures from ca A.D. 1100–1400, at elevations between 3000 and 4000 ft (914–1219 m). It grows on rocky, clayey-loamy igneous derived soils, less frequently on limestone soils in semi-arid desert grassland to pinyon-juniper woodland with *Canotia holacantha, Cylindropuntia acanthocarpa, Hilaria jamesii, Ephedra torreyana* var. *torreyana, Fouquieria splendens, Gutierrezia sarothrae, Juniperus osteosperma*, *Krameria erecta, Larrea tridentata, Opuntia engelmannii, O. phaeacantha, Prosopis velutina, Quercus turbinella, Rhus trilobata, Vachellia constricta*, and *Yucca baccata*.

Phenology.—Flowering late June through early August; flowering is synchronous, i.e., all of the plants that are flowering in a given year are at a similar stage of flowering. Fruiting in late summer to fall.

Etymology and common names.—The plant is named for the county in which it occurs, as well as for the Yavapai tribe that may have used this plant many years ago. Because it only occurs in the Page Springs area, it bears the common name, "Page Springs agave."

Conservation status.—*Agave yavapaiensis* is a rare taxon, and for this reason, detailed locality data is omitted here.

Additional specimens examined. U.S.A. Arizona: Yavapai County: Coconino National Forest, east of Page Springs, 1140 m, 10 Jul 2003, *Hodgson 17245* (DES 2 sheets), *17246* (DES), *17247* (ASU 2 sheets, DES 2 sheets); Coconino National Forest, Tuzigoot National Monument, 1034 m, 10 Jul 2003, *Hodgson 17250* (ASU 2 sheets, DES 2 sheets); Coconino National Forest, east of Oak Creek, 1211 m, 11 Jul 2003, *Hodgson et al. 17251* (DES 2 sheets), Coconino National Forest, west of Page Springs, 1181 m, 17 Jul 2003, *Hodgson et al. 17363* (DES 2 sheets), *17364* (ASU 2 sheets, DES 2 sheets); west of Page Springs, 1167 m, 27 Aug 2003, *Hodgson et al. 17421* (DES); west of Page Springs, 1082 m, 23 Nov 2010, *Hodgson et al. 25900* (DES).

Hodgson first collected the Page Springs agave in June 2003. Additional populations were found with the assistance of Sedona botanists Jean Searle and Max Licher. Subsequent surveys have yielded few additional sites/clones, and only ten sites are known. Plants grow on the dry, exposed ridges overlooking perennial water, usually in agriculturally favorable basalt soils with or near archaeological features. Like the Sacred Mountain agave, the Page Springs agave may have been a regionally important, signature plant for those inhabiting this area.

Both *A. verdensis* and *A. yavapaiensis* rely on vegetative reproduction through the formation of "pups" by the rhizomes. Few capsules with relatively few, small seeds develop only near the upper part of the inflorescence. Their perceived lack of significant variation in rosette, leaf, inflorescence and flower characters also suggest human manipulation. The two species possess traits favorable for harvesting and use for food and fiber. Their caespitose cloning habit, easily cut leaves with deflexed teeth, synchronous flowering, sweet-tasting apical meristem ("heads, cabezas") are all characteristics that may have been selected for by pre-Columbian farmers. The baked heads, particularly those of *A. yavapaiensis*, are exceptionally large and dense, weighing 30-40 pounds (Hodgson, unpublished data).

Agave yavapaiensis differs from the *A. verdensis* agave by its narrowly elliptic to linear-oblanceolate, abruptly acuminate, blue-green leaves that are slightly flushed with maroon, porrect, upturned, recurved or deflexed marginal teeth, dark brown, but not conspicuous calloused tepal lobe apices, green to dark green ovary and conspicuously stipitate, narrower, linear fruit with narrow valves. *Agave verdensis* has short-lanceolate to short-oblanceolate, acuminate, glaucous gray leaves that are tinged with maroon flush distally, strongly deflexed, occasionally porrect, upturned or recurved marginal teeth, conspicuous brown papillose pubescent calloused tips on tepal lobe apices, light green ovary, and short-stipitate, broader fruit with wider valves.

Agave verdensis and *A. yavapaiensis* show affinities with *A. chrysantha* of central Arizona and *A. shrevei* Gentry of Chihuahua and Sonora, Mexico. They differ from *A. chrysantha* by their cloning nature, little variability in morphology of vegetative and sexually reproductive structures, leaf size and shape, marginal teeth number and orientation, flower color, and minimal seed production, favoring reproduction by rhizomatous offsets. *Agave chrysantha* occasionally grows with, or adjacent to, *A. verdensis* clones. *Agave verdensis* shows the greatest affinity on a morphological basis to *Agave shrevei* subsp. *shrevei* and subsp. *matapensis* Gentry, the former from Sonora and Chihuahua, the latter from Sonora, on the northern end of the Sierra Madre Occidental. *Agave shrevei* was a valuable food and beverage resource for indigenous peoples of the Sierra Madre Region (Bye et al., 1975; Gentry, 1982). Their large teats (fleshy prominences below the teeth along the leaf margin), strongly reflexed marginal teeth, pale gray glaucous leaves are comparable to the Sacred Mountain agave, but flower characters and reproductive strategies are significantly different.

Leaf shape and color of the *Agave verdensis* suggests a small *A. delamateri*; indeed, it is difficult to distinguish young plants of either. However, numerous differences including ploidy level ($2n=60$ for the *A. verdensis* and $2n=120$ for *A. delamateri*), rosette, and flower characteristics can differentiate them.

