

PALMS

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FRONT COVER

Washingtonia filifera occurs in a narrow canyon in the Kofa National Wildlife Refuge, Arizona, USA. See article by L. Noblick et al., p. 177. Photo by L. Noblick.

BACK COVER

Adonidia dransfieldii. See article by Z. Jamil, p. 193. Photo by Z. Jamil.

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The flowers and fruits of *Areca macrocalyx*. See article by Z. Jamil, p 193. Photo by Z. Jamil.

PALM NEWS

The palm collection at Ventnor Botanic Garden, Isle of Wight, United Kingdom, has been granted National Plant Collection status by the horticultural conservation organization Plant Heritage. The garden's palm collection began in the 1860s, when few gardens in the UK dared to grow palms outdoors. The garden, which bills itself as "Britain's hottest garden," now holds the National Collection of Palms (hardy and half-hardy) thanks in part to its nearly frost-free site. One gem of the collection: an avenue of *Jubaea chilensis* that will mature in 50–100 years.



In related palm garden news, Montgomery Botanical Center's M. Patrick Griffith et al. published an analysis of how botanical gardens can contribute to ex situ conservation efforts in the palm family. They also identified gaps in palm collections. The gap analysis will help botanical gardens and other conservation organizations target species for ex situ collection. The work, published in *Frontiers in Forest and Global Change* (4: 711414. doi: 10.3389/ffgc.2021.711414) is open access.

Mexico is home to nearly 100 species of palms, but their distribution in the country is poorly known. In a new publication, Macedo-Santana and colleagues modeled distribution patterns and examined environmental factors that contribute to palm species distributions. Only about half of the species had sufficient data to be used in the modeling exercises, which found that precipitation was a major driver of palm distributions for many species. The researchers identified palm-rich areas in the country, especially in the southeast and the central Pacific coast, that could be targeted for palm conservation. The work was published in *Ecoscience* 28: 137–147. 2021.



Some cities in Florida are moving away from palms in municipal landscapes in the belief that other trees might slow climate change because they are better than palms at sequestering carbon and removing ozone. These cities are basing their decisions on comparative data provided by the US Forest Service and the Arbor Day Foundation: A live oak (*Quercus virginiana*) sequesters 487 lbs. of carbon per year, a mahogany (*Swietenia mahagoni*) sequesters 623 lbs. and a thatch palm (*Thrinax radiata*) sequesters a mere 2 lbs. For ozone capture, the scores are oak 48 oz., mahogany 44 oz. and thatch palm 5 oz. One might legitimately question why one of the smallest Florida palms was used in this comparison. Oaks and mahoganies are much larger than the thatch palm, so it is no surprise that their numbers are greater. It would be useful to see carbon sequestration calculated per unit of leaf area.

Furthermore, although palms may not be champions at carbon and ozone capture, they uniquely provide the tropical ambiance that visitors to Florida expect. Their value to the tourism industry likely far exceeds that of oaks and mahoganies.

Calyptrocalyx calcicolus, a New Species from the Highlands of New Guinea

JOHN DRANSFIELD¹ AND LUCY T. SMITH¹

Calyptrocalyx calcicolus, a small undergrowth species from karst limestone in the Southern Highlands of Papua New Guinea, remarkable in its possession of a conspicuous staminal tube, is described as new.

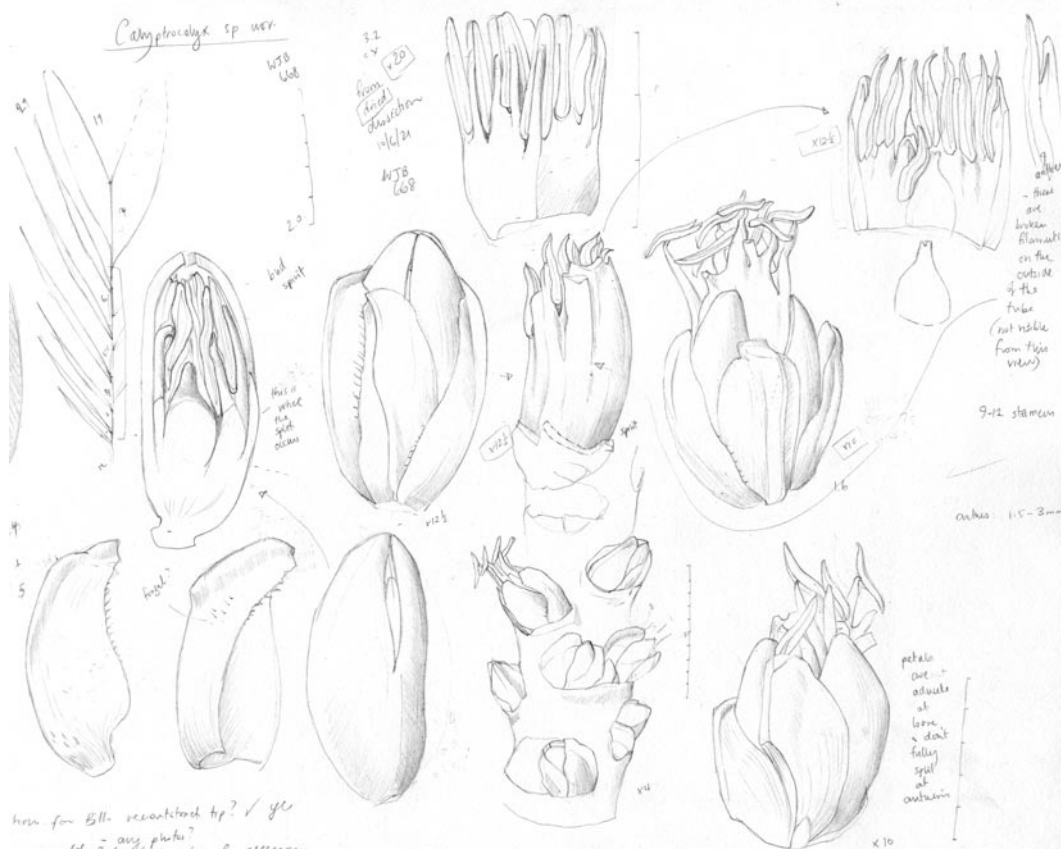
In 1999, John Dowe and Michael Ferrero described an extraordinary new species of *Calyptrocalyx*, *C. doxanthus*, that was grown by Gregori Garnaedi Hambali in his nursery on the outskirts of Bogor in Java (Dowe & Ferrero 1999a, 1999b). The palm had been collected originally in the Cyclops Mountains near Jayapura in Indonesian New Guinea. A beautiful palm with clustering habit and mottled sigmoid leaflets ending in drip tips, the species is most distinctive in its androecium. The filaments of the stamens are united in a fleshy tube, with the anthers pendulous to the inside of the tube. This type of androecium was unknown elsewhere in the genus. While searching through unnamed specimens of *Calyptrocalyx* in Kew in preparation for the account of the genus for the Palms of New Guinea project one of us (JD) came across a collection made by Bill Baker in the Lake Kutubu area of Papua New Guinea that shows a similar, but not identical,

form of androecium (Fig. 1). Indeed, the collector noted in the field that the filaments are united in a tube. Rather than pendulous into the mouth of androecium tube, as in *C. doxanthus*, the anthers are initially erect then at anthesis are spreading. Androecial details were further discovered as the analytical plate was being prepared (LTS) (Fig. 2). It has not been possible to match Bill Baker's collection with any described species, and so it is described and named here for the first time.

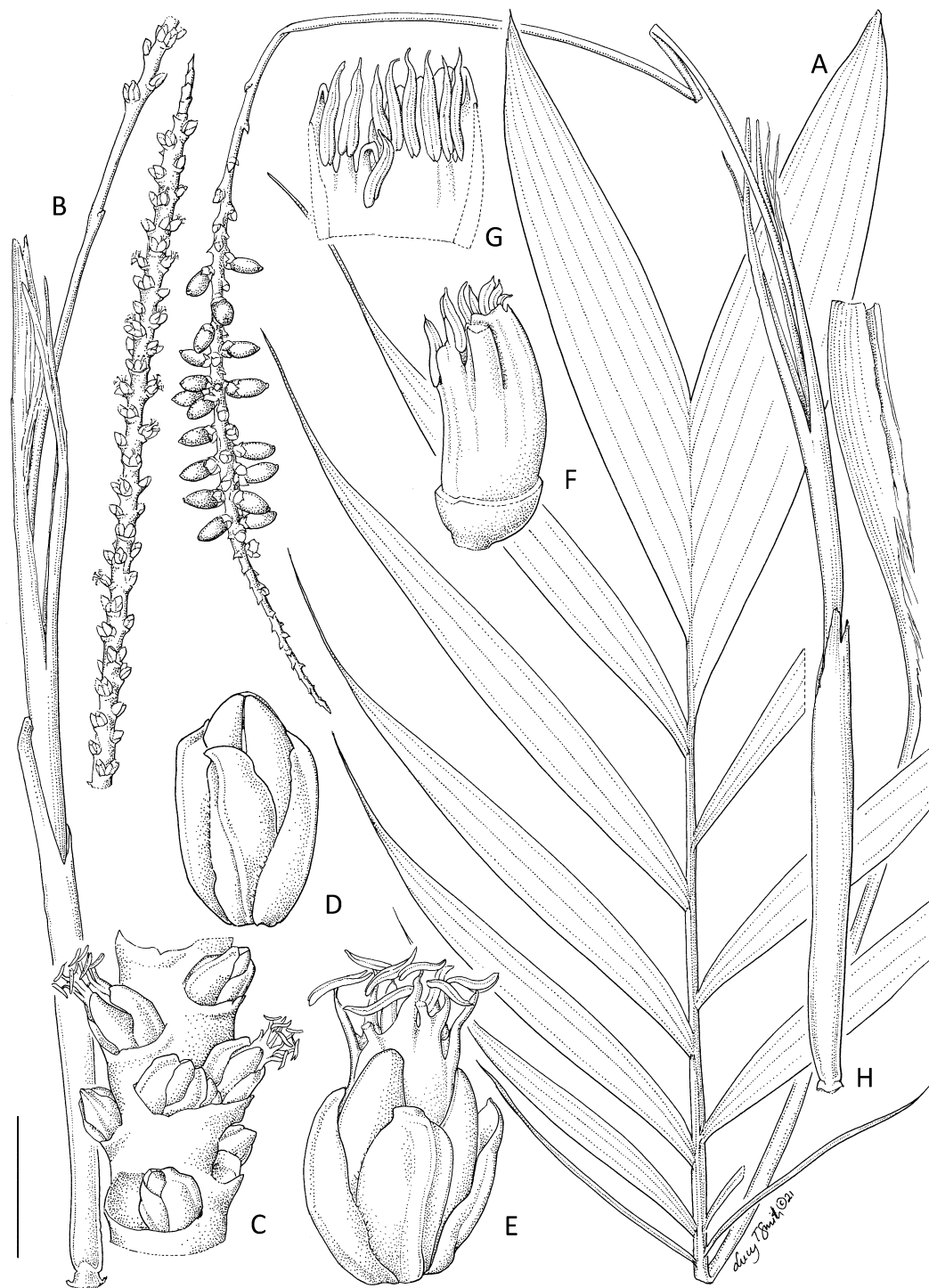
Calyptrocalyx calcicolus J.Dransf. & L.T. Smith, *sp. nov.*

Small clustering palm distinctive in its lanceolate leaflets with long drip tips, inflorescences a solitary spike with the rachilla portion much wider than the peduncle and covered with dense pale brown scales and the androecium composed of 9–12 stamens, the filaments united in a conspicuous cup with erect, later spreading anthers and homogeneous endosperm. Type: Papua New Guinea. Southern Highlands: Lake Kutubu, Wanunuku, forest on karst limestone, 900 m alt., 13 February 1996, W.J. Baker 668 (holotype K; isotypes BH, LAE).

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1 (top). *Calyptrorcalyx callicolus*. Detail of inflorescence, showing stamen tube, Lake Kutubu, Papua New Guinea (Photo: Bill Baker). 2 (bottom). *Calyptrorcalyx callicolus*. Preliminary pencil sketches of floral details illustrating the unusual arrangement of stamens. Drawn by Lucy T. Smith.



3. *Calyptrocalyx callicolus*. A. leaf; B. base of inflorescence; C. close-up of part of spike; D. staminate flower bud; E. staminate flower at anthesis; F. stamen tube; G. stamen tube opened out; H. infructescence. Scale bar: A = 6 cm; B, H = 4 cm; C = 1 cm; D, E = 4 mm; F, G = 3.3 mm. A–G from W.J. Baker 668, H from W.J. Baker 660. Drawn by Lucy T. Smith.

