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A Taxonomic History and Reexamination of Sabal minor in the Mississippi Valley

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Sabal displays a high degree of variability, particularly in characters commonly used to delimit species (Bailey 1944, Uhl and Dransfield 1987, Zona 1989). In particular, the presence or absence of a trunk (height) along with spines, and leaf blade folding caused taxonomic confusion for early explorers and biologists in North America. Although *S. minor* (*S. louisiana*) has received great attention for its stem variability, other North American palmettos also exhibit great trunk variability including *S. etonia*, *S. palmetto* and *Serenoa repens* (Hilmon 1969, Bailey 1944, Brown 1973, Zona and Judd 1986). This paper reviews the early observations and taxonomic history of *Sabal louisiana* (the "trunked palm") and utilizes protein electrophoresis to characterize its affinity with *S. minor* (N. J. Jacquin) Persoon.

History of *S. minor* (*S. louisiana*)

One of the earliest European accounts of New World palms was by Le Clercq (1691) who published an account of the explorations of the Mississippi by La Salle. He stated, "the whole country is covered with palms." In light of the present distribution of palms, the species observed was probably *S. minor*. The earliest taxonomic treatment of the palm was apparently by Adanson (1763) who established the genus *Sabal* presumably in reference to *S. minor* without commenting on the name's derivation (Guernsent 1804).

The earliest reference to a species distinct from *Sabal minor* in the Mississippi Valley is attributed to Robin (1807). He described two species. The first, which he placed in the genus *Chamaerops*, was described as having a trunk that ". . . scarcely emerges from the ground. . . ," leaves (petioles?) that lack spines or teeth and are ". . . folded in a fan." The common name for this palm was given as "latanier". The description fits *Sabal minor* and certainly not *Serenoa repens* which, although essentially without an upright trunk and occurring in southeastern Louisiana, possesses teeth on the petioles. The second species was not named and received only a short statement concerning the leaves, which were described as divided and folded, ". . . somewhat like an old-fashioned cravat or collar." No mention was made of the presence or absence of a trunk. The description of the leaves fits the manner in which leaves break in some populations of *Sabal minor* (i.e., Frenier Beach, Fig. 1C) in which the palms do possess trunks.

A decade later, William Darby published an account of his exploration of Louisiana titled "A geographical description of the state of Louisiana . . . being an accompaniment to the map of Louisiana." Appearing in 1816 (second edition in 1817), this book gives a description of the habitat of a palm he named *Chamaerops louisiana*. Darby stated ". . . there is a specific difference between the *Chamaerops palmetto* [=*Sabal palmetto*] . . . and that of Louisiana. The *Chamaerops serrulata* of Muhlenberg [=*Serenoa repens*] is certainly not the same as the palmetto of Louisiana; the latter bears a much greater resemblance to cabbage tree, though much more humble in elevation, than to the saw-leaved palmetto of Georgia." This statement may suggest that some form of trunk was present in the palms he observed. Obviously he was familiar with the species occurring on the east coast, so it is surprising that no comparison of this palm was made with *Sabal minor*. The habitat he described for this species is between "where the land sinks too low for the

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1. Variability in the stature of *Sabal minor*. A. A "dwarf" individual from a population near Blountstown, Florida. B. Typical acaulescent individuals in a population near New Orleans, Louisiana. C. A caulescent individual with leaves folded in a manner fitting the description made by Robin (1807). D. Caulescent individuals growing along the Mississippi River below Venice, La. The exposed trunk of the center individual is approximately 2.4 meters in height.

Arundo . . . (and) . . . where the inundation exceeds in depth 15 to 20 inches." Trees associated with the palm were also given. These include *Quercus phellos* Linnaeus, *Q. rubra* Linnaeus, *Liquidambar styraciflua* Linnaeus and *Celtis crassifolia* (*C. laevigata* Willd.), species commonly found in bottomland hardwood forests.

