

Palms

Journal of the International Palm Society

Vol. 61(1) Mar. 2017



THE INTERNATIONAL PALM SOCIETY, INC.

The International Palm Society

Founder: Dent Smith

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Palms (formerly PRINCIPES)

Journal of The International Palm Society

An illustrated, peer-reviewed quarterly devoted to information about palms and published in March, June, September and December by The International Palm Society Inc., 9300 Sandstone St., Austin, TX 78737-1135 USA.

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Annual membership dues are US\$55.00 for Individuals (or US\$150 for three years) and include a subscription to the Journal. Donor memberships are US\$500 per year. Individual Lifetime memberships are available for a one-time fee of US\$1000. Benefactor memberships require a one-time payment of US\$2500. Subscription price is US\$55.00 per year for libraries and institutions. Dues include mailing of the Journal by airlift service to addresses outside the USA. Dues may be paid on-line at www.palms.org.

Change of Address: Send change of address, phone number or e-mail to The International Palm Society Inc., 9300 Sandstone St., Austin, TX 78737-1135 USA, or by e-mail to info@palms.org.

Claims for Missing Issues: Claims for issues not received in the USA should be made within three months of the mailing date; claims for issues outside the USA should be made within six months of the mailing date.

Periodical postage paid at Austin, TX, USA and additional mailing offices. Postmaster: Send address changes to The International Palm Society Inc., 9300 Sandstone St., Austin, TX 78737-1135 USA.

PALMS (ISSN 1523-4495)

Mailed at Lawrence, Kansas 15 Mar. 2017
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The full text of PALMS is available on EBSCO Publishing's database.

This publication is printed on acid-free paper.

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FRONT COVER

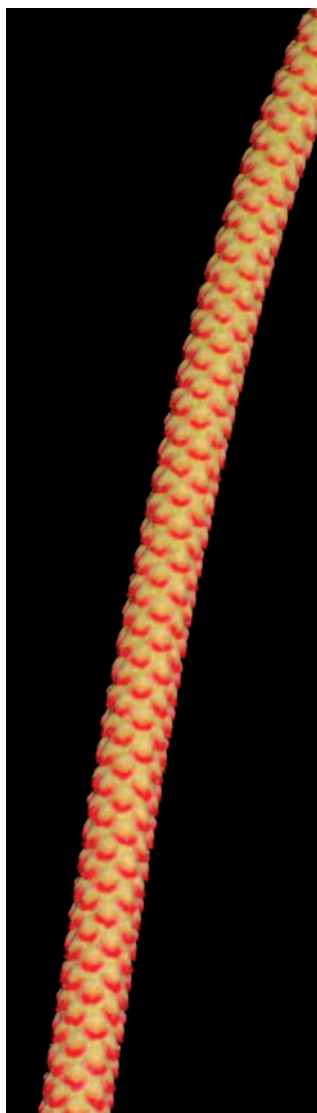
Livistona alfredii was named by Baron Ferdinand von Mueller to honor Prince Alfred, Duke of Edinburgh (second son of Queen Victoria), and husband of Grand Duchess Maria Alexandrovna of Russia. Photographed at Millstream National Park, Pilbara, Western Australia. See article by Dowe p. 21. Photo by J.L. Dowe.

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Adult *Coccothrinax x angelae*. See article by Suárez et al., p. 45. Photo by D. Suárez.

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The long, unbranched inflorescences of *Calyptrogyné costatifrons* hang 2 m under the crown. See article by Cano et al., p. 5. Photo by Á. Cano.

PALM NEWS



Christel Ramos

In November of 2016, M.H. Grayum and J. De Gracia published a **new species of *Synechanthus*** from Panama, *S. dasystachys* (Phytoneuron 71: 1–10). The species, only the third recognized in this small, seldom-seen genus, is characterized by simple, bifid leaves and unbranched inflorescences. The publication is open access and available at www.phytoneuron.net/2016Phytoneuron/71PhytoN-Synechanthus.pdf.

In December of 2016, K. Luo et al. published a **new species of *Guihaia*** from karst limestone hills of central Guangxi, China (Phytotaxa 286: 285–290). It is only the third species of *Guihaia*. *Guihaia lancifolia* is remarkable for having narrow, undivided, lanceolate leaves. The evolution of this palm appears to represent a case of paedomorphism, the retention of juvenile traits (in this case, juvenile leaf shape) into adulthood.



Kawen Luo



C.D. Heatubun

Lastly, C.D. Heatubun described (Phytotaxa 288: 175–180) a palm that he has named *Areca jokowi*. This **newly-discovered wild relative of the betel nut palm** is from western New Guinea. The specific epithet honors the President of Republic Indonesia, His Excellency Joko Widodo-Jokowi. The addition of this species brings the total species of *Areca* in western New Guinea to five.

We have just learned the very sad news that Xavier Metz has passed away, in Antananarivo, Madagascar, after a long illness. He is survived by his wife Nathalie and three daughters. It was Xavier, who, with his family, discovered *Tahina spectabilis* in a remote part of northwest Madagascar, where he managed a cashew plantation. Xavier did much to bring the palm to the notice of botanists, facilitated the collection of scientific specimens, organized the controlled seed harvest from which most, if not all, cultivated plants originate, and who laid the foundation for *Tahina spectabilis* conservation and sustainable use.

Palms of the Darién Gap (Colombia- Panama)

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The Darién Gap is a poorly explored area of pristine forest around the Panama-Colombia border, and it marks the only break in the Pan-American highway that runs from Alaska to Tierra del Fuego. This area has been a crossroad for the migration of plants and animals between North America and South America, ever since the closure of the Panama Isthmus around 10 million years ago. The palms of this unique area are discussed here for the first time.

The Darién Gap is a mythical area that has fascinated biologists and adventurers for decades. Located on the border between Colombia and Panama (Fig. 1), where Central America merges with South America, this land of rugged topography and dense forests is one

of the most poorly explored regions on earth. Few scientists have explored its mangroves and coastal forests, its freshwater swamps, its lowland rainforests or the cloud forests that cover its mountain ranges. However, some expeditions conducted between the 1950s and

the 1970s gave hints of its immense biodiversity. The most famous one was led in 1975 by Alwyn Gentry, a restless North American botanist who revolutionized the biogeographic theories of the Neotropics during the 1980s. Gentry was the first to ascend Cerro Tacarcuna, the highest point of the Serranía del Darién (1875 m), where he discovered 46 species of plants new to science, and found representatives of both the Andean and the Central American floras, vestiges of the floristic exchange between both continents (Gentry 1977). His reports describe, for example, oak forests with abundant wax palms (which are actually *Dictyocaryum lamarckianum*). Today, about 40 years after Gentry's expedition, many plants of this region are still known only from their type specimens and it is thought that hundreds of species still remain to be discovered in the area. Because of this amazing biological richness and the severe threats it faces, the Darién Gap was included in the Tumbes-Chocó-Magdalena biodiversity hotspot (Mittermier et al. 2011).

Several historical and political factors have favored the conservation of this region by preventing the opening or improvement of access routes. The Pan-American highway that runs from Anchorage (Alaska) to Tierra del Fuego (Argentina) has a single, 106 km break, at the Darién Gap. The costs of building a highway through these hills, rivers and swamps were deemed too high in 1984, when the Pan-American road reached its farthest post at the hamlet of Yaviza, in eastern Panama (Fig. 1). The absence of a route cutting through the Darién has hindered the expansion of human settlements into the area. Also, the creation of the Darién National Park in 1980 was an additional contribution from the Panamanian government for the conservation of these ecosystems. On the Colombian side of the border, the Los Katíos National Park preserves also a small portion of the Gap, but conservation on that side has resulted mostly from a different reason: from the early 1980s, traffic of drugs and illegal migrants across the border, as well as fights between the guerrillas

1. Map of the Darién Gap (light green area) showing the localities visited by the authors (pink). National Parks (dark green areas), villages (stars) and hills (triangles) that are mentioned in the text are shown, as well as the most important rivers. The thick dashed line represents the Pan-American highway.



and paramilitary forces in the area added the risk of war to the hardships of Darién's geography. Since then, the area has become renowned for its high rate of kidnappings and murders and fear to access the gap is felt on both sides of the border. This instability has helped to keep away settlers, miners, farmers, and others whose economic interests are a threat to the conservation of this region. The latest attempt to reactivate the construction of the Pan-American highway took place in 2010, when the Colombian president brought back the issue to the Panamanian government, who dismissed it in order to avoid increased drug traffic and illegal immigration, as well as to keep a barrier to the spread of foot-and-mouth disease (FMD), a viral ailment of bovines, prevalent in South America but not in Central America (GAO 2002).

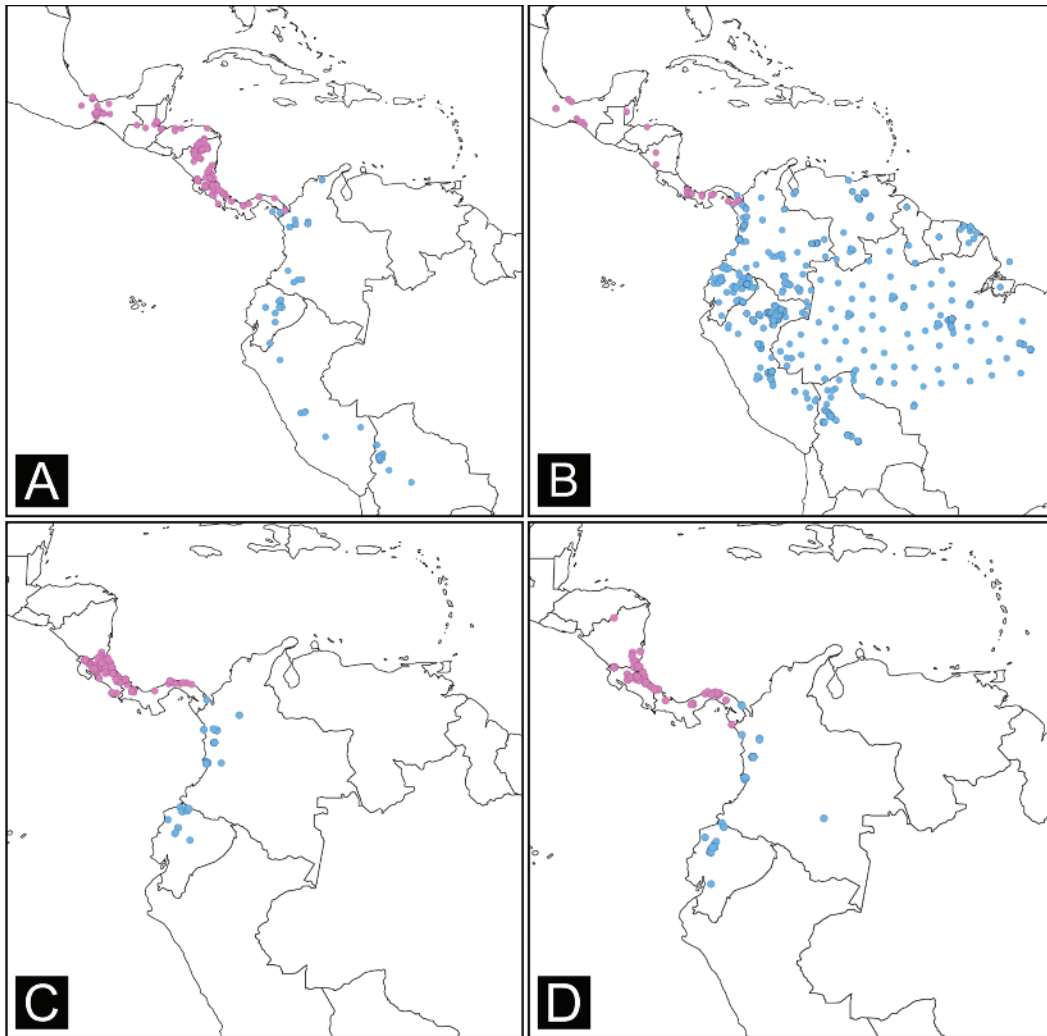
However, Colombia lives today in a period of relative calm and growth, whereas the increasing population in Panama is looking for new areas to exploit, as large lowland areas have already been devastated for livestock or

cereal farming. Human pressure on both sides of the border has intensified and the possibility of completing the missing section of the Pan-American highway is latent, for the purported commercial benefits it could bring to Colombia and Panama. The time has come to reinforce the conservation strategies aiming to protect this site, included in UNESCO's World Heritage List (UNESCO 1981). At the same time, improvement of the political situation in Colombia reopens the possibility to explore it. A race against time has begun, in order to study and protect this area before it is too late. The interest to explore these forests has awakened in the last years and has begun to bear fruit. The most remarkable example is the discovery of the spectacular *Sabinaria*, a new palm genus distributed in the lowlands of the Caribbean side of the Darién Gap in Colombia and adjacent Panama (Galeano & Bernal 2013, Bernal 2014).

Recent studies indicating that the closure of the Panama Isthmus took place earlier than thought, about 10 million years ago (Ma),

2. Members of the expedition to the summit of *Serranía del Darién* in Tatabras, Chocó, Colombia. Standing up from left to right Héctor Favio Manrique, Ángela Cano, Saúl E. Hoyos-Gómez, Norman Echavarría, Darío Toro (our guide), and María F. González; seated from left to right Andrés Upegui and Rodrigo Bernal.





3. Geographic distribution of different palm species whose ranges stop at the Darién Gap. A. *Reinhardtia gracilis* (pink) and *Dictyocaryum lamarckianum* (blue); B. *Chamaedorea woodsoniana* (pink) and *Oenocarpus bataua* (blue); C. *Chamaedorea deckeriana* (pink) and *Desmoncus cirrifer* (blue); D. *Bactris gracilior* (pink) and *Wettinia aequalis* (blue).

instead of 3.5 Ma (Montes et al. 2015), have also aroused new interest in the area. The biogeographic changes brought about by this event were dramatic. The formation of this bridge between the Americas finished the long isolation of 80 Ma of South America and favored species interchange between both continents (Simpson 1980, Bacon et al. 2015).

Using palms as a model to understand the processes that generated the diversity patterns observable today in the Isthmus, one of us, Ángela Cano, started a series of expeditions into the area. The idea was to collect as many palm species as possible, especially focusing on endemics. The Darién represents a key region for this. On the other hand, the

discovery of *Sabinaria* and the continued efforts to complete the Colombian National Palm Collection at the Quindío Botanic Garden, moved Rodrigo Bernal and Héctor Favio Manrique to organize some expeditions to the region, whereas other authors of this paper have had a long-standing interest in the flora of the area. As all these projects coincided in time, we joined forces and our endless desire to explore and we embarked on the adventure of studying the Palm flora of the Darién Gap (Fig. 2).

