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FRONT COVER

Pinanga aff. *brevipes*. Its flowers and fruits are borne under the leaf litter. See article by P. Petoe et al., p. 57. Photo by P. Petoe.

BACK COVER

Eugeissona utilis is widespread throughout Borneo. See article by P. Petoe et al., p. 57. Photo by W.J. Baker.



Leaf sheath spines of *Plectocomia mulleri*. See article by P. Petoe et al., p. 57. Photo by B.G. Kuhnhäuser.

PALM NEWS



Alex Lomas

Pinanga coronata is proving to be a serious invasive palm in Fiji, outcompeting native tree ferns. A study led by Michael J.B. Dyer (*Australian Journal of Botany* 66: 647–656. 2019) examined the distribution of different age classes of native tree-ferns and invasive *Pinanga coronata* in lowland forest in Fiji and demonstrated that the palm seems to be preventing establishment of young tree-ferns. The invasive palm should be controlled and eradicated if there are to be no long-term negative impacts on native biodiversity, and the authors suggest that ultimately there will need for well-implemented legislation to prevent the spread of this palm and other ornamentals.

Five students under the supervision of Dr Reyad El Khazali of the Electrical and Computer Engineering Department at Khalifa University, United Arab Emirates, have created a **prototype drone to assist in pollination date palms (*Phoenix dactylifera*)**. The pollination drone was designed with image processing software that allows it to determine the gender of the palm trees by detecting marks placed on the trees that indicate male or female. The drone will locate female trees and dust it with pollen. Currently, more than 44 million date palms grow in the UAE, and they must be pollinated by hand to



Larry Koester

insure good fruit set. The drone will bring great efficiency to the task. Another team of researchers, also from Khalifa University, published a technique for fusing **graphene, created from date palm syrup**, to sand particles. The resulting hybrid structure can filter anionic, cationic and heavy metal pollutants from water. The project demonstrates the potential for cleaning wastewater using two natural resources that exist in great abundance in the UAE – dates and sand. The open-access paper is Khan et al. Sustainable synthesis of graphene-based adsorbent using date syrup. *Scientific Reports* 9: 18106. 2019.

The coconut gets a new variety. In 1916, the great Florentine palm botanist, Odoardo Beccari described the taxon *Cocos nucifera* forma *palmyrensis* Becc. for coconuts sent to him from the Palmyra Atoll by Joseph F. Rock. The form is characterized by exceptionally large fruits. The late H. Harries, along with L. Pignotti and R.M. Baldini, examined specimens in the Florence herbarium and concluded that the Palmyra populations should be elevated to the rank of variety. They published the new taxon in “Unraveling the taxonomic identity of *Cocos nucifera* f. *palmyrensis* (Arecaceae: Cocoseae).” *Candollea* 75: 25–30. 2020.

Lanjak Entimau Wildlife Sanctuary – a Palm Hotspot in the Heart of Borneo

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With over 300 species, Borneo has the richest palm flora of any Malesian island. Here, we describe an expedition to Lanjak Entimau Wildlife Sanctuary, a remote region of Sarawak in the heart of Borneo and provide a checklist of the 46 palm species that we found there.

Our expedition started in Kuching, the state capital of Sarawak in western Malaysian Borneo. We used the city as a base from which to access nearby localities including Gunung Matang in Kubah National Park, which is known for its astounding palm diversity and for Beccari's efforts to describe it during the 19th century (Beccari 1904), and Bako National Park, home to several populations of the iconic palm *Johannes-teijsmannia altifrons*. Although exploring and collecting within these popular sites was rewarding, we were particularly excited about what was yet to come: an

expedition to the remote and incompletely known Lanjak Entimau Wildlife Sanctuary (LEWS). LEWS is the largest of Sarawak's 66 Totally Protected Areas and is only accessible to scientists and local people living within its immediate vicinity (Forest Department Sarawak 2020). It is probably most widely known for its significant role in the conservation of the critically endangered northwest Bornean orangutan (Ancrenaz et al. 2016). However, the sanctuary protects a large diversity of wildlife, including an estimated 2000 species of plants (Chai 2000). The sanctuary abuts the vast



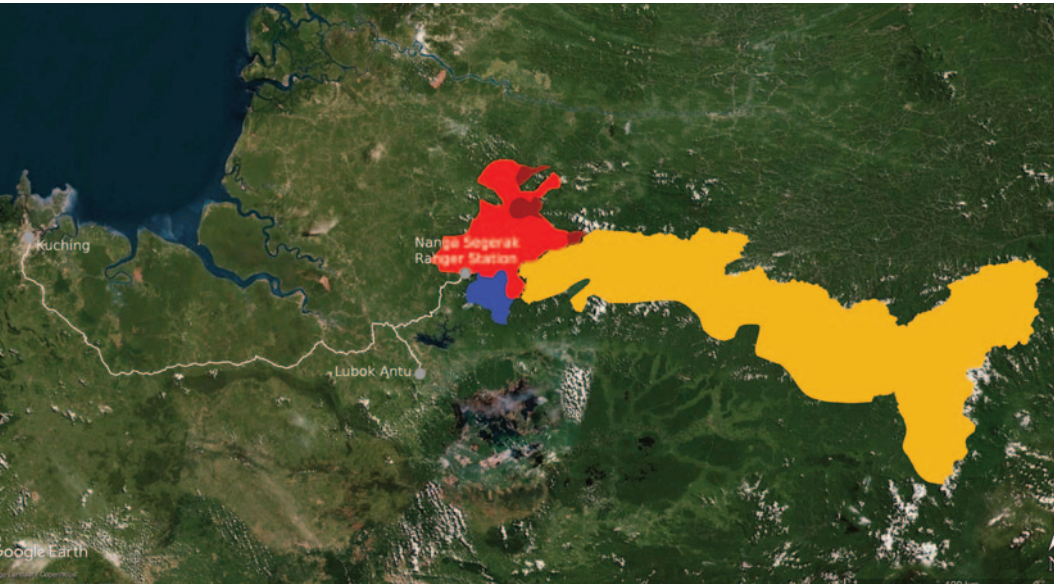
1. The island of Borneo showing Lanjak Entimau Wildlife Sanctuary (red) with extensions (dark red), Betung Kerihun National Park (yellow) and Batang Ai National Park (blue).

Betung Kerihun National Park across the border in Kalimantan, which is more than five times the size of LEWS. Together, the two reserves form the Transboundary Biodiversity Conservation Area (Fig. 1; Brouwer 2012), a core part of the Heart of Borneo initiative, which aims to conserve the remaining intact forests in the center of the island (Rautner et al. 2005). However, the biodiversity of LEWS remains insufficiently known. A checklist of the plants of LEWS has been published,

which records over 100 palm species (Chai 2000), but many palm records are yet to be formally confirmed and further ground-truthing is required.

At 6:30 in the morning of 1 November 2018, we departed Kuching in a fully loaded pickup-truck with the objective of undertaking a rigorous inventory of the palm diversity around Nanga Segerak Ranger Station, which is located in Ulu Engkari, in the southwestern portion of

2. Our route from Kuching to Lanjak Entimau Wildlife Sanctuary. Protected areas color coded as in Figure 1.





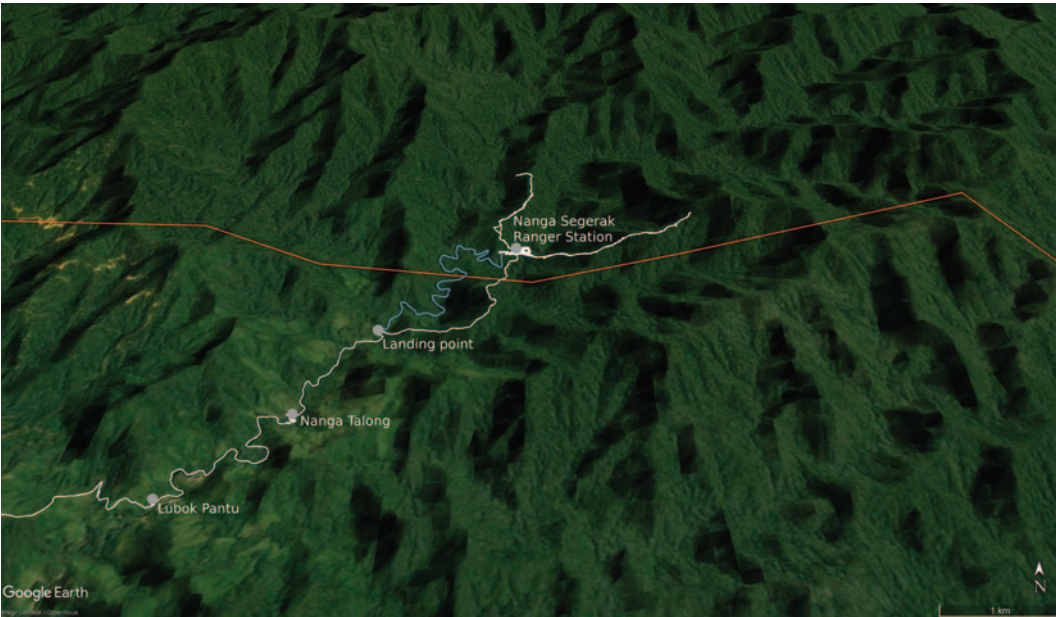
3. Palm cabbage of *Plectocomiopsis geminiflora* (left) and *Eugeissona utilis* (right) sold at local stall near Lubok Antu. Photo: B.G. Kuhnhäuser.