Slender clustering, unarmed, pleoanthic, monoecious palm. Stem erect, 1.2–1.5 m tall, to 1.6 cm diam., internodes 3–5 cm long, crownshaft absent. Leaves 6 in crown, regularly pinnate, to 80–85 cm long, sheath to 13 × 2.5 cm, dull green with scattered dark scales, the margins fibrous; petiole 34–40 cm long, 3 mm wide, with abundant dark scales; rachis 36 cm long, ± triangular in section, tapering to 1.5 mm diam.; leaflets 5–7 on each side of the rachis, arranged regularly, apical pair multifold; proximal leaflets very slender 12 × 0.5 cm, mid leaf leaflets lanceolate, 20–30 × 2–2.5 cm acuminate in a conspicuous drip tip, apical leaflet pair multifold, to 45 × 5 cm, irregularly lobed, both leaflet surface bearing scattered dotlike dark scales. Inflorescences solitary in the axil, spicate, interfoliar, 50–70 cm long, becoming pendulous; peduncle 35–45 cm long, 2.5 mm diam, with scattered dark scales; prophyll papery, apically disintegrating into fibers, 15 × 1–1.5 cm, with abundant dark scales; peduncular bract similar to the prophyll, 30 × 1.5 cm with abundant dark scales; rachilla portion conspicuously fatter than the peduncle, to 10 cm long, 5 mm diam. with congested floral pits and abundant mid brown scales, the rachilla bracts rounded triangular. 3 mm long, 5 mm wide, forming conspicuous lips to the floral pits. Staminate flowers in bud 6 × 3 mm; sepals 3, keeled, free, imbricate, 6 × 3 mm, straw-colored, very densely covered in shiny pale scales; petals valvate, 6 × 2.5 mm, densely covered with shiny pale scales; stamens 9–12, 5 mm long, filaments 4 mm long, united to form a tube, with a short variable free part, inflexed towards the tip, sometimes free filaments borne external to the staminal tube; anthers inflexed, erect in bud, then irregularly spreading at anthesis, 1.5 × 0.3 mm; pistillode small, conical. Pistillate flowers in available specimens immature. Fruit ellipsoid (im-

mature) drying somewhat irregularly angled, dull green, densely covered with scales, stigmatic remains apical. Seed 10–11 × 5 mm, ellipsoid, endosperm homogeneous, embryo sub-basal. (Fig. 3).

Specimens examined: NEW GUINEA. Papua New Guinea. Southern Highlands: Lake Kutubu, Wanunuku, near to Tugiri, WWF Integrated Conservation and Development Project Area, premontane rain forest on karst limestone, 900 m, 13 Feb. 1996, *W.J. Baker 668* (holotype K; isotypes BH, LAE); Moro District, Ulisili, near Sisibiu oil well, WWF Integrated Conservation and Development Project Area, dense forest on exposed limestone ridge, 860 m, 12 Feb. 1996, *W.J. Baker 660* (K, KEP, LAE); Kantobo, between Wassi Falls Lodge and the Falls, alt. 470 m, 9 Feb. 1996, *W.J. Baker 639* (FTG, K, LAE).

All three collections were made in forest developed on karst limestone.

Calyptrocalyx calcicolus can be immediately distinguished from *C. doxanthus*, the only other species with a staminal tube, by its solitary habit, lanceolate, not sigmoid, leaflets and the dense covering of overlapping straw-colored scales on the inflorescence. Relationships with other species in the genus are not obvious and, indeed, it may not be close to *C. doxanthus*.

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Thirty Years of Conserving Sargent's Cherry Palm (*Pseudophoenix sargentii*) in the Florida Keys

JENNIFER POSSLEY¹, JANICE DUQUESNEL² AND VANESSA
McDONOUGH³

Pseudophoenix sargentii H.Wendl. ex Sarg., commonly called Sargent's cherry palm, the Buccaneer palm, or the Florida cherry palm, is a striking palm tree that can reach 8 meters in height (Zona 2002), has prominent leaf scars along its trunk, and densely pinnate, blue-green fronds (Fig. 1). Although *P. sargentii* is the most widely distributed member of the Caribbean genus *Pseudophoenix* (Zona 2002), it is considered globally vulnerable by the IUCN for continued decline and increasing threats throughout its range (Carrero 2021).

Pseudophoenix sargentii, which grows on limestone or sand over limestone (Zona 2002), is primarily distributed in the Bahama Archipelago and the Greater Antilles, with additional occurrences in Mexico's Yucatan Peninsula, Belize, Dominica, and Florida, USA (Zona 2002). Although this species is not federally listed under the US Endangered Species Act, *Pseudophoenix sargentii* is an endangered species in Florida (Weaver &

Anderson 2010), where it is restricted to the Keys.

Florida's beleaguered palm

The Florida population of *P. sargentii* has had several strikes against it since it was first discovered by the American botanist Charles Sprague Sargent in 1886. This beleaguered species bears an unfortunate resemblance to the once highly sought-after royal palm (*Roystonea regia* (Kunth) O.F.Cook), which led to rampant harvesting shortly after its discovery (Ledin et al. 1959). Over-collection was responsible for the severe reduction in what was already a limited range. The palm is extremely slow growing, with first flowering in-situ not occurring for two, sometimes three decades (Maschinski & Duquesnel 2007). An unknown and potentially lethal fungal pathogen affects the crown shaft and apical bud of some mature trees (Ledin et al. 1959, Edelman & Richards 2013, Magellan & Griffith

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1. Adult *Pseudophoenix sargentii* on Elliott Key in 2007. Photo by Kristie Wendelberger (FTBG).

2017). A final strike against the species' persistence in Florida is that wild seedling mortality has been and continues to be high, likely due to herbivory by small mammals (Ledin et al. 1959, Lippincott 1995, O'Hare & Dalrymple 2000, Maschinski & Duquesnel 2007).

In the United States, *P. sargentii* has only been documented on three islands in the Florida Keys: Elliott, Long and Sands Keys (Fig. 2). The habitat and history of human use on each island varies considerably. Elliott Key is a 12 km long, 0.5 km wide limestone ridge that rises no more than one meter above sea level,

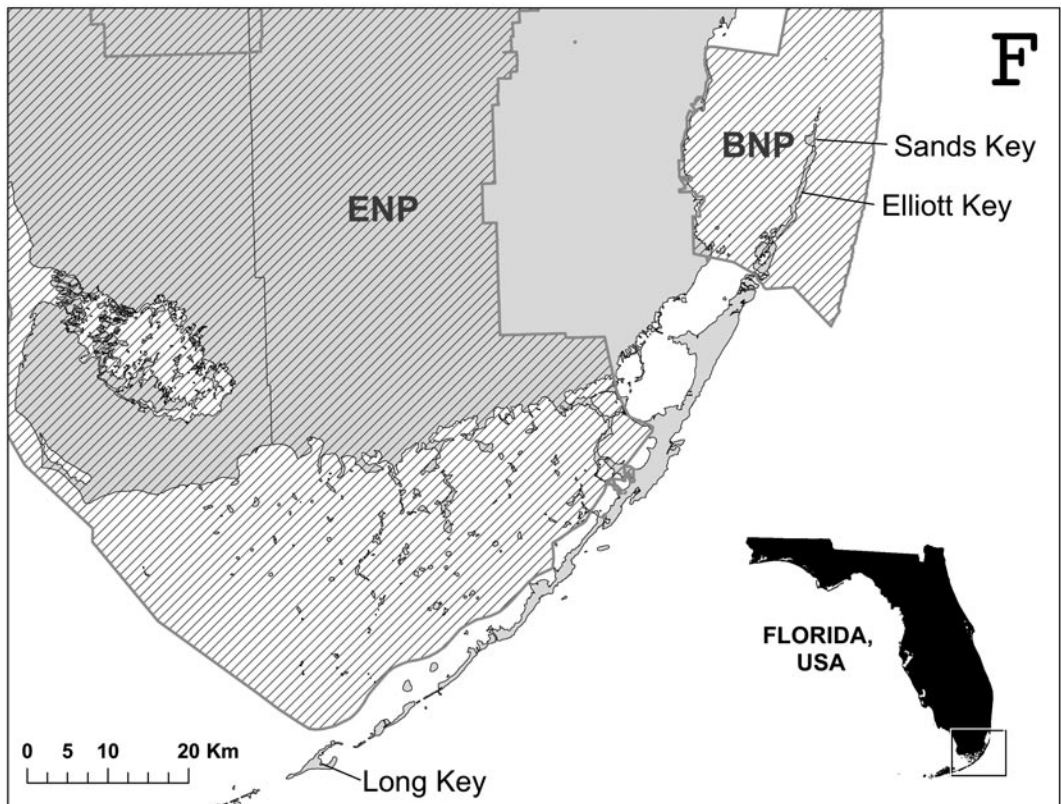
off the east coast of mainland Miami-Dade County. The island and surrounding waters are part of Biscayne National Park (BNP). Although today the island is densely vegetated with hardwood hammock in the (relatively speaking) highest elevation portions and with tidal marsh and mangrove in lower-lying areas, large swaths were razed for a pineapple plantation in the mid-1800s, prior to the species' discovery. Sands Key lies to the immediate north of Elliott Key and is tiny in comparison, at 1.5 km wide by 2.5 km long. Most of the island is mangrove forest, though a narrow band of hammock runs through its center, and small areas were cleared for homesteading in the early 20th century (pers. comm., J. Marano, BNP Maritime Archeologist). Long Key is nearly 90 km south of Elliott Key. It is the only island in the historic range of *P. sargentii* that is connected by road to the mainland, and thus has experienced greater poaching and development pressure. However, much of the island is now protected in Long Key State Park.

Pseudophoenix sargentii was extirpated from Sands Key not long after 1925 (Ledin et al. 1959) and from Long Key at some point in the 1960s (Lippincott 1992). The sole wild population of this species in Florida is on Elliott Key, within BNP.

The last wild population in the United States

To our knowledge, large-scale, island-wide censuses of the last remaining US population of *P. sargentii* on Elliott Key were not conducted until the 1990s when staff from BNP, Florida Park Service (FPS), and Fairchild Tropical Botanic Garden (FTBG) first collaborated to attempt this endeavor. Surveys were conducted by staff and volunteers over multiple days, and in the beginning, were aimed at detecting and mapping all *P. sargentii* on the island, from the smallest seedling to the largest mature tree. This task took several years to "complete," though due to the dynamic nature of wild plants, surveys and mapping efforts continue to this day. During this same period, surveys were conducted on Long and Sands Keys,

2. Locations of the three Florida islands on which *P. sargentii* was historically known to occur: Sands and Elliott Keys are in the Upper Keys and Long Key is in the Middle Keys. Everglades (left) and Biscayne National Parks (right) are indicated by cross-hatching.





3. *Pseudophoenix sargentii* on Elliott Key in 2003. This “large juvenile” has begun to develop a trunk but has not yet flowered. Photo by Kristie Wendelberger (FTBG).

which confirmed that the species was truly extirpated from these islands. By 2003, most of the Elliott Key population was thought to have been mapped and tagged. We thus shifted effort away from detecting new plants and toward re-monitoring known plants, allowing

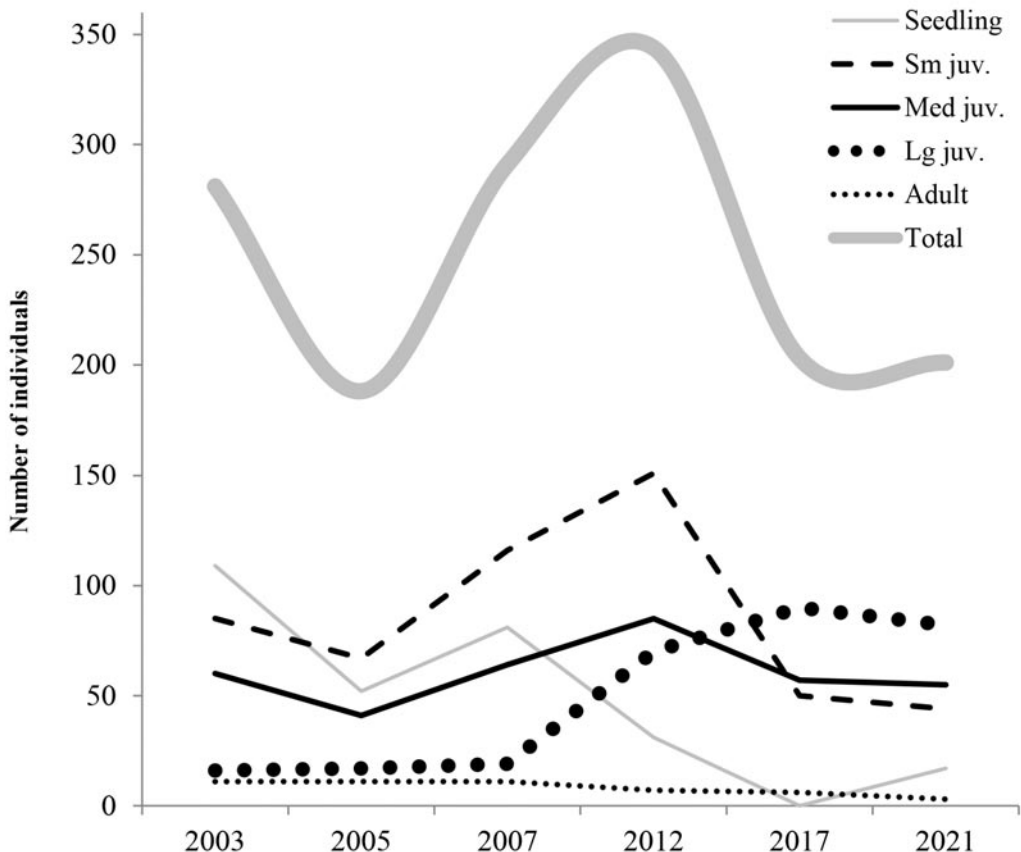
us to draw conclusions about the trajectory of this population (see Maschinski & Duquesnel 2007). Since that time, we have monitored every two to four years, and now have two decades of population trends which can inform conservation management decisions.

