

Palms

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The International Palm Society

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FRONT COVER

Orania regalis, Tamrau Mountains, West Papua (Jan. 2013). See article by Dowe & Latifah, p. 121. Photo by W.J. Baker.

BACK COVER

Pinanga rupestris, Bako National Park, Sarawak, Malaysia. See article by S. Bellot et al., p. 109. Photo by S. Bellot.

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Fruits of *Chuniophoenix hainanensis* in cultivation at Singapore Botanic Garden. See related article by Zaki & Zona, p. 137. Photo by Zaki.

PALM NEWS

A new study of the **pollination ecology of *Bactris guineensis*** was published by E. Brieva-Oviedo et al. (Flora 269: 151628; <https://doi.org/10.1016/j.flora.2020.151628>), who found that the flowers open at night, have a “balsamic” fragrance and are strictly out-crossing (self-pollination does not produce fruits and seeds). The inflorescence is thermogenic (self-heating) and can be up to 12°C warmer than ambient. The authors found that the species is pollinated by minute flower weevils and sap beetles. Knowledge of the pollination is important, as the species is being eyed as a commercial fruit crop along the Caribbean region of Colombia. In a separate paper, E. Brieva-Oviedo and L.A. Núñez-Avellaneda reported on the **pollination biology of *Sabal mauritiiformis***, the only species of *Sabal* that occurs in Colombia and only the fourth *Sabal* to receive such careful study. They found that *S. mauritiiformis* is self-incompatible, non-apomitic and predominantly out-crossing. Of 65 species of insects that visited inflorescences, the stingless bees (Meliponini) were identified as effective pollinators. The paper is Brieva-Oviedo, E. & L.A. Núñez-Avellaneda. 2020. Biología reproductiva de la palma amarga (*Sabal mauritiiformis*: Arecaceae): especie económicamente importante para la Costa Caribe colombiana. *Caldasia* 42:278–293. doi: <https://dx.doi.org/10.15446/caldasia.v42n2.75595>.



Palm botanists have long been aware that palm diversity in terms of growth form and abundance of individuals can vary greatly across the tropics with the general impression that tree palms are just more conspicuous in the American tropics. Now we have the proof. Robert Muscarella and over 200 co-authors (we did not count) have published a paper based on research analyzing 2548 forest plots sited throughout the tropics. They showed that **the abundance of tree palms (with stems greater than 10 cm diameter) is five times greater in the Neotropics than elsewhere**. The paper goes on to make suggestions why the African and Indomalayan regions have relatively low numbers of tree palms. The open-access study is published here: Muscarella et al. 2020. The global abundance of tree palms. *Global Ecology and Biogeography*. <https://doi.org/10.1111/geb.13123>.



How and why did the world's largest seed, that of double-coconut (*Lodoicea maldivica*), evolve? Sidonie Bellot and co-workers recently conducted a detailed phylogenetic analysis of tribe Borasseae, to which the double-coconut belongs, using DNA and seed-size data. They inferred ancestral seed size, dispersal history and rates of change in seed size and evaluated how overall plant size, inflorescence branching, habitat and insularity may have influenced these changes. They concluded that taller plants with fewer-branched inflorescences produced larger seeds, shade-loving members tended to have larger seeds and seed size changed more rapidly on islands (except on Madagascar). The pre-publication manuscript is freely available here: On the origin of giant seeds: the macroevolution of the double coconut (*Lodoicea maldivica*) and its relatives (Borasseae, Arecaceae). *New Phytologist*. 2020. <https://doi.org/10.1111/nph.16750>.

Why and How to Develop DNA Barcoding for Palms? A Case Study of *Pinanga*

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In this article we explain what DNA barcoding means and its utility for palm research and conservation.

Plant DNA Barcoding

Definition: DNA barcoding (Hebert et al. 2003) allows biologists to identify an organism (for instance a palm in your garden) by comparing its DNA with a “reference” library of the DNA sequences of well-identified organisms (for example, all palm species; Fig. 1). The concept is similar to scanning the barcode of a supermarket product to find its price, hence the name. However, in the case of DNA, the code is not made of bars and numbers but of letters (A, T, G, C) representing the four chemical building blocks (nucleotides) that form DNA (Fig. 1).

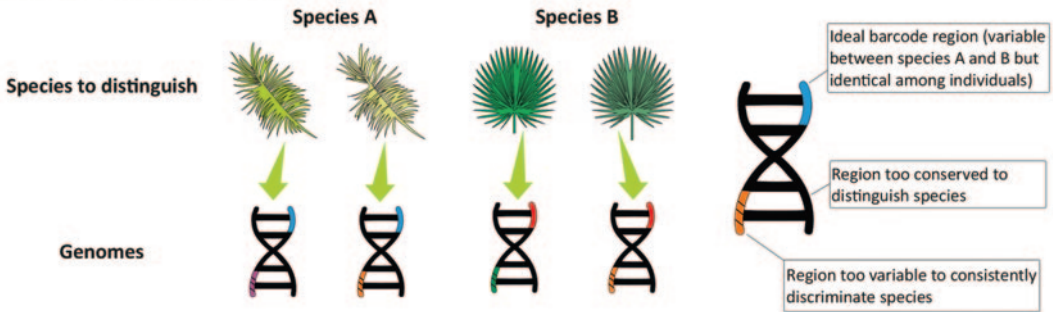
DNA barcoding can be applied to any living organism. For instance, a combination of four distinct DNA regions has been chosen as a barcode to distinguish South African *Encephalartos* cycads. These four regions were

sequenced for the majority of South-African cycad species and the resulting sequences constitute a reliable DNA barcoding reference library for the genus (Williamson et al. 2016). Any cycad material can now be assigned to species or even population of origin by sequencing (reading) these DNA barcode regions and comparing them with the cycad reference library. This permits accurate monitoring of illegal cycad trade and helps to prevent the extinction of these iconic plants.

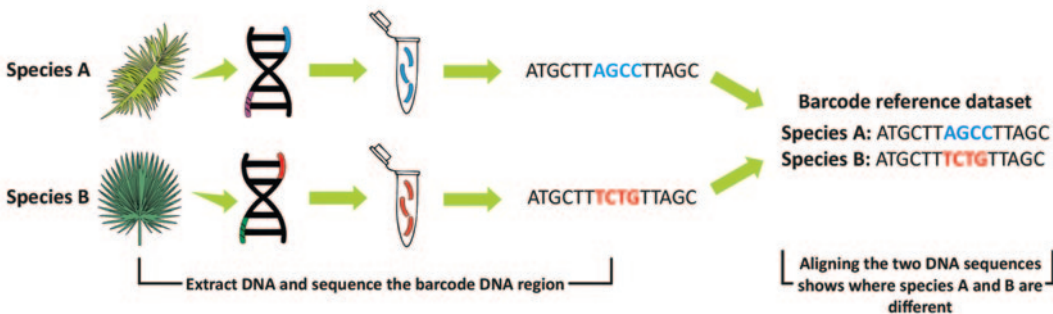
The reference library for all palms is not yet complete, preventing us from identifying palms this way, but biologists are making progress in this direction, as we explain in the next sections.

Applications: DNA barcoding has wide-reaching applications from fundamental studies of biodiversity through ensuring sustainable use.

1. Chose DNA barcode region



2. Create barcode reference library



3. Identify an unknown sample



1. Simplified representation of a DNA barcoding workflow.

DNA barcoding can also help fundamental research. To implement a DNA barcoding approach, one must obtain DNA information for many species (see next section). This information can often be used to understand how the species are related to each other, i.e. to resolve their “family tree,” also known as “phylogeny”, “evolutionary tree” or “Tree of Life”. Finally, DNA barcoding has the potential to expedite the discovery of new species, by revealing individuals with DNA barcodes markedly different from those of any already described species (Fig. 2).

Approaches: Standard barcodes: To achieve the potential of DNA barcoding, selecting the right DNA barcode is crucial. A good DNA barcode region should be a portion of DNA that varies among species but not among individuals of the same species (Fig. 1). So far, there is no single DNA region possessing these characteristics that would allow biologists to distinguish between all species of plants, but

a few regions have proven useful in many plant families. This is the case of four DNA regions called ITS, *trnH-psbA*, *matK* and *rbcL*. The first region is located in the main plant genome: the nuclear genome, which is made up of most of the plant’s DNA. The other regions are located in the plant chloroplast genome, which is a small genome that plants have in addition to their nuclear genome. These DNA regions are referred to as “standard plant DNA barcodes” by the Plant Working Group of the Consortium for the Barcode of Life (CBOL Plant Working Group, 2009).

A new approach: k-mer profiling: To identify an organism using standard DNA barcodes, we compare the DNA barcode sequence of this organism with the sequences of reference organisms by aligning them together and looking for similarities (Figs. 1 & 3A). This is the standard barcoding method. Another approach, called k-mer profiling, does not rely on a specific DNA barcode region, but instead

on calculating the frequencies of all DNA sequences of a chosen length k (called k -mers) that occur in the organism to identify (Fig. 3B). This produces a “ k -mer profile” (Fig. 3B) that is then compared to the k -mer profiles of the reference organisms (Ondov et al. 2016, Sarmashghi et al. 2019).

In both approaches, a higher similarity (of DNA sequence or of k -mer frequencies) is interpreted as evidence of closer relatedness. The advantage of k -mer profiling is that there is no need to select and sequence specific DNA regions, and it can be applied directly to raw genome sequencing data, without having to align DNA, which can be error-prone. However, k -mer profiling can be more costly to implement than standard barcoding, because it requires one to sequence more DNA.