LEWS (Fig. 2). Sirukit anak Dubod from the Sarawak Forestry Corporation accompanied us and had already proven to be a versatile and indispensable companion during our fieldwork in Sarawak. We started out by driving for several hours along the main road to Lubok Antu. Upon reaching this small town, which is near the border with Indonesia, we transferred to a 4-WD truck. We had a brief stop on the roadside where palm cabbage, or *umbut* in Malay, of *Plectocomiopsis geminiflora* and *Eugeissona utilis* was being sold by local people (Fig. 3) and then branched off the main road onto a dirt track that had been constructed for logging purposes and would take us north of Batang Ai National Park toward LEWS. Some common palms, such as *Plectocomiopsis geminiflora* (Fig. 4) and *Eugeissona utilis* flourished in the disturbed vegetation along this stretch of the journey, which lasted for roughly 50 km. Eventually, we reached Lubok Pantu on the Sungai Engkari where we were greeted by our boatmen. The journey upstream would take us first to Nanga Talong and, the following day, on to Nanga Segerak Ranger Station (Fig. 5). The longboats were lined up and ready for departure on the riverbank opposite an idyllic Iban village adorned by *Arenga*

pinnata, *Cocos nucifera* and *Areca catechu* (Fig. 6). After a short and pleasant journey up the river we arrived at Nanga Talong, the last longhouse on Sungai Engkari before LEWS. We were heartily welcomed and hosted by the Headman Bada anak

4. *Plectocomiopsis geminiflora*. Photo: B.G. Kuhnhäuser.





5. Routes travelled in and around Lanjak Entimau Wildlife Sanctuary. The boundaries of the sanctuary are marked with a red line.

Chendai, who gladly accepted several of the *umbut* we had bought earlier in the day, and enjoyed them incorporated into our dinner.

Early on the following morning we took off again in two longboats, which sat low in the water due to the combined weight of us and our provisions. Upstream of Nanga Talong, the river soon became

shallow, with emergent rocks and boulders, forcing us to disembark occasionally to push the boat upstream. Lush vegetation clothed both sides of the river with common riverside palms including *Arenga undulatifolia*, *Salacca vermicularis* (Fig. 7) and several species of *Calamus*. Our three boatmen, Mugu anak Sanggap, Dellie anak Medie and Medie

6. River view of Lubok Pantu showing *Arenga pinnata*, *Cocos nucifera* and *Areca catechu* in the background. Photo: W.J. Baker.





7. *Salacca vermicularis*. Photo: B.G. Kuhnhäuser.

anak Aloh, would be our local guides for the remainder of the expedition. These fearless masters of the river swapped deftly between outboard engine, paddle and punting stick to navigate the shallows, rapids and narrow bends of Sungai Engkari. They also possessed extensive knowledge of the area and the natural resources of the forest. Before the river became impassable for the heavily laden boats, we landed at a riverbank ("Landing point" in Fig. 5) to allow Mugu, Dellie and Medie to continue upstream with the now considerably lighter boats to deliver our provisions to the research station. After a short trek of about two kilometers through the forest we arrived at the station, which is located right inside the boundary of LEWS. Being equipped with electricity, a field laboratory and even internet, the ranger station provides basic but comfortable accommodation and facilities for field workers. In addition, a nearby suspension bridge gives immediate access to excellent collecting grounds for a multitude of palm species. For each of

the five following days, we would explore the trails radiating from the research station from early in the morning until the rains set in, normally during the mid-afternoon, at which point we sought shelter back at base. We were able to make herbarium specimens of almost every palm species that we found. These were deposited at the Sarawak Forest Department herbarium in Kuching, with duplicates for the herbaria at the Royal Botanic Gardens, Kew and Aarhus University. As a result, we were able to confirm our field identifications by comparisons with expertly named specimens after the expedition. The palms we recorded are described in this article and enumerated in Appendix 1.

Palm habitats in LEWS

The sanctuary is geologically complex with several different forest types including riparian, old secondary, lowland mixed dipterocarp and hill mixed dipterocarp forests (ITTO 2001). All of these forest types occur to varying extents within our inventoried area, within an elevational range from 320 m (Nanga Segerak Ranger Station) to 780 m. Although the mixed dipterocarp forest is known to be the most extensive and biologically diverse habitat within the sanctuary, we found the highest species richness and abundance of palms in wet valley bottoms of the riparian forest (Fig. 8). Palms remained conspicuous in the hill slopes and ridge tops of the adjacent mixed dipterocarp forest, although at lower densities and local species richness.

Calamoideae

In the subfamily Calamoideae, we recorded 30 species belonging to the genera *Calamus* (18 spp.), *Eugeissona* (1 sp.), *Korthalsia* (5 spp.), *Plectocomia* (1 sp.), *Plectocomiopsis* (3 spp.), and *Salacca* (1 sp.). They displayed an extraordinary array of morphological and ecological diversity.

Asian calamoid palms are often associated with the climbing growth form. However, about 10% of Calamoideae are not climbing, but self-supporting or stemless



8. Riparian forest understory with *Pinanga* aff. *brevipes*, *Pinanga tomentella*, *Calamus sabalensis* and *Licuala petiolulata* (from front to back). Photo: W.J. Baker.



9. *Calamus ursinus*. Photo: B.G. Kuhnhäuser.

(Couvreur et al. 2015). At LEWS, we encountered five of these species. The remarkable *Calamus ursinus* grew in large numbers on a steep riverbank near the research station (Fig. 9). It was formerly placed in the genus *Pogonotium* (now a synonym of *Calamus* [Baker 2015]), which is immediately distinguished by the long, erect auricles flanking the petiole. Having met with *Calamus ursinus* before on the top of Gunung Matang, we were surprised to find it here again in such a different environment. Indeed, it was previously thought to be constrained to submontane ridgetops (Dransfield 1992).

Calamus collarifer, a self-supporting, litter-trapping palm up to 3 m tall, was one of the most abundant components of the understory (Fig. 10). *Calamus sabalensis*, a slender, stemless species with the appearance of a young palm seedling (Fig. 11), would almost have gone unnoticed, had we not discovered an individual bearing an old inflorescence. Besides these species, we encountered the aforementioned *Salacca vermicularis* and the

massive tree palm *Eugeissona utilis* (locally known as *pantu*), several specimens of which having been felled for their delectable palm hearts (Back Cover).

The aesthetic value of rattans is generally underappreciated! Near the river, we were attracted to the beautiful, bright orange flowers of *Calamus sparsiflorus*, which emitted a sweet fragrance of jasmine. In the specimen we collected, the six stamens were consistently arranged in groups of one, two, and three (Fig. 12). Nearby grew *Calamus pilosellus*, a neat rattan whose regularly arranged, closely adjacent leaflets were interlocked by bristly hairs on the leaflet margins (Fig. 13) and *Plectocomia mulleri*, a robust high-climbing palm with golden spines arranged like eyelashes (see p. 55).

Contrasting with the appeal of these species, several rattans at LEWS lived in close association with belligerent ants. Several species of *Korthalsia* provided living space in their inflated ocreas, i.e. papery elongations of the leaf sheath



10. *Calamus collarifer*. Photo: W.J. Baker.



11. *Calamus sabalensis*. Photo: W.J. Baker.



