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FRONT COVER

Fruits of *Pelagodoxa mesocarpa* are smaller than those of *P. henryana* but still warty. Photographed at Jeff and Suchin Marcus's Floribunda Palms and Exotics, Hawaii, by D.R. Hodel. See article by D.R. Hodel et al., p. 113.

BACK COVER

Pelagodoxa are moderate-sized, solitary, unarmed, tree palms, as seen here with *P. mesocarpa* cultivated in Suva, Fiji. See article by D.R. Hodel et al., p. 113. Photo by D.R. Hodel.

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The distinctive twist in *Syagrus coronata* is analyzed in a new study by L. Noblick. See article p. 109. Photo by S. Zona.

PALM NEWS

The vast regions of southern China continue to yield interesting new palms. A new species of *Guihaia* has been discovered from Chongqing, China, and has been christened *G. heterosquama*. The species has leaves shaped like those of *G. argyrata*, but it differs in having a glabrous petiole and hastula, the soft fibers at the apex of the leaf sheath, and the presence of a pistillode in the male flower. The paper is published by X.Y. Li and colleagues in *Phytotaxa* 405: 248–254. <<https://doi.org/10.11646/phytotaxa.405.5.3>>



M. Manners

Borassus flabellifer is an especially useful palm in Southeast Asia. The sap is harvested for sugar and alcoholic beverages, and the fruits are edible. The palm, however, grows slowly, requiring 12–15 years to achieve reproductive maturity, during which time female and male palms are indistinguishable. A recent project sought to discover molecular markers that could be used to determine the sex of non-reproductive *Borassus* palms. Researchers in Thailand sifted through over 1000 primers and over 10,000 cloned transcripts but found nothing that could serve as a sex-linked marker. They conclude that the sex-determining region(s) of the genome must be very small. A large proportion of transcripts discovered in this research were related to sucrose metabolism, and these transcripts will be useful for further understanding of sucrose production in *Borassus* and other sugar crops or for selecting elite breeding stock. The open-access publication is Pipatchartlearnwong, K. et al. 2019. Towards sex identification of Asian Palmyra palm (*Borassus flabellifer* L.) by DNA fingerprinting, suppression subtractive hybridization and *de novo* transcriptome sequencing. *PeerJ* 7:e7268 <<http://doi.org/10.7717/peerj.7268>. 2019>

Species of *Johannesteijsmannia* are some of the most spectacular understory palms of SE Asia, but aspects of their reproductive ecology are poorly known. Data on the phenology, or timing, of reproduction are essential for developing conservation management plans for these species. A new study by Y.M. Chan and L.S.L. Chua examines the seasonality, timing and fecundity of three species of *Johannesteijsmannia* in Peninsular Malaysia. The authors concluded that flowering peaked during the wet seasons. They also noted that seed loss under natural conditions was as high as 84–98%. The open-access paper is Chan & Chua. 2019. Flowering phenology and seed production of three threatened tropical palms, *Johannesteijsmannia* spp. (Arecaceae). *Gardens' Bulletin Singapore* 71 (1): 243–260. <[http://doi.org/10.26492/gbs71\(1\).2019-13](http://doi.org/10.26492/gbs71(1).2019-13)>



S. Zona

...continued on p. 154

Syagrus coronata and its Twist

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Syagrus coronata is known for its unusual five columns of closely spaced leaf bases that frequently twist to the left or to the right or remain more or less vertical.

This unusual leaf arrangement inspired me to explore whether the direction of the twist is different between palms growing in the northern and southern hemispheres, and whether it more commonly twists to the left (clockwise as observed from above) or twists to the right (counterclockwise as observed from above). This question of spirality (direction of twist) being affected by the geographic location of a palm has been raised by previous studies on coconuts and other palms (Davis & Davis 1987, Minorsky 1995). Finally, I asked whether twisted leaf arrangements are statistically more prevalent than vertical ones (whether direction of leaf arrangement is purely random).

Introduction

Syagrus coronata (Mart.) Becc. has a north-eastern Brazilian distribution that extends from east of the Rio São Francisco in Bahia, persists throughout most of eastern and central Bahia, northern Minas Gerais (i.e., north of the Rio Jequitinhonha), continuing north into southern Pernambuco, through the states of Sergipe and Alagoas. *Syagrus coronata* is one of the very few palms that can survive Brazil's very arid caatinga region (Noblick 2017).

Bondar (1938, 1942) championed the usefulness of *S. coronata*, locally known as *licuri*. He reported that the heart of the palm, fruit and nut are edible, the leaves provide wax, the seeds are used for extracting oil for soap, perfume and other products and the endocarp (nut) is used in regional handicrafts. The fruits have an edible, mucilaginous, sweetish, fibrous mesocarp that is chewed then discarded, and the oily seeds are collected in large quantities for food. They are also used for cooking and lighting oil. The crushed seed meal is fed as a daily ration to domesticated fowl. The leaves of *licuri* can be ground up, mixed with other plants and fed to livestock. Leaves are also used to cover rural shelters and to fabricate doors and walls, and various parts of the leaf, especially the leaflets, are used for making hats, fans, baskets, dusters, sleeping mats, etc.

Syagrus coronata belongs to a section of the genus that has very short internodes and a curious twisted leaf arrangement that gives the appearance of five ascending spires or columns of leaves (Figs. 1–3), which inspired Martius to name it "*coronata*," meaning "crowned." Sometimes these rows are nearly vertical with one leaf base arranged directly above the next



1 (left). Stem with leaf bases twisting to the left. 2 (right). Stem with leaf bases nearly vertical.

(Fig. 2), but more often these leaf base columns are slightly or even strongly twisted to the left or to the right (Figs. 1 & 3). I explored three questions concerning these twists: (1) Is there any significant difference in the direction of their twist between those growing north of the equator (Florida) and those growing south of the equator (Bahia); (2) Does this species more commonly twist to the left (clockwise) or to the right (counterclockwise); and (3) Are frequencies of the left-twisted, right-twisted, and vertical categories equal or significantly different?

Materials and Methods

First, I recorded the leaf arrangement as vertical, left twisted, or right twisted for 316 Brazilian palm specimens in Bahia at the Universidade Estadual de Feira de Santana (ca. 12°11'48"S, 38°58'27"W) and 31 cultivated specimens at the Montgomery Botanical Center (MBC) in Florida, USA (25°39'39.8"N,

80°16'53.2"W). I used the chi-square test to compare the northern and southern populations to see if there was a statistically significant difference in leaf arrangement between the two hemispheres. Second, using the 285 palms with twisted leaf arrangement, I calculated whether leaves were more likely to twist to the left or to the right. Finally, I examined all 347 (316 + 31) observations together of left-twisted, right-twisted and vertical categories to see if there was a significant tendency favoring the twisted vs. the vertical leaf arrangement.

Results and Discussion

In Bahia, of the 316 palms observed in their natural habitat, 58 displayed vertically arranged leaves, 136 had leaf columns twisted to the left (clockwise) and 122 had leaf columns twisted to the right (counterclockwise). In Florida, of the 31 trees observed, 4 were vertical, 10 were twisted to the left



3. Stem with leaf bases twisting to the right.

(clockwise) and 17 were twisted to the right (counterclockwise). Our field observations suggested that the left twist (136[L]) vs. 122 [R]) is more common south of the equator and the right twist (10[L] vs. 17[R]) is more common north of the equator. The chi-square test showed no significant difference in the twist direction between the northern and southern hemisphere populations ($\chi^2 = 3.11$; $df = 2$; $p < 0.05$).

Since our chi-square value of 3.11 is less than the critical chi-square value of 5.99, the variation can be explained by chance alone. Hence, we must accept the H_0 null hypothesis that there is no significant difference in the leaf twist direction between the two hemispheres. The Coriolis Effect was suggested as a possible explanation for the left and right tendencies, but I quickly dismissed it, as this effect is true for fluids or gases, not plants, causing fluids or gases to rotate differently on opposite sides of the equator. For example, hurricanes spin

counterclockwise north of the equator, and cyclones spin clockwise south of the equator. In fact, north of the equator more *licuri* palms were observed to twist clockwise than counterclockwise and south of the equator more *licuri* palms twisted counterclockwise than clockwise, which is the opposite of the Coriolis Effect. The next chi-square test indicates that northern and southern samples do not differ in handedness (spirality).

To test whether one twist direction was more prevalent than the other, I examined all 285 palms from Bahia and Florida with twisted leaf arrangements. The chi-square test showed no significant difference in the twist directions ($\chi^2 = 3.15$; $df = 1$; $p < 0.05$). Since the chi-square value was less than the critical chi-square value of 3.84, we conclude that there is no significant difference in the direction of the leaf twist. Like the flipping of a coin, which frequently lands heads or tails, left and right twists are randomly distributed among our observed palms.

Now that brings us to our third question. Are the left, right and vertical arrangements really analogous to a coin toss? Can we expect our data outcome to be more like a coin toss or an imaginary three-sided die? In the case of dice, we would expect any of the three observed categories to be equally possible, but in the case of a coin, we would mostly anticipate a heads or tails, but would rarely expect a coin to land on its edge and remain there.

To test whether the twisted observations were more common and significantly different than the vertical ones, I pooled all 347 observations and assumed a theoretical expected value of 115.67 (347/3) for each outcome. The chi-square test proved that there was a significant difference between twisted and vertical observations ($\chi^2 = 37.56$; $df = 2$; $p < 0.05$). Since 37.56 is greater than the critical chi-square value of 5.99, we reject the H_0 null hypothesis, which states that the three categories of left and right twisted and vertical are random, with each outcome having an equal chance. Instead, we accept our H_1 alternate hypothesis that there is a difference between the left-twisted, right-twisted and vertical leaf arrangements, such that their outcomes are not equally likely. This is like discovering a loaded die, which in our case is loaded in a way that the vertical category is less common. This makes our palm's twist direction more like a coin toss than a three-sided die.

In conclusion, the twisted leaf arrangement of *Syagrus coronata*, to the left or right or vertical, is randomly determined and not influenced by its location north or south of the equator, nor is one arrangement (left or right) statistically more prevalent over the other. However the right or left twisted arrangement of leaves are statistically more prevalent than the vertical ones.

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Reassessment of *Pelagodoxa*



1. The large, initially undivided leaves and big, curious, warty fruits of *Pelagodoxa* have long fascinated palm botanists, collectors and growers. Here is *P. henryana* with Marianne Hodel at the Jardin Botanique Harrison Smith, Papeari, Tahiti. All photos by Donald R. Hodel unless noted otherwise.

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We document substantial and critical differences between the two populations of the fascinating genus *Pelagodoxa*, establish the validity and resurrect the name of a second species from synonymy, discuss molecular data, phylogeny and phytogeography, ethnobotany and conservation and what impact, if any, they might have had in its speciation and insular distribution. We also summarize the cultivation requirements for these handsome and intriguing palms.

With its large, initially undivided leaves, big, curious, warty fruits, monotypic nature and mysterious, remote, island habitat, *Pelagodoxa henryana* has long fascinated palm botanists, collectors and growers (Figs. 1 & 2). The possibility of a second species of *Pelagodoxa* has generated a substantial amount of interest, but the recent literature on the subject has dismissed this prospect and accepted only one species.

History

In 1916 Charles Henry, a French agriculturist, technical director of the Société française des Îles Marquises, found what would later become *Pelagodoxa henryana*, probably in Taipivai (Taipi) Valley on Nuku Hiva in the Marquesas Islands of French Polynesia (Fig. 3). Henry sent

seeds, notes and photographs to Désiré Bois, editor of the prestigious journal *Revue Horticole* at the Natural History Museum in Paris. Bois forwarded Henry's material to Odoardo Beccari, the great Italian botanist who specialized in palms.

Beccari wrote a formal but brief description, which established the new genus and species, *Pelagodoxa henryana*, and which was included as a footnote in a longer article that Bois wrote about this new discovery (Bois 1917). Two of Henry's photographs, one of two seedlings (one with a seed still attached) and the other of a young adult plant, and two drawings, one of an infructescence (artist unknown) and the other of a longitudinal section of a fruit (drawn by Beccari [Dowe and Chapin 2006]), were included in the article. Bois quoted Henry,

2. The large, curious, warty fruits of *Pelagodoxa* always attract attention, as here with *P. henryana* in the garden of Marianne and Donald Hodel, Papeari, Tahiti. *Butaud et al.* 3494.





3. Several individuals of *Pelagodoxa henryana* emerge above the disturbed forest at the type locality in Taipivai Valley, Nuku Hiva, Marquesas Islands, French Polynesia, a site with extensive signs of ancient human habitation. Butaud et al. 3495.

who, in describing the palm in his notes, stated, "I have never seen a more beautiful palm. Some individuals four to five years of age, straight of stem, have the appearance of adult specimens of *Kentia*; the large, entire, pleated leaves, silvered below, give them a special quality." (Moore 1957).