At present, wild *Pseudophoenix sargentii* palms are located solely within the hardwood hammock plant community on Elliott Key and are distributed in three uneven clusters on the northern third of the island. As of 2021, the total number of known wild *P. sargentii* on Elliott Key is 201. Reproductive palms make up less than 1.5% of the total wild population (just 3 individuals) and seedlings are also scarce, comprising 8.5% of the population (17 seedlings). The bulk of the population is in the juvenile stage. Using subcategories suggested by Maschinski and Duquesnel (2007), nearly half of the population is in the “large juvenile” stage, with a height of at least 1.6 meters (Fig. 3). Since regular monitoring began in 2003, the number of known large juvenile *P. sargentii* on Elliott Key has increased more than 500%, with approximately 2/3 of the individuals being newly located during 2005-2021 monitoring events and 1/3 that were present in 2003 as seedlings or juveniles.

Over the past three decades, the total known number of *P. sargentii* on Elliott Key has fluctuated widely. Lippincott (1992, 1995) reported 47 palms in 1990; this number was reduced to just 28 after a direct hit from Hurricane Andrew in 1992. Eleven years later in 2003, the population had swelled to 281 and reached an all-time high of 344 in 2012 (Fig. 4). More recent surveys in 2017 and 2021 found approximately 200 individuals. Although some variance in population numbers is likely due to differences in sampling effort, we can attest that all population censuses were conducted over one or more days, using the same methods and always with one or more biologists who had participated in a previous survey. Thus, we believe the population fluctuations shown in Figure 4 reflect true shifts in population numbers, and not sampling artifact.

The beleaguered Elliott Key population of *P. sargentii* has weathered its fair share of setbacks.

4: Total number of *Pseudophoenix sargentii* individuals (wild + planted) on Elliott Key, grouped (wide gray line) and separated by size class, during repeated censuses of the same known geographic area conducted by staff of Fairchild Tropical Botanic Garden, the Florida Park Service, Biscayne National Park and collaborators between 2003 and 2021.



The direct hit from (Category 5) Hurricane Andrew was the most dramatic negative impact in recent decades, but more subtle misfortunes have proven more lethal. Almost all adult palms on the island have succumbed to the deadly-but-unidentified fungal pathogen or else have died after their apical bud was damaged by falling branches from adjacent hardwoods (the species seems to be especially sensitive to this). Seedlings and small juveniles often fall victim to herbivory by small mammals that remove nearly all photosynthetic tissue. With heavy losses of young and old, it is clear why juvenile palms comprise the bulk of the wild population.

On the positive side, there are signs of hope for *P. sargentii* on Elliott Key. In 2020, we documented fruiting in one of the three remaining wild adults, adding a much-needed influx of seeds to the population. This individual may have fruited annually in recent years; our monitoring is infrequent enough that we very likely miss some reproductive events. Intriguingly, we documented 13 new seedlings at the largest cluster of *P. sargentii* on Elliott Key this year, despite the fact that the nearest fruiting tree is more than a kilometer away. The last known adult plant at the largest cluster was recorded in poor health in 2012. This species is not known to have a long-lived seed bank, but seeds may exhibit some level of dormancy. Another possible explanation for seemingly new seedlings in areas that lack reproductive adults is that the fruits were dispersed there by one of the few mammals present on the island, namely raccoons, marsh rabbits, or Mexican red-bellied squirrels (O'Hare & Dalrymple 2000). However, in their four-month study using infrared, motion-triggered cameras to record potential dispersers and predators of *P. sargentii* on Elliott Key, O'Hare and Dalrymple (2000) did not detect any direct interactions between mammals and fruits of *P. sargentii*. Finally, it should be noted that *P. sargentii* seedlings could be present for years before they begin to produce pinnate leaves that are likely to catch the eye of a biologist. Seedlings of *P. sargentii* look very similar to those of *Thrinax radiata* Lodd. ex Schult. & Schult.f., which is more plentiful on Elliott Key. Differentiating the two species before pinnate leaves form requires careful study of the point where the petiole meets the base of the blade.

Finally, it is important to acknowledge that thorough systematic surveys of the island for

undetected *P. sargentii* have not been implemented in many years. Staff time and funding typically only allow revisiting of known plants. In 2021, we spent approximately 12 person-hours searching for undetected plants, which resulted in documenting 12 new individuals. These encouraging finds demonstrate the need for further detailed surveys throughout the island.

Ex-situ conservation collections

Prior to and during efforts to recover *P. sargentii* in Florida, FTBG, BNP and FPS have been carefully building an ex-situ collection of *P. sargentii* at FTBG. With such a small wild population that faces so many varied threats, an off-site "back-up" for wild palms was viewed as especially critical.

FTBG's ex-situ collections of *P. sargentii* from Elliott Key began in 1954 when marine taxidermist and conservationist Al Pfeuger dug up one of the trees from the then privately-owned island and gave it to FTBG. One more tree was obtained in 1958 when Gerard Pitt, Stanley Keim and Robert Read extracted a 4-foot-tall palm. Both trees lived for decades (39 and 46 years, respectively) in FTBG's collections. FTBG did not receive *P. sargentii* seeds from Elliott Key until 1982, when BNP staffer Craig Hauke collected 100 fruits for propagation by FTBG and the nearby USDA Agricultural Research Service office at Chapman Field. These seeds were the basis of the reintroduction efforts which began a decade later.

In the 1990s, staff from FTBG, FPS and BNP began periodic collection of *P. sargentii* seeds from Elliott Key, with the intention of establishing conservation collections of the attractive palm. Palms were grown and planted at FTBG. As of 2021, FTBG's living collections of *P. sargentii* originating from Elliott Key include 23 established trees from 8 separate accessions which were directly collected (as seed) from the wild and approximately 120 seedlings that were grown from two of these ex-situ trees (Fig. 5, Table 1). Most wild collections were made between 1990 and 2001, though a single seedling was grown from a seed collected from a wild adult in 2020. Additional wild collections will be made in the future, as seeds are available, and following conservation guidelines (CPC 2019). FTBG has shared *P. sargentii* of Elliott Key origin with other botanical institutions, including Montgomery Botanical Center, Vizcaya



5. *Pseudophoenix sargentii* propagation and cultivation at Fairchild Tropical Botanic Garden. A. A young adult palm (FTG Accession #2001-0920 from Elliott Key) in the Garden's lowlands (2020, R. Hammer). B. Seedlings grown from seeds collected at Fairchild, from palms of Elliott Key provenance (2021, B. Harding). C. Fruits, some with one or two aborted ovaries (2003, C. Lewis). D. Seeds with the endocarp cracked allowing them to imbibe water prior to sowing, which hastens germination (2021, J. Possley).

Museum and Gardens, Naples Botanic Garden, and Naples Zoo at Caribbean Gardens. The importance of ex-situ collections and sharing material cannot be overstated. In this regard, conservation of *P. sargentii* has been highly successful. Recent work by Hoban et al. (2020) suggested that ex-situ holdings of *P. sargentii*

in botanical gardens conserve at least 95% of the species' genetic diversity, when extremely rare alleles are not considered.

Reintroductions: 1990s and today

While comprehensive efforts were underway by the 1990s to document the last remaining

Table 1. Living collections of <i>Pseudophoenix sargentii</i> from Elliott Key at Fairchild Tropical Botanic Garden, as of May 2021, including 23 planted palms and approximately 120 potted seedlings. All material was grown from seed.					
Year Re- ceived	Accession #	Collector	Origin	Location	Quantity
1990	90404	Carol Lippincott (FTBG)	Elliott Key	Garden	1
1991	9170	Ann Deaton (DEP)	Elliott Key	Garden	1
1991	9171	Ann Deaton (DEP)	Elliott Key	Garden	1
1991	9172	Ann Deaton (DEP)	Elliott Key	Garden	1
1991	941066	unknown	Elliott Key	Garden	1
2001	2001-0082	Dena Garvue (FTBG)	Elliott Key	Garden	1
2001	2001-0920	Dena Garvue (FTBG)	Elliott Key	Garden, Farm	14
2020	2020-0001	Brian Harding (FTBG)	FTBG 941066	Nursery	ca. 40
2020	2020-0028	Brian Harding (FTBG)	FTBG 90404	Nursery	ca. 80
2020	2020-0212	Vanessa McDonough (NPS)	Elliott Key	Nursery	1

population of *P. sargentii* in Florida, a movement formed to recover the species throughout its historical range. Concerned citizens and biologists from FTBG, BNP, and FPS formed an ad hoc working group to collect wild fruits, grow palms, and reintroduce them to habitat within the historic range (Lippincott 1995). A total of 168 plants grown from seeds collected from Elliott Key palms were transplanted onto Elliott, Sands, and Long Keys from 1991 through 1994. The three palms that were planted on Sands Key did not survive, and no further efforts were made to reintroduce *P. sargentii* to that island. Efforts on Elliott and Long Keys, however, were met with more success.

Elliott Key: From 1991 to 1994, the ad hoc working group out-planted 63 *P. sargentii* on Elliott Key. Augmentations were conducted in the summer, despite staggering mosquitos, to take advantage of South Florida’s rainy season. Out-planted palms ranged in size from one-year-old seedlings with just two leaves to larger juvenile palms which were seven to ten years old and up to 2 meters tall. Palms were planted in five widely spaced hardwood hammock locations across the island. Fifty-seven of the palms were planted several hundred meters north and south of the naturally occurring

plants, and six were planted among the smallest naturally occurring cluster of 10 seedlings.

Three decades later, in 2021, only seven (11.1%) of the *P. sargentii* planted on Elliott Key have survived. While this ratio is low, it is similar to survival of wild plants we have documented from 2000 to 2021 (9%, 10% and 21% at three separate clusters). Four of the seven surviving outplants are palms that were planted within the naturally occurring population, suggesting that future efforts might focus on augmenting known, natural clusters of *P. sargentii* instead of establishing new ones. Two of the larger outplants installed in the early 90s have flowered, with the first signs of flowering (an old flower stalk) observed in 2017. Unfortunately, the tree which was first to flower was observed to have been damaged by a fallen tree limb in 2017 and died by 2021. But the other flowering outplant survives, and five more will be large enough to flower in the next decade, should they survive. While no seedlings have yet been detected near the palms that flowered, these reproductive and soon-to-be reproductive palms are poised to substantially contribute to the next generation of *P. sargentii* on the island. . . we can only hope.



6. Reintroduced *Pseudophoenix sargentii* on Long Key. A. A young outplant protected by an herbivore exclusion (2008, J. Maschinski). B. Janice Duquesnel measures the height of an outplant (2004, J. Maschinski). C. One of the original outplants from the 1990s which has developed a trunk but has not yet flowered (2019, J. Duquesnel). D. One of the large juveniles that was planted in 2019 (2021, J. Duquesnel).

Long Key: The reintroduction of *P. sargentii* to Long Key is significant not only for the long-term goal of conserving this species, but also because it was the first reintroduction project in a Florida State Park. Initial out-plantings occurred in 1991, 1993 and 1994, with 199 individuals planted at six locations. Four of the chosen recipient sites were coastal berm habitat, and two sites were hardwood hammock. Most out-plants were small juveniles approximately 0.3 m in height. Five medium juvenile palms that were six-years old and 1.2 m in height were out-planted at two locations. In addition, nine seeds were sown at one site, and 19 seedlings were planted at two sites. Monitoring was conducted monthly for the first year to determine survival rate. None of the seeds germinated, and all 19 seedlings died shortly after planting. After the first year, monitoring was conducted annually for nearly 30 years. Compared to the reintroduction on Elliott Key, palm health on the Long Key introduction was monitored much more frequently, and we thus have more insight into what drove population trends of this introduced population on Long Key.

Herbivory on *P. sargentii* fronds was documented soon after outplanting. FPS installed herbivore exclosures (Figure 6) around all but the largest (six-year-old) palms, which were undamaged. Cages remained around the palms and no herbivory was documented again until 1999, when a hermit crab was observed perched on an exclosure eating a palm frond. In 2000, using the original height of the six-year-old palms as a guideline, FPS began removing the exclosures from any palm that was 1.5 m or taller. In rare cases, the cage was removed earlier, if it appeared to be causing damage to the palm.

Growth and development were inconsistent across the Long Key out-planting sites. Although some palms have only grown 0.6–0.9 m in 26 years, others have grown several meters. The six-year-old palms that were out-planted in 1991 were the first to develop trunks. True trunks were first observed in 2005 when these palms were 20 years old.

Causes of Long Key outplant mortality have varied and have included lightning strikes, poaching, and the sometimes-synergistic factors of hurricanes, sea level rise, and habitat loss. These last causes were particularly impactful for *P. sargentii* planted on the coastal berm at the southwest end of Long Key State Park. Shoreline erosion has been problematic

since at least the 1990s. Erosion during the 2004/2005 hurricane season killed 19 palms, and six more died after losing habitat to Hurricane Irma in 2017. As a result of the degree of mortality from hurricanes, FPS planted 12 additional palms of Elliott Key provenance that were sown as seed by FTBG in 2001. In 2019, six medium juveniles and six large juveniles were planted into hammock and coastal berm on Long Key. One was poached, and one died, but the others remain healthy (Fig. 6).