During the same year, Rafinesque (1817) published a flora of Louisiana based on the earlier work of Robin, although he never visited the region himself (Fitzpatrick 1911). Rafinesque assigned binomials to Robin's palms. He called the first *Sabal adansonii* (=*S. minor*) and the second, a new species, *S.?adiantinum* Raf. The description of the latter species appears to be an embellishment of Robin's description. Rafinesque stated that the new species was acaulescent although Robin made no mention of the plant's stature. Ewan (1967) suggested that *S.?adiantinum* is *Serenoa repens* despite the specific reference Rafinesque made to the unarmed petioles. In the same publication, Rafinesque took issue with Darby's species *Chamaerops louisiana* and considered this to be the same as *Sabal adansonii*. It is unfortunate that Darby failed to give fuller description of the palm other than stating that it differed from *Serenoa repens* and was "much more humble in elevation" than *Sabal palmetto*. It was not possible for Rafinesque nor is it possible now to assign Darby's palm without conjecture.

Over the next 40 years there appeared several references to palms found in the Mississippi Valley. In "The Genera of North American Plants . . . ," Nuttall (1818) placed *Sabal adansonii* in Louisiana stating that it is in ". . . troublesome abundance around New Orleans; but less frequent than other species in Georgia and Carolina." The other species referred to were *S. palmetto* and *Serenoa repens*. Darby (1818) maintained the use of *Chamaerops louisiana* in "The Emigrant's Guide, etc." Flint (1828) used the species name *Chamaerops latanier*, a name which must have been derived from Robin's or Darby's work. Martius (1838) described the range of *Sabal adansonii* to include the Mississippi Valley as well as Georgia and Carolina.

Shortly after Martius (1838) another statement was put forward which added to the somewhat confused status of the palms of the Mississippi Valley. Arthur Schott (1857), in a report on the Texas–Mexican border and the lower 80 miles of the Rio Grande, stated "It is also in the lower portion of this belt (where the palm tribe is represented by the *Chamaerops palmetto*) that the Palmetto attains a growth as gorgeous even as in the lower Mississippi." The palm which he observed would have been either *Sabal texana* or *S. mexicana*. The confusion stems from his reference to a "gorgeous" palmetto in the Mississippi Valley. If "gorgeous" is interpreted to mean as having a large stature, as Small (1926) interpreted this statement, then *Sabal palmetto* would be the most obvious comparison. However, *S. palmetto* does not occur within 300 miles of the area (the western edge of its range is in the Apalachicola Valley). His reference may have been to stands of caulescent palms (*Sabal minor*) now only represented by one known stand below Venice on the Mississippi River (Fig. 1D).

The next known reference to trunked palmettos in Louisiana is by Featherman in 1870. In a discussion of the vegetation of Grand Isle, he stated that "tree palmettos are seen here (behind the beach) and there near the beach."

In 1926, J. K. Small was in a position to address the problem of trunked palmettos in Louisiana. He observed a population of trunked palms south of Point aux Herbes (on the southeastern end of Lake Pontchartrain) which were initially taken for *Sabal palmetto*. However, on closer examination he discovered the palm to resemble *S. minor*. Small named this palm *Sabal deeringiana*. Included in his description of the species were characters that he considered significant in distinguishing it from *S. minor*; it is a tree to 4 meters with a trunk of 1 to 2 meters high with petioles longer than the leaf blades, the leaf midrib extends high into the flat blade and the leaves are filamentous. He also indicated that the petals are slightly broader and longer, the stamens are longer, and that the fruit is more depressed than in *S. minor*. The type specimen is deposited at The New York Botanical Garden.

In 1929 Small made further comparisons of *S. deeringiana* with other species of *Sabal*. The habitat of this palm was said to be bottomless gumbo, and he stated that in Louisiana, *S. deeringiana* was much more restricted and less common than *S. minor*. In this publication, Small provided photographs of two individuals of *S. deeringiana* at Frenier Beach on Lake Pontchartrain.

