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Hohokam Lost Crop Found: A New *Agave* (Agavaceae) Species Only Known from Large-scale pre-Columbian Agricultural Fields in Southern Arizona

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Abstract—For over thirty years archaeologists have provided evidence that southern Arizona pre-Columbian Native Americans, the Hohokam, extensively cultivated agave. However, no archeologists reported finding living agaves growing in the rock-piled or gridded Hohokam fields, therefore researchers could only speculate about the species cultivated. Our work expands upon a recent publication noting several agaves growing in prehistoric dry-farmed fields on terraces overlooking the San Pedro River. These agaves have affinities to *A. phillipsiana* W. C. Hodgs. and *A. palmeri* Engelm. based on flower color but differ by their gray-green leaves with thick bases and conspicuous bud imprinting. They are extremely rare, reproduce asexually via rhizomatous offsets with no apparent fruit set, have relatively uniform intra- and inter-population morphology, grow only with archaeological features and are unknown from natural settings: all characteristics expected in a domesticated crop. Here we describe *Agave sanpedroensis*, provide a key to distinguish it from other agaves in south-central Arizona and propose that it is a clonal, relictual crop grown from ca. A.D. 800–1450 by the Hohokam, and thus represents a ‘lost crop’ as sought by archaeologists. The extensive size and wide distribution of Hohokam agave fields that transformed the landscape and are still visible today indicates the crop’s importance in the Hohokam economy. The question of where and when this agave originated has implications for North American domestication centers. Our discovery emphasizes the importance of collaborative research between archaeologists and botanists whose distinctive data can provide a richer understanding of how the Hohokam developed and then sustained one of the American Southwest’s largest prehistoric populations.

Keywords—Dry-farming, landscape modification, rare plant, relictual domesticate, Southwestern ethnobotany.

The importance of agave as a source of Native American food, fiber, and beverage has been well documented (Castetter et al. 1938; Callen 1965; Gentry 1982; Bruman 2000; Hodgson 2001a). Archaeologists proposed that pre-Columbian residents of southern Arizona, the Hohokam, practiced large-scale agave cultivation as evidenced by the many thousands of acres of agricultural features such as rock pile fields and rock alignments, characteristic stone tools for harvesting and processing agave, and large roasting pits used to cook agave (Miksicek 1984; Fish et al. 1985; Fish and Fish 2014). Because stands of living agaves were absent from field localities, researchers could only speculate about the species cultivated and whether Hohokam farmers grew wild local populations or perhaps Mexican cultigen/domesticates obtained by trade. By the time Spanish explorers arrived in the mid-1500s in what is now Arizona, the Hohokam material culture and agricultural land use pattern no longer existed as there was a severe population decline that started ca. 1350 (Hill et al. 2004). There are no ethnographic accounts of the Hohokam culture that can inform archaeologists or ethnobotanists about these fields.

The Hohokam, who farmed the Sonoran Desert in present-day central and southern Arizona, were greatly influenced by pre-Columbian Mesoamerican cultures and cultigens. Their agrarian society emerged from local Archaic hunting and gathering groups who inhabited the area (Andrews and Bostwick 1997) and cultivated maize beginning at least 4000 yr ago (Mabry 2005). Over many centuries, roughly from A.D. 300–1450, the Hohokam developed a sophisticated and intensive agriculture system along the Gila, Salt, San Pedro, Santa Cruz, and Verde Rivers and their tributaries. Hundreds of miles of large and technologically complex irrigation canals and ditches delivered water to crops of maize (*Zea mays* L.), tepary beans (*Phaseolus acutifolius* A. Gray var. *acutifolius*), common beans (*P. vulgaris* L.), lima beans (*P. lunatus* L.), jack beans (*Canavalia ensiformis* (L.) DC.), mixta, butternut, and pepo squashes (*Cucurbita argyrosperma* K. Koch subsp. *argyrosperma*, *C. moschata* Duchesne, and *C. pepo* L. subsp. *pepo*), bottle gourds (*Lagenaria siceraria* (Molina) Standl.), grain amaranth

(*Amaranthus cruentus* L. and *A. hypochondriacus* L.), and cotton (*Gossypium hirsutum* var. *punctatum* (Schumach.) J.B. Hutch) growing in floodplains and adjacent first level terraces (Gasser and Kwiatkowski 1991b; Fish 2004; Fritz et al. 2009). By A.D. 800 large Hohokam pithouse villages, many with public features such as ceremonial ballcourts and platform mounds, spread along rivers like the San Pedro (Clark and Lyons 2012). In the Salt and Gila River basins Hohokam populations fanned out on irrigation canal extensions with large settlements coalescing near the most fertile land, often many miles from the rivers’ canal intakes. Archaeologists estimate that by A.D. 1300 the Hohokam numbered roughly 40,000 people (Hill et al. 2004) and had one of the largest population concentrations in the prehistoric American Southwest.

Archaeologists speculated that agaves were cultivated in the drier areas in some riverine fields (Gasser and Kwiatkowski 1991a: 427; Teague 1998: 16–17), although the primary, extensive evidence of agave cultivation is now only visible on mountain bajadas and terraces as the prehistoric irrigated floodplain fields are buried by alluvium (Clark et al. 2012a). From a distance, while the bajadas and terrace surfaces look “natural”, they actually represent engineered landscapes modified and managed for dry-farming by the construction of terraces, rock piles, and rock alignments from local materials. These constructs served as mulch to slow moisture evaporation and surface water flows, increasing infiltration from local, rare, rainfall events (Fish et al. 1985, Fish and Fish 2014). The rock mulch may also have protected roots and enhanced soil permeability for young plants, as well as deterred gopher predation. While rock pile fields are found intermittently throughout the Southwest, they occur in a “well-delimited and continuous distribution within Hohokam territory” (Fish and Fish 2014: 125).