12. Inflorescence branch of *Calamus sparsiflorus*, with stamens of each flower arranged in groups of one, two and three. Photo: B.G. Kuhnhäuser.



13. *Calamus pilosellus*. Photo: B.G. Kuhnhäuser.

beyond the insertion of the petiole. *Korthalsia rostrata*, *K. cheb* (Fig. 14) and *K. echinometra* (Fig. 15) could be easily distinguished by the shape, size and armature of their ocreas. The long, divergent ocreas of *Korthalsia hispida* (Fig. 16) were inhabited by “noisy ants” producing a rattling sound upon disturbance before rushing out to attack. In *Calamus sabut*, interlocking whorls of spines formed so-called ant galleries (Fig. 17). These were connected by carton tunnels made of bitten off spines. Not all

Korthalsia species accommodate ants; *Korthalsia debilis* bore a tightly sheathing, disintegrating ocrea (Fig. 18).

Other rattans displayed morphological extremes and curiosities. Whilst *Calamus corrugatus* was the most slender of all palms we encountered with a stem diameter of only 5 mm (Fig. 19), *Calamus comptus* had the longest inflorescence at over 7 m. In stark contrast to these rather slender rattans was the massive *Calamus ornatus*, which we encountered only as a seedling. *Calamus myriacanthus*, a usually

14. Inflated ocrea of *Korthalsia cheb* with entrance hole at the right. Photo: W.J. Baker.





15 (left). Inflated ocrea of *Korthalsia echinometra*. Photo: B.G. Kuhnhäuser. 16 (right). Divergent ocrea of *Korthalsia hispida*. Photo: W.J. Baker.

short-stemmed palm widespread throughout Sarawak, here climbed to 8 m despite possessing no specialized climbing organs. The diamond-shaped, discoloured leaflets of *Calamus hallierianus* were strongly reminiscent of *Korthalsia* (Figs. 20 & 21). Apart from this superficial resemblance, *Calamus hallierianus* was easily distinguished from *Korthalsia* by its extraordinary inflorescence, which was enclosed entirely within the pod-like prophyll, a character diagnostic for the group of species formerly included in the genus *Ceratolobus* (now a synonym of *Calamus* [Baker 2015]). The inflorescence is accessible to potential pollinators only via narrow openings at the prophyll tip. *Calamus pseudoulur* caught our interest as it possessed both a cirrus and a vestigial flagellum, whereas most rattans have either one or the other of these two highly specialized climbing organs. The fruits of *Calamus didymophyllus* were covered in red glossy resin, so-called “dragon’s blood,” and *Plectocomiopsis mira*, immedi-

ately distinguished by its truncate, orange ocrea, was the only rattan considered poisonous by our local guides.

Further calamoid palms we encountered at LEWS were *Calamus* cf. *periacanthus*, *C. javensis*, *C. korthalsii* with long, slender spines at the mouth of the sheath, *C. laevigatus* var. *mucronatus*, whose basal leaflets were reflexed across the stem, *C. maculatus*, *C. zonatus*, *Plectocomiopsis geminiflora* and a potentially undescribed species of *Plectocomiopsis* with discoloured leaves and a triangular ocrea.

Coryphoideae

Five species of coryphoid palm belonging to the genera *Arenga* (1 sp.), *Caryota* (1 sp.) and *Licuala* (3 spp.) were recorded. The relatively low diversity of *Licuala* was somewhat surprising given that the genus is particularly diverse in Borneo with 48 known species (Govaerts et al. 2020), but it is possible that the narrow endemism of many of the species causes high species-



17. *Calamus sabot* with interlocking whorls of spines forming ant galleries. Photo: B.G. Kuhnhäuser.



18. *Korthalsia debilis*. Photo: W.J. Baker.



19. *Calamus corrugatus*. Photo: B.G. Kuhnhäuser.



20 (left). *Calamus hallierianus*. Photo: W.J. Baker. 21 (right). Enclosed inflorescence of *Calamus hallierianus*. Photo: W.J. Baker.

turnover within the genus. Nevertheless, *Licuala petiolulata* made up for the dearth of species in its sheer numbers of individuals. It was one of the commonest palms that we found growing around the ranger station, where it occurs in the soggy riparian forest as well as on drier slopes and ridges. Fertile individuals of *L. petiolulata* were very rare at the time of collecting but we could easily identify the palms we saw on account of their conspicuously petiolulate terminal leaf segments (Fig. 22). *Licuala rheophytica* was also rather common but occurred only in the riparian forest and a bit further up the mountain slopes. In contrast to *L. petiolulata*, this is a dainty palm and all the individuals we saw had short 4-segmented leaves and spicate inflorescences (Fig. 23). Very occasionally we would come across mottled *licuala* leaves, which were later attributed to *Licuala* cf. *maculata*. This palm could not be identified unequivocally due to the lack of fertile material, but is likely to be *L.*

maculata, which is known from nearby Batang Ai National Park.

The largest coryphoid palm that we collected was *Caryota mitis*, which grew in the riparian forest to about 12 meters in height. The only other caryotoid palm to be recorded was *Arenga undulatifolia*, which occurred frequently along the banks of Sungai Engkari. Both of these species have broad distributions that extend well beyond Borneo.

Arecoideae

We recorded 11 species of arecoid palm belonging to the genera *Areca* (1 sp.), *Iguanura* (1 sp.) *Oncosperma* (1 sp.) and *Pinanga* (8 spp.). The arecoid palm seen most frequently was *Pinanga* aff. *brevipes*, which was particularly abundant in the riparian forest but also occurred on higher slopes and ridges. The individuals we observed were all small, acaulescent understory palms with relatively short leaves that had three or four pairs of



22. *Licuala petiolulata* with conspicuously petiolulate terminal leaf segments. Photo: P. Petoe.



23. *Licuala rheophytica*. Photo: P. Petoe.

relatively broad pinnae inserted onto the rachis, and bifid inflorescences. Despite demonstrating clear affinities with the type of *Pinanga brevipes*, known from Kuching, the form that occurs around the ranger station seemed altogether smaller and with broader leaflets. Most strikingly, the specimens that we encountered produce their inflorescences buried in the leaf litter or even deeper in the soil, where they successfully flower and set fruit (Figs. 24 & 25).

Areca chaiana, *Oncosperma horridum*, *Pinanga tomentella*, *P. albescens* and *P. sp. 1* all grew within a relatively short distance from the river. Of these palms, *Areca chaiana* was perhaps the most exciting discovery as it is the only species of *Areca* with a spicate inflorescence (Figs. 26 & 27). Having so far been regarded an anomalous member of the genus (Dransfield 1984), the placement of this species in the genus *Areca* may yet be challenged (Bellot pers. comm.). We found only a few, scattered individuals of

Pinanga tomentella and *P. albescens*, which are both small single-stemmed species like *Pinanga* aff. *brevipes* but differ in having entire leaves. In addition, all the individuals of *P. tomentella* that we recorded appeared to be of an unusual form with conspicuously bullate leaves (Fig. 28). Though common elsewhere in Borneo, *Oncosperma horridum* was rare in this area, and we observed only a single, fertile individual of *Pinanga* sp. 1. Despite the existence of a good collection, the identity of *P. sp. 1* with its sigmoid leaflets and bright red, spicate infructescence (Fig. 29) remains unresolved.

On higher slopes and ridges we collected *Pinanga* cf. *ligulata*, *P. lepidota* and *Iguanura chaiana* and recorded, but did not collect, *Pinanga salicifolia* and *P. sp. 2*. These species were all occasional except for *Iguanura chaiana* and *Pinanga* sp. 2 each of which were only represented by one individual. The latter species could not be identified due to a lack of fertile material, although the variegated,



24 (left). *Pinanga* aff. *brevipes*. Photo: W.J. Baker. 25 (right). Entirely subterranean infructescence of *Pinanga* aff. *brevipes*. Photo: P. Petoe.

pinnate leaves displayed by this species stood out among the surrounding vegetation (Fig. 30). Attaining 8 m in height, *Pinanga* cf. *ligulata* was the most imposing of the pinangs we saw in LEWS and was referred to by our guides as *pinang*

mureng. *Iguanura chaiana* was an exciting find because few records exist of this rare species (Fig. 31). In contrast, *Pinanga lepidota* and *P. salicifolia* are widely distributed and rather common throughout much of Borneo.

26. *Areca chaiana*, note the spicate inflorescence. Photo: P. Petoe.