Of the 211 *P. sargentii* that have been outplanted in Long Key State Park, 47 persist. Of these, 37 were planted in the 1990s (18.6% survival) and 10 were planted in 2019 (83.3% survival). As of 2021, only 18 palms have well-developed trunks, and no palms have reached reproductive maturity. However, most of the remaining palms are in the large juvenile stage.

What the future holds

Pseudophoenix sargentii is one of the rarest and most charismatic plant species in Florida. While its status in our flora remains tenuous, the overall population size on Elliott Key has been stable in recent years, with at least 200 individuals and a promising number of large juveniles, many of which will likely reach adulthood in the next decade. Large juveniles have demonstrated high survivorship in the past (Maschinski & Duquesnel 2007), so we feel it is reasonable to expect the number of adult *P. sargentii* on Elliott Key to increase in the future. While some may succumb to crown rot, our monitoring shows that others will survive to reproduce at least once.

At present, a “rebooted” *P. sargentii* ad-hoc working group is taking measures to mitigate threats to wild and reintroduced plants. On Elliott Key, plans include caging a portion of young palms in areas where seedling herbivory is highest and hiring tree trimmers to remove large hardwood limbs that stretch over the top of *P. sargentii* populations, especially adults and large juveniles. Monitoring efforts continue on both Elliott and Long Keys.

Through all efforts to conserve *P. sargentii*, climate change provides an unsettling undercurrent. Increasing severity and frequency of tropical storms threaten the survival of this species, by directly felling the palms, or by causing adjacent trees or branches to fall and damage the apical bud. Saltwater inundation during major storms will likely cause death to *P. sargentii* of any age class that

are subject to prolonged flooding. It is worth noting, however, that storms can also provide opportunity for seedling recruitment. Lippincott (1995) reported that, while Hurricane Andrew killed 19 of the island's tallest of the known 47 palms, shorter palms survived and even thrived in the post-storm canopy openings, "actively producing robust, deep green leaves." The Florida Keys are ground zero for global sea level rise, with loss of species and entire plant communities accelerating as salt water intrudes and habitats change (Ross et al. 1994, Maschinski et al. 2011).

With all of South Florida in the same boat, we carry out our work with imperiled species like *P. sargentii* knowing that the next step may be assisted migration, and that sharing germplasm from documented wild provenance with botanical institutions outside of our region will be paramount to keeping the Florida *P. sargentii* from disappearing forever.

Acknowledgments

The story of *P. sargentii* conservation in Florida is one of long-term commitment which is somewhat unusual in plant conservation, where changes in funding, personnel, and/or institutional priorities can easily extinguish a long-term project such as this one. Individuals are the driving force behind such efforts, but institutional commitment is needed as well. Thank you to our parent institutions FTBG, NPS and FPS for their long-term support of this work. Monitoring in 2021 was funded by the Florida Dept. of Agriculture and Consumer Services, Division of Plant Industry, under Agreement #027132. For assistance with field work and logistics we would like to thank Morgan Wagner, Michael Hoffman, Brian Lockwood, Shelby Moneysmith and Astrid Santini from Biscayne National Park; Eliza Gonzalez from Montgomery Botanical Center; Dallas Hazelton from Miami-Dade County; James Lange, Lydia Cuni, Brian Harding and Sabine Wintergerst, from Fairchild Tropical Botanic Garden; Mark Duncan and Chanell Guillaume from Long Key State Park; and Joseph Montes de Oca and Elizabeth Wu. For helpful comments on the manuscript, we thank Jonathan Flickinger, Andrea England, Rodrigo Bernal and an anonymous reviewer. Finally, thank you to the cooperators whose excellent past work on this project has laid the foundation upon which we stand today, especially Carol Lippincott, Rob Campbell, Ann Deaton, Jim Duquesnel, Dena Garvue and Joyce Maschinski.

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Update from the Authors: Just as this article was going to press, one of the reintroduced palms on Long Key was found by one of us (JD) to have flowered and produced hundreds of fruits (pictured, photographed by Long Key Park Manager David Morris). Undeniably, this long-awaited event (30 years, to be exact) bodes well for the future of *Pseudophoenix sargentii* in Florida!



Washingtonia from the Kofa National Wildlife Refuge, Arizona

LARRY R. NOBLICK¹, DANIELA NOBLICK¹ AND ANDREW STREET¹

In the Kofa National Wildlife Refuge, Arizona, a population of *Washingtonia* grows in a remote narrow desert canyon surrounded by Sonoran Desert vegetation. Some recognize it as a new species, while others do not. A recent study identified this population as a unique outlier, discontinuous from all other populations in the genus based on morphology, raising questions as to its true identity. Here, we examined the structural biology, focusing on leaf anatomy, to determine whether it warrants recognition as a separate *Washingtonia* species. Our results do not support a new classification of this isolated *Washingtonia* population.

History

On December 2, 1923, Orator F. Cook collected a palm from a narrow canyon in the Short Horn Mountains of southwestern Arizona, USA (Fig. 1). Just a few days later (December 5, 1923), the following newspaper headlines ensued: "Find New Species Palm Yuma County" (Anon. 1923), and "Botanist from Washington Establishes Existence of Genuine Palms at Quartzite" (Miller 1990). The Morning Sun of Yuma went on to report the story of how this new palm species had been discovered (Anon. 1923). To paraphrase: William Hoy of Quartzite discovered "genuine palms" in the vicinity of the North Star mine. Peter Robertson published the discovery in the Sun on August 1, 1923. Harry A. Gunning and H.G. McKeever, of the local Department of Agriculture, attempted to confirm the discovery, but not finding any on the first attempt, tried again on October 23 and found the palms with the help of R.D. Martin. They

returned to the site in December with Mr. O. F. Cook, a specialist in palm classification from Washington, D.C. The newspaper went on to report that "Mr. Cook intends to describe it as a new species to be called *Washingtonia arizonica*," and certain unique characteristics were mentioned, like its smaller size and self-pruning properties. Although Cook proposed the name of *Washingtonia arizonica*, he failed to publish it legitimately. Following botanical rules at the time, the simple newspaper article did not serve as a valid publication (fide Bailey 1936). Cook annotated the name "*Washingtonia arizonica* n[ov]. sp." and even added "type locality" on the label of a herbarium collection from Palm Canyon made by Loomis and Peebles in 1930 (AZU). Marcus E. Jones, a major author to the Contributions to Western Botany Journal, is given credit for coining the name *Washingtonia filifera* var. *arizonica* M.E.Jones (Bailey 1936, Tropicos 2021), but he also never legitimately published the name.

The Kofa palm

The *Washingtonia* palms growing at Kofa display certain unique features not commonly observed in *W. filifera*. *Washingtonia arizonica*

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1. Palm Canyon in the Kofa National Wildlife Refuge showing the narrow, steep walls of the canyon with with Daniela Noblick (ca. 5 ft.) for scale.

“*sensu* Cook,” unlike *Washingtonia filifera* (Rafarin) H.Wendl. ex de Bary, is reported to be self-pruning. On their 1930 collection label, Loomis and Peebles wrote: “Maximum height 30 ft., nearly all individuals self-pruning, the

usual ‘skirts’ absent.” Miller (1990), however, dispelled that idea when he visited and found some palms in the canyon with leaf petticoats touching the ground; but to be fair, Loomis and Peebles did report “nearly all.” When we

visited the area in 2015 and 2019, we saw charred marks on the palm stems and presumed that any former petticoats were destroyed by fire. The Forestry Service confirmed that the charred stems were a result of a 1953 fire, which seriously damaged the trees. Forestry Service brochures still insist that the palms are self-pruning as reported by Cook, Loomis and Peebles in the 1920s and 1930s, long before the last recorded fire, thus leaving the validity of this character in doubt. Other morphological differences include a shorter, thinner stem, smaller crown, smaller leaves with stiffer leaflets and most adults with narrower, spineless petioles (Villanueva-Almanza et al. 2018).

The habitat

Palm Canyon is now part of the Kofa National Wildlife Refuge established in 1939 to protect the dwindling big horn sheep population and other wildlife. Miller (1990) wrote:

These palms are still thriving in what is now called Palm Canyon. This is 18 miles south of Quartzite on U.S. 95, then some

eight miles east over a graded but rocky road to the entrance of the canyon in the Kofa Mountains. After a walk upward and inward through the deep canyon, palms may be seen growing on the floor of a very steep sided canyon, with very occasional ones perched hundreds of feet up on the sides where precarious footholds exist.

The *Washingtonia* palms at Palm Canyon (Fig. 1) are considered descendants of those growing there since the last periods of the North American glaciations, ca. 10,000 years ago (US Fish Wildlife Service 2014). As the climate dried and the vegetation transformed into the Sonoran Desert, the palms, once amply distributed, found refuge in isolated canyons sheltered by steep walls. Palm Canyon's main source of water is rainfall. Precipitation funnels from a plateau above cutting down through the narrow rocky canyon through a volcanic rock formation of rhyolite, leaving behind a boulder strewn south facing canyon floor (Fig. 2). The south facing slope of the canyon where the palms grow allows for warmer winter temperatures during the day (Villanueva-

2. Palm Canyon in the Kofa National Wildlife Refuge showing the narrow canyon with its boulder strewn south sloping floor, the small crowned palms lacking leafy skirts, and relatively thin slightly charred stems from the 1953 fire.





3. Palm Canyon's steep canyon walls only allow direct sunlight for a few hours each day.

Almanza et al. 2018), but the high canyon walls and narrow valley allow only a few hours of direct sunlight each day (Fig. 3). Because of the topography of the canyon, moisture is retained allowing the palms to survive there.

Carbon isotope discrimination, which indicates water use efficiency in plants, shows the Kofa palms to be very water-use efficient as evidenced by their high $\delta^{13}\text{C}$ values (-25.35‰), compared to those of the other *Washingtonia* populations (-26.43‰ to -29.31‰) (Pérez et al. 2021). Over the millennia, the slowly desiccating region has led to the selection of drought-resistant individuals, and the Kofa *Washingtonia* has evolved into the most xeric-adapted of all *Washingtonia*. To our knowledge, the next nearest population is in California at Clapp Spring, ca. 44 miles away or possibly spots along the Colorado River, ca. 28 miles away. Because of its geographic isolation, genetic exchange with other *Washingtonia* populations is unlikely.

Current population status

"Thriving" is not a word that should be used to describe the dwindling palm population of Palm Canyon; "tenaciously surviving" is better. Eighty-five years ago, Bailey (1936) recounted that:

This Arizona canyon has been explored recently for palms and Dr. Charles T. Vorhies of the Arizona Experiment Station writes me that in the main part of it and in a still narrower extension there are sixty-five trees. Small seedlings appear to have perished, apparently having been torn out by torrents of water. The big trees, however, are fruitful.

A population size of 65 persisted through 1960 (Kearney & Peebles 1960) but then shrunk to ca. 21 adult individuals according to a 1986 census (US Fish Wildlife Service, 2011) then to only 20 adults by 2014 (US Fish Wildlife Service, 2014) and finally 14 adults in 2018 (Villanueva-Almanza et al. 2018). We saw very few seedlings in Palm Canyon.

Two species or one?

Historically, the *Washingtonia* specimens on the southern end of the Baja California Peninsula have been called *Washingtonia robusta* H.Wendl. and the ones in the north, *Washingtonia filifera*. The two species can be easily distinguished when placed side by side: *W. filifera* has a stocky stem, stiff, dull green leaves with rigid, slightly pendant leaflets, whereas *W. robusta* has a slender stem, lax, glossy dark green leaves with very pendant leaflets (Fig. 4).



4. Side by side comparison of *Washingtonia* palms from (left) Kofa NWR-AZ, (middle) *W. robusta* at Montgomery Botanical Center and (right) *W. filifera*, Carrizo Grove near Castle Hot Springs-AZ.

Villanueva-Almanza (2018) and others conducted a comprehensive study, taking several measurements from numerous *Washingtonia* specimens occurring from the southern tip of Mexico's Baja California Peninsula (*W. robusta*) to its most northern populations in Southern California (*W. filifera*), and they discovered some interesting trends. The morphology of the palms changed gradually with latitude, leading them to question whether *Washingtonia* was really two species or just one. For example, *Washingtonia* stems tend to increase gradually in diameter from south to north along Mexico's Baja California Peninsula and into Southern California, USA. Thicker stems are thought to protect the apical meristem from freezing (Cornett 1987).

The results from Villanueva-Almanza et al. (2018) support a single *Washingtonia* species and the thicker-stem hypothesis with one exception: the palms at the Kofa National Wildlife Refuge (latitude 33.36), which are almost as slender as those from more southern latitudes (Villanueva-Almanza et al. 2018), despite experiencing temperatures as low as -13.9°C (NOAA, 2018). The survival of these slender-stemmed *Washingtonia* may be due to their topographic position more than latitude. Unlike palms in other oases, these individuals are growing on a south-facing slope, rather than at the bottom of a canyon, where winter temperatures are lower and remain so for a longer time as the denser, heavier cold air settles there, a phenomenon known as cold air drainage (Yoshino 1984).