In Small's discussion of this new species he referred to Schott's (1857) reference to a palm of "gorgeous" growth in the Mississippi Valley but was apparently unaware of the earlier observations of trunked palmettos by Robin (1807) and Darby

(1816). Had he known of these, he surely would have noted the similarity of these descriptions. The similarity can be seen by comparing Small's photographs of *S. deeringiana* with Robin's description of the manner in which the leaves split and break over (Fig. 1C).

Bomhard (1935) reviewed these accounts of trunked palmettos and considered Darby's specific epithet to have priority, thus creating the binomial *Sabal louisiana* (Darby) Bomhard. Bomhard (1937, 1940, 1943) provided photographs and a map of population sites. She extended the range of the species to eastern Texas across to the western portion of the Florida panhandle and north to southern Arkansas. She stated that *S. louisiana* is stemless under some conditions while producing an aboveground trunk under others. Unfavorable conditions that contribute to retarded trunk development include exposure to brackish water, direct sunlight, and the deposition or removal of soil around the plant's base (Bomhard 1943). Bomhard suggested that the largest individuals she observed were in excess of 200 years old.

In his first monograph of the genus, Bailey (1934) recognized *S. louisiana*; however in his second monograph (1944), he combined *Sabal minor* and *Sabal louisiana*. He considered the latter to be the final, emergent stage of the former stating that "no clear definite . . . differences are recorded between the acaulescent and caulescent phases . . ." and that if these are two species, characters other than stature need to be found. Since this time, *Sabal louisiana* has been considered a synonym of *S. minor* (except by Bomhard 1950 and Vines 1960 who maintained it as a distinct species). In a recent monograph of the genus, Zona did not separate *S. louisiana* from *S. minor* (Zona 1990).

Acaulescent populations of *S. minor* occur throughout the species' range while trunked palms occur mostly in the western portion of the range (specifically in LA and TX, Figs. 1C and 1D). Typical, acaulescent populations are composed of individuals with leaves reaching 1.5 to 2 meters in height (Fig. 1B). A population of unusually small individuals was observed on the Apalachicola River flood plain near Blountstown, Florida. Here, the largest reproductively mature individuals scarcely reached 40 cm in height (Fig 1A). A similar population of "dwarf" individuals was described by Bailey (1944) from Angelian County, Texas.

In contrast, it is not uncommon in the western half of the species' range to find populations of trunked individuals with a stem height of approximately 1–1.5 meters (total height near 4–5 meters). The tallest individuals have trunks greater than three meters (total plant height approximately six meters, Fig. 1D). The largest individual known, tentatively identified as *S. minor*, has a 19 foot trunk (5.8 meters) with a total height of 27 feet is located in Brazoria County, Texas (Landon Lockett, personal communication).

Gel Electrophoresis Methods

Plant material was collected from six taxa representing three species in two genera. *Serenoa repens* (Bartram) Small was collected from a population near Orlando, Florida and *Sabal palmetto* (Walt.) Loddiges ex J. A. & J. H. Schultes was collected near Crystal River, Florida. Four populations of *Sabal minor* were examined. An acaulescent population sampled near Savannah, Georgia (SVGA), a population of "dwarf" individuals near Blountstown, Florida (BTFL), a caulescent population at Frenier Beach, Louisiana (FBLA), one of the sites of *Sabal louisiana* described by Bailey (1944) and Bomhard (1943), and a caulescent population of *Sabal minor* located below Venice, Louisiana actually growing in the Mississippi River (MRLA). This population previously had been found to have the greatest mean genetic distance (Nei's index, 1972) from 13 populations distributed from Georgia to Texas (Ramp, 1989).

Leaf portions were cut into small pieces then ground with mortar and pestle in a 7.5 pH grinding buffer composed of 0.1 M Tris, 1.0 mM EDTA, 10 mM KCl, 10 mM MgCl, 14 mM 2-mercaptoethanol, and 5% polyvinylpyrrolidone-40 (Gottlieb 1981b). This was absorbed onto 3 × 15 mm paper wicks (Beckman) and placed into 12.9% starch gels.