This article presents the expeditions we have made so far and provides a list of species reported for the region. We also present an analysis of the new reports for Colombia and

Panama and comments regarding the distribution patterns of the species and the conservation state of the visited localities.

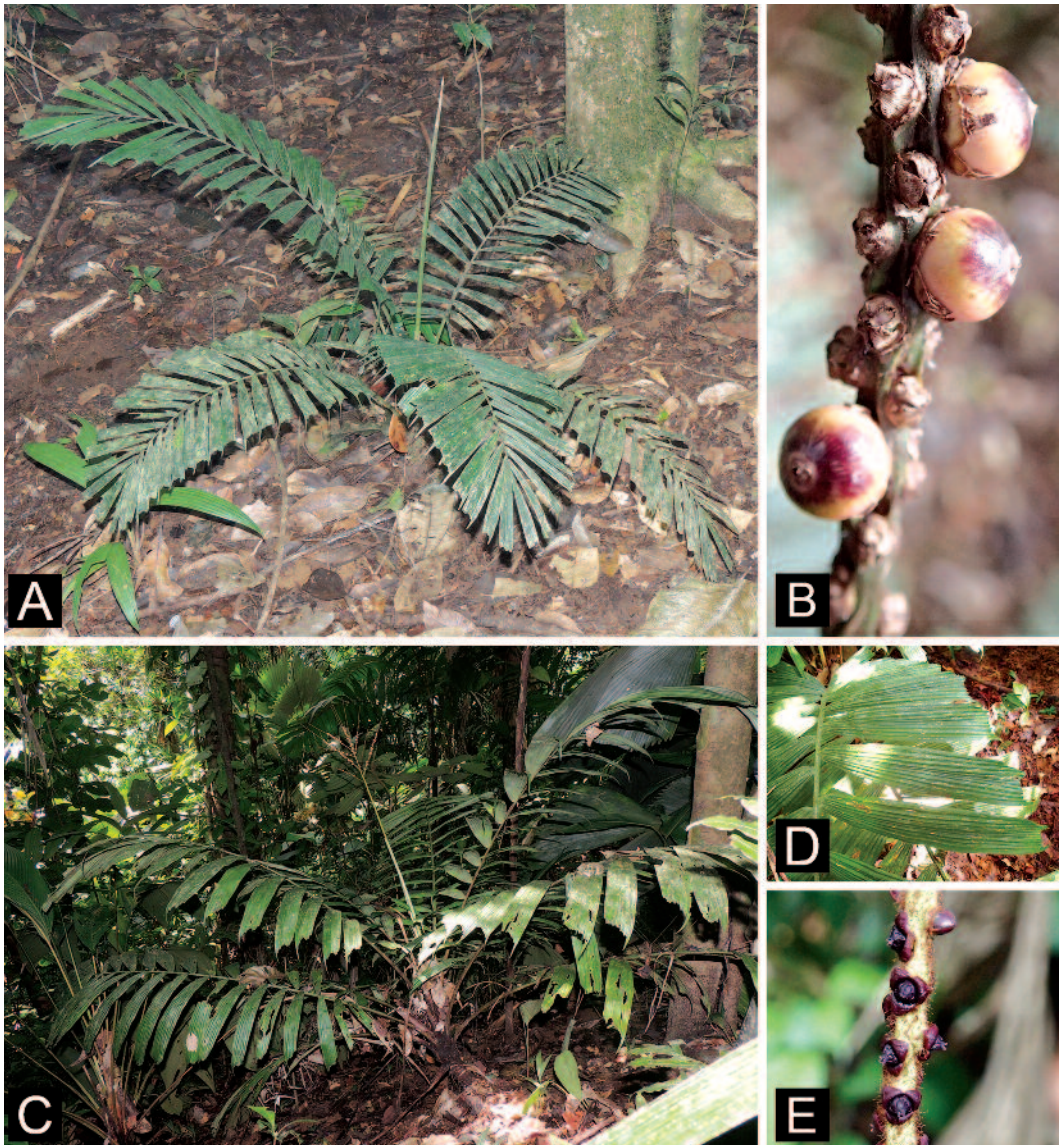
Study sites

Our definition of the Darién gap is based on current vegetation cover, topography and hydrography (Fig. 1). On the Panamanian side, the Tuira river mouth marks the western limit and the Emberá-Wounnan *comarca* the eastern limit. The areas surrounding the Pan-American Highway are very disturbed and therefore we exclude them from our delimitation. On the

Colombian side, the limits follow the Truandó and Atrato basins. As here defined, the Darién Gap has an area of 22,130 km², and ranges in elevation from sea level to 1875 m.

We visited nine localities, seven in Colombia and two in Panama (Fig. 1), following a longitudinal gradient from the Caribbean coast (La Paloma, Sapzurro, Sasardí and Playona), to the Pacific (Cerro Sapo, Punta Ardita), with three inland sites (Balboa, Cerro Pirre and Tatabras). We also considered the altitudinal gradient and chose localities allowing a

4. *Aiphanes* species in the Darién Gap. A, B. *Aiphanes acaulis*, Tatabras, Chocó Colombia. A. Habit, B. Fruit; C–E. *Aiphanes buenaventurae*, La Paloma, Chocó, Colombia. C. Habit, D. Detail of the leaflets, E. Pistillate flowers.



sampling from lowland to higher altitudes. In the site of Playona, near the village of Acandí (Fig. 1), we only visited lowland forest because we were there essentially to collect species typical of coastal swamps, like *Raphia taedigera*, *Manicaria saccifera*, *Elaeis oleifera* and *Euterpe oleracea*. This vegetation type was not present in the other visited localities, where forests were mainly on *terra firme*, and their

composition and characteristics varied with altitude. The maximum altitudes we reached in the highest localities were Cerro Pirre, 1125 m, Cerro Sapo, 961 m and Tatabras, 1200 m.

Sampling

We exhaustively explored the forests of every visited place, collecting at least one herbarium voucher per species, as well as foliar tissue for

5. *Attalea iguadummat*, La Paloma, Chocó, Colombia. A. & C. Acaulescent habit, B. Inflorescence, D. Regularly arranged leaflets





6. *Bactris charnleyae*, La Paloma, Chocó, Colombia. A. Habit, B. Detail of crown and infructescence, C. Infructescence.

DNA extraction. Specimens collected in Colombia were deposited in COL and those collected in Panama are conserved at PMA and G. We photographed all the species in detail (e.g. Figs. 4–13), trying to include their different developmental stages and their morphological variation (seedlings, adults, details of roots, leaves, flowers or fruits). We were particularly careful with dioecious taxa (e.g. *Chamaedorea*), trying to collect and photograph staminate and pistillate individuals. In the Colombian localities we also collected several seeds and seedlings of each species in order to include them in the Colombian National Palm Collection. This project of the Quindío Botanical Garden aims to grow in the same place all the palm species occurring wild in Colombia, as a tool for education, research and conservation. Not only the species but also the populations, with their particular genetic identity, are to be included in the collection. That is why we collected all the species at all the localities, even if some of them were already represented at the Collection.

Other sources of information

We consulted the literature (Galeano & Bernal 2010, Correa et al. 2004, Hodel 1992, Henderson et al. 1995), online herbaria databases (COL, F, K, MO, NY, PMA) and the Global Biodiversity Information Facility (GBIF, accessed 26.08.2015) to complement the list of species observed by us in the field and to prepare Figure 3. We verified the occurrences found in the mentioned herbaria and in GBIF and added to our list only species that had been determined by palm specialists.

Results and discussion

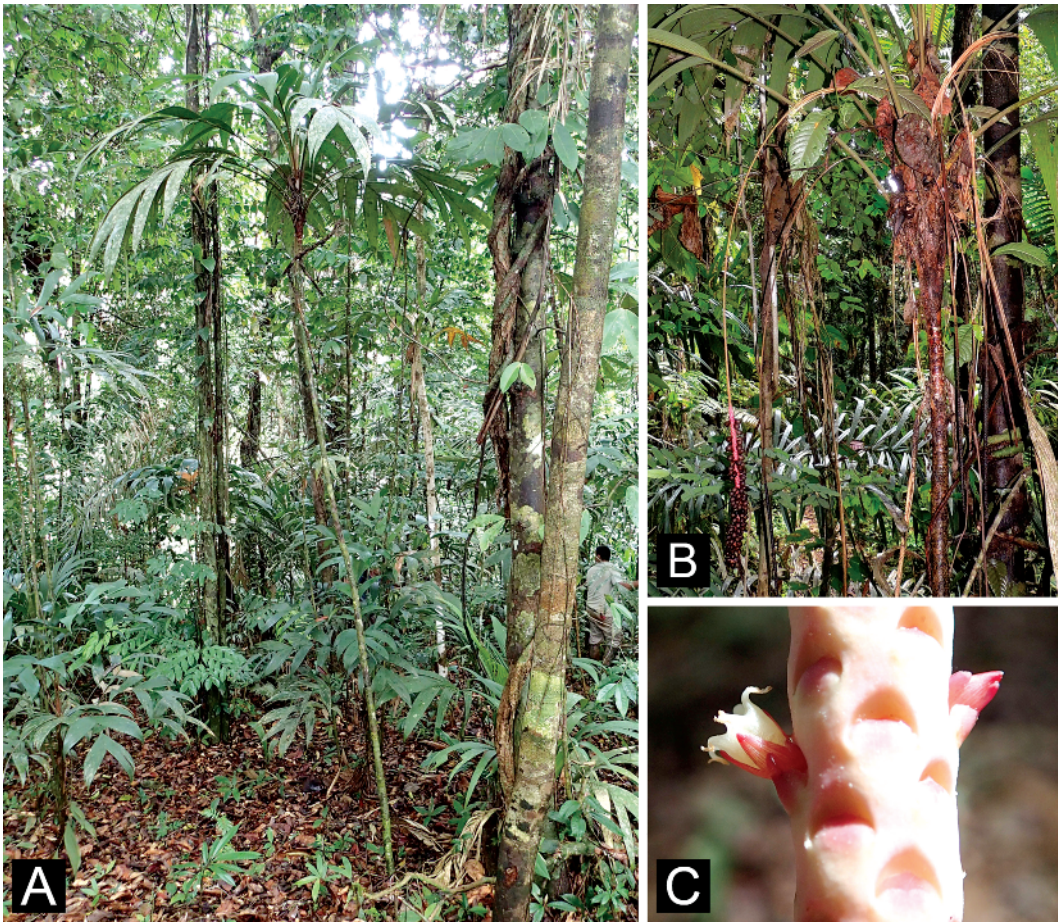
We documented 79 species of palms in the Darién Gap, belonging to 29 genera in 4 subfamilies. Only two species, *Chamaedorea ponderosa* and *Sabinaria magnifica*, are restricted to the Gap area, and three additional species (*Attalea iguadummat*, *Bactris charnleyae* and *Pholidostachys panamensis*) have narrow ranges that scarcely reach neighboring areas in Colombia or Panama (Table 1). As elsewhere in the continental neotropics, the largest

Table 1. List of palm species reported for the Darién Gap. The sources of information are given, from fieldwork: Cerro Pirre (CP), Cerro Sapo (CS), La Paloma (LP), Playona (P), Punta Ardita (PA), Tatabras (T), Sapzurro (SAP), Sasardí (SAS); from the literature: Correa et al. 2004 (C&al.), Galeano and Bernal 2010 (G&B); from virtual herbaria: Missouri Botanical Garden Herbarium (MO), New York Botanical Garden Herbarium (NY), Herbario Nacional Colombiano (COL), Herbario Universidad de Panamá (PMA).

Species	Data source
<i>Aiphanes acaulis</i> (Figs. 4A & B)	T
<i>Aiphanes buenaventurae</i> (Figs. 4C–E)	LP
<i>Aiphanes hirsuta</i>	CP, CS, T, C&AL, G&B, MO, PMA
<i>Asterogyne martiana</i>	LP, PA, C&AL, G&B, MO, PMA
<i>Astrocaryum malybo</i>	PA, G&B, COL
<i>Astrocaryum standleyanum</i>	CP, CS, LP, P, SAP, T, G&B, COL, MO, PMA
<i>Attalea allenii</i>	LP, T, G&B, MO
<i>Attalea iguadummat</i> (Fig. 5)	LP
<i>Bactris barronis</i>	CP, CS, PA, SAP, G&B, COL, MO
<i>Bactris brongniartii</i>	G&B, MO,
<i>Bactris charnleyae</i> (Fig. 6)	LP
<i>Bactris chocoensis</i>	LP
<i>Bactris coloradonis</i>	CP, CS, LP, P, PA, T, C&AL, G&B, COL, MO
<i>Bactris gasipaes</i>	CP, C&AL, G&B, MO
<i>Bactris glandulosa</i>	T, MO
<i>Bactris gracilior</i>	C&AL, MO
<i>Bactris major</i>	SAS, C&AL, G&B, COL, MO
<i>Bactris manriquei</i>	LP
<i>Bactris maraja</i>	CP, CS, LP, P, SAP, T, C&AL, G&B, COL, MO
<i>Bactris obovata</i>	LP, SAS, T, C&AL, G&B, COL, MO
<i>Bactris pilosa</i>	CP, LP, PA, SAS, T, C&AL, G&B, COL, MO
<i>Bactris setulosa</i>	G&B, MO
<i>Calyptrogyne costatifrons</i> (Fig. 7)	SAS, LP, G&B, MO
<i>Chamaedorea allenii</i>	CP, LP, SAS, T, C&AL, G&B, COL, MO, PMA
<i>Chamaedorea subjectifolia</i>	CS, LP
<i>Chamaedorea costaricana</i>	NY
<i>Chamaedorea deneversiana</i>	T, G&B
<i>Chamaedorea lucidifrons</i>	MO
<i>Chamaedorea macrospadix</i>	MO
<i>Chamaedorea matae</i>	MO
<i>Chamaedorea pinnatifrons</i>	LP, SAP, C&AL, G&B, COL, MO
<i>Chamaedorea ponderosa</i> (Fig. 8)	CP, PA, T, C&AL, G&B, MO
<i>Chamaedorea pygmaea</i> (Fig. 9)	CP, C&AL, MO
<i>Chamaedorea tepejilote</i>	CS, C&AL, G&B, COL, MO, PMA
<i>Chamaedorea warszewiczii</i>	CP, T, C&AL, G&B, COL, MO, PMA
<i>Chamaedorea woodsoniana</i>	CP, CS, T, G&B, MO, PMA
<i>Cocos nucifera</i> *	CP, T, C&AL, G&B