The importance of DNA barcode references: The establishment of comprehensive reference libraries is a key challenge in DNA barcoding. If species are missing from the reference library, it will be difficult to interpret a species with a barcode that does not match any of the species in the library; it could be a new species or simply a species absent from the reference library. Public repositories such as the Barcode of Life Data System (BOLD) (Ratnasingham &

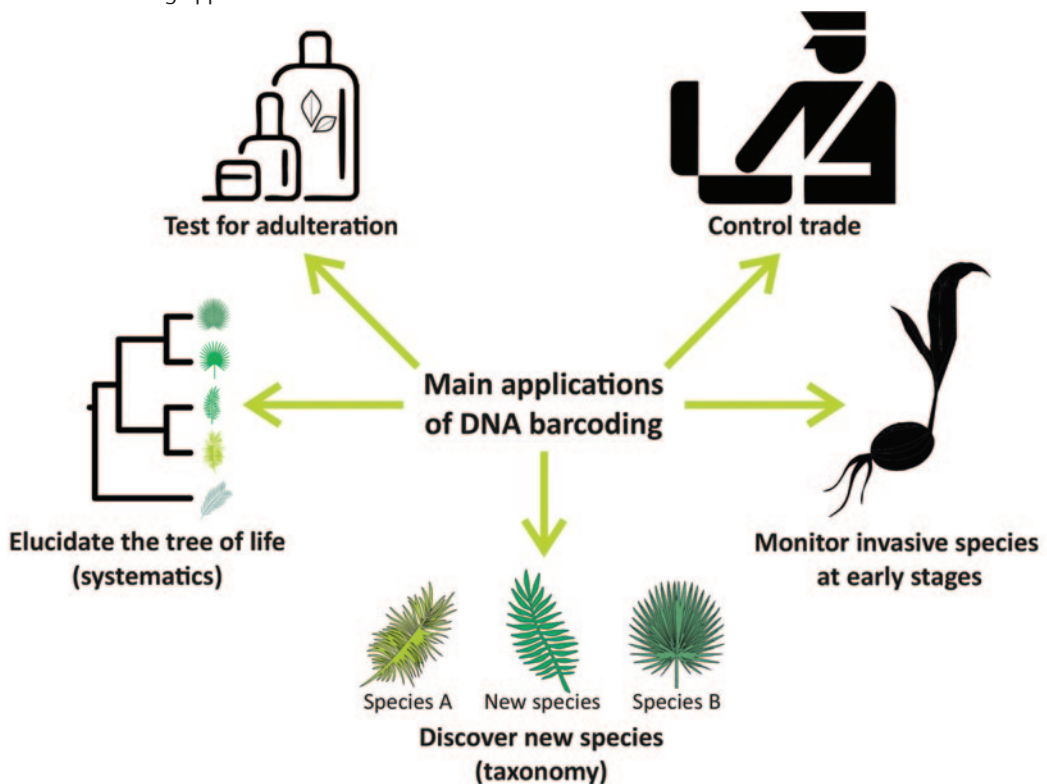
Hebert 2007) and GenBank (Benson et al. 2018) already hold DNA barcode sequences for many species. However, these repositories are far from complete (many sequences are not identified at the species level and many species are missing) and often contain incorrect information, due to misidentification of material, contamination between samples, or DNA sequencing errors (Meiklejohn et al. 2019).

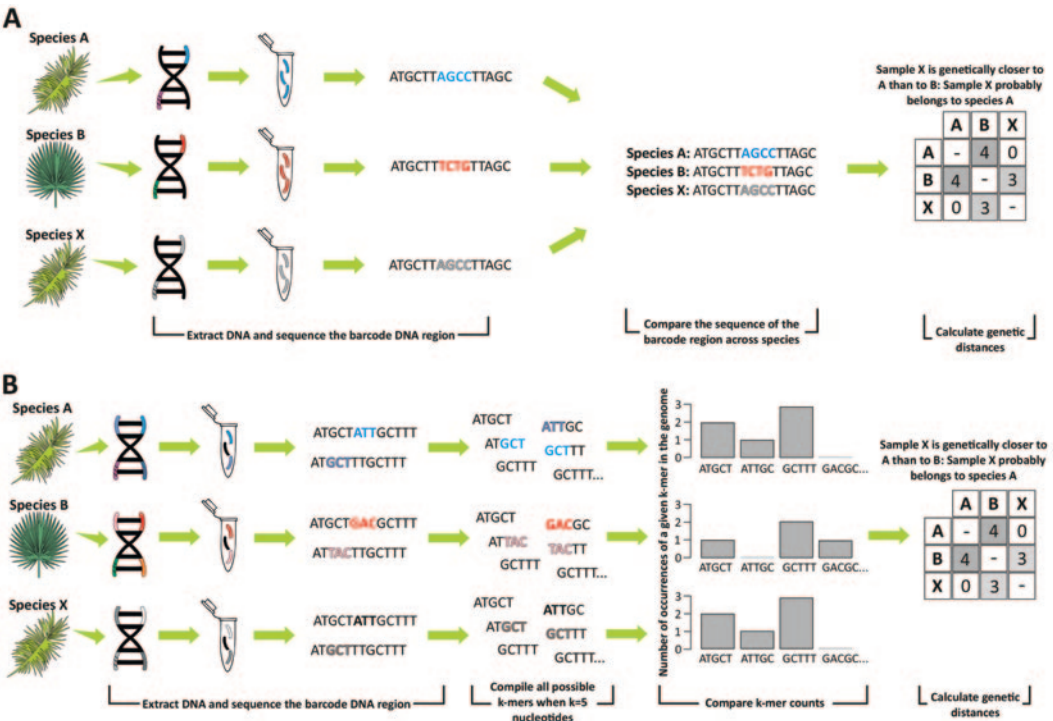
Concerted efforts, global standards and long-term resource allocation are required to develop the high-quality reference libraries that will allow making the most of (plant) DNA barcoding. These efforts will have to take place at every step of barcode design: from collecting as many species as possible, to verifying the identity of each species collected, to sequencing the right barcode region(s), to avoiding cross-contaminations and mix-ups in the field, the lab or the computer, to controlling for sequencing errors, and to uploading the right DNA sequence with the right name to the reference library.

How plant phylogenomics can help plant DNA barcoding: the example of palms

Plant phylogenomics: As explained in the previous section, barcoding studies are often

2. DNA barcoding applications.





3. DNA barcoding approaches. A. Standard approach using one or a few DNA regions. B. High-throughput approach using genome-wide (k-mer profiles) comparisons.

combined with research aimed at understanding how species are related to each other (phylogenetics) because they can both make use of the same DNA regions. The development of high-throughput DNA sequencing in the last fifteen years has led to an age of “phylogenomics” in which relationships between species (phylogenies) are not inferred from one or a few but from dozens to hundreds of DNA regions. The most common high-throughput DNA sequencing approaches to sequence these DNA regions from plants are summarized below, together with their relevance for plant phylogenetics and DNA barcoding.

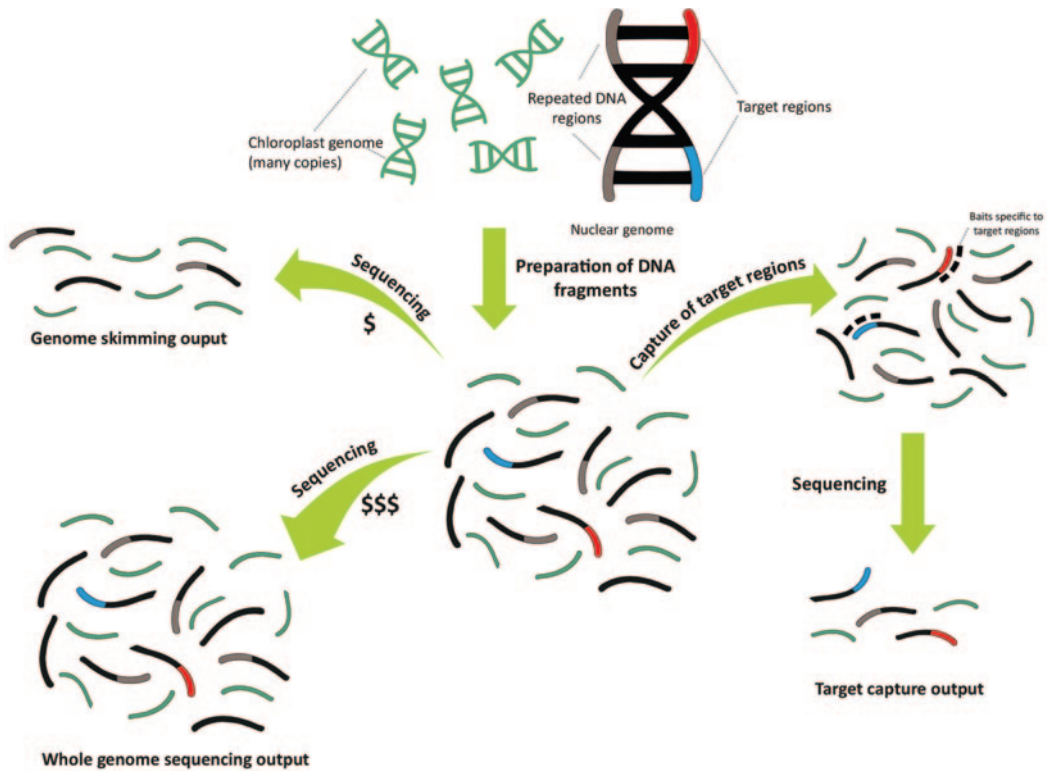
Genome skimming: The “genome skimming” approach consists in randomly sequencing fragments of DNA, but not enough to sequence the whole genome. Because the sequencing is random, regions that are present in multiple copies in the genome will have more chance to be sequenced than regions present only once (Fig. 4).

In plants, the chloroplast genome is often present in many copies for one or a few copies of the nuclear genome. As a result, plant genome skimming yields many DNA sequences from the chloroplast genome but

fewer from the nuclear genome (Fig. 4). One notable exception is the previously mentioned standard DNA barcode ITS (see section 1.3.1), which is repeated many times across the nuclear genome, and therefore often recovered in genome skimming studies.

Chloroplast genes and ITS have proven efficient for both DNA barcoding and phylogenetic studies of some plant families [for instance in orchids, (Freudenstein & Chase 2015)], so genome skimming is a good approach to achieve phylogenetic and DNA barcoding goals at once. It is also cheap (ca. \$20–\$50 per sample) compared to other high-throughput sequencing approaches (see below). Unfortunately, the DNA regions that can consistently be obtained by genome skimming do not always vary enough between species to clarify their family tree or to be used as a DNA barcode (Hollingsworth et al. 2009). In such cases, we need to sequence additional DNA regions.

Whole genome sequencing: One way to sequence more DNA regions is to perform “whole genome sequencing,” which also consists in randomly sequencing fragments of DNA, but with a higher sequencing effort so that all or most of the nuclear and chloroplast genome



4. Main high-throughput sequencing approaches used for DNA barcoding.

is sequenced (Fig. 4). This approach is ideal because it provides a complete representation of the genome of an individual, which can allow many types of studies beyond phylogenetics and DNA barcoding. For instance, one can look for the genes responsible for hardiness or drought tolerance and use this information to breed new varieties. However, whole genome sequencing is still very costly (ca. \$1,000–\$10,000) in plants because they can have large genomes [up to 50 times the size of a human genome! (Pellicer et al. 2018)].