To summarize, the Kofa palms are morphological outliers that have survived in a south-facing, narrow canyon for a long time, as either a relict palm or as an isolated invasive, with slender stems that may be self-pruning, and are the most xeric-adapted of the *Washingtonia*. The objective of this study and purpose of this paper is to examine, document and compare the leaf anatomy of the Kofa *Washingtonia* with other *W. filifera* and *W. robusta* palms and discuss our findings within the context of the recent morphological, ecological and genetic analyses discussed above.

Materials and methods

Material examined: We assembled leaf material from *Washingtonia* palms along its distribution range to examine leaf anatomy across different populations of this genus, including palms from the Kofa population, labelled as *W. filifera*. Fresh palm material from the Montgomery Botanical Center (MBC), Coral Gables, Florida (*W. filifera* and *W. robusta* H.Wendl.) and dried herbarium specimens from Fairchild Tropical Botanic Garden, Coral Gables, Florida (FTG) and the University of Arizona, Tucson, Arizona (ARIZ) were used in this study (Appendix 1). Fresh material was collected from palms grown from seeds that we collected from five mother plants at each of five different non-urbanized localities in Nevada, California and three localities in Arizona (Appendix 1) with the exception of Kofa, where we found seeds from only three adults. The seeds were photographed, sown

and germinated at MBC in the same soil mix. Several were germinated in individual tubes before transplanting to larger pots, while others were germinated in community pots and separated later. All were grown under similar temperature, light and moisture conditions. The 2015 collections from Nevada and California have been planted out in the garden, but the 2019 Arizona collections are still too young to leave the nursery. Whenever possible, one leaf segment halfway between the base and the tip of the fan-shaped blade was sampled, and the sections were taken halfway between the initial split from the leaf blade and where the leaflet splits a second time.

Anatomical preparation and imaging: Methods for hand sectioning follow Noblick (2013, 2017, 2021). For this study, a hand microtome (homesciencetools.com, USA) was used along with a Straight Razor 3" Full Hollow Ground Carbon Steel Blade (Dovo, USA), using a carrot cube for securing the specimen in the hand microtome. Slides were prepared using a drop of 1:1 glycerin. Images were captured with a compound trinocular microscope (AmScope, USA) with a 5 Mb digital camera and 10× objective (100× magnification). The images were cleaned of background spots, adjusted for brightness and sharpened if necessary using Adobe Photoshop. If the entire midrib or leaf margin did not fit into the field of view, adjacent images were photo merged using the automatic photo merging capabilities of Adobe Photoshop. A stage micrometer was used to apply a scale.

Results

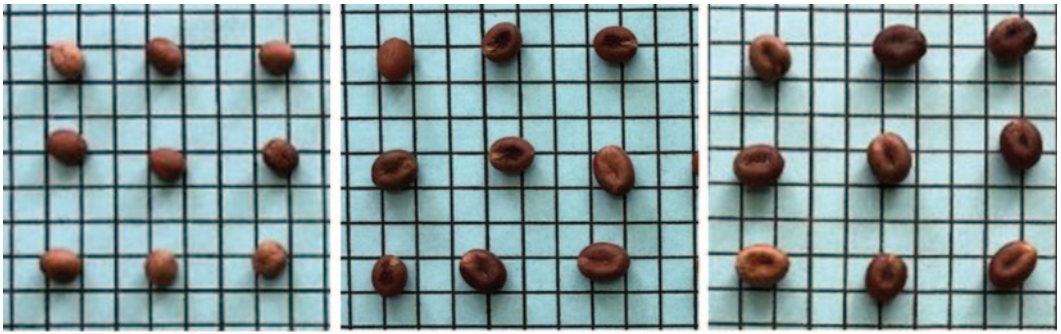
Placed side by side, mature Kofa palms look clearly different from other *Washingtonia* populations (Fig. 4). However young Kofa palms grown from seeds sown on the same day as other *Washingtonia* palms are nearly identical (Fig. 5), growing vigorously as any other *Washingtonia* and with their characteristic spiny petioles. The seeds collected from Kofa were smaller than those collected from either Hassayampa or the Carrizo Grove at Castle Hot Springs, Arizona (Fig. 6).

Leaflet margins of the young palm seedlings germinated from Kofa, Hassayampa and Castle Hot Springs differ little anatomically from one another (Fig. 7). The leaflet margins of 5–6-year-old palms grown from seeds collected in Nevada and Southern California (Fig. 8(top), B, C) are similar to a herbarium collection from Kofa NWR-Arizona (Darrow & Benson 10867) with the exception of extra tannins in the leaflet (Fig. 8(top), A). Mature leaves are consistently thicker with larger fibers than juvenile leaves as observed between juvenile leaves from Arizona (Kofa), Nevada and California, Fig. 8 (top), and mature adult leaves, Fig. 8 (bottom) from these same populations (note the scale).

The first leaflet specimen examined from Kofa (Noblick 5682, Fig. 9A) was markedly different than other *Washingtonia*. It had smaller, numerous fibers on both surfaces of the leaflet and smaller, differently shaped vascular bundles. This result initially prompted us to

5. Seedlings of the same age of *Washingtonia* from (left) Kofa NWR-AZ, (middle) Hassayampa River Preserve-AZ and (right) Carrizo Grove, near Castle Hot Springs-AZ.





6. *Washingtonia filifera* showing the slightly smaller seeds from Palm Canyon (left) as opposed to larger seeds from the Hassayampa River Preserve (center) and the Carrizo Grove near the Castle Hot Springs Resort (right). Grid is 0.5 cm.

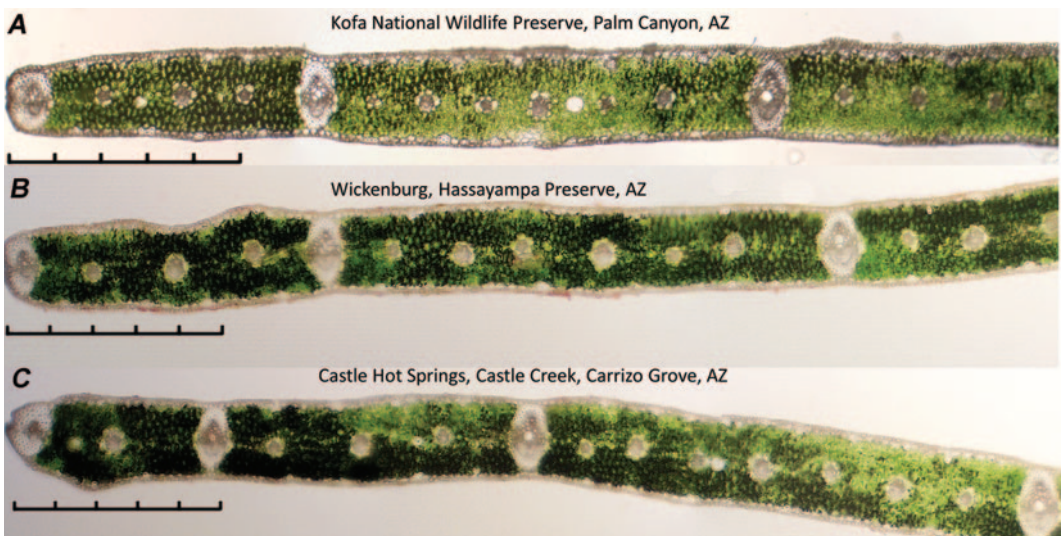
interpret this *Washingtonia* as a separate species just like O.F. Cook in 1923. Then, in order to verify, we sampled a second and third margin from the same leaf, which revealed very little difference from other *Washingtonia* (compare Fig. 9B–D with 9F–J). This illustrates the importance of examining multiple samples from the same leaf to avoid premature conclusions. Comparing Kofa palms (Noblick 5682, and Willson 37782 and Darrow & Benson 10867) on the top row to those from other localities on the bottom row from Arizona, Nevada, California and Mexico we found them all to have similarly large and similarly shaped vascular bundles and large fiber strands (Fig. 9).

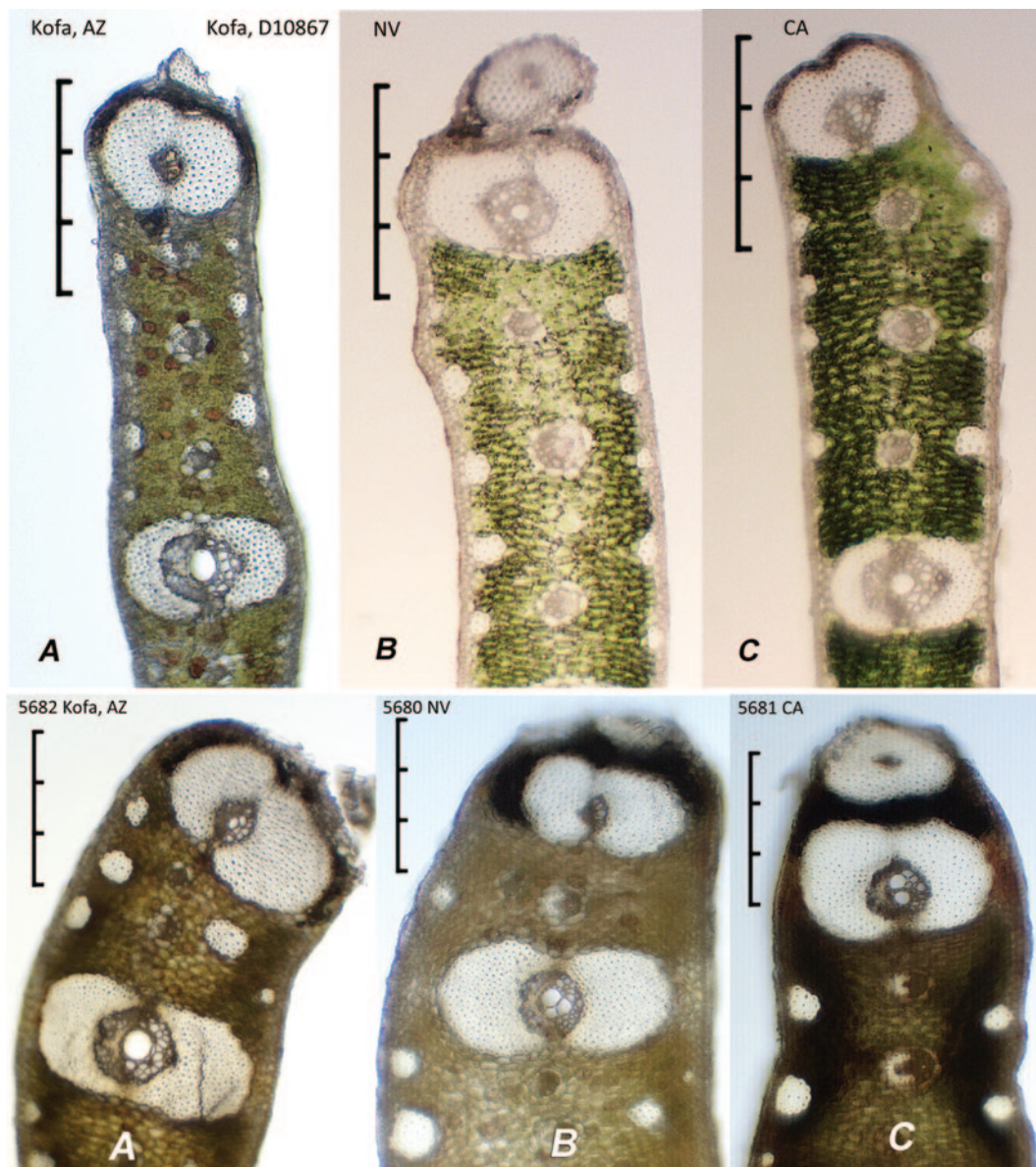
Next, we compared leaflet anatomy between the Kofa palms (Fig. 10A, B) and *W. robusta* (Fig. 10C). Although the margins on the top row are quite similar, the midribs on the

bottom row are different with the *W. robusta* having a narrower and deeper V shape. So even though both *Washingtonia* share a thinner stem, the Kofa palm leaves are stiff with non-pendulant leaf segments and have anatomically different-looking midribs.

There are few differences between the midrib of the Kofa palms and the other *W. filifera* types. The Kofa midrib is a bit smaller (0.9–1.1 vs 1.1–1.5 mm, see Fig. 11)), and sometimes flatter on the adaxial surface (Fig. 11A, 12A, B) when compared to the others that have an open U or even a slight V shape (Fig. 11B–C, E–G). The center midrib parenchyma cells of the Kofa palms are arranged in a more or less radial pattern fanning out from the center of the adaxial surface of the midrib (Fig. 12). Not all Kofa specimens are flat on the adaxial surface (Fig. 12C, D, Willson 37752), but they all clearly show the radial symmetry of their

7. The seedling leaflet margins of *Washingtonia filifera* grown from seed from the Kofa NWR, Hassayampa, and the Carrizo Grove in Arizona showing how anatomically similar they are to one another. Scale is 0.5 mm.





