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A preliminary evaluation of the ancestry of a putative *Sabal* hybrid (Arecaceae: Coryphoideae), and the description of a new nothospecies, *Sabal* × *brazoriensis*

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ABSTRACT

In a coastal plain forest in eastern Texas, USA, occurs a population of a putative *Sabal* hybrid, one of few native, putative palm hybrids in the continental USA. Robust plants with large trunks, they are morphologically dissimilar to the much smaller and acaulescent plants of *S. minor*, with which they co-occur. The only other large *Sabal* species in the USA are *S. mexicana* and *S. palmetto*, with *S. mexicana* native only to Texas. Using Amplified Fragment Length Polymorphisms (AFLPs), we sampled several plants of the putative hybrid and its possible parents in order to evaluate its possible hybrid origin. UPGMA, principal coordinate analysis, and Bayesian analyses indicated that it seems to be a hybrid, but an old one, with clear genetic distinctiveness. However, these results also suggest a closer affinity of the putative hybrid with *S. minor* and *S. palmetto* than with *S. mexicana*, excluding the latter species from possible parentage. Results also suggest that *S. minor*, despite its wide morphological diversity, is a clearly coherent species with minimal evidence of introgression, except for Mexican material that appears to be introgressed with *S. mexicana*. *Sabal palmetto* may also possess a complicated genetic history not necessarily reflected in its morphology.

RESUMEN

En un bosque de la planicie oriental de Texas, EEUU, se encuentra una aparente población híbrida de *Sabal*, una de pocas palmas nativas aparentemente híbridas en los EEUU continental. Plantas robustas con grandes troncos, son morfológicamente disimilares a las mucho más pequeñas y acaulescentes plantas de *S. minor*, con las que coocurren. Las únicas otras especies grandes de Sabal en los EEUU son *S. mexicana* y *S. palmetto*, de las cuales solo *S. mexicana* es nativa a Texas. Utilizando polimorfismos de longitud de fragmentos amplificados (AFLPs), muestreamos varias plantas del híbrido aparente y de sus posibles padres para evaluar su posible origen híbrido. UPGMA, análisis de coordenadas principales y análisis Bayesianos indicaron que parece ser un híbrido, pero uno viejo, con clara distinción genética. Sin embargo, estos resultados también sugieren una más cercana afinidad del híbrido aparente con *S. minor* y *S. palmetto* que con *S. mexicana*, excluyendo a esta última especie de posible parentage. Los resultados también sugieren que *S. minor*, a pesar de su diversidad morfológica, es claramente una especie coherente con mínima evidencia de introgresión, excepto de material Mexicano que aparenta tener introgresión de *S. mexicana*. *Sabal palmetto* puede también poseer una historia genética complicada no necesariamente reflejada en su morfología.

Key words: AFLP, circumscription, hybridization, taxonomy, *Sabal mexicana*, *Sabal minor*, *Sabal palmetto*, Texas flora

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INTRODUCTION

The genus *Sabal* Adanson (1763: 495, 599), as currently recognized, contains 16 species (Zona 2000), although as many as 26 species have been recognized at one time (Bailey 1944). The genus is distributed from the southeastern USA southward through Central America and the Caribbean to northwestern South America. Five species are native to the continental United States (Zona 2000): *S. etonia* Swingle ex Nash (1896: 99), a dwarf species with a generally subterranean stem, native to xeric sand in peninsular Florida; *S. mexicana* Martius (1839: 246), a large, trunked species of subtropical to tropical woodland and savanna, distributed from southern Texas south to El Salvador; *S. miamiensis* Zona (1985: 366), a species native to southeastern Florida, but presumed extinct, that is very similar to and perhaps not distinct from *S. etonia* (Zona 2000), and has more recently been considered a nothospecies: *S.* × *miamiensis* (*Sabal etonia* × *S. palmetto*; Wunderlin 1998); *S. minor* (Jacquin 1776: 8) Persoon (1805: 399), also generally with a subterranean stem and often preferring wetlands, with perhaps the broadest geographic distribution in the genus, native from northeastern North Carolina south to Florida and west to central Texas, with a disjunct population in northeastern Mexico (Goldman 1999); and *S. palmetto* (Walter 1788: 119) Loddiges ex Schultes & Schultes (1830: 1487), a generally large, trunked species of mesic to wet woodland and grassland, native from southern North Carolina to western Florida, south to Cuba, the Bahamas, and the Turks and Caicos Islands. Both *S. minor* and *S. palmetto* show more morphological variation than perhaps any other species in the genus, and with several species of *Sabal* occurring sympatrically, hybridization among species would seem possible. See Zona (1990) for a summary of the genus.

In a floodplain forest in southwestern Brazoria County, Texas, USA, part of the extensive and biologically rich Columbia Bottomlands region (Rosen *et al.* 2008) in the southeastern part of the state, there is an unusual *Sabal* population unlike any congeners native to the United States. Mature plants in this population have trunks, with some plants up to nearly nine meters tall (including crowns), and the leaves have large blades that vary from relatively flat to strongly costapalmate, the latter unlike *S. minor*. Plants in this population have been the source of debate and generally have been included in *S. minor* (Correll & Johnson 1970, Diggs *et al.* 2006). Trunk-bearing specimens of *S. minor* occur occasionally in the western portion of the range of the species, particularly in Louisiana and Texas, where they have been assigned several names, including *S. deeringiana* Small (1929a: 34, 1929b, 1933) and *S. louisiana* (Darby) Bomhard (1935: 44). However, such arborescent individuals are usually just considered robust material of *S. minor* (Bailey 1944, Correll & Correll 1972, Correll & Johnston 1970, Diggs *et al.* 2006, Zona 1990, 2000). Vines (1977) placed the Brazoria population in *S. louisiana*. Yet the leaf blades of the Brazoria population are usually larger, with a longer hastula and costa than those of typical *S. minor*, and it has been suggested that this unusually variable palm population is morphologically intermediate between *S. mexicana* and *S. minor*, therefore that it is probably a hybrid between these two species (Simpson 1988, Lockett 1991, Lockett & Read 1991).

Sabal minor grows in abundance at this Brazoria County site, whereas the nearest native population of *S. mexicana* is approximately 100 km to the west-southwest, and the nearest native populations of *Sabal palmetto* are at least 1000 km to the east. As of the early 1990s the tallest palm in the putative hybrid population was estimated to be over 150 years old (Lockett & Read 1991), and the wide morphological variability of this population might suggest that it is a hybrid swarm that is several generations old, perhaps even predating European settlement of the region.

Hybridization in Arecaceae has been reported several times in nature. Natural intergeneric hybrids have been reported between *Attalea* Kunth and *Orbignya* Mart. ex Endl. (Balick *et al.* 1987; *Orbignya* is now included in *Attalea* [Zona 2002]), and *Coccothrinax* Sarg. and *Thrinax* L.f. ex Sw. (Nauman 1990). Interspecific hybridization is more common, noted in *Attalea* (summarized in Balick 1988, Henderson *et al.* 1995), *Calyptrogyne* H.Wendl. (Henderson 2005), *Caryota* L. (Hahn & Sytsma 1999), *Copernicia* Mart. (summarized in Balick 1988, Henderson *et al.* 1995), *Desmoncus* Mart. (Henderson *et al.* 1995), *Hyospathe* Mart. (Henderson 2004), *Phoenix* L. (González-Peréz *et al.* 2004), and *Syagrus* Mart. (summarized in Balick

1988, Henderson *et al.* 1995). In *Sabal*, the only putative hybrids other than the Brazoria plants are *S.* × *miamiensis* and the *S. louisiana* phase of *S. minor* (as a hybrid between *S. minor* and *S. palmetto*; Simpson 1988).