Target sequence capture: In general, researchers interested in phylogenetics and/or DNA barcoding do not have the means nor the need to perform whole genome sequencing. They therefore apply methods to sequence only the DNA regions that they are interested in, at lower cost (ca. \$15–\$60 per sample). A popular approach in plant phylogenomics is “target sequence capture,” a method that fishes out a specific set of pre-determined DNA regions (Fig. 4). A set of user-designed “baits” capture the target DNA regions by binding to them. These baits and the DNA attached to them are then chemically bound to steel beads, and a magnet is used to retain them while unwanted

“off-target” DNA that did not attach to the baits is washed away.

This way, dozens to hundreds of regions can be sequenced, with a larger choice of regions than when using genome skimming, and at a lower cost than when using whole genome sequencing. Sometimes the off-target DNA is not completely washed-away, which results in the capture of additional regions, typically these present in multiple copies (such as chloroplast genes and ITS) because they are more likely to be captured by chance (Fig. 4). This can be a handy way to keep sequencing the standard barcodes together with the additional DNA regions targeted by the baits.

Towards a complete palm family tree using palm phylogenomics

The Palms Phylogenomics Working Group: Palm phylogenetics (the resolution of the palm family tree) has been an active area of investigation since the early 1990s [see (Dransfield et al., 2008, Baker & Dransfield, 2016) for a historical overview] but a complete species-level phylogeny of the palm family that could also serve as a reference for DNA barcoding has long been out of reach. Four years ago, around half of all palm species had

never been sequenced, and even when combining all the DNA and morphological information available, many parts of the palm family tree remained unresolved (Faurby et al. 2016). This is partly due to the size of the palm family, which with its >2500 species ranks among the 30 largest vascular plant families (WCVF 2019). Moreover, many palm species grow in inaccessible tropical locations, making the collection of “fresh” DNA difficult and expensive. Finally, the DNA regions traditionally used to resolve plant relationships evolve slowly in palms (Barrett et al. 2016), which limits their utility to solve the palm phylogeny and creates the need to study additional DNA regions.

This situation has recently changed due to the development of high-throughput DNA sequencing methods, which, contrary to traditional methods, allow one to sequence many DNA regions at a low cost (Fig. 4), from the intact DNA of fresh plant material as well as from the degraded material of herbarium specimens (Brewer et al. 2019). These new possibilities led palm scientists from all around the world to decide to join efforts to build a comprehensively sampled palm family tree by 2020. The “Palms Phylogenomics Working Group” (PPWG) was born around this idea in 2015, during the third World Palm Symposium in Montenegro, Quindío, Colombia.

The PPWG's approach and progress so far: To be successful, the PPWG had to decide on a standardized DNA sequencing method, so the data produced by all participants could be combined. The chosen method was target sequence capture (Fig. 4), using baits that had been developed specifically to target 176 regions of the palm nuclear genome (Heyduk et al. 2016). More recently, this set of target regions has been extended (Loiseau et al. 2019), so parts of the palm phylogeny will be backed by up to 971 regions of the nuclear genome. Because target sequence capture can accommodate degraded DNA, choosing this technique allowed us to make the most of worldwide herbarium collections. However, good quality DNA remains easier and cheaper to work with, and yields better data than degraded DNA, so field work (including trips funded by the International Palm Society) remained instrumental to our success.

So far, target capture data have been generated for more than half of the palm species, across all subfamilies. Ongoing work is dedicated to closing the remaining gaps, and we expect that

data will be generated for more than 80% of all palm species by the end of 2020. The remaining <20% consist mainly of unclear species names and/or very rare species for which collections were too precious to be sampled or too degraded to yield DNA of sufficient quality. Within the next 2 or 3 years, a complete species-level phylogeny of the family based on hundreds of nuclear DNA regions should therefore be freely available for fundamental and applied palm research.

Using the palm family tree to develop palm DNA barcoding: Linking palm fundamental research and conservation: By knowing the relationships between palm species, we will be able to propose robust hypotheses of how and when palms diversified and spread around the world, how palm diversity responds to different climates, and how the diversity of palm uses relates to their genetic, morphological and chemical diversity. The large amounts of genetic information generated from authoritatively named samples will be made available to other scientists, who will contribute to progress in palm research and conservation. In addition, by developing a well-curated reference library of hundreds of DNA regions, each a potential DNA barcode, for at least one individual per palm species, the PPWG is making an essential first step towards the development of palm DNA barcoding.

On the utility of palm DNA barcoding: Despite the widespread use of palms, we are aware of only few studies that have looked at designing and/or using DNA barcodes to identify palms to the species level. The first study focused on tribe Caryoteae and showed that a combination of three out of the four standard barcode regions tested was able to identify 92% of the species (Jeanson et al. 2011). Further studies attempted to distinguish between 15 Chinese *Calamus* species (Yang et al. 2012) or between 5 Indian *Daemonorops* species (Umapathy et al. 2015) using standard DNA barcodes. In another study, researchers used standard DNA barcodes to control that herbal dietary supplements sold in the USA as containing saw palmetto (*Serenoa repens*) did indeed contain this palm (Little & Jeanson 2013). More recently, (de Oliveira et al. 2019) showed that standard barcodes could also be used to identify the species (and therefore the cultivated or wild origin) of fresh and canned palm hearts despite the degraded nature of their DNA.

These studies yielded encouraging results, but additional work is required to generalize and strengthen the protocols so that they can be applied to real-life challenges such as robust quality controls. With the development and decrease in cost of high-throughput sequencing, palm DNA barcoding could find applications in the following fields:

1. Some important wild-sourced palm products such as rattan canes or palm hearts are traded by major industries that have the need and the means to enforce sustainable sourcing of their materials.
2. Cost-effective DNA barcoding in the field could help conservationists to complete species inventories and census without the need for on-site palm experts, or when morphological features are unavailable or unhelpful to distinguish palm species (which is often the case).
3. Palm DNA barcoding could shed light on some long-standing taxonomic problems, foster the discovery of new palm species and facilitate palm identification by researchers and horticulturists.

Palm scientists are therefore now looking into developing palm DNA barcoding based on the data generated by the PPWG. For example, one such project led by the Royal Botanic Gardens, Kew is applying target sequence capture to identify rattan species that are being utilized in the rattan furniture industry, to improve the sustainability of the rattan supply chain. Other projects at Kew aim at testing different methods, starting with the genus *Pinanga* as a case study.

Using *Pinanga* as a case study to develop palm DNA barcoding

Pinanga, a genus in need of systematic attention: The genus *Pinanga* belongs to tribe Areceae and currently comprises 142 accepted species occurring in South-East Asia. They tend to have local distributions, with levels of endemism close to 100% in the genus' centers of diversity, namely Borneo (38 species), the Philippines (25 spp) and Sumatra (22 spp). *Pinanga* species are diverse in shape, from dwarf understorey palms to sub-canopy trees, including stemless, single-stemmed and clustering species (Figures 5A & 6). Leaves are extraordinarily variable, with entire or divided blades, and this variability even occurs within some species in the adult state (Fig. 5A). Fruits are of various colours and sizes (Fig. 5B). They also have the most diverse pollen structure

and genome size in the palm family. This raises questions regarding the forces driving the evolution of different species, and about the possible use that humans could make of such diversity.

Pinanga species are already used for various purposes, such as handicrafts, food, ornament, timber, medicine or stimulants (Haynes & McLaughlin 2000, Dransfield et al. 2008), but a systematic ethnobotanical account of the genus is missing. Due to their small distribution ranges in areas where rainforests are continuously reduced by land-use change, many *Pinanga* species are likely threatened, but the conservation status of only five species has been formally assessed (IUCN, 2020), calling for urgent attention.

Pinanga was first described by Blume in 1839 (Rumphia 2: 76, 1839). Fifty years later more than 30 species of *Pinanga* were already described, many of them by Beccari, who wrote the only existing monograph of the genus in 1886. Since then, *Pinanga* has been the focus of multiple local taxonomic treatments, notably for Java, Bali (Witono et al. 2002), Sarawak (Dransfield 1991), Peninsular Malaysia (Lim et al. 1998), the Philippines (Fernando 1994), Thailand (Barfod & Dransfield 2013) and Vietnam (Henderson & Dung 2019). However, many taxonomic uncertainties remain, there is no recent monograph of the genus and determination keys are rare and only valid in some geographic areas (Dransfield 1984). This lack of a general taxonomic treatment for the genus slows down efforts to investigate, sustainably use and protect *Pinanga* species.

Towards and beyond a complete species-level phylogeny of Pinanga: The taxonomic difficulties in *Pinanga* could be partly overcome by comparing morphological features with DNA data. Phylogenetic studies of the genus have, however, been rare, with only one phylogeny published so far, comprising 52 species, and based solely on the ITS DNA region (Witono & Kondo 2007). In addition to illuminating taxonomic treatments, a *Pinanga* phylogeny would help us understand how the genus spread and diversified in SE Asia, and how different leaf shapes or genome sizes evolve in palms. Finally, the data generated to infer a full phylogeny of the genus could allow us to design DNA barcodes that would help the taxonomy and monitoring of *Pinanga* species. In return, *Pinanga* is a good case study to design palm barcodes, because regions that



5. *Pinanga* in Borneo. A. Vegetative diversity. B. Fruit diversity. C. Sarawak Forest Corporation employees admiring *P. rupestris* in Bako National Park. All pictures from S. Bellot, except for *P. aristata*, taken by E. Usher.

work on such a taxonomically difficult genus have good chances to work across the palm family.

To infer the phylogeny of *Pinanga* using DNA target sequence capture, we extracted DNA from many herbarium specimens. In addition, S. Bellot went to collect fresh material in Sarawak (Malaysia), with the help of the International Palm Society and of local collaborators (Fig. 5C). This field work in Bako and Kubah National Parks as well as sampling the Semenggoh Botanical Garden near Kuching were instrumental in allowing us to sample almost all *Pinanga* species, develop our understanding of *Pinanga*'s habitat, and make local contacts. Thanks to this trip, high-throughput sequencing data could be generated for most Bornean *Pinanga* species. This provided an ideal setting to compare the performance of different DNA barcodes on a genus where morphological identification remains difficult. We quickly summarize our first findings below.

Traditional and new DNA barcodes seem to perform well in *Pinanga*

Preliminary results: To start building a barcode reference library of Bornean *Pinanga* species, we obtained target capture data for 30 out of the 37 *Pinanga* species occurring in Borneo. We also generated genome skimming data for 17 of these species to compare results from both sequencing approaches. We then used computer programs (Johnson et al. 2016) to retrieve the three standard barcode regions *matK*, *rbcL* and ITS from both types of data for each species. These three regions, which are in multiple copies in the plant genome, were expected to be recovered by the genome skimming approach (Fig. 4). They were not specifically targeted by the target capture approach, but we wanted to see if they would be recovered as a "by-catch". In addition, we computed k-mer profiles (with $k=31$ nucleotides) for all datasets using the program skmer (Sarmashghi et al. 2019) (Fig. 3B).

