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FRONT COVER

The Cuban endemic *Hemithrinax ekmaniana* is easily one of the most unusual, recognizable and yet little-known palms in the world. See article by Rodríguez Lima et al., p. 123. Photo by D.R. Hodel.

BACK COVER

Kerriodoxa elegans cultivated in Hawai'i. See article by M. Dahme, p. 135. Photo by J. Dransfield.

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Pacaya, the inflorescences of *Chamaedorea tepejilote*, are harvested and exported from Guatemala. See related article by Castillo Mont et al., p. 109. Photo by S. Zona.

PALM NEWS

A new species of *Wettinia*, *W. donosoensis*, was described recently by De Gracia et al. (Novon 25: 145–149. 2017.). The species is distinctive by virtue of its small size, few leaflets per leaf, unbranched inflorescence and very long petals on the pistillate flowers. It was discovered on a copper-mining concession in the Donoso District of western Colón Province of Panama, where it grows in lowland rainforests at elevations below 150 m. It is a lovely, small palm, but sadly, it is already endangered.

Biologists have recently published several studies of the insect visitors and pollinators of palms.

Lara et al. (Revista Mexicana de Biodiversidad 88: 106–112. 2017.) documented the flowering sequence and floral visitors of *Wettinia kalbreyeri*, a tall, stilt-rooted palm of the montane forests of Colombia. The researchers documented beetles, bees and flies as the principle floral visitors. Of these, sap beetles of the genus *Mystrops* (Nitidulidae) were identified as the main pollinators. Beetles of the genus *Mystrops* were also identified as the main pollinators of *Syagrus smithii* by Guerrero-Olaya and Núñez-Avellaneda (Revista Peruana de Biología 24: 43–54. 2017.). These researchers studied natural populations of the palm, a species from the western Amazon Basin, and found that the flowers are visited by beetles, flies and bees. *Mystrops* beetles visit both staminate and pistillate flowers to feed and copulate. Curculionid beetles were identified as pollinators of secondary importance. Floral visitors to *Nypa fruticans* in the Philippines were also found to include flies, bees and beetles, as detailed in a recent paper by Mantiquilla et al. (Asia Life Sciences 25: 1–22. 2016.). The authors found that beetles of the genus *Epuraea* (Nitidulidae) and fruit flies of the genus *Drosophila* (Drosophilidae) are the most likely pollinators of this important mangrove palm. Nogueira Mendes et al. (Brittonia 69: 11–25. 2017) reported their findings regarding the pollination of *Mauritia flexuosa*, a keystone species in some ecosystems of the Amazon Basin. In contrast to a recent study that identified wind as the major pollen vector (see PALMS 58: 109–114. 2014.), this study identified Curculionid beetles of the genus *Grasidius* as the most effective pollinators and found that wind played only a minor role. This study is further evidence that the pollination systems of *M. flexuosa* may vary geographically. Taken as a whole, these recent pollination studies document the importance of palms in their ecosystems and the interconnectedness of palms and other organisms. They also seem to show that beetles have “an inordinate fondness” for palms.



Luis Alberto Nuñez

A surprising study published by C.J. Sudsiri and colleagues (Scientia Horticulturae 20: 66–77. 2017) found that **electromagnetic fields substantially increase the percentage of African oil palm seeds germinating and the rate at which they germinate**. The team reported rapid and complete germination (96% in 30 days) for endocarps that were immersed in water and exposed to an EMF at 9 mT for four hours. The control groups had zero germination during the same period. They also noted that seedlings irrigated with EMF-treated water grew three times faster than controls. The authors could posit no known mechanism for the effects that they observed.

The Pacaya Palm, *Chamaedorea tepejilote*: Observations of its Cultivated and Wild Forms in Guatemala

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Within the large neotropical genus *Chamaedorea* (Arecoideae: Chamaedoreaceae), the pacaya palm (*C. tepejilote* Liebm.) is the only species that is cultivated as a food source, for its immature staminate (male) inflorescence.

Pacaya use is particularly common in Guatemala, where the species appears to have undergone domestication, as witnessed by the larger and more highly branched inflorescences produced by cultivated palms, which are solitary in habit. This morphology contrasts with that of wild pacaya palms, which in Guatemala are caespitose, produce smaller inflorescences and have a non-overlapping geographic distribution compared with the solitary/cultivated form. As the first step in a study aimed at understanding how domestication might have occurred in *C. tepejilote* and its underlying genetic basis, we visited several regions in Guatemala to observe and sample the diversity of cultivated pacaya palms and their wild relatives.

The pacaya palm and its importance in Guatemala

The pacaya palm (*Chamaedorea tepejilote*) is a dioecious species native to southern Mexico, Central America and western Colombia (Hodel 1992, Henderson et al. 1995). On the basis of linguistic studies, it is believed to have been exploited by mankind for two or three millennia in Central America (Brown 2009), principally for its comestible male inflorescence, which is harvested when immature. The word *tepejilote* means “mountain corn” in the Native American Nahuatl language, and the young pacaya inflorescence superficially resembles a cob of maize. In some respects, pacaya can be compared to asparagus in that it has a slightly bitter but pleasant taste. Fresh pacaya consumption is limited mostly to Guatemala and neighboring countries such as El Salvador and Honduras; however, the shucked inflorescences may also be bottled in an acidified water solution, allowing their export to other countries. A significant demand for preserved pacaya exists in North America,

especially amongst expatriates from Central America, leading to pacaya sometimes being referred to as a type of “nostalgia food.” Pacayas may be cooked in a number of ways, such as with egg to produce fritters (Fig. 1), in a tomato-based sauce, or simply boiled, then seasoned to taste (Fig. 2). Pacaya is a key ingredient in *fiambre*, the traditional Guatemalan dish prepared and eaten to celebrate the Day of the Dead and All Saints Day (Castillo Mont et al. 1994).

Figure 3 shows a pacaya plantation, and Fig. 4 shows a roadside pacaya stall. As can be seen from the photo, pacayas are usually harvested and sold without removing the inflorescence bracts, which provide protection during transport.

In Guatemala, the most sought after palms in cultivation produce inflorescences that are much larger than those of wild palms and more tightly packed within the inflorescence bracts due to increased branching (Castillo Mont et al. 1994). The contrasting morphologies of wild and domesticated pacaya palms led Cook and Doyle (1939) to consider the solitary, large inflorescence-bearing palms of Alta Verapaz as belonging to a separate species and even a different genus. They proposed the name “*Edanthe veraepacis*” for the cultivated palm; this unorthodox interpretation was not, however, adopted by taxonomists, and the two contrasting morphotypes found in Guatemala have long been considered as belonging to the same species. The fact that the cultivated pacaya palm is solitary in habit is significant in the context of domestication, since it indicates that the only possible means of propagation is through seed production (some caespitose palm species can be cloned via offshoots). The phenotype of present-day cultivated pacaya palms may therefore have resulted from

1 (left). Pacaya fritters (photo by F. Stauffer). 2 (right). Cooked pacaya (photo by D.R. Hodel).





3 (top). Pacaya plantation (photo by D.R. Hodel). 4 (bottom). A roadside pacaya stand (photo by F. Stauffer).

human selection over numerous generations of sexual reproduction. This makes the pacaya palm a particularly interesting case study to investigate domestication in the palm family. One particularly original feature of this species is that the sought-after characters for human

consumption relate to the male plant. Female plants, which produce inflorescences that are too bitter to be eaten, may be either sacrificed for palm heart production or simply left to act as a source of seed production for future generations.

Table 1. General information on sampling localities. Precipitation data are from climatedata.org.

Locality	Altitude (m)	Annual precipitation (mm)	Natural vegetation	Comments
Quetzal Biotope & vicinity, Baja Verapaz Dept.	1500–2348 (sampling at ca. 1500)	2000	Cloud forest	Most palms sampled were in cultivation. All solitary. Inflorescences mostly at optimal stage for consumption.
Cobán & vicinity, Alta Verapaz Dept.	1320	2270	Cloud forest	Most palms sampled were in cultivation. All solitary. Inflorescences mostly at optimal stage for consumption.
Las Escobas nature reserve, Cerro San Gil, Izabal Dept.	Up to 1145 (sampling at ca. 1000)	2750	Tropical rainforest	Clustering habit, inflorescences far less developed than in Alta/Baja Verapaz, no cultivated palms seen.
Chicacao & Suchitepéquez Dept.	470	3515	Tropical rainforest	Cultivated, wild and/or possible garden escape palms, solitary and clustering, some possibly originating from Izabal
Vicinity of Pacaya volcano, Escuintla Dept.	ca. 1500 (volcano rises to 2552)	1480	Scrub forest (much land given up to cultivation)	Palms observed and sampled were probable garden escapes.

Localities

Figure 5 shows the localities where we carried out observations and sampling of Guatemalan pacaya palms in 2014. The chosen itinerary took us to a number of contrasting locations: the central region in which pacaya cultivation is the most developed (Alta Verapaz and Baja Verapaz departments), the Caribbean (Gulf of Honduras) coast (Izabal department) and the Pacific-facing slopes in the south (Suchitepéquez and Escuintla departments). By sampling in several different regions, we had the opportunity to observe a good proportion of natural and cultivated pacaya palm diversity in Guatemala. Our itinerary also allowed us to witness pacaya palm flowering in contrasting environments. Some basic information on the different sites visited and their corresponding climates is given in Table 1.

Our field work consisted of three main activities: firstly, observations of the palms in their wild and domesticated environments along with cultivation practices; secondly the collection of samples for microscopy, RNA extraction and DNA extraction; and thirdly, measurements of the inflorescences produced by the pacaya palms at each locality so as to gain information on their morphological diversity. Samples for RNA extraction needed to be harvested and transported on dry ice, which represented something of a challenge for us as this substance sublimates rapidly in tropical field conditions. For morphometric measurements, a wide range of parameters was measured for each inflorescence harvested, including bract sizes, rachilla (inflorescence branch) length, rachis length and rachilla number. One point is important to note: because flowering in *C. tepejilote* is seasonal



5. Sampling localities (map reproduced from google.com).

and not the result of a continuous production of asynchronously developing inflorescences throughout the year, the inflorescences carried on a given plant will generally be similar in terms of developmental stage. However, some parameters such as rachilla length will vary widely according to the season and phenology (flowering timing) of the ecotype, making morphometric comparisons between sites and ecotypes difficult. One of the few parameters that can be compared relatively easily between sites and between individual palms is the number of rachillae carried on the inflorescence, provided of course that the inflorescence is sufficiently developed to allow

the count to be made. Our findings reinforced earlier observations that the cultivated, solitary pacaya palm morphotype carries larger numbers of rachillae on its inflorescences compared with the wild, clustering morphotype. This general tendency appeared to hold true for inflorescences of both sexes and was particularly striking in the case of the male inflorescence, which carried on average twice as many rachillae in the cultivated form compared to the wild form in our sampling. This approximate figure does not take into account any additional complexity attributable to the abnormal “patush” phenotype (see below). As is often seen in *Chamaedorea* species and palms in general, the number of rachillae is also sex-dependent, with female inflorescences carrying noticeably fewer rachillae than male ones. A brief account of the different localities we visited is given below.