We have undertaken a preliminary study of these putative hybrid palms from Brazoria County, Texas, using Amplified Fragment Length Polymorphisms (AFLPs) to examine if this population is the product of hybridization, and if so what the possible parental origin could be, sampling the other three *Sabal* species that naturally occur closest to this locality (*S. mexicana*, *S. minor*, and *S. palmetto*; all three being diploid, $2n = 36$ [Zona 2000]). AFLPs are a proven tool for examining genetic structure, taxonomic circumscription, and relationships among species and individuals. They also have been used to examine the origins and relationships of hybrids, e.g. in Asteraceae (*Scalesia*: Lindhardt *et al.* 2009); Burseraceae (*Bursera*: Weeks & Tye 2009); Cyperaceae (*Schoenoplectus*/*Scirpus*: Fay *et al.* 2003, Yang *et al.* 2009); Euphorbiaceae (*Manihot* & *Ricinus*: Gedil *et al.* 2009); Orchidaceae (*Calopogon*: Goldman *et al.* 2004; *Dactylorhiza*: Hedrén *et al.* 2001; *Orchis*: Bateman *et al.* 2008; *Ophrys*: Stökl *et al.* 2009); Orobanchaceae (*Castilleja*: Hersch-Green & Cronn 2009); Rosaceae (*Sorbus*: Fay *et al.* 2002); Solanaceae (*Solanum*: Erazzú *et al.* 2009); oomycetes (*Phytophthora*: Hurtado-Gonzalez *et al.* 2009); and birds (*Empidonax* [Tyrannidae]: Rush *et al.* 2009). AFLPs have also been used to examine the genetic structure, variation, relationships, or circumscription of palm species, e.g. in *Chamaedorea* (Bacon & Bailey 2006), *Elaeis* (Billotte *et al.* 2005), *Iriartea* (Sezen *et al.* 2007), and *Metroxylon* (Kjær *et al.* 2004).

MATERIALS AND METHODS

Samples from twenty-nine individuals of *Sabal* were used in this study, collected with voucher herbarium specimens between 1993 and 1998 (Table 1): four of *S. mexicana*, 13 of *S. minor*, five of *S. palmetto*, and seven of the putative Brazoria County hybrid (hereafter referred to as the "Brazoria material"). Nearly all samples were taken from plants growing in their natural habitats within their native geographic ranges. Only the plants sampled from Travis County, Texas, were cultivated. All samples of the Brazoria material were collected in what is now the "Palm Unit" of the San Bernard National Wildlife Refuge. Samples of *S. minor* were collected throughout much of the geographic range of the species, and all plants sampled were the typical form of the species (acaulescent). One *S. minor* sample (#10) was from the same site as the Brazoria material, and another was from Jackson County, Texas (#12), at the same locality of the nearest known native *S. mexicana* population to Brazoria County. Samples of *S. mexicana* and *S. palmetto* were collected from cultivated plants, and from natural populations at or near the geographic margins of these species closest to the Brazoria Co. site (Jackson Co., Texas, and Franklin Co., Florida, respectively; Table 1).

The DNA extractions used the cetyltrimethylammonium bromide (CTAB) method of Doyle & Doyle (1987), purificatied with CsCl/ethidium bromide gradients (1.55 g CsCl/mL; Palmer 1986). The AFLP samples were purified with QIAquick polymerase chain reaction (PCR) purification columns (Qiagen, Crawley, West Sussex, UK). DNA was obtained only from live material.

AFLPs were obtained following the automated ABI AFLP Plant Mapping Protocol (Applied Biosystems Inc. [ABI], Warrington, UK). Template DNA fragments were generated by digesting 0.5 µg genomic DNA, following the protocol of Vos *et al.* (1995). The two combinations of selective bases used in this study were EcoRI-ACC × MseI-CTC ("Tamra 14" [Y14], yellow-labeled) and EcoRI-ACT × MseI-CTT ("Fam 16" [B16], blue-labeled). The fragments were separated using an ABI 377 Genetic Analyzer. Gel analysis was performed using Genescan 2.0.2 and Genotyper 1.1 (ABI). Only amplified fragments with sizes ranging from 50 to 500 bases were scored because bands beyond this size range could not be accurately sized. Fragments were scored as present or absent. Two sets of samples were run, each at different times, with one sample in common between them (sample 8; Table 1). Characters differing in the common sample between the two runs then were excluded from all samples. The resulting data matrix is available from the corresponding author and is also deposited in the Botany Libraries at the Harvard University Herbaria.

TABLE 1: Samples used in this study, numbers at left corresponding to those in the figures. Vouchers for all samples were collected by the first author and are deposited at BH, except for sample 11, which is deposited at MEXU with photographic duplicates at BH and TEX (herbarium acronyms follow Holmgren et al., 1990). An asterisk after a sample number indicates a cultivated plant.

SAMPLE NUMBER	SPECIES	COLLECTION NUMBER	COUNTRY	STATE	COUNTY/ MUNICIPALITY
1	*minor*	464	USA	Texas	Kendall
2	*minor*	465	USA	Texas	Kendall
3	*minor*	466	USA	Texas	Kendall
4	*minor*	467	USA	Texas	Kendall
5	*minor*	468	USA	Texas	Kendall
6	*minor*	469	USA	Texas	Kendall
7	*minor*	509	USA	Florida	Calhoun
8	*minor*	512	USA	Texas	Hardin
9	*minor*	549	USA	Georgia	Camden
10	*minor*	565	USA	Texas	Brazoria
11	*minor*	900	Mexico	Nuevo León	Iturbide or Linares
12	*minor*	1275	USA	Texas	Jackson
13	*minor*	1328	USA	North Carolina	Pender
14	"hybrid"	558	USA	Texas	Brazoria
15	"hybrid"	559	USA	Texas	Brazoria
16	"hybrid"	560	USA	Texas	Brazoria
17	"hybrid"	561	USA	Texas	Brazoria
18	"hybrid"	562	USA	Texas	Brazoria
19	"hybrid"	563	USA	Texas	Brazoria
20	"hybrid"	564	USA	Texas	Brazoria
21	*mexicana*	546	USA	Texas	Jackson
22*	*mexicana*	1238	USA	Texas	Travis
23	*mexicana*	1273	USA	Texas	Jackson
24	*mexicana*	1274	USA	Texas	Jackson
25	*palmetto*	551	USA	Florida	Franklin
26	*palmetto*	1331	USA	South Carolina	Charleston
27	*palmetto*	1333	USA	Florida	Franklin
28*	*palmetto*	1239	USA	Texas	Travis
29*	*palmetto*	1240	USA	Texas	Travis

A UPGMA phenogram of *Sabal* samples was constructed using the program TFPGA 1.3 (Miller 1997). Binary data were input as diploid, dominant values and Nei's (1972) original genetic distance was calculated for each sample. A phenogram was then constructed from the distance matrix, with 10,000 bootstrap replicates used to generate support values for each node.