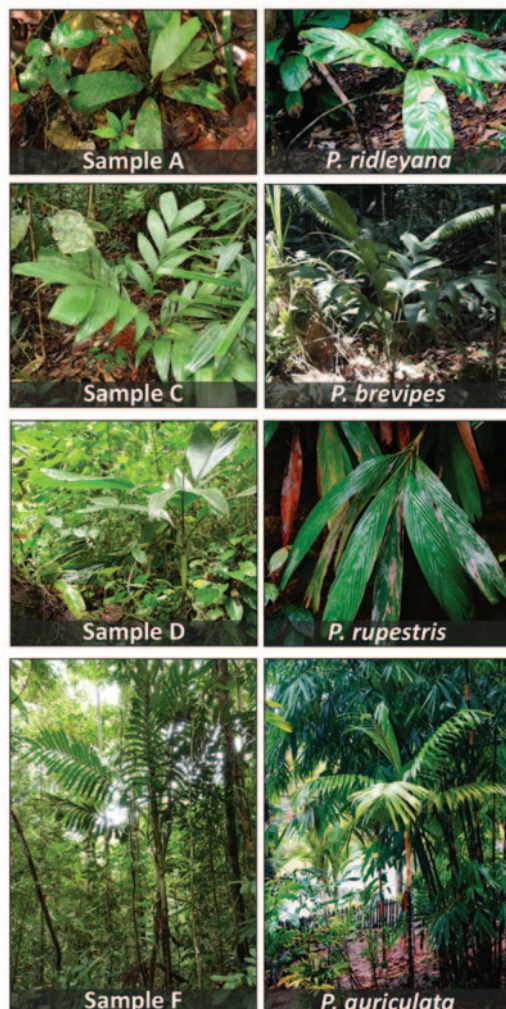
Among the standard barcodes, *matK* and *rbcL* could only be retrieved from genome skimming data, and only for five and six species respectively. We had more success with ITS, which could be recovered from 25 species when considering both genome skimming and target capture data. ITS yielded higher genetic distances between species than *matK* and *rbcL*. Genetic distances estimated from comparison of k-mer profiles [following (Sarmashghi et al. 2019)] were even higher, regardless if the k-mer profiles were computed on target capture or genome skimming data (detailed results available on demand). We therefore concluded that, among the barcodes tested, the most promising to distinguish between Bornean *Pinanga* species would be ITS and k-mer profiles. As a result, we compiled a preliminary barcode reference library with these barcodes, containing the k-mer profiles of 30 species and the ITS region of 25 of them.

We performed a preliminary test of these barcodes by comparing the ITS sequence and the k-mer profiles of seven unidentified *Pinanga* samples to our barcode reference library. Both types of barcodes yielded the same identifications for each unknown sample (Table on Fig. 6). For four of these samples (A, C, D and F; Fig. 6), we had pictures of the collected sample that could be compared with pictures of the reference species to which they best matched. Three of these comparisons supported our barcoding identification, whereas in one of them (sample D vs *Pinanga rupestris*) the pictures did not match (Fig. 6). We found out afterwards that this sample was most likely *Pinanga albescens*. This species is one of the species missing from our reference library, which explains the wrong result obtained and illustrates the importance of having a complete reference.

Next steps for *Pinanga* barcoding: Our small study on *Pinanga* shows that both target capture and genome skimming data can be used to recover standard barcodes or to design new ones, but that modifications of our ongoing target capture protocol will be needed if the goal is to retrieve *matK* or *rbcL* consistently. The robustness of the performance of k-mer profiling will need additional testing, for instance by comparing the results obtained with different k-mer lengths or different sequencing efforts.

Both ITS and k-mer profiles perform well in distinguishing species, but these results will require confirmation by testing more samples after completing our barcode reference library

Sample to identify	Best matching species from the reference	
	ITS	k-mer profiles
A	<i>P. ridleyana</i>	<i>P. ridleyana</i>
B	<i>P. ligulata</i>	<i>P. ligulata</i>
C	<i>P. brevipes</i>	<i>P. brevipes</i>
D	<i>P. rupestris</i>	<i>P. rupestris</i>
E	<i>P. auriculata</i> , F and G	<i>P. auriculata</i> , F and G
F	G, then <i>P. auriculata</i>	<i>P. auriculata</i>
G	F, then <i>P. auriculata</i>	F and <i>P. auriculata</i>



6. *Pinanga* barcoding results. Pictures of samples A, C, D and F are from P. Petoe, other pictures are from S. Bellot.

with the seven missing species. Besides ensuring correct species identification, completing our reference library could allow to discover new species, if the DNA of some samples does not match the DNA of any known species. A complete barcoding study of *Pinanga* would benefit from being undertaken together with a much-needed monograph of the genus, and it would, in return, inform the latter. We hope that these preliminary results will encourage further research in this direction.

Conclusion

Advances in DNA sequencing help us to understand better how palm diversity evolves and have the potential to support a more sustainable interaction between palms and people. Collaborative efforts will be necessary to make the most of the large datasets currently generated by the PPWG, while long-term funding will be required to ensure that future palm research and conservation can rely on accurate curation and preservation of data and samples.

As far as DNA barcoding is concerned, the next challenges include the sampling of multiple individuals per species and the choice of palm barcodes that are suitable for future applications. Our study suggests that since multiple DNA barcoding approaches can be successful on a group as difficult as *Pinanga*, they are likely to be successful across all palms. We therefore argue that the most urgent step now is not to design palm barcodes but to 1) spread the message that DNA barcoding is feasible in palms at various costs, and 2) assess who could benefit from palm DNA barcodes and what their requirements would be. The latter is more easily done when potential users understand the applications of DNA barcoding, so we hope that this article will reach many of them and help them to determine if palm DNA barcodes could fulfil their needs. We encourage anyone interested to contact us or other palm scientists, so that we can develop palm barcoding projects that will support a fair and sustainable development.

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Oranges or Kings? The Cryptic Etymology of Zippelius's *Orania regalis*

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The relevant literature suggests that the rare New Guinea palm *Orania regalis* Zipp. and the genus *Orania* Zipp. were named in honor of William I, Prince of Orange and King of Netherlands. This paper proposes an alternative etymology of the names *Orania* and *O. regalis*.

Orania regalis Zipp. is one of the more unusual palms of New Guinea because of its distinctive habit, floral and fruit morphologies, and rarity (Keim & Dransfield 2012) (Fig. 1). Although not having been recorded by botanists in the wild for over 130 years since it was first observed in 1828, its rediscovery in 1999 provided confirmation of distribution in the Province of West Papua, Indonesia, near Triton Bay, at Nabire and Wandammen Peninsula (Baker et al. 2000). It is also known from the Tamrau Mountains (Bird's Head Peninsula) and the Aru Islands (originally as *O. aruensis* Becc.) (Beccari 1877, Keim & Dransfield 2012).

The species was first collected in 1828 by Alexander Zippelius near the village of Lobo in the vicinity of Triton Bay during the Dutch

government's Natural History Commission expedition to south-west New Guinea (Zippelius 1829a, Macklot 1830). Zippelius first proposed the name *O. regalis* in correspondence to Carl Ludwig Blume, former director of Buitenzorg Gardens (now Bogor Botanic Gardens), who was then director of Leiden herbarium and publishing seminal works on the flora of the East Indies. In the letter, Zippelius provided a summary of his collections of the expedition, including his observations on palms. Translated from the Dutch, Zippelius (1829a) wrote:

On the other hand, there are many palm trees to look out for once you explore the interior and the steep rocky mountains. I discovered an 80 – 100 foot high *Areca*



1. Group of *Orania regalis* in native habitat, Tamrau Mountains, West Papua (Jan. 2013). Photo by W.J.Baker.



2 (left). Habit illustrations of *Orania regalis* (as *Arausiaca excelsa*), right, and *Drymophloeus oliviformis* (as *Ptychosperma appendiculata*), left, Rumphia 2, fig. 119. (1838). Source BHL. 3 (right). Diagnostic illustration of *Orania regalis* (as *Arausiaca excelsa*) in Rumphia 2: tab 122 (1838). This illustration has been designated as the type for *Orania regalis*. Source BHL.

along with a 2nd smaller species, a 2nd *Licuala*, of which I did not collect the smaller as it was not flowering, a *Sagus* from 100–120' high, two magnificent new genera, namely my *Orania regalis*, which is characterized by flowers with three stamens and bitter orange-shaped fruits, and my *Drymophloeus*, of which I found 2 species here and a 3rd on Amboina. It is most closely related to *Areca*, *Caryota* and *Iriarteia* Humb., the leaves have the wedge-like fan-shape of the *Caryota*, appearing gnawed at the edge.

Zippelius's letter was published in a number of journals, first in Dutch and also translated into German and French (Zippelius 1929b, 1829c), and the name *O. regalis* entered the domain of palm nomenclature. A list of palms collected by Zippelius during the expedition was published in an account of the expedition (Macklot 1830).

Publication

During investigation of the broader aspects of the origin of the names of palm genera and species, it became apparent that there was an ambiguity involving the currently accepted etymology of the names *Orania* and *O. regalis*. All taxonomic works examined invariably suggest that *O. regalis* was named to commemorate William I (Willem Frederik, Prince of Orange-Nassau; 24 August 1772–12 December 1843, the first King of the Netherlands and Grand Duke of Luxembourg, who reigned 1815–40) (e.g., Seemann 1870, Dransfield et al. 2008, Kiem & Dransfield 2012, Burckhardt 2016, Mari Mut 2020). However, upon examination of Zippelius's original use of the name *O. regalis*, this may not have been his intention. Zippelius made no mention of persons to be commemorated or any other explanation for the name apart from his original description.



4. Flowering and fruiting *Orania regalis* in Bogor Botanic Gardens (accession XII.141), a third generation individual planted ca. 1970 from the seeds of XII.E.21 (March 2020). Photo by D. Latifah.

As a point of clarification, the brevity of Zippelius's original description of *O. regalis* brings into question whether it meets the requirements for a validating description or diagnosis. Invoking a number of articles in the International Code of Nomenclature for algae, fungi and plants (see Turland et al. 2018: Art. 38.1–38.4), the inclusion of the specific characters of three stamens and orange-shaped fruits is evidently adequate in distinguishing the species, and therefore Zippelius's description provides valid publication of the name. However, this differs from the most recent revisionary work on *Orania* (Keim & Dransfield 2012) where it was proposed that valid publication of *O. regalis* was provided by Blume (1838) and that Zippelius's earlier use of the name rendered it as a *nomen nudum*. Considering that valid publication was achieved by Zippelius in 1829, as is presently accepted by the WCSP (2020) and also accepted here, the authorship would be *O. regalis* Zipp., and the genus name, by means of a single "*descriptio generico-specifica*" [a single description simultaneously validating the names of a genus and its single species – see Turland et al. 2018: Art. 38.5) as *Orania* Zipp.