Alta Verapaz and Baja Verapaz: the heart of pacaya country

Alta Verapaz is the country’s leading department for pacaya production, with neighboring Baja Verapaz also making an important contribution. Both departments contain areas of steep, beautiful mountainous cloud forest that have been significantly eroded by human activities in recent times, but which are now the subject of conservation

6 (left). Removing pacayas from tall palms (photo by J. Tregear). 7 (right). Harvested pacaya enclosed in the inflorescence bracts (photo by D.R. Hodel).





8 (left). Pacayas prior to harvesting. 9 (right). A pile of harvested pacayas waiting to be bagged. (Photos by D.R. Hodel.)

efforts. The prevailing climate is illustrated by the rainy mist known locally as *chipi chipi*, which is experienced throughout much of the year. Coffee production is important in the region, and pacaya palms may often be observed inter-planted with coffee trees. We also observed pacaya palms growing closely with bananas and maize. A typical smallholding is shown in Fig. 2. Our visit was made in April, which falls within the “high season” for pacaya production in Alta and Baja Verapaz. The large numbers of pacaya stalls seen by the roadside (Fig. 3) confirmed the continued importance of pacaya as a vegetable crop in this region of Guatemala. Nevertheless, some changes were seen to have occurred since observations made in the 1990s (Hodel 1992, Castillo Mont et al. 1994). As previously, the pacaya stands were observed to be usually small in size (less than 500 square meters); moreover, some plantations observed in the 1990s had disappeared. Although co-cultivation was still apparent, we saw signs that plantations were less intensively managed, and several abandoned pacaya stands were noted. This general trend towards less intensive cultivation and even abandonment could be explained by at least two possible factors. Firstly, rural depopulation might affect the availability of manpower for the upkeep of some plantations. Secondly, “westernization” of consumer habits in recent years might have

resulted in a lower demand for traditional Mayan vegetables such as pacaya. Unfortunately, given the lack of official data relating to the cultivation, consumption and trade of pacaya (Castillo Mont et al. 1994), it is not possible to make any generalized conclusions at present.

Thanks to the kind assistance of pacaya growers and stallholders, we were able to observe the cultivation, harvesting and selling of this vegetable at close hand. As can be seen in Fig. 6, a typical pacaya holding often contains other species of plants. Given the relatively tall size of adult palms (*C. tepejilote* is one of the largest species of the genus), a pole may be required to harvest pacayas from the tallest individuals. The enormous size of the cultivated pacaya inflorescence, even when immature and still enclosed by the bracts, can be seen in Fig. 7. In this case the total inflorescence bud length, including the bracts, was about 70 cm. Figure 8 shows a group of inflorescence buds still attached to the palm just prior to harvesting. A productive palm like the one shown will typically carry about half a dozen pacaya buds per season. Figure 9 shows a pile of harvested pacayas ready to be bagged and sold.

The patush phenotype: In addition to their larger overall size and increased branching, the inflorescences of Alta and Baja Verapaz palms



10 (left). Appearance of a “patush” inflorescence of *Chamaedorea tepejilote*. 11 (right). Fasciated portion of a severely affected inflorescence. (Photos by F. Stauffer.)

may also sometimes display a morphological character known as “patush” (Fig. 10). “Patush” inflorescences are even more highly branched than normal ones, but the phenotype appears to be a type of fasciation rather than a branching phenomenon per se. Indeed inflorescences displaying an extreme “patush” phenotype have what can only be described as an anarchic organization (Fig. 11), due to a presumed meristem dysfunction involving the abnormal fusion of neighboring organs. The “patush” character is sought after by consumers, since the tissues tend to be particularly tender and perhaps less bitter than those of “normal” pacayas.

Culinary notes: After a day of observing pacaya palms and taking samples, we were fortunate to be able to savor the “fruits” of our labors. Although pacaya was not on the menu at our hotel, the owners kindly agreed to cook some pacayas that we had brought back with us. We

were thus treated to cooked pacaya in two different forms, namely those shown in Fig. 1 (simply boiled/seasoned and fritters). Both were found to be very tasty, although the group vote seemed to weigh in favor of the fritter as the preferred cooking approach. It was interesting to note that pacayas harvested from different palms had slightly different tastes – presumably a reflection of natural diversity and perhaps a sign of potential for varietal selection.

Pacaya palm husbandry: As regards germplasm management, during our survey we saw no evidence of hand pollination being used as a tool to obtain pacaya palms of a precisely defined parentage. Nor indeed did we see any evidence of seeds being sown by the grower: all palms exploited appeared to have germinated in situ from naturally dispersed fruits. Nevertheless, management of the density and structure of the plantation was



12 (top). Repositioning of self-seeded palms in a pacaya plot. 13 (bottom). Probable “feral” pacaya palms growing in Alta Verapaz. (Photos by J. Tregear.)

observed to be achieved either by the repositioning of self-sown seedlings (Fig. 12) or by the elimination of unwanted plants. We can therefore draw the preliminary conclusion that genetic selection has taken place through the selective maintenance in the plantation of

male plants displaying desirable characteristics for human consumption. Although these plants do not produce seeds, the desirable pacaya characters that they contain in their genetic makeup can be transmitted to the next generation through the pollination of nearby

female palms, which will produce and shed fruit that later germinate in situ. This scenario requires that from time to time, a male inflorescence with desirable characteristics should be left unharvested so that it can complete its development and shed pollen. This is likely to happen on a regular basis in a pacaya plantation, probably mostly by chance rather than by deliberate planning.

Although the majority of our sampling in the Alta/Baja Verapaz departments was carried out in cultivated pacaya plots, we also attempted to find individuals on sites as far away as possible from civilization to assess whether any truly wild populations of solitary pacaya palm existed. Although we found the occasional small population in woodland or ravine sites (Fig. 13), we were unable to find *C. tepejilote* on any site that could be considered with certainty as being unaffected by human activity. The relationship between the “wild” palms we found in Alta/Baja Verapaz and the cultivated ones therefore remains to be determined. Clearly studies of genetic diversity should help to shed light on this question.

Izabal department: home of the wild clustering pacaya palm

The department of Izabal is situated immediately to the east of Alta Verapaz and contains a stretch of coast on its north-eastern side which opens into the Gulf of Honduras and Caribbean sea. We carried out our sampling in the Las Escobas nature reserve near the coast not far from Puerto Barrios. This is a site where various palm genera such as *Chamaedorea*, *Geonoma*, *Reinhardtia* and *Synechanthus* are well represented. At this location, only the clustering morphotype of pacaya palm can be found. No pacaya cultivation occurs in the area and all pacaya palms are considered to be wild. It became quickly apparent that the seasonality of flowering (i.e., phenology) was different from that seen in Alta and Baja Verapaz: whereas the pacaya palms observed in the latter region a few days earlier were nearing anthesis, the majority of their wild cousins in the Las Escobas reserve carried either old infructescences (Fig. 14) or very young infructescences. After a certain amount of searching, which involved climbing to the highest point of the reserve from which there was a tantalizing sea view, we eventually found a few pacaya palms with infructescences of a suitable stage for sampling, albeit much



14. Wild clustering morphotype of pacaya palm with infructescence (Las Escobas nature reserve) (photo by J. Tregear).

younger ones than those seen in Alta and Baja Verapaz.

Suchitepéquez and Escuintla departments: pacaya cultivation on the volcanic slopes

The medium altitude volcanic soils in the south of the country that suit coffee cultivation are also a favorable growing environment for the pacaya palm. Indeed, in this part of the country can be found the Pacaya volcano, which, it has been speculated, may have given its name to the comestible inflorescence, since *C. tepejilote* has been cultivated on its slopes for many centuries (Castillo Mont et al. 1994). We observed and sampled palms growing within sight of the latter volcano near the village of San Vicente Pacaya in the Escuintla department. We also made observations and took samples in the neighboring department of Suchitepéquez, on the slopes of the volcano San Pedro near Chicacao. In both of these departments, as well as in the adjoining department of Santa Rosa, the cultivated pacaya palm is thought to have been introduced (Castillo Mont et al. 1994). As seen earlier in the Izabal department,

we noticed that the flowering season in Suchitepéquez and Escuintla was significantly different from that of Alta and Baja Verapaz; indeed, in this part of the country, the pacaya harvest season is usually in September and October. Clearly it will be of great interest in the future to determine whether these differences in flowering behavior are explained by differences in environment or in genotype, or a combination of the two. As an additional reference point for future molecular studies, we sampled a few palms growing in cultivation for their ornamental value in the Suchitepéquez department. These palms, which were of the clustering morphotype, had been introduced at an earlier date from the Izabal department. Interestingly, their flowering was significantly more advanced than those seen near Puerto Barrios only two days before, possibly reflecting the importance of environment in the determination of flowering time.

Conclusions

Our short tour of the pacaya habitats of Guatemala allowed us to observe the flowering behavior of this species at close hand and to collect a range of tissue samples for molecular and histological studies. It also allowed us to talk with growers and sellers of pacaya and to witness the importance of this traditional Mayan vegetable in Guatemala. Last but not least, it gave us the chance to sample this culinary delicacy! Despite an apparent decrease in the numbers of pacaya plantations since the 1990s, it was clear that the pacaya palm continues to occupy an important place in Guatemalan cuisine and culture. Perhaps the increasing interest in “exotic” fruit and vegetables seen in Europe and elsewhere might one day result in pacaya being better known worldwide than it is today.

From a scientific point of view, this trip started us on our quest to understand how domestication might have occurred in the pacaya palm. A number of important questions need to be resolved, the most central one perhaps being the following: did domestication occur before or after the separation of the clustering and solitary forms observed in Guatemala today? Comparative studies incorporating pacaya palm ecotypes from other countries should help shed light in this area. It is interesting to note that the wild pacaya palms of Colombia and Panama are solitary: are these palms more closely related

to the cultivated solitary palms of Verapaz or to the wild clustering palms of Izabal? Much insight will be gained from studies of genetic diversity, but we also hope to identify, from a functional point of view, those genes which have been affected by the domestication process and which might therefore contribute to the striking appearance of the prized pacayas sold in the markets of St Cristobal and Cobán.

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Natalie Uhl (1919–2017)



Natalie Uhl died in the hospital from pneumonia on 28 March 2017 at the age of 97. She had a long life during which she developed a most distinguished career as a plant morphologist and anatomist and will be known to all interested in palms in her own right and as a long-term associate of Harold E. Moore Jr. She was a Co-Editor of *Principes*, later to become *Palms*, and co-author of two editions of the standard taxonomic reference to palms – *Genera Palmarum: a classification of palms based on the work of Harold E. Moore Jr. (GP1)* and *Genera Palmarum: Evolution and classification of palms (GP2)*.

Natalie was born in Rhode Island in 1919. She was educated at Rhode Island State College and at Cornell University, working under Professor Arthur J. Eames. In 1943, she gained her MS degree and then went to work on a PhD on the floral morphology and anatomy of a group of aquatic plants now known as the Alismatales, completing it in 1947.