To assess the relative clustering of *Sabal* samples in ordination space, principal coordinate analysis (PCoA) was performed using NTSYS-PC 2.1 (Rohlf 1997). Binary, dominant AFLP data were input and converted to a Jaccard (1908) coefficient similarity matrix for two-state data. The DCENTER and EIGEN data conversion procedures were then utilized to generate eigenvectors. The vectors associated with the three most informative eigenvalues, which accounted for the greatest amount of variation, were then plotted in three-dimensional principal coordinate space. Significance of axes was determined by comparing the variance represented by each axis against random expectation by using a broken stick distribution (Frontier 1976, Jackson 1993).

Levels of genetic differentiation among species were assessed using Weir & Cockerham's (1984) θ (theta), calculated in the program TFPGA 1.3, with 1000 bootstrap replicates across loci (bands) used to detect significant deviations from 0. The value θ is analogous to Wright's (1951) F_{ST} but accounts for small and unequal sample sizes, as well as for the size and number of populations. Although θ is classically used to assess intraspecific population genetic differentiation, it can be used in studies of interspecific hybridization to assess differentiation between a putative hybrid population and possible parental species (Field *et al.* 2009). These analyses initially included all samples, but later excluded the *S. minor* specimen from Mexico (#11; see Table 1) because some of our other analyses indicated its unusual placement or characteristics relative to other samples of *S. minor*.

We used a method of Bayesian clustering for further examination of the parentage of the Brazoria material, the Markov Chain Monte Carlo (MCMC) algorithm applied in STRUCTURE version 2.3.2 (Falush *et al.* 2007). This provides a measure of the proportional membership that an individual has within any of the groups examined, whether an individual can be assigned to a single group or (as with a hybrid) to more than one group (Field *et al.* 2009). STRUCTURE is a valuable tool for assessing hybrid origins (e.g. Field *et al.* 2009, Lexer *et al.* 2010, Weeks & Tye 2009, Yang *et al.* 2009). All MCMC analyses used the admixture model, with 1,000,000 initial burn-in iterations followed by 1,000,000 MCMC iterations, with independent allele frequencies assumed. Population assignments (e.g. species and putative hybrid identities) were not used as supplementary data in the analyses, but rather we relied on the AFLP data alone to determine how the tested number of genotypic groups would be allocated across all samples. To examine how AFLP genotypes were distributed across the plants and species we sampled, analyses limited the number of possible groups to two ($K = 2$; the Brazoria material presumed to belong with two of the three possible putative parental species), three ($K = 3$; the putative Brazoria material presumed to belong with at least one of the three possible putative parental species), four ($K = 4$; the putative Brazoria material presumed to be its own entity, distinct from the other three species), and 14 ($K = 14$; the number of *Sabal* populations sampled for this study, to see how distinct the various populations are from one another, thus further assessing the distinctiveness of the Brazoria material). We used as a threshold for hybrid identity, or at least of introgression, a q-value (the inherited proportion of an individual's genome from another species) of 0.10. Vähä and Primmer (2006) determined that detecting hybrids using STRUCTURE was most efficient (= the proportion of individuals in a group that were correctly identified from the analysis) and accurate (= the proportion of an identified group that is actually part of that group) when a minimum of 48 loci were used, with increasing F_{ST} (sensu Weir & Cockerham 1984) between parental populations, ideally ≥ 0.21. However, with fewer loci and lower F_{ST} values efficiency was optimal at $q = 0.10$ and accuracy at $q = 0.20$.

RESULTS

AFLPs provided 177 bands or characters, 127 (71.8%) of which were variable, with 107 (60.5%) of these present in two or more samples. Overall, the Brazoria material shows some evidence of a hybrid origin, with greater similarity to *Sabal minor* and *S. palmetto* than to *S. mexicana*, but it also shows coherence as an independent group, distinctive from the other species sampled. Nine bands were unique to the Brazoria material, 11 to *S. mexicana*, nine to *S. minor*, and 14 to *S. palmetto*. However, almost none of these species-specific bands were fixed, except for three in *S. mexicana*. The Brazoria material had 114 bands, of which 14 were shared with only one other species: none shared only with *S. mexicana*, four shared only with *S. minor*, and ten shared only with *S. palmetto*. Only one of these 114 bands was fixed in both the Brazoria material and a compared species (*S. palmetto*). Eighteen bands were shared by the Brazoria material with only two of the three other species: none with both *S. mexicana* and *S. minor*, five with both *S. mexicana* and *S. palmetto*, and 13 with both *S. minor* and *S. palmetto*. Only three of these 18 bands were fixed-present for the Brazoria material and the compared two species (*S. minor* and *S. palmetto*).

UPGMA:—The UPGMA analysis shows the Brazoria material as a coherent cluster (Figure 1), although with low bootstrap support (bootstrap percentage, BP, < 50). It occurs with the *S. minor* cluster (BP < 50), with all but one of the *S. minor* samples forming a strongly supported cluster (BP 92) adjacent to the Brazoria cluster, and with only the Mexican sample of *S. minor* (#11, see table 1) outside of the Brazoria cluster. Most Texas samples of *S. minor* form a weakly supported cluster (BP 63), which includes the Brazoria County sample of this species (#10). *Sabal palmetto* samples occur to the outside of the *S. minor*-Brazoria material cluster, but this species does not are contained within a coherent cluster itself. *Sabal mexicana* is the outlier in the tree, forming a strongly supported cluster (BP 90).