The presence of specialized stone tools such as tabular stone knives, steep-edge pulping planes, and hammer-stones, as well as roasting pits are archaeologists’ key clues to identify the crop being raised in these fields, as these tools were utilized to process agave foods, beverages, and fibers throughout

prehistory. Carbonized agave remains recovered from central and southern Arizona Hohokam sites include isolated fibers, leaf bases, and caudex fragments, while terminal and marginal leaf spines are not as common (Fish et al. 1985). Macrobotanical charred agave remains suggest that two or more agaves were cultivated (Bohrer 1987; Fish et al. 1985). Unfortunately, these botanical remains are too fragmentary for species-specific identification, leading researchers to propose that either the rare *Agave murpheyi* F. Gibson, wild agaves from Arizona, or even cultivars of Mexican origin were grown. Furthermore, these prehistoric structural remains and tools generally occur at elevations below the natural range of many southeastern and central Arizona wild agaves such as *Agave chrysantha* Peebles, *A. deserti* subsp. *simplex* Gentry, *A. palmeri* Engelm., and *A. parryi* Engelm. The latter two are primarily desert grassland (Chihuahu Desert), chaparral, and oak to pine woodland plants.

Beginning in the 1980s, Hodgson and other botanists at the Desert Botanical Garden initiated various field studies of *Agave* species in Arizona and northern Sonora, Mexico to identify potential prehistoric cultigens. In central Arizona, they found remnant populations of agaves growing in prehistoric fields and provided evidence that *Agave murpheyi* and *A. delamateri* W. C. Hodgson & L. Slauson are pre-Columbian domesticates, not just wild agaves cultivated by the Hohokam. Both species have traits common among domesticated plants. They produce little if any seed, can reproduce asexually readily via rhizomes (*A. murpheyi* also produces bulbils), show very little morphological variability, and are only found growing associated with archeological features like rock piles and terraces and not in natural settings (Hodgson and Slauson 1995; Hodgson 2001a). Subsequently, Parker et al. (2007) demonstrated that both plants have lower genetic diversity than wild agave species, a trait expected in crop plants. Only approximately 75 populations of *A. murpheyi* are known, occurring in the Lower Colorado Valley and Arizona Upland subdivisions of the Sonoran Desert in Arizona and northern Sonora between 400 and 1000 m elevation. Roughly 200 populations of *A. delamateri* occur primarily within the Arizona Upland or pinon-juniper woodlands of central Arizona between 700 and 1600 m elevation. Their present distributions overlap the northern Hohokam region but do not occur in the southern Hohokam region.

Clark and Lyons' (2012) publication of San Pedro River archaeological research documented the first known presence of living agaves in the southern Arizona Hohokam dry-farming fields' terraces overlooking Holocene floodplains. Significantly, it documented rock pile sites within 2 km of the Holocene floodplain along more than 60 miles of the river. Some of the agricultural sites measured over 60 hectares (60,000 m²) (Clark et al. 2012a: Fig. 5.1). The publication, including a picture of an agave in a field (Doelle et al. 2012: Fig. 2.17), was called to the senior author's attention. Unable to ascertain the plant's identity, Hodgson and Salywon visited the site and determined that it was an undescribed species. After contacting Doelle, together we visited 12 localities where archaeologists noted agaves occurring within these ancient agricultural fields.

In 2015, an archaeological site steward showed Hodgson and Salywon a small population of agaves growing in Hohokam dry-farming fields near the Tortolita Mountains, ca. 45 km west of the San Pedro River site. These agaves morphologically match those at the San Pedro River sites. This locality is only ca. 12 km east of the Marana study area

where Fish et al. (1985: Fig. 1) first identified Hohokam agave fields.

Herein we describe this recently discovered new agave species known only from southern Arizona Hohokam agricultural fields bringing together both archaeological and botanical evidence. We also provide a key to differentiating this agave from other similar agaves in south-central Arizona and discuss the implications of finding this putative domesticate and potential Hohokam 'lost crop.'

Agave sanpedroensis W. C. Hodgson & A. M. Salywon sp. nov. TYPE: USA. Arizona: Pima Co., south of San Manuel along the San Pedro River, 12S 535235E 3608075N (in order to protect site locations, coordinates are for the nearest town, San Manuel), elev. 914 m, Upper Sonoran Desert scrub, with numerous pre-Columbian rock piles and terraces, 7 Aug 2014, W. C. Hodgson & A. Salywon 29603 (holotype: DES [3 sheets: DES00078831–3]; isotypes: NY, US).

Agave sanpedroensis W. C. Hodgson & A. M. Salywon is similar to *A. phillipsiana* W. C. Hodgson and *A. palmeri* Engelm. by its flower color (tepal lobes, filaments, style cream, cream-yellow, green, pink, maroon, or maroon-flushed). The sigmoid/sinuuous slender inflorescence and large, thick flowers of *A. sanpedroensis* are similar to those of *A. phillipsiana*. It differs from the usually stout inflorescence of lateral branches of *A. palmeri*. The gray-green leaves with thick base and conspicuous bud imprinting of *A. sanpedroensis* differs from the leaves of *A. phillipsiana* and *A. palmeri*, which are darker green and without conspicuously thickened bases and bud imprinting.

