SABAL ETONIA (PALMAE): SYSTEMATICS, DISTRIBUTION, ECOLOGY, AND COMPARISONS TO OTHER FLORIDA SCRUB ENDEMICS[1]

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A taxonomic study of *Sabal etonia* Swingle ex Nash and related taxa (involving field work throughout Florida along with the study of more than 800 herbarium specimens) has shown that this palm is morphologically and ecologically distinctive and most closely related to *S. palmetto* (Walt.) Lodd. ex J. A. & J. H. Schultes and *S. miamiensis* Zona (see Zona 1983). *Sabal etonia* differs from the more widespread *S. palmetto* in its usually subterranean trunk (vs. erect and aerial), crown of usually only 3 – 5 leaves (vs. 14 – 40), narrower petioles (ca 0.6 – 2 vs. 2 – 4 cm), blades with fewer segments [20 – 46(-56) vs. 44 – 80(-90)], shorter median leaf segments [32 – 66(-69) vs. (55-)60 – 110(-120) cm], shorter hastulas [1 – 2.7 vs. (2.8-)3 – 13.3 cm], inflorescence structure (2 orders vs. 3 orders of branching), larger fruits (diameter usually 12 – 15 vs 9 – 12 mm), and larger seeds (diameter of usually 8 – 10 vs. 6 – 8 mm). *Sabal miamiensis* is intermediate between *S. etonia* and *S. palmetto* in most vegetative characters, but has a subterranean trunk like the former and three branch orders in its inflorescences like the latter; its fruits and seeds are typically larger than either species (see Zona 1985, for a detailed discussion of *S. miamiensis*).

The morphological character most obviously distinguishing *Sabal etonia* from *S. palmetto* is acaulescence. Authors of recent treatments of the flora of Florida (Long & Lakela 1976, Wunderlin 1982) have placed great emphasis on the above-ground trunk of *S. palmetto* versus the subterranean trunk of *S. etonia*. Usually, the trunk of *S. palmetto* is emergent and erect, but that of *S. etonia* is subterranean and sigmoid. An excellent illustration of the

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peculiar trunk of *S. etonia* may be found in Bailey (1944). While these character states are typical for the species, they are by no means consistent. Occasionally, one encounters individuals of *S. etonia* with well developed emergent trunks. Bailey (1944) mentioned *S. etonia* in Marion County with six foot (ca 2 m) trunks; however, such individuals are encountered very infrequently in dry habitats (such as sand pine scrub). Individuals of *S. etonia* growing in more mesic habitats, such as those of coastal Volusia and Dade counties, also exhibit caulescence. These plants grow in what appears to be "mesic scrub," a scrub in the process of succession toward a mesic hammock (Kurz 1942). The short-emergent trunks of these individuals may be the result of mesic edaphic conditions. There also exist individuals of *S. palmetto* with only shortly emergent trunks to 1 m tall. Such individuals may be seen in dry coastal dunes such as those near Cedar Key (Levy Co.) or Merritt Island (Brevard Co.). There are also acaulescent to short-emergent plants on the Everglades pine keys of Dade County. These "stunted" plants also are likely the result of edaphic conditions. It appears that either excessively dry soil or a confined root system results in acaulescent or short-trunked *S. palmetto*. The morphological plasticity of these species has not been fully appreciated by many taxonomists.

The trunk of *Sabal etonia* is smooth, even on those plants with emergent trunks. The trunk of *S. palmetto* may be more or less smooth or clad with old leaf bases. The petioles, and consequently, the leaf bases are smaller in *S. etonia* as compared with those of *S. palmetto*.

As indicated above, the leaves of *Sabal etonia* are smaller on average than those of *S. palmetto*: the hastula and petiole are narrower and shorter, and there are fewer, shorter and narrower segments. The lamina of *S. etonia* and of *S. miamiensis* is characteristically yellow-green, but that of *S. palmetto* is slightly blue-green.