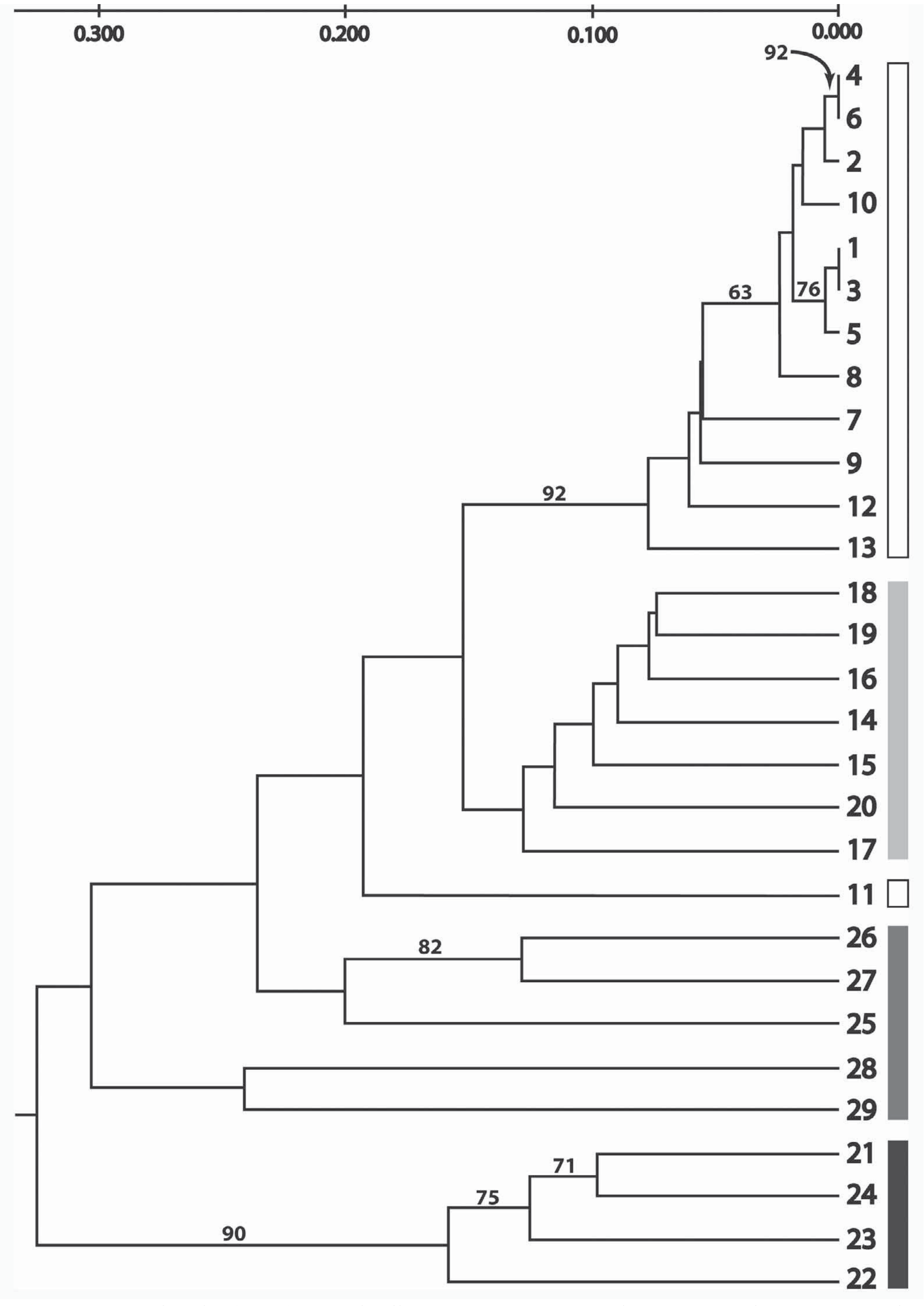

FIGURE 1: UPGMA tree of Nei's (1972) genetic distances. Bootstrap values greater than 50% are shown. Sample numbers correspond to those in Table 1. Bars indicate different taxonomic groups: white = *Sabal minor*, light gray = Brazoria material, dark gray = *S. palmetto*, and black = *S. mexicana*.

PCoA:—The first principal coordinate axis represented approximately 26.1% of the variation, the 2nd approximately 16.2%, and the third 7.3% (total variation = 49.6%). According to the broken stick null model only the first two axes were statistically significant (values not shown). The three species and Brazoria material each form discrete groups (Figure 2), without any samples of these four groups occurring within a cluster formed by another group. Axis one shows *Sabal mexicana* to be most similar to *S. palmetto*, and *S. minor* most similar to the Brazoria material. Axis two shows the Brazoria material to be most similar to *Sabal palmetto*, and *S. mexicana* most similar to *S. minor*. In axis three, the least significant axis, the Brazoria material is most similar to *S. mexicana*, both of them are less similar to *S. minor* and much less similar to *S. palmetto*, whereas *S. minor* and *S. palmetto* appear most similar to each other.

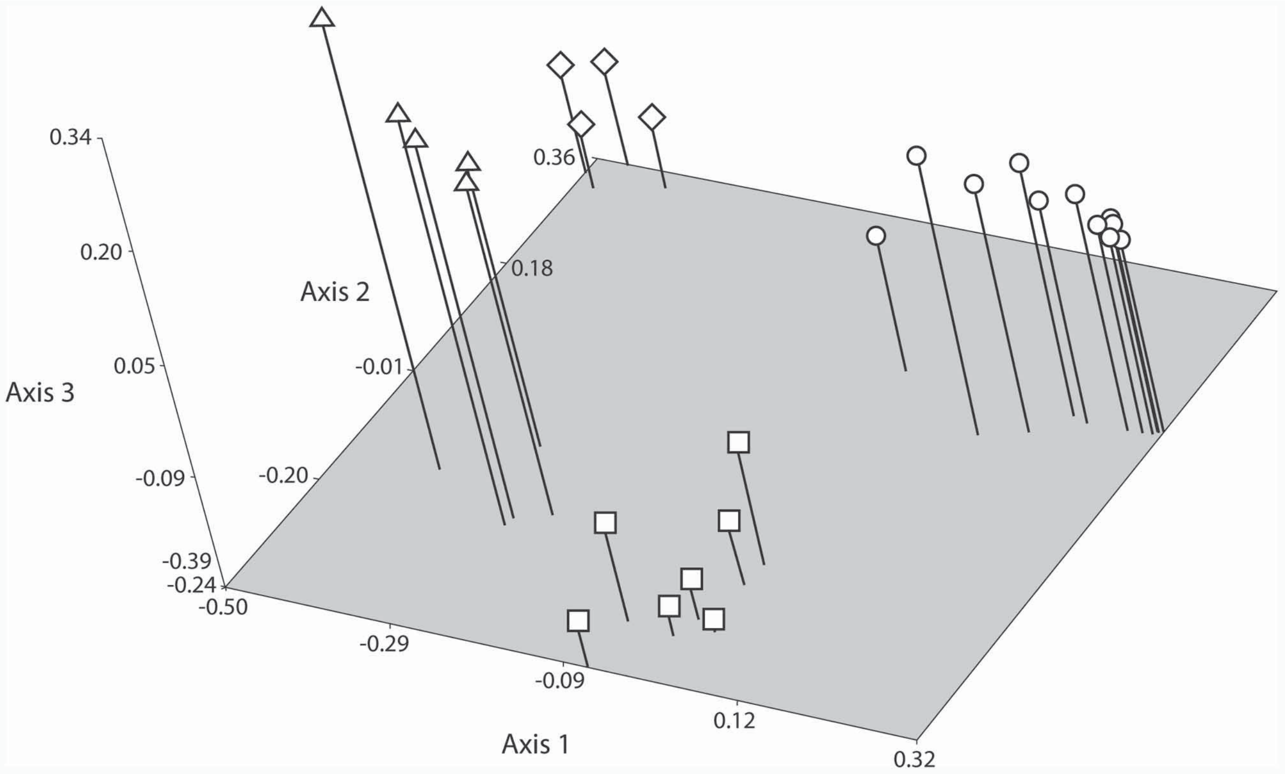

FIGURE 2: Principal coordinate plot of the first three axes. The samples of the Brazoria material are represented by squares, *S. mexicana* by diamonds, *S. minor* by circles, and *S. palmetto* by triangles.

Genetic differentiation:—Between each of the *Sabal* species, and between the species and the Brazoria material, genetic differentiation was strong (Table 2; significance $P < 0.01$). Average values of θ, with all samples included, ranged from 0.4700 (between the Brazoria material and *S. palmetto*) to 0.7274 (between the Brazoria material and *S. mexicana*), indicating the least and greatest differentiation, respectively. When the Mexican *S. minor* sample (#11) was excluded, the values of θ in comparisons of other groups with *S. minor* increased slightly, the highest with *S. mexicana* (0.7467). The level of differentiation of the Brazoria material from *S. minor* was intermediate to those of the other two species, with $\theta = 0.5919$ when sample 11 was included and 0.5257 when it was not.

TABLE 2: Comparisons of genetic differentiation between the three *Sabal* species and the Brazoria material, according to average θ values. Comparisons where the Mexican sample of *S. minor* (#11, see Table 1) is included are above the diagonal, whereas those below are with sample 11 excluded from the analysis. All values were significant at $P < 0.01$. CI = confidence interval.

