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Features

A garnet-red new leaf emerging on *Geonoma poeppigiana*. See article by Couvreur et al., p. 161. Photo by Thomas L.P. Courvreur.

THE INTERNATIONAL PALM SOCIETY
Conserve. Learn. Grow.

FRONT COVER

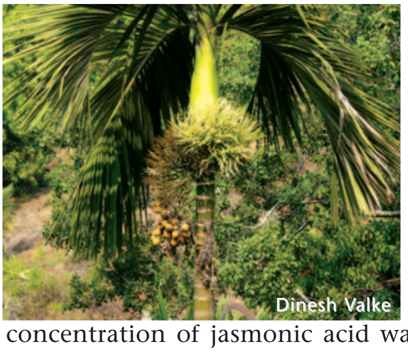
A hybrid between *Howea belmoreana* and *H. forsteriana* occurring naturally on Lord Howe Island. See article by A. Henderson, p. 177. Photo by W. Baker.

BACK COVER

A stand of *Syagrus sancona* in the Kapawi region of Ecuador. See article by Couvreur et al., p. 161. Photo by Thomas L.P. Courvreur.

PALM NEWS

New research from Sidonie Bellot and colleagues finds that **more than half of the world's palm species are threatened**. The team used machine learning to assess extinction risk predictions for 1,381 palm species. Those predictions were integrated with published conservation assessments for 508 species to point to areas with the greatest need for conservation. Madagascar, New Guinea, the Philippines, Hawaii, Borneo, Jamaica, Vietnam, Vanuatu, New Caledonia and Sulawesi were identified as priority regions for palm conservation. The publication is at *Nature Ecology & Evolution* 6: 1710–1722 (2022).



Molecular tools are continuing to allow botanists to reveal the chemical pathways that control the growth and development of plants. One such study examined the **development in male and female flowers in the inflorescence of the betelnut palm, *Areca catechu***. The work, published by G. Zhou et al. in *New Phytologist* (https://doi.org/10.1111/nph.18471), found that jasmonic acid, a common signaling chemical in plants, was expressed in female flowers at about ten times the concentration found in male flowers. They also found that in inflorescences bearing abnormal bisexual flowers, the concentration of jasmonic acid was about twice that of normal male flowers. The author proposed a mechanism by which jasmonic acid promotes the development of female flower organs.

John Dowe and coauthors recently published "**The botanical expedition of Hermann Wendland in Central America: a nomenclatural study and travel report**" in *Boissiera* 73, a publication of the Conservatoire et Jardin Botaniques, Geneva, Switzerland. The work details Wendland's travels and botanizing in Central America, an expedition that resulted in 185 named taxa, many of which were palms. This publication examines the nomenclatural history and typification of those names

Kapawi: A Mega-Diverse Palm Community in the Eastern Amazon of Ecuador

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The Achuar Kapawi community is located in the eastern Amazonian region of Ecuador. It is adjacent to the Kapawi river, a tributary of the large Pastaza river and is just 20 km from the Peruvian border. Because of its proximity to Peru, this region might harbor several species of palms not yet recorded in Ecuador. The present article is a personal account from a 5-day expedition to the region by the first author, and a preliminary synthesis of results from an expedition led by Henrik Balslev (ecology) and Rodrigo Cámara-Leret (ethnobotany) to investigate the diversity, abundance, and uses of palms in the region.

Ecuador is one of the richest countries in palm diversity of South America when related to its size. To date, around 140 species in 32 genera are recorded (Valencia et al. 2013). Yet, some areas of the Amazon remain relatively little explored for palms (Borchsenius et al. 1998, Couvreur et al. 2008, 2021), especially those close to the Peruvian border. This is the case

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1. A view of Kapawi Eco Lodge, deep in the Ecuadorian amazon, in the region of Pastaza, close to the Peru border. Notice *Astrocaryum chambira* (tall palm), and just under a juvenile *Iriartea deltoidea*. Photo by Thomas L.P. Couvreur.

of the Kapawi community of the Achuar, one of the most recent Indigenous ethnic groups to have been contacted.

The Achuar are one of the 13 Indigenous ethnic groups living in Ecuador. The word "Achuar" comes from the union of the words "shuar" or person and "achu" or *morete* palm (*Mauritia flexuosa*). The 'Achuar' are thus the people of the *morete* palm. The lifestyle and traditions of Achuar were famously described by the French anthropologist Phillipe Descola who visited Kapawi in the 1970s (Descola 1993). And yet, far too little is known about the Achuar people's knowledge of Amazonian biodiversity or about palms and their uses.

Kapawi, which refers to the name of a sort of flat fish in the Achuar-Shiwiar language (Descola 1993), is located deep in the Ecuadorian Amazon in the region of Pastaza, some 175 km southeast from the Amazonian town of Puyo and 20 km from the Peruvian border. This region is covered by a dense lowland rainforest drained by the large Pastaza river, which starts high in the Andes near Baños, and ends in the Mariño river in Peru (a tributary of the Amazon). Besides the relatively flat region close to Pastaza, there is a hilly area to the north, with peaks of about 350–400 m, providing some geological diversity to the region.

Kapawi was the focus of two palm expeditions that took place ten years apart, one in October 2011 led by Henrik Balslev (ecology team) and Rodrigo Cámara-Leret (ethnobotany team) and one in February 2021 led by Thomas Couvreur. The base for both expeditions was the Kapawi Eco Lodge (www.kapawi.com) (Figs. 1 & 2), a community-based project which aims to use ecotourism for the economic, social, and cultural development of local Achuar communities. The project, which is managed by the indigenous residents themselves, serves as an added source of income for the Kapawi, Wachirpas, Ishpingo, Kusutkau, Wayusentsa, Sharamensa and Suwa communities. Ecotourism revenues have served to increase local incomes. Importantly, ecotourism provides an added incentive for local communities to conserve the natural resources in the area.

To reach Kapawi, one needs to take a plane from the aerodrome located in the village

2. Example of the understory rain forest near Kapawi the common *Hyospathe elegans* subsp. *elegans* in the foreground. Photo by Thomas L.P. Couvreur.

called Shell, just north of Puyo. Once in the air, the small 3-passenger plane takes an eastern bound direction, leaving behind the mighty Andes. On a good day, one can see to the right the Sangay, one of the numerous active volcanoes in Ecuador spitting its fumaroles. As we progress into the Amazon, the impact of humans on the rainforest becomes less and less apparent. After a short 45 min flight, the plane makes an expert

3. Our Achuar guide, Jhonny Saant in the Kapawi rainforest. Photo by Thomas L.P. Couvreur.

landing on the short dirt runway of the Kapawi community. Several people come out of nowhere and check with the pilot if some relatives in Puyo sent them some food or a letter. After a short stop, the plane turns and takes off again.

One of our guides was Jhonny Saant, a 30-year-old Achuar student in pedagogy and father of three (Fig. 3). After being a guide for the lodge for several years, he decided to resume higher education thanks to a government scholarship. Thomas was also accompanied by two other young Achuar students at the Kapawi community school.

The plan for Thomas's teamwas to walk as much as we could and collect as many palms as we saw. This general collecting approach allows one to cover more ground but with less detail. In contrast, the ecology team set up a much more thorough protocol to document palm diversity, results of which are partially presented here. A total of 11 transects measuring 5 × 500 m each were installed, covering different lowland evergreen forest types: terra firme (4 transects), intermediate (1 transect) and floodplain (6 transects). In these transects, all palm individuals including seedlings, juveniles, sub-adults and adults are meticulously counted, measured, identified and photographed. Finally, the ethnobotany team undertook several interviews to document to the importance of palms and their uses across the Achuar communities.

A mega-diverse palm community

After one week of painstaking work in October 2011, the ecology team (led by Henrik Balslev) documented 7505 palm individuals representing a total of 40 palm species in 21 genera across the 11 transects covering 2.75 ha (Table 1). That means there are 2729 palms per hectare and between 9 to 29 species per transect! In addition, four species were documented outside of the transects (*Bactris gasipaes* var. *gasipaes* (Fig. 4), *Cocos nucifera*, *Syagrus sancona* and *S. smithii*) leading to 44 palms known from Kapawi. *Oenocarpus bataua* was by far the most abundant palm in the region with 1529 individuals registered over the 11 transects. We can refer to such species as being super-abundant. The two other most abundant palms were the understory *Geonoma macrostachys* (953 individuals) and *Geonoma stricta* subsp. *arundinacea* (857 individuals reported). Both species are morphologically very variable and taxonomically hard to classify. *Geonoma macrostachys* is, in fact, so

4 (left). *Bactris gasipaes* var. *gasipaes*, or *uví* in Achuar. Here one morphotype with red fruits (left) and one with white fruits (right) growing in Jhonny's *chacra* (community garden). Photo by Thomas L.P. Couvreur. 5 (right). *Wendlandiella gracilis* var. *simplicifrons* in flower (a new genus and species record for Ecuador). Photo by Henrik Balslev.

variable that it was impossible to define into different subspecies (Henderson 2011). Nevertheless, it is a spectacular understory palm with large (to 2 m tall) generally undivided leaves and a long erect generally unbranched inflorescence. It is common across the Ecuadorian Amazon growing sympatrically with many different morphotypes. Even though this morpho-diversity is a headache for taxonomists, it is a blessing for evolutionary biologists who are using the *Geonoma macrostachys* species complex model to unravel the impact of Amazonian environmental heterogeneity on understory plant speciation (Roncal 2006, Bacon et al. 2021).