A lithium hydroxide buffer system (Soltis et al. 1983) was used to examine seven enzyme systems; alcohol dehydrogenase (ADH), leucine aminopeptidase (LAP), glutamate-oxaloacetate transaminase (GOT), peroxidase (PER), superoxide dismutase (SOD), phosphoglucosisomerase (PGI) and malic enzyme (ME). Staining procedures followed Soltis et al. (1983).

The unbiased estimate of mean heterozygosity per locus (H) for each taxa and the unbiased genetic distances were calculated (Nei 1978). Although sample sizes are small for *Sabal palmetto* (n = 5) and *Serenoa repens*, (n = 10) empirical studies have found that samples of 8–

Table 1. Allozymes observed for three American palmettos. Sabal minor *populations are given in text.*

Locus	*Serenoa repens*	*Sabal palmetto*	*Sabal minor* SVGA	BTFL	FBLA	MRLA
PGI-1	1.0		—	1.0	1.0	1.0
	1.0					
PGI-2a	0.50	—	0.0	0.0	0.0	0.0
b	0.50	—	0.0	0.0	0.0	0.0
c	0.0	—	0.07	0.20	0.89	0.50
d	0.0	—	0.93	0.80	0.11	0.50
PER-1	1.0	—	—	—	—	—
PER-2a	0.0	1.0	1.0	1.0	1.0	1.0
b	1.0	0.0	0.0	0.0	0.0	0.0
LAP-1a	1.0	0.0	0.0	0.0	0.0	0.0
b	0.0	1.0	1.0	0.0	1.0	1.0
LAP-2a	1.0	0.0	0.0	0.0	0.0	0.0
b	0.0	1.0	1.0	1.0	1.0	1.0
GOT-1a	1.0	0.0	0.0	0.0	0.0	0.0
b	0.0	1.0	0.0	0.0	0.0	0.0
c	0.0	0.0	0.83	0.73	0.53	0.50
d	0.0	0.0	0.17	0.27	0.47	0.50
ME-1a	1.0	0.0	1.0	1.0	1.0	1.0
b	0.0	1.0	0.0	0.0	0.0	0.0
SOD-1a	1.0	0.0	0.0	0.0	0.0	0.0
b	0.0	—	1.0	1.0	1.0	1.0
SOD-2	1.0	1.0	1.0	1.0	1.0	1.0
SOD-3	1.0	—	1.0	1.0	1.0	1.0
SOD-4a	0.0	—	1.0	1.0	1.0	1.0
b	1.0	—	0.0	0.0	0.0	0.0
ADH-2a	—	0.0	0.98	0.85	0.41	0.33
b	—	1.0	0.02	0.15	0.89	0.67

12 individuals usually give heterozygosity estimates within 1% of estimates based on much larger samples and that samples even as small as two individuals generally give estimates within 2.5% (Gorman and Renzi 1979). There is even a smaller effect of sample size on genetic distance. Results indicate that for interspecific comparisons, a sample size of one is sufficient to estimate genetic distance within 0.1 in over 90% of the cases studied and that the error is to systematically overestimate D (Nei 1978, Gorman and Renzi 1979). Both heterozygosity and genetic distance estimates are much more severely affected by the number of loci sampled. Gorman and Renzi (1979) found that a sample of two individuals scored for all loci studied (23) gave a better estimate of heterozygosity than all individuals (20–41 per species) scored for a subset (up to 20) of the loci in eight species of *Anolis*.