Henry (1918) briefly described *Pelagodoxa henryana* as "another sort of palm, maybe unknown, with entire and silvery leaves of the most beautiful appearance" in an article about the flora and agriculture of the Marquesas Islands. Shortly thereafter, Bois (1919) gave a summary of this unique palm and later noted that Henry had sent seeds to the horticulture department at the Natural History Museum in Paris, which arrived desiccated or died soon after germination from a fungal disease (Bois 1924).

A few years later, Martelli (1932) provided the most detailed and thorough account yet of *Pelagodoxa henryana*, although pistillate flowers were lacking. He relied on new material provided by Father Simeon Delmas, a French missionary who had made collections from Taipivai Valley, which Martelli thought was the same location where Henry had made his

original collections. Father Delmas was the first to note that *P. henryana* grew at Puawan (Puamau) on Hiva Oa and on nearby Tahuata; however, the occurrence on this latter island is tenuous, and Father Delmas likely had confused *P. henryana* with the then unnamed palm *Pritchardia tahuatana* (Butaud & Hodel 2017).

Beccari (posthumously) and Pichi-Sermolli (1955) added to the description of *Pelagodoxa*, basing it on Beccari's unpublished notes of the Arecoideae. Unfortunately, pistillate flowers were still lacking. Uhl and Dransfield (1987) and Dransfield et al. (2008) provided the most detailed and complete descriptions of *Pelagodoxa*, including, finally, pistillate flowers.

Burret (1928) named and described a second species, *Pelagodoxa mesocarpa*, which differed from *P. henryana* primarily in its significantly smaller fruits and seeds but also in its thinner pericarp and the larger quantity of corky warts in relation to the size of the fruits. The provenance of *P. mesocarpa* is uncertain. Accompanying the holotype at B, which consists of two empty fruit halves, is a label reading "Verschaffelt comm. 65" on one line and below it "New Caledonia Cuming leg."



4. The fruit exocarp of *Pelagodoxa* is prominently cracked into low, pyramidal corky warts, as here with *P. henryana* in the garden of Marianne and Donald Hodel, Papeari, Tahiti. *Butaud et al.* 3494.

This first line means that Verschaffelt, likely Ambroise Verschaffelt, distinguished 19th-century Belgian horticulturist, nurseryman and author, “communicated,” gave, or provided

the fruits in 1865. The second line means that Hugh Cuming, renowned English naturalist and prodigious collector of plants and especially shells, should be credited with

making the collection in New Caledonia, or he simply prepared the specimen. However, Cuming never visited New Caledonia; he spent nearly all of his collecting time in Chile, Mexico and, after passing through French Polynesia (apparently without stopping in the Marquesas), the Philippines (Dance 1980, Layard 1895, Melville 1895, St. John 1940). Thus, Burret theorized that the provenance of *P. mesocarpa* might be the Philippines, where Cuming was active for an extended period of time. Nonetheless this notion seems unlikely because *Pelagodoxa* has never been collected in the Philippines. Perhaps Cuming picked up immature fruits of *P. henryana* while passing through French Polynesia. Several collections of a small-fruited *Pelagodoxa* that match up well with *P. mesocarpa* have been made in Fiji, Vanuatu and the Solomon Islands in Melanesia, always cultivated or in disturbed sites near human habitation, but Cuming never visited these areas. Either way, it seems that Verschaffelt had some of these small-fruited *Pelagodoxa* and might have attempted to grow them in his nursery, and somehow Burret ended up with a few fruits.

Also accompanying the holotype of *Pelagodoxa mesocarpa* at B is a single sheet with four pencil drawings of one fruit and three seeds, all annotated with handwritten German text. In the lower left-hand corner, handwritten in ink is “gen. nov. e-Mus. brit. Mann fecit 1863.” This notation roughly says “new genus at British Museum, made by Mann 1863.” Perhaps Mann is German botanist Gustav Mann, who was a gardener and botanical author at the Royal Botanic Gardens, Kew, and who collected in Africa and India, including palms. Nonetheless, Burret used this sheet of drawings in developing his description, even reproducing the figures in his article.

All or nearly all technical accounts of *Pelagodoxa* up until now have considered it monotypic. The only species was *P. henryana*. *Pelagodoxa mesocarpa* was considered a synonym, although most accounts noted its smaller fruits.

Taxonomy

Pelagodoxa Becc. in Bois, Rev. Hort. (s. 2), 15: 302. 1917. Type species: *P. henryana*.

Typification: The typification of *Pelagodoxa* has been problematic and several possible scenarios have been considered.

One candidate for holotype material of *Pelagodoxa henryana* is a fruit collection in a

box at Paris (P) with two labels, one stating it was a collection by Henry in 1917 and the second lacking a reference to collector or date. However, Dowe and Chapin (2006), in their excellent account of *P. henryana*, discounted this fruit collection as the holotype because they stated in their opening paragraph that Henry collected his original material “in 1916 from Nuku Hiva . . .” Thus a 1917 collection would post-date 1916 and have to be excluded. Even if one accepted the 1917 fruit collection as original material, though, it likely would have been a logistical impossibility to get fruits collected in 1917 from the Marquesas to France well before the protologue was published in July 1917!

A second possible holotype specimen is one consisting of a small portion of an inflorescence and flowers and identified as “*Pelagodoxa henryana* Becc. Marquise, Taiohae 7/1916 Henry, ex O. Dubois” in Beccari’s Herbarium Palmarum at Florence (FI) (Cuccuini & Nepi 2006, Dowe & Chapin 2006). When lent specimens for study, Beccari had a frequent practice of retaining fragments before returning the loan, and this specimen appears to be of that nature. Nonetheless, Dowe and Chapin discounted this specimen as the holotype, saying it was “not relevant to the protologue,” perhaps because the fragments of the inflorescence at FI are too meager to match with the description in the protologue. Interestingly, Taiohae is a village and valley adjacent to Taipivai Valley but separated by a high ridge and is about five kilometers distant (on a straight line) from the type locality in Taipivai Valley, where the famous stand of *P. henryana* exists. *Pelagodoxa* is unknown from the wild in Taiohae Valley or village, but cultivated specimens are in the latter. If this 1916 Henry collection proves to be original material, then the type is likely from a cultivated plant.

Dowe and Chapin (2006) stated that after a thorough search of herbaria, they concluded that Henry’s original 1916 collection of fruits of *Pelagodoxa henryana*, which would serve as holotype material, had been lost, destroyed, or was unable to be positively identified; thus, because no specimen could be conclusively identified as the holotype, they designated a lectotype consisting of the two original drawings from the protologue, one of an infructescence (Fig. 76, artist unknown) and the other of a longitudinal section of a fruit (Fig. 79, drawn by Beccari).

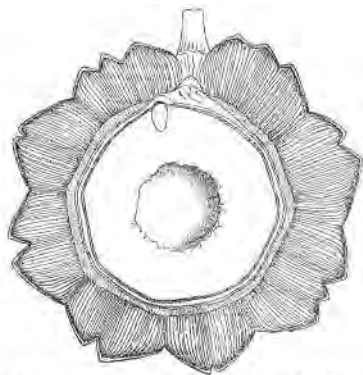


Fig. 79. — Section anatomique verticale à lavers l'endosperme, du fruit de *Pelagodoxa henryana* Boiss. (franchise naturelle).

5. The type of *Pelagodoxa henryana* (lectotype) is an illustration in Beccari's hand of a cross section of a fruit, Fig. 79, in D. Bois, *Rev. Hort. n. s.* 15: 304. 1917.

We concur with Dowe and Chapin's reasoning that absence of a holotype means that lectotypification is necessary; however, the International Code of Botanical Nomenclature for algae, fungi, and plants (Turland et al. 2018) clearly states in two places that (Art. 9.3): "A lectotype is **one** specimen or illustration..." Also, (Art. 7.2): "A nomenclatural type (*typus*) is **that element...**" (in both cases emphasis ours). In both instances, the lectotype or type is singular. Thus, one of the two, not both drawings, would have to be selected as the lectotype. Below we designate Beccari's drawing of a section of fruit, Fig. 79 in the original publication (Bois 1917), as the lectotype.

Type Locality: Surprisingly, the date 1916 and Taipivai (Taipi) Valley (the locale of Herman Melville's *Typee*), on Nuku Hiva in the Marquesas Islands of French Polynesia, commonly accepted as the year of discovery and the type locality of *Pelagodoxa henryana*, are not in the 1917 protologue and do not appear in any of the other later papers of the time about this palm (Henry 1918, Bois 1919, 1924).

As noted earlier under the second candidate for typification, the date 1916 does appear on a Henry specimen of *Pelagodoxa henryana* in Beccari's Herbarium Palmarum at Florence (FI) but any reference to Taipivai Valley is lacking. It was not until 15 years later that Martelli (1932, p. 248) speculated that Taipivai Valley was the possible type locality, basing his finding on notes that Father Delmas had provided. These notes indicated that Father Delmas had collected material of *P. henryana*

in 1930 at the base of a large waterfall in Taipivai Valley, which Martelli thought was the same place at which Henry had collected his original material ["... *a piedi della grande cascata di Vai-pivai, a Nord del corso del torrente. 5 Settembre 1930. (Credo che questa sia la stessa località ove la scopri il Sig. HENRY)*"]. Thus, we consider the Taipivai Valley site as the putative type locality, although we refer to it simply as the type locality in this paper.

Nomenclature: The protologue of *Pelagodoxa henryana* is unusual and rather intriguing. Bois authored the paper, but it contained lengthy quotes from both Beccari and Henry. The genus and species names are clearly attributed to Beccari, but not so the Latin description. The quote from Beccari contains minimal descriptive information and is preceded by a paragraph that Bois wrote suggesting that Beccari's subsequent appraisal was based only on information and photographs. The final paragraph of Beccari's quote states the following: "If you [i.e., Bois] can obtain from your correspondent [i.e., Henry] specimens of the spadix with flowers, some ripe fruits, and a photograph of the leaf of an adult plant, I would be able to provide a complete description...", which suggests that Beccari did not provide all or even a majority of the Latin description. However, it is evident that at one point (and prior to the publication of the protologue), Beccari saw fruits that Bois had provided, which he used to make the illustration, and he at least saw an inflorescence and flowers, as fragments of these organs Henry collected and are dated 1916 are at FI.

Thus, it seems that much of the description in the protologue could have come from Henry (and perhaps the fruit description as well). Whether Henry himself was knowledgeable or sufficiently experienced to have prepared a Latin description and diagnosis is another matter (he lacks an "official" INPI standard author abbreviation and has never been credited with any other names). More likely, Bois (or Beccari?) compiled the Latin description based (entirely, or at least largely) on information Henry had provided. Nevertheless, Latin descriptions or diagnoses were not required in 1917 for the validation of new taxon names (see Turland et al., 2018: Art. 39.1), and the descriptive information provided in Beccari's quote would likely be deemed sufficient for that purpose (R. Govaerts, in litt.; 4 June 2019). That being the case, we accept *Pelagodoxa* Becc. (in Bois) and

Pelagodoxa henryana Becc. (in Bois) as authority citations, in accordance with Turland et al. (2018: Art. 46.2, Note 2, Ex. 11).

Description of *Pelagodoxa*

The following description is from Bois (1917), Brown (1931), Moore (1957), Chapin et al. (2001), Stauffer et al. (2004), Dransfield et al. (2008), Butaud (2014a) and our field observations and measurements of plants at the type locality of *Pelagodoxa henryana* in the Marquesas Islands and cultivated plants of *P. henryana* in Tahiti and Hawaii and cultivated plants of *P. mesocarpa* in Tahiti, Hawaii, Fiji and Vanuatu.