In terms of species richness, the 2011 fieldwork showed that Kapawi is one of the most species rich palm communities across the whole of tropical America (Balslev et al. 2011). The terra firme evergreen forest was the most diverse with 29 species, while the intermediate lowland was the poorest, with 18 species. Even when we compare with similar habitats, Kapawi stands out as very species rich. For example, Kapawi is comparable to Yasuni, in lowland Ecuador Amazon and one of the most biodiverse places on earth. A recent survey documented between 30 and 33 palm species on terra firme over a surface of 2.5 ha (Balslev et al. 2011, although there might be different species concepts between studies). The region around Kapawi is thus a truly mega-diverse palm community in western Amazon.

Most of these species were already documented from Ecuador, although generally not reported for this region. Interestingly, and as we hypothesized before our expeditions, we documented the presence of two genera, one species and one subspecies as new records for Ecuador.

The two genera new to Ecuador are the monotypic genus *Wendlandiella* and *Iriartella* (two species). *Wendlandiella* represents a single polymorphic species, *W. gracilis*, distributed mainly in Peru and the State of Acre in Brazil (Eychenne et al. 2018). Kapawi harbors the most northern population of *W. gracilis* representing the variety var. *simplicifrons* (Fig. 5). It is a small understory palm, with entire-bifid leaves and an erect once branched inflorescence with several rachillae. It can easily be confused with other understory bifid-leaved palms such as *Chamaedorea pauciflora*

6. *Iriartella stenocarpa* in fruit (another new genus and species record for Ecuador). Photo byThomas L.P. Couvreur.

(*yaun*) also present in the Kapawi region. This species is locally abundant, with 157 individuals all being recorded in a single transect (HB032) in a floodplain habitat.

Iriartella stenocarpa (Fig. 6) is a small understory palm up to 5 m tall with fishtail leaves and small stilt-roots, typical of the Iriarteinae subtribe (which also contains the genera *Dictyocaryum*, *Iriartea*, *Socratea*, *Wettinia*). One needs to be very careful with species of *Iriartella*, because, unlike the other genera, the leaf sheath is covered in small spines. If you inadvertently grab the leaf sheath, you will spend the rest of the day and night with tweezers plucking away at the spines like the first author experienced once in Brazil. Despite

7 (left). *Wettinia drudei*, a new species record for Ecuador. 8 (right). *Geonoma maxima* subsp. *camptoneura*, a new subspecies record for Ecuador. Photos by Thomas L.P. Couvreur.

being the first record of the genus for Ecuador, the species is quite common and can be present in dense populations.

The genus *Wettinia* is a mainly Andean centered genus (Pintaud et al. 2008), but one species occurs in the lowland rainforests of the Amazon, *Wettinia drudei* (Fig. 7). It is the smallest species of the genus, reaching to about 5 m, and is similar to *Iriartella stenocarpa* but without the nasty spines of the leaf sheath. In Kapawi, it is locally common, being quite abundant when present.

Finally, we also documented a new subspecies for Ecuador: *Geonoma maxima* subsp. *camptoneura* (Figs. 8 & 9). *Geonoma maxima* is a beautiful widespread Amazonian palm, reaching to about 5 meters. It is morphologically very variable in the number and arrangement of its pinnae. In the latest revision of the genus, Henderson described 10 subspecies. To date, only *G. maxima* subsp. *multiramosa* was documented from Ecuador, occurring in the northern part of the Amazon (Yasuni and Cuyabeno). The *camptoneura* subspecies has few (3 or 4) irregularly inserted and sized pinnae forming a sharp angle with the midrib. It differs from the numerous regularly inserted pinnae found in subsp. *multiramosa* (Henderson 2011). We were lucky enough to have collected it in flower, during the female phase, revealing its bright white petals and stigmas.

Besides these new records for Ecuador, we also documented the presence of other interesting palms. One of them is the impressive *Elaeis oleifera*, the South American relative of the infamous African oil palm (*Elaeis guineensis*). Its documentation in Ecuador is fairly recent, dating to 1986 (Balslev & Henderson 1986, Montufar et al. 2018). This species grows in swampy areas and has a prostrate stem with only the terminal part erect and topped by several 6 m long leaves (Fig. 10). Its presence in the swamps brings a special feel to the forest. Another interesting species recorded for Kapawi is *Bactris simplicifrons*. Even though it is widely distributed and abundant (Henderson 2000), it is one of the few species of *Bactris* (together with *B. schultesii* and *B. killipii*) that have almost no noticeable spines, which is very unusual for this genus. One has to pass one's fingers along the margin of the leaves to feel them.

Palm uses

Besides species richness and abundance, diversity of uses is an important way to evaluate the dependence between a community and the environment. Palm uses

9. Flower (female phase) of *Geonoma maxima* subsp. *camptoneura*. Photo by Thomas L.P. Couvreur.

were documented in 2011 by the ethnobotany team (led by Rodrigo Cámara-Leret) with the assistance of Justo Saant by interviewing 65 informants of the Kapawi, Kusutkau and Wayusentsa communities, noting the common name of the species mentioned and the different associated uses. Uses were categorized into seven major groups: Animal food (a), Construction (b), Cultural uses (c), Human food (h), Medicinal and veterinary (m), Utensils and tools (u), and Other uses (o). In addition, in 2021 the first author had open and informal discussions with the guide Jhonny Saant. The 2011 survey noted a total of 36 species used by Achuar in Kapawi, with 1–24 uses reported for each species. Below and in Table 2, we present a summary of important palm species for the Achuar, based on the book co-authored with the Achuar (Cámara-Leret et al. 2018):

Iriartea deltoidea, *tuntuam*, was the most used species with 24 uses documented in five categories. Out of the 65 informants, it was cited 542 times! This means that on average, tuntuam was mentioned eight times per informant. This is one of the most important Construction palms: the whole stems serve as house posts, the split stems are used as house

10. *Elaeis oleifera* in a swampy forest near the Kapawi community. Notice the young inflorescence at the base of the leaves. Photo by Thomas L.P. Couvreur.

floors and walls, the strips from the stem serve for the lower tapes of the roof and as support on which to weave leaves for thatch, while the rods from the stem are used to make chicken pens. Also, the split stem is used to make spears and blowguns and the strips from the stem are used to build fences on the river banks where plant poisons are used to fish. Beds are also made from boards obtained from the stem. The Achuar built the houses of the

11. *Muntish* (Achuar), grubs extracted from the rotting trunk of *Mauritia flexuosa* and ready to be eaten. Photo by Thomas L.P. Couvreur.

12. *Uví* (*Bactris gasipaes* var. *gasipaes*) fruits. The white ones are called *Kuyu uví*, and the red ones *Kapuku uví*. Photo by Thomas L.P. Couvreur.

Kapawi Ecolodge entirely with *tuntuam* and not a single iron nail was used in the building process!

In addition to being the most abundant palm species, *Oenocarpus bataua* or *kunkuk* is also one of the most used for the Achuar community, used in 16 different ways across five of the seven uses categorized. For instance, the leaves are used for thatching forest huts, the spear leaves for making brooms, the fibers of the leaf sheath are extracted to weave the Achuar headdress or *tewasan*, the raw palm heart is edible, the fruit is matured in water and eaten or drunk in juice, and its oil is applied directly on the hair as a pomade.

Mauritia flexuosa, or *achu*, was another well cited species in the surveys, and the second most used palm in terms of different categories. The fallen and rotting stems of achu are a well-known breeding ground for palm grubs called *mundish* (Fig. 11). After a full day walking in the forest with Jhonny one day, Thomas stopped near a fallen *Mauritia flexuosa*. Jhonny then pulled out his machete and began chopping away at the trunk. After a few minutes, he found several large white larvae, with a black head. He swallowed them raw one after the other. Thomas tasted a raw one handed by Jhonny. As you chew, the head cracks under your teeth like a chip, before giving way to a warmish liquid. The taste is quite neutral, but on the greasy side, and is not unpleasant. Palm larvae are delicacies across the tropics. Jhonny explained the culinary variety of palm larvae depending on the palm species. “Each palm species has its own larva, with its own distinct taste,” he said. That of the *puntish* Achu is described as being greasy with a sweet flavor, while the one of *tuntuam* (*Iriartea deltoidea*) is said to be less greasy with a more watery taste.