Alexander Zippelius (1797–1828)

Alexander Zippelius (also Zippel) (born 1797, Würzburg, Germany; died 1828, Timor), was a German-born Dutch horticulturist and botanical collector whose lasting contribution to botany was his work undertaken in the East Indies (now Indonesia) between 1823 and 1828 (van Steenis-Kruseman 1950). Zippelius was appointed assistant curator at 's Lands Plantentuin te Buitenzorg (now Bogor Botanical Gardens) after Blume's return to Leiden in 1826, and through that connection was engaged as a naturalist/botanical collector on the Natural History Commission expedition to the south-west coast of New Guinea in the company of scientific leader, mineralogist Heinrich Christian Macklot, naturalist Salomon Müller, illustrator Pieter van Oort and taxidermist Gerrit van Raalten (Macklot 1829, Müller 1857, Glaubrecht 2002, Wonu Veys 2018).

The expedition started from Ambon 21 April 1828, and returned on 5 September 1828. One outcome of the expedition was the establishment of a Dutch colony, known as Fort Dubus near Triton Bay, but this was

5. Crown of *Orania regalis* showing the characteristic, congested, broom-like inflorescence, Bogor Botanic Gardens (accession XII.141) (March 2020). Photo by D. Latifah.



abandoned a few years later. Many of Zippelius's New Guinea botanical collections were made in the vicinity of Fort Dubus and the village of Lobo, as almost five weeks (ca. 27 June–31 August) were spent there whilst the Fort was established (Modera 1830a, 1830b, Glaubrecht 2002). During this time, Zippelius was able to explore the local area and climb to high elevation in the hinterland.

After returning to Ambon, the naturalists from the expedition, including Zippelius, travelled onto Timor in October 1828 to undertake searches for minerals and to collect natural history specimens (Modera 1830a, 1830b, Mörzer Bruyns 2018). In Kupang, Zippelius succumbed to “fever” (malaria?) and died on 28 December 1828, at the age of only 31 years (Glaubrecht 2002). He was lamented as a victim of the “murderous climate of New Guinea” and considered a “botanical martyr” (Anon. 1829, 1830a, 1830b). Zippelius kept extensive and meticulous notes on the plants he observed and collected, and for a botanical collector his Latin descriptions were of a very high quality. His notes eventually found their way into the hands of botanists in both the East Indies and Leiden (Mees 1994) where they were later used as the basis for numerous descriptions of new species, many of which bore the names that Zippelius had originally proposed (see Spanoghe 1841, Zollinger 1854, Mettenius 1856, Blume 1849–1856, Scheffer 1876, Beccari 1885). Most of Zippelius's botanical collections are held in the Naturalis Biodiversity Center (formerly the National Herbarium of the Netherlands), about 2900 collections, and his notes on the palms he observed and collected are in the herbarium archives [NB: Zippelius's original field notes for *O. regalis* have not been located]. Nothing is known of Zippelius's early life and education, and there are no known portraits of him. Zippelius is commemorated in about 100 plant names (IPNI 2020), including three palms, *Areca macrocalyx* var. *zippeliana* Becc. [= *Areca macrocalyx* Zipp. ex Blume], *Ceratolobus zippelii* Blume [= *Korthalsia zippelii* Blume] and *Drymophloeus zippelii* Hassk. [= *Caryota mitis* Lour.] (WCSP 2020).

The House of Orange

Blume (1838), in his work on the palms of the East Indies in his magnificent publication *Rumphia*, provided expanded descriptions of *Orania* and *O. regalis* and included two superb illustrations that clearly identified the species (Figs. 2 & 3). Blume noted that the fruit were



6. Spontaneous seedling of *Orania regalis*, Bogor Botanic Gardens (March 2020). Photo by D. Latifah.

drawn from specimens preserved in “spirit of wine”. These illustrations have been proposed as possible typifying elements in the absence of any surviving herbarium specimens collected by Zippelius (Baker et al. 2000, Keim & Dransfield 2012). Further to this, Blume suggested that the palm was named for the Prince of Orange, William I, and wrote that “... it is supposed that the late Zippelius named this beautiful palm in honor of William I, King of the Netherlands” [... *videtur nomen, quod divus Zippelius in honorem Guilielmi I, Nederlandiae Regem, Palmae huic speciosissimae indidit*]. The emphasis here is on “supposed.” With that one word, Blume admitted that he did not know with certainty the etymology of *Orania*.

A further complication to this etymological intrigue involves the name *Arausiaca excelsa* Blume, and the genus *Arausiaca* Blume, which were nomenclaturally illegitimate names proposed by Blume (1838) to ostensibly replace *O. regalis* and *Orania*. Blume, in the same publication corrected this and noted that the name of the taxon in question was indeed *O. regalis* and that the proposed replacement name (i.e. *Arausiaca excelsa*) was a “printing error” in that the plates had been prepared earlier with his new name included in the



7 (top). Ripening fruit of *Orania regalis*, accession XII.E.141, ex Bogor Botanic Gardens (March 2020): scale in cm. Photo by D. Latifah. 8 (bottom). Ripening seeds of *Orania regalis* taken from accession XII.E.141, ex Bogor Botanic Gardens (March 2020): scale in cm. Photo by D. Latifah.

caption and references to these names were therefore maintained in his text. Nevertheless, Blume elaborated on the name, and wrote that *Arausiaca* was intended to commemorate the House of Orange, founded by Willem Prince of Orange (1533–1584), and based in the southern French city of Orange, the Roman name of which was Arausia. William I, also a Prince of Orange and later the first King of the Netherlands, was in power during Blume's time and was a reluctant supporter of scientific work in the East Indies, of which Blume was a possible beneficiary (Weber 2018).

In addition to this complication, illustrations in Rumphia of *Arenga porphyrocarpa* (Blume ex

Mart.) H.E. Moore were incorrectly captioned as *O. regalis*, although the caption explanations used the name *Wallichia oranii*, and included a brief note to say that it was also named to honour the House of Orange (Koch 1872). It appears that Blume was determined to dedicate the names of palms (and other plants) to Netherlands royalty.

From this, the etymology of *O. regalis* became, over time, inextricably associated with Blume's latter work, a situation that has persisted into the present. Perhaps Blume's intention was to win favor with the ruling royals who were his benefactors. During his time at Buitenzorg and later at Leiden, Blume was in a continual

struggle for adequate financing and other support for his botanical endeavors (Weber 2018). In recognition of the support given to Blume by the royal family of the Netherlands, he dedicated a number of his publications to them. For example, in the preface to *Flora Javae*, Blume (1828) wrote that if it were not for the generosity and foresight of William I, his work on the East Indian flora would not have been possible, whilst in the first volume of *Rumphia*, Blume (1836) dedicated it to the Queen Consort of the Netherlands, Friedricke Luise Wilhelmine (wife of William I).

Oranges or Kings?

With Zippelius's early death, his work on the flora of the East Indies was not completed. It is therefore not possible to be definitive about his intentions with regards to the names he applied to the new species he recognized. A list of the names that he created, preserved in his unpublished manuscripts and labels on herbarium specimens, numbers to over 400 entries (IPNI 2020), many of which were published as synonyms or basionyms by subsequent taxonomists. From examination of the names it is apparent that he rarely named taxa for persons, but rather for distinguishing morphological characteristics. Of the 400 names, only eight persons were commemorated, including botanists (Robert Brown, Franz Gerhard Eschweiler, David Heinrich Hoppe, David Nelson and Philipp Franz von Siebold,) and his fellow biologists in the East Indies (Heinrich Boie, Heinrich Christian Macklot and Salomon Müller).

It is clear that Blume ascribed the dedication of *Orania* to William, Prince of Orange but it is not clear that Zippelius had the same intention. Zippelius, in describing the genus, wrote that the palm was "magnificent" and with "orange-shaped fruits." We believe that the resemblance to oranges could be the meaning behind the name *Orania*. Nowhere have we found evidence of Zippelius's intention to dedicate the name *Orania* to Dutch royalty. Etymological accuracy is sometimes difficult to unravel in older palm names, and this paper provides an alternative to the commonly accepted etymology of *Orania* and *O. regalis*.

Zippelius's living legacy at Bogor

Although no accession records survive for the earliest plantings of *O. regalis* at Bogor, it is likely that Zippelius collected the fruit and/or seedlings that were used to establish the palm



9. Dissected ripening fruit of *Orania regalis* taken from accession XII.E.141, ex Bogor Botanic Gardens (March 2020): scale in cm. The central hollow shows that it is not fully ripened. Photo by D. Latifah.

there. There are at least four generations of *O. regalis* known to have been, or are being grown, at Bogor. The oldest extant individual, XII.E.21, appears to be senescent and has not flowered or fruited since 1965. It, along with an individual identified as XII.E.21a that died in 2004, is recorded as the progeny of either two individuals identified as II.F.5 or II.F.5a, the former dying in 1970 and the latter in 1995, and which were possibly among the first generation. XII.E.21 was planted in 1906 and therefore can be aged at 114 years as of March 2020. It has a stunted crown although the leaves remain green and are being produced on a regular basis. Two other individuals from the 1906 plantings, X.D.35 and X.D.35a, both died in 1997, and progeny from these, V.H.63 and V.H.63a, were planted in 1959 and both died in 2010. Located nearby to XII.E.21 is the third-generation individual, XII.141, the only one that is presently flowering and fruiting; it was planted in ca. 1970 (Figs. 4 & 5). Below this are at least four seedlings and these are being nurtured for replacement of the aging specimens (Fig. 6). The fruit collected from XII.141 mostly conform to the expected morphology for the species (Figs. 7–9). The local name of *Kiboera*, derived from the Sundaican language, was given for *O. regalis* that were cultivated at Bogor (Hasskarl 1844), although use of this name has not persisted.

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The Sabal Palm Sanctuary, Brownsville, Texas

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Texas, despite its large area, has only three native palms, all in the genus *Sabal*. All three taxa can be found in protected areas. This article spotlights *S. mexicana* and the Sabal Palm Sanctuary

The palmetto palm (*S. minor*) is widespread in eastern and southern Texas and gives its name to Palmetto State Park near Gonzales, east of San Antonio (Fig. 1). *Sabal minor* is the most common native palm in the USA, occurring in nine other states and extends in distribution into northeastern Mexico. In this paper, conservation status as defined by NatureServe and The Nature Conservancy's Natural Heritage Program is referenced. NatureServe's rankings are analogous to IUCN categories but also provide information about status at the US state level (natureserve.org/conservation-tools/conservation-status-assessment). A global conservation status of G5 (Secure) has been assigned to this palm (Master et al. 2012).