Moderate, solitary, unarmed, pleonanthic, monoecious, tree palms (Figs. 1, 3). Trunk to 12 m tall, 15 cm diam., erect, rarely leaning or prostrate, brown, bare, $\pm$ smooth but lightly and closely marked with ring-like leaf scars (Fig. 10), slightly flared at base and typically with visible roots. Leaves to 15–20, crowded at distal end of trunk, ascending to drooping, often persisting temporarily and hanging dead and brown against trunk before falling, initially simple and with a bifid apex but typically becoming irregularly split (from wind) into single or multi-ribbed pinnae (Figs. 1, 3); base crescent-shaped, thickened, $\pm$ bulbous, densely covered abaxially with whitish, $\pm$ mealy tomentum, splitting opposite petiole, not forming a crownshaft; petiole curved, flat to channeled adaxially, rounded abaxially and covered with whitish, $\pm$ mealy tomentum especially proximally and less so distally, slender marginal fibers present; rachis curved, slightly channeled to flat adaxially, rounded and covered with silvery gray indumentum abaxially; blades relatively large, simple and pinnately ribbed or irregularly pinnate, gradually narrowed to the base, abruptly narrowed and cleft apically, coarsely toothed apically, the teeth representing the apices of the primary nerves (folds), $\pm$ coriaceous, dark glossy green adaxially, green abaxially but densely to lightly covered with a thin felt of gray tomentum; primary nerves raised and conspicuous adaxially and abaxially secondary nerves conspicuous, transverse veinlets obscure; rachis slightly curved, 5 cm wide proximally and there flat adaxially, rounded abaxially, attenuate distally and becoming slightly ridged adaxially, 8 mm wide distally, densely to lightly covered abaxially with whitish, $\pm$ mealy tomentum. Inflorescences 12–15 per individual, interfoliar, solitary, protandrous, and ascending to spread-

ing in flower, drooping when heavily laden with fruits, sometimes infrafoliar in fruit, exceeding petiole, branched to 2 or 3 orders; peduncle green but densely covered with silvery tan indumentum, oval in cross-section, longer than leaf base; prophyll inserted near base of peduncle, incompletely enclosing inflorescence in bud, splitting dorsally, beaked, coriaceous to nearly woody, densely covered with whitish, $\pm$ mealy tomentum; peduncular bract similar to prophyll and inserted just above the latter's base, enclosing inflorescence in bud, extending on to rachis for 20 cm but typically falling away early and leaving only a short, truncate base 2–2.5 cm high, tubular, thin, beaked, densely covered with whitish, $\pm$ mealy tomentum; panicle greenish, rachis green, variously longitudinally angled, with tan to whitish indumentum especially proximally, tapering distally, branches becoming smaller, shorter and with fewer and shorter rachillae and smaller subtending bracts distally; rachillae green except quickly turning brown and withering where staminate flowers only, lightly covered with small, fine, mostly inconspicuous, patchy indumentum, subtended by a small, green bract, longitudinally angled, $\pm$ stiff, spreading or only slightly drooping, tapering to a pointed tip 1.5 cm long, devoid of flowers in distal and proximal 2–3 cm; bearing spirally arranged, shallow but abrupt, floral pits subtended by bracts forming a low, triangular lip proximally. Flowers in triads of two earlier-opening staminate flowers flanking a central, later-opening pistillate flower in proximal $\frac{1}{4}$ – $\frac{1}{2}$ of each rachilla, paired or solitary staminate flowers distally; floral bracteoles low, rounded, inconspicuous, lower than pit, flowers partially exerted ca. $\frac{1}{2}$ from pit; nectaries present. Staminate flowers sessile, in bud $\pm$ globular and angled from mutual pressure to $\pm$ symmetrical and dome- or bullet-shaped, at anthesis to 4×2.5 mm, yellowish white; sepals 3, distinct, broadly ovate-triangular, imbricate, strongly keeled, chaffy; petals 3, broadly ovate, striate, connate proximally, free and valvate distally, adnate proximally to receptacle forming a stalk-like base; stamens 6, inflexed in bud, spreading at anthesis, filaments stout, triangular-columnar above insertion of free portion of petals, swollen proximally and there connate and adnate to pistillode, anthers medifixed, sagittate proximally, dehiscence latrorse; pistillode much shorter than stamens, conic-pyramidal, short apical tip, tricarpellate, each carpel with medial keel; pollen ellipsoid, asymmetric. Pistillate flowers sessile, in bud



6. The panicle of *Pelagodoxa henryana* is green in flower except for the rachilla tips, which have turned brown after the earlier opening staminate flowers have dropped off. Garden of Marianne and Donald Hodel, Papeari, Tahiti. *Butaud et al.* 3494.

dome-shaped, at anthesis slightly larger than staminate, globose, tending to spread and crack the floral pit; sepals 3, distinct, broadly ovate-triangular, yellowish white, briefly connate proximally and adnate to receptacle, imbricate in proximal half, free in distal half and there triangular, acute distinct, distinct, broadly ovate or rounded, greenish white, free distally, imbricate proximally; petals 3, broadly ovate-triangular, yellowish white, briefly connate proximally and adnate to receptacle, imbricate in proximal half, free in distal half and there triangular, acute; staminodes 3–6, 0.8×0.8 mm, triangular, flattened, connate proximally and there adnate to gynoecium; gynoecium broadly ovoid-rounded, greenish, trilocular, uniovulate, symmetrical but quickly becoming asymmetrical or lopsided due to bulging and overdevelopment of fertile locule, stigma branches 3, sessile, short, papillate, initially erect, reflexed at anthesis, raphides present. Fruits nearly spherical but slightly wider than long, perianth persistent; exocarp thin, light brown to tan, prominently cracked into low, pyramidal corky warts (Fig. 4), these

smaller basally, larger apically; stigmatic remains basal; mesocarp with large, abundant, radiating fibers; endocarp thick, hard, woody, operculum lacking. Seeds attached basally; endosperm homogenous; embryo nearly basal. Germination: adjacent-ligular; eophyll bifid. Cytology: $2n = 32$.

Two Species of *Pelagodoxa*

In the middle and late 1970s, the senior author returned to Hawaii with seeds of the large-fruited *Pelagodoxa henryana* that he had collected in Tahiti from cultivated plants grown from seeds from the Marquesas and a small-fruited *Pelagodoxa* that he had collected in Fiji, the latter of which long-time International Palm Society member Dick Phillips had recently found in cultivation (Phillips 1996). Although two species had been validly published in the genus, which had dramatically different fruit sizes, botanists and collectors simply attributed the size difference to natural and accepted variability. For the next 40 years, in order to distinguish plants of the two fruit sizes, collectors and dealers



7. Flowers of *Pelagodoxa henryana*: staminate above, pistillate below (both type locality, Taipivai Valley, Nuku Hiva, Marquesas Islands, French Polynesia). Butaud et al. 3495.

informally called them the “large-fruited,” “Marquesan” or “Polynesian” *P. henryana* and the “small-fruited,” “Vanua Lava” or “Melanesian” *P. henryana*. No other differences other than fruit size were documented.

Hodel had planted in his wife’s garden in Papeari, Tahiti, a small-fruited *Pelagodoxa henryana* in the late 1970s to go with the more than 20 large-fruited *P. henryana* that he and his wife had planted. The presence of both small- and large-fruited *P. henryana* growing in the same garden enabled Hodel to make careful comparison of the two taxa. As mature, adult palms, the differences in leaf blade shape and rachis color were still present, although the orange rachis of the small-fruited taxon tended to become orangish brown or tan in adulthood. As the palms flowered, another critical difference became apparent: the large-fruited *P. henryana* had inflorescences branched to two orders while the small-fruited *P. henryana* had inflorescences branched to three orders. Table 1 is a summary of the primary morphological differences between the two species. We feel these differences and others are sufficient to recognize two species.

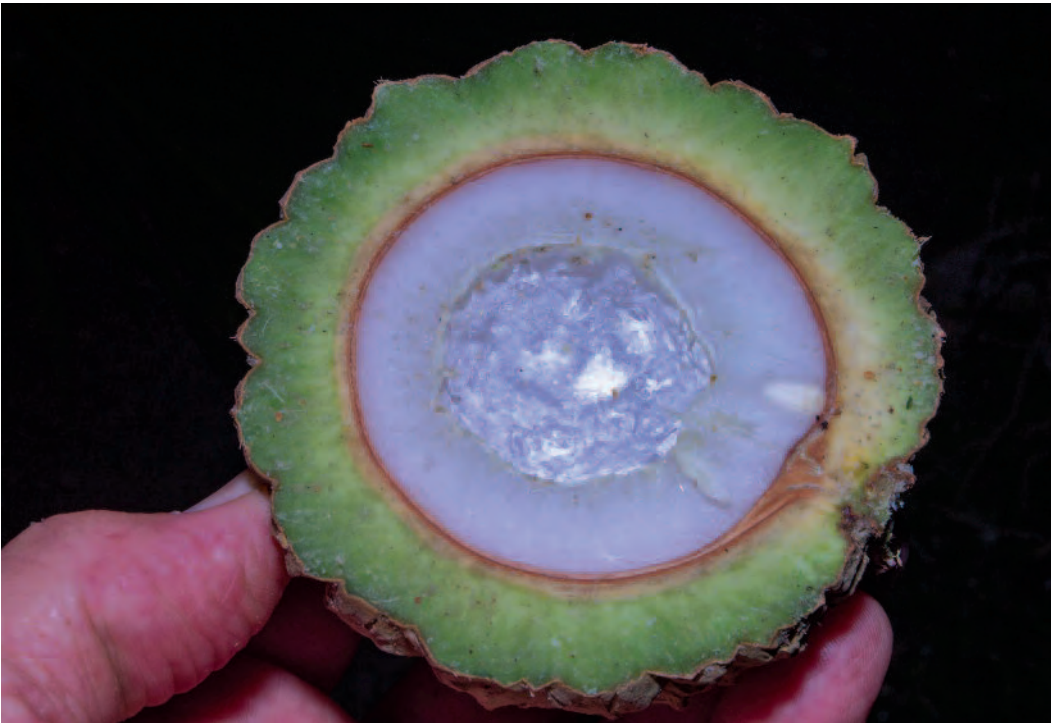
Key to the Species of *Pelagodoxa*

Leaf rachis light green; inflorescence branched to two orders; fruits 85–94 × 88–99 mm . . .
 *Pelagodoxa henryana*

Leaf rachis orange-brown to tan; inflorescence branched to three orders; fruits 63–71 × 60–70 mm *Pelagodoxa mesocarpa*

Pelagodoxa henryana Becc. in Bois, Rev. Hort. (n. s.) 15: 302. 1917. Type: Lectotype (here designated), illustration in Beccari’s hand of a cross section of a fruit, Fig. 79, in D. Bois, Rev. Hort. n.s. 15: 304. 1917. (here reproduced, Fig. 5).

Leaf base 8 × 20 cm; petiole 50 cm long, 10 cm wide at base, 4.5 cm wide at blade, light green, green and rounded abaxially, slender marginal fibers to 25 cm long extending nearly the full length of the petiole; rachis 180 cm long, green to light green (Figs. 15, 16); blade 2.35 × 1.55 m, ± broadly oblong, apical cleft 32 cm deep, up to 73 primary nerves or potential pinnae per each side of rachis, these to 111 × 3 cm, primary nerves light green adaxially, and silvery green abaxially. Inflorescences 12–15, to



8. A cross section of the fruit of *Pelagodoxa henryana* shows the green mesocarp and the seed with the grayish white endosperm with a hollow chamber and the white embryo just slightly to the right and above of the point of attachment. Garden of Marianne and Donald Hodel, Papeari, Tahiti. *Butaud et al.* 3494.