One important spot when visiting Amazonian communities is at the *chacra*, or the community garden. The most important palm is *uví* or *Bactris gasipaes* var. *gasipaes* (Fig. 4), the only fully domesticated palm of the Amazon. *Uví* was the only species in the survey to have been cited in all seven categories, underlining its central importance for Amazonian communities. The main product is the fruit which is eaten boiled or used to make the traditional *chicha* across the Amazon.

13. Harvesting of *chapi* (*Phytelephas tenuicaulis* leaves) for thatching of the Achuar houses. The living plant is in the background. Photo by Thomas L.P. Couvreur.

Jhonny's *chacra* contained three different morphotypes, mainly distinguished by the color and shape of the fruits: yellow, red and, the most weird one of all, white (Fig. 12). Every morphotype can be characterized by a different taste, from oily to floury, depending on what they use it for.

After visiting the *chacra* we made a brief stopover in Jhonny's house. All seated around the fire, Jhonny's wife served us typical cassava beer, or *nijiamanch* (this brew was not yet fermented, luckily!). It is a creamy, whitish drink with a slightly acid taste. Jhonny lives in a typical Achuar house, which is oval with a high roof made of the leaves of *Phytelephas tenuicualis* (*chapi*) which can last 10 to 20 years (Fig. 13). The interesting thing about Achuar houses is the fact that they do not have walls, which gives an impression of openness and freedom.

Conclusion

These two expeditions underlined the importance of Kapawi for palm diversity and the Achuar's diverse palm knowledge. Kapawi's proximity to Peru allowed us to document several species and genera not previously recorded for Ecuador. As we flew back towards Shell (yes, our 3-passenger plane did come back to pick us up!), we waved goodbye to Jhonny and Kapawi Eco Lodge and hoped that ecotourism will protect this palm paradise for many generations to come.

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Table 1: Checklist of palm species recorded for Kapawi with total number of individuals recorded across 11 transects. HB: Henrik Balslev (vouchers deposited at AAU, QCA); TC: Thomas Couvreur (Vouchers deposited at QCA, WAG).

Species	**Total individuals in 11 transects**	**Voucher**
Aiphanes ulei (Dammer) Burret	20	HB8509
Aphandra natalia (Balslev & A.J.Hend.) Barfod	4	HB8520
Astrocaryum chambira Burret	32	HB8515
Astrocaryum urostachys Burret	237	HB8534
Attalea butyracea (Mutis ex L.f.) Wess. Boer	218	HB8517
Attalea maripa (Aubl.) Mart.	33	
Attalea phalerata Mart. ex Spreng.	6	
Bactris acanthocarpa Mart.	110	HB8527
Bactris corossilla H. Karst.	134	HB8531
Bactris gasipaes var. *gasipaes* Kunth	n.a.	
Bactris hirta Mart. var. *hirta*	13	HB8540; TC1367
Bactris maraja Mart. var. *juruensis* (Trail) A.J.Hend.	2	
Bactris maraja Mart. var. *maraja*	34	TC1337
Bactris schultesii (L.H.Bailey) Glassman	46	HB8526; TC1351
Bactris simplicifrons Mart.	54	TC1357
Chamaedorea pauciflora Mart.	43	HB8519; TC1372
Chamaedorea pinnatifrons (Jacq.) Oerst.	121	HB8513
Cocos nucifera L.	n.a.	
Desmoncus giganteus A.J.Hend	2	HB8530
Desmoncus mitis Mart. var. *mitis*	3	
Desmoncus polyacanthos Mart.	21	
Elaeis oleifera (Kunth) Cortés	72	HB8512; TC1365
Euterpe precatoria Mart.	190	
Geonoma brongniartii Mart.	6	HB8529
Geonoma camana Trail	2	
Geonoma longepedunculata Burret	161	HB8522
Geonoma macrostachys Mart. (var. *acaulis* (Mart.) Skov)	441	HB8536; TC1339
Geonoma macrostachys (var. *macrostachys*)	31	HB8511
Geonoma macrostachys (var. *atrovirens* Borchs. & Balslev)	13	
Geonoma macrostachys (as *Geonoma supracostata* Svenning)	468	HB8521

Table 1: Continued.

Geonoma maxima Kunth		
subsp. *multiramosa* A.J.Hend.	79	HB8537; TC1369
Geonoma poeppigiana Mart.	59	HB8525
Geonoma multisecta (Burret) Burret		
(as *Geonoma polyandra* Skov)	49	
Geonoma stricta (Poit.) Kunth subsp. *arundinacea*		
(Mart.) A.J. Hend. (*stricta* var.		
piscicauda (Dammer) A.J.Hend.)	180	HB8510
Geonoma stricta subsp. *arundinacea*		
(*stricta* var. *stricta*)	630	HB8506
Geonoma stricta subsp. *arundinacea*		
(*stricta* var. *trailii* (Burret) A.J.Hend.)	47	HB8532; HB8538; TC1338
Hyospathe elegans Mart.	256	HB8524
Iriartea deltoidea Ruiz & Pav.	536	HB8514
Iriartella stenocarpa Burret	371	HB8528; HB8535; TC1350; TC1373
Mauritia flexuosa L. f.	11	
Oenocarpus bataua Mart.	1529	HB8516
Oenocarpus mapora H. Karst.	43	HB8523
Phytelephas tenuicaulis (Barfod) A.J.Hend.	558	HB8533
Prestoea schultzeana (Burret) H.E.Moore	37	
Socratea exorrhiza (Mart.) H.Wendl.	260	HB8518
Syagrus sancona H.Karst.		
Syagrus smithii (H.E.Moore) Glassman		
Wendlandiella gracilis Dammer var.		
simplicifrons (Burret) A.J.Hend.	157	HB8507; TC1356
Wettinia drudei (O.F.Cook & Doyle) A.J.Hend.	143	HB8539
Wettinia maynensis Spruce	43	HB8542

Table 2: Scientific and Achuar names of palms mentioned, different categories, number of uses mentioned and number of times the name was cited after 64 interviews. The table is ordered based on the decreasing number of citations. Animal food (a), Construction (b), Cultural uses (c), Human food (h), Medicinal and veterinary (m), Utensils and tools (u), and Other uses (o).

Species	Local names	Use categories	No. of uses	No. of citations
Iriartea deltoidea	Tuntuam	b, c, h, u, o	24	542
Oenocarpus bataua	Kunkuk	b, c, h, u, o	16	452
Astrocaryum chambira	Kumai	a, c, h, u, o	18	401

Table 2: Continued.

Bactris gasipaes var. *gasipaes*	Uví	a, b, c, h, m, u, o	16	398
Mauritia flexuosa	Achu	b, c, h, m, u, o	16	344
Attalea butyracea	Katira	b, h, o	10	342
Astrocaryum urostachys	Awan; Kurugurupish	b, c, h, u, o	9	286
Attalea maripa	Iñayoa; Tsentsak	b, h, u, o	13	270
Aphandra natalia	Kintiuk	a, b, c, h, u, o	14	267
Attalea phalerata	Kuñua	b, h, u, o	11	259
Euterpe precatoria	Saké	b, c, h, o	11	244
Phytelephas tenuicaulis	Chapi	b, c, h, o	7	219
Oenocarpus minor	Shimpi	b, c, h, u, o	11	186
Socratea exorrhiza	Kupat	b, c, u, o	12	175
Wettinia maynensis	Teren	b, h, u, o	11	159
Attalea sp.	Kamacriña	b, h, u, o	10	148
Bactris corossilla	Murayá kamanchá	b, c, h, m, u	11	85
Syagrus sancona	Chuchuk	b, u, o	5	80
Bactris maraja	Pakaña kamanchá	b, c, h, m, u	9	79
Hyospathe elegans	Sapap	b, u	3	68
Iriartella stenocarpa	Kuuntas	b, u	4	66
Geonoma macrostachys var. *acaulis*	Turuji	b	1	65
Pholidostachys synanthera	Kampanak	b	1	63
Elaeis oleifera	Yunchik	a, h, u	5	62
Chamaedorea pauciflora	Yaun	c	1	61
Geonoma sp.1	Shushui turuji	b	1	61
Geonoma cf. *deversa*	Yunkup	b, h, u	3	57
Aiphanes ulei	Tuntuam janki	h, m, u	5	56
Syagrus smithii	Koemiank	b, u	2	48
Geonoma cf. *longe-pedunculata*	Murayá turuji	b	1	47
Desmoncus spp.	Makayai	b, m, u	5	45
Bactris concinna	Kamanchá	b, h, u	5	31
Geonoma stricta	Wapas turuji	b	1	16
Mauritiella armata	Achuku	b, u	4	15
Astrocaryum jauari	Wiriria	a, b, m	3	4
Geonoma sp.2	Pakaña turuji	b	1	3
Bactris riparia	Miririao	-	0	0

A Review of Naturally Occurring Hybrids in Palms (Arecaceae)

ANDREW HENDERSON[1]

A review of the literature on naturally occurring hybrids in palms is presented. Approximately 114 instances of putative hybridization were found. Hybridization in palms appears to be relatively uncommon, although it may be under-reported. Within the family, there is a preponderance of records from two, taxonomically distant tribes: Trachycarpeae (Coryphoideae) and Cocoseae (Arecoideae). There does not appear to be any association between hybrids and habitat, region or morphology. Hybrids can be problematic in systematic studies, and their identification based on morphological data is challenging. There are very few polyploids in palms, and these do not appear to be a result of hybridization.