The second is the natural hybrid Brazoria palm (*S. × brazoriensis*) an endemic natural hybrid of *S. minor* × *S. palmetto*; the latter species is not now found wild in Texas, but likely was present in the past. The hybrid has a very limited geographic range in the Brazos River Valley, west of Houston, and a small population of fewer than 300 palms (Fig. 2). The Brazoria palm is protected in the Palm Unit of San Bernard National Wildlife Refuge (Goldman et al. 2011). Natural hybrids are not assigned a conservation status; however, if the

Brazoria palm were a described species, it would be considered to have a status of S2 (Imperiled).

The third native palm, *S. mexicana*, occurs nowhere else in the USA but with a global distribution extending into Mexico and Central America. Its conservation status globally is G5 (Secure) but within the USA is N1 (Critically Imperiled). The Sabal Palm Sanctuary in Brownsville, Texas serves as an exemplary conserved area protecting the habitat of *S. mexicana* and numerous other plant and animal species.

Prior to significant human settlement, the natural vegetation of the Lower Rio Grande Valley consisted of what is now classified as Tamaulipan Riparian Scrub Forest (USNVC 2020). This plant group occurs in mesic environments, including riparian and floodplain areas, largely in the northeastern Mexican state of Tamaulipas as well in a narrow strip of land along the Rio Grande extending across the international border into southern Texas. The plant group consists of low woodlands, trees and shrublands. Native plants are floristically diverse; keystone tree species are *S. mexicana*, *Ebenopsis ebano* (Texas ebony) and *Ulmus crassifolia* (Texas cedar elm).



1 (top). *Sabal palmetto*, Palmetto State Park, Gonzales TX. Photo by Texas Parks & Wildlife. 2 (bottom). *Sabal × brazoriensis*, San Bernard National Wildlife Refuge, Brazoria TX. Photo by John Williams, Flickr.

Early Spanish explorers encountering the forested banks of the Lower Rio Grande reportedly called it *Rio de las Palmas* because of the prominence of *S. mexicana* (Jahrsdoefer & Leslie 1988). In the mid-19th century, Mexican sabal palms were described as occurring along both the Mexican and American sides, as much as 80 miles inland from the river. The rich alluvial soils along with a sunny, semi-tropical climate led to extensive land clearing for agriculture (sugarcane, cotton, fruits and vegetables), and by 1937, only a few native palm stands

remained on the American side of the river. A mapping of the distribution of *S. mexicana* in 1996 revealed that several isolated small populations existed in (downstream order) Starr, Hidalgo and Cameron counties (Everitt et al. 1996). Two of these remnant stands are within officially designated multiuse protected areas. One is inland, the 2,000-acre Santa Ana National Wildlife Refuge created in 1943 in Hidalgo County, south of the City of Alamo, on the banks of the Rio Grande. This site may represent the upstream limit of *S. mexicana* described in the mid-19th century.



3 (top). Drone aerial view, looking southeast, Sabal Palm Sanctuary. Old growth forest with prominent *Sabal mexicana* palms is in center right. Rio Grande visible center near the top. Cleared agricultural land upper left is in Mexico. 4 (bottom). Drone aerial view of Rabb Plantation House, 1892. Photos by Gorgas Science Foundation.

The second remnant stand is the private Sabal Palm Sanctuary located six straight-line miles southeast of Brownsville, also on the Rio Grande. It was established in 1971 by the National Audubon Society through the purchase of 170 acres of the former Rabb Plantation. Subsequent adjacent land acquisitions of former agricultural lands have expanded the Sanctuary to cover 557 acres. Since 2010, the Sanctuary has been operated under a long-term lease agreement by the Gorgas Science Foundation, Brownsville. Both

of these areas protecting sabal palms were created primarily to conserve the habitat of Texas Gulf Coast resident and migratory bird stopover sites.

The Sabal Palm Sanctuary is a level tract of delta land located on the water at the south most bend of the Rio Grande, about 18 straight-line miles from the river's mouth. A 32-acre tract of old growth forest within the Sanctuary is known locally as the *boscaje de la palma* (palm forest) (Fig. 3); it was conserved



5. Sabal Palm Sanctuary. Entrance to old growth forest. Photo by Wikimedia Commons.

during an earlier era of the landholding. In addition to the sabal palm forest, the Sanctuary includes former farmland reverting to nature and a lovely restored Queen Anne style plantation house completed in 1892 (Fig. 4), now functioning as the Sanctuary visitor center and Gorgas Science Foundation office. The Sanctuary acreage lies just south of the Mexico–US barrier but is accessible by an open street. An overlook structure on the river, about one-fourth of a mile from the Rabb Plantation House, provides a view across to Mexico, but no sabal palms are visible there. Steamboats called at the Rabb Plantation back when the meandering river was much closer to the house than it is now (Ralph 2013).

A unique feature of the Sanctuary is that it includes many native plants and animals at the northern limit of their Mexican range.

Nature enthusiasts can ramble through the Sanctuary along excellent trails and walkway systems among the sabal palms, which occur singly or in groupings with a good representation of age classes, an indication of natural regeneration and sustainability (Figs. 5 & 6). It is possible to observe wildlife especially birds at feeding stations and from enclosures, such as one on a now oxbow lake, which was the river course when the plantation was established. The Sanctuary's avifauna is exceptional with hundreds of migratory and resident birds; annual sightings record 339 bird species (ebird.org). Emblematic are the flocks of garrulous green jays with their brilliant green, yellow and blue plumage (Fig. 7). For the palm enthusiast, nature lover, birder and history buff, the Sabal Palm Sanctuary exceeds expectations in every way.



6. *Sabal mexicana* palms within the Sanctuary. Photo by Jane MacKnight.

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7. Green jays (*Cyanocorax luxuosus*), colorful resident birds of the Sanctuary. Photo by Jane MacKnight.

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Pseudovivipary in *Chuniophoenix hainanensis*

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1. *Chuniophoenix
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Singapore Botanic
Garden.

This report documents pseudovivipary, the formation of plantlets in the inflorescence, in *Chuniophoenix hainanensis*.



2. The plantlets formed on the infructescence as the fruit began to fall.



3. An individual plantlet on *Chuniophoenix hainanensis*.

Social media is facilitating the discovery and documentation of the biological world in some unexpected ways. Readers of this journal will remember the thrilling discovery of *Tahina spectabilis* on PalmTalk (Dransfield et al. 2008), but a Brazilian sundew (*Drosera magnifica*), a Javanese waxvine (*Hoya amicabilis*) and a Turkish snowdrop (*Galanthus bursanus*) also owe their discoveries to photos posted online.

Videos of heretofore unknown animal behaviors are being posted on social media, and users of iNaturalist are documenting the natural world to an extent undreamt of a decade ago. The senior author has observed *Chuniophoenix hainanensis* in Singapore Botanic Gardens over the last two years and photographed it in February, 2020 (Fig. 1). He posted photos of plantlets forming on the inflor-

escence (Fig. 2) on Instagram, where they were seen by the junior author, who solicited more information. Additional photographs and data were obtained, and the findings are presented here.

The production of plantlets in the inflorescence is termed pseudovivipary, in contrast to true vivipary, which is the germination of seeds while fruits are still attached to the mother plant (Elmqvist & Cox 1996). Pseudovivipary is not uncommon in grasses and other monocots, including *Phalaenopsis* orchids and onion relatives (*Allium* spp.). It occurs infrequently in palms. Edelman and Richards (2019) recently summarized the occurrence of pseudovivipary in several species of *Calamus* and *Salacca*, as well as in *Hyospathe elegans* (Skov & Balslev 1989), *Socratea salazarii* (Pintaud & Millan 2004) and *Wendlandiella gracilis* (SZ, pers. obs.). This case of pseudovivipary in *Chuniophoenix* was briefly noted by Benezet (2020), who also photographed the same palm in Singapore Botanic Gardens.

This individual of *Chuniophoenix hainanensis* was observed in the final stages of fruiting. The infructescence bore scattered fruits, which were ripening from orange to deep red. At the bases of the rachillae, small plantlets were forming (Fig. 2). None of these plantlets had roots at the time of observation (Fig. 3). One of us (Z) detached some unrooted plantlets and tried establishing them in moist sphagnum moss, but they perished before they could produce roots. We believe that roots will form on the plantlets if the infructescence contacts the soil.

This report of pseudovivipary in *Chuniophoenix hainanensis* is from a single, cultivated plant, so we cannot assess how widespread the phenomenon might be in wild populations. A synopsis of the genus in cultivation made no mention of pseudovivipary (Zona 1998) nor did recent field guides (Henderson 2009, Henderson & Dung 2019). Palms that do not

ordinarily produce plantlets in the inflorescence have occasionally been observed doing so, often as single, aberrant individuals (Davis et al. 1981). It is doubtful that these rare occasions of pseudovivipary constitute a successful evolutionary strategy of asexual (clonal) reproduction (Elmqvist & Cox 1996). Even if this plant of *C. hainanensis* proves to be a one-off occurrence, it is nevertheless of great interest to the study of morphogenesis and the genetic control of vegetative meristems.

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New Localities of *Dypsis leptocheilos* in the Western Region of Madagascar

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New localities of *Dypsis leptocheilos* (Red Neck Palm), a poorly known palm species have recently been found in the western part of Madagascar. These new localities provide more data to suggest an update of the IUCN conservation status of the species.

Madagascar is one of the most important biodiversity hotspots in the world and it has a high number of endemic species (Myers et al. 2000). It is home to around of 10% of palms species in the world and more than 50% of genera existing in the island are endemic. The Palms of Madagascar published by Dransfield and Beentje (1995) and a Field guide to the palms of Madagascar by Dransfield et al. (2006) show that most of the species of palms are distributed to the east and 90% of Madagascar palms are restricted to humid forests (Rakotoarinivo et al. 2014). With the last four newly described species (Eiserhardt et al. 2018), 209 native palms species are now recorded in Madagascar (Govaerts et al. 2020).

The western parts of Madagascar carry a numerically much smaller palm flora with

only a few species that can tolerate the strongly seasonal climate. Endemic species such as *Bismarckia nobilis* Hildebr. & H.Wendl. and *Dypsis madagascariensis* (Becc.) Beentje & J. Dransf., and the non-endemic species, *Phoenix reclinata* Jacq. and *Hyphaene coriacea* Gaertn., are widespread and abundant throughout the West (Dransfield et al. 2008). In 2016, KMCC team observed during a field trip 11 species (Table 1) and the exploitation of certain of these palms (Fig. 1; Table 1). They are threatened by overexploitation, repeated fires and habitat loss due to agricultural expansion.