In 1945 she married Charles H. Uhl, a plant cytologist specializing in Crassulaceae, also in Cornell University, at the School of Plant Sciences. They settled down in Ithaca, started a family and raised four children, Jean, Mary, Charles Jr. (Butch) and Betsy. They were

married for 65 years until Charlie's death in 2010. Once the children were more independent, Natalie was able to get back to academic life. In response to the launch of the Soviet Sputnik in the late 1950s, the US government, determined not to lose the space race, increased hugely the amount of funding available to universities for scientific research. Harold E. Moore, Jr. (Hal), one of the many beneficiaries of this increase in academic funding, was able to employ Natalie in 1963 as a research associate working on aspects of palm floral morphology, anatomy and development. Women scientists were few and far between in those days and Natalie was to see at first hand the gradual change in attitudes to women in academia. Hal was undoubtedly the preeminent palm scientist of that generation and was working towards a generic account of all palms, his *Genera Palmarum*. It was during this period in the late 1960s and 1970s that Natalie, either as a co-author or as an author in her own right, published a long series of critical and exemplary studies that provided essential insight into the structure and evolution of palms. In those pre-cladistic, pre-molecular phylogeny days, much of the phylogenetic structure of the palm family was developed intuitively, and Natalie's work



Charlie and Natalie Uhl in the garden. (Photo by Charles Uhl Jr.)

provided a remarkably robust set of anatomical and developmental characters informing taxonomic decisions.

When Hal Moore became gravely ill in 1980, he planned the succession for the editing of *Principes* and the continuation of his grand project, *Genera Palmarum*, passing the baton to Natalie and suggesting that I should somehow also be involved. In late 1980, I was invited to visit the Bailey Hortorium in Cornell to discuss how *Genera Palmarum* might be completed.

Here began a period of six years of very close collaboration during which we worked together to write the book that was eventually published as *GPI*. This involved twice-yearly visits for me to Cornell University of a month each. I remember these visits so clearly, the times we spent discussing palm morphology and classification, the enjoyable meals together, walks in the Finger Lakes district and the warm hospitality shown by the Uhls. Occasionally Natalie made visits to Kew.

During this period, Natalie worked away on co-editing *Principes* and, as co-editor and Board Member, frequently attended Palm Society meetings, watching as the society changed from the Palm Society to the International Palm Society with a much broader outlook and membership base.

The first edition of *Genera Palmarum* spawned new interest and research into the family and new data accumulated rapidly. New genera and species were published, and the limits of genera recognized in *GPI* were in some instances called into question. Molecular research burgeoned and methods for analyzing large datasets using cladistic methodology became more and more refined and available, allowing the re-examination of the inter-relationships of genera. Quite soon, the need for a second edition of *Genera Palmarum* became evident. Natalie and I continued our collaboration, meeting every year at the Montgomery Botanical Center in Miami for two-week sessions of discussion and data matrix compilation, using the unparalleled resources of the living collections at the Center. We co-opted William (Bill) Baker, Connie Asmussen, Madeline Harley and Carl Lewis into the authorship of *GP2*, which was finally published in 2008.

Natalie was awarded the Founder's Medal, Fairchild Tropical Garden (1988), the Engler Medal, International Association of Plant Taxonomists (1990), the Asa Gray Award, American Association of Plant Taxonomists (2002), The Dent Smith Award, International Palm Society (1999), Robert Allerton Medal, the National Tropical Botanical Garden (2003) and Honorary Membership of Montgomery



Charles Uhl Jr.



Natalie Uhl and John Dransfield hold a copy of *Genera Palmarum* edition 2 at a launch party, L.H. Bailey Hortorium, Cornell University, Ithaca, New York, in 2008. (Photo by Soejatmi Dransfield)

Botanical Center (2004). Natalie's great contribution to palm botany was celebrated at the World Palm Conference in 2015 in Colombia, which, sadly, she was unable to attend.

Natalie was a quiet, unassuming person of great dignity and elegance, polite and concerned for other people. In her scientific career, she was perceptive, critical and extremely thorough. Behind this dignified

exterior, however, she was immense fun and a real joy to work with. Out of the tragic death of Hal Moore came a wonderful collaboration. I count myself immensely lucky to have known and worked with Natalie. She was a very special person.

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Hemithrinax ekmaniana, Jewel of the Cuban Palms

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The Cuban endemic *Hemithrinax ekmaniana* is easily one of the most unusual, recognizable and yet little-known palms in the world. Here we update its description, provide information about its history, habitat and phenology and discuss threats to its survival.

Joseph Dalton Hooker erected the genus *Hemithrinax* in 1883, basing it on the previously named species *Trithrinax compacta*, which August Heinrich Rudolf Griesbach and Hermann Wendland had named in 1866 (Griesbach 1866). This species was based on a

collection that Charles Wright had made in Cuba (Wright 3222). Max Burret named the amazing *Hemithrinax ekmaniana* in 1929, one of four species in the endemic Cuban genus, basing it on a collection that the Swedish botanist and explorer Erik Leonard Ekman had



1 (top). *Hemithrinax ekmaniana* is endemic to the Mogotes de Jumagua, a set of eight, karst limestone hills surrounded by agricultural fields near Sagua La Grande, Villa Clara. 2 (bottom). Mogote no. 4 is one of three of the set of eight mogotes that has *Hemithrinax ekmaniana*. Note the barely visible palms on the north (right) side of the hill (Photos by D.R. Hodel).

made in 1924 in central Cuba (*Ekman 18536*). Borhidi and Muñiz (1985) transferred it to *Thrinax* but later Lewis and Zona (2008), using mostly molecular data, returned it to *Hemithrinax*.

Ekman on his herbarium specimens and Burret in his article cited the locality of *Hemithrinax ekmaniana* as "Sagua La Grande." A few years later, in 1940, Leon made a collection of this species and cited the location as "Caguaguas-



3. *Hemithrinax ekmaniana* is an unarmed, solitary, tree palm, to 7 m tall. The green, living and brown, dead, persistent leaves form an obovoid-shaped canopy (Photo by D.R. Hodel).

Sagua la Grande," a community near the east end of Mogotes de Jumagua, a few kilometers from the city of Sagua La Grande (a *mogote* is

a hill of karst limestone, which is typically composed of uneven, multi-sized limestone rocks with extremely sharp, fissured, pitted



4. Leaf bases of *Hemithrinax ekmaniana* are split at the base (Photo by D. Suárez).

surfaces). When publishing his treatment of *Hemithrinax* in his series on Cuban palms, Leon (1941) gave the more precise location where *H. ekmaniana* grew, the “Mogotes de Jumagua,” currently in the province of Villa Clara, municipality of Sagua La Grande.

Mogotes de Jumagua is a set of eight, connected, upper Cretaceous, karst limestone hills belonging to the geological formation known as Alturas Heights in the northern Cordillera de Las Villas, about five kilometers from Sagua La Grande (Fig. 1). The connected hills, which attain a maximum height of 86.8 masl, are arranged in a linear fashion in a more or less southeast to northwest orientation. In the 19th century, Pezuela (1866) stated that they were known as “the Hills of the Jumagua” and described them as “...calcareous in character, that running north are separated to the O. [west] by a marshy terrain between

mountains called by navigators Mogotes...” The eight hills are in two groups separated by a small valley and are crisscrossed and connected by an extensive network of caves. In the southeast one group has hills 1 and 2 while to the northwest the second group has hills 3, 4 (Fig. 2), 5, 6, 7 and 8.

In 1976, a quarry was established on one of the hills of Mogotes de Jumagua for the mining and extraction of limestone aggregates. This activity, which was responsible for destruction and significant loss of biodiversity at the site, drew the attention of the speleological and archaeological group Sabaneque in early 1977. Based on the site’s natural and historical value, Sabaneque made the successful case for protecting the Mogotes de Jumagua from mining and other destructive activity, and it was soon declared an ecological reserve as part of the National System of Protected Areas of Cuba. Conservation activity began in 1984 when it was formally named the Mogotes de Jumagua. In 2008 the Council of State of the Republic of Cuba legally established Mogotes de Jumagua, designating 453 ha as an area of national significance because of its interesting flora and fauna and its archaeological, paleontological and historical value (CNPAP 2011–2015). The Mogotes de Jumagua contains 442 species of vascular plants belonging to 302 genera of 106 families (Castañeda 1996). In addition to *Hemithrinax ekmaniana*, another endemic of exceptional merit at the site is the small tree *Tabebuia saxicola*.

Materials and Methods

During the last ten years, we observed and collected data on *Hemithrinax ekmaniana* at the Mogotes de Jumagua on multiple occasions. We reviewed the literature, including the original account of the species (Burret 1929), and located herbarium specimens, including Ekman’s types, in Cuban and foreign herbaria (GB, HAC, HAJB, ULV, NY and S). We cite herbarium acronyms according to Index Herbariorum (Thiers 2012).

We defined three basic stages of plant development to describe population structure accurately: seedling (leaves only, without visible stem); juvenile (with visible stem but non-reproductive); and adult (reproductive).

We used a Garmin® GPS (62s series, accuracy ± 5 m) to determine the spatial area of the population of *Hemithrinax ekmaniana*. We collected phenological data monthly from 100 individuals. We obtained floral measurements

using a stereo-microscope Comecta SA at 200X magnification and measured and recorded data from 10,000 fruits and seeds. For fruit, seed and stem diameters (the latter 1.3 m above ground) we used a metric micrometer (accuracy ± 0.05 mm) and weighed fruits and seeds on a Gibertini balance (EU-C5001, precision ± 0.1 g). Depending on palm size and location, we used a Suunto hypsometer (0.1 m accuracy) or 10-meter tape (mm and cm fractional units) to determine height and annual growth rate.

We followed Borhidi and Muñiz (1986) to describe the phylogeographic location and Capote and Berazaín (1984) to define the type of plant formation where *Hemithrinax ekmaniana* occurs. We obtained companion species information from Castañeda (2006) and Falcón et al. (2013–2014). For conservation status, we supplemented our data with information from Berazaín et al. (2005), Borhidi and Muñiz (1983), Dransfield et al. (1988), IUCN-BGCS (1989), Johnson et al. (1996), Peña et al. (1998), Walter and Gillett (1998) and Zona et al. (2007) and determined the conservation category on criteria from IUCN (2012). The laboratory of the “Marta Abreu” Central University of Las Villas identified pests associated with *H. ekmaniana*.

Results and Discussion

Hemithrinax ekmaniana Burret, Kongl. Svenska Vetensk. Acad. Handl., n. s., 6(7): 9. 1929. Type: Cuba. Villa Clara: Sagua La Grande, “on steep rock,” 20 February 1924, *Ekman 18536* (S05-5546) lectotype (here designated) S (photo!); isolectotypes (S-R-2860, S05-5547, S05-5548) S (photos!), NY (photo!), GB.

Thrinax ekmaniana (Burret) Borhidi and O. Muñiz, Acta Bot. Hung. 31: 227. 1985.

Unarmed, solitary, tree palm, to 7 m tall but attaining maturity and fruiting when less than 1 m tall (Fig. 3). Trunk erect, 6.4–7.6 cm diam. at base and 5.1–6.9 cm diam. at 1.30 m above ground, smooth, very faintly ringed, grayish. Leaves palmate, very densely inserted, ca. 40–60 green and 50–70 brown persistent, forming an obovoid-shaped canopy (Fig. 3); base 18–22 cm long, 13–15 cm wide, proximal part split (Fig. 4), this 14.1–17.8 cm long, 10 cm wide where attached to trunk, proximal margin composed of slender, grayish, unbranched fibers 13–16 cm long, 0.8–1.3 mm diam., arranged in 2 densely woven layers, distal margins composed of slender, cream-colored, unbranched fibers 45–65 cm long, 1–2 mm thick, becoming thread-like distally and

5. Distal margins of the leaf bases of *Hemithrinax ekmaniana* are composed of slender fibers 45–65 cm long that protrude conspicuously from among the leaves (Photo by D.R. Hodel).