The inflorescence structure is variable and of taxonomic importance in the genus *Sabal*. Inflorescences of the group are axillary and enclosed by a series of open-ended tubular bracts which protect the primary axis of the inflorescence. The inflorescence of *S. etonia* is nearly erect, but as the fruits develop, it frequently becomes prostrate on the ground from its own weight. The branches of the inflorescence of *S. palmetto* are arrayed loosely along the main axis. There are three orders of branches (discounting main axis). In *S. etonia* the branches are crowded tightly on the main axis and are ascending, and there are only two orders of branches. Terminology used here, particularily that of axis enumeration, corresponds to Tomlinson & Zimmermann (1968).

Floral morphology varies very little among these species, and the taxonomic usefulness of floral features is not great. The petals of *Sabal*

etonia average 3.1 mm long, while those of *S. palmetto* average slightly shorter (i.e., 2.9 mm), and those of *S. miamiensis* slightly longer (i.e., 3.5 mm). However, fruit and seed size has proved to be of taxonomic value in the species complex. As indicated above, the fruits of *S. etonia* are intermediate between those of *S. palmetto* and *S. miamiensis*.

Sabal etonia is a member of the characteristic and highly endemic flora occurring on the white or yellow sands of the upland areas of the central "backbone" of the Florida peninsula. One of the most common plant communities in this region is the sand pine/xerophytic oak scrub (e.g., vegetation dominated by *Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg., *Quercus geminata* Small, *Q. myrtifolia* Willd., *Q. inopina* Ashe, and *Q. chapmanii* Sarg.). The species occurs in central Florida from Clay Co. south to Highlands Co. along the Trail Ridge, Mount Dora Ridge, and Lake Wales Ridge, and along the Atlantic Coastal Ridge from St. Lucie to Dade County (Figure 1). (See White 1970, for a summary of the geology of these ridges). In contrast, *S. palmetto* occurs from coastal North Carolina (Brunswick Co.) south through South Carolina and Georgia to northeastern Florida, throughout peninsular Florida, and in the Bahama Archipelago. This species shows a distinctive affinity for water. It is abundant in mesic to hydric hammocks, tidal flats, river banks, coastal strand and dunes, and pine flatwoods and savannas. The species is the canopy dominate in peninsular Florida's tidal flats just above the *Juncus roemerianus* Scheele zone. *Sabal miamiensis* is limited to the pinelands (i.e., *Pinus elliottii* Engelm. var. *densa* Little & Dorman) occurring on the oolitic limestone of the Miami region. Thus *S. etonia* is typically ecologically isolated from both *S. palmetto* and *S. miamiensis*.

The authors conclude that *Sabal etonia* is clearly distinct from both *S. palmetto* and *S. miamiensis* in both morphology and ecology. This study has demonstrated the unreliability of cauline characters in this complex. The morphology of adult leaves, particularly leaf number, lamina color, segment number, and hastula length, has proven taxonomically valuable. Inflorescence structure is also an important and useful character, as is fruit and seed size. No one morphological character is reliable enough to separate the three species due to the amount of overlap in the range of variation, however, *S. etonia* is clearly delimited from related taxa when a suite of characters is used. A summary of the nomnenclatural synonymy along with a brief description and citation of representative specimens for *S. etonia* is given below.

SABAL ETONIA Swingle ex Nash, Bull. Torrey Bot. Club 23:99–100. 1896. TYPE: FLORIDA: vicinity of Eustis, 16–30 Jun 1894, *Nash* 999 (HOLOTYPE: NY!; ISOTYPES: BH!, GH!, MO!, US!).