Dypsis leptocheilos distribution

According to the field guide, *D. leptocheilos* was described from a palm grown in a garden in Tahiti (Dransfield & Beentje 1995); this case is similar to that of *Dypsis madagascariensis*,



1. A Sakalava house thatched with the leaves of *Hyphaene coriacea* and with walls made from *Raphia farinifera* petioles.

which was described from cultivated palms in the botanical gardens at Calcutta and Buitenzorg. *Dypsis leptocheilios* was also observed in Ambilobe in 1903 (Perrier de la Bâthie 15802; P), and in Maevatanana in 2007 (Rakotoarinivo 363; K, TAN). *Dypsis leptocheilios* has not been seen in the Ambilobe area since 1903.

In 2009, during a field inventory led by Steve Goodman in Beanka, the team discovered and collected a species of *Dypsis* (Letsara 925; TAN). The species is similar to *Dypsis lastelliana*, which is distributed in the rainforest of northern Madagascar, by virtue of the red-brown hairs on the leaf sheath and inflorescences branched to three orders (Fig.

2). After critical identification using the field guide of the palms of Madagascar and discussion with palm specialist Mijoro Rakotoarinivo, we identified the specimen as *Dypsis leptocheilios* (Fig. 3).

Four recent inventory fieldtrips have been conducted by Kew Madagascar Conservation Centre (KMCC) team, and these allowed the location of *D. leptocheilios* in the field:

(1) In January 2017, during the KMCC and the Parc Botanique et Zoologique de Tsimbazaza (PBZT) expedition, in Andafiha, Melaky region (17°15'15"S, 44°37'48"E, 230 m), two species of *Dypsis* attracted their attention; the first is *D. madagascariensis*, well known in the western part of Madagascar, and



2. *Dypsis lastelliana*, Analalava, Antsinanana region.



3. *Dypsis leptocheilos*, Andafiha, Melaky region.

Table 1: Palm species inventoried in Menabe and Melaka regions during 2016 trip (western region of Madagascar).

Species	Habitat	Localities and regions	IUCN Category	Uses
<i>Dypsis madagascariensis</i>	Deciduous forest, Gallery forest	All areas in Menabe and Melaky regions	LC	Floorboards, edible heart
<i>Dypsis oropedionis</i>	Gallery forest	Belalomanga in Menabe	EN	Unknown
<i>Dypsis baronii</i>	Submontane to montane forest	Belalomanga in Menabe	LC	Edible heart & fruit, ornamental
<i>Dypsis leptocheilos</i>	Remnant riverine forest	From Andafiha to Beanka in Melaky	CR	Unknown
<i>Raphia farinifera</i>	near villages at edges of water courses	All areas in Menabe and Melaky	LC	Fibers from young leaf for weaving, petiole for hut construction, edible heart & fruit
<i>Bismarckia nobilis</i>	Grasslands or woody grassland	Common in Menabe and Melaky	LC	Flattened trunk for construction, leaves for thatch & basketry, palm wine, pith for bitter sago
<i>Hyphaene coriacea</i>	Grassland or woody grassland	Common in Menabe and Melaka	LC	Handicrafts, thatch leaf fiber for basketry, hat, rope, edible heart, wine
<i>Borassus madagascariensis</i>	Grassland	Around Morondava in Menabe and Maroserana in Melaky	NE	Edible heart, pith starch, basket, fruit fermented for alcohol, edible shoots of germinating seedling, wine
<i>Phoenix reclinata</i>	Banks of streams & small rivers or marshes	Around Bekopaka in Melaka and Kirindy in Menabe	NE	Leaflets for baskets, edible fruit
<i>Ravenea robustior</i>	Humid forest in valleys	Belalomanga in Menabe	LC	Floorboards, house walls
<i>Ravenea madagascariensis</i>	Humid forest	Belalomanga in Menabe	LC	Stem wood for house walls & floorboards

the second is *D. leptocheilos* very rarely seen in the field. In this locality, the team found 34 adults of the second species in 1.7 ha areas. In Andafiha, the population of *D. leptocheilos* is threatened by wildfire and *hatsaka* or *tavy* (slash and burn agriculture). Around the Beanka protected area (reserve managed by Biodiversity Conservation Madagascar), a large population was observed with two sub-populations (pers. obs., 2017) consisting respectively of 36 adults in an area about 0.8 ha and of 25 adults in an area of approximately 1.5 ha. Everywhere, seedlings are numerous,

estimated to be two or three times more abundant than the adults. From our rapid inventory, we found that *Dypsis leptocheilos* grows mainly in association with *D. madagascariensis* (Arecaceae), *Breonadia silicina* (Rubiaceae), *Elaeis guineensis* (Arecaceae), *Ravenala madagascariensis* (Strelitziaceae), *Raphia farinifera* (Arecaceae), *Syzygium sakalavarum* (Myrtaceae), *Dioscorea antaly* (Dioscoreaceae) and *Albizia lebbeck* (Fabaceae)

(2) In February 2017, during the preparation of a visit of students of Royal Botanical



4. *Dypsis leptocheilos*: seedlings growing in the nursery of Parc Botanique et Zoologique de Tsimbazaza.

Gardens, Kew, the team took advantage to visit Maevatanana (Betsiboka region) where *Dypsis leptocheilos* was collected in 2007 (specimen: Rakotoarinivo 363; K, TAN). In this locality, along a small river, we have seen one adult plant and 35 seedlings. According to the local guides, the lack of adult plants is due to the collection of seeds because harvesters chop palm trees to collect them. About 17 km from the first locality, near the National Road 4, two adult plants were recorded.

(3) In March 2017, another inventory was done around Ikalamilotrakely (Betsiboka region) during a field trip to Bongolava (district of Port-Bergé). The team found two adult plants and 64 seedlings. According to local guides, hundreds of adult plants and thousands of seedlings are estimated to occur 20 km west of Ikalamilotrakely bridge, where people extract gold.

(4) In November 2017, during an expedition to Montagne des Français, the KMCC team observed 2 adult plants with 14 seedlings along a small river in Maromandia, Ambanja district,

Diana region. Seeds were collected on March 2019 by KMCC team and now in cultivation at PBZT (Fig. 4).

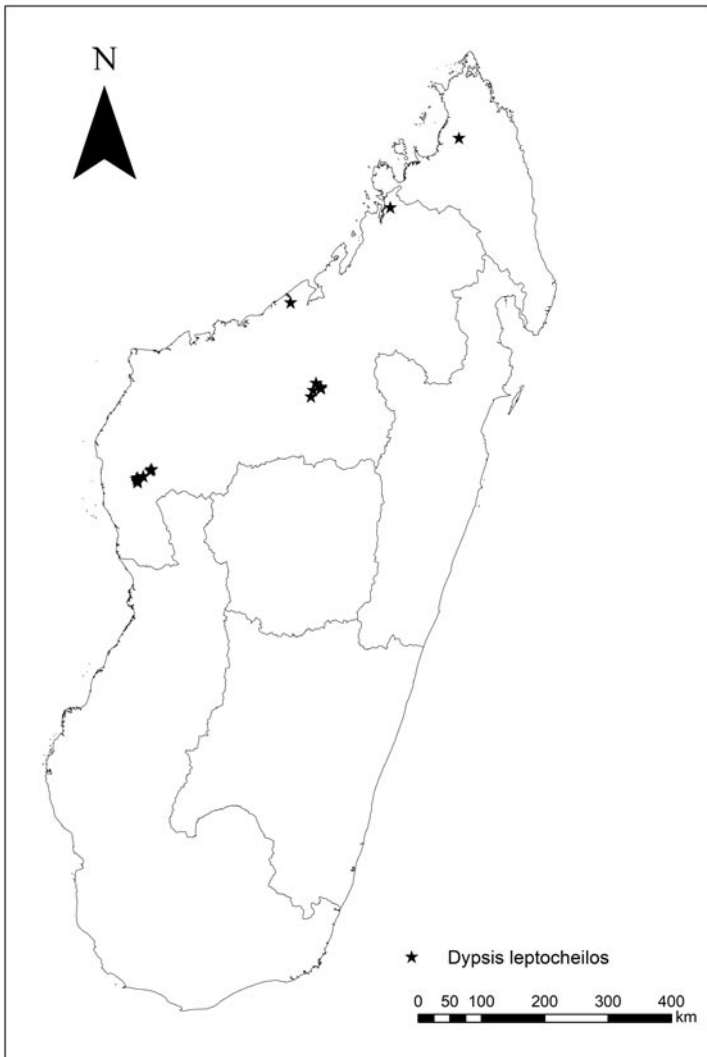
The regeneration rates in observed sites, Andafiha, Beanka, Maevatanana and Maromandia, were respectively obtained by the proportion of seedlings and mature individuals: $80/34 \times 100 = 235\%$, $142/61 \times 100 = 232\%$, $99/3 \times 100 = 3300\%$ and $14/2 \times 100 = 700\%$. The higher regeneration rate in Maevatanana does not signify an adequate rate of seedling survival because of the low number of adult plants. In this area, harvesters of seeds cut trees to facilitate collection. Outside of Beanka protected area, the survival of this species is affected by habitat loss. Based on these recent data, *Dypsis leptocheilos* is distributed in western and north-western Madagascar in Mahajanga and Antsiranana provinces (Fig. 5).

Update of *Dypsis leptocheilos* on IUCN Conservation status.

These new investigations and distributions could improve the IUCN conservation status of *Dypsis leptocheilos*. According to Rakotoarinivo and Dransfield (2012), *D. leptocheilos* is Critically Endangered (CR) under criteria B1ab(iii, v) + 2ab(iii, v); C2a (i, ii), considering the collection made in 2007 in Maevatanana. In the assessment, they mentioned that conservation action for this species is very urgent because of threats to the palm and suggested further exploration of other sites to find other sub-populations.

Based on data obtained over the last five years, we believe that the conservation status of *D. leptocheilos* needs to be reassessed. There are now ten subpopulations inventoried in Mahajanga and Antsiranana provinces. According to the Botanic Gardens Conservation International (BGCI 2020), living collections of the species are held in 27 botanic gardens in far-flung locations such as Tahiti, Singapore and Miami.

The extent of occurrence (EOO) and the area of occupancy (AOO) are calculated by using the Geospatial Conservation Assessment Tool (GeoCAT) with the standard 2×2 km grid cells (Bachman et al. 2011). Madagascar data observations are provided by the Global Biodiversity Information Facility website (<https://www.gbif.org/fr/>), which is largely fed by iNaturalist.org/Zavamaniry gasy from Kew observations and the catalogue of the plants of Madagascar (<http://legacy.tropicos.org/Project/Madagascar>).