8. Comparison of juvenile (top) and mature (bottom) *Washingtonia* margins from the same areas. (A) *Washingtonia*, Darrow and Benson 10837 (top) and Noblick 5682 (bottom) from the Kofa NWR-AZ. (B) Noblick 5680 (top and bottom) from Moapa NWR-NV. (C) Noblick 5681 (top and bottom) from the Coachella Preserve-CA. The Kofa collection (Darrow and Benson 10837) was most likely collected from a young palm as it is similar to the leaflet margins top B and C from 5–6 year old MBC palms grown from seed. Scale = 0.3 mm.

parenchyma cells. The arrangement of the parenchyma cells in the other specimens appeared to be layered or randomly arranged (Fig. 13A, C, D), although a slight radial arrangement appears in the Carrizo Grove, Arizona specimen (Fig. 13B). The *W. robusta* midribs (11D, H) have a narrower shape than the Kofa palm (Fig. 11A) and all other *W. filifera* (11B, C, E–G) represented here.

Discussion

Fibers and Tannins: *Washingtonia* palms are desert plants. They have adapted to survive harsh and water challenging environments. The thicker leaf fibers serve to add structural integrity to the fan leaf in times of low water, thus allowing the leaf to retain its shape, while continuing to photosynthesize. The abundant presence of thicker fibers also make them more

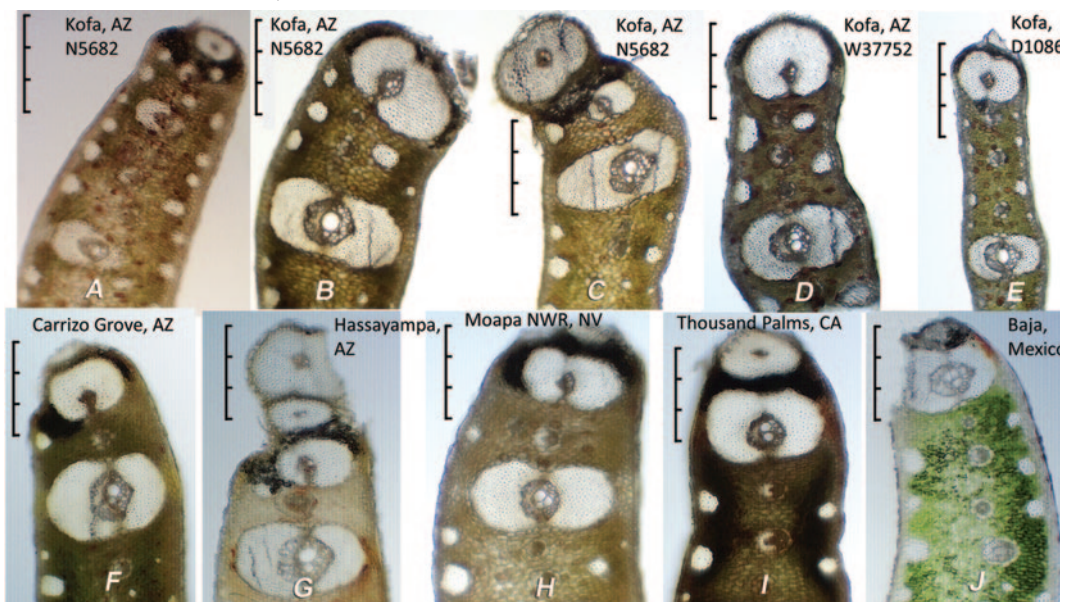
difficult for herbivores to bite off and chew. The presence of tannins in the leaf, not only impart a bitter, astringent and disagreeable taste, but also causes weight loss and bloating. The tannins specifically inhibit rumen fermentation, thus inhibiting the digestion of proteins and cellulose (Managan 1988).

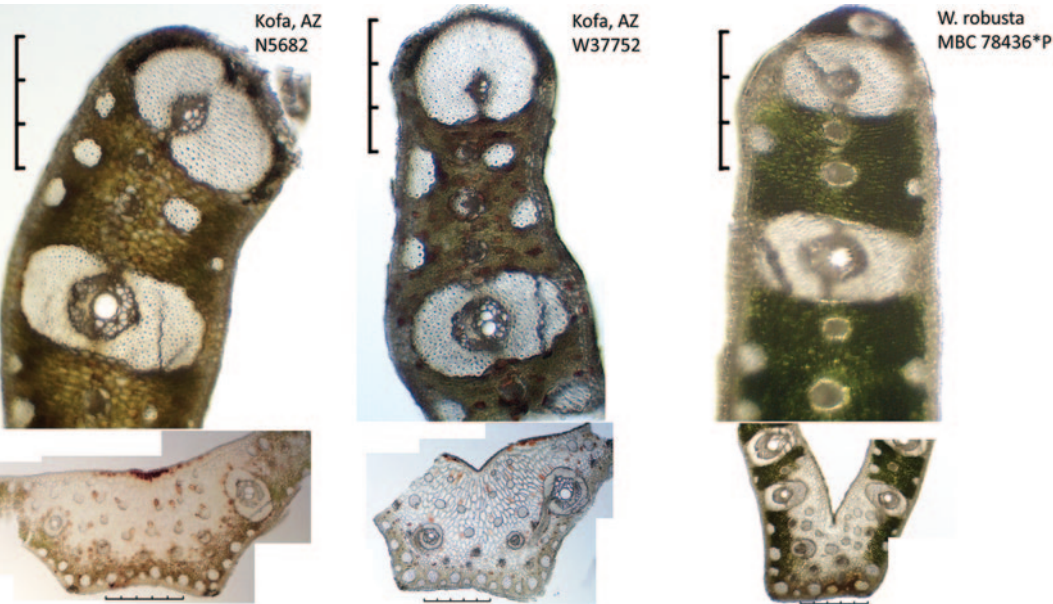
Washingtonia the relic, or an invasive species: As mentioned above, the Kofa palms are thought to be descendants of those growing in the area since the last period of the North American glaciations, ca. 10,000 years ago (US Fish Wildlife Service 2014). Axelrod (1950, 1977) claimed all native *Washingtonia* to be a relic population for the following reasons: they belong to a tropical family (Arecaceae) that is now surviving in a region too cold for the genus today, palm fossils have been discovered in the Mojave Desert, native *Washingtonia* palms are scarce, and finally, they are widely scattered over its present range in small isolated oases. On the other hand, Cornett (1989) theorized that *Washingtonia* represent a relatively recent palm invasion from the south and challenged Axelrod's 1950 use of the word "relic" to describe their current distribution in the US. Cornett stated that the evidence suggests that *Washingtonia filifera* has

never been more widely distributed than at present, and he does not acknowledge any verifiable fossil evidence indicating that this species was once widespread in the Mojave Desert. The fan-leaved fossils referred to by Axelrod (*Sabalites*) lack *Washingtonia*'s characteristic petiole spines, a character that Cornett considers important in the positive identification of the genus. Finally, a "relic" species should be in decline and yet compared to the first census (Henderson, 1961), they are more abundant. There are presently more individual native desert fan palms than ever before with a distribution expanding to the north. Cornett (1989) also pointed to a study by McClenaghan and Beauchamp (1986) that showed a great degree of genetic similarity between populations, which would lend credence to a recent appearance and rapid expansion in the US.

Axelrod (1977) later retracted his former claim that fossils in the Mojave Desert could be accurately assigned to the genus *Washingtonia*, but Spencer (1999) stepped up to defend Axelrod's original point of view. The fossil genus *Sabalites* found all over the Southwest and as far north as Canada, has been defined by Read and Hickey (1972) as any palmate leaf

9. Leaflet margin comparison. Top row images are *Washingtonia* from Kofa National Wildlife Refuge (NWR) in AZ and bottom row (F–J) are from elsewhere (see below). Images A–C are from the same leaf, Noblick 5682 (FTG). D. Willson 37752 (ARIZ) is from an adult specimen, but E. Darrow and Benson 10867 (ARIZ) from Kofa was collected from a younger palm (see Figure 8). F. Noblick 5734 (FTG) Carrizo Grove, Castle Hot Springs, AZ. G. Noblick 5733 (FTG) Hassayampa River Preserve near Wickenburg, AZ. H. Noblick 5680 Moapa Valley NWR-NV. I. Noblick 5681 (FTG) Coachella Valley Preserve near Thousand Palms-CA. J. MBC 9644*C grown from seed from Cataviña, Baja California, Mexico. Scale is 0.3 mm.



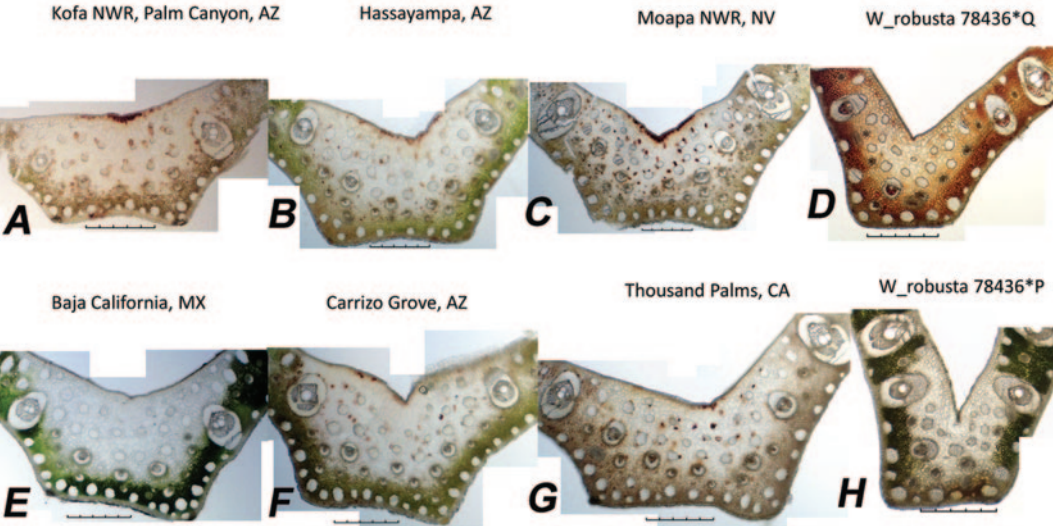


10. Comparison of Kofa *Washingtonia* (left and middle) and a cultivated *W. robusta* (right). Scale is 0.3 mm top and 0.5 mm bottom.

“with a definite costa or extension of the petiole into the blade.” There is no mention of spines or lack of spines on their petioles in that definition. Cornett (1986) himself recorded spineless *Washingtonia* petioles on tall, aging specimens and admitted that the fossilized palms formerly assigned to the genus

Sabalites may be in error. As *Washingtonia* palms grow older and taller, they first lose spines on the distal portion of their petioles and ultimately lose all of their spines. We confirmed that the tallest *Washingtonia* at MBC and also the adult specimens in the Kofa National Wildlife Refuge follow this pattern

11. *Washingtonia* midrib comparison. A–C, E–G are *W. filifera* and D and H are *W. robusta*. A. Noblick 5682 (FTG) Kofa NWR-AZ. B. Noblick 5733 (FTG) Hassayampa Preserve-AZ. C. Noblick 5680 (FTG) Moapa Valley NWR-NV, note the reddish tannin bodies. D. *W. robusta* MBC 78436*Q locality unknown. E. MBC 9644*C Cataviña, Baja California, Mexico. F. Noblick 5734 (FTG) Carrizo Grove-AZ. G. Noblick 5681 (FTG) Coachella Valley Preserve near Thousand Palms-CA. H. *W. robusta* 78436*P locality unknown. Note the differences between the *W. filifera* and *W. robusta* midribs. Scale 0.5 mm.



of spine loss. Thus, some of the *Sabalites* fossil palm leaves could very well be spineless *Washingtonia* leaves, supporting the relic hypothesis. Spencer argued that palm populations should be expected to expand or contract during favorable or less favorable periods of time.

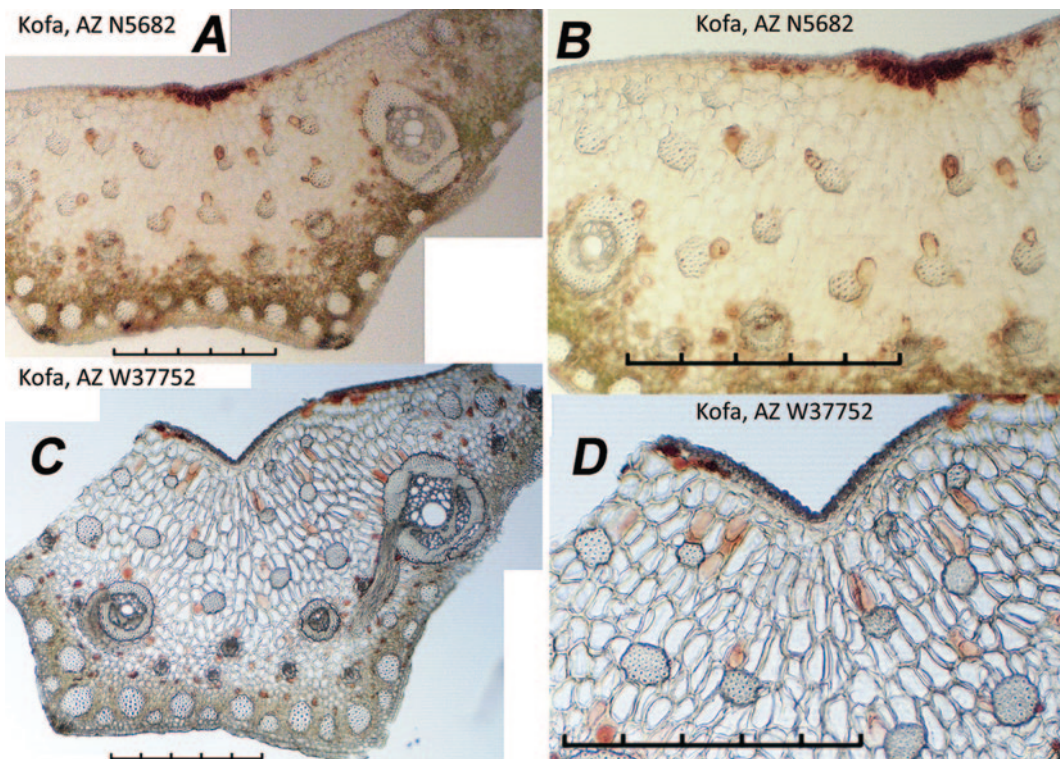
Cornett also assumed that the original census count of *Washingtonia* conducted in the Southwestern US by Henderson (1961) was comprehensive and accurate. However, current census counts of *Washingtonia* now include newly discovered populations, like Castle Hot Springs (Brown et al. 1976). The fact that more palms are being discovered farther North may indicate newly discovered populations rather than recent expansions of *Washingtonia* into these areas.