Hybrids are the result of sexual reproduction between two different taxa, usually congeneric species or subspecific taxa but sometimes between species from different genera. As such they may be isolated occurrences with no particular consequences. However, by repeated hybridization, alleles of one species may be incorporated into another (introgression). Sometimes large populations of hybrids, or hybrid zones, can form between two different, adjacent taxa. The processes of introgression and formation of hybrid zones have significant evolutionary consequences and have played a major role in the evolution of several plant families (Reiseberg & Wendel 1993).

Polyploidy, the heritable increase in genome copy number, commonly occurs in plants and may be derived from the same species (autopolyploidy), or, more often, from hybridization between different species (allopolyploidy). Wood et al. (2009) considered that most, or possibly all, plant species ultimately had a polyploid ancestry. It is estimated that 15% of angiosperm speciation events were accompanied by ploidy increase (Soltis et al. 2007). It is also estimated that from one half to two-thirds of flowering plants are polyploids, including about 80% of the species in the grass family (Levy & Feldman, 2002, Soltis & Soltis 2009).

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The goal of this paper is to review the literature on naturally occurring hybrids in palms and then to use the results to discuss several topics: the extent of hybridization in palms and the distribution of hybrids amongst subfamilies, tribes and subtribes; the association between hybrids and habitat, region or morphology; the implications of hybridization for palm systematics, both for revisionary and phylogenetic studies; and the role of hybrids in speciation of palms, particularly in ploidy levels.

Materials and Methods

A survey of the relevant literature on palms was carried out, and the results presented according to the most recent classification of the family (POWO 2022). In a few cases, personal observations from researchers were

1. *Coccothrinax argentata* × *Leucothrinax morrisii* on Big Pine Key, Florida. Photo by Paul Craft.

2. *Coccothrinax macroglossa* × *C. pseudorigida* in Camagüey, Cuba. Photo by D.R. Hodel.

3. *Coccothrinax crinita* subsp. *brevicrinis* (left), *C.* × *angelae* (center) and *C. miraguama* subsp. *roseocarpa* (right). Photo by Paul Craft.

included. Numbers of species per genus and nomenclature were taken from POWO (2022) or from the most recent monographs, and distributions were taken from Dransfield et al. (2008). References to cultivated palms were omitted because there are so many of them and they are not directly related to the subject. Many of the hybrids reported here are somewhat anecdotal and based on little data and are often referred to as possible hybrids or potential hybrids. All published reports are here assumed to represent actual hybrids regardless of their level of supporting data. Genera for which no natural hybrids are known are listed in Appendix 1.

Results

CALAMOIDEAE

CALAMEAE, METROXYLINAE

The subtribe comprises one genus (*Metroxylon*, 7 species) distributed in the Asian tropics. McClatchey (1998) reported that, on Samoa, two species (*M. paulcoxii* and *M. warburgii*) were sympatric and that one specimen might be a hybrid between the two. However, the sympatry of the two species was possibly an artifact of human activity.

CALAMEAE, CALAMINAE

The subtribe comprises one genus (*Calamus*, 411 species) widely distributed throughout the Asian tropics with one species in Africa. Henderson (2020a) reported one possible naturally occurring hybrid, involving *C. bacularis* and *C. myriacanthus*, and a few, other potential cases (*C. javensis* and *C. tenompokensis*; C. *leloi* and an unknown species; *C. insignis* and *C. longiusculus*).

CORYPHOIDEAE

SABALEAE

The tribe comprises one genus (*Sabal*, 16 species) distributed in Central America and the Caribbean. In one of the most detailed studies of hybridization in palms, Goldman et al. (2011), using molecular data (AFLPs), considered that a population of *Sabal* in Texas was a hybrid between *S. minor* and *S. palmetto* (*S.* × *brazoriensis*). They postulated that the initial hybridization event could have taken place thousands of years ago when the geographic distribution of the parent species was different. They considered it possible that caulescent plants of *S. minor* as well as *S.* × *brazoriensis* could represent an extensive regional hybrid swarm between acaulescent *S. minor* and *S. palmetto* (see also Simpson 1988). Their data also suggested that a Mexican sample of *S. minor* showed evidence of introgression with *S. mexicana*.

CRYOSOPHILEAE

The tribe comprises 11 genera (*Schippia*, 1 species; *Trithrinax*, 3 species; *Zombia*, 1 species;


4 (left). *Copernicia × vespertilionum* in Sancti Spíritus, Cuba. 5 (right). *Copernicia × sueroana* in Las Tunas, Cuba. Photos by Paul Craft.

Coccothrinax, 56 species; *Hemithrinax*, 3 species; *Leucothrinax*, 1 species; *Thrinax*, 3 species; *Chelyocarpus*, 3 species; *Cryosophila,* 10 species; *Itaya*, 1 species; *Sabinaria*, 1 species) distributed throughout the Neotropics.

Naturally occurring intergeneric hybrids between *Coccothrinax* and *Thrinax* have been reported from the Florida Keys (Nauman 1989, 1990) (Fig. 1). These hybrids were found to be sterile.

In *Coccothrinax*, hybridization is common amongst cultivated species (particularly in botanic gardens), and there appear be several naturally occurring hybrids in Cuba (Craft 2017). Craft considered that *C. orientalis* and *C. pauciramosa* could hybridize, and also *C. macroglossa* and *C. pseudorigida* (Fig. 2). Suárez Oropesa (2015), based on morphological data, described a naturally occurring hybrid from Cuba between *C. crinita* and *C. miraguama* as *C. × angelae* (Fig. 3).

PHOENICEAE

The tribe comprises one genus (*Phoenix*, 13 species) widely occurring in Old World tropical and subtropical areas. The species are well-known to hybridize freely in cultivation (Dransfield et al. 2008, Gros-Balthazard 2013). González-Peréz et al. (2004), using molecular data (RAPD markers) reported that on the Canary Islands, the naturally occurring *P. canariensis* hybridized with the introduced *P. dactylifera*. Pérez-Escobar et al. (2021) discussed the ancient hybrid origin of the date palm, *P. dactylifera*. They considered that its evolution was influenced by gene flow from two wild relatives, *P. theophrasti*, currently restricted to Crete and Turkey, and *P. sylvestris*, widespread from Bangladesh to the West Himalayas (see also Flowers et al. 2019).

TRACHYCARPEAE, LIVISTONINAE

The subtribe comprises six genera (*Livistona*, 28 species; *Licuala*, 167 species; *Lanonia* 13 species; *Johannesteijsmannia*, 4 species; *Pholidocarpus*, 6 species; *Saribus*, 9 species) distributed throughout the Asian tropics and subtropics and just reaching north-east Africa.

There are several anecdotal reports of hybridization in *Livistona* in Australia. Tucker (1975) reported a natural hybrid between *L. australis* and *L. humilis*. Dowe (2009) considered that the ranges of *L. australis* and *L. decora* overlapped in some areas and there could be hybridization between the two. Rodd (1998) mentioned possible hybrids between *L.*

6. *Copernicia* × *shaferi* in Camagüey, Cuba. Photo by D.R. Hodel.

humilis and *L. inermis* and considered it possible that *L. leichhardtii* hybridized with *L. lorophylla* and *L. mariae*. Henderson and Nguyen Quoc Dung (2019) considered that *L. jenkinsiana* and *L. saribus* formed hybrids in northern Vietnam.

Miyamoto et al. (2006) studied a population of *Licuala* at a site in lowland rainforest in Brunei, using morphological and molecular data. They considered that intermediate plants between *L. paludosa* and *L. bruneiana* could be hybrids between the two species.

Bacon et al. (2016a) found no evidence of hybridization between *Johannesteijsmannia* species, despite the species occurring in close proximity in Peninsular Malaysia.

UNPLACED GENERA OF TRACHYCARPEAE

This group comprises seven genera (*Acoelorraphe*, 1 species; *Serenoa*, 1 species; *Brahea*, 11 species; *Colpothrinax*, 3 species; *Copernicia*, 22 species; *Pritchardia*, 29 species; *Washingtonia*, 2 species) distributed in the New World tropical and subtropical regions, with the exception of the Pacific island *Pritchardia*.

Bacon et al. (2012a) considered that there was no evidence of hybridization in *Brahea*. Ramírez-Rodríguez et al. (2011, 2012), based on morphological and molecular data, showed evidence of hybridization between *B. dulcis* and *B. calcarea* in Mexico.