<i>Cryosophila kalbreyeri</i>	CP, CS, PA, SAS, C&AL, G&B, COL, MO
<i>Desmoncus cirrhifer</i>	T, MO
<i>Desmoncus myriacanthos</i>	LP, P, T, COL, MO
<i>Desmoncus obovoideus</i>	SAP
<i>Dictyocaryum lamarckianum</i>	CP, CS, T, C&AL, G&B, MO
<i>Elaeis oleifera</i>	CP, CS, P, PA, T, C&AL, G&B, COL, MO
<i>Euterpe longivaginata</i>	T, PMA
<i>Euterpe oleracea</i>	P, G&B, MO, PMA
<i>Euterpe precatoria</i>	CP, CS, C&AL, G&B, MO
<i>Geonoma calyptrogynoides</i>	PA, C&AL, G&B, COL, MO
<i>Geonoma cuneata</i>	CP, CS, LP, PA, T, C&AL, G&B, COL, MO, PMA
<i>Geonoma deversa</i>	CP, LP, PA, SAS, T, C&AL, G&B, COL, MO
<i>Geonoma frontinensis</i>	T
<i>Geonoma interrupta</i>	CP, CS, LP, PA, SAP, T, G&B, COL, MO
<i>Geonoma lehmannii</i>	T
<i>Geonoma maxima</i> subsp. <i>dispersa</i>	PA
<i>Geonoma procumbens</i>	LP, SAP, COL, MO
<i>Geonoma triandra</i> (Fig. 10)	CP, T, C&AL, G&B, MO
<i>Geonoma undata</i>	G&B, MO
<i>Hyospathe elegans</i>	LP, T, C&AL, G&B, MO
<i>Hyospathe pittieri</i>	G&B, MO
<i>Iriarte deltoidea</i>	LP, SAP, T, C&AL, G&B, COL, MO
<i>Manicaria saccifera</i>	P, G&B, MO
<i>Oenocarpus bataua</i>	CP, CS, LP, T, C&AL, G&B, MO, PMA
<i>Oenocarpus minor</i>	CP, CS, LP, P, SAP, T, C&AL, G&B, COL, MO, PMA
<i>Pholidostachys dactyloides</i>	CS, LP, T, C&AL, G&B, MO, PMA
<i>Pholidostachys panamensis</i> (Fig. 11)	LP
<i>Phytelephas macrocarpa</i>	CP, CS, LP, C&AL, G&B, COL, MO, PMA
<i>Prestoea acuminata</i>	CP, MO
<i>Prestoea decurrens</i>	LP, PA, G&B, COL, MO
<i>Raphia taedigera</i>	P, G&B, COL, MO
<i>Reinhardtia gracilis</i> (Fig. 12)	T, C&AL, G&B, COL, MO
<i>Reinhardtia koschnyana</i> (Fig. 13)	CP, C&AL, G&B, MO, PMA
<i>Reinhardtia simplex</i>	CS, C&AL, G&B, MO
<i>Sabal mauritiiformis</i>	CS, C&AL, G&B, MO
<i>Sabinaria magnifica</i>	LP
<i>Socratea exorrhiza</i>	CP, CS, LP, SAP, T, C&AL, G&B, COL, MO, PMA
<i>Synechanthus warscewiczianus</i>	CP, LP, PA, SAP, T, C&AL, G&B, COL, MO, PMA
<i>Welfia regia</i>	CP, SAS, G&B, COL, MO
<i>Wettinia aequalis</i>	LP, MO
<i>Wettinia quinaria</i>	LP, SAS, T, C&AL, G&B, COL, MO
<i>Wettinia radiata</i>	CP, PA, C&AL, G&B, COL, MO, PMA

*We have included the coconut, *Cocos nucifera*, in the list, as there is a long-standing debate on its wild occurrence along the Pacific coast of Panama and northern Colombia in pre-Columbian times.



7. *Calypstrogyne costatifrons*, La Paloma, Chocó, Colombia. A. Habit, B. Hanging infructescence, C. Detail of the inflorescence with typical pits and staminate flower.

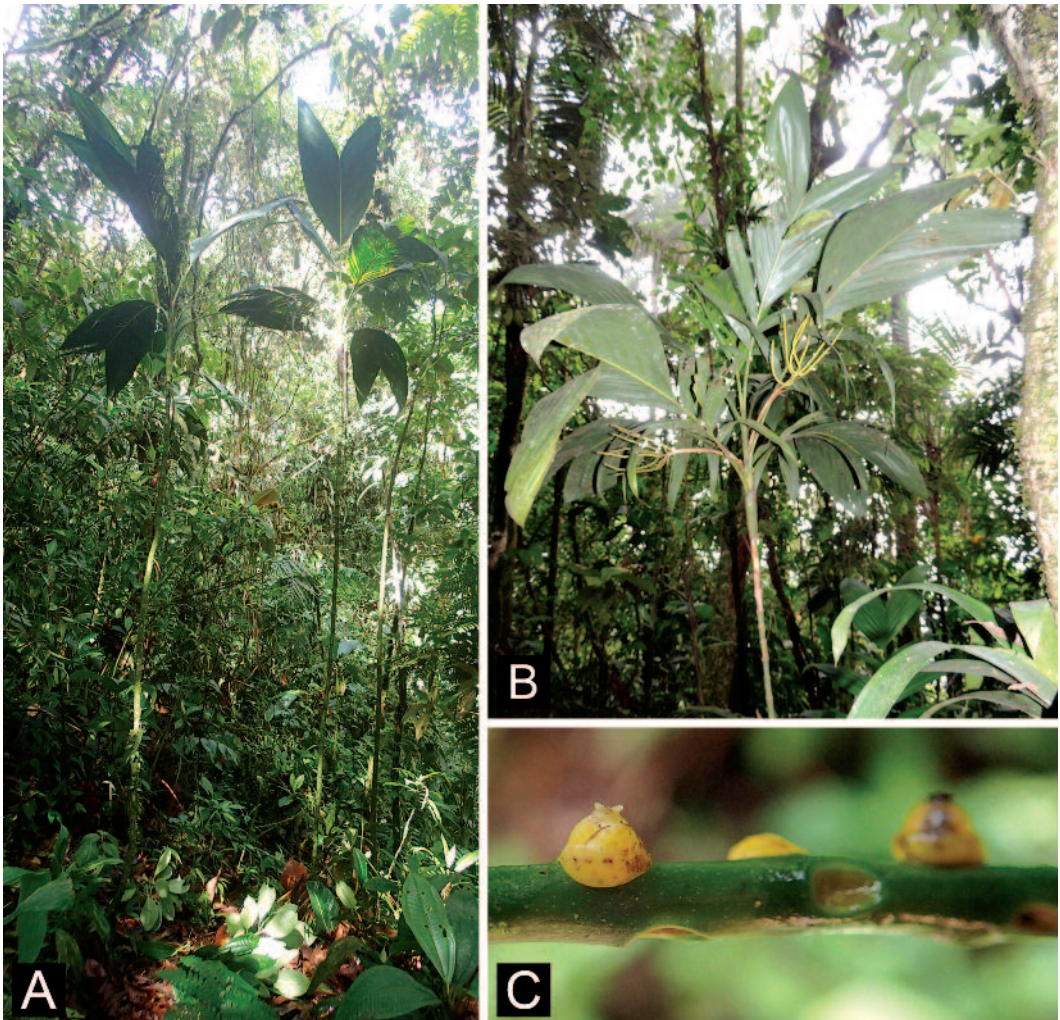
genera are the understory *Chamaedorea*, *Bactris* and *Geonoma*.

For many of the palms occurring in the Darién Gap, this area marks a southern or northern limit to their ranges. Figure 3 shows several examples of this. Other species having a southern limit in this area are *Chamaedorea ponderosa* and *C. warszewiczii*. In contrast, *Aiphanes acaulis*, *A. buenaventurae*, *Astrocaryum malybo*, *Bactris chocoensis*, *B. manriquei*, *B. setulosa*, *Geonoma calypstrogynoidea*, *G. triandra*, *Hyospathe pittieri* and *Wettinia aequalis* have their northern range limit in this area.

Why is this particular area the distributional limit of so many species from the north and from the south? From the Late Cretaceous (ca. 100 Ma), when the most recent common ancestor of all palms appeared in the life scenario (Couvreur et al. 2011), and until the Miocene, South America was isolated from Central and North America and between both

land masses there was an oceanic passage (Simpson 1980). During that long period, the palms, originally distributed in the Laurasian supercontinent (northern hemisphere), showed an impressive capacity of dispersal over the oceans and seas (Baker & Couvreur 2013a) and became widespread in the pantropical region. From the Miocene on, the Panama Isthmus started emerging, and around 10 Ma, a complete land-bridge enabled the southern species to disperse northwards and vice-versa (Montes et al. 2015). It has been suggested, for example, that the South American species of *Copernicia* crossed the Isthmus from North America (Bacon et al. 2013).

The biogeographic evolution of American palms is a complex story (see Baker & Couvreur 2013a, 2013b) that is starting to become clearer thanks to the development of molecular and computational technologies. However, there are still many blurred aspects of the evolution



8. *Chamaedorea ponderosa*, Cerro Pirre, Darién National Park, Darién, Panama. A. Habit, B. Leaves and inflorescence, note that the leaves can be simple or irregularly pinnate, C. Pistillate flower.

of palm lineages regarding the effect of the emergence of the Panama Isthmus. Was it a corridor that allowed the conquest of new niches? Or did it generate a bottleneck effect? When looking at cases like those of Fig. 3, one could think that the Darién Gap acted as a barrier, e.g., blocking the colonization of South America for the species mapped in pink. However, that is not the only possibility: their ancestor could have originated in the Darién Gap, and the species could have dispersed to the north afterwards. Or the Darién Gap may represent just the southernmost area they have reached so far. A deeper biogeographic study, based on comprehensive, species-level, time-calibrated phylogenies is needed to solve these conundrums, and that is being tackled at the Botanic Garden of Geneva.

Although large tracts of forest in the Darién Gap still lack exploration in search of palms, our field work has already revealed many interesting findings. Besides the discovery of the new genus *Sabinaria*, four species have been recorded for the first time in Colombia –*Attalea iguadummat* (Fig. 5), *Bactris charnleyae* (Fig. 6), *Chamaedorea subjectifolia* and *Pholidostachys panamensis* (Fig. 11) (Bernal 2014). Similarly, two species have been recorded for the first time in Panama –*Aiphanes buenaventurae* (Fig. 4C–E) and *Sabinaria magnifica*. On the other hand, the spiny *Astrocaryum malybo* has been collected in northwestern Colombia, ca. 7 km from the Panamanian border (Galeano & Bernal 2010), and its occurrence in southwesternmost Panama is highly likely.

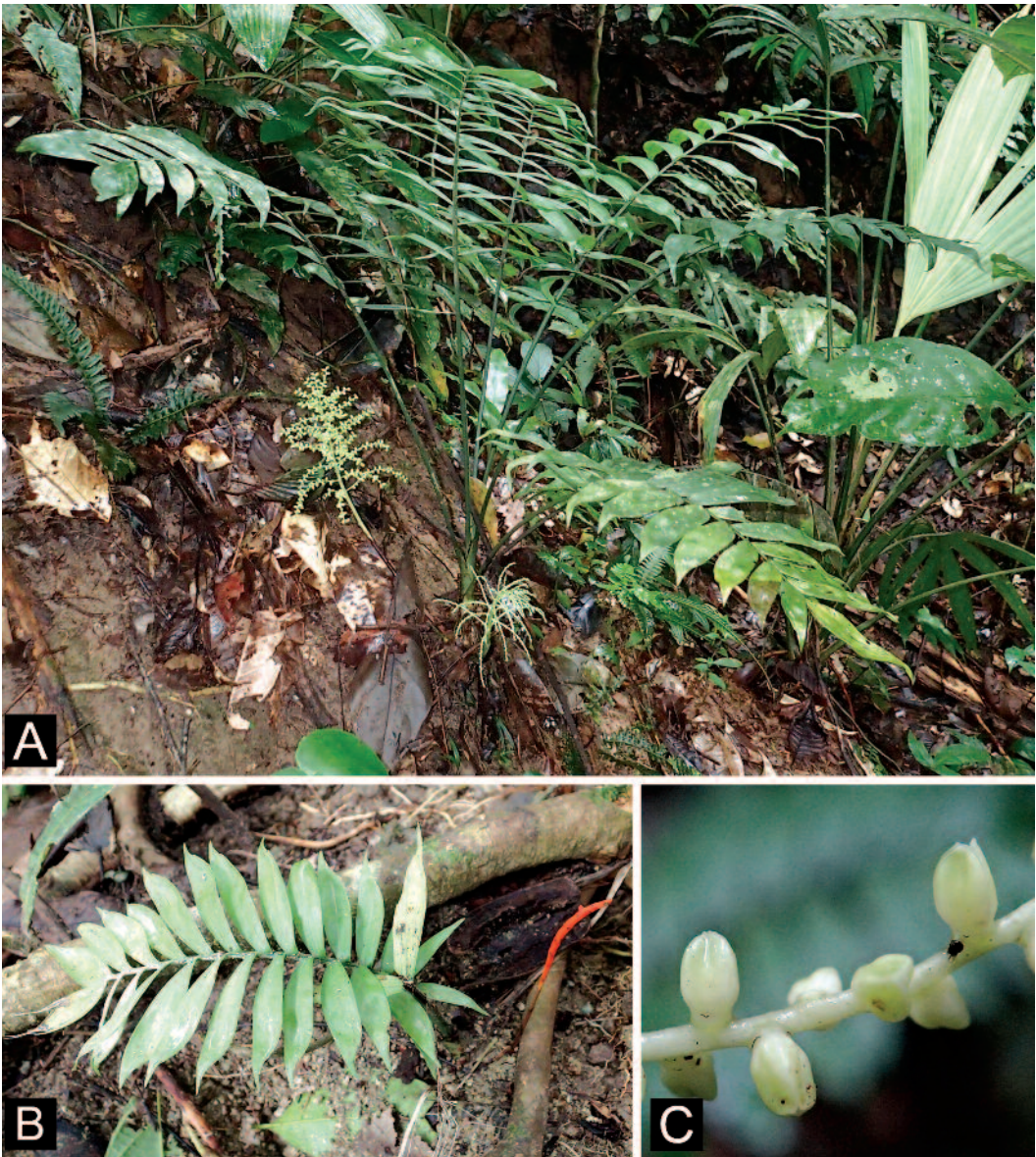
For some species, the Darién Gap has represented a significant extension of their known ranges. An interesting example is *Aiphanes buenaventurae* (Fig. 4C–E), formerly known only from two collections made in the Buenaventura area, in the southwestern coast of Colombia, where it had been unsuccessfully sought after by two of us (RB and HFM) in 2013. In the Darién Gap we found a small population of eight adult individuals exactly at the border. This suggests that the species grows throughout the lowlands of Chocó for at least 500 km. Its scarcity at the two known