90 cm long in flower, to 110 cm long in fruit, holding 15–30 mature fruits; peduncle 41 cm long, 12.5 cm wide at base, 6.5 cm wide and 3.5 cm thick at prophyll attachment, 3.7 cm wide and 1.8 cm thick at first branch, prophyll attached 2.5 cm distally of base, 33 cm long, peduncular bract attached 25 cm distally of

prophyll attachment, 37 cm long; panicle branched to 2 orders, in flower 60 × 60 cm (Fig. 6), in fruit 68 × 55 cm, rachis 38 cm long in flower, 56 cm long in fruit, 8 primary branches proximally and 17 simple rachillae distally, most proximal branch the largest, others progressively decreasing distally in size,

Table 1. Summary of Major Morphological Differences between <i>Pelagodoxa henryana</i> and <i>P. mesocarpa</i> .		
Character	<i>P. henryana</i>	<i>P. mesocarpa</i>
Leaf Length/Width Ratio*	ca. 1.3	ca. 2.25
Leaf Rachis Color	green	orange aging to tan
Degree of Inflorescence Branching	2 orders	3 orders
Inflorescence Bract Length (most proximal on rachis)	5–8 cm	2.5 cm
Fruit size (mm) and shape	85–94 × 88–99, spherical	63–71 × 60–70, nearly spherical
Mesocarp (ripe fruit)	green, not sweetly fragrant	orange, sweetly fragrant
Seed size (mm) and shape	57–70 × 55–68, spherical	41–53 × 35–43, broadly ovoid
* Leaves taken for measurement from plants of similar size and age (mature) and growing in similar conditions of full sun.		

complexity and number of rachillae, 1st branch 38 cm long, sub-peduncle 8 × 2 × 1.2 cm, subtended by bract 5–8 cm long, sub-rachis 10 cm long, 3.3 cm wide at base, 8 mm wide at apex, with 9 rachillae to 24 × 0.8 cm, 8th branch 25 cm long, sub-peduncle 2.5 × 1.2 × 0.5 cm, subtended by 2 bracts 7 × 7 mm, no sub-rachis, 2 rachillae to 22 × 0.7 cm, simple rachillae 12–24 × 0.6–0.8 cm, bract subtending 1st simple rachilla 6 × 7 mm, bract subtending 17th simple rachilla 1 mm high. Flowers in pits 3 × 1 × 2 mm. Staminate flowers at anthesis 4 × 4 mm (Fig. 7), sepals 2–2.5 × 2–2.5 mm; petals 3.5–4 × 3.5 mm, ca. equaling filaments; stamens 2.5–3 mm long, filaments 1.5–2 × 0.7–1 mm, anthers 1–1.25 × 0.8 mm, medifixed, sagittate proximally, latrorse; pistillode 0.4–1 × 0.6–2 mm. Pistillate flowers in bud 2 × 2 mm, not exerted beyond pit, at anthesis 4 × 4 mm (Fig. 7); sepals 1.5–2 × 2.5–3 mm; petals 2.5–3 × 3–3.5 mm; gynoecium 4 × 4 mm, stigma branches 1 mm long. Fruits 15–35 per panicle, 85–94 × 88–99 mm (Fig. 17); exocarp 0.2 mm thick, corky warts to 3 × 2.7 × 1 cm; mesocarp 20 mm thick, fibrous, green (Fig. 8), aromatic or odoriferous; endocarp 1.6 mm thick; seed testa 1.6 mm thick. Seeds 57–70 × 55–68 mm, nearly spherical, with a projection at basal point of attachment, this 3 × 3 mm, rounded-blunt; endosperm 60–65 mm diam., with a large central hollow to 20–25 mm diam.; embryo 4.5–9 × 3.2–6 mm (Fig. 8).

Specimens Examined: FRENCH POLYNESIA: Marquesas Islands, Nuku Hiva, Taipivai Valley, Teuakueenui Falls region (type locality), drawing in Beccari's hand of transverse section of fruit (FI [photo!]) and in Bois [1917], lectotype); drawing by unknown hand of branch of infructescence with fruit (FI and in Bois [1917]); 17 July 1916, *Henry s.n.* (fragments of rachillae and flowers, FI [photo!]); 1917, *Henry s.n.*, fruit collection (P); undated, *Henry s.n.*, (fruit collection in a plastic bag, P); October 1919, *Henry s.n.* (fragments of rachillae and immature flowers, FI); 21 August 1920, *Henry s.n.* (P); September 1921, *S.F.I.M.* 146 (P); 19 August 1921, *Brown* 646 (BISH); 6 March 1973, *Sachet & Fosberg* 2409 (P); 18 August 1970, *Gillett* 2232 (BISH, P); 25 June 1977, *Wood* 6370 (10 trees observed (fr, PTBG); 22 September 2016, *Butaud, Taata & Hodel* 3495 (PAP); Hatiheu valley, terrain de la mission au Sud-Est de l'ancien dépotoir, 15 October 2012, *Butaud & Huioutu* 3165 (PAP); leaf, anonymous and undated (FI [photo!]); ex Bois, fruit, anonymous and undated (FI

[photo!]). CULTIVATION. FRENCH POLYNESIA: Marquesas Islands, Nuku Hiva, Taipivai Village, Clark residence, 30 July 1970, *Gillett* 2213 (BISH, P); Ua Huka, Vaipae Village, local church grounds, 24 June 2004, *Wood* 10784 (PTBG, US); Tahiti, Papeari, P.K. 49.8, *côte de mer*, garden of Marianne and Donald Hodel, 17 September 2016, *Butaud, Falchetto & Hodel* 3494 (PAP); Austral Islands, Raivavae, Vaiuru, *marae* Temahara, 15 April 1922, *Stokes* 60 (BISH). HAWAIIAN ISLANDS: Kauai, National Tropical Botanical Garden in Lawai Valley, Bamboo Bridge section, *NTBG* # 770290.001 (seed from Tahiti), 14 March 1994, *Lorence* 7448 (PTBG, US), 14 December 1994, *Reuter* 35 (PTBG).

Distribution: Endemic to French Polynesia, *Pelagodoxa henryana* is unknown in the wild state (Butaud 2004a). Ancient populations were known on Raivavae island in the Austral archipelago, where they are now extinct, and are still known on Nuku Hiva in the Marquesas archipelago in the form of two anthropogenic stands, the type locality in Taipivai Valley with 11 adult individuals (Fig. 3) and many juveniles and seedlings and the new locality of Hatiheu with a single mature individual and several juveniles in 2017.

The type locality of *Pelagodoxa henryana* is in upper Taipivai Valley, close to the base of Teuakueenui waterfall and near an old Marquesan house foundation (as noted by Gillett on his 2232 specimen). There the small population of this striking palm grows on a slope above a stream in dense, wet, disturbed lowland forest composed predominantly of *Inocarpus fagifer* (*ihī*, *mape* or Tahitian chestnut), *Cocos nucifera* (*'ehi*, *e'ehi*, coconut) and *Hibiscus tiliaceus* (*hau*, *purau*), a site with extensive signs of ancient human habitation (Fig. 3). In 2012, a new population was identified with the help of Marquesan informants in Hatiheu valley on the northern coast of Nuku Hiva growing on an isolated archeological structure, confirming the statement of Brown (1931) that "according to native informants, there were also a few trees growing at low altitudes in the north-eastern part of Nukuhiva." A single tree was known in 1921 at Puamau on Hiva Oa island and was considered recently introduced from Nuku Hiva (Brown 1931).

On Raivavae in the Austral Archipelago, several trees were cultivated at least on two ritual sites, *marae* Unurau and *marae* Temahara, according to the ethnologist J.F.G. Stokes in 1922 (Brown 1931; Matthew Prebble, pers. comm. 2012)

and several informants (Linda Tumarae & André Ani, pers. comm. 2012). All these trees had died by the 1980s, and *P. henryana* is now extinct on this island. Apparently, it formerly inhabited nearly all the Austral Archipelago because palm pollen dated before the arrival of Polynesian people and described as belonging either to the Iguanurinae subtribe (Prebble 2014, Prebble & Wilmhurst 2009) or the Arecoideae subfamily but differing from *Cocos* (Prebble & Dowe 2008) was identified in swamp sediments from Rimatara, Tubuai, Raivavae and Rapa Iti islands.

Thus, *Pelagodoxa henryana* was most likely native in the Austral Islands. It probably was also native in the Marquesas Islands as no clear traditional link exists between Polynesians from both archipelagoes. Not yet known from the Cook Islands, we consider it a French Polynesian endemic species extinct in the wild and subsisting only in the cultivated state because of Polynesian domestication; the situation of *P. henryana* is then similar to that of *Pritchardia tahuatana* (Butaud & Hodel 2017).

Today, *Pelagodoxa henryana* is widely cultivated on nearly all the high islands of French Polynesia, mainly in the Marquesas, the Society and the Gambier. It also has been disseminated to other tropical locales like the Hawaiian Islands, Australia, Singapore and Thailand.

Ecology: The two populations on Nuku Hiva occur at 140–300 m elevation in lowland wet forest dominated by *Hibiscus tiliaceus* with some *Inocarpus fagifer* and *Cocos nucifera*. Minor tree species are *Annona muricata*, *Artocarpus altilis*, *Cananga odorata*, *Cerbera manghas*, *Glochidion marchionium* and *Pandanus tectorius*. The understory is composed of the ferns *Angiopteris evecta*, *Asplenium tenerum*, *Diplazium harpeodes*, *Lepisorus mucronatus*, *Nephrolepis biserrata*, *N. hirsutula* and *Ophioderma pendulum*; the grasses *Centotheca lappacea* and *Oplismenus compositus*; the bananas *Musa troglodytarum* and *M. x paradisiaca*; the herb *Procris pedunculata*; and the vines *Dioscorea bulbifera*, *Stephania japonica* var. *timoriensis* and *Vanilla x tahitensis*. This habitat is clearly of anthropogenic origin and corresponds to a kind of fallow forest, one growing on what was previously inhabited and cultivated land, which archeological structures prove. On Raivavae in the Austral Archipelago, *Pelagodoxa henryana* was cultivated on ceremonial structures, currently dominated by a similar

wet forest of *Hibiscus tiliaceus* with some individual *Inocarpus fagifer*.

Thus, the original habitat of *Pelagodoxa henryana* is unknown. Several authors hypothesized it was part of the mid-elevation wet forest, at 300–900 m elevation, with *Hibiscus-Pandanus-Angiopteris* formation and *Ficus prolixa*, *Cyclophyllum barbatum* and *Inocarpus fagifer* (Hallé 1978, Schäfer 1977). Based on the rather good floatation capacity of fruits of *P. henryana*, which is due to the large central hollow (see below in Phytogeography section), the lack of a past or present dispersing animal (either bird or bat) and the main conclusions of Prebble and Dowe (2008) about the decline of palms on Pacific islands, we suggest the hypothesis that *P. henryana* was an inhabitant of lowland wet forest, probably swampy and not far from rivers and the sea. The ability of *P. henryana* to grow well in shade, sometimes deep shade, is also compatible with a position in the understory of such riparian, swampy or littoral forests.

Pelagodoxa mesocarpa Burret, Notizbl. Bot. Gart. Berlin-Dahlem 10: 288. Type: *H. Cuming s.n.* (B, holotype [photo!] Fig. 9).

Leaf base 12 × 14 cm; petiole 56 cm long, 10 cm wide at base, 4.5 cm wide at blade, yellow distally, green proximally, tan abaxially, slender marginal fibers to 15 cm long in proximal three-quarters; rachis 220 cm long, orange to yellow-orange when young becoming orange-tan to tan with age (Figs. 15, 16); blade 2.5 × 1.1 m, ± narrowly oblong, apical cleft 25 cm deep, 62 primary nerves or potential pinnae per each side of rachis, these to 120 × 3.2 cm, primary nerves greenish yellow to orange adaxially, orange-tan to tan abaxially. Inflorescences 12–15, to 90 cm long in flower, to 115 cm long in fruit (Fig. 11), holding 15–40 mature fruits; peduncle 46 cm long, 12 cm wide at base, 6 cm wide and 2.1 cm thick at prophyll attachment, 4 cm wide and 2.4 cm thick at first branch; prophyll attached 2.5 cm distally of base, 43 cm long, peduncular bract attached 35 cm distally of prophyll attachment, 33 cm long and; panicle branched to 3 orders, in flower 55 × 75 cm (Fig. 12), in fruit 75 × 95 cm, rachis 52 cm long in flower, 65 cm long in fruit, indumentum ± scurfy, 14 primary branches proximally and 13 simple rachillae distally, 1st branch 32 cm long, sub-peduncle 5.5 × 2.5 × 0.9 cm, subtended by bract 2.5 cm long, sub-rachis 15 cm long, 1 cm wide at base, 8 mm

wide at apex, sub-peduncle $3 \times 1 \times 0.7$ cm, with 16 rachillae to 21×0.6 cm, 14th branch 17 cm long, sub-peduncle $2.5 \times 0.9 \times 0.5$ cm, subtended by 2 bracts 2×7 mm, sub-rachis 5×4 mm, 3 rachillae to 15×0.5 cm, simple rachillae 13, 9–18 $\times 0.5$ –0.8 cm, bract subtending 1st simple rachilla 2×6 mm, bract subtending 17th simple rachilla 1×5 mm. Flowers in pits $4 \times 2 \times 2$ mm. Staminate flowers at anthesis 5–5.5 $\times 5$ –5.5 mm (Fig. 13), sepals 2.5–3 $\times 2.5$ –3 mm; petals 3.8–4.2 $\times 3.5$ mm, slightly shorter than filaments; stamens 3–3.5 mm long, filaments 2.5 $\times 0.7$ –1 mm, anthers 0.9 $\times 0.6$ mm; pistillode 0.5–1 $\times 0.6$ –2 mm. Pistillate flowers in bud 2.5 $\times 2.5$ mm, barely exerted beyond pit, at anthesis 4.5 $\times 4.5$ mm (Fig. 13); sepals 2–2.5 $\times 3$ –3.5 mm; petals 3 $\times 3.5$ –4 mm; gynoeceum 4.5 $\times 4.5$ mm, stigma branches 0.5–0.75 mm long. Fruits 25–50 per panicle, (20–)63–71 $\times$ (20–)60–70 mm (Figs. 17, 18); exocarp 0.45 mm thick, corky warts to $2 \times 1.8 \times 0.8$ cm; mesocarp 11 mm thick, pulpy, orange (Fig. 18), sweetly fragrant; endocarp

1.4 mm thick; seed testa 1 mm thick. Seeds 41–53 $\times$ 35–43 mm, broadly ovoid (Fig. 14), with a projection at basal point of attachment, this 5 $\times 2.5$ mm, sharp-pointed; endosperm 36–39 mm diam., solid, lacking a central hollow; embryo 5.5–7.9 $\times$ 3.2–3.9 mm.