5. Map showing distribution of *Dypsis leptocheilos*.

The value of AOO estimated by using Geocat with 17 data records is less than 500 km² (vs 60 km²), and the ten subpopulations are severely fragmented in seven threatened locations, distributed in two provinces (Antsiranana and Mahajanga). The observed subpopulations outside of the protected area are inferred to be declining in the area of occupancy, the extent of occurrence and the number of mature individuals. In Maevatanana, *Dypsis leptocheilos* trunks were cut for mature seeds, its habitat was destroyed by forest logging and deforestation to extend the surface for agriculture. In Andafiha, the edge the gallery forest is threatened by *tavy* or *hatsaka* (slash and burn agriculture). These threats may suggest that the number of mature individuals is therefore decreasing, and the

same situation may appear in other unexplored sites suggesting the criteria B2ab(ii,iii,v). In each subpopulation, the total number of mature individuals was estimated to be 34 in Andafiha, 61 in Beanka, 3 in Maevatanana and 2 in Maromandia, which is less than 250 under criterion C2a(i), and the observed total number of mature individuals is less than 1000 (vs 100), under criterion D. Therefore, we propose that *Dypsis leptocheilos* is assessed as Endangered B2ab(ii,iii,v); C2a(i); D.

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Foraging of *Licuala* *ferruginea* Fruits by Long-tailed Macaques (*Macaca* *fascicularis*) in Singapore

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Zoochory, i.e. animal-mediated seed dispersal, is the most common mode of dispersal of palm seeds (Dransfield 1981). Data on palm seed dispersal collected across a range of studies showed that the animals capable of dispersing palm seeds range across several animal classes from insects, fish, reptiles, birds, bats to other vertebrate mammals such as primates and palm civets (Zona & Henderson 1989, Corlett 1998, Corlett 2017).

While there is little evidence of obligate plant-animal mutualism in palm seed dispersal ecology, interacting mutualistic networks may still be important in maintaining the persistence of rare palm species in localized populations in rainforests, i.e. interacting

networks where a plant species may rely on various frugivores for seed dispersal, and the frugivores, in turn, depend on other plant species during periods of fruit scarcity (Bascompte & Jordano 2006). The documentation of animal frugivory in rare palm

populations therefore contributes useful information for their conservation.

There are three *Licuala* palms recorded from Singapore: *L. triphylla*, which is extinct, *L. spinosa*, which is vulnerable and found in mangroves, and *L. ferruginea* (Chong et al. 2009). *Licuala ferruginea* Becc. is the only *Licuala* palm that occurs in the understory of rainforest in Singapore. It is endangered and known to occur in localized patches of relatively undisturbed rainforest (Loo et al. 2015). Flowering is irregular and has been observed to be synchronized in some years (A.L., pers obs.). This note presents the first record of Long-tailed macaque (*Macaca fascicularis*) foraging on the fruits of *L. ferruginea*.

A single mature *L. ferruginea* plant (2.8 m in height and circa 4.7 m across, consisting of 11 leaves – the largest leaf with a 3.8 m long petiole and a frond diameter of 1.4 m) with one infructescence was encountered in early April 2020 in the Bukit Timah Nature Reserve (BTNR). Bukit Timah Nature Reserve is the oldest rainforest reserve in Singapore. It is 163 ha in size and comprises primary rainforest at its core, with mature secondary forest around it. The *L. ferruginea* plant was located along South View Path; it was monitored by a video camera trap as part of a wildlife management surveillance program. A Bushnell Trophy Cam HD Aggressor trap was deployed around the palm, approximately 30 cm above ground. The camera trap was set to record videos of 15 seconds per trigger, with a two seconds delay period between triggers. The video camera trap captured four different animals visiting the plant on five occasions in May 2020. During those visits, the fruits were pink, indicating that they were still unripe. The mature fruits of *L. ferruginea* are dark red to almost black (Saw 1997). The video captures are summarized as follows (see video in supplementary materials):

18 May 2020; 1428 hrs (Fig. 1). A green imperial pigeon (*Ducula aenea*) visited the plant, but did not take approach the fruits.

21 May 2020; 1223 hrs (Fig. 2). A clouded monitor lizard (*Varanus nebulosus*) visited the plant but did not approach the fruits.

22 May 2020; 1131 hrs (Fig. 3). Two common tree shrews (*Tupaia glis*) visited the plant and approached the fruits but did not take them.

13 May 2020; 1618 hrs (MP4 media). A troop of long-tailed macaques (*Macaca fascicularis*),

comprising a single adult male, several adult females and infants, visited the plant and took the fruits (Fig. 4). The adult females and infants were observed to share the palm by picking the individual fruits directly off the infructescence by hand. This contrasts with the adult male, which removed part of the infructescence of the palm and consumed the fruits by bringing them up to its mouth. The foraging behaviour suggests that the adult females and infants prefer to forage together. Females are philopatric and form a stable core in a troop, developing strong bonds and relationships with other females (Wrangham 1980). Other than the difference in the way the fruits were obtained, the macaques generally processed the fruit individually and removed the outer layer by the incisors in front of the mouth. Their hands were also used to help position and rotate the fruit. Continued movement of their mouths suggests that the seeds were cleaned inside the mouth. Pronounced cheek pouches could be seen on the infants in the video. The macaques also spent time foraging on the leaf litter when there were no fruits left on the palm. This suggests that the leaf litter likely had fruits and seeds that were partially processed or leftover.

The video camera footages showed that the clouded monitor lizard, green imperial pigeon and common tree shrews did not take the fruits of the *L. ferruginea*, leaving them eventually for the long-tailed macaques. Studying the morphology of *Licuala*, Saw et al. (2003) noted that the fruits are animal dispersed and the most likely dispersal agents are birds and small forest mammals. Hence, it is surprising that the green imperial pigeon and common tree shrews did not take the fruits of the *L. ferruginea*. Perhaps, the common tree shrew is unable to detect the pink immature fruits as they have dichromatic vision, compared to the long-tailed macaques, which have developed trichromatic vision (i.e. able to detect red and green). The clouded monitor lizard is also dichromatic. Recent work by Onstein et al. (2020) showed that palm fruit colors, especially conspicuous reddish fruits, could be linked to the broad-scale distribution and diversification of primate color vision. However, we are unable to explain why the green imperial pigeon avoided the fruits as birds are tetrachromatic and have a preference for red and black fleshy fruits, over yellow and green fruits (Duan et al. 2014). It may be that the immature fruit of *L. ferruginea* is pink, rather than red, and has higher green and blue wavelengths.



M PUCT 191

80°F 26°C

05-18-2020 14:38:36



M PUCT 191

82°F 27°C

05-21-2020 12:23:50

1 (top). A green imperial pigeon (*Ducula aenea*) visited the plant, but did not take approach the fruits. 18 May 2020; 1428 hr. 2 (bottom). A clouded monitor lizard (*Varanus nebulosus*) visited the plant but did not approach the fruits. 21 May 2020; 1223 hrs.



3. Two common tree shrews (*Tupaia glis*) visited the plant and approached the fruits but did not take them. 22 May 2020; 1131 hrs.

The foraging of the *L. ferruginea* fruits by the macaques suggests that they could be important dispersers or destroyers of *L. ferruginea* seeds. A study of a group of 30–40 long-tailed macaques at BTNR in the 1980s suggested that the macaque could be an important vertebrate disperser of fruits from a range of plant species. Specifically, Lucas and Corlett (1992) reported 223 records of foraging on ripe palm fruits and 33 records on unripe fruits. Of these records, 143 records involved the consumption of rattan fruits of which *Calamus oxleyanus* was dominant. Other species included *C. luridus*, *C. insignis*, *Calamus sp.* and *Korthalsia sp.* In addition to rattan fruits, there were 65 records of foraging on oil palm (*Elaeis guineensis*) fruits, 16 records of foraging on *Oncosperma horridum* fruits and 33 records of unripe fruits of *Caryota mitis*. However, there were no records of the foraging of *L. ferruginea* or other understory palms such as *Rhopaloblaste singaporensis*. Corlett and Lucas (1990) and Lucas and Corlett (1998) also showed that the fate of seeds in ripe, fleshy fruits was determined by seed size – swallowed seeds in feces (length <4 mm and width <2.3 mm); spat seeds (length 4–30 mm and width 2.3–20.0 mm); destroyed (length 20–30 mm); dropped (length >30 mm). This is also within

the range reported by Tsuji and Su (2018) in a review of macaques in Asian forests. Lucas and Corlett (1992) reported that the rattan palms (i.e., *Calamus* and *Korthalsia*) were almost certainly dispersed by the spitting of seeds by the macaques on the move.

The *L. ferruginea* seed is globose to ovoid, approximately 8 by 7 mm in length (Saw 1997). While the fate of the seeds is not clear in the video, the size of the seed falls within the category of seeds that macaques may clean in the mouths, store in their cheek pouches and spit them out a distance away from the parent plant. As the video camera footages did not capture the spitting of seeds and we also could not find any seeds on the ground around the palm, we are unable to confirm this.

It is likely that the macaques could have destroyed the seeds. In any case, the macaques had foraged on immature fruits, and the seeds would have been unviable even if they were dispersed. Macaques at the Penang Botanic Gardens had also been observed feeding on immature fruits of *Licuala grandis* and *L. peltata* var. *sumawongii*, amongst other palms, after a non-feeding (by visitors) policy was implemented in the gardens (Saw, L.G. 2020, pers comm).



4. The adult male (foreground) feeding from a part of the infructescence it had removed. The adult females (background) and infants were observed to share the palm and picked the individual fruits directly off the infructescence by hand.

While this may be a single record of the foraging of *L. ferruginea* fruits by long-tailed macaques, it suggests that macaques could have an effect on the persistence of small rare understorey palm populations, either as dispersers or destroyers of seeds. Further studies will need to be undertaken, especially during years of synchronized fruiting of individual palms in the forest, where the high abundance of fruit compensates for predation and brings about predator satiation. This will provide insights into the dispersal strategy of *L. ferruginea* and its close congeners, *L. thoana*, *L. bayana* and *L. kemamanensis* as they all have immature pink fruits (Saw, L.G. 2020, pers comm.).

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Camera trap video

13 May 2020; 1618 hrs (MP4 format). A troop of long-tailed macaques (*Macaca fascicularis*) foraging on *Licuala ferruginea*. 23 10-second videos were stitched together. High exposure segments lasting 1–2 seconds at the start of each 10-second video were cropped out.

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