6. The interfoliar inflorescences of *Hemithrinax ekmaniana* are ascending to spreading in flower and drooping in fruit (Photo by D.R. Hodel).



7 (top). Inflorescences in flower of *Hemithrinax ekmaniana* are ascending in flower. Note the densely placed flowers (Photo by D. Suárez). 8 (bottom). Fruits of *Hemithrinax ekmaniana* are yellow to creamy at maturity and densely placed (Photo by D.R. Hodel).

protruding conspicuously from among the leaves (Fig. 5); petiole to 10 cm long, 1.6 cm wide and 8 mm thick at base, 1.3 cm wide and

6 mm thick at apex, biconvex, green, margins sharp and with deciduous hairs; hastula adaxially triangular, light green, to 1.4 cm high

Table 1. Population Age Structure of *Hemithrinax ekmaniana*, Mogotes de Jumagua, Villa Clara, Cuba, 2004–2014.

Mogote	Seedling		Juvenile		Adult		Total	
	2004	2014	2004	2014	2004	2014	2004	2014
4	7	3	0	0	5	6	12	9
6	59	63	102	108	243	247	404	418
7	11	12	6	7	50	58	77	77
Total	77	78	118	115	298	311	493	504

with 0.8 mm apical point, 2 cm wide and 8 mm thick at base, abaxially +/- triangular, pale green, to 3 mm high with 0.5 mm apical point, 1.8 mm wide and 0.7 mm thick at bases; blade cuneate to broadly cuneate, 50 cm wide, rigid, pale green to slightly waxy green adaxially, conspicuously waxy silvery gray abaxially (Fig. 5), composed of 28–32 segments, these with thickened margins, midrib impressed adaxially, raised abaxially, 6–9 conspicuous primary nerves on each side of midrib, transverse veinlets barely visible, central segments 36–42 cm long, connate in proximal 1/3 and free in distal 2/3, narrowing to bifid apex to 1 cm long, rarely to 7 cm long, lateral segments to 27 cm long, connate in proximal 3 cm only, otherwise free, a filament-like appendage 8.9–14.6 cm long, 0.1–0.3 mm diam. frequently arising from the junction of adjacent segment margins. Inflorescences interfoliar, 60–80 cm long, slightly shorter than subtending leaf in flower to exceeding the subtending leaf in fruit, ascending to spreading in flower, drooping in fruit (Figs. 6 & 7); peduncle to 64.5 cm long, 0.8 cm diam. at base, clothed with 6–8, tubular, tomentose, densely striated bracts, prophyll to 11.5 cm long, acute at apex, peduncular bracts 8.3–13.0 cm long, acuminate at apex, distal most bract exceeding the peduncle and extending on to rachis; rachis 8–12 cm long with 1–3 primary branches, these 21–28 cm long, 3.5 mm diam. at rachis, secondary branches 1–3 per primary branch, 0.9–1.1 cm long, 2 mm diam. at primary branch and subtended there by a thin, deciduous bracteole 0.8 mm wide; rachillae up to 9 per inflorescence, 4–5 cm long, 1.5–1.8 mm diam., each averaging 42 flowers, each subtended by a deciduous bracteole to 0.6 mm long. Flowers solitary, densely and irregularly placed (Fig. 7), sessile on a short tubercle-like pedicel, whitish, lacking bracteoles; perianth cupular, 2 mm wide, 6 lobed, lobes small, ovate; stamens 6, sessile, filaments lacking,

bases connate; anthers oblong, 0.7 mm long with a very broad connective. Fruit averaging 233 per infructescence, 28 per rachilla, densely but irregularly placed (Fig. 8), 4.5–5 mm diam., globose, yellow to creamy at maturity, placed on a on a short tubercle-like pedicel; seed 3.9–4.0 mm diam., depressed-globose, seed 3.9–4 mm in diameter, hilum basal, endosperm homogenous, embryo subapical.

Additional Specimens Examined: Cuba. Villa Clara: Caguaguas-Sagua la Grande, Mogotes de Jumagua, 5 April 1940, *León, Carabia & Marie-Victorin 17637* (HAC); April 1992 *Henderson & Galeano s.n.*, (NY, [photo]); 26 March 1992 *Castañeda 4567* (ULV); 2 November 1994, *Castañeda 5188* (ULV); 5 October 1996, *Morici 350* (HAC); 12 October 1998, *Castañeda 1914* (ULV); 28 February 2012, *Borsch et al. 5196* (HAJB, B, ULV); 18 January 2013, *Rodríguez & Suárez 42764* (AJBC); 12 October 2013, *Pérez-Obregón 10701* (ULV); 26 September 2015, *Rodríguez 10991* (ULV).

Distribution and Ecology

Hemithrinax ekmaniana is endemic to Mogotes de Jumagua, Sagua La Grande, Villa Clara, about 16 km from the northern coast of Cuba, where it grows mostly on north-facing cliffs at and near the tops of mogotes 4 (Fig. 2), 6 and 7 only, from 20 to 80 masl. There it is perhaps the most conspicuous element of the semi-deciduous, mesic forest and Mogote Vegetation Complex.

This area, which is exposed to the prevailing north and northeast winds, has a pronounced and lengthy dry season, and native plants at the site, including *Hemithrinax ekmaniana*, are predominantly xerophytes. Indeed, *Morici* (2000) referred to *H. ekmaniana* as the most xerophytic species of the genus. Extreme drought, warm temperatures, wind, high solar radiation and a porous substrate characterize the site. For six months the palms survive with



9. Senior author Milián Rodríguez stands with several of the more than 300 adults and a few of the more than 100 juveniles at the Mogotes de Jumagua (Photo by D.R. Hodel).

only about 20% of the already low annual rainfall; average rainfall for the last 10 years is about 1,020 mm in the rainy season (May 20 to October 15) and only about 270 mm for the dry season (CMPVC 2015). That the palms are mostly on the sides of north-facing cliffs where solar radiation is lower and even shade is present for part of the year, especially when they are young and establishing, undoubtedly helps with their survival.

Companion species include *Agave legrilliana* Jacobi (Asparagaceae), *Capparis grisebachii* Eichler (Capparaceae), *C. cynophallophora* L. (Capparaceae), *Forestiera segregata* (Jacq.) Krug & Urb. (Oleaceae), *Guapira discolor* (Spreng.) Little (Nyctaginaceae), *Hybanthus havanensis* Jacq. (Violaceae), *Hyperbaena racemosa* Urb. (Menispermaceae), *Malpighia pallens* Small (Malpighiaceae), *Philodendron lacerum* (Jacq.) Schott (Araceae), *Picramnia pentandra* Sw. (Picramniaceae), *Pseudocarpidium ilicifolium* (A. Rich.) Millsp. (Lamiaceae), *Selenicereus grandiflorus* (L.) Britton & Rose (Cactaceae), *Sideroxylon foetidissimum* Jacq. (Sapotaceae), *Tabebuia myrtifolia* (Griseb.) Britton (Bignoniaceae), *T. saxicola* Britton (Bignoniaceae) and *Trichostigma octandrum* (L.) H. Walter (Phytolaccaceae).

Population Age Structure

Table 1 shows the age distribution of the population of *Hemithrinax ekmaniana* for 2004 and 2014. The 2014 census counted 311 adults (Fig. 9), 115 juveniles and 78 seedlings, figures that differed little from the 2004 census, indicating that the population has remained stable over the 10-year period.

Phenology

Hemithrinax ekmaniana initiates flowering at the beginning of the rainy season, about late May, and continues until the middle of September, while fruits are produced from late June to the middle of October to (Albert and López 1993). Fruit maturation averages about three months. Fruits can persist on the tree for up to one year (Morici 2000). The average weight and volume of 1000 fruits are 56.58 g and 86 cm³, respectively. The average weight and volume of 1000 seeds are 42.70 g and 64 cm³, respectively. The growth rate is slow, about 1.27cm of trunk per year.

Conservation Status

The narrow, restricted range of *Hemithrinax ekmaniana* increases its susceptibility to a random, single, disruptive event, like a

hurricane (tropical cyclone), and to potential damage from weeds, animals, disease and human activity. A large plain with extensive agricultural activity surrounds the Mogotes de Jumagua, where *H. ekmaniana* is endemic. This agricultural activity could threaten fragile biotic relationships and the entire *mogote* ecosystem. Construction of an agricultural drainage canal at the base of the north side of the *mogotes* has altered surface water runoff patterns. On the south side of the *mogotes* the use of agricultural pesticides can negatively affect local fauna, mainly insects, including pollinating beetles (Coléoptera: *Carybrychus* sp.). We have also observed insect-predated seeds and termites in trunks of *H. ekmaniana*, both of which could be affected by nearby pesticide use. Another threat is the common occurrence of summer thunder storms, which in the past have killed five individuals of *H. ekmaniana* with lightning strikes.

With a single population occupying only 2.3 ha of a 10-ha site, *Hemithrinax ekmaniana* is one of the most narrowly distributed and vulnerable Cuban palms. Fortunately, because it is located in a legally protected area with difficult access, well preserved vegetation and soils unsuitable for agriculture, we do not predict a decline in its population size; thus, we confirm its inclusion in the vulnerable category, Vu (D1-2), according to IUCN (2012) criteria, which González-Torres et al. (2016) confirmed.

Ex Situ Conservation

Hemithrinax ekmaniana is cultivated in several botanical gardens in Cuba, including the National Botanical Garden (Havana), Cienfuegos Botanical Garden, Las Tunas Botanical Garden and the Botanical Garden of the "Marta Abreu" Central University of Las Villas. Outside Cuba it is cultivated in the Palmetum of Santa Cruz de Tenerife in the Canary Islands, Spain; Orto Botanico di Messina in Italy; and Fairchild Tropical Botanic Garden and the Montgomery Botanical Center in Florida, USA (Palmpedia 2015). It is also cultivated in a few private gardens in Sagua La Grande, Cuba and South Florida, USA.

Ornamental Potential

Because of its unique habit and leaves, *Hemithrinax ekmaniana* has great ornamental potential and would be especially suitable for subtropical and tropical gardens in areas with a pronounced and lengthy dry season and poor, rocky and/or limestone soils. Although

slow growing, it is easily propagated from seeds and cultivated using traditional nursery methods.

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Observations on Reproduction in *Kerriodoxa elegans*

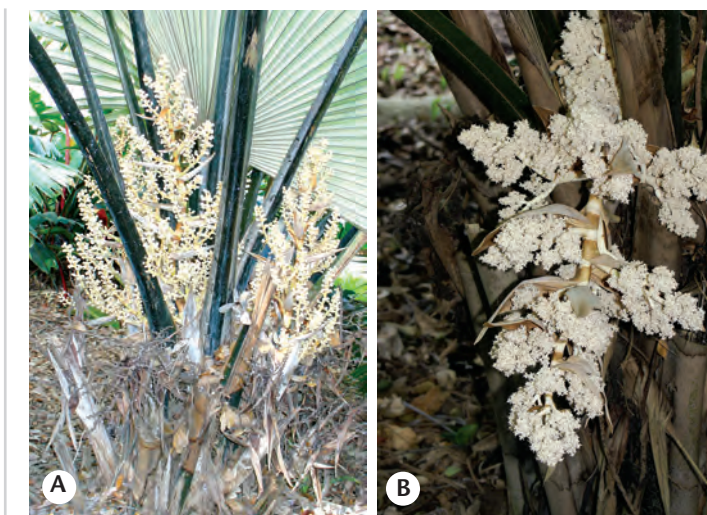
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1. Inflorescences of *Kerriodoxa elegans* are sexually dimorphic.
A. Pistillate (female).
B. Staminate (male).
(Photos by S. Zona).