	Sabal minor	**Brazoria material**	***Sabal mexicana***	***Sabal palmetto***
Sabal minor	–	0.5275 (CI 95% 0.4313–0.6138)	0.6853 (CI 95% 0.6055–0.7564)	0.5725 (CI 95% 0.5086–0.6381)
Brazoria material	0.5919 (CI 95% 0.4944–0.6813)	–	0.7274 (CI 95% 0.6653–0.7794)	0.4700 (CI 95% 0.3943–0.5374)
Sabal mexicana	0.7467 (CI 95% 0.6710–0.8097)	0.7274 (CI 95% 0.6653–0.7794)	–	0.5012 (CI 95% 0.4191–0.5802)
Sabal palmetto	0.6241 (CI 95% 0.5568–0.6792)	0.4700 (CI 95% 0.3943–0.5374)	0.5012 (CI 95% 0.4191–0.5802)	–

AFLP genotypes:—STRUCTURE analyses of proportional membership of individual samples within their assigned groups showed both the distinctiveness of the Brazoria material and a greater similarity of this group to *S. minor* and *S. palmetto* than to *S. mexicana*. The last is especially clear when two groups were assumed (Figure 3A). STRUCTURE indicated that the Brazoria material was in the same genotypic group (in white) as *S. minor* (samples 1–13). All samples of the Brazoria material (samples 14–20) and *S. minor* showed little influence from the other genotypic group, in gray, which was present at $q \leq 0.005$ (average 0.002). The exception to this was the *S. minor* sample from Mexico, #11, which had a q-value of 0.285 for the gray group, suggesting hybridization. *Sabal mexicana* (samples 21–24) was nearly defined by the other genotypic group (in gray) and the small representation of the white genotypic group within this species was ≤ 0.012 (average 0.005). However, all individuals of *S. palmetto* (samples 25–29) were an admixture of the two genotypic groups, suggestive of hybrids, with the alternate genotypic group with q-values of 0.156–0.559 (average 0.399).

When three groups were assumed (Figure 3B; white, light gray, and dark gray), the Brazoria material likewise shows more in common with *S. minor* and *S. palmetto* than *S. mexicana*. Both the Brazoria material and *S. palmetto* were dominated by one genotypic group (light gray). However, Brazoria plants exhibited a mixture with the genotypic group that dominated *S. minor* (white), with q-values of 0.003–0.403 (average 0.159). *Sabal minor*, with the exception of the Mexican sample, had very little representation of the other two genotypic groups (cumulative q-values of 0.001–0.019, average 0.004). The Mexican sample had a cumulative q-value of 0.292 from the other two genotypic groups, suggesting hybridization. *Sabal mexicana* was defined by the third genotypic group (dark gray), with cumulative q-values of the other two groups of 0.002–0.006 (average 0.003). This third genotypic group is also represented to a small to moderate extent in *S. palmetto* (q-values 0.007–0.360, average 0.155). The two individuals of *S. palmetto* showing the greatest genotypic admixture were sample 25, a wild-collected plant from Franklin Co., Florida, and sample 29, a cultivated plant in Austin, Texas.

When four groups were assumed (Figure 3C), the Brazoria material appears nearly distinct, but still with greater affinity to *S. minor* and *S. palmetto* than *S. mexicana*. The Brazoria material has strong membership in a single genotypic group (light gray), which otherwise is associated minimally with *S. palmetto*. Most Brazoria material individuals have a cumulative q-value for the other three genotypic groups of 0.002–0.029 (average 0.009), the exception being sample 20, with a cumulative q-value of 0.309, with moderate membership ($q = 0.307$) in the genotype that dominates *S. minor*. *Sabal minor* is nearly defined by a single genotypic group (in white) that is present to a small degree in the Brazoria material and *S. palmetto*. The cumulative q-value for the other three genotypic groups in each of the *S. minor* samples is 0.001–0.010 (average 0.003), with the exception of the Mexican sample, which has a cumulative q-value of 0.304, with a moderate membership ($q = 0.296$) in the genotypic group that includes *S. mexicana*. *Sabal mexicana* shows the least genetic admixture of all palm groups studied here, being defined by a single genotype (medium gray). The cumulative q-value for the other three genotypic groups in each of the *S. mexicana* samples is 0.002–0.005 (average 0.003). *Sabal palmetto* is dominated by another genotypic group (dark gray), with a cumulative q-value for the other three genotypic groups in each of the *S. palmetto* samples of 0.004–0.278 (average 0.107); a wild-collected sample from Franklin Co., Florida (#27), with the strongest indication of hybridization. Overall, *S. palmetto* shows a more substantial expression of the four genotypic groups than any other species.

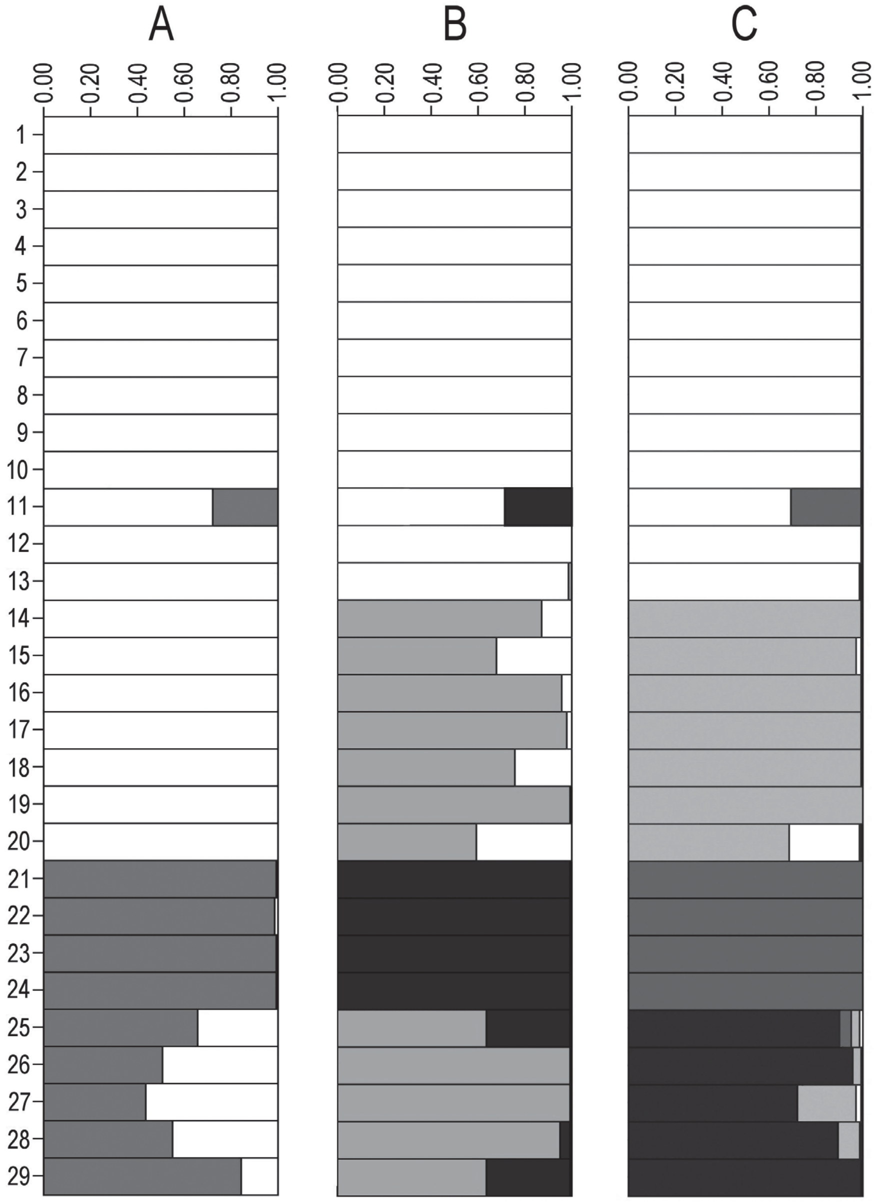

FIGURE 3: Ancestry estimates for the 29 *Sabal* samples, provided by STRUCTURE, for 2–4 genotypic groups. Numbers at top are the proportional membership of an individual in a given genotypic group, whereas the numbers at left are the sampled individuals used in the study (Brazoria material = 14–20, *S. mexicana* = 21–24, *S. minor* = 1–13, *S. palmetto* = 25–29; table 1). A. Two genotypic groups (represented by white and gray). B. Three genotypic groups (white, light gray, and dark gray). C. Four genotypic groups (white, light gray, medium gray, dark gray).