Specimens Examined: ORIGIN UNKNOWN: *H. Cuming s.n.* (B, holotype [photo!]). CULTIVATION. FRENCH POLYNESIA: Tahiti, Papeari, P.K. 49.8, côte de mer, garden of Marianne and Donald Hodel, 17 September 2016, Butaud, Falchetto & Hodel 3493 (PAP). HAWAIIAN ISLANDS: Kauai, National Tropical Botanical Garden in Lawai Valley, Bamboo Bridge section, NTBG # 800426.001 (seed from Fiji), 12 May 2003, Lorence 9070 (PTBG, US), 28 March 1998, Chapin 40 (PTBG).

Distribution: Likely unknown in a truly wild state, *Pelagodoxa mesocarpa* has been recorded (as *P. henryana*) several times from the Solomon Islands and Vanuatu, where it is always found near houses and other places of human

9. The holotype of *Pelagodoxa mesocarpa* comprises two empty, shell-like exocarps at B. Photo courtesy of the Botanischer Garten und Botanisches Museum Berlin-Dahlem, Zentraleinrichtung der Freien Universität, Berlin.





10. Both *Pelagodoxa* spp. have an erect, smooth, brown trunk as here on *P. mesocarpa*. Note the orange to tan leaf blade rachises of this species. Garden of Marianne and Donald Hodel, Papeari, Tahiti. *Butaud et al.* 3493.



11. Inflorescences of *Pelagodoxa mesocarpa* are sometimes infrafoliar in fruit. Jeff and Suchin Marcus' Floribunda Palms and Exotics, Hawaii.



12 (top). The panicle of *Pelagodoxa mesocarpa* is green in flower except for the rachilla tips, which have turned brown after the earlier opening staminate flowers have dropped off. Garden of Marianne and Donald Hodel, Papeari, Tahiti. *Butaud et al.* 3493. 13 (bottom). Flowers of *Pelagodoxa mesocarpa*: staminate above (cultivated, Fiji), pistillate below Jeff and Suchin Marcus's Floribunda Palms and Exotics, Hawaii.

activity. In some cases, it has escaped into adjacent, highly disturbed secondary or regrowth forest.

Corner (1969) reported that *Pelagodoxa* was of recent occurrence on San Cristobal in the Solomon Islands, where it had grown from fruits washed ashore on the southern coast in the mid-1950s, and that the islanders were unfamiliar with it. Corner continued and noted that Geoff F. C. Dennis of the Forest Department had reported to him that a grove of this palm was at Makiri Harbour, also on the southern coast of San Cristobal, and perhaps Catholic missionaries, who had originally come from the Marquesas Islands, introduced it. When the senior author was doing botanical work in the Solomon Islands in 1976, Dennis, who was then retired, recounted this story of the small-fruited *Pelagodoxa* in the Solomon Islands and repeated it several times in subsequent correspondence. Later, Dennis and McQueen (1989) provided a brief summary that differed somewhat from previous accounts. They stated that the first seeds of this palm were brought from the Marquesas Islands in the 1800s. A few of the palms are currently growing at Tetera village at the head of a deep harbor on the southern coast of San Cristobal, and the recently-retired Anglican Archbishop of Melanesia collected seeds of the palm from an island in Tetera Harbour. Nonetheless, it seems highly unlikely that *P. mesocarpa* could have been introduced into the Solomon Islands from the Marquesas Islands, because the small-fruited *P. mesocarpa* had never been found in this latter area.

Dowe (1989) and Dowe and Cabalion (1996) reported that *Pelagodoxa* occurred on Vanua Lava, Malekula and Erromango in Vanuatu, where it was cultivated but had become naturalized. Chapin and Dowe (2005) theorized that French missionaries stationed between Vanuatu and French Polynesia in the 1800s and 1900s might have brought seeds or plants of *Pelagodoxa* to Vanuatu as they did with other plants, but again, this notion seems unlikely because only the large-fruited *P. henryana* has ever been found in French Polynesia. Recent correspondence with the Forestry Department of Vanuatu showed that *Pelagodoxa mesocarpa* is also present on Gaua and Vanua Lava islands in the Banks Archipelago, and the Forestry Department cultivates it on Efate.

Pelagodoxa mesocarpa has been reported several times from Fiji, as early as 1948 and again as



14. Seeds of *Pelagodoxa mesocarpa* are broadly ovoid. Garden of Marianne and Donald Hodel, Papeari, Tahiti. Butaud et al. 3493.

P. henryana, but always cultivated in a garden (Parham 1948, 1972, Phillips 1996).

Ecology: Little is known about the ecology of *Pelagodoxa mesocarpa*. Where it is found in the Vanuatu and the Solomon Islands and how it performs in cultivation suggest that *P. mesocarpa* likely is from a habitat of partial shade in moist to wet, tropical lowland forest, similar to that of *P. henryana*. Its fruit morphology and anatomy seem to support dispersal by birds (*Ducula* spp., Imperial pigeons) or fruit-bats (*Pteropus* spp.).

Major Morphological Differences Between *Pelagodoxa henryana* and *P. mesocarpa*

Leaf: Other than the fruits and seeds, leaves of the two species might show the most conspicuous differences. Leaf blades of *Pelagodoxa henryana* tend to be proportionately shorter and wider than those of *P. mesocarpa*. When comparing leaves of both species of the same- or similar-aged plants grown in the same light conditions of full sun, leaf blades of *P. henryana* have a length-to-width ratio of 1.3 while those of *P. mesocarpa* are 2.25 (Fig. 15). Also, leaf blades of *Pelagodoxa henryana* have up to 73 primary nerves per side of the green to light green rachis while those of *P. mesocarpa*



15 (top). Leaf blades of *Pelagodoxa henryana* (left, Butaud et al. 3494) tend to be proportionately shorter and wider than those of *P. mesocarpa* (right, Butaud et al. 3493). 16 (bottom). Leaf blade rachises of *Pelagodoxa henryana* (left, Butaud et al. 3494) are greenish, while those of *P. mesocarpa* (right, Butaud et al. 3493) are orange. All photos from garden of Marianne and Donald Hodel, Papeari, Tahiti.

have 62 primary nerves per each side of the orange aging to tan rachis (Fig. 16).

Inflorescence: Inflorescences of *Pelagodoxa henryana* are branched to two orders while



17 (top). Fruits of *Pelagodoxa mesocarpa* (left, Butaud et al. 3493) are significantly smaller than those of *P. henryana* (right, Butaud et al. 3494). 18 (bottom). Mature ripe, fruits of *P. mesocarpa* (right, Butaud et al. 3493) have a sweetly fragrant, pulpy, orange mesocarp, while those of *P. henryana* (left, Butaud et al. 3494) have an aromatic or odoriferous, fibrous, greenish mesocarp. Both photos from the garden of Marianne and Donald Hodel, Papeari, Tahiti.

those of *P. mesocarpa* are branched to three orders (Figs. 6, 12). Also, rachis bracts subtending the first-order branches of *P.*

henryana tend to be larger than those of *P. mesocarpa*. For example, the rachis bract subtending the most proximal branch of *P.*



19. Seeds of *Pelagodoxa mesocarpa* (left, Butaud et al. 3493) are smaller, somewhat oblong or ellipsoid and have a sharp-pointed protuberance at the attachment point while those of *P. henryana* (right, Butaud et al. 3494) are larger, nearly spherical and have a broadly rounded protuberance at the attachment point. Garden of Marianne and Donald Hodel, Papeari, Tahiti.

henryana is 5–8 cm long while the corresponding rachis bract on *P. mesocarpa* is only 2.5 cm long.

Fruits and Seeds: Fruits of *Pelagodoxa mesocarpa* are significantly smaller than those of *P. henryana* (Fig. 17). Average length and width are 20 mm and 25 mm smaller in *P. mesocarpa*, with differences of 19 mm and 23 mm significant at $p < 0.05$. Not surprisingly the fruits have significant differences in volume. Those of *P. henryana* are on average 237 cm³ larger (ca. 240%) in volume than fruits of *P. mesocarpa*.

Outliers of fruit size for both species have been reported; fruits as little as 2–3 cm in diameter were reported for *Pelagodoxa mesocarpa* (as *P. henryana*) in Vanuatu (Chapin & Dowe 2005) while fruits to 15 cm in diameter were reported for *P. henryana* in French Polynesia (Bois 1917). In the case of the former, these were likely immature, unfertile, or aborted fruits because they failed to germinate even though in some instances the pericarp had become soft, fragrant and orange. Nonetheless, Vanuatians or ni-Vanuatu have described the fruits as only 2 cm in diameter, have cultivated them (propagated?) and report an inland population on at least one island (Chapin & Dowe 2005). Further work on *Pelagodoxa* in Vanuatu would surely be rewarding. In the case of *Pelagodoxa henryana* fruits have never been found in

recent times that were much larger than 10 cm in diameter; although difficult to explain, fruits to 15 cm in diameter were likely estimations and perhaps erroneous ones at that.

Fruits of both species tend to have circular shapes with high eccentricity (a measurement of how circular a shape is) (Fig. 17). A small but significant difference of 0.01 exists between the two species (significant at $p < 0.05$). Fruits of *Pelagodoxa henryana* tend to be slightly more spherical than those of *P. mesocarpa*, which tend to be slightly more oblong or ellipsoid.

On average, fruits of *Pelagodoxa mesocarpa* have 10% fewer warts than those of *P. henryana* but this difference is not significant at $p < 0.05$. Although we found a significant difference in the number of warts per square centimeter, this difference is likely attributable to the significant difference in fruit size. Overall, a similar number of warts on *P. mesocarpa* tend to have a high density over a smaller surface area. Burret (1928) also noted that the fruits of *P. mesocarpa* have a considerably thinner pericarp, as well as a relatively large number of warts relative to their circumference.

When mature and ripe, fruits of *Pelagodoxa henryana* have an aromatic or odoriferous, fibrous, greenish mesocarp while those of *P.*

mesocarpa have a sweetly fragrant, pulpy, orange mesocarp (Fig. 18).

As with the fruit size, the seeds also differ significantly, with seeds of *Pelagodoxa mesocarpa* being smaller than those of *P. henryana* (Fig. 19). The average difference in seed length, width and volume was 11 mm, 20 mm and 64 cm³, respectively. Differences of 8 mm, 18 mm and 54 cm³ were significant at $p < 0.05$.

Seeds of *Pelagodoxa henryana* are nearly spherical with a small, broadly rounded protuberance proximally adjacent to the embryo while those of *P. mesocarpa* are slightly longer than wide (oblong or ellipsoid) with a small, somewhat sharp-pointed protuberance proximally adjacent to the embryo (Fig. 19). The difference in shape is significant; seeds of *P. mesocarpa* show significantly lower eccentricity of 0.78 on average, with a difference in eccentricity from *P. henryana* of 0.16 (significant at $p < 0.05$).

Seedling: After germination differences are apparent in the bifid seedling leaves. Seedlings of *Pelagodoxa henryana* have broader, shorter leaf blades with a more spreading apical cleft and a greenish rachis while those of *P. mesocarpa* have longer, narrower leaf blades with a more acute apical cleft and a distinctive orange rachis (Fig. 20).

A few, recent descriptions of fruit and seed size and shape of the two *Pelagodoxa* species (Chapin et al. 2001, Chapin & Dowe 2005) are not as dramatically different as earlier measurements (Bois 1917, Burret 1928). In such recent cases, fruits used for study were taken from sites where both species were cultivated, suggesting that hybridization was a distinct possibility (see Molecular Analysis below) although other factors might also be responsible. As with many other plants, suspected hybrids between *P. henryana* and *P. mesocarpa* show intermediate character, especially in fruits, seeds, leaf blade shape and leaf rachis color.

20. Seedlings of *Pelagodoxa henryana* have broader, shorter leaf blades with a more widespread apical cleft and a greenish rachis while those of *P. mesocarpa* have longer, narrower leaf blades with a more contracted apical cleft and a distinctive orange rachis. Garden of Marianne and Donald Hodel, Papeari, Tahiti.



Molecular Analysis

We undertook DNA analysis to determine if molecular support existed for our thesis that *Pelagodoxa* comprised two species.