Given the preponderance of archaeological and botanical evidence, we speculate that agaves were an exceedingly important domesticate during pre-Columbian times in the area that is now Arizona and adjacent Mexico. Of the 21 *Agave* taxa in Arizona, 12 are endemic, and of these, five are pre-Columbian cultivars. We believe the five cultivars may have originated in northern Mexico involving species within Gentry's (1982) Ditepalae group, such as *A. shrevei*, and were traded/transported as far north as

Grand Canyon (Hodgson, 2001b). Further research among agaves in northern Mexico, particularly those in Sonora and Chihuahua, is necessary to seek their wild progenitors and other potential undiscovered ancient cultivars. Interdisciplinary research, using systematic, nutritional, ethnobotanical and archaeological studies is necessary to answer many taxonomic and cultural questions regarding these plants. In closing, we are reminded that botanists must look at "natural" landscapes as possibly being culturally modified, and that such landscapes may still harbor plants purposely manipulated by man. We agree with, and have provided additional evidence for, Doolittle's (2000: 81) assessment that "the legacy of native North Americans' husbandry of large and woody plants is much richer than previously thought."

Key to *Agave shrevei*, *A. palmeri*, and agaves found in the Verde Valley, Arizona

1. Leaves dense, closely imbricate, with largest teeth along upper ¼ of leaf, soon drying brown upon initiation of flowering; inflorescence broadly paniculate, dense, usually with 20–40 lateral branches; tepal lobes 13–27 mm long, soon wilting, narrowing and incurving after anthesis . . . . . *A. parryi*
1. Leaves open, not closely imbricate, with largest teeth along most of leaf margin, persistently green after initiation of flowering, sometimes for 1+ years; inflorescence paniculate to narrowly paniculate, usually with 8–20 lateral branches; tepal lobes 8–22 mm long, drying leathery, broad and persistently erect after anthesis.
   2. Tepal lobes, filaments, style golden yellow; apices of outer tepal lobes dark yellow to light brown, not conspicuously calloused; leaves lanceolate to broadly-lanceolate; marginal teeth 4–11 mm long, 1–4 cm apart, the interstitial teeth (0–)1–3(–5) on upper 2.3 of leaf margin on one side of leaf; capsules oblong to obovoid. . . . . *A. chrysantha*
   2. Tepal lobes, filaments, style cream, cream-yellow, green, pink, maroon, or maroon-flushed; apices of outer tepal lobes usually conspicuously calloused, brown, reddish-brown or maroon; leaves linear-lanceolate, lanceolate, elliptic, oblanceolate, narrrowly obovate or ovate; marginal teeth generally less than 7 mm long, 0.2–2.5 cm apart, the interstitial teeth (2–)3–12 on upper 2/3 of leaf margin on one side of leaf; capsule, when present, linear-oblong or obovoid.
      3. Rosettes 50–70 cm high; flowers 4.2–5.7 cm long; floral tube 13–16 mm high; outer tepal lobes 7.8–12 mm long; filaments and style cream to cream-yellow, without pink, red or maroon flush; endemic to central Arizona.
         4. Leaves short-lanceolate to short-oblanceolate, acuminate, glaucous gray, tinged with maroon flush distally; marginal teeth strongly deflexed, occasionally porrect, upturned or recurved; ovary light green; fruit linear-oblong to obovoid, the valves 11–18 mm wide, the stipe 1–4 mm long; mature seed 5×6.5 mm. . . . . *A. verdensis*
         4. Leaves narrowly elliptic to linear-oblanceolate, abruptly acuminate, blue- green, usually without maroon flush distally; marginal teeth porrect, upturned, recurved or deflexed; ovary green to dark green; fruit linear to linear-oblong, the valves 8–12 mm wide, the stipe 4.5–6 mm long; mature seed 4×5 mm. . . . . *A. yavapaiensis*
      3. Rosettes 50–100 cm high; flowers 4.7–8.6 cm long; floral tube 11–23 mm high; outer tepal lobes 10–22 mm long; filaments and style cream, light yellow, green, pink, red, maroon or maroon flushed; species of Arizona, New Mexico and northwestern Mexico.
         5. Leaves short-lanceolate to ovate, short-acuminate, pale gray glaucous; marginal teeth at or basal to mid-blade strongly reflexed, with prominent teats; floral tube 15–23 mm high . . . . . *A. shrevei* ssp. *shrevei* ssp. *matapensis*
         5. Leaves linear-lanceolate, lanceolate to oblanceolate, acuminate to long acuminate, glaucous gray-green or green to dark green; marginal teeth at or basal to mid-blade porrect, upturned or recurved, generally with low teats; floral tube 11–20 mm high.
            6. Leaves erect or erect-ascending, conspicuously incurved at apex, glaucous gray-green with maroon tinge; interstitial teeth (3–)6–12 on distal 2/3 of leaf margin; filaments inserted at same level on perianth tube; lateral branches widely spaced, perpendicular to main axis . . . . . *A. delamateri*
            6. Leaves ascending to spreading, flaring outward, not conspicuously incurved at apex, green to dark green; interstitial teeth (2–)3–7 on distal 2/3 of leaf margin; filaments inserted at 2 levels or subequally on perianth tube; lateral branches widely spaced, perpendicular to main axis or ascending.
               7. Flowers 4.5–7.5 cm long; tepal lobes (6–)9–18 mm long; filaments inserted at 2 levels on perianth tube; scape (1.7–)4–7.2 m tall, the lateral branches perpendicular to main axis; marginal teeth firmly attached, 0.5–2 cm apart; rosettes solitary, rarely suckering . . . . . *A. palmeri*
               7. Flowers 7.4–8.6 cm; tepal lobes 15–22 mm long; filaments inserted subequally on perianth tube; scape 2.7–6 m tall, the lateral branches sinuous-ascending; marginal teeth easily detached, 1–2.5 cm apart; rosettes sparingly to freely suckering. . . . . *A. phillipsiana*

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