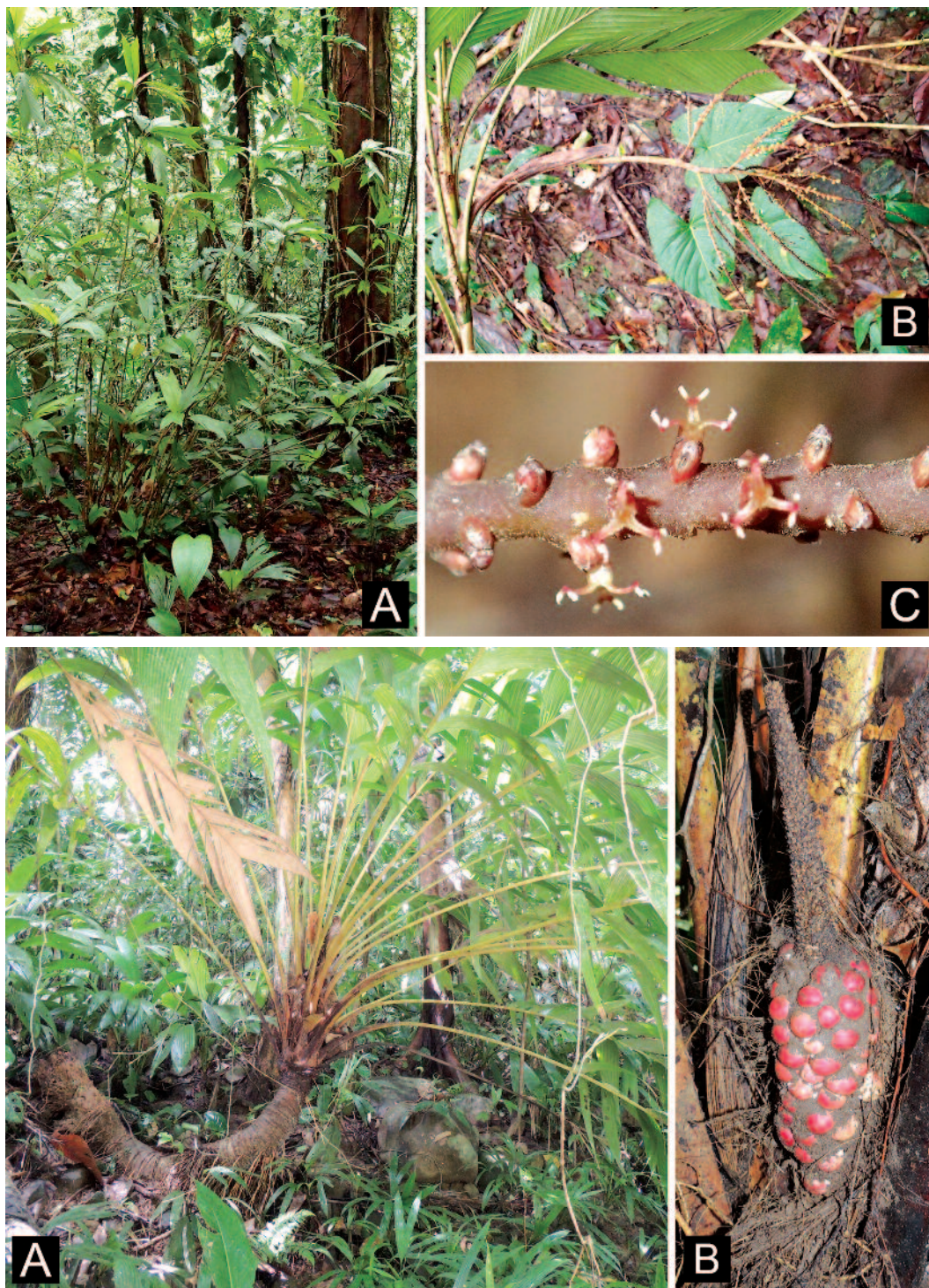
localities probably accounts for its having been overlooked in intervening areas.

Another species in this genus, *Aiphanes acaulis* (Fig. 4A & B), was abundant at Tatabras, where we built our camp amid them. This locality represents a 300 km northwestward extension for the range of this beautiful acaulescent palmlet, formerly known only from central Chocó department, in Colombia.

Although most of the Darién Gap is still densely covered with forest, deforestation is already evident in its marginal areas. On the

9. *Chamaedorea pygmaea*, Cerro Pirre, Darién National Park, Darién, Panama. A. Habit of staminate individual, B. Habit of pistillate individual, C. Staminate flowers.



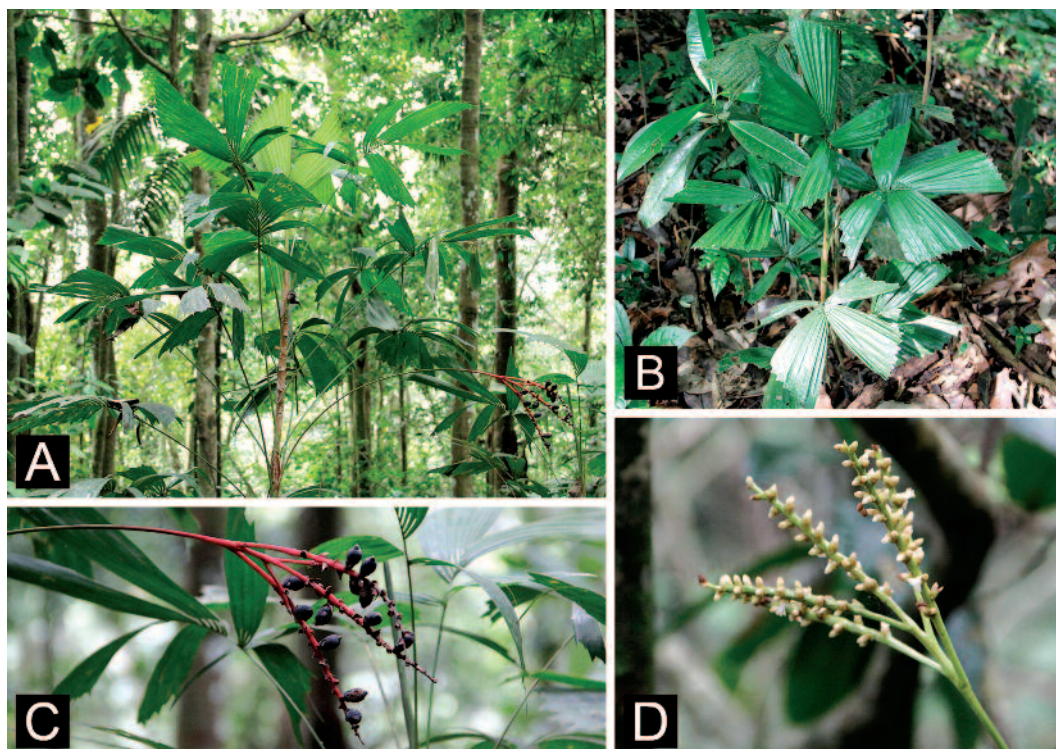


10 (top). *Geonoma triandra*, Cerro Pirre, Darién National Park, Darién, Panamá. A. Habit, B. Inflorescence, C. Staminate flowers with three stamens (to which the specific epithet alludes).

11 (bottom). *Pholidostachys panamensis*, La Paloma, Chocó, Colombia. A. Habit, B. infructescence.

Colombian side, the Darién is bordered by the Urabá region, one of the most severely deforested areas in the country. From the

towns of Unguía, Acandí and Capurganá, deforestation fronts are already evident and clearly advancing. Between 2014 and 2015, a



12. *Reinhardtia gracilis*, Tatabras, Chocó, Colombia. A. Habit, B. Leaves, C. Infructescence and leaves (note the windows at the base of the leaflets), D. Inflorescence.

few hectares of the forest where *Sabinaria magnifica* grows were cleared for agriculture, and soon thereafter they were abandoned. On the Panamanian side, the Pan-American Highway has already devastated a large area of the former forests of the Gap, up to the village of Yaviza (Fig. 1). In the remaining areas, deforestation occurs in the lowlands, especially nearby towns or indigenous communities, even inside the Darién National Park area. In the *Serranía* the vegetation is better conserved or intact. That is also the case towards the Caribbean coast of Panama, because there are no roads or human settlements in the continent; the indigenous people that inhabit the area live in the islands near the coast.

The 79 species of palms found at the Darién Gap, as well as their interesting distribution patterns, provide an insight into the extremely rich flora of this area, and its vital role in the evolution of the current neotropical biota. Despite our work, the upper ranges of the *Serranía* still remain poorly known, particularly in the most inaccessible central areas. Many new records and perhaps even novelties are still to be expected, not only for the palm family, but also for other plant groups. Evidence of this is what we found after only a

few days exploring the Tatabras region; *Lozania glabrata*, (Lacistemataceae) a species apparently known only from the type specimen, a new record for Colombia (*Maytenus schippii*, Celastraceae) and a possibly new species of Bombacoideae.

Conservation of the forests in the whole Darién Gap, not just in the current protected areas, should be of the utmost priority for both Panama and Colombia. Deforestation of this historical crossroad of biological and cultural exchange between South America and North America would deprive us of a vital source of information on the Earth's remote past.

Acknowledgments

Exploration of the Darién Gap was sponsored by the International Palm Society endowment fund, the Palm Research Team of Universidad Nacional de Colombia, the Quindío Botanical Garden, the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (Colombia), and the Dr. Joachim de Giacomini Foundation of the Swiss Academy of Natural Sciences. Field work was supported by the Fundación Darién, in particular Sergio Márquez and Hugo Ortega (Acandí), Gloria



13. *Reinhardtia koschnyana*, Cerro Pirre, Darién National Park, Darién, Panama. A. Habit, B. Inflorescence bearing staminate and pistillate flowers, C. Fruits.

Upegui (Sapzurro), Orlando Martínez, Angie Henao, Germán Henao, and Cristina Lopera (Capurganá), Julio Restrepo, Darío Toro and the Toro family (Balboa), Marcos Gonzalez, Alipio Canupia, Luis Pacheco (Darién National Park).

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Baron Ferdinand von Mueller, the “Princeps of Australian Botany,” and a Historical Account of his Australasian Palms

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Baron Ferdinand von Mueller was Australia's most celebrated botanist of the nineteenth century. Although a broad-based plant taxonomist, he described 19 new palm taxa, including two genera and 15 species in Australia, and one species each in New Guinea and Fiji. Significantly, Mueller's taxa represent about 25% of all the palms thus far recognized for Australia and its off-shore dependencies, and he remains the single most important taxonomist to have worked on Australian palms.

Baron Ferdinand von Mueller (1825–96) (Fig. 1) was Australia's most productive plant taxonomist of the nineteenth century (Stevens 1997), describing over 2400 taxa of which more than half remain as the currently used names (APNI 2015). Migrating from Germany to Australia in 1847, Mueller was engaged as the Victorian Government Botanist in 1853 (a position he held until his death) and established the Phytologic Museum of Melbourne (now the National Herbarium of Victoria) in the Melbourne Botanic Gardens.

His vast correspondence, estimated to be over 12000 surviving letters (Anon. 2015), and capacity to publish and disseminate widely his taxonomic work (Churchill et al. 1978), provide an extensive resource upon which to understand his botanical methods and resolve his continuing taxonomic influence. The appellation “*Princeps of Australian Botany*” was first given to him by William Thiselton-Dyer, Director of Kew Gardens, in recognition of his pre-eminence as a taxonomist and champion of the Australian flora (Mueller 1878a).



1. Baron Ferdinand von Mueller, c. 1877, *carte de visite* by J. Botterill, Melbourne.

Despite his authority over Australian plant taxonomy, Mueller received criticism because of his methodology in determining genera and species limits and changes that he made to contemporary plant classification systems (Maroske 2006). Early in his career, the prominent English taxonomist George Bentham (1853) claimed that Mueller described too many species on questionable and inconsequential differences and that some of his generic limits were too broad. Bentham bluntly told Mueller in correspondence (quoted in Moore 1997) that his:

...wholesale amalgamation of genera, without any indication of the characters to be assigned to the new compound genus, or of its relations to allied genera retained as distinct, has no other effect than the unnecessary addition of many hundred names to the already over-loaded synonymy.

An anonymous obituarist (Anon. 1896) wrote a scathing though patently unfair criticism of

Mueller with regards to his taxonomic work, writing that:

He was insatiable in his desire for titles and notoriety. This weakness caused him to publish botanical contributions in every possible organ open to him and occasionally led him to the commission of regrettable inconsistencies in botanical nomenclature... he needlessly added to the synonymy of Australian plants by simultaneously publishing many of them under two generic names, so that whichever view one might take of generic limits, his name would still stand as the authority!

It is difficult to justify such negative criticism considering Mueller's exceptional output, and it is inconceivable that he willfully created potential taxonomic and nomenclatural problems. The vastness of Mueller's taxonomic works expedited the possibility of the unintentional creation of potentially problematic synonymies. Nevertheless, and as examples, he created some nomenclatural difficulties for future taxonomists with regard to palms, as with the genera *Bacularia* and *Normanbya*. Both were first introduced by Mueller as proposed alternative genus names, actions that subsequently created taxonomic and nomenclatural challenges. However, it must be understood that during Mueller's active years there was a lack of precision and cohesion in the collective rules of plant nomenclature. Issues of nomenclatural priority ('primogeniture' in Mueller's terminology) and what is now known as 'valid publication' were imperfect concepts. There were many attempts by taxonomists to stabilize the rules of plant nomenclature but there was no mechanism to ensure conformity among taxonomists. Mueller (1892a) ostensibly supported the rules of priority, as he wrote to Adolf Engler, stating that:

...the binomial name which at first was used in the correct genus can have priority, which certainly always follows from the date.