Six naturally occurring hybrids were reported in *Copernicia* from Cuba by Dahlgren and Glassman (1963): *C.* × *vespertilionum* (Fig. 4), *C.* × *sueroana* (Fig. 5), *C.* × *burretiana*, *C.* × *shaferi* (Fig. 6), *C.* × *textilis*, and *C.* × *occidentalis*. Moya López et al. (2019) accepted a seventh species, *C.* × *escarzana*. The widely distributed *C. hospita* is a parent of five of these hybrids. Other species such as *C. curbeloi*, *C. longiglossa* and *C. molinetii*, may also be of hybrid origin, as well as *C. oxycalyx* (Craft 2017). Craft noted that most hybrids occurred in central and eastern Cuba, where species of *Copernicia* occurred in close proximity (see also Moya López & Mayotte 1996). In some places large numbers of hybrids occurred. Verdecia Pérez (2016), based on morphological data, described a natural hybrid, *C.* × *dahlgreniana*, in Cuba with intermediate characteristics of *C. cowellii* and *C. macroglossa*. Most species of *Copernicia* are endemic to Cuba and the common occurrence of hybridization has been a challenge for taxonomic revisions.

For *Pritchardia*, Hodel (1980) reported that species freely hybridized in cultivation, although Hodel (2007a) did not report any naturally occurring hybrids. He noted that species seldom occurred sympatrically. Bacon et al. (2012b) noted the difficulty of delimiting sympatric Hawaiian species because of their similarity due to recent divergence and their phenotypic plasticity. They suggested that hybridization had played an important role in the diversification of species from regions of sympatry, for example in Kauai (*P. flynnii*, *P. napaliensis*, *P. minor*, *P. waialealeana* and *P. viscosa*) and Oahu (*P. bakeri*, *P. kahukuensis* and *P. martii*).

CARYOTEAE

The tribe comprises three genera (*Arenga*, 24 species; *Caryota*, 14 species; *Wallichia*, 8 species) widely distributed in the Asian tropics.

Whitmore (1998) described "hybrid swarms" in Peninsular Malaysia between *Arenga westerhoutii* and *A. pinnata*, although he considered the latter to be introduced to the region.

Hahn (1993) suggested that *Caryota sympetala* was of hybrid origin, an idea not supported by Jeanson (2011). Hahn and Sytsma (1999) considered that there were several instances of hybridization in *Caryota*, including between sympatric species from the Philippines (*C. cumingii* and *C. rumphiana*; *C. cumingii* and *C. mitis)* and from Vietnam (*C. monostachya* and *C. maxima*).

Henderson (2007) proposed that one specimen of *Wallichia* could be a hybrid between *W. marianneae* and *W. caryotoides*, but this specimen was determined as *W. gracilis* by Jeanson (2011).

CEROXYLOIDEAE

CEROXYLEAE

The tribe comprises four genera (*Ceroxylon*, 12 species; *Juania*, 1 species; *Oraniopsis*, 1 species; *Ravenea* 22 species) distributed in South America, Madagascar, Australia, and Juan Fernandez.

María José Sanín (pers. comm.) reported isolated individuals of *Ceroxylon* in Colombia being morphologically intermediate between *C. quindiuense* and *C. parvifrons*, *C. quindiuense* and *C. alpinum*, and *C. quindiuense* and *C. vogelianum*. In Peru, a population of individuals appeared intermediate between *C. peruvianum* and *C. echinulatum*.

PHYTELEPHEAE

The subtribe comprises three genera (*Ammandra*, 1 species; *Aphandra*, 1 species; *Phytelephas*, 6 species) distributed in the Neotropics.

Barfod (1991) considered that *Phytelephas seemannii* subsp. *brevipes* from Panama was similar to *P. macrocarpa* subsp. *schottii* and could a hybrid between *P. seemannii* and *P. macrocarpa*.

ARECOIDEAE

IRIARTEEAE

The tribe comprises five genera (*Iriartella*, 2 species; *Dictyocaryum*, 3 species; *Iriartea*, 1 species; *Socratea*, 5 species; *Wettinia*, 22 species) widely distributed in the Neotropics.

Bacon et al. (2016b) considered that in Colombia there was high potential for hybridization between the widely distributed *Wettinia kalbreyeri* and the more narrowly distributed *W. disticha*. Galeano and Bernal (2010) considered that *W. oxycarpa* could be a natural hybrid between *W. quinaria* and *W. kalbreyeri*.

CHAMAEDOREEAE

The tribe comprises five genera (*Hyophorbe*, 5 species; *Wendlandiella*, 1 species; *Synechanthus*, 3 species; *Chamaedorea*, 104 species; *Gaussia*, 5 species) widely distributed in the Neotropics, with the exception of *Hyophorbe* from the Mascarene Islands. There are no records of natural hybrids in the tribe. Hybrids between species of *Hyophorbe* are common in cultivation (e.g., Hung & Pan 2014; see also Maunder et al. 2002). Hodel (1992) considered that natural hybrids probably did not occur in *Chamaedorea*, although several artificial hybrids are known from cultivation.

COCOSEAE, ATTALEINAE

The subtribe comprises 10 genera (*Beccariophoenix*, 3 species; *Jubaeopsis*, 1 species; *Voanioala*, 1 species; *Allagoptera*, 6 species; *Attalea*, 30 species; *Butia*, 22 species; *Cocos*, 1 species; *Jubaea*, 1 species; *Syagrus*, 67 species; *Parajubaea* 3 species) widely distributed in the Neotropics, southern Africa, and Madagascar.

Noblick (2017) reported a hybrid between *Butia odorata* and *Syagrus romanzoffiana*, × *Butyagrus nabonnandii*. This cross was first made from cultivated plants in Europe in the 19th century but was later found to occur naturally in Uruguay.

Moraes (1996) considered that there might be hybrids between *Allagoptera campestris* and *A.*

Fig. 7. *Attalea piassabossu* in eastern Brazill. Photo by L. Noblick.

leucocalyx in areas where the two species overlapped, and from where intermediate specimens are known.

Henderson (2020b) considered that in at least half of the 30 species of *Attalea* there was evidence of hybridization, including single instances of hybrids as well as large scale hybrid zones. Hybrids greatly complicated the taxonomy of the genus. Some of the most detailed studies of hybrids in *Attalea*, based on morphological data, were carried out by Michael Balick and colleagues (e.g., Balick et al. 1987a, 1987b; see also Anderson & Balick 1988). The following hybrids have been postulated (Henderson 2020b; see also Pinheiro 1997): *A.* × *minarum*, *A.* × *teixeriana*, *A. piassabossu* (Fig. 7), *A.* × *voeksii*, *A. camopiensis*, *A. degranvillei*, (*A. maripa* × ?*A. guianensis*), *A. salvadorensis*, *A. dahlgreniana*, , (*A. nucifera* × *A. butyracea*) and (*A. sagotii* × *A. barreirensis*).

Gaiero et al. (2011) studied genetic diversity in four species of *Butia* in Uruguay, *B. lallemantii*, *B. paraguayensis*, *B. yatay* and *B. capitata*. They found that variability within populations was high, possibly due to gene flow, past hybridization or life history traits. In particular, they considered that current or recent hybridization between *B. lallemantii* and *B. paraguayensis* could explain the high number of admixed genotypes observed in both species. Brussa and Grela (2007) considered that *B. lallemantii* and *Syagrus romanzoffiana* formed hybrids in Uruguay. They also listed × *Butyagrus nabonnandii* as occurring naturally in riverine forests and hills in eastern Uruguay. Engels et al. (2021) described a new hybrid between *B. eriospatha* and *S. romanzoffiana*, which they called × *Butyagrus paranaensis*. It occurred in forests in the central-south region of Paraná state, Brazil. Soares et al. (2014) described × *Butyagrus alegretensis* from southern Brazil, a hybrid between *B. lallemantii* and *S. romanzoffiana*. Noblick (2014) suspected hybridization between *B. paraguayensis* and *B. yatay* along the Paraná River, which defines part of the border between Paraguay and Argentina.

Hodel (2011) discussed *Syagrus* hybrids in both cultivation and the wild. Noblick (2017) recognized 14 naturally occurring hybrids in *Syagrus*, mostly from eastern Brazil. He considered that hybrids had a low frequency of occurrence and were often characterized by low fruit production, low seed germination and by hybrid vigor, making the hybrid more robust than either of its parents. Some species were remarkably promiscuous. *Syagrus coronata* formed hybrids with several other species, including *S. vagans*, *S. microphylla*, S. *schizophylla*, *S. botryophora* and *S. romanzoffiana*. *Syagrus romanzoffiana* formed hybrids with other species including *S. coronata*, *S. flexuosa*, *S. oleracea* and *S. glaucescens*. Noblick (2017) recognized the following hybrids: *S.* × *lacerdamourae*, *S.* × *costae*, *S.* × campos-*portoana*, *S.* × *mirandana*, *S.* × *tostana*, *S.* × *matafome*, *S.* × *andrequiceana*, *S.* × *serroana*, (*S. loefgrenii* × S. *romanzoffiana*), *S.* × *teixeiriana*, *S.* × *altopalacioensis*, (*S. pleioclada* × *S. glaucescens*), *S.* × *cipoensis* and (*S. comosa* × *S. elata*).