Plants 50–70 cm high and broad, rosettes open, freely offsetting via rhizomes, forming clones of few to many plants. Leaves numerous, linear-lanceolate to linear-oblongate, 44–49 cm × 5–7.3 cm, broadest at, just below, or just above middle, firm, acuminate, erect-spreading, guttered, thick at base, glaucous-gray, cross-zoned with alternating bands of gray and gray-green, with conspicuous white bud-imprinting, the margins undulate; marginal teeth firmly attached, strongly deflexed, occasionally porrect or upturned in basal and distal 1/4–1/6 of leaf margin, glaucous gray (-brown), with brown ring at base; interstitial teeth (0)–4–6 along distal 2/3 of leaf margin; terminal spine 2.4–3.5 cm, gray with dark gray-mahogany brown at tip. Inflorescence narrowly paniculate, stalk 4.75–6 m tall × 25–32 mm at 1 3/4 m from ground, maroon-green glaucous, with 9–13 lateral, perpendicular to sigmoid/sinuuous-ascending maroon-glaucous branches in upper 1/3–2/5 of stalk, these ca. 22 cm long at widest point of inflorescence, bracts broadly lanceolate, acuminate to long-acuminate. Flowers 21–31 within individual clusters, 55–65 mm long, with a sweet-musky fragrance at anthesis; tepal lobes persistently erect, clasping filaments, becoming leathery with age, with margins sometimes strongly involute, in two series, unequal to slightly unequal to equal, the outer series 15.2–19.25 mm long, cream-light yellow (to very light chartreuse), sometimes lightly flushed with maroon, with conspicuous brown, papillose, cucullate tips, those of inner series 13.5–16.25 mm long, cream-light yellow (to very light chartreuse), with less cucullate and lighter tip, white ciliate hairs within apices, strongly keeled; floral tube 11.5–14 mm high × (11)–13.5–17 mm wide, light green, thick, bulging at base of tepal lobes; filaments light chartreuse-cream, sometimes becoming lightly flushed with maroon distally, 51–60 mm long, unequally to subequally or equally inserted 5–6.9 mm

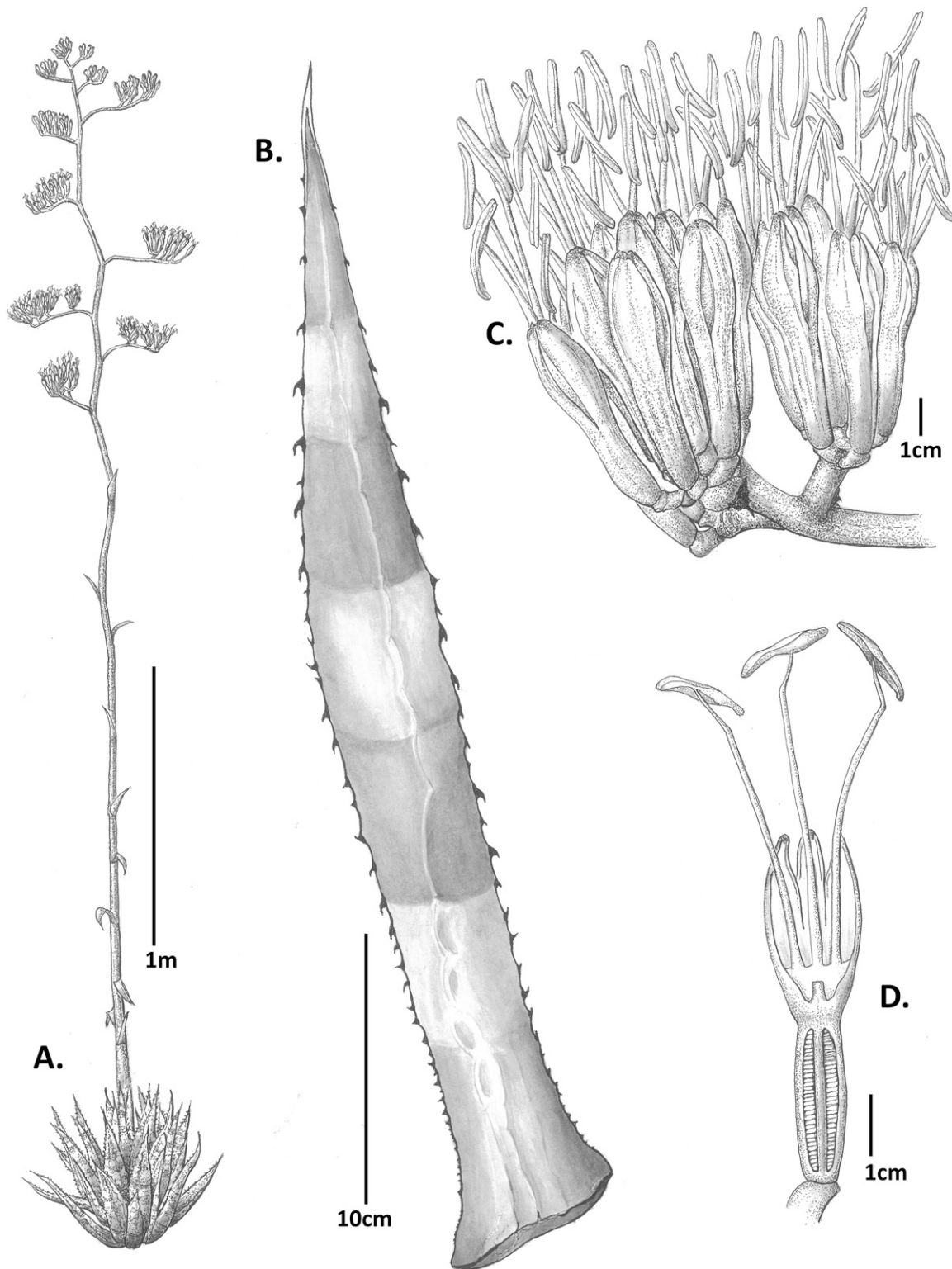


FIG. 1. *Agave sanpedroensis*. A. Habit. B. Leaf. C. Flower cluster. D. Flower, longitudinal section (Hodgson & Salywon 29603).