Mueller (1893) summarized his views on priority in a later letter to Joseph Hooker writing that:

...even if we have ever so many congresses or conferences or deliberations, they will be overthrown like all other unjust legislature, unless all arbitrariness is avoided. I often wonder, what they will

think of us about the agitation now on priority of plant names, a hundred years hence. As I said, permanency and unanimity can only be secured by absolute justice. Of course no one is bound to accept decisions of Congresses which he did not attend.

Matters regarding priority and nomenclature of Mueller's palm taxa will be further discussed individually below.

Mueller's palm taxonomy

Author's note: In the following, Mueller's original nomenclature is maintained in the text and currently accepted nomenclature follows in square brackets.

During Mueller's era, Australian palms were primarily seen, at least by botanists based in southern Australian cities, as plants of unpopulated, wild places of the tropical northern outposts of the Australian colonies. Mueller (1880a) wrote to Joseph Hooker that:

...my material on palms is very scanty, but I will send you what I have. In North Queensland the palms (even there like bamboos not numerous) occur in fever-jungles beset by cannibals; indeed I rather meet a tiger or *Naja* in India or a lion in Africa, than savage bipeds in the forest-recesses of N. E. Australia.

Mueller (1880b) variously noted the difficulty in obtaining herbarium specimens of palms because of their remoteness (from his herbarium in Melbourne), their occurrence in environments which necessitated special collecting techniques, and the infrequency which his collectors entered those environments.

In addition to herbarium specimens, Mueller supplied seeds and propagation materials of palms to botanical institutions such as the Botanic Garden of the University of Florence (Mueller 1865a), Kew Gardens in Britain and Herrenhausen Gardens in Germany (Wendland & Drude 1875). Mueller (1865b) wrote in a letter to Carl von Martius that he had:

...seen to it to distribute the frost resistant species of the far southern palms *Ptychosperma*, *Seaforthia* [*Archontophoenix cunninghamiana*], *Areca* *sapida* [*Rhopalostylis sapida*] and *Livistona australis* in large quantities by sending of seeds around the Mediterranean.

Mueller promoted the horticultural value of Australian plants and palms, not only to Australian institutions but also to European gardens and acclimatization societies, by supplying seeds and propagation materials (Naudin & Mueller 1887, Parkin 1996). He experimented with supplying live plant materials as well as seeds (Mueller 1874a). An attempt was made in 1882 to despatch a live stem of the Australian cabbage palm (*Livistona australis*) to Kew Gardens from Melbourne, but it did not survive the rigors of long-distance sea travel. Mueller (1882a) wrote in a letter to Joseph Hooker that:

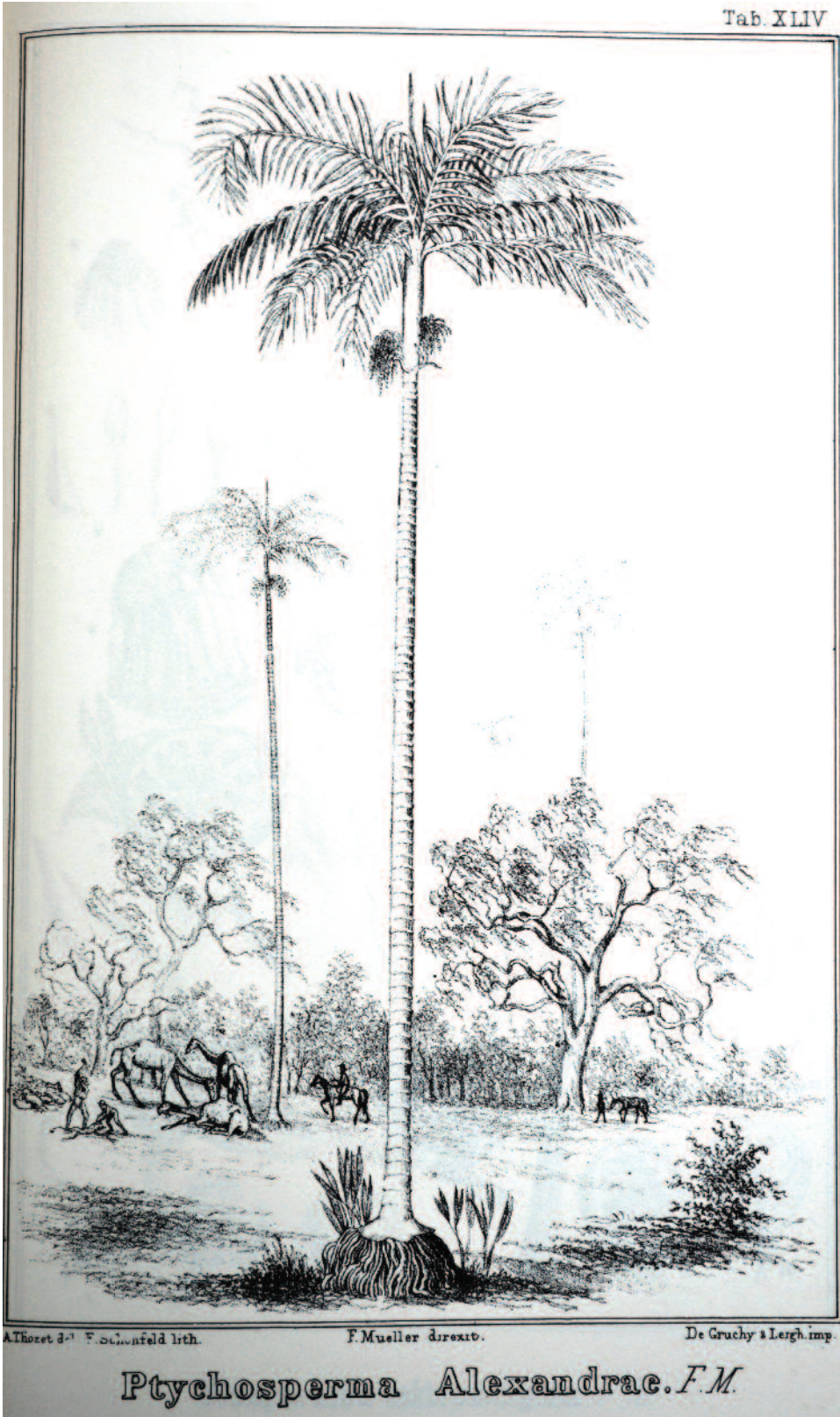
...the experiment with the *Livistona* did not succeed, is not surprising, the distance of shipping is too far. Stems, quite similarly treated, have grown here in gardens quite well and made at once a magnificent show, but then it took only 2 or 3 weeks, to bring the stems from Illawarra to Port Phillip.

He was also a grateful recipient of palms that could be grown in Melbourne, especially if the species was readily adaptable to the temperate climate of southern Australia. On receiving seeds and plants of *Rhopalostylis sapida* (nikau palm) from New Zealand, Mueller (1865c) wrote to Governor Grey:

I have to express to your Excellency my most grateful acknowledgement for your goodness in causing my establishment to be supplied not merely with a quantity of seeds of the N. Z. *Areca* [*Rhopalostylis sapida*], but also with a number of living plants of this noble palm. As the species is so hardy I am anxious to introduce it into all the cooler latitudes, in which among tall palms only the N. Z *Areca* and our Australian southern *Livistona* [*L. australis*] & *Seaforthia* [*Archontophoenix cunninghamiana*] will grow. The latter palms are within my reach, but I am glad to be able through Your Excellency's kindness to add now also the New Zealand palm to those others rendered already available to my correspondents.

Mueller's first synoptic assessment of Australian palms was in 1864, the year prior to his naming his first Australian species. Mueller (1864) summarized the family in a letter to Carl von Martius:

...palms, which are evidently sparsely represented in Australia, even though this noble family of plants reaches its southern limit here at the southern latitude of



2. Illustration of *Ptychosperma alexandrae* (*Archontophoenix alexandrae*), Tab XLIV in *Fragmenta phytographiae Australiae* vol. 5 (1865), "A. Thozet del F. Schonfeld lith. ... F. Mueller direxit ... De Gruchy & Lergh. Imp."



3. *Archontophoenix alexandrae* (F. Muell.) H. Wendl. & Drude was named [as *Ptychosperma alexandrae*] by Baron Ferdinand von Mueller in 1865 to commemorate the wedding of Princess Alexandra of Denmark to Edward Prince of Wales, later King Edward VII of Great Britain. Photo taken at Eungella National Park, Queensland, Australia. Photo by J.L.Dowe.

Table 1. Palm taxa named by Ferdinand Mueller. The currently used names follow the treatment of the Arecaceae in *Flora of Australia* (Dowe & Jones 2011)

Original name	Currently used name
<i>Areca alicae</i> F. Muell.	<i>Areca triandra</i> Roxb. ex Buch.-Ham.
<i>Bacularia</i> F. Muell.	<i>Linospadix</i> H. Wendl.
<i>Calamus obstruens</i> F. Muell.	<i>Calamus australis</i> Mart.
<i>Caryota albertii</i> F. Muell. ex H. Wendl.	unchanged
<i>Kentia beccarii</i> F. Muell.	<i>Hydriastele montana</i> (Becc.) W.J. Baker & Loo
<i>Kentia belmoreana</i> C. Moore & F. Muell.	<i>Howea belmoreana</i> (C. Moore & F. Muell.) Becc.
<i>Kentia canterburyana</i> C. Moore & F. Muell.	<i>Hedyscepe canterburyana</i> (C. Moore & F. Muell.) H. Wendl. & Drude
<i>Kentia forsteriana</i> C. Moore & F. Muell.	<i>Howea forsteriana</i> (C. Moore & F. Muell.) Becc.
<i>Kentia mooreana</i> F. Muell.	<i>Lepidorrhachis mooreana</i> (F. Muell.) O.F. Cook
<i>Kentia wendlandiana</i> F. Muell.	<i>Hydriastele wendlandiana</i> (F. Muell.) H. Wendl. & Drude
<i>Livistona alfredii</i> F. Muell.	unchanged
<i>Livistona drudei</i> F. Muell. ex Drude	unchanged
<i>Livistona leichhardtii</i> F. Muell.	<i>Livistona humilis</i> R.Br.
<i>Livistona mariae</i> F. Muell.	unchanged
<i>Livistona ramsayi</i> F. Muell.	<i>Licuala ramsayi</i> (F. Muell.) Domin
<i>Normanbya</i> F. Muell. ex Becc.	unchanged
<i>Pritchardia thurstonii</i> F. Muell. & Drude	unchanged
<i>Ptychosperma alexandrae</i> F. Muell.	<i>Archontophoenix alexandrae</i> (F. Muell.) H. Wendl. & Drude
<i>Ptychosperma beatriceae</i> F. Muell.	<i>Archontophoenix alexandrae</i> (F. Muell.) H. Wendl. & Drude

37°30'. The particular limits of the other Australian *Livistona* species have so far not been precisely determined, and therefore the geographical limits of the individual species of this genus cannot yet be defined. They extend, however, only along the wooded east and north coasts, with the exception of one noble species, which the unhappy Leichhardt, as well as I personally met with occasionally in the open plains or on slopes of Arnhem Land. *Areca monostachya* [*Linospadix monostachyos*] is restricted to subtropical eastern Australia. *Cocos nucifera* is found on one or another of the small islands of Torres Strait, and *Caryota urens* [*Caryota albertii*] in far north-eastern Australia. *Seaforthia elegans* [*Archontophoenix cunninghamiana*] extends intermittently from Illawarra along the east coast, and perhaps belongs also to North Australia. *Calamus australis* is distributed fairly widely through tropical and extra-tropical littoral eastern Australia. There is no evidence of palms, neither on

the west nor on the south coast, nor in the distant interior of Australia.

Taxonomic progression

The first new palm species to be described by Mueller were published in 1865 in his journal *Fragmenta phytographiae Australiae*. These included three taxa, *Ptychosperma alexandrae* [*Archontophoenix alexandrae*] (Figs. 2 & 3), *Calamus obstruens* [*Calamus australis*] and *Livistona leichhardtii* [*L. humilis*] (Table 1) (Mueller 1865d). The protologue of *Ptychosperma alexandrae* included a dedication to Princess Alexandra of Denmark on her marriage to Edward Prince of Wales (later King Edward VII of Great Britain) (Mueller 1865e). When it came to naming new palm species, the eponymous dedication to royalty and nobility was to become one of Mueller's favored approaches considering the 'princely', 'noble' and 'majestic' character of palms (Dowe & Maroske 2016). *Calamus obstruens* was named for the palm's characteristics, which, with long barbed whips, obstructed the passage



4. Illustration of *Kentia belmoriana* (*Howea belmoreana*) (right) and *K. forsteriana* (*Howea forsteriana*) (left), 'From a sketch by R. Fitzgerald', in *Fragmenta phytographiae Australiae*, un-numbered plate, Vol. 7 (1870).

of persons if unfortunate enough to get caught in their grip. The last taxon of the group, *Livistona leichhardtii*, was a proposed name included in a summary of *Livistona* species that were thus far described for Australia. The name was later validated by Mueller (1874b). The species was named for the explorer and naturalist Friedrich Wilhelm Ludwig Leichhardt (1813–1848?). Leichhardt and his party attempted an east to west crossing of Australia in 1848, but they were never heard of again and the circumstances of their disappearance remain an enduring legend of Australia's outback (Lewis 2013). Mueller espoused an ongoing interest in the fate of Leichhardt, and was instrumental in promoting and organizing a number of searches for the lost explorer and his party (Mueller 1865f). Also included in this treatment of the Palmae was a brief synopsis of the twelve Australian palm species described by other botanists up to that time (Mueller 1865d).

It is around this time that Mueller began to send his palm herbarium specimens from Melbourne to specialists in Europe. He dispatched the whole palm collection to von Martius in Munich, Germany, in 1868 in anticipation of a taxonomic contribution, as described in a letter from Mueller (1868a) to von Martius:

...it gives me particular pleasure to be able to place the little material, that in this respect evidently poor flora of Australia has displayed so far, before the great expert on these princely plants. Nonetheless, there are 17 species (as far as I can judge), and that, after all, quadruples the number of palms expounded by Robert Brown. Unfortunately these plants were accessible to me only under the most unfavorable conditions, and that must excuse the inadequacies of the specimens. I fear that you, exalted friend, will not consider the poor material worth a close examination. However, should you do so nonetheless, we should gain a classic, eternally memorable contribution for the 6th volume of the Flora of Australia. I beg you, to retain any one specimen, which ever it may be, for your own palm collection, but send the rest through Dr Sonder to Bentham during 1868, as Bentham in any case wishes to compare my original material with that of Robert Brown's and Hooker's collections.