COCOSEAE, BACTRIDINAE

The subtribe comprises five genera (*Acrocomia*, 9 species; *Astrocaryum*, 39 species; *Aiphanes*, 38 species; *Bactris*, 79 species; *Desmoncus*, 24 species), widely distributed throughout the Neotropics.

Wessels Boer (1971) described a hybrid, *Bactris* × *moorei*, between *B. acanthocarpa* and *B. oligoclada* in Venezuela. Henderson (2000) reported several hybrids in *Bactris*: (*B. mexicana* × *B. gracilior*), (*B. acanthocarpa* × unknown species), (*B. barronis* × *B. gasipaes*), (*B. brongniartii* × *B. major*), (*B. caudata* × *B. coloradonis*), (*B. corossilla* × *B. maraja*), (*B. setulosa* × *B. major*) and (*B. setiflora* × *B. corossilla*). Couvreur et al. (2006) reported possible hybrids between wild and cultivated *B. gasipaes* in western Ecuador.

Henderson (2011a) reported that several, suspected hybrids were present amongst specimens of *Desmoncus*. Most of these involved *D. polyacanthos*, the most widespread and variable species, and either *D. pumilus*, *D. mitis* or *D. horridus*. All hybrids came from the central and western Amazon region, and none occurred in other regions: (*D. polyacanthos* × *D. horridus*), (*D. leptoclonos* × unknown species), (*D. polyacanthos* × *D. mitis*), (*D. parvulus* × unknown species) and (*D. polyacanthos* × *D. pumilus*).

EUTERPEAE

The tribe comprises five, Neotropical genera (*Hyospathe*, 6 species; *Euterpe*, 7 species; *Prestoea*, 10 species; *Neonicholsonia*, 1 species; *Oenocarpus*, 9 species).

Henderson (2004) reported that therei were hybrids between subspecies of *Hyospathe* *elegans*, and a possible hybrid zone between *H. elegans* and *H. pittieri* along eastern Andean slopes.

Pereira et al. (2022) found two geographical genetic groups in *Euterpe edulis* from the Atlantic Coastal Forest of Brazil, a northern and a southern group, with a region of hybridization in the contact zone.

Balick (1991) described a hybrid between *Oenocarpus bacaba* and *O. minor*, *O.* × *andersonii*, from a single locality near Manaus in Brazil. Balick (1988) reported on hybrids between *O. bataua* and *O. bacaba* in Colombia, and Henderson et al. (1995) listed hybrids between *O. bataua* and *O. bacaba* and *O. bataua* and *O. mapora*.

GEONOMATEAE

The tribe comprises six, Neotropical genera (*Welfia*, 2 species; *Pholidostachys*, 8 species; *Calyptrogyne*, 18 species; *Calyptronoma*, 3 species; *Asterogyne*, 5 species; *Geonoma*, 68 species).

Henderson (2005) reported hybrids between *Calyptrogyne trichostachys* and *C. brachystachys*, and between *C. panamensis* and *C. fortunensis*, and a possible hybrid zone in Central America between *C. brachystachys* and *C. ghiesbreghtiana*.

There are numerous sympatric species of *Geonoma* in Neotropical forests. Knudsen (1999), Borchsenius (2002), and Borchsenius et al. (2016) have shown how differences in phenology and floral scent contribute to reproductive isolation in sympatric species or forms. Henderson (2011b) reported numerous hybrids in *Geonoma*, including three possible hybrid zones. The most convincing of these was a hybrid zone in the northeastern Amazon region involving *G. deversa* and *G. leptospadix*. He also reported numerous hybrids between subspecies within species. Henderson reported the following interspecific hybrids, four of which involved the widespread *G. deversa*: (*G. deversa* × *G. brongniartii*), (*G. deversa* × *G. leptospadix*), (*G. deversa* × *G. occidentalis*), (*G. deversa* × *G. longivaginata*), (*G. poeppigiana* × *G. brongniartii*), (*G. camana* × *G. macrostachys*), (*G. elegans* × *G. pauciflora*), (*G. orbignyana* × *G. undata*), (*G. interrupta* × *G. pinnatifrons*), (*G. poeppigiana* × unknown species), (*G. pohliana* × *G. pauciflora*), (*G. schottiana* × *G. pauciflora*) and (*G. undata* × *G. trigona*).

ARECEAE, BASSELINIINAE

The subtribe comprises six genera (*Basselinia*, 14 species; *Burretiokentia*, 5 species; *Cyphophoenix*, 4 species; *Cyphosperma*, 5 species; *Lepidorrhachis*, 1 species; *Physokentia*, 7 species), distributed in New Caledonia, Vanuatu, Fiji, the Solomon Islands, and the Bismarck Archipelago.

Pintaud (2006) reported on hybrids in Basselinia in disturbed forests in New Caledonia between *B. pancheri* and *B. gracilis* and between *B. pancheri* and *B. deplanchei*. In some areas *B. vestita* formed hybrids with *B. gracilis* and *B. pancheri*.

ARECEAE, LINOSPADICINAE

The subtribe comprises four genera (*Calyptrocalyx*, 27 species; *Linospadix*, 7 species; *Howea*, 2 species; *Laccospadix*, 1 species) distributed in the Moluccas, New Guinea, Australia, and Lord Howe Island.

Babik et al. (2009) and Hipperson et al. (2016) reported hybrids between *Howea belmoreana* and *H. forsteriana* on Lord Howe Island (Figs. 8 & Front Cover). However, they considered that gene flow between the two species was extremely limited.

ARECEAE, ONCOSPERMATINAE

The subtribe comprises four genera (*Oncosperma*, 5 species; *Deckenia*, 1 species; *Acanthophoenix*, 3 species; *Tectiphiala*, 1 species) widely distributed in the Asian tropics and Indian Ocean islands.

Adorador and Fernando (2017) considered that a population of *Oncosperma* on Samar Island in the Philippines could be of hybrid origin, although neither of the putative parents (*O. horridum* and *O. gracilipes*) occurs on Samar.

Ludwig (2006) reported that the allopatric distribution of *Acanthophoenix* meant that the possibility of hybridization in the wild was remote. However, she reported hybrids in plantations.

UNPLACED MEMBERS OF ARECEAE

The group comprises ten genera (*Bentinckia*, 2 species; *Clinostigma*, 11 species; *Cyrtostachys*, 7 species; *Dictyosperma*, 1 species; *Dransfieldia*, 1 species; *Heterospathe*, 39 species; *Hydriastele*, 39 species; *Iguanura*, 34 species; *Loxococcus*, 1 species; *Rhopaloblaste* 6 species) widely distributed throughout the Old World tropics.

Hodel (2007b) reported that a possible hybrid between *Clinostigma samoense* and *C. warburgii* occurred on Samoa.

Discussion

There are 180 currently recognized genera of palms. Naturally occurring hybrids have been

8. *Howea belmoreana* (front left), *H forsteriana* (front right) and putative hybrid (back left) on Lord Howe Island. Photo by W. Baker.

reported in 26 of these (14% of the total). However, of the 180 genera, 54 are monospecific and about 40 have few, allopatric species. This leaves about 90 genera having two or more species some of which are distributed sympatrically in which hybrids could potentially occur. Hybrids are reported in 29% of these genera.

There are about 2,533 currently recognized species of palms, and of these 26 are hybrid species (i.e., ones that have been officially described and currently recognized). These represent <1% of the total number of recognized species. About 114 instances of naturally occurring hybridization have been reviewed here. Because several of these have the same parent, only about 156 species (6% of the total number of recognized species) are involved in hybridization.

Hybrids are not evenly distributed amongst subfamilies, tribes and subtribes. At the subfamily level, most hybrids occur in the Arecoideae (73 hybrids, 64% of the total). However, there are many more species overall in the Arecoideae, about 50% of the total number of palm species. Fewer hybrids occur in the Coryphoideae (31 hybrids, 27% of the total), and fewer still in the Calamoideae (5 hybrids, 4% of total) and Ceroxyloideae (5 hybrids, 4% of total). At the tribal level, in the Arecoideae there are 48 hybrids reported for the Cocoseae, 16 for the Geonomateae, 4 for the Euterpeae, 4 for the Areceae, and 1 for Iriarteeae. The high number for the Cocoseae is based mostly on three genera in the subtribe Attaleinae (*Attalea*, *Butia*, *Syagrus*) and two in the subtribe Bactridinae (*Bactris*, *Desmoncus*). At the tribal level in the Coryphoideae, there are 20 hybrids reported for the Trachycarpeae, 4 each for the Cryosophileae and Caryoteae and 2 for the Sabaleae. The relatively high number for Trachycarpeae is based mostly on *Livistona* and *Copernicia*. Within genera it appears that the most widespread and variable species are more likely to form hybrids. Examples are *Attalea maripa* and *A. speciosa*, *Syagrus coronata* and *S. romanzoffiana*, *Bactris acanthocarpa* and *B. major*, *Desmoncus polyacanthos*, *Oenocarpus bacaba*, *Geonoma deversa*, *Sabal palmetto*, *Livistona australis* and *Copernicia hospita*.