Methods: We processed 11 samples/accessions of the large-fruited *Pelagodoxa henryana* and five of the small-fruited *P. mesocarpa*, using 3 × 6 cm sections from the newest, fully open leaf. Sampled plants were from Floribunda Palms and Exotics (FP) (Kurtistown, Hawaii, USA); the National Tropical Botanical Garden (NTBG) (Kalaheo, Hawaii, USA); and previously published data in GenBank from one accession identified as *P. henryana* at Kew. All samples/accessions of *P. henryana* except two were taken from plants grown from seeds collected at the type locality on Nuku Hiva, Marquesas Islands, French Polynesia and all samples of *P. mesocarpa* were taken from plants grown from seeds likely collected from one tree in Fiji (Appendix 1). We used *Sommieria leucophylla* (previously published GenBank data) as an outgroup, which has a strong, well established sister-group relationship with *Pelagodoxa* (Lewis and Doyle 2002, Asmussen et al. 2006, Loo et al. 2006, Norup et al. 2006, Baker et al. 2011).

We extracted DNA following the CTAB protocol of Doyle and Doyle (1987). We then conducted polymerase chain reactions and Sanger sequencing of two nuclear intron loci that were used in a previous study of arecoid phylogenetics (Baker et al. 2011). We chose intron 4 of phosphoribulokinase (*PRK*) and intron 23 of the second largest subunit of RNA polymerase II (*RPB2*) using the primers of Lewis and Doyle (2002) and Roncal et al. (2005). We chose these loci because the newly generated sequences then could be incorporated into a previously published, densely sampled phylogenetic dataset and because these loci carry significant phylogenetic signal at the species level (Baker et al. 2011).

We amplified both loci under the same thermal cycle: 94°C (4 minutes); followed by 25 cycles of 94°C (2 min), 55°C (1 min) and 72°C (2 min), with a final extension step of 72°C (4 min). PCR reactions were conducted with 12.5 µl Apex PCR 2× Taq master mix (Genesee Scientific, San Diego, California, USA), 8 µl nanopore water, 1.25 µl of forward and reverse primer (PRK-717F, GTG ATA TGG AAG AAC GTG G and PRK-969R ATT CCA GGG TAT GAG CAG C; RPB2-F, CAA CTT ATT GAG TGC ATC ATG G and RPB2-R, CCA CGC ATC TGA

TAT CCA C, respectively), 1 µl of 5M Betaine (Thermo Scientific, Waltham, Massachusetts, USA) and 1 µl of template DNA (50–100 ng/µl).

PCR products were visualized on a 1% agarose gel stained with ApexSafe DNA loading dye (Genesee Scientific, San Diego, California, USA) and cleaned with Axygen AxyPrep magnetic beads (Corning-Axygen, Corning, New York, USA, 1.4% by volume), followed by two washes with 200 µl 70% ethanol. Cycle sequencing was carried out in 10 µl reactions with the BigDye™ Terminator v3.1 cycle sequencing kit (Thermo Scientific, Waltham, Massachusetts, USA) following manufacturer protocols and cleaned using Sephadex (70g/L, GE Healthcare, Chicago, Illinois, USA) in a 96-well filter plate (Phenix Technologies, Accident, Maryland, USA). Sequencing was conducted on an Applied Biosystems 3130 Genetic Analyzer (Thermo Scientific, Waltham, Massachusetts, USA) at the West Virginia University Genomics Core Facility using manufacturer protocols.

Resulting electropherograms were edited in Geneious v.10 (Biomatters Inc., Auckland, New Zealand) and consensus sequences from forward and reverse reads were exported and merged with *PRK* and *RPB2* data matrices from Baker et al. (2011), downloaded from TreeBase (www.treebase.org; accession S11041). Alignments were generated with Muscle (Edgar 2004) and manually trimmed to reduce missing data at the ends of the alignment. Phylogenetic trees were constructed using maximum likelihood in RAxML v.8 (Stamatakis 2014), under a GTR+GAMMA model with the default number of rate categories. We conducted 10 independent runs from random starting seeds to check for convergence. We assessed branch support with 1,000 standard bootstrap replicates in RAxML under the same search parameters.

Results: The resulting trimmed alignments were 1507 and 1440 bp, with 509 and 693 parsimony informative characters for *PRK* and *RPB2*, respectively. For *PRK*, all samples of *Pelagodoxa* formed a monophyletic group (Bootstrap = 100%) that does not include *Sommieria leucophylla* (Fig. 21). *PRK* was invariant within *Pelagodoxa*, however, with all samples sharing a single sequence type. For *RPB2*, *Pelagodoxa* sequences formed a monophyletic group (bootstrap = 100%) that does not include *S. leucophylla* (Fig. 21). Two sequence variants were recovered, largely corresponding to *P. henryana* (nine samples/accessions) and *P. mesocarpa* (seven

samples/accessions) (hereafter termed the 'henryana' and 'mesocarpa' types). These two sequence variants differed by ten substitutions and included an 85-bp insertion in the *mesocarpa* type relative to all other arecoid palms. Two accessions initially identified as *P. henryana* had the *mesocarpa* type variant for *RPB2* and clustered with the latter (Fig. 21).

Discussion and Conclusions: Both *PRK* and *RPB2* data place all samples/accessions of *Pelagodoxa* as a monophyletic group (though *PRK* is invariant within *Pelagodoxa*) with strong bootstrap support. *RPB2* further differentiates *Pelagodoxa* into two relatively divergent sequence types, with the *henryana* type comprising 9 of 11 *P. henryana* samples and the *mesocarpa* type comprising all five of the *P. mesocarpa* samples and two of the 11 *P. henryana* samples.

Three possible explanations exist for the two anomalous *Pelagodoxa henryana* samples/accessions harboring *mesocarpa*-type sequences: 1) one or more of the samples/accessions were misidentified; 2) these sequences represent unsorted ancestral polymorphism among *Pelagodoxa*; or 3) these sequences are in fact unique to each species, but the two *P. henryana* bearing the *mesocarpa*-type sequences may be the result of pollen transfer from *P. mesocarpa* to *P. henryana* (hybridization). Indeed, the first of the two anomalous samples of *P. henryana* in question corresponds to an F1 offspring from *P. henryana* seed (F1 offspring = accession *NTBG 040506.001*; parental plant = *NTBG 770290.001*). However, this plant is in proximity (ca. 50 m) to an individual of *P. mesocarpa* (*NTBG 800426.001*), representing a highly plausible instance of pollen transfer from *P. mesocarpa* to *P. henryana*. Furthermore, honeybees have been frequently observed to pollinate the plants at the National Tropical Botanical Garden in Hawaii (David Lorence pers. obs.). The *P. henryana* parental plant (*NTBG 770290.001*) was grown from seed from a large-fruited individual from the Jardin Botanique in Papeari, Tahiti (first or second generation, originally from the type locality on Nuku Hiva, Marquesas Islands). The small-fruited individual (*NTBG 800426.001*) that grows close to *NTBG 770290.001* was grown from seed from the small-fruited plant from Fiji. Thus, it is plausible that *040506.001* represents a hybrid, resolving this anomaly. Regardless, variation in *RPB2* lends further evidence of divergence among individuals of *P. henryana* and *P. mesocarpa*, especially because

all sampled individuals of the small-fruited *P. mesocarpa* share the same sequence variant.

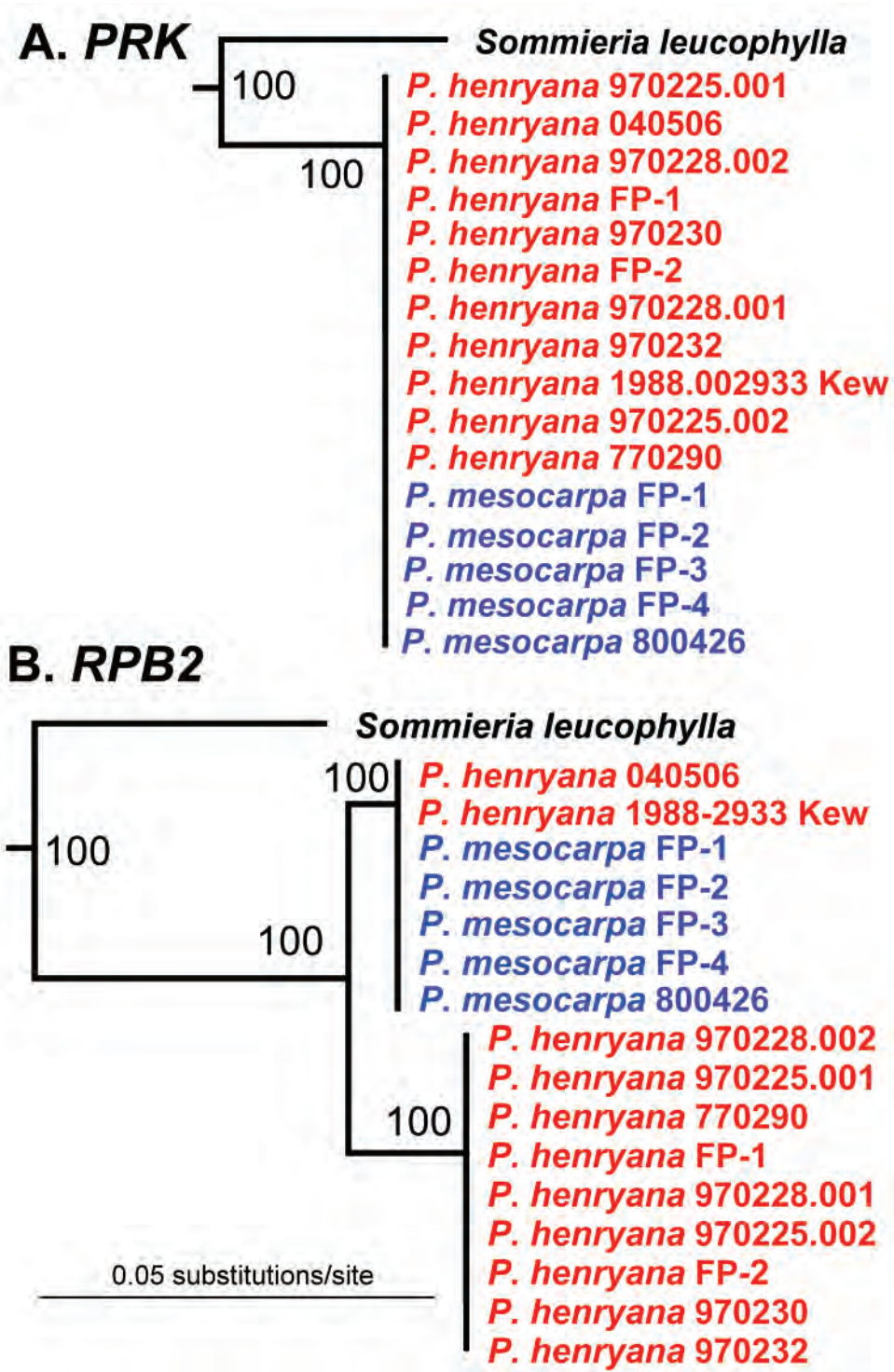
The second anomalous sample (accession) of *Pelagodoxa henryana* in question was the original plant included in Baker et al. (2011). This plant grows at the Royal Botanic Garden, Kew, England (voucher 1988-2933 [K]; GenBank accession numbers *AJ831321/AJ830135*). Kew accession data show that they had received the seeds from which their plant was grown from the Royal Botanic Garden, Edinburgh, Scotland. Alistair Watt had obtained these seeds (*Watt 1156*) from the late Dick Phillips in Fiji (Watt pers. comm.); thus, it was likely the small-fruited *P. mesocarpa*, the only *Pelagodoxa* to which Phillips had access at that time (Phillips 1996). Indeed, while fruits are not visible in photos of the plant at Kew, the leaf blade seems longer and narrower, corresponding more with that of *P. mesocarpa*. We conclude that the Kew plant is, in fact, *P. mesocarpa*, now making the GenBank data mislabeled, and resolving this anomaly.

Thus, the molecular data tend to support our thesis that *Pelagodoxa henryana* and *P. mesocarpa* are two distinct species.

Phylogenetic Relationships and Phytogeography

Phylogenetic relationships can allude to or support biogeographical theories, including origin, migration and distribution, which in turn can help define speciation. The first workers investigating *Pelagodoxa* based their theories about its relationships with other taxa on gross but distinctive morphological characters, especially its curious, large, corky-warted fruits and large, undivided leaves (Bois 1917, Burret 1928, Martelli 1932, 1935, Beccari & Pichi-Sermolli 1955, Satake 1962). Indeed, in his response to Bois after receiving a description and perhaps a fruit or two of *P. henryana*, Beccari noted the similarity of *Pelagodoxa* to the southeast Asian *Teymannia altifrons* (now *Johannesteijsmannia altifrons*) and the American *Manicaria saccifera*, likely based on their large simple leaves and warty fruits, but he was unable to determine its taxonomic position.