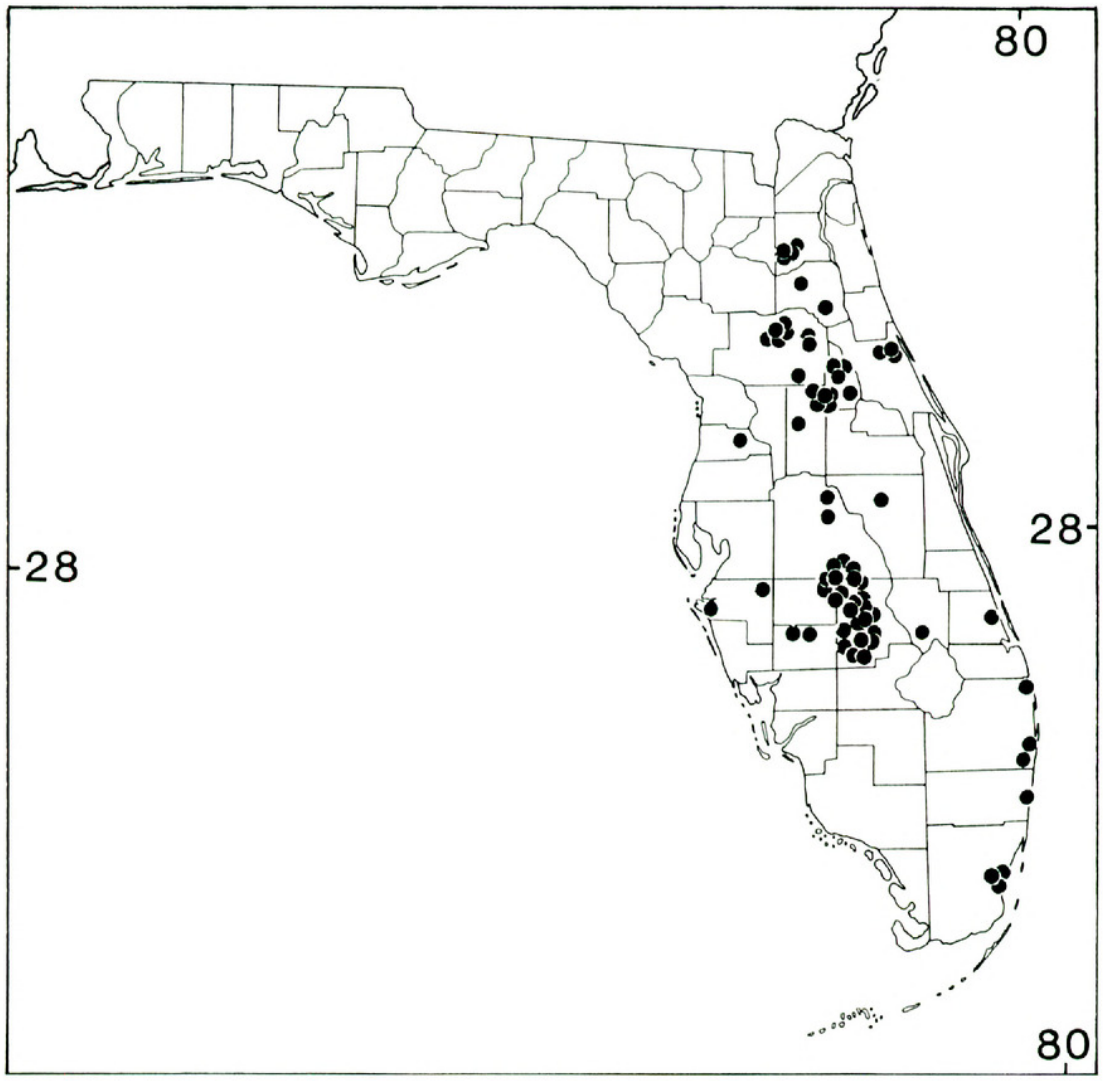

Figure 1. The distribution of *Sabal etonia*.

Sabal adansonii Guerns. var. *megacarpa* Chapm. Fl. South. U.S., 2nd ed. 651. 1883. *Sabal megacarpa* (Chapm.) Small, Fl. SE. U.S. 223. 1903. TYPE: SOUTH FLORIDA: *Garber s.n.* (LECTOTYPE: MO!).