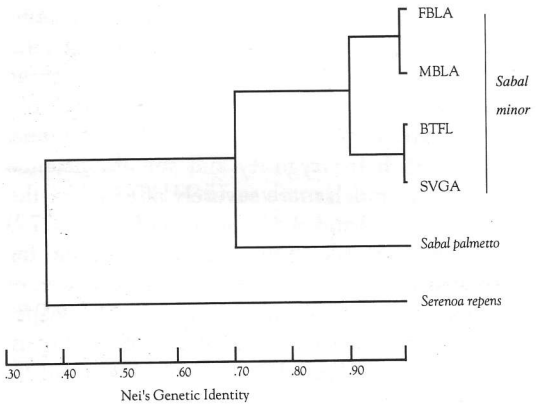
Results and Discussion

Thirteen loci were resolved (Table 1). Mean heterozygosity values for these loci (on the diagonal of Table 2) were similar for all taxa ranging from H = 0.081 in BTFL (*Sabal minor*) to H = 0.000 in *Sabal palmetto*. Mean heterozygosities for these palms are low compared to the average of H = 0.156 found in plants (Hamrick et al. 1979) but are similar to those calculated for *Washingtonia filifera*, H = 0.009 (McClenaghan and Beauchamp 1986). When values for these palms are compared with other long-lived perennials (average heterozygosity, H = 0.27), the difference is striking. It would be interesting to know if low heterozygosity is characteristic of palms in general or if the low heterozygosity observed here is the result of similar evolutionary histories (e.g., populations undergoing similar bottlenecks).

The smallest genetic distances were between the four populations of *Sabal minor*, ranging between 0.011 and 0.132. Genetic distances and identity are given in Table 2 and a phenogram of genetic identity in Figure 2. The high genetic identity within the populations SVGA, BTFL,

Table 2. Nei's (1978) unbiased estimates of genetic identity (above diagonal), genetic distance (below diagonal), and heterozygosities (on the major diagonal).

	Serenoa repens	*Sabal palmetto*	*Sabal minor* SVGA	BTFL	FBLA	MRLA
Serenoa repens	(0.043)	0.372	0.376	0.388	0.386	0.381
Sabal palmetto	0.989	(0.000)	0.578	0.619	0.725	0.684
Sabal minor (SVGA)	0.978	0.548	(0.038)	0.989	0.910	0.876
Sabal minor (BTFL)	0.947	0.480	0.011	(0.081)	0.924	0.924
Sabal minor (FBLA)	0.952	0.322	0.094	0.079	(0.076)	0.980
Sabal minor (MRLA)	0.965	0.380	0.132	0.079	0.020	(0.075)



2. Phenogram of Nei's (1978) unbiased genetic identities for *Serenoa repens*, *Sabal palmetto* and three populations of *Sabal minor*.

MBLA, and FBLA indicated that *Sabal louisiana* is probably not genetically isolated from *S. minor* and supports Bailey's (1944) conclusion that *S. louisiana* should not be separated from *S. minor*. Studies of other species have found that genetic identity between intraspecific populations are usually quite high, nearly always 0.90 or above (Gottlieb 1977, 1981a, Crawford 1983).

Between congeneric species, most studies have found that genetic identity are much lower than within species (Gottlieb 1981a, Crawford 1983). For 13 species pairs in 8 genera, Gottlieb (1977) found a mean genetic identity of I = 0.67. Identities between the three populations of *Sabal minor* and *S. palmetto* certainly fall in this range (I = 0.662).

Between *Serenoa repens* and the two species of *Sabal* sampled, the mean genetic identity is 0.379. However, for comparisons between genera and higher taxonomic levels, the utility of allozyme data is increasingly limited. This is due to underlying assumptions in data interpretation. To interpret two different electromorphs from different genera as representing genetic divergence equal to two different electromorphs within a genus distorts the data, forming closer genetic affinities between taxa than may exist. Also, the assumption that electromorphs with identical mobilities represent identical proteins when derived from widely separated taxa is undesirable (Crawford 1983). The results of these taxonomic comparisons indicate that the use of electrophoretic techniques to detect genetic differences should be a valuable tool in unraveling the systematics of *Sabal*.

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