Mueller (1868b) subsequently wrote to Joseph Hooker, that:

...after several requests of the great and venerable von Martius I have sent to that excellent man the whole of my Australian palms on loan, 6 or 7 large packages, comprising 17 species.

It was unfortunate that von Martius was not able to commence any new work on the Australian palms as he died shortly after, on 13 December 1868 (Egge 1979).

Mueller's next episode of palm taxonomy involved specimens collected from Lord Howe Island in 1869 by Charles Moore, William Carron and Robert David Fitzgerald (Moore 1870), and another specimen received from northern Australia collected by Benjamin Gulliver (Mueller 1870). In addition to describing the five new species at this time, Mueller established a new genus, *Bacularia*, to accommodate a single species, *Kentia monostachya* [*Linospadix monostachyos*], that was originally described as *Areca monostachya*. The genus was suggested by name only, and therefore was nomenclaturally invalid, as there was no description or formal transfer of taxa. Although not validly published, Mueller (1878b) continued to use *Bacularia* in his own publications, and later provided a summary of his *Bacularia* species. *Bacularia* was later validated by Hooker (1882), although its identity remained obscure and is now a synonym of *Linospadix* (Dowe & Irvine 1997).

Returning to the Lord Howe Island species, Moore (1870) provided a report on their plant collecting activities on Lord Howe Island, in which he listed four unnamed palm species, two in the genus *Kentia*, one in the genus *Areca*, and another in an undescribed genus. In his report, Moore used descriptive common names that were quoted by Mueller as part of his protologues, and which are currently still in use for the respective species. Mueller described all these new species within the genus *Kentia* as *K. belmoreana* [*Howea belmoreana*], *K. forsteriana* [*Howea forsteriana*] (Fig. 4), *K. canterburyana* [*Hedyscepe canterburyana*] (Fig. 5), *K. mooreana* [*Lepidorrhachis mooreana*] and *K. wendlandiana* [*Hydriastele wendlandiana*]. The genus *Kentia* at that time was among the largest palm genera consisting of 40–50 species, functioning as an admixture of Arecoid palms from eastern Indonesia, New Guinea, New Caledonia, Fiji, New Zealand and Australia (Govaerts & Dransfield 2005). With



From a Sketch by R. Fitzgerald.

Kentia canterburyana

Dracophyllum Fitzgeraldii

5. Illustration of *Kentia canterburyana* (*Hedyscepe canterburyana*), 'From a sketch by R. Fitzgerald', in *Fragmenta phytographiae Australiae*, un-numbered plate, Vol. 7 (1870).

regard to the Lord Howe Island palms, Mueller (1869) noted in a letter to Joseph Hooker that:

There are also 4 palms on the island, which seem all to belong like the 8 New Caledonians to *Kentia*, with which Miquel & Blume unite the New Zealand *Areca sapida* [*Rhopalostylis sapida*]. Possibly *Kentia* is only a section of *Areca*. I shall investigate the matter as far as my material admits.

The evident taxonomic disharmony within *Kentia* was soon to be recognized by palm taxonomists (Brongniart 1873, Wendland & Drude 1875, Beccari 1877, 1885), and the genus was partitioned into a number of small or monotypic genera, with *Kentia sensu stricto* remaining as a much diminished genus, distributed in the Moluccas, New Guinea, northern Australia and Fiji. All of Mueller's *Kentia* species were transferred to other genera through early works by other botanists. Of interest is that Bentham, though an otherwise persistent critic of Mueller's taxonomic methodologies, followed Mueller's assignment of *Kentia* species *verbatim* in his treatment of the *Palmae* in *Flora Australiensis*. Bentham (1878) wrote that:

The genus [*Kentia*] has however been variously extended or restricted by different phoenicologists. I have followed in its delimitation the views of F. Mueller, which appear most in conformity with those of Blume, although in the original species the male flowers are hexandrous. In the Australian species the number of stamens varies considerably but always more than 6, they would therefore be referable to A. Brongniart's genus *Kentiopsis* (Comptes Rendus 1873) which appears to me to be too artificially separated from *Kentia*.

Perhaps showing some taxonomic stubbornness, Mueller continued to maintain his *Kentia* species in his own publications (Naudin & Mueller 1887; Mueller 1889), although his taxa had been assigned to different genera by other botanists as synonyms. Some botanists continued to maintain *Kentia* as a valid taxon well into the twentieth-century, though much reduced in species number (Beccari 1923; Martelli 1935; Burret & Potztl 1956). All the species that were formerly included in *Kentia* are now distributed to other genera, and it is considered an invalid and misapplied taxon (Dransfield et al. 2008).

Following on with new palm taxonomy, two more species, *Livistona ramsayi* [*Licuala ramsayi*] (Fig. 6) and *L. mariae*, were published by Mueller (1874b) in Volume 8 of *Fragmenta*. Mueller first received information about the former species in a letter from the naturalist Edward Ramsay who provided a description and a sketch of a leaf and inflorescence and suggested it was a species of *Livistona* (Barford & Dowe 2005). Ramsay soon after dispatched to Mueller a specimen that he collected from Rockingham Bay. Ramsay's (1874) letter to Mueller included:

My No.5 is quite distinct from any *Livistonea* I know of the leaves are almost peltate and the pinnae joined for more than ½ their length it forms a flat stiff shieldlike disc – look at a short distance as if quite peltate near entire or plicate. Disc 6 to 8 feet in diameter on young tree 20 ft high they were 6 ft across. Hill [Walter Hill] found this and says he thinks he met it but has no specimens I gave him seed – it is the only one of this form I ever met with...I used a leaf for an umbrella during a very heavy storm without getting at all wet.

Perhaps as an indication of his non-specialized interest in palms, Mueller failed to recognize that it belonged to the genus *Licuala*, and not *Livistona*. What might have been an "excuse" for Mueller (1874c) for not correctly identifying the genus was provided in a reply to Ramsay:

I labor under especial disadvantage for working on palms this moment, because I lent my whole normal collection to Mr. H. Wendland, who works exclusively on palms: but although this took place several years ago, I have up to date not a single line from him on the subject of their elucidation, nor has he returned the original specimens, placing me thus at great inconvenience for further comparisons.

As to be discussed further on, Wendland was at that time preparing the first monograph on Australasian palms and Mueller had dispatched to him at Herrenhausen Gardens, Germany, most of the palm specimens then presently held in the Melbourne herbarium.

Almost at the same time that Mueller published his description of *Livistona ramsayi* [*Licuala ramsayi*], Wendland and Drude (1875) described another taxon established on the



6. *Licuala ramsayi* (F. Muell.) Domin was named by Baron Ferdinand von Mueller to honor the collector of the type specimen, Edward Pierson Ramsay [as *Livistona ramsayi* F. Muell.]. Ramsay, an ornithologist and zoologist, was Curator of the Australian Museum, Sydney 1874–94. Photo taken at Djiru National Park, Mission Beach, Queensland, Australia. Photo by J.L. Dowe.

same species, which they named *Licuala muelleri* [*Licuala ramsayi*] as a dedication to Mueller, but based on a different specimen that had been collected by John Dallachy from Dalrymple Gap, Queensland. Seemingly unaware of the association between their *Licuala muelleri* and Mueller's *Livistona ramsayi*, Wendland and Drude (1875) maintained the latter as a species within *Livistona* and proposed that it was a possible synonym of *L. inermis* (which was their interpretation of *Livistona decora*). Wendland and Drude also noted that they found it difficult to reconcile *L. ramsayi* as they had not seen adequate specimens. The publication of two names concurrently, for the same species, explains the confusion that was to eventuate in the identity of this palm. Bentham (1878) appeared to recognize the anomaly, and he chose *Licuala muelleri* as the 'legitimate' name, and placed *Livistona ramsayi* as a synonym of it. However, this action would, by current nomenclatural rules at least, be deemed "illegal" as he should have maintained Mueller's original epithet, *ramsayi*, as it antedated Wendland and Drude's *muelleri* and therefore had nomenclatural precedence (McNeil et al. 2012). Bentham (1878) wrote in *Flora Australiensis* that:

Although the flowers are unknown it is probable that Wendland and Drude are correct in transferring this palm from *Livistona* to *Licuala*, but its precise affinities must remain for the present undetermined.

The correct (and currently accepted) combination, *Licuala ramsayi* was eventually provided by Domin (1915), and the taxon that Wendland and Drude proposed to be the "true" *Livistona ramsayi* from Rockingham Bay is now attributed to *L. drudei* (Rodd 1998).

The second taxon established by Mueller (1874d) in the same issue of *Fragmenta* was *Livistona mariae* named for Grand Duchess Maria Alexandrovna on the occasion of her marriage to Prince Albert, son of Queen Victoria (Dowe & Maroske 2016). At first, Mueller only provided a name in a note, simply as "*L. mariae*," and without a description. Soon after, he provided an additional brief entry as a footnote in Ernest Giles' *Geographic Travels in Central Australia* after that explorer located a population of palms in the "Glen of Palms" (Palm Valley) and thus revoking the earlier statement by Mueller (1864) that no palms were found in

central Australia. Later in the same publication, in the list of species collected by Giles, Mueller provided the full name: "*Livistona Mariae*, F. M., *Fragm. IX., ined.*" but noted that it was *ineditus*, i.e. unpublished (Giles 1875). The validating description was eventually provided in 1878 (Mueller 1878b)

As mentioned above, the first monograph on Australasian palms was at that time being prepared by the German botanists Hermann Wendland and Oscar Drude, which resulted in the publication of *Palmae Australasiae* in the journal *Linnaea* (Wendland & Drude 1875). Hermann Wendland (1823–1903) was Director of Herrenhausen Gardens 1870–1903, and during the late 1800s was considered an authority on palms (Anon. 1903a). Wendland had described many species of palms from Africa, the Americas, Australia and the south Pacific (Wittmack 1903). He was also a renowned horticulturist, and the living collection of palms that had been assembled at Herrenhausen Gardens was to surpass that at Kew and was the largest in Europe at that time (Regel 1891, Anon 1903b). The living palm collection at Herrenhausen had developed over many decades, mainly housed in technically-advanced large heated glass-houses that were designed and constructed to allow tropical palms to be grown to maturity in an otherwise temperate climate (Wendland 1882, Auhagen 1882, Palm & Rettich 2006). Many new palm species were described on specimens that were cultivated at Herrenhausen Gardens (Hodel 1992). Over his career, Wendland described about 600 palm taxa, primarily from the Americas and Africa (IPNI 2015). Wendland's collaborator, (Carl George) Oscar Drude (1852–1933) was Assistant at the Göttingen University Herbarium during this time, later a lecturer and Professor in Botany at Dresden Polytechnikum, becoming one of the world's leading ecologists and biogeographers and Director of Dresden Botanical Gardens, 1879–1920 (Güttler 2011, Egerton 2015). Drude was an active palm taxonomist, describing about 300 taxa during his career, mostly from the Americas (IPNI 2015).

As acknowledged in their introduction to *Palmae Australasiae*, Wendland & Drude (1875) considered that Mueller had made a significant contribution to the monograph, with collaboration on some species, and the co-authorship of one taxon, *Caryota albertii*, which was named for Prince Albert, husband of Queen Victoria, and another example of

Mueller naming palms to honor royalty (Dowe & Maroske 2016). Wendland & Drude also noted Mueller's contributions to the living collection at Herrenhausen Gardens, as well as acknowledging the herbarium specimens sent by him to Wendland specifically for the study of the Australasian species. In dedication, they named two species in honor of Mueller in *Palmae Australasicae*: *Calamus muelleri* and *Licuala muelleri* [*Licuala ramsayi*]. Most of the Australasian palm specimens that Mueller housed in Melbourne, at least up to early 1875, were sent to Wendland for the monograph and were temporarily kept in Wendland's Herbarium at Herrenhausen Gardens. The Wendland herbarium, previously maintained at Herrenhausen Gardens, was incorporated into Göttingen Herbarium in 1969 (Wagenitz 1972). There is evidence that some duplicates or fragments of Mueller's Melbourne specimens are extant at Göttingen, but a full inventory of the Wendland palm collection has yet to be completed (Marc Appelhans, GOET. pers. com.).

Bentham, at this time, was preparing the *Palmae* for the seventh, and last, volume of *Flora Australiensis*, and Mueller (1872) told Bentham in a letter that the Australian palm specimens that Bentham required for descriptive purposes for *Flora Australiensis* were with Wendland at Herrenhausen. Many of the specimens that Wendland & Drude cited in *Palmae Australasicae* were also cited in Bentham's treatment of the *Palmae* in *Flora Australiensis*, so it is evident that Bentham examined the same specimens. The specimens were received by Bentham at Kew from Herrenhausen in late 1876 (Bentham 1876), and returned to Mueller in Melbourne in early 1877 (Bentham 1877). All of the specimens sent to Wendland eventually, and somewhat miraculously if the travel distances are considered, found their way back to Melbourne, where many are the type specimens for the new taxa that were described in *Palmae Australasicae* (Dowe 2010).

Mueller (1875) provided a summary in Volume 9 of *Fragmenta* of the taxonomic changes that had been adopted by Wendland & Drude in *Palmae Australasicae*. He noted that the Australian palms had been thoroughly revised, and that *Kentia* had been reduced to a single species in Australia, *Kentia acuminata* [*Carpentaria acuminata*], but otherwise Mueller gave no indication of his true thoughts, at least in published accounts, on the extensive nomenclatural changes that Wendland &

Drude had introduced in their monograph. However, it was evident that Mueller rejected many of the changes as he continued to maintain his own genus and species names in subsequent publications. In correspondence to Bentham, Mueller (1876) wrote disapprovingly that:

The limitation of the genera [in *Palmae Australasicae*] is too narrow, as you will likely observe by a mere walk through the Kew palm-house. What an unnecessary burden to the memory such superfluity of genera! How many intermediate species among such genera may still be discovered. I do not know, at what date or even year this publication of W. & D. appeared; but it must have been later than when I made my last remarks on Palms, wherein I brought myself *Kentia moorei* to *Clinostigma* [*Lepidorrhachis mooreana*], if that genus should be adopted. It seems strange, that these authors do not quote the note. As for *Livistona ramsayi* it has no resemblance to *L. inermis*; the leaves indeed are like those of *Licuala peltata* and *Corypha taliera*; but with short indentations only, not cleft. Should not *Licuala* be reduced to *Livistona*? Can you kindly tell me, when Wendland's & Drude's paper did appear?