Observations of plants in cultivation reveal that the species is not always strictly dioecious. The exact nature and stability of the gender expression in *Kerriodoxa elegans* (Fig. 1) need further investigation.

Some years ago, following a friend's suggestion that more is better than less, I planted about 40 *Kerriodoxa elegans* in the mountains of Puerto Rico's central cordillera. About two dozen survived. The first to mature was in December 2014, a female. The inflorescences in this dioecious species are distinctive, and the two sexes are readily distinguished by appearance (Fig.1). A year later, four more

flowered bringing to total number of adults to two staminate (male) plants and three pistillate (female) plants. A sixth plant, another female, began flowering in late 2016/early 2017. Flowering is annual. Here in Puerto Rico, the flowering season is late November into January, with peak flowering in December. Flowers were well attended by bees, and in due time, fruits appeared on the females. After



2 (top). Staminate inflorescences at or just after anthesis, 23 December 2016. 3 (bottom). Small fruits visible on infructescence, 1 January 2017.

initially noticing the flowers and fruits, I paid little attention to the plants. It was not until around March 2016 that I noticed that one of

the supposed males was also carrying fruits. I did not have photographs of this plant's inflorescences when it was in bloom, and with



4. Fruits forming on two of the infructescences, April 2017.

the old inflorescences now decayed, I could not rule out an identification error. I resolved to pay closer attention the next flowering season.

In December 2016, I confirmed that the palm I had identified as male was indeed so, though it had produced viable fruit (Figs. 2 & 3), which it is now [April 2017] again doing (Fig. 4). In Dec/Jan 2015/16, it had four inflorescences, but only one of which produced fruits. A year later, it had five inflorescences, two of which are developing fruits. The palm carries fewer fruits than the female plants, and the size of the fruits is noticeably smaller. However, several seeds from this plant germinated, a fact that demonstrates their viability. Is it possible that some staminate inflorescences contain some female flowers as well, or that some male flowers have functional pistils (and are thus perfect or bisexual)? This would perhaps account for the preponderance of female plants in Phuket, as noted in the description of the species (Dransfield 1983).

When I left the island in September 2016, I was not sure that the fruits were mature, so I harvested 20 or so for planting and left the

remaining fruits on the plants. I wrapped the infructescences of the four fruiting palms with wire mesh to protect them from rodents. On my return, in December 2016, I found that these 100 or so fruits had detached from their infructescences and germinated among the leaf litter but had not yet produced roots. In contrast, all but one of the 20 seeds sown in community pots had masses of roots and were difficult to separate. Germination is remote ligular, there being a short stalk (similar to that of *Bismarckia nobilis*) between the seed and the point of root and eophyll production. Fruit maturation is a nine-month process, and germination is very fast.

A final observation is that the six plants that are the first to mature are also the six closest to water, an ever-flowing stream that, in flood, reaches three of them. This species is a water lover.

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Photo Feature



Ravenea madagascariensis. A staminate plant in full flower; note the many narrow leathery bracts that hang down on either side of the flowers. The flowers are very sweetly scented (with a scent very similar to that of *Chamaedorea fragrans*). They attract large numbers of insects, including beetles (inset). Andasibe, Madagascar.

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A New Species of *Pritchardia* from the Marquesas Islands with Notes on the Genus in French Polynesia

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The genus *Pritchardia* includes 27 species of fan palms, of which 24 are restricted to the Hawaiian Islands and three are widespread in the South Pacific – *P. pacifica*, presumably from Fiji but known exclusively from cultivated specimens, *P. thurstonii* from Fiji and Tonga, and *P. mitiarioana* from the Tuamotu Archipelago in French Polynesia and the Cook Islands (Hodel 2007, 2009, 2012) (Fig. 1). In the Hawaiian Archipelago, these palms are found from sea level to 1200 m elevation in dry to wet forests on volcanic soils, whereas in the South Pacific they are mainly lowland species inhabiting uplifted coral limestone (Montaggioni et al. 1987, Pirazzoli et al. 1988). Here we provide a name and description of a new species from the Marquesas Islands, which prompted us further to investigate and review material of *Pritchardia* in French Polynesia.

From old botanical literature, a species of *Pritchardia*, incorrectly identified as *Corypha umbraculifera* (Forster 1786a, 1786b, Bennett 1840, Jouan 1865), *Chamaerops humilis* (Stewart 1831), and then later *Pritchardia pacifica* (Seemann 1865–73, Drake del Castillo 1886–1892, 1893), was noted from the Marquesas Islands under the Marquesan names of *vahane* on Tahuata Island in the southern Marquesas and *vahake* on Nuku Hiva Island in the northern Marquesas. Old herbarium specimens of Forster in 1774 and Langsdorff in 1804, cited by Seemann (1865–73) and Drake del Castillo (1893), were not located.

In November 2009, during surveys aimed at gathering Marquesan vernacular names to produce booklets on the Marquesan flora (Butaud 2013a, 2013b), several inhabitants of the island of Tahuata (Jeanne Timau & Félix Barsinas, pers. comm. 2009) identified the name *vahane* with two old palm trees growing in Hapatoni village, one of which is the type specimen of the new species here described (Fig. 2).

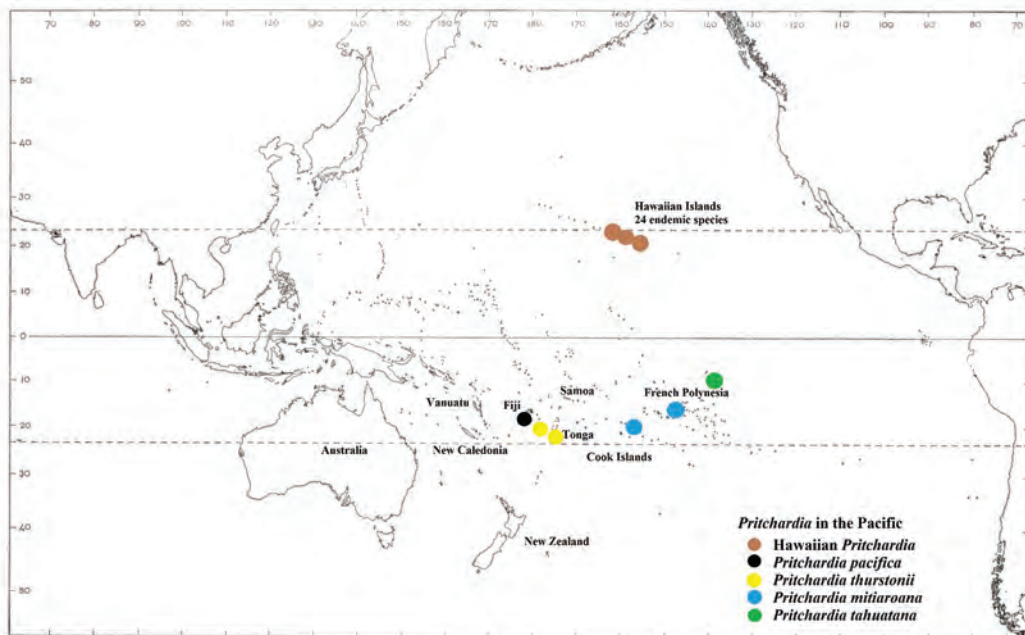
***Pritchardia tahuatana* Butaud & Hodel sp. nov.**

Pritchardia tahuatana differs from all other species in the genus by a combination of its non-ventricose trunk and inflorescences branched to four orders. Also, the red to purple cotyledonary sheath of young, newly

germinated seedlings is unique in the genus. Type: Cultivated: FRENCH POLYNESIA: Marquesas Islands, Tahuata, Hapatoni, Chez Kiri et Pauro Vaimaa en littoral au début de l'allée des Anciens, UTM 7 X 705 482 Y 8 897 259, 9 m elev., 24 September 2016, J.-F. Butaud 3496, with D. Hodel, M. Hodel, and R. Hodel (Holotype PAP, isotype P).

Solitary, moderate, tree palm, 10–20 m tall. Trunk 17–27 cm DBH, smooth, grayish tan, longitudinally striated, straight proximally but sometimes curved distally on old specimens, flared basally and there sometimes with conspicuous root boss, frequently notched with hand- and foot-holds. Leaves palmate, 20–35, ascending to drooping, 1.85–2.75 m long, forming a hemispherical to spherical canopy (Fig. 2), sometimes older ones persistent and forming a short skirt; base ca. 30 cm long, 20 cm wide, margins with abundant and conspicuous tan, papery to hair-like fibers to ca. 25 × 1.25 cm (Fig. 3), these extending on to proximal petiole, densely clothed with thick, brownish tan tomentum; petiole 75–100 × 5.5 cm, flat adaxially, convex abaxially, margins sharp, densely clothed with partially deciduous, thick, tan to whitish tomentum especially proximally; blade 110–150 × 150–175, undulate, slightly less than semi-circular (Fig. 4), green with scattered, moderately dense, whitish lepidia abaxially (Fig. 5), ridges of segment folds proximally and

1. Distribution of the genus *Pritchardia* in the Pacific Ocean.





2. *Pritchardia tahuatana* typically has 20–35, ascending to drooping, palmate leaves that form a hemispherical to spherical canopy. (Hapatoni, Tahuata, type, J.-F. Butaud et al. 3496). (photo by D.R. Hodel).

hastula clothed with partially deciduous, thick, whitish tomentum, sometimes with long, slender, curled filaments at segment junctions especially on juvenile plants; rachis to 18 cm long, segments ca. 65, center ones 135 × 6 cm, free for 67 cm, tip bifid for 7 cm, lateral ones 140 × 5.5 cm, free for 66 cm, tip bifid for 3 cm, basal ones 80 × 3 cm, free for 50 cm, tip bifid for 8 cm, tips stiff to drooping, hastula 4 × 5 cm. Inflorescences interfoliar, 3–12, slightly ascending to spreading in flower, spreading in fruit, curved, persisting when dead, branched to 4 orders (Fig. 6), to ca. 115 cm long, shorter than to ca. equaling petiole; peduncle 60–85 cm long, 20–33 × 15–22 mm diam., slightly flattened in cross-section, densely clothed with whitish tan tomentum; prophyll ca. 20 cm long, peduncular bracts 5, most distal reaching 1st panicle branch; panicle 50–65 cm long,

spreading in flower, nodding when heavily laden with fruit, composed of up to 16 branches and 7 simple rachillae, most proximal branch largest, to ca. 25 cm long and with several sub-branches and up to 42 rachillae; rachis 40–50 cm long; rachillae to 145 × 3–3.5 mm, straight, glabrous, brownish in flower, green in fruit. Flowers in moderately dense spirals 2–3 mm distant, fresh flowers at anthesis not seen, in bud slightly distal pointing (Fig. 7), 8 × 3.5 mm, long-ovoid, subtended by reddish brown, long-acuminate, nearly filament-like bracteole to 3 mm long; calyx tubular, 5.2 × 3.5 mm, coriaceous, brownish green, dotted with minute whitish protuberances, 3-lobed, lobes 1 mm high, short-acuminate; corolla greatly exceeding calyx, 8 mm long, long-ovoid, coriaceous, tubular proximally, divided into 3 valvate lobes



3. Leaf base margins of *Pritchardia tahuatana* typically have abundant, tan fibers. (Haaioipu near Hanatetena, Tahuata, J.-F. Butaud et al. 3497). (photo by D.R. Hodel).

distally, these greenish proximally, tinged with brown distally; flowers at post-anthesis 8-9 × 9 mm (Fig.8); calyx cupular, 5 × 4 mm, green

to brown, shallowly 3-lobed, lobes 1 mm high, acute, finely striate nerved longitudinally when brown and dry; corolla lobes fallen away, remaining base lower than calyx; stamens 6, 7-8 mm long, exceeding calyx and ca. equaling pistil, filament bases connate in a ring ca. equaling calyx lobes with 6 slender tips extending 1.8 mm above ring, these brownish, erect to spreading beyond calyx and bearing the anthers, these 2.5-3.2 mm long, oblong, dorsifixed below middle, brownish orange; pistil greenish, extending ca. 2.5 mm above staminal ring and calyx, columnar, truncate distally. Fruit 23 × 21 mm fresh (Fig. 9), 17-21 × 16-19 mm dry, ± globose, green when mature but ripening glossy black, set on a short, stubby pedicel 4 × 4 mm; seed 16 × 16 mm, globose; embryo sub-basal. Cotyledonary sheath or ligule of seedlings distinctly red to purple.