Conclusion

After six intense days, we had to leave LEWS behind us. Having focused on taking an as complete as possible inventory of the palms of Nanga Segerak Ranger Station, we had met with an astonishing diversity of palms in its immediate surroundings. In a radius of less than 2 km around the research station, focusing mainly on easily accessible habitats such as riparian forest and ridge tops, we had recorded 46 palm species and collected herbarium vouchers for 42 of them, with accompanying leaf samples for ongoing research on palm evolution. We had also gained insights into the many uses of the palms of the



27. *Areca chaiana*. Photo: W.J. Baker.



28. *Pinanga tomentella*, form with bullate foliage. Photo: P. Petoe.



29. *Pinanga* sp. 1. Photo: W.J. Baker.



30. *Pinanga* sp. 2. Photo: P. Petoe.

wildlife sanctuary. We had eaten the freshly cooked *umbut* of two *Calamus* species for lunch while sitting on the leaves of *Licuala petiolulata*, had enjoyed a delicious vegetarian curried *pantu*, and had watched our guides collect canes of the slender and flexible *Calamus corrugatus* and *Calamus laevigatus* var. *mucronatus*.

Now, we had to surrender our precious collections to the mercy of the winding rapids of the Sungai Engkari (Fig. 32). The ride down the narrow river was both thrilling and terrifying, adrenalin peaking when one of our boatmen fell overboard. Drenched to the skin, we were glad to reach the calmer waters of Nanga Talong



31. *Iguanura chaiana*. Photo: P. Petoe.

safely with our collections intact. As our onward journey was planned for the next day, we took the opportunity to collect a specimen of *Arenga pinnata* growing next to the longhouse. Being well aware of the old tradition of headhunting practiced by the Iban people in the past, we couldn't resist the temptation to ascertain whether skulls from former times still existed at the longhouse. When we were presented with an unearthly assortment of nine skulls (Fig. 33), we were amazed to find that some of these were kept in harnesses made of woven rattan canes! On the next morning, we continued our journey back to Kuching, passing through a melancholy landscape of secondary forest necklaced with low-hanging clouds (Fig. 34). At Kuching, our specimens were pressed and dried at the Sarawak Forestry Corporation's Semenggoh Arboretum, and sorted into duplicates.

The richness of palms we documented around Nanga Segerak Ranger Station bears witness to the importance of LEWS as a refuge for Borneo's palm diversity. As indicated by the existing checklist of the

flora of LEWS (Chai 2000), we feel confident that further fieldwork would bring to light many more palm treasures.

Acknowledgments

We thank the CEO of the Sarawak Forestry Corporation Haji Zolkipli Mohamad Aton for allocating resources and staff making this fieldwork possible. In particular, Julia Sang was instrumental with regards to planning and formalities, Sirukit anak Dubod took on a multitude of essential tasks including supporting our field collecting effort, cooking, and drying our specimens and Embahalbana anak Jangoh was our host and local contact at Nanga Segerak Ranger Station. In addition, the advice given to us by our three boatmen Mugu anak Sanggap, Dellie anak Medie and Medie anak Aloh was invaluable on the rapids of the river as well as in the forest collecting, and the inhabitants of Nanga Talong including the Headman Bada anak Chendai, who accommodated us in his home, all made us feel very welcome. We thank Dr John Dransfield, Dr Andrew Henderson and Dr Leng Guan



32. Boat journey from the ranger station to Nanga Talong. Photo: W.J. Baker.



33. Nanga Talong longhouse resident with collection of headhunting skulls in rattan harnesses. Photo: B.G. Kuhnhäuser.

Saw for helping with determining specimens and for general advice on palms. Dr Paul Chai provided valuable information about the field site. Sarawak Forest Department kindly granted permission to collect (permits No. (207)JHS/NCCD/600-7/2/107 and No. WL107/2018) and export plant specimens (permit No. 18642). This work was supported logistically by the Royal Botanic Gardens, Kew. It was made possible thanks to generous funding from the Aarhus University Research foundation (grant AUFF-E-2017-7-19 to Wolf L. Eiserhardt), a Bentham-Moxon Trust grant (BMT1-2017) to WJB and BGK, a Society of Systematic Botanists Graduate Student Research Award to BGK, and a Brasenose College Student Support Funding grant to BGK.

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34. Landscape near Lanjak Entimau Wildlife Sanctuary. Photo: W.J. Baker.



Appendix 1. Palms recorded around Nanga Segerak Ranger Station, Lanjak Entimau Wildlife Sanctuary. Specimen codes represent herbarium collections: BK = Benedikt G. Kuhnhäuser, PP = Peter Petoe, X = no voucher specimen collected (sight record).

Subfamily	Genus	Specific epithet	Specimen
Arecoideae	<i>Areca</i>	<i>chaiana</i>	PP35, PP50
	<i>Iguanura</i>	<i>chaiana</i>	PP45
	<i>Oncosperma</i>	<i>horridum</i>	PP41
	<i>Pinanga</i>	<i>aff. brevipes</i>	PP32, PP34
		<i>albescens</i>	PP39
		<i>cf. ligulata</i>	PP38
		<i>lepidota</i>	PP43
		<i>salicifolia</i>	X
		<i>sp. 1</i>	PP36
		<i>sp. 2</i>	X
		<i>tomentella</i>	PP37
Calamoideae	<i>Calamus</i>	<i>cf. periacanthus</i>	X
		<i>collarifer</i>	BK25
		<i>comptus</i>	BK27, BK46
		<i>corrugatus</i>	BK41
		<i>didymophyllus</i>	BK48
		<i>hallierianus</i>	BK37
		<i>javensis</i>	BK32
		<i>korthalsii</i>	BK33, PP33
		<i>maculatus</i>	BK39
		<i>myriacanthus</i>	BK28, BK30, BK45
		<i>ornatus</i>	PP44
		<i>pilosellus</i>	BK52, BK53
		<i>pseudoulur</i>	PP42
		<i>sabalensis</i>	BK31
		<i>sabut</i>	BK36
		<i>sparsiflorus</i>	BK51
		<i>ursinus</i>	BK26
		<i>zonatus</i>	BK43
	<i>Eugeissona</i>	<i>utilis</i>	BK38
	<i>Korthalsia</i>	<i>cheb</i>	PP40
		<i>debilis</i>	BK47, BK55
		<i>echinometra</i>	BK50
		<i>hispida</i>	BK40
		<i>rostrata</i>	BK34
	<i>Plectocomia</i>	<i>mulleri</i>	BK54
	<i>Plectocomiopsis</i>	<i>geminiflora</i>	BK49
		<i>mira</i>	BK44
		<i>sp.</i>	BK35
Coryphoideae	<i>Salacca</i>	<i>vermicularis</i>	BK56
	<i>Arenga</i>	<i>undulatifolia</i>	X
	<i>Caryota</i>	<i>mitis</i>	PP48
	<i>Licuala</i>	<i>cf. maculata</i>	PP46
		<i>petiolulata</i>	PP47
		<i>rheophytica</i>	PP31, PP49, PP51

***Pritchardia arecina*, a Rare Hawaiian Palm Native to East Maui**

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1. *Pritchardia arecina*.



Kahanu Garden and Preserve, located in Hana on the Hawaiian Island of Maui, is part of the National Tropical Botanical Garden (NTBG). The remote Kahanu Garden and Preserve focuses on conservation of Polynesian-introduced and native Hawaiian plant species, including *Pritchardia arecina* Becc., a species of the only palm genus native to the Hawaiian Islands. Located at the foundation of Kahanu Garden is Pi'ilanihale Heiau, a National Historic Landmark, which is considered to be one of the largest cultural sites in Polynesia. Part of NTBG's work includes the collection of rare and endangered plants and using its botanical gardens as safe havens for taxa threatened by climate change, habitat loss and a myriad of other threats



2. *Pritchardia arecina* in flower. Note that the petals fall as a cap at anthesis. Photo by Mike Opgenorth.