Plants usually acaulescent, rarely caulescent to 2 m, stems sigmoid, to 10 – 15 cm in diameter, or if upright, 15 – 20 cm in diameter. Leaves 3 – 5, usually yellow-green, costapalmate; petiole 23 – 55 cm long, 0.6 – 2(-2.1) cm wide; hastula triangular, 1 – 2.7 cm long, segments 20 – 46(-56), bifid, filiferous, 32 – 66(-69) cm long, 1.5 – 3 cm wide. Inflorescence paniculate, densely branched with two orders of branching (discounting main axis), upright at first then prostrate as fruits develop. Flowers subsessile, perfect, white, sweetly fragrant, protogynous; calyx three-lobed, 1 – 1.4 mm long, cup-shaped; petals three, 3 – 3.2 mm

long, ovate; stamens 6, the same length as the petals, connate slightly at the base and basally adnate to the petals; gynoecium composed of three fused carpels, 2.5 – 3.5 mm long; ovary superior, stigma papillose. Fruit a one-seeded berry developing from one carpel (rarely more than one carpel develops, the fruit is then a strongly lobed two- or three-seeded berry), globose, shiny black, (11-)12 – 15 mm in diameter with a fleshy pericarp; seed oblate, concave on the funicular end, brown, (6-)8 – 10(-11) mm in diameter, embryo sublateral, endosperm bony. (Figure 2, see also Bailey 1944, Small 1925).

Distribution and Ecology: Florida, from Clay Co. to Highlands Co. in the sand pine scrub of the Central Florida Ridge, also in the scrub on older coastal dunes of Volusia, St. Lucie, Palm Beach, Broward, and Dade counties, and in isolated patches of scrub in DeSoto, Hernando, Manatee, Okeechobee, and Seminole counties (Figure 1). Associated species are discussed by Harper (1914, 1915, 1927), Kurz (1942), and Mulvania (1931). Flowering occurs from late May through July.

Representative Specimens: UNITED STATES: FLORIDA. **Broward Co.**: Ft. Lauderdale, *Bailey 473* (BH). **Clay Co.**: Goldhead Branch State Park, *Skean 850* (FLAS), *Ward 5490* (FLAS). **Dade Co.**: Miami, *Bailey 6472* (BH); North Miami, *Zona 68* (FLAS). **De Soto Co.**: west of Horse Creek, *Shuey 1853* (USF). **Highlands Co.**: Lake Placid, *Brass 33413* (USF); near Sebring, *Judd 2498* (FLAS); just west of Lake Jackson, *Judd 2846* (FLAS); without definite locality, *Small 11572* (NY); off U.S. Rt. 27, *Zona 10* (FLAS); south of Josephine Creek, *Zona 60* (FLAS). **Lake Co.**: near Eustis, *Nash 975* (US). *Savage 79* (BH). **Marion Co.**: near Salt Springs, *Judd 2774* (FLAS); Ocala National Forest, *Wunderlin, et al. 6549* (USF), *Zona 1* (FLAS). **Okeechobee Co.**: near Okeechobee City, *Bailey & Small 6211* (BH). **Osceola Co.**: east of Alligator Lake, *Shuey s.n.* 27 Oct 1974 (USF). **Palm Beach Co.**: Jupiter, *O'Neill s.n.* (FLAS, US); Boca Raton, *Zona 63* (FLAS); Boynton Beach, *Zona 104* (FLAS). **Polk Co.**: near Frostproof, *Judd 2840* (FLAS), *Zona 3* (FLAS). **Putnam Co.**: north of Florahome, *Wilson s.n.* 16 May 1959 (FLAS). **Volusia Co.**: near Ormond Beach, *Zona 31* (FLAS), *Zona 60* (FLAS).

Economic Uses: *Sabal etonia* is of potential ornamental use in areas where the edaphic conditions would permit its growth.