above base of tube; anthers (dehiscing) 15–19 mm long; ovary 24–30 mm high, 8–9 mm wide, light chartreuse green-cream or chartreuse green, neck 1.5–4.7 mm long, light chartreuse green-cream or chartreuse green; style 32–59 mm long, cream or light chartreuse cream with or without slight maroon flush. Capsules and seed not observed. Figures 1, 2A, B.

Phenology—Flowering late July through August. Fruits apparently aborting early in development, none known.

Distribution and Ecology—*Agave sanpedroensis* is known from fewer than a dozen populations/sites, along the San Pedro River between Benson and San Manuel, and from one locality near the Tortolita Mountains, Arizona. All occur within pre-Columbian agricultural fields with numerous rock piles and terraces in the Arizona Upland subdivision of the Sonoran Desert, with no known occurrences in more natural (non-anthropogenic) settings. Most of the rock piles documented

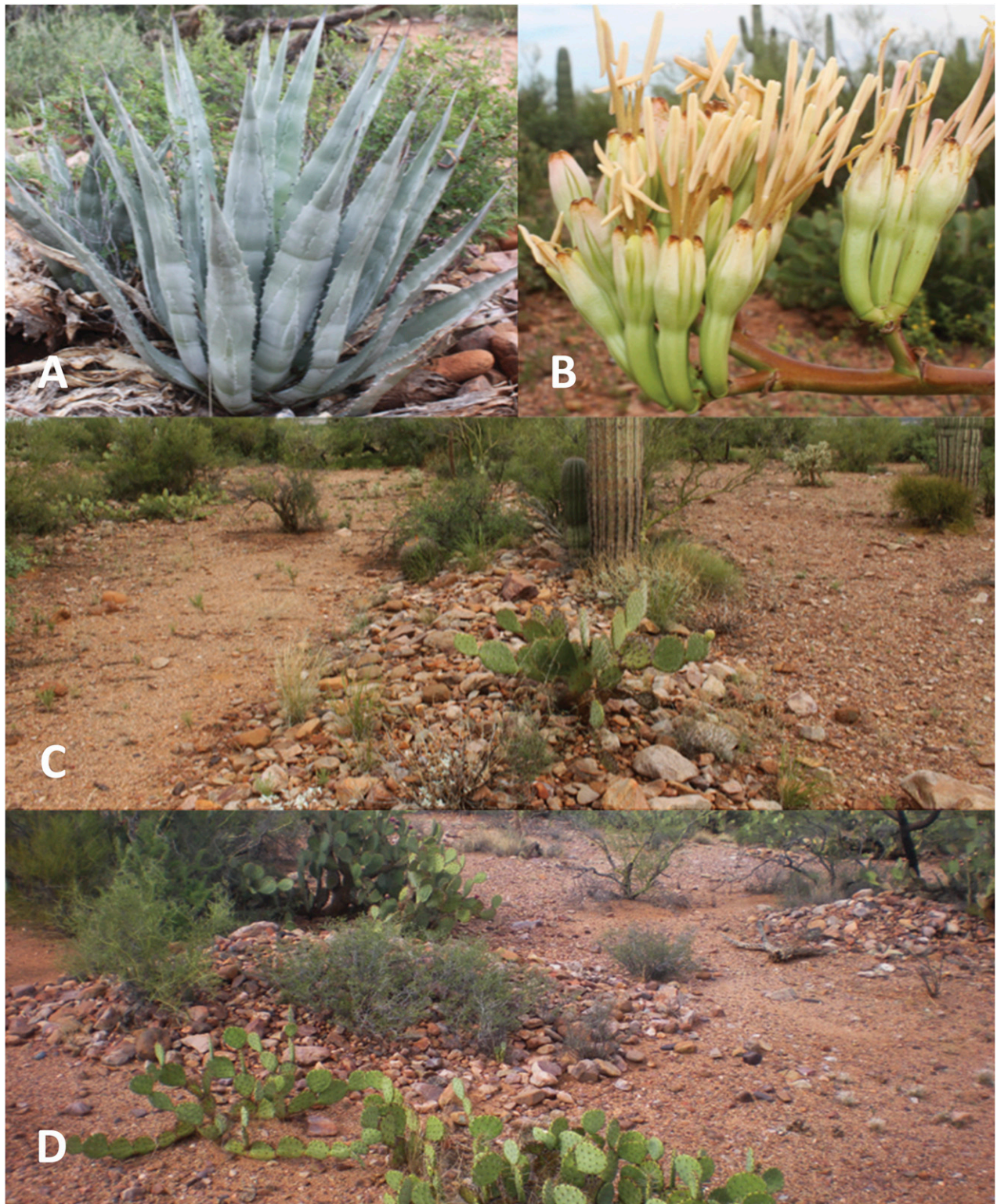


FIG. 2. *Agave sanpedroensis* and pre-Columbian rock piles and linear alignment. A. Rosette (type locality). B. Flower cluster (Hodgson et al. 30580). C. Rock linear alignment perpendicular to the slope with upslope to the left. (Note the accumulation of fine sediments on the upslope side). D. Two large rock piles typical of the agricultural sites.

along the San Pedro River are circular in area and range from one to three meters in diameter and are less than 75 cm in height (although there occur some that are much larger); additionally, there are linear features with some over 50 m in length (Fig. 2C, D). The density and morphology of the rock

piles is quite variable, ranging from a single rock pile (1–3 m²) to sites over 60 ha in size with thousands of these rock pile features (Clark et al. 2012a). Archaeologists also identified roasting pits and several potential “gridded fields” within the San Pedro River agricultural field systems. Extensive

“gridded fields” thought to have been used for agave cultivation have been documented in Safford Basin along the Gila River, northeast of the San Pedro River (Doolittle and Neely 2004).