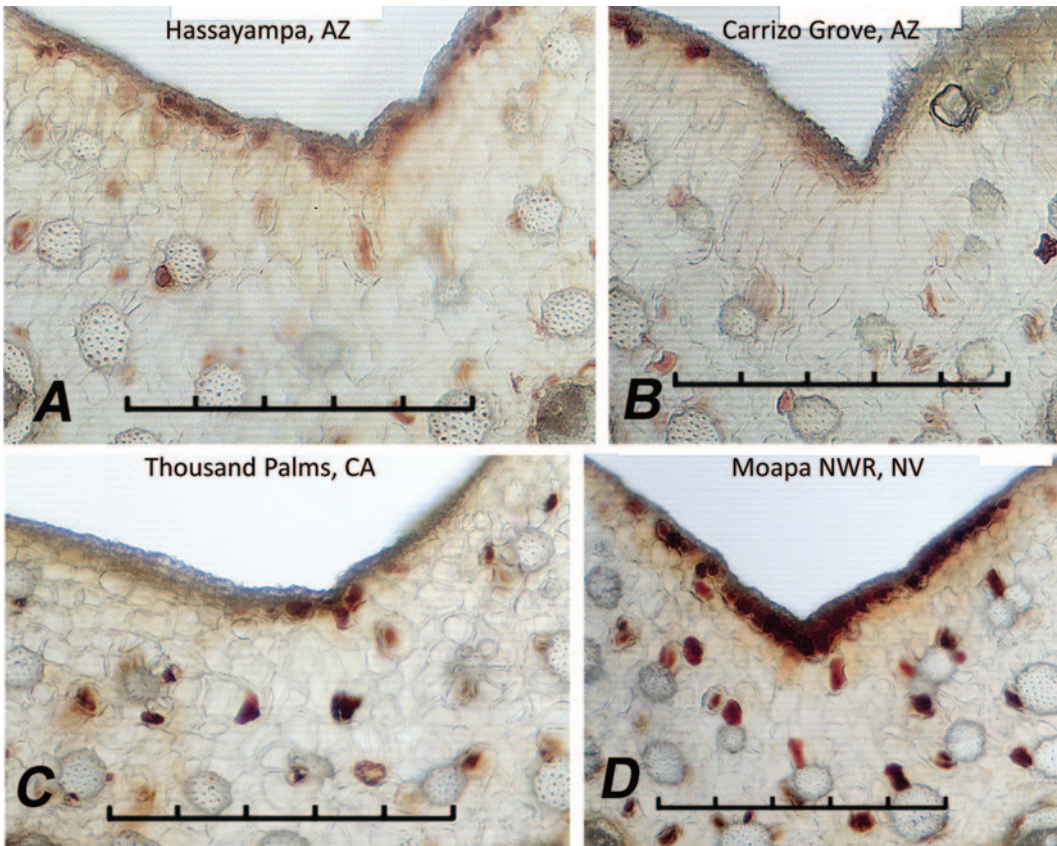
Spencer (1999) further argued that since most of the fossil palm leaves have been found in abundance in the Rocky Mountains of Wyoming, northern Oregon, British Colombia, Vancouver Island and as far north as Alaska, the palms are likely retreating from the north rather than advancing towards it, thus

suggesting that the presently scarce and isolated *Washingtonia* oases are relicts of a much broader palm distribution. Recent genetic work by Villanueva-Almanza (2019) and Villanueva-Almanza et al. (2021) over the entire distributional range of *Washingtonia* showed a great deal more genetic diversity than detected in previous work (McClenaghan & Beaucamp 1986), which examined only populations of *W. filifera*. Their results reveal four highly structured *Washingtonia* populations resolved into four geographic regions: (1) Southern Peninsula, (2) Mid-Peninsula, (3) Northern Peninsula and (4) Sonoran mainland.

Recently Cornett (2021) reported that *W. filifera* is in decline, evidence by an absence of juvenile recruits and the die-offs of once vigorous palms from the largest native desert fan palm oasis in Palm Canyon of Riverside County, California (Cornett et al. 1986). He referred to *Washingtonia filifera* as a keystone species on which many birds, mammals and other organisms rely for food, shelter and nesting materials and lamented its current decline from many desert oases due to climate

12. *Washingtonia filifera* midribs from Palm Canyon, Kofa NWR-AZ. A. Noblick 5682 (FTG). B. Close-up of Noblick 5682 showing the flattish adaxial surface and the radial symmetry of the parenchyma cells. C. Willson 37752 (ARIZ). D. Close-up of Willson 37752 clearly showing the radial symmetry of the parenchyma cells. Scale is 0.5 mm.





13. Close-up of the center portion of *Washingtonia filifera* leaflet midribs. Note the random or near radial arrangement of the parenchyma cells. A. Noblick 5733 (FTG) from the Hassayampa Preserve-AZ. B. Noblick 5734 (FTG) from the Carrizo Grove-AZ. C. Noblick 5681 (FTG) from the Coachella Preserve near Thousand Palms-CA. D. Noblick 5680 (FTG) from Moapa Valley NWR-NV. Scale 0.5 mm.

change. This reflects a contradiction to his earlier 1989 statement that *W. filifera* is a rapidly spreading, invasive species that is more numerous than ever before.

Much of the present-day expansion and increasing abundance of *W. filifera* can be blamed on human dispersal and the popular use of this species in urbanized settings, which exposes it to more favorable growing conditions. Although *W. filifera* is not mentioned as an invasive, *W. robusta* is. It is specifically listed as an invasive of riparian areas, orchards and landscaped areas by the California Invasive Plant Council (<https://www.cal-ipc.org>).

Kofa palms, a unique species: The Kofa palms failed to fit the clinal north to south pattern discovered by Villanueva-Almanza et al. (2018) for *Washingtonia filifera*, so they excluded this population from the rest of their study and labelled it an outlier. The Kofa *Washingtonia* are small, with smaller crowns and thinner

stems, and are the most xeric-adapted, water-use-efficient palms among the *Washingtonia*. Although questionable, the US Fish and Wildlife service (2014) maintained that they are self-pruning, which can be tested long-term by growing them in an ex-situ garden environment, which is being done at MBC and on the University of Arizona campus.

In spite of all the differences highlighted above, DNA analysis of the Kofa palms shows this population to fall firmly within the other *Washingtonia filifera* specimens of the northern Baja California Peninsula (Villanueva-Almanza et al. 2021). Genetic data show that the Kofa palms are most closely related not to other palms in Southern California, but rather to other specimens in northern Mexico from Cañón Palomar, Cañón de Tajo and Guadalupe Canyon (Villanueva-Almanza et al. 2021). A specimen from Guadalupe Canyon (Felger 8185) anatomically resembles those from Kofa with their adaxially flattened midrib and slightly radially arranged parenchyma cells

(Fig. 14). This could just be coincidence, but it could also serve as another example of how anatomy often confirms molecular results. This has been seen in the Attaleinae (Meerow et al. 2009) with the relationship of *Parajubaea*, *Polyandrococos* and *Allagoptera* and also with several relationships in the genus *Syagrus* (Noblick 2013, 2017).

To conclude, no significant anatomical differences were noted in the current study that would support recognition of the Kofa palms as a new taxon. Despite being morphologically distinct enough to be excluded from the Villanueva-Almanza et al. (2018) study, molecularly and anatomically these palms are not distinct from other *Washingtonia* and therefore cannot be recognized as a different species. Nevertheless, their morphological and ecological uniqueness does prompt the need for both in-situ and ex-situ conservation. Furthermore, by growing this palm under common conditions with other *Washingtonia*, we can examine the morphological plasticity and verify if the Kofa palms will continue to maintain its morphological differences. Perhaps under equivalent growing conditions, Kofa palms will develop a larger crown, thicker trunk and hold a full skirt of leaves as seen in other *Washingtonia* populations. If not, then perhaps we should address the possibility recognizing it as a distinct form of *Washingtonia filifera*.

In summary, the *Washingtonia* from Palm Canyon in Arizona's Kofa National Wildlife Refuge is of special interest due to its morphological and ecological uniqueness, despite the fact that such differences are not currently resolvable via molecular or anatomical means.

Botanical account of the Kofa palm

Description: Palm solitary with trunk 3–8 m × 32–46 cm with persistent leaf bases split at the base and often forming a short skirt of persistent dead leaves near the base of the crown, but not necessarily down the trunk. Leaves appear to be self-pruning. Ca. 14–16 spirally arranged green short costapalmate fan leaves in the crown. Petiole unarmed as adult (armed only as juveniles), adaxially channeled and abaxially rounded, 60–70 cm long × 2.2–3.5 cm wide and 1 cm thick. Lamina or leaf blade measures 71–98 long × 91–135 cm wide. Leaf rachis 9–19 cm long. Hastula 3.4–5.2 cm. 54–57 leaf segments in all, which are relatively stiff and non-pendulant. Basal leaflets 34–45 × 0.7–1.0 cm with the lowest ones not split or split to 18 cm; middle leaflets 79–87 × 3.8–4.5 cm with each split to 40–47 cm; apical leaflets 88–91 × 4.7–5.5 cm with each split to 39–54 cm. Inflorescence interfoliar, branches to 4 orders and is 270–300 cm long. The peduncle is 100 cm long and 2.5 × 2 cm thick near the first branch of the inflorescence. The

14. *Washingtonia filifera* midribs of *Felger 8185* (ARIZ) from Guadalupe Canyon in the northern state of Baja California, Mexico. Genetic data show that it is close to the palms in the Kofa NWR. Note flattish adaxial surface of midrib and nearly radial arrangement of the parenchyma cells. Scale = 0.5 mm.



inflorescence first branches into three main branches (not 2 as collected elsewhere) and each of these have 5–6 branches resembling grape-like clusters. These secondary inflorescence branches have a secondary peduncle 54–95 × 1.5 cm and are 73–109 cm from the lowest branch to the apical branch. The smaller grape-like branches are 12–22 cm long at the apex, 16–28 cm near the middle and 23–35 cm long near the base. Flowers ca. 2–3 mm long. Fruits not measured but appear to be pedicellate, seeds small (Fig. 6).

Distribution and habitat: The total distribution of this palm is found and protected within the Kofa National Wildlife Refuge just south of Quartzite, Arizona. Habitat is desert. Steep narrow-sided canyon with large boulders, and very rocky soils. The floor of the canyon is a steep south-facing slope. Water funnels down through this valley from the plateau above. Narrow canyon walls block the sun most of the day with the palms only getting a few hours of direct sun each day.

Conservation: These specimens grow within the confines of a protected refuge and are not under any threat from humans, but the population has been in decline for many years and because of the extended droughts, the population has not flowered and fruited regularly for several years. Because of the tiny area of its current distribution, low numbers of reproductive individuals and evidence of continual decline this palm population, if treated as a separate species, would be classified as critically endangered CR B2ab(v); D (IUCN 2001).

Phenology: This palm flowers in spring and early summer and fruits in late summer, fall and winter. We personally noted herbarium specimens with flowers in April and June, immature fruit in July, August and October and mature fruit in December and January. Our fruit and seed collections were made in November.

Uses: No uses are currently being made of this palm. However, it may have ornamental landscape value where a xeric-adapted palm is required.

Notes: This species is distinguished from the other closely related *Washingtonia* by its smaller and less robust stature. Palms are about half the size of those seen in California, Nevada and even in other areas of Arizona near Wickenburg and Castle Hot Springs.