The sand pine/xerophytic oak scrub of the Central Florida Ridge supports many endemic species (Harper 1949, James 1961, Ward 1979). *Sabal etonia* is almost always found wherever there is scrub, and the taxonomy and distribution of this species may provide some insight into the probable origin of this and other scrub endemics. Noteworthy endemics of this region include: *Asclepias curtissii* A. Gray, *Bonamia grandiflora* (A. Gray) Heller, *Bumelia lacuum* Small, *Calamintha ashei* (Weatherby) Shinners, *Carya floridana* Sarg., *Chapmannia floridana* Torr. & Gray, *Chionanthus pygmaeus* Small, *Clitoria fragrans* Small, *Conradina brevifolia* Shinners, *Dicerandra frutescens* Shinners, *Eriogonum floridanum* Small (*E.*

longifolium Nutt. var. *gnaphalifolium* Gandoger), *Eryngium cuneifolium* Small, *Garberia heterophylla* (Bart.) Merr. & Harper, *Hypericum cumulicola* (Small) P. Adams, *H. edisonianum* (Small) P. Adams & Robson, *Ilex opaca* Ait. var. *arenicola* (Ashe) Ashe, *Lechea cernua* Small, *Liatris ohlingerae* (Blake) Robins., *Lupinus aridorum* McFarlin ex Beckner, *L. cumulicola* Small, *Nolina brittoniana* Nash, *Osmanthus megacarpus* (Small) Small ex Little, *Palafoxia feayi* Gray, *Paronychia chartacea* Fern., *Persea humilis* Nash, *Pityopsis graminifolia* (Michx.) Nutt. var. *aequilifolia* Bowen & Semple, *Polygala lewtonii* Small, *Polygonella basiramia* (Small) Nesom & Bates, *P. robusta* (Small) Nesom & Bates, *P. myriophylla* (Small) Horton, *Prunus geniculata* Harper, *Quercus inopina* Ashe, *Sabal etonia* Swingle ex Nash, *Sisyrinchium xerophyllum* Greene, *Stylisma abdita* Myint, *Warea amplexifolia* (Nutt.) Nutt., *W. carteri* Small, and *Ziziphus celtata* Judd & Hall.

An understanding of the origin of many of the scrub endemics is aided through a study of the distribution and morphological variation of the various endemics and their close relatives, an appreciation of past geological events in the area of endemism, and a knowledge of the region's edaphic and climatic conditions [see discussion of endemism in Stebbins (1942), Mason (1946), and Woodson (1947)].

The Central Highlands of the Florida peninsula, as they are called by Cooke (1945), are a series of disconnected ridges which may represent the remnants of a single ridge extending through Florida from Baker to Highlands County (White 1970). This geomorphological feature is now seen as a series of separate smaller ridges including the Trail Ridge to the north in Baker, Bradford, and Clay counties; the Mount Dora Ridge extending through eastern Marion, Lake, and Orange counties; and, by far the largest of the individual ridges, the Lake Wales Ridge of Lake, Orange, Osceola, Polk, and Highlands counties. McNeil (1949) showed that much of the land that is now the Trail Ridge and Lake Wales Ridge was exposed even during the Pleistocene interglacial periods when the sea level was considerably higher than its present level. In the Pliocene, portions of the Florida-Georgia border and probably portions of the ridges were above sea level (White 1970). Another ridge which is relevant to this discussion is the Atlantic Coastal Ridge which extends down the entire Atlantic coast but supports scrub only in its higher areas such as those found in Volusia, St. Lucie, Palm Beach, Broward, and Dade counties. In its southerly parts the Atlantic Coastal Ridge was formed from sand dune deposits overlaid on the Miami Ridge, a calcareous bar formed in Pamlico times (100,000 B.P.) and was submerged until very recently (White 1970). The areas of Florida that were exposed in the Pleistocene presumably were suitable for plant habitation. Watts (1969) noted that sclerophyllous oak pollen is well