Unfortunately, both these characters have arisen independently in several (fruits) or many (leaves) varied and sometimes only distantly related genera. Genera commonly associated with *Pelagodoxa* included *Manicaria*, *Phytelephas*, *Sommieria* and even the palmate-leaved *Johannesteijsmannia* and *Pholidocarpus*.



21. Results of DNA analysis of *Pelagodoxa henryana* and *P. mesocarpa* showing the PRK tree (A) above and the RPB2 tree (B) below.

Supra-generic taxa linked to *Pelagodoxa* included the informal “*Orania*” group, the tribe Areceae, the subtribe Iguanurinae and the subfamily Phytelphantoideae.

Moore (1973) was the first worker to take a more modern, evolutionary approach to phylogenetic analysis. Incorporating an extensive suite of morphological and

anatomical and vegetative and floral characters, he placed *Pelagodoxa* in the informal “*Clinostigma*” alliance and close to *Iguanura*, *Neoveitchia* and *Sommieria* within the Arecoid palms.

Dransfield and Uhl (1986) placed *Pelagodoxa* in the subtribe Iguanurinae of the tribe Areceae and subfamily Arecoideae and alluded to a possible relationship with *Heterospatha* but recognized and remarked about its isolated nature. However, Pintaud (1999) determined *Pelagodoxa* was sister to *Sommieria*, while Chapin et al. (2001) noted that the lack of an operculum (lid or covering of the embryo) in *Pelagodoxa* would exclude it from the Iguanurinae, which has as one of its determining characters the presence of the operculum.

Starting after the turn of the 21st century, numerous workers, relying mostly on DNA sequence data, placed *Pelagodoxa* and *Sommieria* as sister genera isolated from other genera in their phylogenetic trees. In acknowledgement of their unique characters and isolation from other genera, Dransfield et al. (2005), based on then several yet-to-be published phylogenies, placed *Pelagodoxa* and *Sommieria* in their own tribe, Pelagodoxeae, within the subfamily Arecoideae, a placement still recognized in recent phylogenies.

In supra-generic relationships, Dransfield et al. (2008) remarked that “no obvious morphological explanation” exists for the exclusion of the Pelagodoxeae from the tribe Areceae with which it has much in common biogeographically, yet no modern phylogenetic study placed it in, or even sister to, the Areceae. However, shortly thereafter studies documented its sister relationship to the Areceae (Baker et al. 2009, Baker & Couvreur 2013a) or its inclusion within the “core arecoids” group with the Areceae (Comer et al. 2015, 2016). Surprisingly, some recent studies show that the Pelagodoxeae is more closely related to the American tribes Leopoldineae (Norup et al. 2006, Baker et al. 2011, Faurby et al. 2016) or a clade of Geonomateae, Leopoldineae and Manicarieae (Baker et al. 2009). This information supports the theory of Dransfield et al. (2008) that the Pelagodoxeae arrived independently from the Areceae in the western Pacific, likely from the Americas. This theory would seem to be unusual or even unlikely but is supported by the parallel case of *Pritchardia* (Coryphoideae: Trachycarpeae), which is also theorized to have

arrived in the Pacific from the Americas, in this case from North America (Bacon et al. 2012).

After *Pritchardia* likely arrived in the western Pacific from North America, first as a more easily dispersed, small fruited prototype, it then moved back toward the east through Fiji, Tonga, Cook Islands and finally French Polynesia and Hawaii where, in the latter two places, fruit size increased dramatically (Hodel 2007, 2009, 2012b, Butaud & Hodel 2017). Dramatically increased fruit size and accompanying loss of dispersal in isolated island groups, like Polynesia and Melanesia, is called “fruit gigantism” and is a documented and recognized phenomenon (Corner 1966, Carlquist 1980). A similar, plausible, parallel process could have occurred in the Pelagodoxeae. The ancient ancestor of the Pelagodoxeae was likely small-fruited, associated with more easy dispersal. After arriving in the western Pacific, it evolved into *Sommieria* in New Guinea, with fruits only about 1.5 cm diam., and then moved back toward the east to give *Pelagodoxa mesocarpa* in Melanesia, with fruits 63–71 x 60–70 mm, and then even farther east with *P. henryana* in the Marquesas Islands in French Polynesia, with fruits 85–94 x 88–99 mm.

Critical, recent work supports the concept that the Arecoideae originated in South America (Baker & Couvreur 2013a, b, Comer et al 2015, 2016); however, the way its various sub-lineages dispersed from there varies. Comer et al. (2015, 2016) suggested that the Pelagodoxeae dispersed directly from South America to the Pacific, while Baker and Couvreur (2013a, b) suggested that the Pelagodoxeae migrated from South America to the-Pacific region through Eurasia and shows a closer relationship with Old World rather than New World genera.

Whatever the scenario, the large fruits of *Pelagodoxa* present an obstacle to efficient and ready distribution over vast distances within the South Pacific. Long distance dispersal must be responsible for *Pelagodoxa* reaching the Marquesas and Austral Islands. Perhaps a now extinct bird or bat played a role in its dispersal but fruit flotation or hydrochory has also been proffered as a possible dispersal mechanism. In informal trials we found that mature, fresh fruits and seeds of *P. henryana* immediately floated in sea water (Fig. 22). A few fruits and all seeds were still floating after more than two months (total length of the floating

experimentation) while all fruits and seeds of *P. mesocarpa* sank immediately, which is in contrast to findings of Chapin et al. (2001), who stated that fresh fruits of *P. henryana* would float only after drying for two weeks; however, because the two taxa were not distinguished then, they could have been working with *P. mesocarpa*.

These informal trials introduced the possibility of two distinct dispersal mechanisms: hydrochory for *Pelagodoxa henryana* with relatively large, round fruits, floating because of their central hollow, and with a green, unfragrant mesocarp, and zoochory for *P. mesocarpa* with relatively small oval fruits, sinking because of the absence of central hollow, and with an orange, sweetly fragrant mesocarp. Unfortunately, we were unable to conduct germination studies on these floating fruits and seeds; thus, we do not know if they would have germinated after floating in sea water for more than two months.

That the two morphologically and geographically distinct fruit morphs exist and are well documented, the smaller one in Melanesia and the larger one in Polynesia, seems to cast doubt on the earlier theories that people moved *Pelagodoxa* from the Marquesas Islands in French Polynesia to Vanuatu and the Solomon Islands in Melanesia.

However, people obviously played a role in the local distribution and perhaps extirpation and conservation of these two species. Both species are always at sites of past or current human habitation or other activity or are growing nearby in secondary or highly disturbed forest (Dowe & Cabalion 1996, Gillett 1971).

Ethnobotany

Next to nothing is known about the ethnobotany of *P. mesocarpa*, except that it is called *martiab* in the Burmbar language at Black Sands on Malekula in Vanuatu (Dowe and Cabalion 1996). Indeed, more field research is sorely needed for this species.

In contrast to the ethnobotanical data of *Pritchardia tahuatana* reported in Butaud & Hodel (2017), much less is known about that of *Pelagodoxa henryana*. Nevertheless, recent research on Nuku Hiva and Raivavae islands provided interesting results.

Local and Common Names: The local Marquesan name on Nuku Hiva is *'enu*, sometimes incorrectly spelled *enu* or *etu*, (Brown 1931,

Butaud 2013, Chaulet 1890, Christian 1910, Dordillon 1904, Hallé 1978). In the Austral archipelago on Raivavae, local names are *ha'ari gohutu* and *ha'ari rohutu*, the latter an alternative writing of the former (Brown 1931, Butaud 2014b). Interestingly, *ha'ari* means coconut tree and *gohutu* and *rohutu* is the residence of a departed soul in the world of gods and spirits. The name *ha'ari rohutu* could have been also the name of *P. henryana* on Rapa iti because the ethnologist J.F.G. Stokes recorded that name for a palm goddess in 1920 (Prebble & Dowe 2008). Some confusion with the name *vahane*, which refers to *Pritchardia tahuatana*, arose in the Marquesas. The French names for this palm are *palmier des Marquises*, *palmier marquisien*, *palmier de Nuku Hiva* or *palmier de Taipivai*, whereas in English its name is Marquesas palm.

Myths: On Nuku Hiva the fruits of *Pelagodoxa henryana* are linked with the amniotic sac of pregnant women; it could have originated from a buried eel head (Tehina Teikitohe, pers. com. 2012). On Raivavae this palm is linked with the half-god Maui who learned from the gods how to ignite fire and subsequently brought it to Earth, sheltered in a *Pelagodoxa* fruit (Linda Tumarae & Gahiti Teipoarii, pers. com. 2011). Stokes, on his specimen number 60 (BISH) collected on Raivavae in 1922, indicated a "legendary origin and from heaven," which corresponds with the preceding information. Moreover, Stokes "recorded from informants in 1920 a local tradition referring to *Ha'ari rohutu*, a palm goddess represented by an idol figure wrapped in palm fiber" (Prebble and Dowe 2008).

Sites: On Raivavae *Pelagodoxa henryana* was planted for unknown purposes on the sacred places called *marae*. The specimen Stokes 60 and local informants in 2011 noted it was planted on the *marae* Temahara where two trees survived until 1970 to 1980; Stokes also indicated the ancient presence of two trees on *marae* Unurau in 1922 (Matthew Prebble, pers. com. 2012). In the Marquesas Islands, this palm was also cultivated on ancient lithic sites at Taipivai and Hatiheu on Nuku Hiva and perhaps Puamau on Hiva Oa.

Seeds: On Nuku Hiva, "immature endosperm [of *Pelagodoxa henryana* fruits] was sometimes consumed as food, especially in time of famine" and "a watery extract from the endosperm was used as medicine" (Brown 1931). The consumption of young fruits was confirmed recently on Nuku Hiva (Sylvain



22. Fresh fruits and seeds of *Pelagodoxa henryana* (Butaud et al. 3494) float in sea water while those of *P. mesocarpa* (Butaud et al. 3493) sink. Garden of Marianne and Donald Hodel, Papeari, Tahiti.

Falchetto, pers. comm. 2018) whereas a *monoi* (lotion) made from the dried endosperm was used to massage newborns to heal minor injuries and spots and to repel mosquitoes (Lucien Puhetini, pers. com. 2018). On Raivavae Stokes noted on his specimen 60 that children ate the seeds.

Leaves: In the Marquesas leaves of *Pelagodoxa henryana* because of their often unsplit nature were probably used, as were those of *Pritchardia tahuatana*, for thatching, especially on sacred houses and other structures or those of royalty but we were unable to find documenting evidence. Moreover, confusion is likely with the formerly more common *P. tahuatana*, which was also called palm or palmetto in the literature. On Nuku Hiva, a medicinal extract taken from the boiled leaves of *P. henryana* was employed for an unknown ailment (Lucien Puhetini, pers. com. 2018).

Conservation

Pelagodoxa henryana is considered Critically Endangered (CR) on the IUCN Red List of Threatened Species (Johnson 1998) and Data

Deficient (DD) on the IUCN France Red List for endemic plant species of French Polynesia (UICN et al. 2015). The DD evaluation was due to the previous undetermined status, natural or anthropogenic, of the stands on ancient sites on Nuku Hiva. The CR evaluation was due to its very restricted occurrence (<10 km² on Nuku Hiva); and a single, small population (one “natural” population of about 10 mature individuals in Taipivai Valley); and the threats posed by feral pigs and adjacent land clearance for agriculture and human habitation.

As we have suggested, no natural stand of *Pelagodoxa henryana* is extant, either in the Austral or in the Marquesas Archipelagoes, and all known individuals are of cultivated origin; thus, we recommend an Extinct in the Wild (EW) IUCN Red List designation for *P. henryana*.

Pelagodoxa henryana is protected under the French Polynesian regulation (Code de l'Environnement) and the Environment Department (DIREN) has undertaken

conservation activities on Nuku Hiva since 2006, aiming to erect an *ex situ* conservation planting of seedlings originating from the mature trees at both known ancient sites: Taipivai Valley and Hatiheu. Also, both ancient sites have been regularly cleaned of weeds and encroaching vegetation (Butaud 2014a).

The National Tropical Botanical Garden on Kauai in Hawaii has established a conservation planting of seven *Pelagodoxa henryana* from seeds gathered from 5 of the 10 mature individuals known at the type locality in Taipivai Valley in 1997. However, the presence of *P. mesocarpa* at the National Tropical Botanical Garden raises the possibility of hybrids with *P. henryana*, and if pure, unhybridized seeds are desired, precautions must be taken to preclude hybridization.