We have seen and documented only two flowering specimens of *Agave sanpedroensis* and neither has produced any fruit. Although it appears to be sterile, it readily reproduces asexually via rhizomatous offsets and thus has persisted for centuries in these fields since they were abandoned. It remains to be determined why *A. sanpedroensis* may be sterile. Perhaps it is not self-compatible, grows outside of the range of its wild progenitor and the environmental conditions are not conducive to fruit set, has some genetic incompatibilities as a result of artificial selection, or was purposefully selected for asexual reproduction. Human selection on many agaves has been widespread through time and in some cases has resulted in species only known from cultivation that do not produce fruits and seeds at all (or only very rarely) but reproduce asexually quite readily. Besides Arizona species above, others include *A. cantala* (Haw.) Roxb. Ex Salm-Dyck, *A. fourcroydes* Lem., *A. sisalana* Perrine ex Engelm., and *A. karatto* Miller, to name a few (Gentry 1982; Rogers 2000).

Associates—*Calliandra eriophylla* Benth., *Carnegiea gigantea* (Engelm.) Britton & Rose, *Cylindropuntia fulgida* (Engelm.) F.M. Knuth, *Ferocactus wislizeni* (Engelm.) Britton & Rose, *Fouquieria splendens* Engelm., *Opuntia engelmannii* Salm-Dyke, *O. phaeacantha* Engelm., *Parkinsonia microphylla* Torr., *Prosopis velutina* Woot., and *Eragrostis lehmanniana* Nees.

Conservation—*Agave sanpedroensis* is an extremely rare taxon, and for this reason, detailed locality data is omitted here (the UTM coordinates given are for the nearest town, San Manuel). We know of fewer than a dozen populations/sites of this species, consisting of roughly 200 individuals. Given the thousands of acres of Hohokam rock pile fields that archeologists have identified and their cultivation potential one could deduce that the Hohokam grew this species (and perhaps others) on a large scale. The few remaining individuals represent relicts that have survived drought and predation via asexual reproduction in these same fields for over 550 yr, probably since their abandonment with the dissolution of the Hohokam culture. At a San Pedro site that has experienced extended drought over the past 15 yr, one cluster noted by archeologists in the early 1990s had died during the past two decades. The Endangered Species Act does not provide protection for domesticated species and the Archaeological Resources Protection Act does not provide protection for plants. Therefore, there is no legal status to bestow upon this species to protect it under the law. In fact, since *A. sanpedroensis* is a putative domesticated species and is not known from the wild, it cannot be included on the IUCN red list (IUCN Standards and Petitions Subcommittee 2017: Sec. 2.1.1). Human cultivation, once again, is needed to bring this ‘lost crop’ back from the brink of extinction.

Etymology—The species is named for the San Pedro River Valley, where archeologists have documented large-scale Hohokam dry-farming fields and where this species was presumably farmed.

Additional Specimens Examined—USA.—ARIZONA: Pinal Co.: south of San Manuel, along San Pedro River, 12S 535235E 3608075N (in order to protect site locations coordinates are for the nearest town, San Manuel), elev. 914 m, Upper Sonoran Desert scrub, with numerous pre-Columbian rock piles and terraces, 19 Jul 2014, Hodgson & Salywon 29595 (DES 2 sheets), 29596 (DES); 7 Aug 2014, Hodgson & Salywon 29602 (ARIZ, ASU, DES 3 sheets); 5 Sept 2014, Hodgson & Salywon 29867 (DES 2 sheets), 29869 (DES);

23 Oct 2014, Hodgson et al. 30116 (DES 2 sheets), 30117 (DES); 31 July 2015, Hodgson et al. 30580 (DES 5 sheets).

The Hohokam people subsisted by cultivating maize, beans, squash, amaranth, and agave along with exploiting wild plant and animal resources. Limited paleobotanical analyses from test excavations along the San Pedro River, the southern region of Hohokam cultural influence, reveal that, in order of ubiquity in the samples, maize, mesquite pods/beans (*Prosopis velutina*), common beans, saguaro fruit (*Carnegiea gigantea*), prickly-pear (*Opuntia* spp.), juniper “berries” (*Juniperus* species), squash, agave, and cheno-am (*Chenopodium* species & *Amaranthus* species) seeds were the most frequent food plants recovered (Clark et al. 2012a).