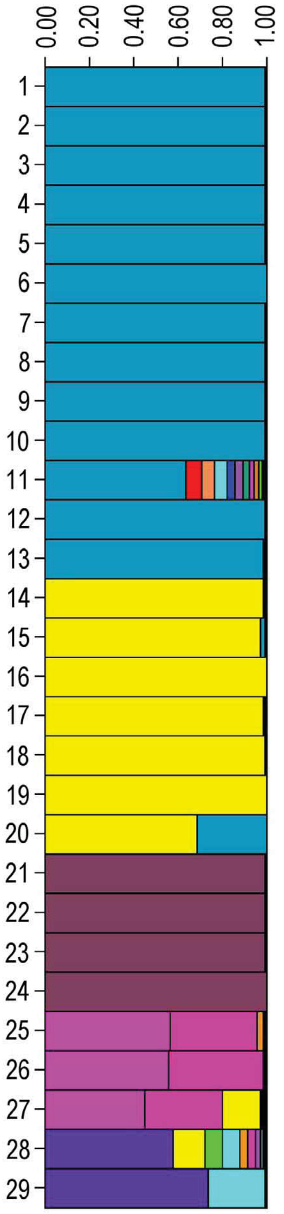

FIGURE 4: STRUCTURE ancestry estimates for the 29 *Sabal* samples, using 14 genotypic groups. Sample numbering and the proportional membership scale follow that of Figure 3.

When 14 groups are assumed, representing number of populations sampled, genotypic groups rarely corresponded to actual populations, and often were restricted to a portion of the genome of only one or a few individuals, whereas some genotypic groups nearly define whole species (Figure 4). The Brazoria material was again highly dominated by one genotypic group, *S. minor* by a second, and *S. mexicana* by a third. The Brazoria material contains a cumulatively small proportion of the other 13 genotypic groups (q = 0.005–0.028, average 0.012), with the exception of sample 20, with a cumulative q-value of 0.318, and 12 of those 13 groups, except the genotypic group dominating *S. minor*, are generally absent altogether from the Brazoria material. The genotypic group dominating *S. minor* is present in the Brazoria material to a small extent (but more than any of the other 12 genotypic groups), but is most noticeable in samples 15 (q = 0.022), and 20 (q = 0.313). In *S. minor*, the cumulative q-value for the 13 genotypic groups not dominating this species was 0.003–0.016 (average 0.005), with the exception of the Mexican sample which contains most of the other genotypic groups, with a cumulative q-value for these other groups of 0.361. *Sabal mexicana* shows minimal representation for any of the other genotypic groups, with a cumulative q-value for the other 13 genotypic groups of 0.005–0.009 (average 0.007). *Sabal palmetto*, however, does not seem to be dominated by any single genotypic group, shows representation of most of the 14 genotypic groups, and although the genotypic groups dominating *S. minor* and *S. mexicana* are poorly represented in *S. palmetto* (respectively q = 0.001–0.012, average 0.005; q = 0.001–0.002, average 0.001), the group dominating the Brazoria material is found in a greater proportion in samples 27 (q = 0.176) and 28 (q = 0.143).

DISCUSSION

The arborescent Brazoria *Sabal* population shows evidence of a hybrid origin, best illustrated by the group membership analysis in STRUCTURE. Analyses assuming three, four, and 14 groups show admixed individuals within the Brazoria group, most evident when three genotypic groups were assumed. Sample 20 consistently produced a hybrid signature among these three analyses. This individual was the most morphologically intermediate of any of the Brazoria material sampled, with deeply costapalmate leaves similar to those of *S. palmetto*. Furthermore, in the UPGMA tree the Brazoria material occurs in an intermediate position between the majority of *Sabal minor* and the *Sabal* species with trunks.

If of hybrid origin, the parentage of the Brazoria material apparently lies with *S. minor* and *S. palmetto*, not *S. mexicana*. The number of bands the Brazoria material shares with only one or two other species suggests the most distant relationship is with *S. mexicana*. In the UPGMA tree the Brazoria material occurs between *S. palmetto* and the majority of *S. minor*, with *S. mexicana* the outlier. The PCoA indicates the Brazoria material is much more similar to *S. minor* and *S. palmetto* than to *S. mexicana*. Average values of generic differentiation (θ) show the greater distinctiveness of the Brazoria plants from *S. mexicana* than from *S. minor* and *S. palmetto*, with the last species the least genetically differentiated from the Brazoria material, and *S. minor* the next-most distinct. Finally, the STRUCTURE analyses indicate the Brazoria plants have substantial membership in the genotypic groups that dominate *S. minor* and *S. palmetto*, especially the former (in contrast to what is indicated by the results of the genetic differentiation analysis) but essentially no membership in the genotypic group that defines *S. mexicana*.

The Brazoria material, however, is surprisingly well-defined as a group, as if it were a distinct species. Possessing a similar number of unique bands to the other species, the Brazoria material forms its own cluster in the UPGMA tree (but BP < 50). Likewise it is a distinct, separate cluster in the PCoA, and genetic differentiation values (θ) are also very high between it and the other three species. Wright (1978; summarized in Hartl & Clark 2007) defined F_{ST} values in excess of 0.25 as "very great genetic differentiation". Finally, STRUCTURE analyses of four and 14 genotypic groups also suggest its distinctiveness. When STRUCTURE seeks four groups among all plants, the Brazoria material is almost completely dominated by a genotypic group nearly restricted to this group of plants, with a lesser genotypic partition associated with *S. minor*. When STRUCTURE seeks 14 genotypic partitions among all samples it did not assign several partitions, each in relatively large proportion, to the Brazoria plants, but rather only two, one nearly restricted to and greatly dominating the Brazoria material, and the other, when present, associated with *S. minor*. The Brazoria County sample of *S. minor* (#10), collected in the middle of the arborescent Brazoria population, is not part of the arborescent Brazoria material in any of the analyses. However, the widely varying phenotypes among individuals in this group give it the appearance of a hybrid swarm: some individuals look like little more than enlarged *S. minor* plants with a trunk, and others resembling *S. palmetto*. Balick (1988) suggested that abnormal levels of morphological variation in a palm population that co-occurs with congeners, where intermediate character states are observed, would indicate that hybridization has occurred. All of the evidence together suggests that if the Brazoria material is of hybrid origin, the initial hybridization event may have taken place thousands of years ago when the geographic distributions of parents were different and presumed reproductive barriers were relaxed. Since that time they seem to have reproduced primarily with each other, and segregation of morphological traits seems to be occurring now. There is no evidence of backcrosses to *S. minor*, exemplified by the lack of introgression of the *S. minor* individual (sample 10) that is sympatric with the Brazoria material. It is possible they represent a hybrid-derived species, but one with extreme morphological variability.