Additional Specimens Examined. Cultivated. FRENCH POLYNESIA. Marquesas Islands: Tahuata, Haaioipu, peu après le col séparant Hanatetena de Haaioipu, en contrebas du chemin, UTM 7 X 710 854 Y 8 899 432, 131 m elev., 24 September 2016, J.-F. Butaud 3497 with D. Hodel, M. Hodel & R. Hodel (PAP); au cœur de la cocoteraie de Haaioipu, à l'amont du chemin, UTM 7 X 711 196 Y 8 899 572, 121 m elev., 24 September 2016, J.-F. Butaud 3498

4. Leaf blades of *Pritchardia tahuatana* are slightly less than semi-circular. Ruler = 15 cm. (Hapatoni, Tahuata, type, J.-F. Butaud et al. 3496). (photo by D.R. Hodel).



with D. Hodel, M. Hodel & R. Hodel (PAP); Motopu, haute vallée Kaavai, UTM 7 X 711302 Y 8 902 114, 455 m elev., 1 September 2012, J.-F. Butaud & F. Jacq 3157 (PAP); Hapatoni, village, UTM 7 X 705 480 Y 8 897 258, 9 m elev., 28 November 2009, J.-F. Butaud 2477 (PAP)

Prior to naming and describing *Pritchardia tahuatana*, we considered four other names in the genus attributed to French Polynesia, including *P. mitiaroana*, *P. pacifica* var. *marquisensis*, *P. pericularum* and *P. vuylstekeana*. However, *P. tahuatana* is clearly distinct from all as explained above in the protologue and below in notes of the genus in French Polynesia.

Distribution

Endemic to the Marquesas Archipelago, *Pritchardia tahuatana* is known only from eight cultivated plants, always at ancient house sites (sometimes currently occupied) or religious sites, on Tahuata Island at Hapatoni (at currently occupied houses), at Haaioipu near Hanatetena [in coconut (*Cocos nucifera*) plantation] (Fig. 10), and at Motopu (in secondary forest with *Hibiscus tiliaceus* and *Pandanus tectorius* on an old trail linking ancient stone platforms). It was also formerly present on Fatuiva Island at Hanavave village



5. Leaf blades of *Pritchardia tahuatana* are green with scattered, moderately dense, whitish lepidia abaxially. (Hapatoni, Tahuata, type, J.-F. Butaud et al. 3496). (photo by D.R. Hodel).

(on a small trail leading to coconut plantations) where the last tree died in 2009 (pers. obs., October 2009).

6. Inflorescences of *Pritchardia tahuatana* are branched to four orders. (Hapatoni, Tahuata, type, J.-F. Butaud et al. 3496). (photo by D.R. Hodel).





7 (top). Flower buds of *Pritchardia tahuatana* are distal pointing and long-ovoid. (Hapatoni, Tahuata, type, J.-F. Butaud et al. 3496). 8 (bottom). Slightly post-anthesis flowers of *Pritchardia tahuatana* are 8–9 × 9 mm. (Hapatoni, Tahuata, type, J.-F. Butaud et al. 3496). (photos by D.R. Hodel).

Pritchardia tahuatana was once likely much more common and widespread in the Marquesas Archipelago, even up to relatively recent times. Palaeoecological records (pollen and seeds) document several probable South Pacific *Pritchardia* taxa, which were formerly common and widespread in the Austral and Society Islands. This information suggests that prior to Polynesian contact, *P. tahuatana* was also a common and widespread species of lowland, mixed, mesic to wet forests in the Marquesas Archipelago (Fig. 11). After arrival, Polynesians destroyed most lowland forest to plant breadfruit (*Artocarpus altilis*) and other crops (Cuddihy & Stone 1990, Kahn et al. 2015), but they cultivated or conserved some of the palms, likely for rituals or other uses (leaves for thatch and hats, fruit for food). We suggest that *P. tahuatana* was a lowland tree palm, in mesic to wet forests, like other South Pacific *Pritchardia* and several Hawaiian species. Indeed, if it was a montane species like some Hawaiian *Pritchardia*, it should have survived longer in the wild. Schäfer (1977), who

considered it as a possible component of the lower valley vegetation, shared this view.

From historical sources (Forster 1786a, Bennett 1840, Jouan 1865), *Pritchardia tahuatana* was present throughout the entire Marquesas Archipelago, being more common in the southern Marquesas (especially on Tahuata where it was quite common in the interior of valleys, notably Vaitahu) than in the northern Marquesas (where it was only reported from the northern valleys of Nuku Hiva, notably Hooumi) (Fig. 11).

From contemporary sources, *Pritchardia tahuatana* can be documented as recently occurring on many islands in the Marquesas Archipelago (Table 1).

Ecology

Pritchardia tahuatana is considered extinct in the wild and exists only as a domesticated and cultivated species, with all the known trees on Tahuata and Fatuiva being associated with human occupation, either ancient stone



9. Fruits of *Pritchardia tahuatana* are green when mature but ripen to glossy black and have seeds with sub-basal embryos. (Hapatoni, Tahuata, type, J.-F. Butaud et al. 3496). (photo by D.R. Hodel).

platforms probably built between Polynesian colonization of the Marquesas Islands around the 12th century and before the arrival of Europeans in the late 18th century (Allen 2014) or along old pathways; thus, the original ecology of the species remains largely unknown. On both islands it was found from near sea level to 455 m elevation in anthropogenic forests with introduced species, including *Artocarpus altilis*, *Cananga odorata*, *Cocos nucifera*, *Inocarpus fagifer*, *Mangifera indica* and native species such as *Ficus prolixa* and *Morinda citrifolia*, and in secondary forests dominated by native *Angiopteris evecta*, *Cyclophyllum barbatum*, *Hibiscus tiliaceus* and *Pandanus tectorius*.

We performed two, salt-water float tests, one with 10 fruits and the other with 30 fruits, to assess ocean-water dispersal potential. In both tests 100% of the fruits sunk within seven days, indicating the ocean-water dispersal likely played an insignificant role in distribution. Because its fruits are somewhat fleshy, endemic frugivorous birds like the fruit dove (*Ptilinopus*) and pigeon (*Ducula*) probably dispersed fruits of *P. tahuatana* among the Marquesas Islands.

Ethnobotany

The Marquesan names are *vahake* in Nuku Hiva (sometime *vahane* in Taipivai Valley) and *Ua Pou* and *vahane* in Ua Huka, Hiva Oa, Tahuata, and Fatuiva (Christian 1910, Crook 2007, Rollin 1929). Interestingly, *wahane* is the Hawaiian name of *Pritchardia* fruits, whereas the tree itself is called *loulu* (Beccari & Rock 1921, Brown 1931, Hodel 2012).

Several uses of this palm have been reported in the old literature and in conversations with Marquesan inhabitants, including seeds and fruits for food, medicine, and children's games; the wood of the trunk for house construction; and the leaves for hats, fans, umbrellas, house roofing, and rituals. Indeed, steps notched in the trunk, so trees could be more easily climbed to gather fruits and leaves, was a common practice and are still visible on both trees at the type locality in Hapatoni (Fig. 12).

Seeds: After being broken with a stone, the not quite mature-ripe seeds were eaten in Tahuata and Fatuiva (S. Vaki, Fatuiva, pers. comm. 2009; L. Teikipupuni and C. Vaimaa, Tahuata, pers. comm. 2009, 2012), as was done in Hawaii. Bennett (1840) reported that "the



10. The plants of *Pritchardia tahuatana* that occur at Haaopu near Hanatetena, Tahuata in coconut plantations are mostly overtopped and shaded and are not as vigorous as the two plants around residences in Hapatoni. (J.-F. Butaud et al. 3497). (photo by D.R. Hodel).

kernel of the nuts is eaten as a native delicacy," and Brown (1931) added that "the fruits served as food in time of famine." Chaulet (1890) reported that the fruits (*puku vahake*) were used as a purgative, to treat thrush. Children in Hoomi Valley on Nuku Hiva used the dried fruits to play marbles (G. Tekohuotetua, pers. comm. 2012).

Wood (Trunk): The wood or trunk was used for the head board of Marquesan houses (Testard de Marrans 2004) and to make the ridgepole of these houses (Handy 1923).

Leaves: Marquesans employed the leaves for many uses. The most significant might have been for rituals performed by the aristocratic class (Bennett 1840), many of which were reserved exclusively for chiefs or priests. Ritualistic uses of the leaves included wrapping the chief's food, adorning ritual structures or canoe seats, head wreaths for the chief, and priest's blessing of sacred artefacts (Porter 2014). Leaves were also used to make baskets to hold the heads of the dead after they had

been mummified (Brown 1931). One of the main archeological sites (a public place or *tohua*) of Taipivai Valley, Nuku Hiva, is known as *vahakeku'a* or *vahaneku'a* (Suggs 1961), which means the sacred *vahane*, suggesting that *Pritchardia tahuatana* formerly played an important role in Marquesan rituals.