The Hawaiian Islands provide an incredible example of what is possible when millions of years of gradual geological and biological processes converge in the middle of the Pacific. Over 1300 native vascular plants have been identified from the Hawaiian archipelago, 89% of them found nowhere else on earth (Wagner et al. 1999). Of these native plants, *Pritchardia* is the only palm genus native to the islands (Figs. 1 & 2). While some members of the genus *Pritchardia* can be found in other areas of the Pacific, such as Fiji and Marquesas Islands, the Hawaiian Islands are home to 24 of the 28 currently recognized *Pritchardia* species (Butaud & Hodel 2017, Hodel 2007, 2012). Of the Hawaiian Islands, Kaua'i has the greatest number of species (seven, all endemic), followed by O'ahu (five, but one shared with Moloka'i), Maui (five, but two shared with Moloka'i), Hawai'i (five, all endemic), Moloka'i (four, but two shared with Maui and one with O'ahu) and Lana'i, Ni'ihau and Nihoa (one endemic species each).

Should you find yourself in a stand of native Hawaiian forest, one of the things you might be fortunate to see are *Pritchardia* palms (known locally as *loulou*, less commonly as *hawane*) projecting above the forest canopy

(Fig. 3). In East Maui above Kahanu Garden *Pritchardia arecina* historically occurred in the upper rain forest 450–1300 meters in elevation, but recent observations indicate the range receded to 600–1200 m, with an estimated 500 individuals remaining (Wood & Bily 2000, Chapin et al. 2004). Like many other *Pritchardia* native to the Hawaiian Islands, it is thought they were vastly more common prior to the introduction of the Polynesian rat, pig and mongoose, which eat the tasty seeds and tender young plants. While this plant was once considered a Species of Concern by the US Fish and Wildlife Service, Chapin et al. (2004) reported that *P. arecina* is Critically Endangered (CR) when evaluated using the IUCN Red List criteria (IUCN, 2020) and faces a high risk of extinction in the wild. It has not yet been formally assessed for the IUCN Red List, but botanists familiar with this species' are currently doing so.

Pritchardia arecina is distinguished from other Hawaiian loulou species by its robust growth habit reaching 15 m tall, petioles with an abundance of fibers toward the base, large leaves with stiff segment tips, the blade rusty brown to golden silvery or grayish white beneath with wooly pubescence on the ribs

3. Hana Forest Reserve habitat of *Pritchardia arecina* in upper Kawaipapa, above Kahanu Garden. Photo by Kenneth Wood.





4 (top). Closeup view of leaf midrib and rusty brown tomentum, a distinguishing characteristic of *Pritchardia arecina*. 5 (bottom). Fruit set of *Pritchardia arecina*. As fruits mature, they transition from green to black. Photos by Mike Opgenorth.

(Fig. 4), inflorescences equaling to longer than the petioles but shorter than the blades, inflorescence branches completely covered with a reddish brown feltlike cottony or wooly pubescence (tomentum), and large, ellipsoid fruits to 45 mm long and 40 mm wide (Fig.5).



6. *Pritchardia arecina* at Kahanu Garden with traditional *hale* (canoe house). The brown leaves were used for the thatching. Every five years or so, the thatch needs to be replaced. Photo by Mike Opgenorth.

Four other *Pritchardia* species occur on Maui, all which are either still lacking formal IUCN Red List assessments or having outdated assessments: *P. woodii* (on East Maui) and, *P. forbesiana*, *P. glabrata* and *P. munroi*, all on West Maui. The rare *Pritchardia woodii* (not IUCN Red List assessed) occurs in East Maui to the south-southeast of *P. arecina* but in slightly drier areas and differs by its leaf blades being green beneath, densely velvety pubescent inflorescences and having slightly larger fruits to 50 × 45 mm. Of the West Maui species, *Pritchardia glabrata* (EN; Gemmill 1998a) is an endangered species growing in dry to moist, steep to nearly vertical slopes in the 'Iao Valley region and also occurs on Lana'i. It is a small, sometimes dwarf palm reaching only 5 m tall with leaf blades green beneath, glabrous inflorescences and smaller, ellipsoid fruits about 30 mm × 25 mm. The Critically Endangered *Pritchardia munroi* (CR; Gemmill 1998b) occurs on Moloka'i and is also known from a few plants on West Maui, where it grows in moist, scrubby forest. It is distinguished by its densely pubescent leaf blades, which are green beneath, woolly inflorescences, branches covered with short grayish hairs, and smaller globose fruits 25 mm long and wide. *Pritchardia forbesiana* (EN; Gemmill 1998c) is an endangered species that occurs in West Maui and eastern Moloka'i. It

is a smaller species to 10 m tall with more sparsely pubescent blades green beneath, loosely pubescent inflorescence axes and relatively large fruits 45 mm long and 35–40 mm wide.

Ethnobotanical uses of *Pritchardia* species range from building materials, to food, clothing (hats), weapons and likely more applications that have not yet been documented. The mature *lau* (leaves) can be used as thatch for different types of Hawaiian *hale* (houses). Often picked as they reach a horizontal or downward orientation, these *lau* are best for thatching immediately after they turn brown. Leaves are not used once rot sets in. At Kahanu Garden, it is still possible to experience a traditional hale thatched with *Pritchardia* leaves (Fig. 6).

The seeds, a favorite food of birds and rats, were also documented to be eaten by early Hawaiians (Beccari & Rock 1921). There was even an endemic Hawaiian honeycreeper (*Ciridops anna*) on Hawai'i Island named '*Ula 'ai Hawane*, or "the red bird that ate *Pritchardia* [fruits]." This bird relied heavily on the delectable, miniature coconut-type fruits. Due to habitat loss and the introduction of mosquitos that are spreading avian malaria, this bird is now declared extinct and has not been observed since 1937 (Clements 2019).



7. Habit of mature *Pritchardia arecina* in pristine Hawaiian rainforest near Kuhiwa, Maui. Photo by Donald R Hodel.

NTBG's Kahanu Garden's project to conserve East Maui's *Pritchardia arecina* began in 1999 as Kenneth Wood (NTBG), Robert Hobdy (State Division of Forestry and Wildlife) and Pat Bily (The Nature Conservancy of Hawai'i) observed large, mature palms in primary forest in the upper Hana Forest Reserve and only a few seedlings. The dominant plant communities where *P. arecina* still occurs are montane *Metrosideros-Cheirodendron* wet forest and shrubland (Fig. 7). Other native vegetation near this palm includes Hawaiian hydrangea (*Hydrangea arguta*), native lobeliads (*Clermontia* and *Cyanea*) and many others. The area includes a rich combination of tree ferns, such as *Cibotium* and *Sadleria* species, and terrestrial ferns including *Athyrium microphyllum*, *Clyorus sandwicensis* and *Selaginella arbuscula*, along with species of Aspleniaceae and Dryopteridaceae.

The remaining East Maui *loulou* are scattered in isolated stands under increased pressure from invasive flora and fauna. Considering the current loss in biotic diversity, Wood, Hobdy and Bily teamed together and collected fruit from multiple locations along its 30-linear mile habitat ranging from Honaman to Kawaipapa. This approach captured a wide range of *P.*

arecina genetics for *ex situ* conservation in NTBG's botanical gardens. In case a stand is lost in the wild, having genetically diverse collections in our botanical gardens will best allow us to maintain diversity of this species and someday return them to the wild.

Seeds collected from these wild specimens were delivered to the NTBG Horticultural Center on Kaua'i for propagation, and young plants were later out-planted at Kahanu Garden on Maui. Since then, the trees have thrived in their location close to their natural habitat (Fig. 8). All of the trees now produce abundant fruit, paving the way for future protection of these palm populations. However, future work at Kahanu Garden requires strategic hand-pollination of these trees in order to produce seeds true to type. Controlled pollination techniques should be initiated to maintain wild genetic diversity and investigate the opportunity for cross-pollination between selected individuals that may increase genetic diversity and help mitigate inbreeding.

Palms are a key part of tropical ecosystems and have cultural importance for humans. From the sheer appreciation of palms as a symbol of lush, tropical islands to their many ethnobotanical uses, it is important they are



8. *Pritchardia arecina* in cultivation at NTBG's Kahanu Garden. Honoma'ele, Hana, Maui. Photo by Mike Opgenorth.

protected. With all of Maui's five native species currently endangered, it is critical that we continue to conduct research to understand and conserve these enigmatic species into the future.