The Brazoria material likely is a part of a larger taxonomic issue involving the trunk-bearing members of *S. minor* found primarily in Louisiana and Texas. Aside from having stems, such arborescent individuals of *S. minor* generally look mostly like robust versions of acaulescent *S. minor*, with relatively little other morphological evidence of introgression with other species, unlike most of the Brazoria material. Bailey (1944) refused to recognize such arborescent individuals as a distinct taxon, despite his reputation for describing numerous species in other groups (e.g. *Carex*, *Rubus*), and yet he had described several other *Sabal* species, most no longer recognized (Zona 1990). However, Bomhard (1935) and Small (1929a, 1929b) advocated recognition of these arborescent individuals of *S. minor* as a distinct species. Allozyme analyses (Ramp 1989, Ramp & Thien 1995), however, showed that they were not a distinct taxon, and that they should be included in *S. minor*. Yet, these allozyme analyses also showed a greater genetic identity and smaller genetic distance between *S. palmetto* and arborescent *S. minor* than between *S. palmetto* and typical (acaulescent) *S. minor*. Natural populations of *S. palmetto* do not occur within the geographic range of arborescent *S. minor*, instead at least 300 km east of it. Populations of typical *S. minor* that were sampled in the allozyme study and used in comparisons of genetic distance and identity were from the southeastern part of the species range, where *S. palmetto* also occurs, whereas the arborescent individuals of *S. minor* in these comparisons were sampled from southeastern Louisiana. It is possible that all arborescent individuals of *S. minor* and the Brazoria material represent an extensive regional hybrid swarm between typical *S. minor* and *S. palmetto* (or related to the latter), in partial agreement with Simpson (1988). In the context of these allozyme analyses and our AFLP results, it raises the possibility that *S. palmetto* once occurred in the lower Mississippi Valley or adjacent west Gulf coastal plain but is now extirpated. Schott (1857: 44) referred to palms in the lower portion of the Rio Grande valley of southern Texas as attaining "a growth as gorgeous even as that on the Lower Mississippi", where he identified them as *Chamaerops palmetto* (Walt.) Michaux (1803: 206), a synonym of *S. palmetto* (although it is only the similarly arborescent *S. mexicana* that occurs in southernmost Texas). Featherman (1871) likewise reported *S. palmetto* from southern Louisiana, as did Langlois (1887). However, Bomhard (1935) considered these reports of *S. palmetto* from the lower Mississippi Valley to be erroneous, suggesting that they were misidentifications of the arborescent *S. minor*-like palms of the region. Darby (1816: 194) referred to an unusual, large palm from the lower Mississippi valley, historically abundant there, calling it *Chamaerops louisiana*, but distinguished it from *Chamaerops palmetto* (*Sabal palmetto*) by its relatively smaller size. Small (1929b) referred to the trunked palms of the lower Mississippi (*S. deeringiana*) as intermediate in character between *S. minor* and *S. palmetto*. Such controversy suggests that the Brazoria material and arborescent *S. minor* may present an intriguing aspect of *Sabal* evolution and historical biogeography.

Sabal minor is still a morphologically diverse species even if arborescent specimens are excluded. Mature individuals can have leaves from about 0.5–1.6 m diameter and inflorescences about 0.5–3.0 m in length.

Genetically based dwarf individuals are known (illustrated in Ramp & Thien 1995; sample 7 in this study), and edaphically dwarfed individuals are also known (sample 8, later cultivated and obtaining more typical stature). *Sabal minor* usually has relatively flat leaves and inflorescences with two orders of branching (excluding the main axis), but plants bearing leaves with a considerable three-dimensional structure (approaching those of other *Sabal* species) and robust inflorescences branched to three orders are also known (samples 1, 3, and 5). It is also an ecologically diverse species, preferring damp, especially riparian, woodlands, but rarely can grow in semi-xeric or subtropical uplands (samples 2 and 11). Despite this wide diversity, samples of this species used in this study, with the exception of #11, form a strongly coherent group that is relatively uniform genetically. Furthermore, individuals of *S. minor* occurring sympatrically with the Brazoria material (sample 10) and *S. mexicana* (sample 12) show no evidence of introgression with their sympatric congeners.

However, the Mexican sample of *S. minor* (#11) does show evidence of introgression with *S. mexicana*. This is best illustrated in the UPGMA tree by the sample's intermediate position between *S. mexicana* and the remainder of *S. minor* (Figure 1), as well as its prominent partial membership in the *S. mexicana* genotypic group in the STRUCTURE results for two to four genotypic groups (Figure 3). Yet the STRUCTURE analyses of 14 genotypic groups showed several genotypic partitions within this plant, but with the group dominating *S. mexicana* poorly represented. Plants from this population from eastern Nuevo León have the morphology of *S. minor* (see Goldman 1999), but occur near the western periphery of the natural distribution of *S. mexicana*. *Sabal minor* may have been widespread in northeastern Mexico prior to the end of the Pleistocene, but its distribution contracted as the climate became warmer and possibly drier, leaving populations isolated from the broader, expanding distribution of this species to the north and east. Exposed to the far more abundant *S. mexicana* in the region, hybridization may have taken place. Other similar populations of *S. minor* occur nearby in the state of Tamaulipas, known among palm enthusiasts and within the horticultural trade as "*Sabal* sp. Tamaulipas" or "*Sabal* Tamaulipas", although these plants are reported to be more robust than typical *S. minor*. Whether these *Sabal* plants from the central Sierra Madre Oriental of northeastern Mexico are truly *S. minor*, introgressed *S. minor*, or an undescribed species, remains an issue for debate and further research. Northeastern Mexico contains several species of plants and animals that are either disjunct from their larger distributions in eastern North America, or are otherwise closely related to species in that region (Johnston et al. 1989, Martin & Harrell 1957).

The Brazoria material and *S. minor* each are morphologically diverse, but each also seem to be genetically coherent (excluding the Mexican *S. minor* specimen). In contrast, material of *S. palmetto* sampled for this study did not show much morphological variation, but from the STRUCTURE results in particular one could infer that this species may contain a surprising amount of genetic variation. For example, the two plants sampled near the western geographic limit of the species, from Franklin County, Florida (samples 25 and 27), were less than 500 meters apart and nearly identical in appearance but showed some genetic distinctiveness from each other, best illustrated in the UPGMA and STRUCTURE results. Yet this species can show a large amount of morphological variability over its geographic range, especially near its southern geographic limit as inferred from the existence of several synonyms described from that region (see Zona 1990), so this species may be unusually genetically diverse within the genus.

Although this was a preliminary study of the Brazoria County arborescent *Sabal* population, we do believe it is of hybrid origin, derived from *S. minor* and *S. palmetto*, not from *S. mexicana* and *S. minor* as previously reported. However, its unexpected genetic distinctiveness suggests that it may be an old hybrid complex or a distinct species of hybrid origin, with little continuing introgression with sympatrically occurring *S. minor*. Nonetheless, minimally it deserves recognition as a hybrid taxon.

TAXONOMIC TREATMENT

Sabal* × *brazoriensis* D.H.Goldman, L.Lockett, & R.W.Read, *nothosp. nov. (Figure 5).