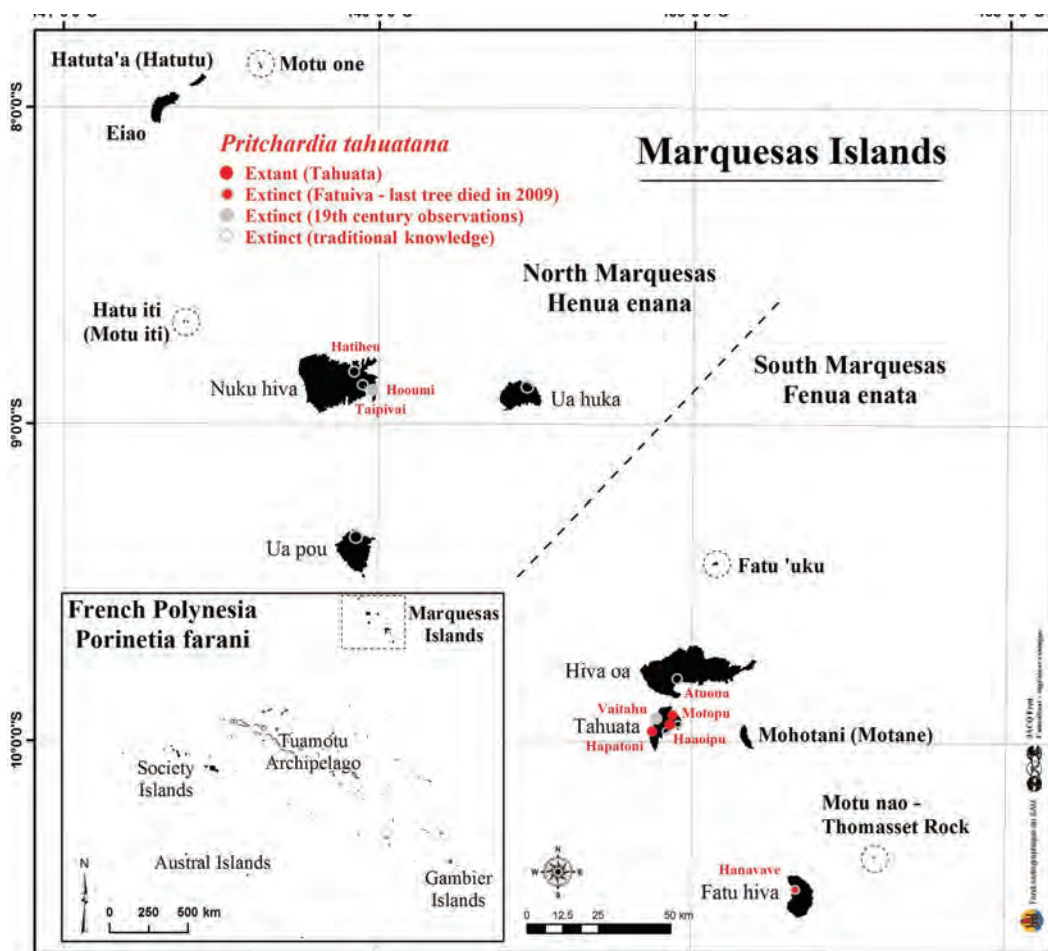
The aristocratic class also used the leaves for roofing to cover the houses of chiefs or burial places, especially the interior part of the roof (Stewart 1831, Bennett 1840, Gracia 1843, Seemann 1865–73, Jouan 1865, 1876, Chaulet 1890, Handy 1923, Linton 1923, Rollin 1929, Testard de Marrans 2004, Crook 2007, Porter 2014). Stewart (1831), quoted by Crook (2007), explained:

"But the Palmetto affords the most valued covering, and that most used – especially for the roof – wherever found in sufficient abundance. Its fan-like leaves are fastened one by one, with their centres about a foot from each other, upon long, split pieces of the hibiscus, which are then ranged upon the roof, sixteen or eighteen inches apart, and, thus disposed, lap considerably, every way, over each over. All these kinds of thatch, instead of becoming dark and sunburnt, like the grass of the Sandwich Island huts, bleach beautifully; and, when seen at a distance, gleam among the groves, in the brightness of the day, like neatly whitened cottages in our own country."

Indeed, many observers were surprised by the few structures covered with leaves of *Pritchardia tahuatana*, despite their excellent qualities for this type of use, which supports the assertion that the leaves were mostly reserved for use by the aristocratic class.

Two kinds of hats were made either with boiled petiole fiber (L. Teikitepupuni, Tahuata and S. Vaki, Fatuiva, pers. comm. 2009) (Fig. 13) or with portions of the blade. European sailors, who bought leaves under the name of *brab* in the 19th century (Bennett 1840, Jouan 1865, 1876, Chaulet 1890), likely to make hats for protection from the tropical sun, might actually have initiated this practice.

Entire leaves or leaf parts were used as fans, parasols, and umbrellas (Gracia 1843, Rollin 1929, Nicolson & Fosberg 2004, Testard de Marrans 2004, Crook 2007, Porter 2014). Leaf blades can also be woven into baskets, mats, and similar products.



11. Distribution of *Pritchardia tahuatana* in the Marquesas Archipelago (English names of North Marquesas, South Marquesas and French Polynesia are inflected in their Polynesian names on the map).

Conservation

Pritchardia tahuatana is currently known from only eight mature palms in three populations about eight km apart on Tahuata. One consists of two palms in the village of Hapatoni on the west coast of Tahuata, the second consists of four scattered palms (one group of two palms and two single palms) in coconut plantations in Haaoiipu beyond Hanatetena on the east coast of the island and the third includes two palms in a mid-elevation valley of Motopu on the north coast.

A slow but steady decline in palm numbers is clear. Several populations have been extirpated or have lost individuals, including Hanatetena and Vaitahu on Tahuata and Hatiheu, Hooumi and Taipivai on Nuku Hiva. A third palm was known with the current pair at the type locality on Hapatoni and another was also present elsewhere in the village (C. Vaimaa, pers. comm. 2012). Dead trunks were seen in

the Motopu and Haaoiipu populations. The last tree on Fatuiva died in 2009. This decline can also be deduced from the observation of Jouan (1865), who wrongly believed that this palm was a recent introduction: "To see the small number of this tree, we can believe that they are not in the island for a long time."

The two specimens of *Pritchardia tahuatana* at the type locality on Hapatoni are emergent above the surrounding, cultivated vegetation and are significantly healthier and more vibrant and reproductive than their counterparts in the coconut plantations in Haaoiipu. The former have canopies composed of more leaves (25 to 35 vs. 20 to 25), more inflorescences (12 vs. 3 or 4), and are producing fruits in abundance. In contrast, the palms in Haaoiipu, which are overtopped, crowded, and largely in the shade of adjacent, taller coconut palms, are less vigorous in appearance with fewer and smaller leaves (Fig. 10), and seem largely unproductive; we were

Table 1. Past locations of *Pritchardia tahuatana* in the Marquesas Archipelago (see Fig. 11).

Island	Location	Period	Source
Nuku Hiva	Taipivai, Hoomi, and Hatiheu Valleys	Before 1980	G. Tekohuotetua, pers. comm. 2012; A. Puhetini, pers. comm. 2013
Ua Pou	Not specified.	Before 1920	Known from legends and traditional stories, T. Teikiehuupoko, pers. comm. 2012; quoted by Linton (1923) for a roof of an old chief's house.
Ua Huka	A site at 550 m elev., close to the main ridge of the caldera	Undetermined	The site is known as <i>tevahane</i> , a derivation of <i>vahane</i> .
Hiva Oa	Wet valleys above Atuona village	Before 1980	A. Lebronnec, pers. comm. 2012.
Tahuata	Known from the few current trees but also formerly from Vaitahu and Hanatetena Valleys; also from a small rocky gulch, east of Haaopu, 0–300 m elev.	Continuing decline but still extant	Several village elders, pers. comm. 2012; the small rocky gulch is known as <i>tevahane</i> , a derivation of <i>vahane</i> .
Fatuiva	Known from only one tree, which disappeared in 2009, at Hanavave village; also at a cape at the entrance of Hanavave Valley.	2009	The cape is known as <i>maiivahane</i> , a derivation of <i>vahane</i>

unable to find mature fruits on the trees, which is probably because of the much fewer leaves and inflorescences and the presence of rats.

Threats to survival of *Pritchardia tahuatana* include rats, pigs (domestic and wild) and crowding and overtopping by adjacent, cultivated vegetation. Its IUCN conservation status is extinct in the wild (EW) and in cultivation it is extremely endangered because of the small quantity of mature palms and the threats to their survival. Fortunately, through the efforts of the senior author, interest in *P. tahuatana* among local residents has blossomed, plants have been grown from seeds, and now several juvenile specimens grow next to the school in Vaitahu north of Hapatoni on Tahuata and also on Nuku Hiva and Tahiti in areas managed for rare species conservation by the department of environmental conservation (DIREN). Also, seeds have been distributed to several avid palm collectors in Tahiti.

Related Species

Pritchardia tahuatana appears to have more in common with the Hawaiian than the South Pacific species of the genus. It shares the mostly drooping leaf segment tips with the Hawaiian species. Also, its fruits are in the same size category as the smallest-fruited Hawaiian species, which are significantly larger than those of the other South Pacific species. It and the South Pacific *P. mitiaroana* are unique in the genus, though, in having inflorescences branched to four orders (Fig. 6). The red to purple cotyledonary sheaths of just germinated seedlings of *P. tahuatana* are colorful and unique in the genus although the colors fade with age (Fig. 14).

Pritchardia tahuatana is difficult to key out in Hodel (2007), the problem arising at the very first couplet. Neither couplet 1a (*P. mitiaroana*) nor 1b (all other species in the genus) is an adequate choice. If following couplet 1a, the South Pacific *P. mitiaroana* differs in its slightly



12 (left). Trunks of *Pritchardia tahuatana* are frequently notched with hand- and foot-holds to aid in climbing to gather leaves and fruit. (Hapatoni, Tahuata, type locality). (photo by D.R. Hodel). 13 (right). This modern hat was made from petioles of *Pritchardia tahuatana* on Fatuiva Island (photo by J.-F. Butaud).

ventricose trunk, white-waxy abaxial leaf blade surface, and much smaller fruit (5–7 mm diam.). It and *P. tahuatana* do share the inflorescences branched to four orders, and are the only species in the genus with this character. If following couplet 1b, *P. tahuatana* would key out at *P. glabrata* in couplet 26b at the very end of the key. The Hawaiian *P. glabrata* differs in its significantly shorter habit (only to 5 m tall), only a few fibers on leaf bases margins, and inflorescences with up to three panicles, each branched only to three orders.

Notes on *Pritchardia* in French Polynesia

How *Pritchardia* arrived in the remote and far-flung islands of French Polynesia is one of the intriguing mysteries of palm biogeography. It has long been thought that the ancestral *Pritchardia* originally arrived from the west in Asia and moved eastward across the Pacific (Beccari & Rock 1921). This theory might be only partially true. Bacon et al. (2012) constructed a phylogenetic analysis on 22 Hawaiian and the three South Pacific species that revealed the colonization of the Hawaiian Islands by a South Pacific ancestor close to *P. thurstonii*. However, her work appears to show that the ancestral *Pritchardia* likely arrived in

the Pacific basin from the northeast, in the Americas, rather than from the west.

Here we discuss the previously named *Pritchardia mitiaroana*, the other native member of the genus in French Polynesia; cultivated and introduced *P. pacifica* and *P. thurstonii*; and extinct *Pritchardia* in the Society and Austral Archipelagos in French Polynesia.

Pritchardia mitiaroana

Before the discovery of *Pritchardia tahuatana* in the Marquesas, the only native members of the genus in French Polynesia were on the uplifted limestone island of Makatea and the atoll of Niau in the Tuamotu Archipelago. These were thought to be *P. vuylstekeana* and *P. pericularum*, respectively. However, Hodel (2007) and Hodel et al. (2009) showed that these native palms were actually *P. mitiaroana*, first described from Mitiaro Island in the Cook Islands (Dransfield & Ehrhart 1995). Bacon et al. (2012) confirmed this finding through genetic studies, which showed that the *Pritchardia* from Mitiaro, Makatea, and Niau were very closely grouped. (See Fig. 16 for distribution of *P. mitiaroana* in the Cook Islands and French Polynesia). Furthermore, Hodel (2007) showed that the names of the two species erroneously attributed to the Makatea



14 (left). The cotyledonary sheath or ligule of seedlings of *Pritchardia tahuatana* are distinctly reddish purple, a condition unique in the genus. (Hapatoni, Tahuata, type, *J.-F. Butaud et al.* 3496). (photo by J.-F. Butaud). 15 (right). On Anaa atoll in the Tuamotu Archipelago, *Pritchardia mitiaroana* is a recent discovery. (photo by J.-F. Butaud).

and Niau palms were poorly documented. Both were described from juvenile and/or sterile plants grown in European glasshouses and known only from the leaves and the few fruits and seeds from which they were propagated; the information was insufficient for proper identification. Nonetheless, their significantly larger fruit and seeds easily exclude *P. mitiaroana* and the leaves devoid of lepidia exclude *P. tahuatana*.