Representative specimens: United States, Arizona: Yuma County, Short Horn Mountains, 2 December 1923, O.F. Cook s.n. (US); 11 May 1927, R.E. Beckett s.n. (US); Yuma County, Palm Canyon, Kofa Mountains, S.H. Mountains (= Kofa Mountains), 31 March 1930, H.F. Loomis & R.H. Peebles 6775 (ARIZ); 853 m, 33.36226, -114.09834, October 1938, R. Willson 37752 (ARIZ); Kofa Refuge, 914–1219 m, 33.3608, -114.09923, 3 February 1941, W.B. McDougall s.n. (ARIZ) [Seedlings]; 3 February 1941, W.B. McDougall & O.F. Cook s.n. (ARIZ); 33.36223, -114.09836, 17 April 1941, A. Darrow & L. Benson 10867 (ARIZ); Kofa Mountains, 762 m, 33.360598, -114.103179, 19 May 1950, C.F. Deaver 3010 (ASC); Fish-tail Canyon (erroneously called Palm Canyon), 25 June 1955 H.E. Ahles 8885 (CM); W side of Kofa Mountains, Palm Canyon, 610 m, 31 March 1983, E. Neese s.n. (BRY); ca. 18 mi S of Quartzite on Hwy 95 and ca. 8 mi E on rd to Palm Canyon, 33.3594, -114.106, 25 May 1987, L.R. Landrum 5484 (ASU); Highway 95 S to mile post 85. Ca. 18 miles S of Quartzite watch for brown Palm Canyon sign indicating the junction of the dirt road. Follow dirt road E for 7 miles to a parking lot and hike into Palm Canyon. 369 m elevation. 33°21'42.6"N, 114°05'31.1"W (33.3618, -114.092), this reading ca. 200–300 m from actual collection, 6 November 2015, Larry R. Noblick & Daniela Noblick 5682 (FTG, US); Sonoran Desert: Kofa Mountains, Palm Canyon, 11km on the dirt road that branches east from US 95, 31 km south of Quartzite., 33.36222 -114.09833, 893 m, 14 October 2017, Lorena Villanueva-Almanza et al. 644 (SD); 33.36231, -114.09831, 893 m, 14 October 2017, Lorena Villanueva-Almanza et al. 651 (UCR).

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Appendix 1. Specimens examined.			
Specimen	Origin	Source	Type
78436*P	Unknown	MBC	Living collection
78436*Q	Unknown	MBC	Living collection
9644*C	Cataviña, Baja Cal., MX	MBC	Living collection
20150367*A	Moapa NWR, NV	MBC	Living collection
20150377*A	Coachella Valley, CA	MBC	Living collection
20190501	Kofa Mountains, AZ	MBC	Living collection
20190504	Hassayampa River, AZ	MBC	Living collection
20190512	Castle Hot Springs, AZ	MBC	Living collection
Darrow & Benson 10867	Kofa Mountains, AZ	ARIZ	Herbarium specimen
Felger 8185	Guardeloupe, Baja Cal., MX	ARIZ	Herbarium specimen
Noblick 5680	Moapa NWR, NV	FTG	Herbarium specimen
Noblick 5681	Coachella Valley Pres., CA	FTG	Herbarium specimen
Noblick 5682	Kofa Mountains, AZ	FTG	Herbarium specimen
Noblick 5733	Hassayampa River, AZ	FTG	Herbarium specimen
Noblick 5734	Castle Hot Springs, AZ	FTG	Herbarium specimen
Willson 37752	Kofa Mountains, AZ	ARIZ	Herbarium specimen

New Palms for Singapore's Landscapes

ZAKI JAMIL¹

The tropical climate in Singapore is ideal for growing a wide variety of palms. Palms, which are largely found in the tropics, are commonly used in Singapore's landscape, and exotic species, along with many of Singapore's native taxa, are prized for use in both public and private gardens.

As a palm grower for Singapore's landscapes including the Botanical Gardens, I have over 200 species of palms under my care (Fig. 1). The Botanic Garden is a government entity, part of Singapore's National Parks Board, and its nursery supplies plants for public landscaping projects outside the garden, as well as for display and research within the garden. There are rare species that are cultivated for conservation purposes, and more common ones for large-scale planting at parks, street side verges and at national gardens. I grow uncommon palms, both native and exotic, and introduce them into Singapore's landscape, with the goal of expanding the palette of palms suitable for landscape use.

As most growers know, some palms are more demanding in their habitat requirements than others. For use in public landscapes, palms have to be vigorous and able to withstand challenges that they might not have in their natural habitat. For example, palms for street

planting must be able to tolerate automobile exhaust and extra heat reflected from the road surface, while palms in public parks must be able to deal with soil compaction and wind. Of the many species we trial at the Board's nursery, three species have risen to the top of the list of unusual palms that thrive in cultivation and deserve wider use.

One of the easiest to grow is *Actinorhytis calapparia* or the Calappa palm (Fig. 2). It is native to New Guinea and the Solomon Islands, but it has naturalized in parts of Malaysia, Indonesia and Thailand. Calappa Palm is a fast-growing, water-loving palm. I like to call it the rich man's Carpentaria palm (*Carpentaria acuminata*) for its extravagant and neat appearance. Like Carpentaria, it has elegantly arching, pinnate leaves and an upright, solitary growth habit. The Calappa palm is good for instant landscaping in confined space, and I am working on introducing more of this species to the landscape. Apart from its stunning features, this species has its ethnobotanical uses too; in some Asian countries the fruits are used as a betel nut substitute.

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1. A small portion of the many palms under my care. Seeds are germinated in flats, and seedlings are transferred to individual pots once their first true leaf emerges. Seedlings and young palms are grown under shade cloth.

The fruits are large and start off green before ripening into red. To propagate this palm, the thick flesh is removed before sowing to prevent odor from decomposition and pests such as rodents from feasting at the seed trays. The seeds generally take between two to three months to germinate. This palm is so easy to grow that its scarcity in cultivation is surprising.

The next palm I would like to highlight is relatively new in cultivation. It is *Adonidia dransfieldii* or Dransfield's Elegant palm (Fig. 3). Native to Sabah, Malaysia, this palm was described in 2015. In size and habit, it is similar to its more famous cousin, the Christmas palm (*Adonidia merrillii*), but it has glaucous-green fronds and a white crownshaft. It is a real stunner of a Malesian palm. The fruits (Fig. 4) are similar to those of the Christmas palm's but juicier and cause skin irritation. Gloves are needed when handling them! Dransfield's Elegant palm seeds take about a month to germinate.

The juvenile stage is critical, as this palm is susceptible to squirrel attack. The squirrels feed

on the terminal bud of juvenile palms. I have lost hundreds of palms and subsequently learned that netting the crownshaft helps to keep squirrels away. Juvenile Christmas palms do not suffer the depredations of squirrels, proving that squirrels are excellent taxonomists. This palm has a rapid growth rate comparable to Christmas palm, and it has been introduced into the street planting of Singapore.

The third palm, one valued for its big, ornamental, spidery leaves, is *Borassodendron machadonis* or the Machado's palm (Fig. 5). This is a large, solitary palm that retains its old leafbases on its trunk. Although the leaves are unarmed, the petioles are as sharp as knife blades! This palm is dioecious, meaning that male and female flowers are borne on separate plants. The female flowers, while not showy, are strongly fragrant. Flowers are followed by large, glaucous, blue fruits (Fig. 6) resembling giant blueberries, and each fruit contains two to three seeds covered in a bright yellow pulp.

The Machado's palm occurs naturally just north of us, in the Malay Peninsula and



2. *Actinorhynchus calapparia* is an easy-to-grow palm that is gaining popularity as a landscape palm in Singapore. When ripe the large fruits are bright red.



3. *Adonidia dranfordii* is a welcome change to the more common species, *A. merrillii*. At maturity, the palm will have a glaucous, white crownshaft.



4. The fruits of *Adonidia dranfildii* look just like those of its relative *A. merrillii*, and they are just as decorative. The flesh from the fruits can cause skin irritation.

Thailand. Although Machado's palm is not native to Singapore, it seems perfectly at home here. It tolerates a wide range of soil pH.

Propagation of this palm is slow, as each seed takes nearly a year to produce its first leaf. As the Machado's Palm are remote germinators, shallow germination trays are not the best choice for germination as the roots would grow through the trays. Each seed is planted in individual, tall bags instead. The slow germination and the difficulties of handling the seedlings are likely the reasons this species

is not more widely propagated in commercial nurseries.

For example, one of the more unusual palms is a beautiful form of the highly variable Papuan *Areca macrocalyx*. This species, widespread throughout New Guinea and offshore islands, varies greatly in size and leaf form, from forms with narrow leaflets to those with very few very broad leaflets. This has resulted in several forms being described as separate species; however, they all seem to intergrade. The form we grow in Singapore has



5. *Borassodendron machadonis*, the Machado's palm is a large, solitary palm.



6. *Borassodendron machadonis* is dioecious. Only the female individuals bear these showy, blue fruits.

been called *A. rheophytica*, which is a slender short palm occurring on the banks of fast-flowing streams on ultramafic rock in northern Borneo, but that species has a very different inflorescence, reminiscent of that of *A.*

triandra. The palm I illustrate, on the other hand, has all the fruit concentrated towards the bases of the inflorescence branches. The narrow leaflets of this particular form do suggest that the palm may be a rheophyte like



7. *Areca macrocalyx* thrives in a garden setting.

A. rheophytica, but we are uncertain about the exact origin of our plants.

Palms are also propagated in the nursery for conservation purposes. A great example is *Orania sylvicola*, a critically endangered Singaporean native (Fig. 8). This palm occurs naturally in much of Thailand, Malaysia and

Indonesia, but in Singapore, only a handful of individuals are left in the wild. This species is legendary for its allegedly toxic fruits. One fruit is said to be sufficient to kill an elephant, but this claim of toxicity has never been thoroughly investigated. If the fruits are toxic, one can only wonder what animal can eat them and disperse the seeds.

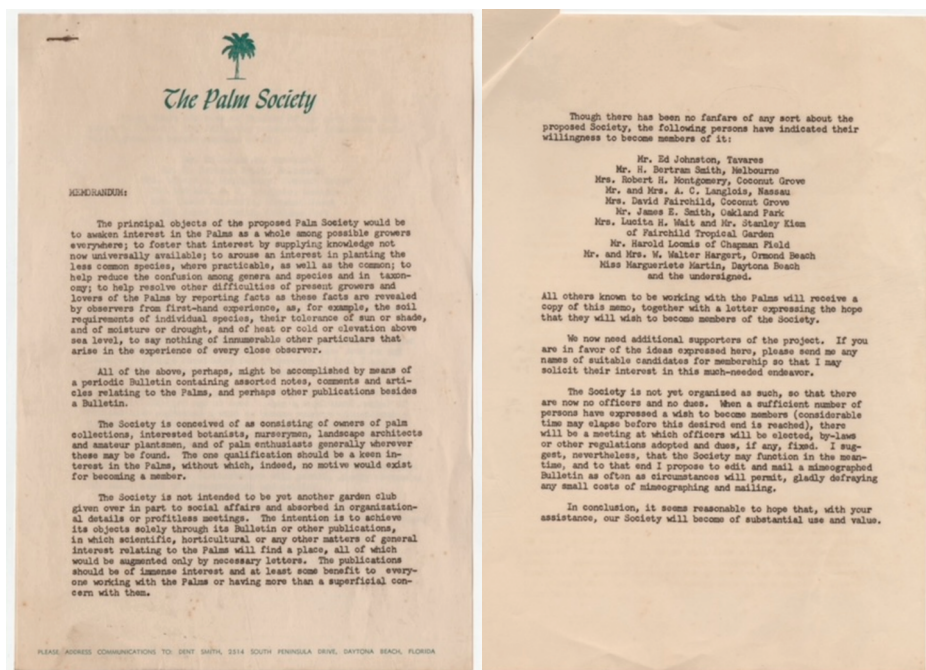


8. *Orania sylvicola* is a beautiful, solitary, pinnate-leaf palm, but the fruits are allegedly toxic.

Horticulture plays a central role in Singapore Botanic Gardens' mission. We are actively seeking new palms to introduce into gardens and landscapes. By harvesting seeds from wild

palms and cultivating them in a nursery environment, we are able to discover new palms for landscaping as well as safeguard the future of these species in Singapore.

The 65th Anniversary Fundraising Campaign



Earlier this year, the International Palm Society established a fundraising campaign in honor of the 65th anniversary of our founding. Historically, the IPS, in acknowledgement of its mission, has supported an astonishing number of endeavors. In fact, IPS Administrative Secretary Dr. Larry Noblick reported, “Since its inception 35 years ago, the IPS Endowment Program has donated more than \$400,000 to over 115 research & education projects on six continents.” A quick perusal of PALMS finds the ubiquitous phrase “generous support from International Palm Society” (e.g., PALMS, 62: 87. 2018). The IPS is not a large society, but its global importance in the areas of palm research, education and conservation is disproportionately large.

As the custodians of the IPS, we are standing on the shoulders of countless famed researchers, professional horticulturalist and hobbyists whose dedication and philanthropy allowed the IPS to flourish. Yet there is still much work to be done, and our reach exceeds our grasp. Conservation of species and preservation of habitat are urgent concerns that require considerable funding. Out of this need, the 65th Anniversary Fundraising Campaign was launched.

We are enormously grateful to the many participants in this year's fundraising campaign. The following donors contributed \$1000 or more, qualifying for inclusion in the Dent Smith Founder's Society. They are: **Jeff Brusseau, Anthony Glomski, Andy Hurwitz, Tom Jackson, Leland Lai, Jill Menzel, Haresh R. and Colin Wilson.**

The IPS will soon launch an exciting new conservation initiative in South America. Its success will depend on the participation of the membership and other sponsors. We are looking forward to an exciting future as we continue to advance the study of palms, their culture, conservation and biology.

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