Hybrids do not appear to be strongly connected with any particular habitat. Using the rather broad categorization of habitats of Henderson (2002)—lowland moist forests; montane moist forests; dry forests; grasslands, savannas and shrublands; and desert and xeric shrublands—most hybrids occur in lowland moist forests (55%), followed by dry forests (21%), and grasslands, savannas and shrublands (16%). Few hybrids are found in montane moist forests (6%) or desert and xeric shrublands (2%). These are approximately the same percentages of habitat distribution for all species of palm.

Hybrids do not appear linked to any particular continent, region, or island, although the majority (83%) are from the Neotropics. Two neotropical areas have high numbers of hybrids: Cuba and eastern Brazil.

Hybrids do not seem to be associated with any particular aspect of morphology, such as stem type, inflorescence type or germination type (Henderson 2002), nor with any particular type of pollination (although pollinators are not recorded for most parent species).

Most hybrids reviewed here are reported by systematists who are revising genera based on herbarium specimens. Different systematists have different propensities to recognize hybrids. Hybrids are anyway difficult to detect from specimens and may be under-reported. They are usually postulated based on sympatry of putative parents and morphological intermediacy of putative hybrids. Furthermore, the sample size of most species in herbaria is extremely small compared with population size, and thus few hybrid specimens may be present in samples. Hybrids appear to be a limited problem for systematists. Most reported hybrids (about 70%) appear to be isolated occurrences and may have little significance. About 20 hybrids are said to be relatively widespread, and seven hybrid zones have been reported. Some genera certainly appear to be more problematic than others for systematists, for example *Attalea*, *Syagrus* and *Copernicia*. As yet there are no studies that address the problem of palm hybrids in inferring phylogenies.

Most of the hybrids reviewed here are presumed to be contemporary or recent events, and most studies are based on morphological data. Only a few studies are based on molecular data, and of these some have addressed ancient hybrid events. Molecular data will no doubt become the norm for investigating hybrids and in studying the role of hybridization, if any, in the formation of species complexes.

Polyploidy, the duplication of whole genomes, is thought to have occurred in virtually all lineages of angiosperms (Alix et al. 2017). However, polyploidy appears to be uncommon in palms. Barrett et al. (2019) found evidence for a whole genome duplication event early in the evolution of the family. In general, they found that an ascending dysploid series of chromosome numbers (i.e., $2n$ = 26, 28, 30, 32, 34, 36) appeared to be the predominant mode of chromosomal change in palms, rather than repeated evolution of polyploidy. Dransfield et al. (2008), in a review of chromosome numbers in palms, found that only four cases of polyploidy had been reliably reported, presumably all autopolyploids, and thus not involving hybridization (compared with estimates of 60–75% polyploids in monocotyledons in general, Keeler 1998). Two of the palm polyploidys (*Arenga caudata*, *Rhapis humilis*) were tetraploids in otherwise diploid genera. The remaining two were polyploids in monotypic genera in the subtribe Attaleinae; *Jubaeopsis* from South Africa ($2n$ = 160–200) and *Voanioala* from Madagascar ($2n$ = ca. 600), the latter having the highest chromosome number amongst the monocotyledons. Though not a polyploid, *Beccariophoenix*, another monotypic member of the Attaleinae from Madagascar, was also distinct in having a diploid count of $2n$ = 36 as opposed to $2n$ = 32 in the remaining species of the Attaleinae. Gunn et al. (2015) considered that genome size in the Attaleinae suggested that polyploidy also occurred in the neotropical *Allagoptera caudescens*. The unusual chromosome numbers in the subtribe Attaleinae are concentrated in the three genera (*Beccariophoenix*, *Jubaeopsis*, *Voanioala*) that occur outside the subtribe's principal distribution in the Neotropics. The remaining neotropical genera of the subtribe produce a high number of hybrids, particularly *Attalea*, *Butia* and *Syagrus*. The significance of this is unknown.

In summary, many of the records of naturally occurring hybrids appear somewhat anecdotal, and many seem to have been as a result of human disturbance. This review gives the general impression that congenerics can hybridize if brought together artificially but seldom do so naturally. However, it is certainly possible that hybrids are under-reported. Just over half of all reported hybrids are from two tribes: Trachycarpeae and Cocoseae.

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Appendix 1. Taxa for which no natural hybrids have been reported.

CALAMOIDEAE

EUGEISSONEAE

Eugeissona, 6 spp. .

LEPIDOCARYEAE, ANCISTROPHYLLINAE

Oncocalamus, 4 spp.

Eremospatha, 11 spp.

Laccosperma, 7 spp.

LEPIDOCARYEAE, RAPHIINAE

Raphia, 22 spp.

LEPIDOCARYEAE, MAURITIINAE

Mauritia, 2 spp.

Mauritiella, 4 spp.

Lepidocaryum, 1 sp.

CALAMEAE, KORTHALSIINAE

Korthalsia, 28 spp.

CALAMEAE, SALACCINAE

Eleiodoxa, 1 sp.

Salacca, 23 spp.

CALAMEAE, PIGAFETTINAE

Pigafetta, 2 spp.

CALAMEAE, PLECTOCOMIINAE

Plectocomia, 14 spp.

Myrialepis, 1 sp.

Plectocomiopsis, 6 spp.

NYPOIDEAE

Nypa, 1 sp.

CORYPHOIDEAE

TRACHYCARPEAE, RHAPIDINAE

Chamaerops, 1 sp.

Guihaia, 4 spp.

Trachycarpus, 10 spp.

Rhapidophyllum, 1 sp.

Maxburretia, 3 spp.

Rhapis, 11 spp.

CHUNIOPHOENICEAE

Chuniophoenix, 3 spp.

Kerriodoxa, 1 sp.

Nannorrhops, 1 sp.

Tahina, 1 sp.

CORYPHEAE

Corypha, 5 spp.

BORASSEAE, HYPHAENINAE

Bismarckia, 1 sp.

Satranala, 1 sp.

Hyphaene, 8 spp.

Medemia, 1 sp.

BORASSEAE, LATANIINAE

Latania, 3 spp.

Lodoicea, 1 sp.

Borassodendron, 2 spp.

Borassus, 5 spp.

CEROXYLOIDEAE

CYCLOSPATHEAE

Pseudophoenix, 4 spp.

ARECOIDEAE

PODOCOCCEAE

Podococcus, 2 spp.

ORANIEAE

Orania, 30 spp.

SCLEROSPERMEAE

Sclerosperma, 3 spp.

ROYSTONEEAE

Roystonea, 10 spp.

REINHARDTIEAE

Reinhardtia, 6 spp.

COCOSEAE, ELAEIDINAE

Barcella, 1 sp.

Elaeis, 2 spp.

MANICARIEAE

Manicaria, 2 spp.

LEOPOLDINIEAE

Leopoldinia, 3 spp.

PELAGODOXEAE

Pelagodoxa, 2 spp.

Sommieria, 1 sp.

ARECEAE, ARCHONTOPHOENICINAE

Actinorhytis, 1 sp.

Archontophoenix, 6 spp.

Chambeyronia, 9 spp.

Appendix 1. continued.

ARECEAE, ARECINAE

Areca, 47 spp.

Nenga, 5 spp.

Pinanga, 143 spp.

ARECEAE, CARPOXYLINAE

Carpoxylon, 1 sp.

Satakentia, 1 sp.

Neoveitchia, 2 spp.

ARECEAE, CLINOSPERMATINAE

Cyphokentia, 2 spp.

Clinosperma, 4 spp.

ARECEAE, DYPSIDINAE

Chrysalidocarpus, 54 spp.

Dypsis, 106 spp.

Lemurophoenix, 2 spp.

Marojejya, 2 spp.

Masoala, 2 spp.

Vonitra, 10 spp.

ARECEAE, PTYCHOSPERMATINAE

Ptychosperma, 29 spp.

Ponapea, 4 spp.

Adonidia, 2 spp.

Balaka, 10 spp.

Veitchia, 11 spp.

Carpentaria, 1 sp.

Wodyetia, 1 sp.

Drymophloeus, 3 spp.

Normanbya, 1 sp.

Brassiophoenix, 2 spp.

Ptychococcus, 2 spp.

Jailoloa, 1 sp.

Manjekia, 1 sp.

Wallaceodoxa, 1 sp.

ARECEAE, RHOPALOSTYLIDINAE

Rhopalostylis, 2 spp.

Hedyscepe, 1 sp.