How was this important agave crop (and perhaps others) lost from the Hohokam past? The rock pile fields where these agaves occur are difficult to date because they contain few diagnostic artifacts. However, archeologists estimate that the Hohokam used these fields along the San Pedro from roughly 800–1450 A.D., with peak agave cultivation between A.D. 1000–1275. The peak population for this area probably occurred in the early 1300s (Clark et al. 2012b). Paleobotanical data indicates that agave cultivation rapidly declined in the late 1300s and was replaced with more intensive maize agriculture and mesquite pod/bean harvesting. At the same time people coalesced from dispersed farmsteads and hamlets to walled villages, events likely precipitated by the migration of Kayenta/Tusayan immigrants from the Four Corners region (northeastern Arizona, southeastern Utah, southwestern Colorado, and northwestern New Mexico) to this area. Clark et al. (2012b) argue that because agave may take a decade or more to reach maturity and the dry-farming field systems were so dispersed within the landscape, the farmers would have had difficulty in defending these fields. Thus, the cultivation of agave field systems indicates a time of low social tension. Conversely, the shift away from agave farming and a coalescing of people into defensive villages in the 1300s is suggestive of social tension and heightened security concerns. The dramatic population decline and the reorganization of populations post-1450 led to, over the centuries since, the subsequent decrease and near extinction of agaves that they once tended in their fields and the transformation of the formerly cultivated landscapes to its modern “natural” appearance.

Because archeologists documented (Clark and Lyons 2012) the few populations of this relic cultigen *Agave sanpedroensis*, scientists now have the unique opportunity to study the living plant in its archaeological context and also to bring this plant back into cultivation for conservation purposes. In contrast, another crop probably domesticated by the Hohokam, little barley (*Hordeum pusillum* Nutt.), is only known from charred caryopses, spikelets, and rachis fragments in archaeological sites (Bohrer 1991; Adams 2014), and there is no chance of resurrecting the crop from these remnant pieces. With the critical need to diversify agriculture, grow less water-dependent crops, and stimulate new industries in the southwestern United States, we have the opportunity to bring this ancient agave crop back to life. Because *A. sanpedroensis* has persisted solely by asexual reproduction, the remaining clones are genetically identical to those planted by the Hohokam. These clones are keys for understanding what favorable traits Hohokam farmers might have selected for, such as edibility, yield, fiber quality, ease of harvest, growth rate, etc. For example, an offset of *A. sanpedroensis* brought into cultivation at the Desert Botanical Garden in 2014 appears to have a much faster growth rate than other native

agaves of similar size (Hodgson and Salywon pers. obs.), suggesting that the Hohokam selected for a shorter life-cycle.

Naturally, the question of where and when this putative domesticated species arose has implications for understanding of North American domestication centers. Because corn, beans, squash, amaranth, and cotton grown by the Hohokam are Mesoamerican cultigens it may be assumed that the agaves cultivated by the Hohokam might have the same origin. However, the ease with which humans can cultivate and transport agaves with rhizomatous offsets would enable ancient farmers to quickly select and perpetuate agave genetic variants (Gentry 1982). Previous studies provide the context to look outside of Mesoamerica for the origin of domesticated agaves. Arizona cultivators living in sedentary agrarian villages developed the earliest and eventually the most extensive irrigation system in North America. Over several thousand years, the advanced agricultural Hohokam had sufficient time to domesticate agaves from wild native ancestors. Archaeobotanical specimens suggest the Hohokam also domesticated little barley (Bohrer 1991; Adams 2014). Recent findings also indicate that the domesticated turkey used by non-Hohokam pre-contact Native American cultures in the American Southwest has a distinct history and origin from contemporary domestic turkey that originated in Mesoamerica (Speller et al. 2010). Moreover, two putative pre-Columbian domesticated agaves described from central Arizona, within the area occupied by the Sinagua culture, have affinities to agaves from Arizona and northern Mexico, rather than Mesoamerica (Hodgson and Salywon 2013).

Both morphological and chloroplast sequence data from the *rpoC1* intron and the *psbA-trnH* and *rps15-ycf1* intergenic regions place *Agave sanpedroensis* in a relationship to both *A. palmeri* s. l. and *A. phillipsiana*, although the molecular data is based on very few informative characters (Salywon et al. unpubl. data.). Morphologically they have similarly shaped leaves (linear-lanceolate to linear-oblong) and flower color (tepals lobes, filaments, style cream, cream-yellow, green, pink, maroon, or maroon-flushed). The sigmoid/sinuuous slender inflorescence of *A. sanpedroensis* is very similar to that of *A. phillipsiana* but different from *A. palmeri*, which

usually has a stout inflorescence comprised of lateral branches often perpendicular to the stalk. *Agave palmeri* is native to southeastern Arizona, southwestern New Mexico, and northern Sonora and northwestern Chihuahua, Mexico. *Agave palmeri* is one of the sweeter agaves with little or no sapogenins and was used historically for food and for making mescal in northern Sonora (Gentry 1982). Historical accounts also report the Akimel O'odham [as Pima], Tohono O'odham [as Papago], and Apache Native Americans using *A. palmeri* (Castetter et al. 1938; Hodgson 2001a). *Agave phillipsiana* occurs in Coconino, Gila, and Yavapai counties, Arizona, and its southernmost populations lie in the northeastern periphery of the Hohokam cultural area. It too is a putative domesticated species (Hodgson 2001b), based on the same characteristics outlined above for *A. sanpedroensis*. Informal tastings of roasted agave comparing wild and domesticated species from Arizona have shown that *A. phillipsiana* is among the sweeter and better tasting samples (Hodgson unpubl. data). Because of the rarity of *A. sanpedroensis*, no samples of it have been roasted and tasted, but because of its close relationship to two other sweet-tasting agaves it would be reasonable to believe it too is sweet. It remains to be determined if *A. palmeri* is the wild progenitor of both *A. sanpedroensis* and *A. phillipsiana*, and when they were derived. Going forward, we have initiated a genome skimming study to address these questions as part of a broader phylogenetic study of the genus.