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PALM LITERATURE

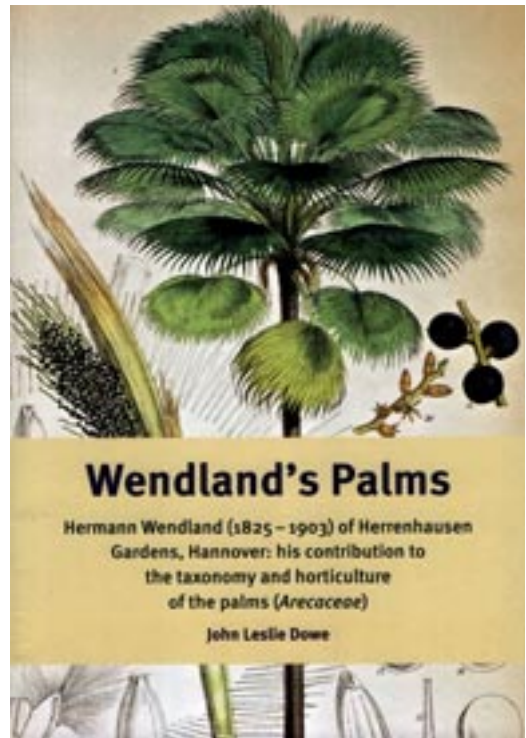
WENDLAND'S PALMS. HERMANN WENDLAND (1825–1903) OF HERRENHAUSEN GARDENS, HANNOVER: HIS CONTRIBUTION TO THE TAXONOMY AND HORTICULTURE OF THE PALMS (ARECACEAE) – John Leslie Dowe, Botanic Gardens and Botanical Museum, Berlin. 2019. Softcover. Engleria 36. ISBN: 978-3-946292-31-9. Price: €25.00. 137 pages, color and black & white illustrations.

For readers of these pages, John L. Dowe will need no introduction. Although he is best known for his work on palms from Australia and surrounding regions, his latest work takes us to Germany, and from there, on a grand tour of the palm world. His topic is the taxonomic work of Hermann Wendland, one of Europe's most important and prolific palm botanists of the late 19th century.

The book opens with a biographical sketch of Wendland, who was the son and grandson of respected plantmen and who rose to become the director of the Royal Gardens at Herrenhausen, including its fabulous Palm House. The palm collection grew to be the most famous living collection of palms on the continent. It was the focus of taxonomic work, where Wendland (and other botanists) could supplement their studies of dried specimens with observations of living plants.

The key to his success at growing palms was, by Wendland's admission, the practice of keeping the pots of palms in trays of standing water. Bear in mind, the tropical glasshouses of Europe were heated, and potted plants quickly dried out under such conditions. Wendland believed that one could not be too liberal in the application of water. He even wrote that, "as a rule, the more spiny a palm is, the more moisture it requires."

The bulk of Dowe's deep-dive into Wendland's palm taxonomy is his analysis of 549 names that are associated with Wendland. Dowe picks through the names, assesses their nomenclatural legitimacy and provides the currently accepted names. Of these, 60 of Wendland's genera and 249 of his species names are still in use. Dowe also provides an outline of Wendland's classification of the tribes and



subtribes of palms, which was based largely on characters of the seed. Wendland's system was not widely taken up and is superseded by the modern synthesis of morphological, anatomical and molecular data. One wonders if his emphasis on seed characters grew from his interest in germinating seeds and growing these new arrivals to Europe.

Wendland's taxonomic work included major publications of big genera, such as *Chamaedorea*, *Geonoma* and *Bactris*. Dowe examines each of these in turn for Wendland's nomenclatural contributions. Dowe does the same for Wendland's regional studies of palms in Africa, the South Pacific, the islands of the Indian Ocean and the Caribbean. Throughout these chapters, Dowe reproduces some of the most beautiful botanical illustrations from Wendland's publications. Hand-colored illustrations from a time before photography are a treat to see. They capture the romance and excitement of the heyday of Europe's exploration of the tropics.

Dowe's latest book is aimed squarely at the palm taxonomist and those with an interest in the history of palm taxonomy. Wendland played a starring role in early days of palm classification, and this book gives Wendland his due.

SCOTT ZONA

Germination Strategies of Three Palms that Coexist in the White Sands of Western Cuba

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Seed characteristics, dormancy classes and germination requirements of three endemic palms of Cuba that coexist in the white sands in the west of the island were described and compared among them according to their breadth of distribution.

Germination plays a key role in the life cycle of plants, since it determines the mortality risk depending on the time and conditions under which it happens (Donohue et al. 2010). A set of environmental and intrinsic factors of the seeds influences the species germination and determines species distribution (Baskin & Baskin 2014a). It often coincides that the species with the widest geographical distribution also has large germination niches, that is, they are capable of germinating under a broad scenario of environmental conditions (Donohue et al. 2010, Cochrane et al. 2015).

The palms, typical in all the tropical and subtropical regions of the world, show complex spatial patterns of distribution and

high species diversity (Svenning 2001, Eiserhardt et al. 2011). Despite their ecological and economic importance, there is poor information on the biology of palm seeds and variations in the amplitude of the germination niche (Orozco-Segovia et al. 2003, Baskin & Baskin 2014b, Braz et al. 2014). Water availability, temperature and lighting are among the environmental factors affecting the germination niche (Bewley et al. 2013, Baskin & Baskin, 2014a).

Cuba has a rich palm flora, being the center of evolution of genera such as *Copernicia* and *Coccothrinax* (Moya & Leiva 2000, Jestrow et al. 2018). Unfortunately, of the 83 native taxa of Cuba, 51 are under threat (González-Torres



1. A. *Copernicia brittoniorum*. B. *Copernicia glabrescens*. C. *Coccothrinax acuminata*. Photos by J.C. Álvarez.

et al. 2016). However, research on seed biology in Cuban palms is limited to the work of Muñoz et al. (1992, 2006) on some aspects of the germination of *Roystonea regia* (Kunth) O.

F. Cook and *Coccothrinax fragrans* Burret, as well as those developed with *Coccothrinax crinita* (C. Wright) Becc. subsp. *crinita* (Pinares 2004, Pernús & Sánchez 2017).

Knowing germination requirements can be decisive in the management and conservation of plant species and the areas where they live. This acquires greater relevance when dealing with species with restricted distribution, as well as extreme ecosystems such as the savannas of white quartzite sands of Western Cuba. These ecosystems have a high endemism determined by the lack of nutrients and alternating periods of flood/drought, which results in a highly specialized flora on these substrates with seasonality conditions and extreme nutrients (Cejas & Herrera 1995, Urquiola et al. 2010).

The objective of the present work was to study the germination strategies of three endemic palms to Cuba that coexist in these savannas, but that have different distributions on the island. We identified seed characteristics, dormancy classes and germination requirements in relation to temperature and lighting in *Copernicia brittoniorum* León, *Copernicia glabrescens* H. Wendl. ex Becc. and *Coccothrinax acuminata* Becc. The first of these species is Critically Endangered (Verdecia et al. 2015). We hypothesize that the amplitude of the germination niche will be in correspondence with the geographical distribution of these palms.

Materials and Methods

The species: The information on distribution, habitat and threat category of the species was taken from the latest categorization of the taxa of the flora of Cuba (González-Oliva et al. 2015). The work of Moya and Méndez (2018) was also taken into account, who recently demonstrated the legitimacy of the name *Coccothrinax acuminata*, which is treated by González-Oliva et al. (2015) as *Coccothrinax miraguama* subsp. *arenicola* (León) Borhidi & O. Muñiz.

The three palms studied are Cuban endemics that live in the white sands of Pinar del Río but differ in their distribution outside this ecosystem. *Copernicia brittoniorum* (Fig. 1A) is Critically Endangered, with only two individuals known to date in these savannas. In fact, individuals from this locality were considered in the past a variety of the species (Cejas & Herrera 1995). This species also lives in the provinces Matanzas and Cienfuegos, in coastal and subcoastal, xeromorphic shrubland and secondary shrubland. On the other hand, *C. glabrescens* (Fig. 1B) and *C. acuminata* (Fig. 1C) are of Least Concern. *Copernicia glabrescens* is the most widely distributed of the three

palms studied, with individuals in the provinces Pinar del Río, Artemisa, Mayabeque, Matanzas and Sancti Spiritus. The plant formations in which it inhabits are also the most varied: seminatural savanna, pine forest, thorny xeromorphic thicket on serpentine, complexes of vegetation of sandy and rocky coast, as well as semi-deciduous mesophilic forest. *Coccothrinax acuminata* has the most restricted distribution, since it occurs only on sandy-quartzite substrate in Pinar del Río, Isla de la Juventud and Artemisa. The species grows in secondary savannas, seminatural savannas, coastal and subcoastal thorny shrublands and pine forest, on sandy-quartzite substrate, mainly on white sandy soils, alluvial soils and rarely on limestone.