Plantae erectae 2–7(–11) m altae. Caulis erectus 0.3–5(–9) m altus, basibus foliorum exceptis 30–45 cm diametro. Folia 2.0–2.5 m; petiolis 0.9–1.5 basibus longe persistentibus; laminis modice vel valde costapalmatis, comparate planis vel profunde plicatis, sparse vel modice filiferis, 0.9–1.5 m × 1.2–2.3 m, segmentis 46–68, partibus liberis segmentorum 35–70 × 2.5–7.0 cm, apice fissis, parte conjuncta longissima segmentorum (30–)40–50 cm; costa recurvata 39–86 cm, 0.45–0.6 partes longitudinis laminae aequanti; hastula 4.5–13 cm. Inflorescentiae (1–)2–3 m, plerumque folia aequantes vel eis paulo longiores, 2–3 ordinibus ramorum (axe primario excluso), ramis patentibus, ramis primariis 20–100 cm, secundariis 10–20 cm, tertiariis 10–15 cm vel nullis. Flores fragrantes 0.5–0.8 cm lati; sepalis deltoideis ± 1.5 mm, basi viridibus, in partibus distalibus fere albis; petalis ovatis ± 3 × 1.5 mm, marginibus involutis, albis, leviter striatis; staminibus 3–4 mm, filamentis anguste lanceolatis, antheribus ellipsoideis ± 0.5 mm flavis. Fructus globosus 8–10 mm, seminibus oblatis, 6–8 mm diametro.

Type:—USA. Texas: Brazoria County, "Palm Unit" of the San Bernard National Wildlife Refuge, 28°58'20.0"N, 95°40'46.3"W, UTM 15R 238893E, 3207868N (NAD83/WGS84), elev. ± 5 m, 8 June 2011, *Goldman & Adams 4178* (holotype BH, isotypes GH, K, NCU, NY, TEX).

Plants erect, 2–7(–11) m tall. *Stem* erect, 0.3–5 (–9) m tall, 30–45 cm diameter excluding leaf bases. *Leaves* 2.0–2.5 m; petioles 0.9–1.3 m, bases long-persistent; blades moderately to strongly costapalmate, relatively flat to deeply folded, sparsely to moderately filiferous, 0.9–1.5 m × 1.2–2.3 m, segments 46–68, free segment portions 35–70 × 2.5–7.0 cm, apically cleft, longest fused segment portion (30–) 40–50 cm; costa recurved, 39–86 cm, 0.45–0.6 × blade length; hastula 4.5–13 cm. *Inflorescences* (1–)2–3 m, generally of similar length to the leaves or slightly longer, with 2–3 orders of branching (excluding the main axis), branches spreading, primary branches 20–100 cm, secondary branches 10–20 cm, tertiary branches 10–15 cm or absent. *Flowers* fragrant, 0.5–0.8 cm wide; sepals deltoid, ± 1.5 mm, green at base to nearly white distally; petals ovate, ± 3 × 1.5 mm, margins involute, white, faintly striate; stamens 3–4 mm, filaments narrowly lanceolate, anthers ellipsoid, ± 0.5 mm, yellow. *Fruit* globose, 8–10 mm, seeds oblate, 6–8 mm diameter.

Phenology:—Flowering in June, fruiting late summer to early autumn.

Distribution and habitat:—To date known only from a small area in southwestern Brazoria County, Texas, in a humid, subtropical, medium-aged floodplain woodland within the Columbia Bottomlands region (Rosen *et al.* 2008), with most trees ± 50 yrs old or less except for occasional older live oaks, on dark brown to black clay soil (Pledger Clay; very fine, smectitic, hyperthermic Typic Hapluderts). Growing with *Berchemia scandens*, *Callicarpa americana*, *Campsis radicans*, *Celtis laevigata*, *Cornus drummondii*, *Fraxinus pennsylvanica*, *Ilex decidua*, *I. vomitoria*, *Juniperus virginiana*, *Malvaviscus drummondii*, *Morus rubra*, *Parthenocissus quinquefolia*, *Pleopeltis polypodioides*, *Quercus nigra*, *Q. shumardii*, *Q. virginiana*, *Rubus pensilvanicus*, *Sabal minor*, *Sapindus saponaria*, *Smilax bona-nox*, *Tillandsia recurvata*, *T. usneioides*, *Toxicodendron radicans*, *Ulmus americana*, *U. crassifolia*, and *Vitis mustangensis*.

Fewer than 300 individuals of this hybrid are known in the wild, all within the vicinity of the "Palm Unit" of the San Bernard National Wildlife Refuge, with about 200 individuals known to exist within the approximately 46 acres of the "Palm Unit" (M. Lange, pers. comm.). Fortunately this site is protected and these plants probably are increasing in number. This hybrid is poorly represented in herbaria and would benefit from further field documentation.

Etymology:—For Brazoria County, Texas, USA, where it is apparently endemic.

The morphological description given above is based upon measurements given in Lockett & Read (1991), a table of measurements given to the first author by L. Lockett in 1995 (now deposited in the Botany Libraries at the Harvard University Herbaria), and observations by the first author. This new name, *Sabal* × *brazoriensis*, is given as a proper alternative to the invalidly published "*Sabal* × *texensis*" (Lockett & Read 1991), the latter which has become widely used in the horticultural trade for these same Brazoria palms.

FIGURE 5: A. Type individual of *Sabal ×brazoriensis*, Goldman & Adams # 4178, Brazoria County, Texas, June 8, 2011. Smaller palms in the photo are *S. minor* and possibly some seedlings of *S. ×brazoriensis*. Scale bar = 1 m. B. Flowers of a different plant of *Sabal ×brazoriensis* at the type locality, same date; scale bar = 0.5 cm. Photographer: Douglas Goldman.

"*Sabal* × *texensis*" was not validly published because no type was designated (Art. 37.1 of the Code; McNeill *et al.* 2006), and no Latin description or diagnosis was provided (Art. 36.1), as the requirements for publishing nothotaxa at the rank of species or below are the same as those of publishing non-hybrid taxa at the same ranks (Art. H.10.1). Furthermore, the name "*Sabal* × *texensis*" was an unfortunate choice because of its similarity to the name *Sabal texana* (Cook 1901: 534) Beccari (1907: 78), a synonym of *S. mexicana*. If "*Sabal* × *texensis*" were to be validated and it was decided later that it was not a hybrid then the multiplication sign indicating hybridity simply would be removed, resulting in "*Sabal texensis*", likely to magnify confusion with *S. texana*. This confusion probably would be further compounded by some morphological similarity that *Sabal* × *brazoriensis* has to *S. mexicana*, and also by the implication by some authorities of the latter species in the creation of the Brazoria hybrids. Therefore, we chose not to take up "*Sabal* × *texensis*" and instead use *Sabal* × *brazoriensis*.

We encourage further molecular and morphological research on this intriguing problem, with a broader sampling of the species studied here, including more arborescent material of *S. minor*. Furthermore, because the Columbia Bottomlands region of coastal Texas is a known part of a major avian tropical-temperate migratory pathway (Barrow *et al.* 2005; J. McNeal, pers comm.), other *Sabal* species should be sampled that occur closest to southeastern Texas in eastern Mexico or possibly western Cuba, e.g. *S. maritima* (Kunth in Humboldt *et al.* 1815: 298) Burret (1933: 101), *S. yapa* Wright ex Beccari (1907: 64), and possibly *S. mauritiiformis* (Karsten 1856: 244) Grisebach & H.Wendland (in Grisebach 1864: 514). Overall, *Sabal* is a relatively small but morphologically and ecologically diverse genus that merits intensive genetic research to study relationships, circumscription, and population biology. Such work likely will reveal a number of surprises.

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