Previous archeological studies documenting the extensive size and wide distribution of Hohokam agave fields recognize the crop's importance in the Hohokam world. The discovery of *Agave sanpedroensis* as a living, domesticated relict from within these fields illuminates the sophistication of Hohokam dry-land agricultural practices. It reveals that the Hohokam grew not just multiple and varied cultivars in irrigated fields, for which they are famous, but also dry-land domesticates. Our discovery emphasizes the importance of collaborative research between archeologists and botanists whose distinctive data can provide a richer understanding of how the Hohokam developed and then sustained one of the American Southwest's largest pre-Columbian populations.

KEY TO THE PANICULATE AGAVE SPECIES IN SOUTH-CENTRAL 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 *A. parryi*
1. Leaves of rosettes usually open, not closely imbricate, with largest teeth along most of leaf margin; leaf blade linear-lanceolate to lanceolate or oblanceolate; inflorescences open, usually with 6–26(–32) lateral branches 2
2. Perianth tube shallow, 2–10 mm high, much shorter than tepal lobes; filaments inserted at or near middle of tube; tepal lobes ascending or spreading, occasionally erect, equal or subequal, wilting soon after anthesis; flowers 3–6 cm *A. deserti* var. *simplex*
2. Perianth tube not shallow, 6–20 mm high, frequently equaling or exceeding tepal lobes; filaments inserted near perianth tube base to ca. mid tube; tepal lobes erect to erect-ascending, unequal, persistent and often leathery during and after anthesis; flowers 3.5–8.6 cm 3
3. Tepal lobes, filaments, style usually golden yellow; apices of outer tepal lobes dark yellow to light brown, not conspicuously calloused; leaf marginal teeth 4–11 mm long, 1–4 cm apart; inflorescence with peduncles lateral to ascending; capsules oblong to obovoid *A. chrysantha*
3. 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; leaf marginal teeth generally less than 7 mm long, 0.2–2.5 cm apart; inflorescence with peduncles usually perpendicular to perpendicular-ascending to stalk or sigmoid/sinuuous-ascending; capsule, when present, linear-oblong or obovoid 4
4. Rosettes 50–70 cm high, leaves stiffly ascending, gray to gray-green, conspicuously cross-zoned and with conspicuous white bud-imprinting, the margins undulate; inflorescence sinuous, narrow, the peduncles sigmoid/sinuuous-ascending in upper 1/3–2/5 of stalk; capsules none *A. sanpedroensis*
4. Rosettes 50–100 cm high, leaves rigid or somewhat lax, dark green to green to pale green or reddish-tinged, usually not conspicuously cross-zoned and not with conspicuous white bud-imprinting, the margins straight or undulate; inflorescence stout or sinuous, narrow or thick, the peduncles perpendicular to stalk or sigmoid/sinuuous-ascending in upper 1/3–4/5 of stalk; capsules none or present 5
5. Leaves erect or erect-ascending, blade glaucous-gray to bluish, interstitial teeth (3)–6–12 on distal 2/3, apex often conspicuously incurved; filaments inserted at 1 level ca. mid perianth tube; central and south-central Arizona *A. delamateri*
5. Leaves ascending to spreading, blade variously colored, interstitial teeth (2)–3–7 on distal 2/3 of margins, apex not conspicuously incurved; filaments inserted at 2 levels or subequally on perianth tube; Arizona, New Mexico 6

6. 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 usually perpendicular to main axis; capsules present; leaf marginal teeth firmly attached, 0.5–2 cm apart; rosettes solitary, rarely suckering, capsules and seed present *A. palmeri*
6. 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; capsules absent; leaf marginal teeth easily detached, 1–2.5 cm apart; rosettes sparingly to freely suckering, capsules and seeds not observed. *A. phillipsiana*

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AUTHOR CONTRIBUTIONS

WCH, AMS, and WHD designed and performed the research; WCH and AMS analyzed data; and WCH, AMS, and WHD wrote the paper.