Collection site and plant material: We collected the seeds near the Managed Floristic Reserve San Ubaldo-Sabanalamar (84°3'15" W, 22°9'2" N), in the Southwestern portion of Pinar del Río, Cuba, in May (*C. brittoniorum*) and August 2015 (*C. glabrescens* and *C. acuminata*). The site belongs to the Sabaloense phytogeographic district, characterized by a sandy-quartzite substrate deficient in nutrients and very acidic, with an annual historical average of minimum temperature close to 23°C. The region experiences annual floods in the humid hydrological wet period (from May to November), while at the end of the dry period it suffers extreme drought (Urquiola et al. 2010).

Mature fruits of 10 individuals were collected per species, except in *C. brittoniorum*, since to date only two individuals of this taxon are known in this site. The mature fruits of each species were combined in a single batch and washed in running water, eliminating the pericarp. After 48 hours on filter paper at room temperature, laboratory tests were carried out.

Morphophysiological characterization of the seeds: We measured fresh mass (g), dry mass (g), initial moisture content (%), seed length (mm), embryo length (mm) and the ratio between the length of the embryo and the length of the seed (E:S) for each individual seed of 50 per species. The dry mass and initial moisture content were obtained according to the standards of the International Seed Testing Association (ISTA 2007).

Germination requirements and seed dormancy classes: The germination tests were carried out in growth chambers (FRIOCEL 111L, Germany) under a completely randomized design with a factorial arrangement of the

Table 1. Mean values and standard error of morphophysiological variables of fresh seeds of *Copernicia brittoniorum*, *Copernicia glabrescens* and *Coccothrinax acuminata*.

Seed traits	<i>C. brittoniorum</i>	<i>C. glabrescens</i>	<i>C. acuminata</i>
Fresh mass(g)	1.72 ± 0.03	0.71 ± 0.03	0.17 ± 0.01
Dry mass (g)	1.34 ± 0.02	0.54 ± 0.02	0.14 ± 0.01
Moisture content (%)	22.40 ± 0.43	25.11 ± 0.84	15.59 ± 0.11
Length of the seed (mm)	13.83 ± 0.08	10.55 ± 0.17	6.10 ± 0.12
Embryo length (mm)	4.84 ± 0.09	3.43 ± 0.06	1.42 ± 0.03
Embryo: Seed	0.35 ± 0.01	0.33 ± 0.01	0.23 ± 0.01

treatments (temperature x light). The seeds, previously sterilized with sodium hypochlorite (1%, 10 min), were placed in Petri dishes on filter paper saturated with sterile distilled water. They were incubated under light and dark conditions at a constant temperature at 25°C and alternating temperatures of 25/30°C, 25/35°C, 25/40°C and 25/45°C (12 hours at 25°C, eight hours at the highest temperature and a transition between they four hours). The illumination (40 molm⁻²s⁻¹, 400–700 nm) coincided with the period of highest temperature for each treatment. Constant darkness was achieved by wrapping the dishes in two layers of aluminum foil. The location of the dishes in the incubators was changed regularly.

For the three species, five replicates of 15 seeds each were used per treatment and the seeds were considered germinated once the operculum was displaced by elongation of the cotyledon petiole. The germination was checked weekly for seeds exposed to light, and for seeds exposed to darkness, germination was counted at the end of the experiment, which lasted four weeks (*C. brittoniorum* and *C. glabrescens*) and 13 weeks (*C. acuminata*). In both lighting conditions and for each temperature range, the percentage of final germination was determined.

To express the light requirements in germination, the germination index relative to light (GRL) was calculated (Milberg et al. 2000), where $GRL = GL / (GO + GL)$, with GL being the percentage of germination to the light, and GO the percentage of germination in darkness. For this, the average germination values were taken in the optimum temperature range for germination (where the highest germination percentage was obtained in the shortest time possible). The GRL index varies between 0 (germination only in darkness) and

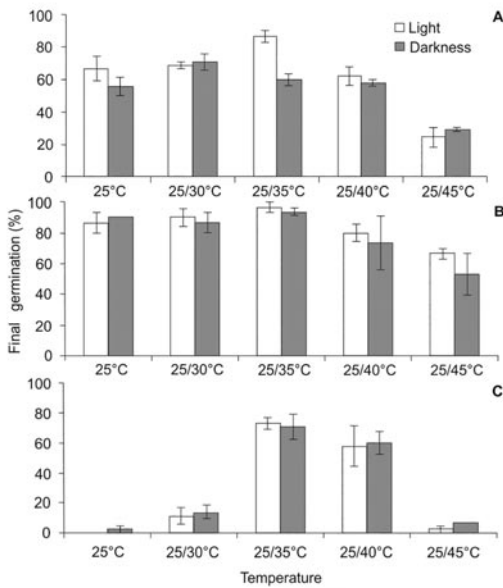
1 (germination only in light). According to Funes et al. (2009), if the GRL index is higher than 0.75, the species is considered to be light dependent (positive photoblastic); if it is less than 0.25, the species is considered light repellent (negative photoblastic); and if the GRL value is between 0.25 and 0.75, then the species is taken as indifferent to light.

We used the classification system and the dichotomous key proposed by Baskin and Baskin (2014a) for the identification of seminal dormancy classes. The seeds of *C. acuminata* that did not germinate in light at 25°C, 25/30°C and 25/45°C were transferred for five weeks to the optimum temperature range to determine possible thermoinhibition or thermodormancy. If reseeded results in high percentages of germination, the seeds are considered to be thermoinhibited; otherwise, a thermodormancy occurs if the seeds stay alive (Baskin & Baskin 2014a). In the three cases, the final germination percentage and the percentage of dead and live non-germinated seed were determined. The germination count was weekly, and the planting conditions as described above for light. Live non-germinated seeds were considered those that presented firm embryos (Baskin & Baskin 2014a).

Statistical analysis: The mean and the standard error were calculated for each variable. The final germination percentages were analyzed for each species through multivariate analysis of variance based on permutations, PERMANOVA (Anderson 2005), because the data did not meet the parametric premises.

Results

The seeds of the three palms varied in mass and dimensions (Table 1), but in all cases the embryos were poorly developed ($E:S < 0.5$). The seeds of *C. acuminata* were the smallest and



4. Effect of temperature and illumination on the percentage of final germination of fresh seeds of *Copernicia brittoniorum* (A), *Copernicia glabrescens* (B) and *Coccothrinax acuminata* (C). The bars indicate the standard errors of the means.

those with the lowest moisture content. The largest seeds were those of *C. brittoniorum*; but the highest moisture content corresponded to the seeds of *C. glabrescens* (Table 1).

The percentage of final germination of *C. brittoniorum* seeds was significantly affected by the light factors ($F=4.92$; $p<0.05$) and temperature ($F=26.76$; $p<0.001$), as well as by their interaction ($F=3.05$; $p<0.05$). Light ($F=10.38$; $p<0.01$), temperature ($F=50.78$; $p<0.001$) and their interaction ($F=7.94$; $p<0.001$) also significantly influenced the germination of *C. acuminata*. However, light ($F=0.80$; $p>0.38$) and its interaction with temperature ($F=0.27$; $p>0.89$) were not significant in the germination of *C. glabrescens*; while the temperature was ($F=5.61$; $p<0.01$). Temperature was the most important factor for the three palms.

The highest percentages of final germination were obtained at light at 25/35°C (Fig. 4). In this temperature, the GRL index was 0.59 for *C. brittoniorum* and 0.51 for *C. glabrescens* and *C. acuminata*; corresponding to germination indifferent to light. The seeds of *C. glabrescens* reached high percentages of germination ($>50\%$) in all the conditions tested (Fig. 4B), while in *C. acuminata* the germination was very low ($<20\%$) at 25°C, 25/30°C and 25/45°C both in light and dark (Fig. 4C). The seeds of *C. brittoniorum* showed an intermediate behavior (Fig. 4A).