As an indication of the slow-down in the detection of new palm species in Australia, Mueller continued to describe palms but at increasingly longer intervals. In volume 11 of *Fragmenta*, Mueller (1878b) provided one new species, *Livistona drudei*, and a new genus, *Normanbya*, as well as emended descriptions and generic alterations to already established taxa, including a summary of his otherwise illegitimate *Bacularia* species, which he had included previously as *Kentia* species. He also provided the validating description of *Livistona mariae*, the taxon for which he had previously, in 1874, only given an informal identity as a name without a description (see above). The same situation also applied to the new species *L. drudei*, in which Mueller initially only provided a proposed name as: "this distinctive species is named after Doctor Oscar Drude," but without a validating description. The name, *L. drudei*, was later included in the index of that particular issue by Mueller (1881a) with reference to the alluded name, but the citing of a name was not enough to validate the taxon. Validation was later provided when Drude (1893) monographed the Australian

species of *Livistona*, thus giving Mueller co-authorship of the taxon.

It is around this time that Bentham & Hooker were completing their *Genera Plantarum*, in which they were to introduce a substantial rearrangement of palm genera. Mueller (1881b), having received advance notification of taxonomic changes, voiced his opposition at their proposed actions, and wrote to Joseph Hooker saying that:

...you must not be angry with me, when I express my regret at the impending multiplication of the genera of palms. As still more spec. will be discovered, more generic limits will break down. We can as a rule attain much better by sections in a large genus, what by severance of them is accomplished under generic names.

Mueller (1885a) attempted to clarify some of the confusion regarding the identity of a number of Australian species, and wrote to Joseph Hooker that:

...you wrote to me about Australian palms inquiringly before, I would like to add, that the lamented Bentham rightly united *Livistona ramsayi* and *Licuala muelleri* [*Licuala ramsayi*]. That is a Palm restricted to the East-Coast of Queensland, while *Livistona inermis* [their interpretation of *L. decora*] under which *L. ramsayi* is placed in the Kew Catalogue (or Report) belongs to the North-Coast exclusively. As Bentham thought *L. humilis* seems merely the young state of *L. inermis*; the latter is neither unarmed; so both names are misleading and these two palms might well be united under the name *Livistona leichhardtii* [*L. humilis*]. At last I have some hope of getting flowers of the Australian *Licuala*, so that its generic position may become definitely settled.

The generic name *Normanbya* was first proposed by Mueller derived from the specific epithet used in Walter Hill's (1874) protologue for the species *Cocos normanbyi* [*Normanbya normanbyi*]. In a letter to Edward Ramsay, Mueller (1874e) claimed that he had 'saved' Hill's name from taxonomic obscurity, in that:

...when Mr Hill's palm fruits arrived, that his supposed *Cocos*! is an *Areca*, near the common Indian Betel nut (*A. catechu*), and his supposed *Areca* is a true *Kentia*. It is singular, that he should venture to send descriptions almost of no diagnostic value and on such ill digested data, as he

obtained, into an official report. To protect him to some extent, I have placed his name along with mine as authority of the Normanby palm, so that his dedication may not be destroyed; and that is more than likely anyone else would have done for him! Pray do not mention this to any one, until you get the new number of the *fragmenta*, which is printed, but not yet issued.

Regarding the suggestion that *Normanbya* be established as a new genus, Mueller (1878b) referred to the possibility that with more collections the relevant species, by then renamed *Ptychosperma normanbyi* [*Normanbya normanbyi*] may be deemed sufficiently distinct to warrant placement in a new genus. However, that was only a proposed (and nomenclaturally illegitimate) use of the name *Normanbya* by Mueller, as there was no formal transfer of species or genus description. Validation of the name was eventually provided by Beccari (1885), with whom Mueller (1885b) by that time was exchanging his concepts about Australian and Papuan palm genera and species, as well as sending Beccari herbarium specimens of Australian palms (Mueller 1887a).

The last five palm species to be described by Mueller were published in various publications other than *Fragmenta*, between 1879 and 1892. As with most of Mueller's previous palm taxonomy, he promptly described these species as he received specimens of them.

The name *Areca alicae* [*Areca triandra*], named for Princess Alice, the third child and second daughter of Queen Victoria and Prince Albert, was first used by Mueller (1879a) in a brief pre-publication note in the *Gardeners' Chronicle* giving notification that a description of the species was to appear in the forthcoming December issue of *Gartenflora*. In the latter publication, Mueller (1879b) noted, somewhat resignedly, that 'it seemed unlikely that many new discoveries could be expected in this group of plants [the palms]' and he was 'particularly happy to be able to add another palm to those already described from Australia'. It was apparent that Mueller considered that most Australian palms had been located and described by this time. Unfortunately, Mueller was incorrect in his identification of his *Areca alicae*, as the palm was an already described Asian species, *Areca triandra*, that had been introduced into cultivation in north Queensland and the

Brisbane Botanic Gardens (Dowe 2010).

The name *Kentia beccarii* was introduced by Mueller (1880c) in the Indian edition of his *Select extra-tropical plants readily eligible for industrial culture or naturalisation*, and named after the Italian botanist and explorer Odoardo Beccari (1843–1920), who by this time had become the world authority on the palms as well as a confidant and regular correspondent of Mueller. Based at the University of Florence, Beccari had travelled extensively throughout south-east Asia and New Guinea (Cuccuini & Nepi 2006). Mueller (1880c) associated this species with *Nengella montana*. The identity of *K. beccarii* remains unresolved as there are no known specimens or diagnostic description related to that name. Notwithstanding, the name has been placed as a synonym of *Hydriastele montana* (Baker & Loo 2004). However, in the absence of specimens directly related to the name *K. beccarii*, and lacking an identifying description, this allocation is questionable, and the name perhaps should be relegated to a *nomen superfluum*. Beccari was to produce some of the most extensive and influential monographs on the palm family and eventually amassed the world's largest palm herbarium in Florence. He named about 1200 palm taxa during his career, mainly from New Guinea, Borneo and Sumatra (Cuccuini & Nepi 2006).

The third species to be described by Mueller (1882b) in this period was *Ptychosperma beatrixae* [*Archontophoenix alexandrae*] for a collection made by Eugene Fitzalan in 1881 from Mount Elliot in northeastern Queensland. The species was described in the Australasian supplement of the trade journal *Chemist and Druggist* and named for Princess Beatrice third daughter of Queen Victoria. Although the generic name of *Ptychosperma* for some Australian species had been superseded by *Archontophoenix* by Wendland & Drude in 1875, Mueller persisted with the generic name of *Ptychosperma* without explanation (Dowe & Hodel 1996). Mueller characterized his new species on the structure of immature flowers and fruit. This is a good example of Mueller describing a new species on questionable and unreliable characters, which was a common criticism from some of his contemporary botanists, as well as publishing taxonomic items in obscure periodicals.

The fourth species to be described was a Fijian species, *Pritchardia thurstonii*, in collaboration

with Drude (1887), and was published in the German-language gardening periodical *Gartenflora*. In 1886, Fijian Governor John Thurston visited the eastern islands of Fiji where he took photos of a palm. The photos were sent to Mueller who determined that it was a new species. Drude evidently received specimens as he provided a detailed description and prepared diagnostic illustrations of flowers and fruit (Anon. 1887). It appears that the specimens were sent directly to Drude as there are no labels recording that the specimen went through Mueller's herbarium in Melbourne. The type specimen is now conserved at Kew Herbarium, and with only a fragmentary duplicate at Melbourne herbarium. Thurston was a correspondent of Mueller (Home *et al.* 2002), and the botanical gardens in Suva, Fiji, now named Thurston Gardens, were founded by him in 1879 (Watling 2005).

In early 1892, Mueller (1892b) provided a summary of the Australian fan palms in the genus *Livistona* in the *Gardeners' Chronicle* writing that:

In the Census of Australian plants, I admitted only three species of *Livistona*, inasmuch as dubious or very imperfectly-known species are omitted in that work, and retained for further consideration till another census can be instituted. Thus, I have recorded there besides *Livistona australis*, only *L. leichhardtii* [*L. humilis*] and *L. mariae*.

In a second instalment of that article, Mueller (1892c) explained his reasons for rejecting the two species named by Robert Brown, i.e. *L. inermis* and *L. humilis*, and noted that:

...*L. humilis* is a youthful *L. inermis*, I kept up the name *L. leichhardtii* for the united species, their original names having become inapplicable now.

This was an illegitimate nomenclatural proposal, and the correct action would have been to use the original name *L. inermis* for the species, as it had precedence over all other names according to Mueller's interpretation. Both *L. humilis* and *L. inermis* are now considered valid species, and *L. leichhardtii* as a synonym of the former (Dowe & Jones 2011).

Although Mueller had seemed to resolve the complexities of the genus *Livistona* for Australia, he was soon to name another species which was to be the last palm to be formally

described by him. In a second article in the *Gardeners' Chronicle* on Australian fan-palms, Mueller (1892c) alluded to a new species in his summary of *Livistona*, as a palm in which:

The fruitlets are globular, and particularly large, from the Western Australian locality in contrast with those of *L. australis* from which species *L. mariae* is also distinguished by the paler leaves, with elongated rachis, which forms a solid axis sometimes nearly 1 foot long beyond the petiole, whereby the leaf gets a somewhat cuneate form: on this account it seems likely that the unnamed *Livistona*, referred to in the *Gardeners' Chronicle* may be *L. mariae*.

Seemingly to contradict his appraisal of the 'Western Australian' species that he named as *L. mariae* in his *Gardeners' Chronicle* summary, Mueller (1892d) soon after described it as a new species, *L. alfredii*, named for Prince Alfred Ernest Albert, husband of Grand Duchess Marie Alexandrovna, and based on the Western Australian collections of what he had previously identified as *L. mariae* (Mueller 1878b). Although the description was more of an informal note than a diagnostic account, the article in the *Victorian Naturalist* provided some manner of distinguishing it from *L. mariae*, and discussed leaf colour and fruit size. The article did not mention any specific specimens, although specimens collected from the Fortescue River, Western Australia, by Forrest were cited by Mueller (1878c) in a previous account of the distribution of what he thought was the occurrence of *L. mariae* in Western Australia. The specimens related to that earlier interpretation were therefore concomitant as types for *L. alfredii*.

Taxonomy summary

Mueller's last comprehensive summary of the Australian palms was presented in his *Second Systematic Census of Australian Plants* (Mueller 1889). In that he listed 25 species under the *Palmae*, and one species in the *Nipaceae*. He later published one more species in 1892 (Mueller 1892d), whilst other botanists described five additional Australian species between that time and Mueller's death in 1896, thus bringing the total number of Australian palms to 32 species by the end of the "Muellerian Era."

Mueller played no particular attention to the palms with regards to monographic treatments, and most of his palm taxonomy involved single or small groups of species

promptly treated as he received specimens of them. Over time, he increasingly assigned Australasian palm taxonomy to specialists such as Hermann Wendland, Oscar Drude and Odoardo Beccari (Mueller undated pre-1875, 1885c, 1887a, 1887b).

Mueller's palm taxonomy can be characterized as intermittent and non-specialized. Periodically, Mueller provided synopses of the palm taxa described for Australia, but these were mainly annotated lists without critical consideration of generic placement or synonymy in the broad sense, and sometimes tending to either ignore or openly contradict the synonymizing work of specialist palm taxonomists. Mueller remained conservative in his palm taxonomy and preferred to use his own nomenclature, despite its contemporary invalidity, even into his later years. Mueller was often accused of describing too many taxa and thus producing confusing synonyms for later botanists. However, this situation does not strictly apply to his palm taxonomy. Of the 19 palm taxa established by Mueller, six retain his original binomial or generic name, seven are now homotypic synonyms that retain Mueller's specific epithet, five are now heterotypic synonyms, and one is a generic synonym. In regard to nomenclatural and taxonomic longevity, much of Mueller's palm taxonomy is relevant today and he remains the single most important taxonomist to have worked on the Australian palms.

Acknowledgments

I would like to thank Sara Maroske and Arthur Lucas for access to letters and transcriptions in the Mueller Correspondence Project (Royal Botanic Gardens Victoria); Chiara Nepi assisted with Mueller's specimens at Florence Herbarium (FI); Marc Appelhans at Göttingen Herbarium (GOET) provided information about Hermann Wendland's herbarium in Herrenhausen Gardens; Nimal Karunajeewa provided information about specimens and labelling of the palm collection at the National Herbarium of Victoria (MEL); and William Baker provided information about Beccari's herbarium specimens at the Royal Botanic Gardens Kew (K). Sara Maroske is thanked for comments on the original draft and for her suggested improvements to the text.

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Status of *Pseudophoenix sargentii* on Elliott Key, Florida

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1. One of three surviving adult *Pseudophoenix sargentii* on Elliott Key. Inflorescence/Infructescence branch can be seen in the canopy of this individual.



The last Florida population of Buccaneer Palm is barely surviving.

The only wild U.S. population of *Pseudophoenix sargentii* H.Wendl. is struggling on an off-shore island in Miami-Dade County, Florida, called

Elliott Key. Elliott Key is a small island about 8 mi (12.8 km) long by 1 mi (1.6 km) wide in the upper Florida Keys (Ledin et al. 1959,

Lippincott 1992, Zona 2002), only accessible by boat. The vegetation on Elliott Key has weathered many hurricanes. In February of 1968, a bulldozer operator widened Elliott Key Highway to 125 feet, destroying more than 120 acres of hammock in what is now called Spite Highway (Lippincott 1992), in an attempt to prevent the island from being acquired by the National Park Service. The attempt was unsuccessful and Elliott Key is currently part of Biscayne National Park in the National Park Service Bureau of the U.S. Department of the Interior.

On Elliott Key, *Pseudophoenix sargentii* (Fig. 1) is found in coastal hammocks with *Agave decipiens*, *Bursera simaruba*, *Caesalpinia major*, *Chiococca alba*, *Coccoloba uvifera*, *Conocarpus erectus*, *Eugenia axillaris*, *Laguncularia racemosa*, *Metopium toxiferum*, *Nectandra coriacea* and *Thrinax radiata* (Fig. 3). *Pseudophoenix sargentii* has been associated with *Thrinax radiata* in the Yucatan, Mexico (Quero 1981, Johnson 1996), and in some areas of Elliott Key it appears as if there are a large number of young *Thrinax radiata* in the understory and very few *Pseudophoenix sargentii*. This last remaining wild U.S. population is listed as Endangered in the State of Florida (Duran 1995, Coile and Garland 2003).