LITERATURE CITED

- Adams, K. R. 2014. Little barley grass (*Hordeum pusillum* Nutt.): A prehistoric New World domesticate lost to history. Pp. 139–179 in *New Lives for Ancient and Extinct Crops*, ed. P. E. Minnis. Tucson: University of Arizona Press.
- Andrews, J. P. and T. W. Bostwick. 1997. *Desert Farmers at the River's Edge: The Hohokam and Pueblo Grande*. Phoenix: Pueblo Grande Museum and Cultural Park.
- Bohrer, V. 1987. The plant remains from La Cuidad, a Hohokam site in Phoenix. Pp. 67–238 in *Specialized Studies in the Economy, Environment, and Culture of La Cuidad: Environmental Data*. Arizona State University Anthropology Field Papers 20, part III, eds. J. Kisselburg, G. Rice, and B. Shears. Tempe: Office of Cultural Resource Management, Arizona State University.
- Bohrer, V. L. 1991. Recently recognized cultivated and encouraged plants among the Hohokam. *The Kiva* 56: 227–235.
- Bruman, H. J. 2000. *Alcohol in Ancient Mexico*. Salt Lake City: University of Utah Press.
- Callen, E. 1965. Food habits of some pre-Columbian Mexican Indians. *Economic Botany* 19: 335–343.
- Castetter, E., W. Bell, and A. Grove. 1938. *The Early Distribution and Utilization of Agave in the American Southwest*. University of New Mexico Bulletin No. 335. Albuquerque: University of New Mexico.
- Clark, J. J. and P. D. Lyons (eds.). 2012. *Migrants and Mounds: Classic Period Archaeology of the Lower San Pedro Valley*, Anthropological Papers No. 45, Tucson: Center for Desert Archaeology.
- Clark, J. J., M. W. Diehl, J. A. Waters, J. B. Hill, and J. L. Adams. 2012a. Plant and animals utilization. Pp. 309–344 in *Migrants and Mounds: Classic Period Archaeology of the Lower San Pedro Valley*, Anthropological Papers No. 45, eds. J. J. Clark and P. D. Lyons. Tucson: Center for Desert Archaeology.
- Clark, J. J., J. B. Hill, P. D. Lyons, and S. N. Lengyel. 2012b. Of migrants and mounds. Pp. 345–405 in *Migrants and Mounds: Classic Period Archaeology of the Lower San Pedro Valley*, Anthropological Papers No. 45, eds. J. J. Clark and P. D. Lyons. Tucson: Center for Desert Archaeology.
- Doelle, W. H., H. D. Wallace, and J. J. Clark. 2012. Lower San Pedro survey results and research design for test excavations. Pp. 29–65 in *Migrants and Mounds: Classic Period Archaeology of the Lower San Pedro Valley*, Anthropological Papers No. 45, eds. J. J. Clark and P. D. Lyons. Tucson: Center for Desert Archaeology.
- Doolittle, W. E. and J. A. Neely (eds.). 2004. *The Safford Valley grids: Prehistoric Cultivation in the Southern Arizona Desert*. Tucson: University of Arizona Anthropological Paper no. 70.
- Fish, S. K. 2004. Corn, crops and cultivation in the North American Southwest. Pp. 115–166 in *People and Plants in Ancient Western North America*, ed. Paul Minnis. Washington, D. C.: Smithsonian Books.
- Fish, S. K. and P. R. Fish. 2014. Agave (*Agave* spp.): A crop lost and found in the US-Mexico Borderlands. Pp. 102–138 in *New Lives for Ancient and Extinct Crops*, ed. P. E. Minnis. Tucson: University of Arizona Press.
- Fish, S. K., P. R. Fish, C. Miksicek, and J. Madsen. 1985. Prehistoric agave cultivation in southern Arizona. *Desert Plants* 7: 107–112, 100.
- Fritz, G. J., K. R. Adams, G. E. Rice, and J. L. Czarzasty. 2009. Evidence for domesticated amaranths from a sedentary period Hohokam house floor at Las Canopas. *The Journal of Southwestern Anthropology and History* 74: 393–419.
- Gasser, R. E. and S. M. Kwiatkowski. 1991a. Food for thought: Recognizing patterns in Hohokam subsistence, Pp. 417–459 in *Exploring the Hohokam: Prehistoric Desert Peoples of the American Southwest*, ed. G. J. Gumerman. Albuquerque: University of New Mexico Press.
- Gasser, R. E. and S. M. Kwiatkowski. 1991b. Regional signatures of Hohokam plant use. *The Kiva* 56: 207–226.
- Gentry, H. S. 1982. *Agaves of Continental North America*. Tucson: University of Arizona Press.
- Hill, J. B., J. J. Clark, W. H. Doelle, and P. D. Lyons. 2004. Prehistoric demography in the Southwest: Migration, coalescence, and Hohokam population decline. *American Antiquity* 69: 689–716.
- Hodgson, W. C. 2001a. *Food Plants of the Sonoran Desert*. Tucson: University of Arizona Press.
- Hodgson, W. C. 2001b. Taxonomic novelties in American *Agave* (Agavaceae). *Novon* 11: 410–416.
- Hodgson, W. C. and L. Slauson. 1995. *Agave delamateri* (Agavaceae) and its role in the subsistence patterns of pre-Columbian cultures in Arizona. *Haseltonia* 3: 130–140.
- Hodgson, W. C. and A. M. Salywon. 2013. Two new *Agave* species (Agavaceae) from central Arizona and their putative domesticated origins. *Brittonia* 65: 5–15.
- IUCN Standards and Petitions Subcommittee. 2017. Guidelines for using the IUCN red list categories and criteria. Version 13. <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>.
- Mabry, J. B. 2005. Changing knowledge and ideas about the first farmers in southeastern Arizona. Pp. 41–83 in *The Late Archaic Across the Borderlands: From Foraging to Farming*, ed. B. J. Vierra. Austin: University of Texas Press.
- Miksicek, C. 1984. Historic desertification, prehistoric vegetation change, and Hohokam subsistence in the Salt-Gila Basin. Pp. 53–80 in *Hohokam Archaeology Along the Salt-Gila Aqueduct, Central Arizona Project*, eds. L. S. Teague and P. L. Crown. Tucson: Arizona State Museum Archaeological Series 150.
- Parker, K., J. Hamrick, W. C. Hodgson, D. Trapnell, A. Parker, and R. Kuzoff. 2007. Genetic consequences of pre-Columbian cultivation for *Agave murpheyi* and *A. delamateri* (Agavaceae). *American Journal of Botany* 94: 1479–1490.
- Rogers, G. K. 2000. A taxonomic revision of the genus *Agave* (Agavaceae) in the Lesser Antilles, with an ethnobotanical hypothesis. *Brittonia* 52: 218–233.
- Speller, F. C., B. M. Kemp, S. D. Wyatt, C. Monroe, W. D. Lipe, U. M. Arndt, and D. Y. Yang. 2010. Ancient mitochondrial DNA analysis reveals complexity of indigenous North American turkey domestication. *Proceedings of the National Academy of Sciences USA* 107: 2807–2812.
- Teague, L. S. 1998. *Textiles in Southwestern Prehistory*. Albuquerque: University of New Mexico Press.