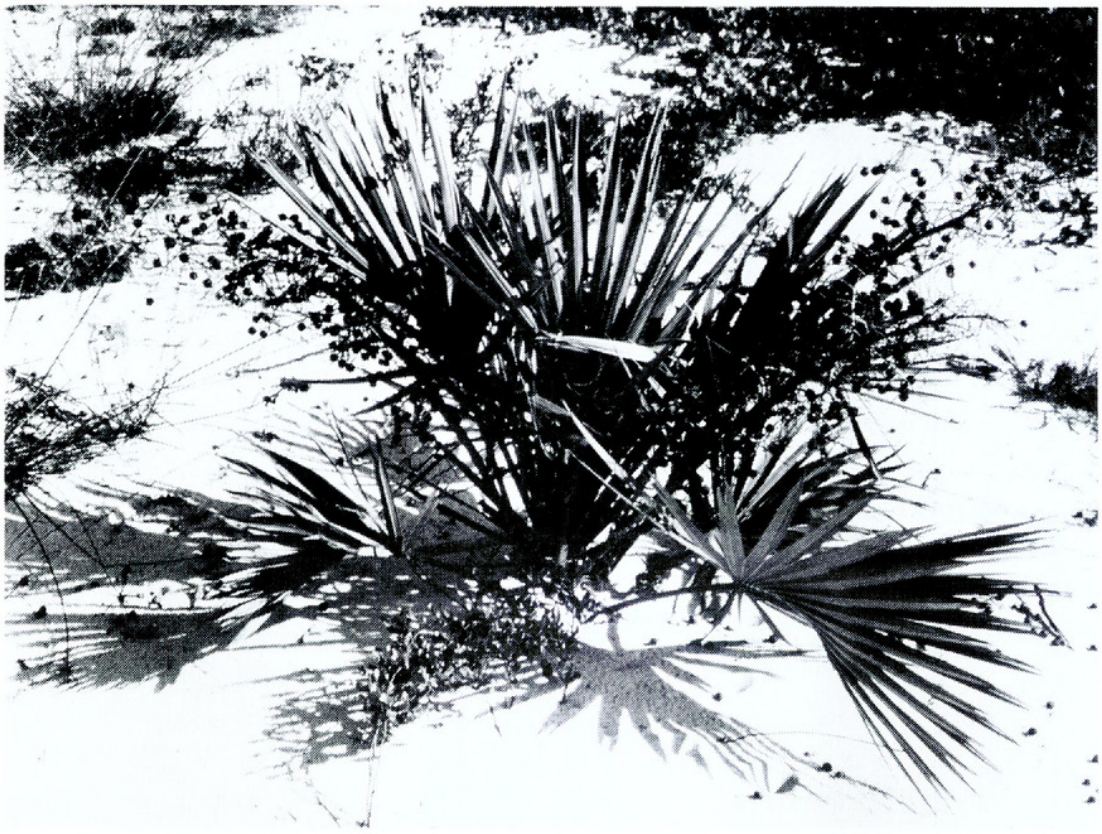

Figure 2. Habit of *Sabal etonia*; photograph taken in Highlands Co., Fla.

represented in Pleistocene lake sediment in Marion County. Discontinuities in sedimentation suggest periods of time when the environment was drier than it is now. In addition, Watts (1975) reported that the fossil pollen record from a lake in Highlands County indicated a dominate scrub community in the Pleistocene.

The genus *Sabal* is well represented in fossil deposits in the southeastern United States (Daghlian 1978, Moore 1973, Read & Hickey 1974). Many of these deposits predate the formation of the land masses in Florida. The fossil record of *Sabal* suggests that it has long occurred in North America, and a refugium, similar to that suggested by Woodson (1947), may have been instrumental in the speciation of the genus in Florida. Moore and Uhl (1982) stated that dwarfism in palms is an evolutionarily advanced condition, so it is likely that *S. etonia* evolved from caulescent ancestors that colonized the ridges of Florida as they formed. *Sabal etonia* now inhabits some of the geologically oldest formations in Florida. However, the Atlantic Coastal Ridge is geologically recent and has been colonized successfully by *S. etonia*. Thus *S. etonia* is likely capable of invading new scrub habitats as they form.

Mason (1946) stated that the area occupied by any species is determined by environmental conditions and that, of the many factors contributing to the overall environment, only edaphic factors occur in sharply defined, often small areas. The soil of the central ridges of peninsular Florida is clearly extreme; Mulvania (1931) described the sand pine scrub inhabitants as "rooted in a bed of silica, to which the term soil is but remotely applicable." The soil underlying the scrub is a coarse white or yellow silica sand that extends to a depth of ca 3.5 – 4.5 m, and the scrub vegetation, including *Sabal etonia*, is found almost exclusively on these xeric sands. This specificity suggests that the distribution of *S. etonia* is the result of the limited occurrence of xeric white sands, and the species may have developed through selection in response to the extreme xeric environment of these sandy ridges.