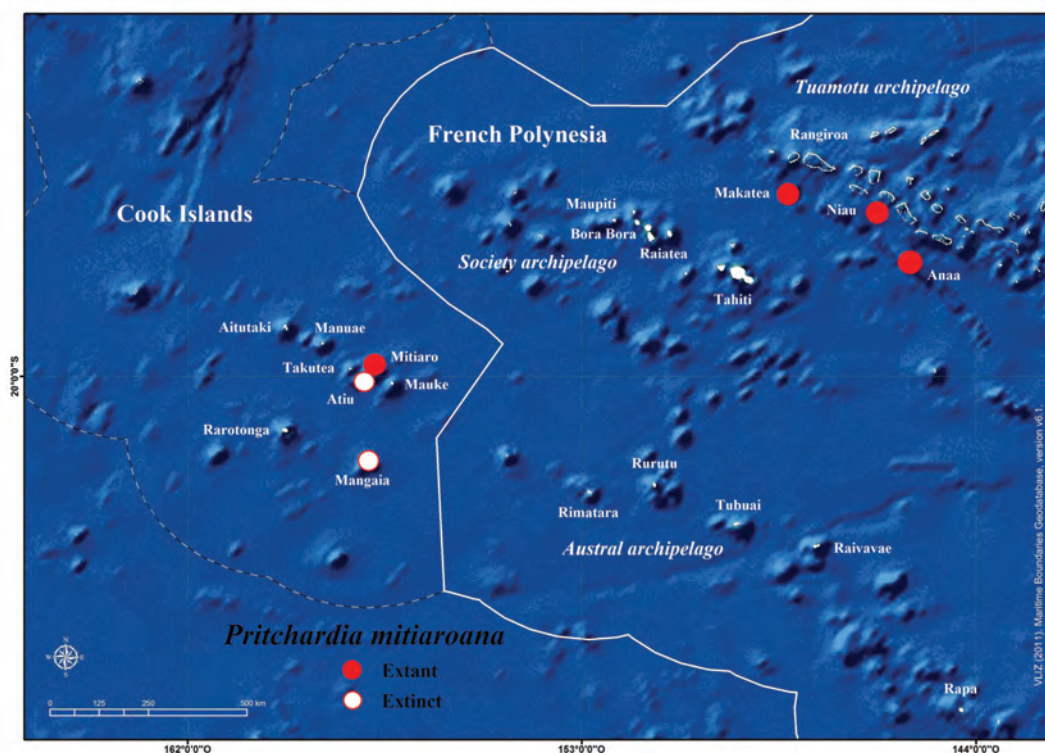
In 2010, after field exploration and inquiries with inhabitants, especially the elder Rosalie Auméran (per. comm. 2008) and the field guide Reubena Matai (pers. comm. 2009), *Pritchardia mitiaroana* was documented for the first time on Anaa, an uplifted atoll also in the Tuamotu Archipelago (Fig. 15); it was formerly known by its Anaa vernacular name *umeume* (Stimson 1964) but was overlooked because of its scarcity. Restricted to the western part of the atoll on the islet of Otika-Omana, four mature trees and scores of trunkless juveniles have been counted. Local informants knew of additional palms several decades ago but they have since died. Extensive burning to clean coconut plantations of weedy growth and rat predation of fruits (both *Rattus rattus* and *R.*

exulans) threaten *P. mitiaroana* on Anaa. Since 2012, a local group has instituted conservation measures on Anaa to preserve natural populations of the palm. A nursery was established to propagate and grow *P. mitiaroana* for replanting and scores have been grown and will be planted in the main village of Tukahora.

In the Cook Islands, *Pritchardia mitiaroana* was probably also the *Pritchardia* that Parkes (1994, 1997) and Ellison (1994) found in their palynological studies on the islands of Atiu and Mangaia (now extinct on both islands) next to and geologically very similar to Mitiaro (Wood 1967) (Fig. 16).

Pritchardia mitiaroana is called *umeume* on Anaa and Niau atolls, *tavevo* on Makatea (Butaud & Jacq 2009), and *niao* on Mitiaro (McCormack 2007).

Specimens Examined. FRENCH POLYNESIA. Tuamotu Islands: Anaa, Piere, bordure de heo, coté lagon, à 50 m au Nord du sentier allant coté océan, mature tree, UTM 6 X 649 017 Y 8 078 990, 4 m elev., 14 March 2010, *J.-F. Butaud 2616* (PAP); same locality, juvenile, UTM 6 X 649 034 Y 8 078 959, 4 m elev., 14



16. Distribution of *Pritchardia mitiaroana* in the Cook Islands and French Polynesia.

March 2010, *J.-F. Butaud 2617* (PAP); Omana, terre Tepaheno, dans la cocoteraie, mature tree, UTM 6 X 649 055 Y 8 078 905, 3 m elev., 31 July 2012, *J.-F. Butaud, J. Hauata & Tenati 3155* (PAP).

Introduced *Pritchardia*

Two introduced and cultivated *Pritchardia* species are known in French Polynesia. The first, *P. pacifica*, which is common on most of the high islands of the Society Archipelago and sparingly in the Marquesas Archipelago, played a significant role in our treatment and documentation of *P. tahuatana* (see below under Cultivated *Pritchardia pacifica* on Nuku Hiva). The second, *P. thurstonii*, is mainly encountered in the Tuamotu Archipelago where it is grown on coral limestone atolls, a habitat similar to its native Fijian and Tongan habitat. In the Marquesas Archipelago, both species are known from a few individuals. *Pritchardia pacifica* was probably introduced by the end of the 19th century or at the beginning of the 20th century whereas *P. thurstonii* appeared in the second half of the 20th century.

Cultivated *P. pacifica* on Nuku Hiva

Pritchardia tahuatana is not the first species of the genus reported from the Marquesas Islands

in modern times. Brown (1931) named and described *P. pacifica* var. *marquisensis* from a specimen collected in 1921 at Hakapuuvai Bay on Nuku Hiva, and we initially considered the possibility that *P. tahuatana* could be included here. However, close and critical examination of the types and additional material of both taxa quickly and readily showed that they differed significantly and that *P. pacifica* var. *marquisensis* is but a synonym of *P. pacifica*.

Pritchardia pacifica, which is also unknown in a truly wild, natural state but is widely cultivated in tropical regions (Hodel 2007), including French Polynesia, differs from *P. tahuatana* in having only a few fibers on its leaf bases margins, the leaf blades with stiff segment tips, inflorescences branched to only two orders and smaller fruits to 12 mm diam.

A search on the type locality of *Pritchardia pacifica* var. *marquisensis* at Hakapuuvai Bay in November 2016, where two other collections of this taxon have also been made, failed to find living *Pritchardia* despite precise description of the locality by a local farmer (S. Falchetto, pers. comm. 2016). We suggest that *P. pacifica* was introduced to Hakapuuvai in the latter half of the 19th century when both this location and nearby Hakapaa bay had

settlements and extensive agricultural operations in cotton, sugarcane and coconut (Rollin 1929).

Specimens Examined. Cultivated. FRENCH POLYNESIA. Marquesas Islands: Nuku Hiva, Western Taipi Vai, Hapaa region, Hakapuu Vai, a small valley, 19 August 1921, *F. Brown 647* (BISH, holotype of *P. pacifica* var. *marquisensis*); Palmier rare et cultivé, August 1921, *SFIM 142* (P); Baie du Contrôleur, Hakapaa, anse Sud, 5 m elev., 24 March 1987, *S. Jourdan 158* (PAP).

Extinct *Pritchardia* in the Society and Austral Archipelagoes

Very recently, Prebble et al. (2016) found *Pritchardia* pollen in a wetland (Vaifanau-ura'amo'ora, Tamanu Plateau, Punaru'u Valley) on Tahiti in the Society Islands, which could correspond to the unidentified species found from Vaihiria Lake on Tahiti (Parkes et al. 1992, Parkes 1994) and Temae Lake on Moorea (Parkes 1994, 1997).

In the Austral islands, palaeoecological records of *Pritchardia* were found in several wetlands on the islands of Rimatara (Prebble & Dowe 2008, Prebble & Wilmshurst 2009 [pollen in Maunutu swamp]) and Tubuai (Prebble & Dowe 2008 [pollen and seeds 16 to 20 mm in diameter in Mihi'ura swamp]).

Thus, these palaeoecological and palynological studies have shown that unidentified species of *Pritchardia* formerly inhabited several islands in the Society and Austral archipelagos, which were thought to be devoid of these palms. From these range extensions of the genus and based on the geographic position, elevation, and biogeography of French Polynesian islands and on the bioecology of *Pritchardia*, we can suggest the hypothesis that these palms were also present in the Leeward Islands in the Society Archipelago, and in Rurutu and Raivavae in the Austral Archipelago, and were probably different from *P. mitiaroana*, which has smaller seeds than the Tubuai specimen. Their extinction or extirpation is probably linked with the arrival of the first Polynesian settlers and the destruction of the lowland vegetation for cultivation purposes but also the introduction of the Polynesian rat (*Rattus exulans*), which feed on its fruits (Prebble & Dowe 2008, Prebble & Wilmshurst 2009, Prebble et al. 2016).

Key to South Pacific *Pritchardia*

1a. Lepidia on abaxial leaf blade arranged in conspicuous, distinct, parallel lines;

inflorescences greatly exceeding leaves *P. thurstonii*

1b. Lepidia on abaxial leaf blade surface scattered or lacking; inflorescences not exceeding leaves. 2

2a. Trunk smooth, dark gray, slightly ventricose, emitting a distinct, drum-like sound when sharply struck; fruit 7 × 7 mm *P. mitiaroana*

2b. Trunk not as above; fruit 12 × 12 mm or more. 3

3a. Abaxial leaf blade with scattered, moderately dense, whitish lepidia; fruit 23 × 21 mm *P. tahuatana*

3b. Abaxial leaf blade mostly lacking lepidia; fruit 12 × 12 mm *P. pacifica*

Conclusion

The discoveries of the new Marquesan palm *Pritchardia tahuatana* and of a new island record for *P. mitiaroana* were primarily due to Polynesian traditional knowledge and the study of old ethnobotanical literature. They demonstrate the possibility of new discoveries in areas already well studied by botanists and also the profound alteration of the original lowland vegetation of these islands. The palaeoecological and palynological studies, which have documented extinct *Pritchardia* species and their distribution, give a similar view of past and continuing disturbances. We encourage ethnobotanical studies in all Polynesian archipelagos not only to preserve traditional knowledge but also to rescue some remnants of the original lowland flora, and especially useful and nearly overlooked species like these *Pritchardia*.

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