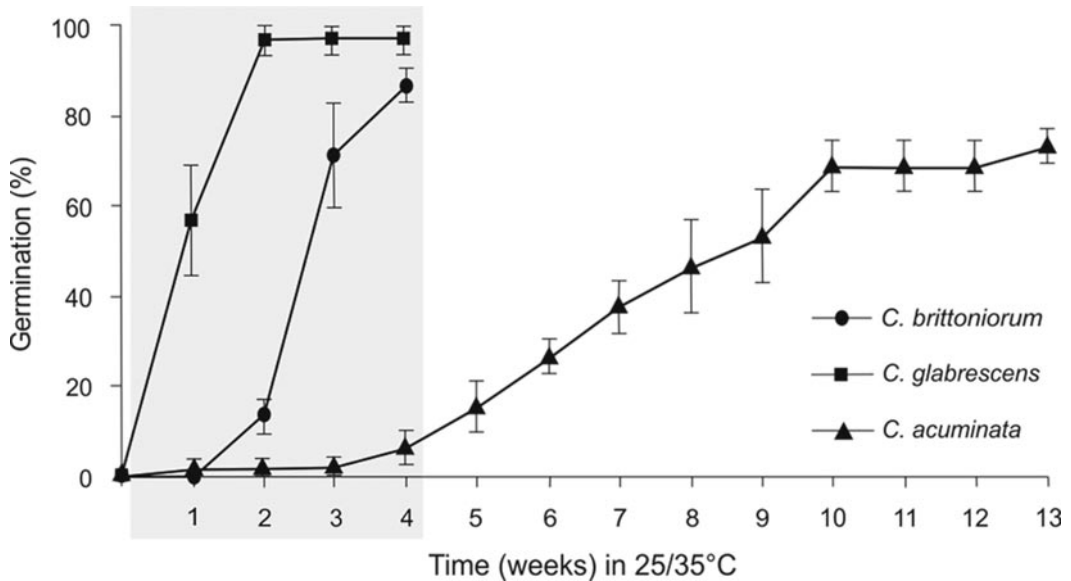
The alternating temperature of 25/35°C also increased the rate of the germination process. For the three species, germination began at this temperature. In the case of the two copernicias, germination was completed before four weeks, indicating morphological dormancy (Fig. 5). On the other hand, for the seeds of *C. acuminata* the morphophysiological dormancy was the most important. For the latter species, only 11% of the germination occurred before the four weeks (morphological dormancy), so the rest of the seeds that germinated had morphophysiological dormancy (Fig. 5).

Germination of the seeds of *C. acuminata* that were at 25°C and 25/30°C and were transferred to the optimum temperature range (25/35°C), was resumed from the second week of being in this condition. In five weeks, final germination percentages were higher than those reached at the optimum temperature were: 88.89 ± 4.45 for the seeds that were at 25°C and 93.33 ± 6.67 for the seeds that were at 25/30°C. In both cases, the seeds that did not germinate were dead. However, the same did not happen with seeds that were at 25/45°C. In this case the reseeding results were as follows: germinated seeds, 17.78 ± 4.45 ; live non-germinated seeds, 8.89 ± 2.23 and dead seeds, 73.33 ± 6.67 .

Discussion

All the seeds presented poorly developed linear embryos, which coincides with that reported for palms in general and determines the component of morphological dormancy in the family (Baskin & Baskin 2014b). On the other hand, the time it took to germinate reflected the existence of morphological dormancy in the two copernicias, as well as morphological and morphophysiological dormancy in *C. acuminata*. These results confirm the dormancy classification that had been inferred for *C. glabrescens* and *C. acuminata* (Baskin & Baskin 2014a). This is the first report of morphological dormancy for *C. brittoniorum*.

The presence of morphological and morphophysiological dormancy in the same lot of seeds was identified in another species of the genus *Coccothrinax* (Pernús & Sánchez, 2017). For *C. acuminata*, which constitutes the most restricted distribution species in the present study, this asynchronous germination could represent an adaptive strategy to guarantee greater establishment of its seedlings. The presence of morphophysiological dormancy could prevent a part



5. Cumulative germination of fresh seeds of *Copernicia brittoniorum*, *Copernicia glabrescens* and *Coccothrinax acuminata* at 25/35°C. The bars indicate the standard error of the means and the shaded area is the part of the seed lot that has morphological dormancy.

of the seed lot from germinating during periods that are only ephemerally favorable, such as isolated rains within the wet season. On the other hand, although the seeds of *C. acuminata* were collected in the middle of the wet season, the phenology of the species is still unknown. According to Willis et al. (2014), the sensitivity to the environment contributed by dormancy, in particular by its physiological component, appears as a key characteristic in the diversification of plants with seeds. Since dormancy controls the appropriate timing of germination, it can strongly affect plant survival; influencing both at the species level and at the population level in processes such as colonization, adaptation, speciation and extinction (Willis et al. 2014).

If we take into account that seeds of *C. acuminata* had the lowest moisture content and size (mass and dimensions), we can expect greater tolerance to desiccation in this species, a feature that might secure seed survival for a longer period. The weight, the moisture content and the ecology of the plants are among the criteria used to predict the storage behavior of seeds (Hong & Ellis 1996). Therefore, species like *C. acuminata* that have small seeds with moisture content lower than 20% and live in dry habitats, are potentially tolerant to desiccation.

Copernicia glabrescens was the only species for which the light factor was not significant according to the statistical results. However,

the three palms showed indifference to light in their germination, as indicated by the high percentages of germination in both light and constant darkness and the GRL index *s* values. Orozco-Segovia et al. (2003) suggest that in most palms, the seeds are indifferent to light. In this sense, the results indicate that these three species are capable of germinating in more or less shaded microsites, where if the rest of the other factors that influence germination allow it.

In all cases, temperature was the most important factor and the optimum temperature was 25/35°C. After water, temperature is considered the main environmental factor that controls germination (Bewley et al. 2013) and in most palms, the optimum germination temperatures exceed 30°C (Orozco-Segovia et al. 2003). Our results also correspond to the high temperatures reported in the collection site (Urquiola et al. 2010). Concerning temperature, the two copernicias showed the broadest germination niches. *Copernicia glabrescens* was the one with the greatest plasticity, reaching high germination percentages even at 25/45°C. This corresponds to its greater distribution and suggests that *C. glabrescens* could germinate under a broad environmental scenario, even in those proposed by the models of climate change (Sánchez et al. 2011). The results of this study are also encouraging for *C. brittoniorum*, since

they demonstrated not only their germination plasticity, but their seeds are viable and produce normal seedlings (data not shown) that can be used for reintroduction into their natural habitat as part of conservation projects with the species.

On the other hand, *C. acuminata* showed the narrowest germination niche in relation to temperature. It reached its highest percentages of germination at 25/35°C and 25/40°C; but unlike the copernicias, in other temperatures germination was low or nil. The experiment of resowing the seeds showed that 25°C and 25/30°C cause thermoinhibition, since the germination process resumed at the optimum temperature. However, 25/45°C could be considered a lethal or sublethal temperature for the species, since on resowing the germination percentage was also low and most of the seeds that did not germinate were dead. Perhaps some of the seeds were already dead when they were transferred to optimal condition or they had exhausted all their reserves at 25/45°C and failed to germinate or survive in the new conditions. Improper planting conditions can lead to accelerated seed ageing and consequently death (Bewley et al., 2013).

As to thermoinhibition, this behavior has also been observed in *Coccothrinax crinita* (Pernús & Sánchez 2017). Although Muñoz et al. (2006) did not find significant differences in rate and percentage of final germination in seeds of *Coccothrinax fragrans* sown at 25°C and 25/35°C. A period at these temperatures (25°C or 25/30°C) could act as a stratification treatment that promotes germination when the temperature increases. Many effective treatments to break dormancy simulate the natural conditions at which the species are adapted and include stratification at low or high temperatures (Baskin & Baskin 2014a).

In conclusion, the hypothesis that the species with greater geographic distribution have greater amplitude of the germination niche was fulfilled. For the two copernicias the dormancy was morphological. Because the requirements for the embryo to grow in this type of dormancy are a moist substrate and adequate temperatures (Baskin & Baskin 2014a) and taking into account the high percentages of germination in all conditions evaluated, the arrival of the rains should be enough to trigger the germination of these palms. On the other hand, *C. acuminata*, with morphophysiological dormancy in most of its

seeds and an optimum narrower temperature range, may have fewer opportunities for germination, but greater establishment in this ecosystem where seasonality is so extreme. These results may contribute to the reproduction of these species in nursery conditions for future conservation actions.

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Photo Feature

Pritchardia pacifica



Pritchardia pacifica, photographed in evening light in Mauritius.

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