In an interesting account of *Pseudophoenix sargentii*, Sargent (1886) noted finding a relatively small population of six individuals in two localities approximately 2 or 3 miles (3.2–4.8 km) apart. He mentioned immature orange or red fruit were observed in April. Sargent (1888) later mentioned about 200 *P. sargentii* were found on Long Key, but these no longer remain on that island (Lippincott 1992 & 1995, Zona 2002). Britton (1904) and Small (1922) found only one adult *P. sargentii* on Elliott Key, which supported the low number of *P. sargentii* reported by Sargent. More recently, in 1992, Lippincott described dozens of eroding *Pseudophoenix sargentii* stumps on Elliott Key as a sign that hurricanes, excessive salt, disease and old age may contribute to a high natural mortality (Lippincott 1992). This is a similar conclusion to what is now seen, 23 years later. The last published count listed eight living adults on Elliott Key (Fotinos et al. 2015).

Tracy Magellan and Jeremy Schnall set sail on February 11, 2015 and reached Elliott Key in 5.5 hours from Florida City. On the first day, GPS points were tested and the first adult individual was found on the island, in an area



2. Two dead *Pseudophoenix sargentii*. One with dead leaves still attached.

called Scorpion Bite. The individual found had no fruit or flowers. After observing the palm, we returned to camp and prepared our plan to visit the remaining adults the next day. The mosquitoes were swarming in dense clouds; on Elliott Key mosquitoes are active in all seasons, including winter.

On February 12th, we began our trek to visit the remaining known adults on the island and collect data. The first stop was a location called "Predator South." The second adult found also had no fruit, but did have an old infructescence/inflorescence still attached (Fig. 1). A voucher collected from that individual was deposited at the South Florida Collections Management Center (FNPS). The third adult was standing dead with no leaves (Fig. 2). The fourth individual was standing dead with wilted leaves remaining (Fig. 2). The fifth individual was also dead, but the top half of the trunk had broken off and was on the ground next to what remained of the standing dead trunk. The sixth individual was found alive, but had no flowers or fruit. The seventh, eighth, ninth, tenth, and 11th individuals were standing dead with no leaves.



3. Young, planted *Pseudophoenix sargentii* with black discoloration on the crownshaft.

In summary, during the expedition to Elliott Key three living adults were observed with no flowering or fruiting in February 2015. It is unknown whether Hurricane Sandy (2012) affected this population by killing off many of the remaining adults, whether the remaining adults are reaching senescence, or whether there is a greater pest or pathogen issue involved. This conclusion parallels strikingly the conclusions of Lippincott (1992); 23 years later the same issues are repeating themselves. Sargent (1886) only observed six individuals 130 years ago. It appears as if *Pseudophoenix sargentii* populations continue to remain low, though from 1990–1992, before Hurricane Andrew, a high estimate of 47 wild individuals of all age classes were observed with at least 20 noted adults (Lippincott 1995, Lippincott personal communication) and ongoing restoration projects aim to increase the island population.

The number of wild adults in the latest survey is worrying, particularly because the three remaining adults do not show current signs of reproduction. There are a few planted juveniles that appear to be healthy and some

small grass-like wild seedlings that appear to have been flagged as part of a 2012 survey by Fairchild Tropical Botanic Garden (Joyce Maschinski, pers. comm.). Those wild seedlings appeared to be very small for 3 years old. A juvenile *P. sargentii* planted near the visitor center appeared to have a blackened crownshaft, possibly due to fungus or another issue (Fig. 3). Edelman and Richards (2013) recently discussed this mysterious ailment but the darkening of the crownshaft does not appear to be a new concern, as it or something similar can be seen in historic black and white photos of *P. sargentii* (Ledin et al. 1959, Read 1968, Lippincott 1992).

Pseudophoenix sargentii can take approximately 30 years to mature (Maschinski & Duquesnel 2006), so let us hope that in the next few years the restoration project funded by the South Florida chapter of the International Palm Society establishing juvenile seedlings on Elliott Key in 1991 (Lippincott 1995, Maschinski & Duquesnel 2006) from seeds collected by Biscayne National Park in 1984 (Lippincott 1995) leads to a viable, healthy and reproductive restocked adult population adding genetic diversity to the existing wild population.

Acknowledgments

We thank the International Palm Society Endowment Fund for a generous grant, which allowed us to conduct fieldwork on Elliott Key. We thank The National Park Service and its employees, Elsa Alvear, Brian Carlstrom, Bradon Falls, Hayley Matteson, Jennifer Stafford and P. J. Walker, for help with permits, collection rules and access to Biscayne National Park, Carol Lippincott for communications regarding her 1995 paper, Joyce Maschinski and Jennifer Possley from FTBG for sharing their maps from 2007 marking the remaining adults on Elliott Key, Larry Noblick for his insight and guidance and Jeremy Schnall for donating his time, his sailboat and his camp equipment to support the expedition.

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***Coccothrinax* × *angelae*, the First Natural Hybrid of the Genus**

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Coccothrinax, a diverse genus of perhaps more than 50 species of small to medium fan palms primarily from the Caribbean basin, is especially rich in Cuba. Over the last nearly 80 years or so, several workers have investigated *Coccothrinax* in Cuba and elsewhere, including León (1939, 1946), Borhidi (1991), Borhidi and Hernandez (1993), Borhidi and Muñiz (1985), Muñiz (1978), Muñiz and Borhidi (1981, 1982), and Nauman and Sanders (1991a, 1991b), yet none produced a definitive monograph of the genus that resolved the several pressing taxonomic problems on the Island. Indeed, the number of recognized species for the genus ranges from 14 (Henderson et al. 1995) to 53 (Govaerts and Dransfield 2005). For Cuba, Moya and Leiva (2000) listed 37 species and seven subspecies. Later Moya (per. comm. 2014) recognized 54 species (38 from Cuba) and seven subspecies.

Although intergenetic hybridization between *Coccothrinax* and *Thrinax* had been reported (Nauman 1990), hybrids within *Coccothrinax*, which might contribute to the difficulty in

resolving the taxonomy of the genus, have not been recognized until recently when Suárez (2015) formally named and described *Coccothrinax × angelae*, a putative natural

hybrid between *C. crinita* subsp. *brevicrinis* and *C. miraguama* subsp. *roseocarpa* (Fig. 1). The discovery and documentation of this new putative hybrid from central Cuba was made after extensive herbarium and field work and a rigorous review of the literature, a process that began in 1999 and culminated with the naming and describing of the new hybrid in 2015.

Here we provide a review of this putative hybrid, including a description, etymology, a discussion of its distribution and ecology, threatened status, and local uses. This work is part of a larger project we are undertaking that will lead to a monograph of the palms of Cuba.

Description

Commonly known as *guano macho* or *guano barbudo*, *Coccothrinax* × *angelae* displays nearly no intermediate characters between each putative parent; rather, it shares several characters with either one or the other parent. Table 1 summarizes the differences and similarities among the three taxa. One parent, *C. miraguama* subsp. *roseocarpa* differs in its

smaller habit and leaf blades darker green adaxially and waxier abaxially with more but shorter segments; the two are similar, though, in inflorescence length and fruit size and color. The other parent, *C. crinita* subsp. *brevicrinis*, differs in its much longer leaf base fibers, longer inflorescence and larger, red-purple fruits; the two are similar, though, in their habit and leaves (color, waxiness, quantity and size of segments). *Coccothrinax* × *angelae* differs from both parents in its rigid, ascending leaf base fibers (Fig. 2). Nonetheless, additional study might show that this hybrid is actually sufficiently distinct to merit species status.

Cultivated plants of *Coccothrinax* × *angelae* in Cuba have been confused with one of its parents, *C. crinita* subsp. *brevicrinis*. Two plants that G.C. Rowe introduced to the Cienfuegos Botanical Gardens (formerly Atkins Gardens of Harvard University) in December, 1929 from Carso de Buenos Aires, a locality where no *Coccothrinax* now exists, were subsequently identified as *C. crinita* subsp. *brevicrinis*. However, recent studies showed that both these plants, still living in the Garden, are

1. *Coccothrinax* × *angelae* growing in habitat in southeastern Cienfuegos, Cuba (D. Suárez).



Table 1. Some Distinguishing Characters of the Hybrid *Coccothrinax × angelae* and its Parents.

	<i>C. crinita</i> ssp. <i>brevicrinis</i>	<i>C. × angelae</i>	<i>C. miraguama</i> ssp. <i>roseocarpa</i>
Height (m).	5–8	5–8	4–5
Leaf color.	Light green adaxially, light waxy gray abaxially	Light green adaxially, light waxy gray abaxially	Dark green adaxially, waxy gray abaxially
Leaf segments (number; length cm)	30–32; 60–70	30–32; 60–70	40–42; 40–50
Leaf-base fibers (length cm; diam. mm)	145 cm long, light brown, flexible tip	40 cm long, 2–3 mm diam., light brown, rigid and ascending tip	40 cm long, 0.5–2 mm diam., dark brown, curved tip
Inflorescence (length cm)	145	40	40
Fruit (diam. mm; color)	15–20; red-purple	5–12; pink-purple	5–12; pink-purple

actually the hybrid *C. × angelae*. Also, the National Botanical Gardens of Cuba in Havana has two plants very near the office of the Director that have been identified as *C. crinita* subsp. *brevicrinis* but which are actually *C. × angelae*.

Habit, Stem, and Leaves: *Coccothrinax × angelae* grows to about 8 m tall and, like nearly all members of its genus, has a solitary, cylindrical stem to 8 cm in diameter (Fig. 1). Mature specimens often show vertical cracks in the proximal portion of the stem. Leaves have oblong-obovate bases up to 70 cm long, with the free part up to 40 cm long. They are triangular-obtuse at the apex and have along each margin a network of coarse fibers in two layers. These fibers, to 25 cm long, are rigid and ascending distally. Petioles are up to 155 cm long and 1.4 to 1.8 cm wide. The orbicular blades have 30 to 32 segments of which the central ones, the largest, are 60 to 70 cm long and 4 to 5 cm wide. Segment tips are bifid and rigid to slightly drooping. Blades are light green adaxially and with a coating of white wax and glabrescent ferruginous indumentum abaxially. The hastula is dark brown, triangular, rigid, and up to 1.5 cm long.

Inflorescences and Fruits: The interfoliar inflorescences of *Coccothrinax × angelae* are relatively short, only up to 40 cm long. Downward curved in fruit, they have 4 to 6 first-order branches, each one with 27 to 30

rachillae up to 5 cm long (Fig. 3). The flowers were not seen. Ripe fruits are pink to purple, globose, 5 to 12 mm in diameter. The rounded, dark-brown seeds are 3 to 5 mm in diameter, slightly compressed, 5-lobed, and with ruminate endosperm.

Etymology

The specific epithet honors the late Dra. Ángela T. Leiva Sánchez, who was director of the National Botanical Gardens of Cuba from 1972 until her passing in June, 2014 and who dedicated many years of her life to the study and conservation of Cuban palms.

Distribution and Ecology

Although unrecognized as a hybrid at the time, Borhidi (1991) noted that this taxon (*Coccothrinax × angelae*) was endemic to Casildense in Yaguanabo Valley in south central Cuba. There it occurred on hills and slopes at mostly low elevations, commonly on nutrient-poor calcareous rocks at La Yaba, La Vega, Las Campanillas, Yaguanabo Arriba, and San Juan, all on the Guamuhaya massif in Cumanayagua Municipality, Cienfuegos Province, about 45 km southeast of the city of Cienfuegos.

In habitat *Coccothrinax × angelae* occurs in seasonally dry, rather open, semideciduous forest from 90 to 312 m elevation although one record puts it as low as 8 m elevation.



2. Leaf base fibers of *Coccothrinax × angelae* showing their rigid, ascending nature (D. Suárez).

Companion plants include *Albizia* (*Samanea saman* (algarrobo), *Annona squamosa* (anón), *Bursera simaruba* (almácigo), *Ceiba pentandra*

(ceiba), *Cordia gerascanthus* (varía), *Erythroxylum havanense* (jibá), *Eugenia axillaris* (guairaje), *Gymnanthes lucida* (yaití), *Harrisia taylori* (jijira),



3. Inflorescences of *Coccothrinax × angelae* showing downward-curved nature and pink-purple fruits (D. Suárez).

Sabal maritima (guano cana), and *Zanthoxylum caribaeum* (bayúa). The exotic, invasive *Dichrostachys cinerea* was observed at all localities.

Both parents are always present with *Coccothrinax × angelae* nearly everywhere it occurs. At one locality, the parent *C. crinita* subsp. *brevicrinis* is currently not present but it once occurred there; unfortunately, human activity recently extirpated it from that locality. This hybrid could possibly affect survival of *C. crinita* subsp. *brevicrinis*, in particular, by reducing its reproductive capability due to genetic erosion through production of hybrid seeds, decreasing population numbers, and increasing spatial competition. Further study is needed to confirm this possibility.

Animals, including several birds and at least two introduced mammals, the wild boar (*Sus scropha*) and deer (*Odocoileus virginianus*), consume fruits of *Coccothrinax × angelae* and help to disseminate the seeds and propagate the hybrid. Indeed, excrement from these animals nearly always contains viable seeds.

Bats (*Chiroptera* spp.) and rodents (*Capromys pilorides* and *Mysateles prehensilis*), eat the external part of the fruit, which also contributes to dissemination of the seeds.

Threatened Status

According to the IUCN threatened species status, *Coccothrinax × angelae* should be considered Critically Endangered (CR) (based on the criteria A2+ 3 abcde; B1+ 2 abc; C1+2 ab; D1+ 2.) because of its limited distribution, extremely fragmented populations, and severe threats from fire and over-harvesting of leaves for handicrafts.

Uses

Local people use *Coccothrinax × angelae* for several purposes. Trunks are used in the construction of crude houses and other structures. Leaf base fibers are used to make brushes for washing and painting, brooms, and for filling pillows and mattresses; they are also fashioned into crude filters to strain fruit pulp and sift flour. Leaves are used to thatch roofs and can be fabricated into unusually strong rope for securing cattle.

Acknowledgment

We should like to thank an anonymous reviewer for constructive comments that helped to improve our paper.

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