ARECEAE, VERSCHAFFELTIINAE

Nephrosperma, 1 sp.

Phoenicophorium, 1 sp.

Roscheria, 1 sp.

Verschaffeltia, 1 sp.

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Exploring for New Localities of *Tahina spectabilis* in North-eastern Madagascar

David Rabehevitra[1]

***Tahina spectabilis*, the most massive fan palm in Madagascar, was discovered in 2006 in a very remote locality northeast of Mahajanga. Recent field work has documented thirteen additional populations of this globally imperiled palm.**

The plant was described as a new Coryphoid genus in 2008 (Dransfield et al. 2008a) with a statement on the restricted distribution of the species. The IUCN assessment categorized *Tahina spectabilis* as Critically Endangered (CR) (Rakotoarinivo et al. 2012), which triggered the hunt for new populations using the predictive distribution map published in the two first papers on the species (Dransfield et al. 2008a)

A second population of *Tahina spectabilis*, was discovered by researchers from Royal Botanic Gardens Kew (RBG Kew), Parc Botanique et Zoologique de Tsimbazaza (PBZT) and the University of the Sunshine Coast (USC) in 2017, after the first one where the species was described and published in 2008 (Dransfield et al. 2008b). The discovery was sparked off by the recognition of the species from a photo sent by a local guide to the Royal Botanic Gardens Kew office in Antananarivo, the Kew Madagascar Conservation Centre (KMCC). The team mounted an expedition, first visiting the original type population and then visiting the new site where the photo was taken. The plant photographed was checked with local guide communities, recognized as *Tahina spectabilis* (Fig. 1) and published (Gardiner et al. 2017). This new discovery, occurring outside the area predicted in the original paper (Dransfield et al. 2008a) suggested that the palm might be more widespread. Researchers from Royal Botanic Gardens visited a new area to explore for potential populations.

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How it started

The trip to Amparihibe where the second population of *Tahina spectabilis* (Gardiner et al. 2017) was discovered, was an opportunity for RBG Kew team to launch a public awareness campaign with the local community on just how important the discovery of *T. spectabilis* is, and why the species is a natural legacy they have the obligation to take care of, for the present and for future generations. This campaign was followed by the distribution of a *T. spectabilis* poster and T-shirts several months later, with the emblem “let us protect *Tahina spectabilis*” in their own Malagasy dialect, emblazoned under a photo of *T. spectabilis* (Fig. 2).

Talk chains

As community members meet people wearing the *Tahina spectabilis* T-shirt and see the photo of the plant, conversations start with what the

1. *Tahina spectabilis* individual discovered in 2017.

plant is, why it is special and ending with "I know a place where there are some too." The site-based KMCC employee – Theophile Rajaonilaza – collected these "site names" along with the names of individuals linked with the information. He visited them on a later date to talk about the species, check with them if possible or plan a later visit and

2. *Tahina specabilis* T-Shirt created to heighten awareness and initiate discussions about the palm.

distribute the T-shirts to expand the publicity campaign. These same people were the ones to guide the team to the sites when they were available.

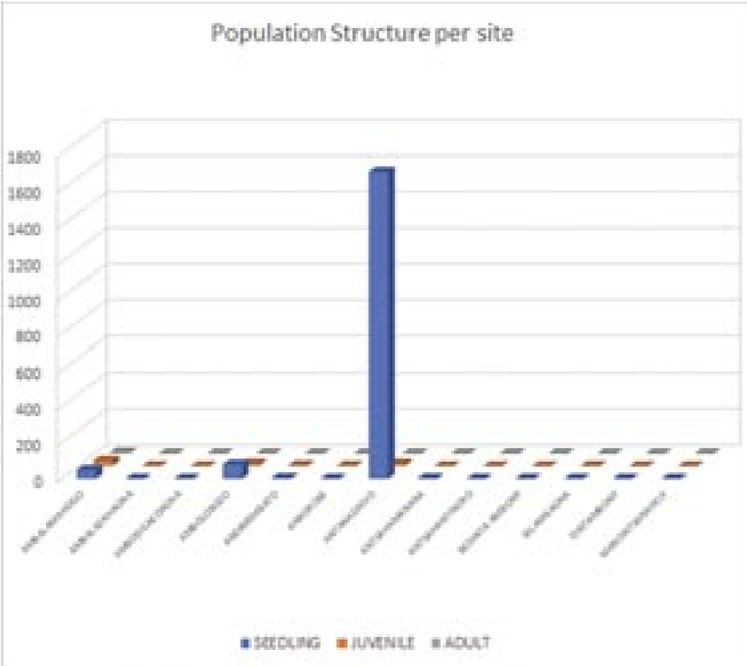
Thirteen new localities

These talk chains amongst community members enabled the recording of thirteen new localities (Fig. 3) – twelve on the eastern side, belonging to the commune of Maromandia, and one, within the commune of Ankaramy on the western side of National Road No. 6, between Befotaka village in the south and Ankaramihely in the north. We took the road as a geographical reference as it is the most obvious landmark for the area. However, the distribution map shows a possible positive correlation with the Ano Malaza River, except for the Antanagnivo population on the western side of the road. These newly discovered localities cover a wide latitude range which will bring an important change in the species' Area of Occupancy and Extent of Occurrence.

Few adults and numerous seedlings

The population structure was categorized into seedlings (S), juveniles (J) and adults (A), with two subcategories each, based on their relative size compared to adult human height for S and J, and the relative height of the trunk for A. This population structure is marked by a very high number of seedlings, ca. 1970, and a low number of juveniles (74) and adults (18) for the thirteen new localities (Fig. 4). The most important concentration of seedlings was recorded in Antanagnivo on the western side

3. Distribution map of the new *Tahina spectabilis* populations. On the left is the map of Madagascar with insets showing the region in the northwest where the palm is found. On the right is enlarged map showing the locations of the 13 newly discovered populations.



4. A graph showing the population structure of *Tahina spectabilis* in the 13 newly documented populations. Size classes are indicated. The number of seedlings in Antanagnivo is striking. The cause of this disparity is not currently known.

of the National Road No. 6, which consists of over 1800 plants and more than 100 individuals per square meter (Fig. 5).

Seeds and Nursery

The RBG Kew team had the luck to observe a flowering *Tahina spectabilis* in the beginning of 2018 in Manerinerina, which produced several hundred seeds (Fig. 6) that the team collected for nursery purposes in collaboration with the PBZT. Unfortunately, too many of the seeds collected dried out before they reached Antananarivo (Fig. 7), and germination was disappointingly low. Parc

5. The high density of seedlings in the population at Antanagnivo.

6. Flowering *Tahina spectabilis* in Manerinerina. The inset at the lower right shows a flower and a developing fruit.

Botanique et Zoologique de Tsimbazaza is now taking care of about 200 nursery seedlings, and about 50 seedlings are held in Theophile's village (Fig. 8).

Further comments

The high concentration of seedlings observed in Antanagnivo suggests a very prolific fruiting

7 (top). Germinating *Tahina spectabilis* seeds. 8 (bottom). *Tahina spectabilis* seedlings thriving in the nursery in Theophile's village.

event but a critical lack of natural dispersers, highlighting the importance of ecosystem interdependence for species survival. A community member living close to several *Tahina spectabilis* individuals in Ambolobozo mentioned seeing fruit bats visiting the fruiting palm and discarding the fleshless seeds, suggesting that bats may be the natural disperser of the palm.

It is also worth mentioning that more than ten site names are known to host *Tahina spectabilis* individuals, but some people are reluctant to allow the visit of strangers for different reasons that are not yet understood by the RBG Kew Team.

Finally, that *Tahina spectabilis* is a distinct palm different from the co-occurring fan palms *Borassus* spp. and *Bismarckia nobilis* is well understood in a few communities, and the local name, *bilambagna*, comes from the fact that their ancestors used the large leaf of the palm as a mat (*lambagna*) for eating during ceremonies. The KMCC Team is currently running a project which supports the community-led conservation of *Tahina spectabilis* near Maromandia through the promotion of yam cultivation, tree planting, well-drilling and classroom building within villages surrounding the best remaining habitat of the species, with an ultimate goal of implementing a community-managed Protected Area.

Conclusions

The second population of the *Tahina spectabilis* revealed in Amparihibe in 2016 has led researchers from Royal Botanic Gardens Kew to discover thirteen other localities, thanks to sustained collaboration with local communities and a continuous in-the field presence. These discoveries were the result of effective communication and public awareness undertaken – T-shirts and individual communication – to reveal people, localities and other key information. These newly discovered localities confirmed the possibility of a wider distribution of the species in this region and a wider AOO/EOO. Undertaking this research work enables the community to deliver their own knowledge of *Tahina spectabilis* and build a productive trust. These results open the door to further research in genetics and other fields such as history. Finally, researchers at RBG Kew hope to support the creation of a protected habitat for the species and reviewing the IUCN status of *Tahina spectabilis* soon.

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