Stebbins (1942) maintained that species with a great deal of genetic variability within populations are more likely to spread over large areas and many habitats than are species whose populations are genetically homogeneous. It is of interest that *Sabal etonia* is morphologically uniform, especially when compared with *S. palmetto*, a species found in many habitats throughout the southeastern United States and the Bahamas (Brown 1976, Zona 1983). Furthermore, Stebbins (1942) defined two different kinds of rare genetically homogeneous species: the "depleted species" and the "insular species." Depleted species are those which were once more common but their present rarity is due to depletion of the store of genetic variability. An insular species, which need not be found only on islands, is one which was never common but has diverged from a more widespread ancestor and has become established in a small insular or isolated area. Stebbins suggested that if the endemic is closely related to a widespread species, which occurs on an adjacent continental area, it is probably a strictly insular species, but if it is closely related to no other living species, or has its close relatives in a geographically distant region, it is more likely a depleted species. A second criterion given by Stebbins (1942) is that an insular species is typically morphologically and/or ecologically specialized in relation to its continental relatives. According to these guidelines *Sabal etonia* is clearly an insular endemic, and likely evolved from mesophytic, more widespread, *S. palmetto*-like ancestors. Many of the other characteristic scrub species also appear to be insular, e.g., *Asclepias curtissii* (related to *A. purpurascens*, Woodson 1954), *Chionanthus pygmaeus* Small (*C. virginicus* L., Hardin 1974), *Ilex opaca* var. *arenicola* (Ashe) Ashe (*I. opaca* var. *opaca*, Wunderlin 1982), *Osmanthus megacarpa* (*O. americana* (L.) Benth. & Hook. f. ex A. Gray, Hardin 1974), *Persea humilis* Nash (*P. borbonia* (L.) Spreng., Wofford 1973), *Polygonella basiramia* (*P. ciliata* Meisn., Nesom & Bates 1984), *P.*

robusta (*P. fimbriata* (Ell.) Horton, Nesom & Bates 1984), *Prunus geniculata* (*P. angustifolia* Marsh., Harper 1911), *Quercus inopina* (*Q. myrtifolia* Willd., Johnson & Abrahamson 1982). *Sabal etonia* is typical of these endemics. The ancestral species presumably inhabited the southeastern United States, and *S. etonia* shows the morphological specializations so typical of scrub endemics: dwarf stature, small leaves, large fruits, and large seeds (see Hardin 1974). These morphological features are likely adaptations to the xeric conditions of the sand pine scrub. Isolation, both in past refugia of emergent land masses and present-day "ecological islands," has preserved the genetically divergent biotypes of the scrub endemics. However, the floristic affinities of the scrub endemics are complex, and some [e.g., *Ziziphus celata* and *Nolina brittoniana* (Judd & Hall 1984), *Eriogonum longifolium* var. *gnaphalifolium* (Horton 1972), *Bonamia grandiflora* (Myint & Ward 1968), *Palafoxia feayi* (Turner & Morris 1976), and *Carya floridana* (Hardin & Stone 1984)], appear to have western affinities. Additional systematic studies of the endemic species of the Central Florida Ridge are urgently needed.

It is the unique combination of historical and edaphic features which makes the sand pine scrub habitat so rich in endemic species. The Florida peninsula, by virture of its absence of glaciation, recent geological activity characterized by many fluctuations in its coastline, relative isolation from the remainder of the continent, proximity to the species-rich tropics, and unique climatic patterns, is an area which supports many endemics. Peninsular Florida is also being subjected to rapid urban and agricultural development, and the natural plant communities of the Central Florida Ridge are very rapidly being destroyed. At this time less than 3% of the total land area of the southern Lake Wales Ridge is currently protected from development (Peroni & Abrahamson 1985). For these reasons, action to preserve the distinctive flora of the Central Florida Ridge is essential.

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