Little is known about the conservation status of *Pelagodoxa mesocarpa* in Vanuatu and the Solomon Islands. Like *P. henryana* in French Polynesia, all known individuals of *P. mesocarpa* appear to be of cultivated origin. Whether any populations of this species are truly natural requires further research. Until then, and like *P. henryana*, we recommend an Extinct in the Wild (EW) IUCN Red List designation for *P. mesocarpa*.

Chapin and Dowe (2007) listed various recommended conservation management strategies for *Pelagodoxa*. Some of these and others that we suggest include thorough surveys of the Solomon Islands and Vanuatu populations of *P. mesocarpa* to determine population numbers, range and health; for both species, protection of habitat in the Marquesas, Solomon Islands and Vanuatu; invasive species (plant and animal) management; long-term population monitoring; establishment of new wild and *ex situ* populations and augmentation of existing wild populations (in the case of *P. henryana* plants propagated only from seeds from the two known extant populations or isolated individuals of known origin to preclude hybridization with *P. mesocarpa*); weed eradication and suppression; rat control; installation of pig-proof fencing around key populations; and education to promote conservation and appreciation for these palms.

We also suggest that genetic studies of all known mature plants of *Pelagodoxa henryana* at both ancient sites on Nuku Hiva and *P. mesocarpa* at selected sites in Vanuatu and the Solomon Islands to assess residual genetic diversity of both species to assist *in situ* and *ex*

situ conservation management, propagation and out planting would be beneficial and rewarding. Genetic studies could also confirm the likelihood of hybridization between both *Pelagodoxa* species in cultivation.

Cultivation

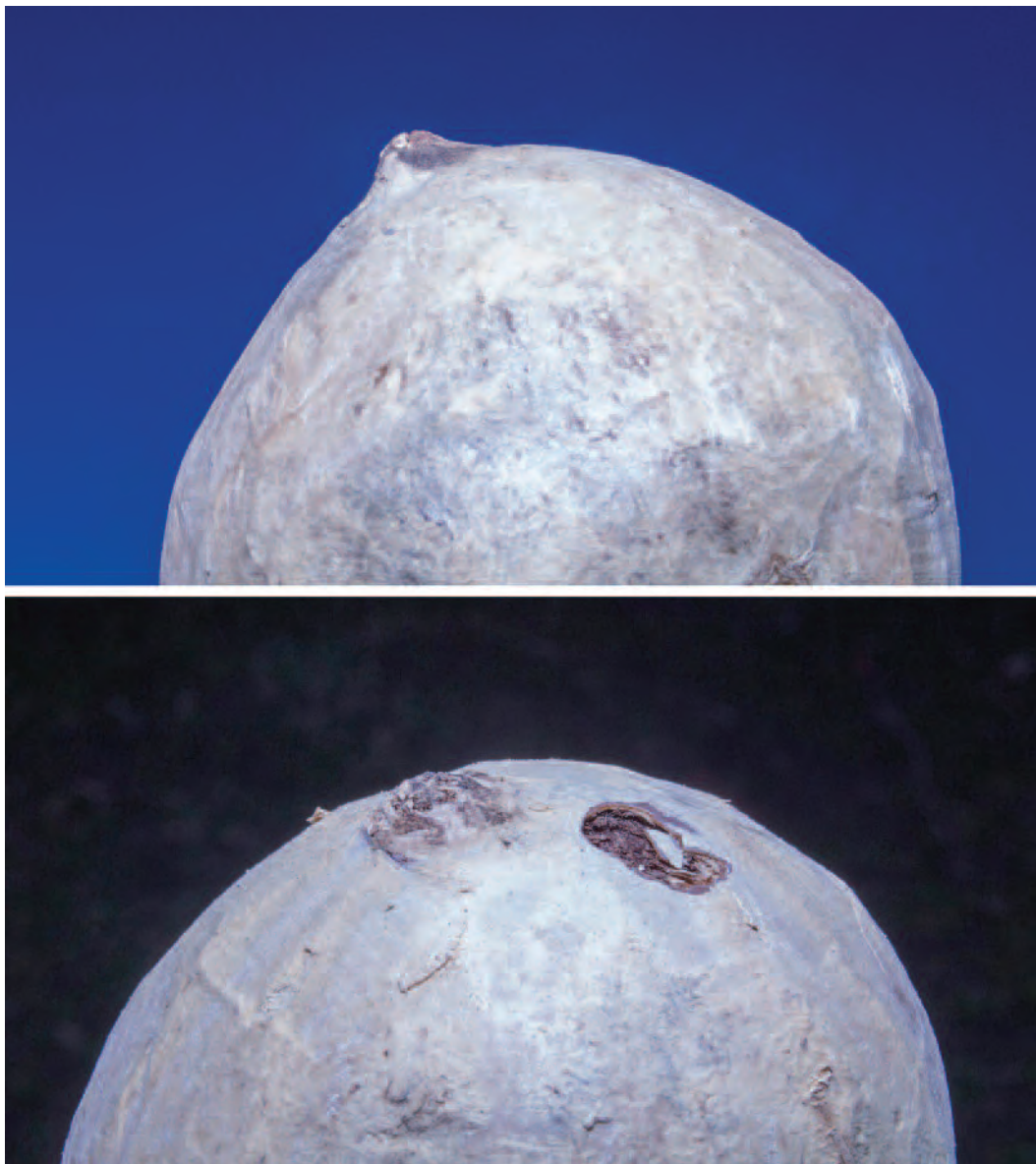
The two species of *Pelagodoxa* are palms of warm, moist to wet, tropical locales. Intolerant of even brief periods of cool or cold, they need sustained warmth and moisture not just to grow and attain their full beauty but to survive. They grow best with daytime temperature of 27–32°C and nighttime temperatures of 21–25°C, high humidity and moist root zones. A few brief periods of night temperatures 16–21°C can be tolerated. In subtropical and temperate regions these species must be grown in an environmentally controlled greenhouse, but even then, they can prove difficult to grow. Excellent, recent reviews of palm horticulture are Broschat et al. (2014) and Hodel (2012a).

Propagation: Seed is the only way to propagate *Pelagodoxa*, and successful germination is relatively easy to attain. Perhaps in the future micro-propagation will be able to produce new plants. Select full size, freshly fallen fruits or ones that knock very easily off the infructescence; it appears that fully mature fruits are critical for good germination.

Several successful methods have been devised for treating and planting seeds of *Pelagodoxa* and all encompass the same principles: fresh, fully mature fruits, cleaned of the mesocarp; cleaned seeds placed in a clean, moist but well aerated medium in clean containers; and the temperature maintained at 25–32°C.

Fruits can be scraped clean of the mesocarp immediately after harvesting or placed in a plastic bag for three to six weeks until the mesocarp is soft and fragrant or aromatic and easily rubbed or scraped off. Once the mesocarp is removed, wash and clean the seeds then allow them to air dry indoors or in the shade for a day or two.

Germination media should be porous, well aerated and well drained yet hold enough water. Clean, disease-free media composed of an organic component like peat moss or coir, for water-holding and an inorganic component like perlite, sand or volcanic cinders for aeration and porosity should meet these requirements. Place the clean, disease-free medium in clean, disease-free pots or other containers.



23. The embryo of *Pelagodoxa henryana* is at 12 o'clock (just to the right of the protuberance) (top). In the bottom photo the seed coat has been broken at the location of the embryo. Garden of Marianne and Donald Hodel, Papeari, Tahiti. *Butaud et al.* 3494.

To plant the seed, locate the small protuberance or projection at the point of attachment. The embryo is about 1.5 cm away on the "high side" of the protuberance (Fig. 23). The seed coat is typically softer here, which marks the embryo. Imagining an equator of the seed running through the protuberance and the embryo, submerge the seed half-way into the medium so that the imaginary equator is at the level of the medium; thus, the seed would be half buried and half exposed with the embryo right at the medium line. Water well and cover with

plastic. Place the planted container off the ground out of full sun in a warm location and maintain the temperature in the appropriate range. Germination should occur in about 4–16 weeks. At his nursery in Hawaii, co-author Marcus prepares the seeds as described above and then places them in moist sphagnum peat moss in a sealed, plastic zip-lock bag maintained in the appropriate temperature range.

A technique that a Marquesan used for quicker germination was to push with the fingers near the bump on the seed as described above to

locate the soft place that marks the embryo and then carefully break the seed coat covering the embryo to expose it (Fig. 23).

In the senior author's garden in Tahiti, fruits simply fall on the ground and after the mesocarp has disintegrated the seeds often germinate right beneath the mother palm. Nonetheless, to ensure highest germination, we place the seeds in ground beds of 100% cleaned, fine, black, river sand, submerging them half-way in the sand as described above. We cover the germination beds with coconut (*Cocos nucifera*) leaves to provide shade from the intense tropical sun. Typically, it rains sufficiently in our area of Tahiti to keep the seeds and medium moist. If necessary, though, we water to keep the medium evenly moist.

The likelihood that the two species of *Pelagodoxa* can hybridize in cultivation, which the molecular analysis supports, must be considered. If both species are present in gardens or collections precautions must be taken to preclude hybridization.

Potting Up and Growing On: Once the seedlings produce their first bifid leaf, remove them carefully from the germination bed or container and pot them individually into 3.8-l (15-cm) containers. Soil for container growing should be porous, well aerated and well drained yet hold sufficient water and nutrients and be slow to break down (Broschat et al. 2014). Maintain potted *Pelagodoxa* in partial shade, gradually transitioning them to higher light or even full sun. When the young plants are firmly rooted and roots have filled the 3.8-l container, shift them up into 20-l containers. When the roots have filled out this larger container, they are ready for planting out.

Planting Location: *Pelagodoxa* attain their fullest beauty and elegance when protected from the wind and afternoon sun. At the type locality of *P. henryana*, palms emergent above the forest canopy have shorter, variably wind-split leaves while those protected in the understory have longer, undivided leaves. Protected palms are more stunning, elegant and impressive than unprotected palms. Too deep shade can be detrimental to the palms' appearance, also, stretching out the leaves so they appear abnormally long and slender. *Pelagodoxa* will perform well in just about any type of soil if it is well drained, holds nutrients and can be kept evenly moist.

Maintenance: Keep root zones evenly moist. Apply a palm-special fertilizer, one with an N-

P-K-Mg ratio of 2-1-3-1 or similar ratio. Maintaining five to eight cm of good quality mulch from the trunk out to at least two meters is beneficial. Remove dead, brown leaves and old inflorescences. Gently pull on them to see if they fall away easily. If not, they can be removed by neatly and carefully cutting them as close to the trunk as possible without damaging the trunk. Pulling and tearing them off the trunk with force can cause permanent, unsightly wounds that can serve as disease and pest entry sites. Serious pests and diseases have yet to be documented for *Pelagodoxa* although it might be susceptible to some of the serious and/or newly emerging problems like palm weevils, Texas palm decline and various Fusarium diseases (Broschat et al. 2014, Hodel 2012a).

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Appendix 1. Sources of *Pelagodoxa* Samples/Accessions Used in this Study. FP = Floribunda Palms and Exotics; NTBG = National Tropical Botanical Garden, Hawaii; 'Type Locality' = Nuku Hiva, Marquesas Islands, French Polynesia; 'RPB2 type' refers to which of the two sequence variants was present in each accession.

Species	Seed Origin	Source and Accession/ID No.	RPB2 type	GenBank (PRK, RPB2)
<i>P. henryana</i>	Type Locality	FP-1	<i>henryana</i>	MK830987, MK825770
<i>P. henryana</i>	Type Locality	FP-2	<i>henryana</i>	MK830988, MK825771
<i>P. henryana</i>	Type Locality	NTBG 970225.001	<i>henryana</i>	MK830979, MK825762
<i>P. henryana</i>	Type Locality	NTBG 970225.002	<i>henryana</i>	MK830980, MK825763
<i>P. henryana</i>	Type Locality	NTBG 970228.001	<i>henryana</i>	MK830981, MK825764
<i>P. henryana</i>	Type Locality	NTBG 970228.002	<i>henryana</i>	MK830982, MK825765
<i>P. henryana</i>	Type Locality	NTBG 970230.001	<i>henryana</i>	MK830983, MK825766
<i>P. henryana</i>	Type Locality	NTBG 970232.001	<i>henryana</i>	MK830984, MK825767
<i>P. henryana</i>	Cult., Tahiti, ex Type Locality	NTBG 770290.001	<i>henryana</i>	MK830985, MK825768
<i>P. henryana</i>	Cult. NTBG	NTBG 040506.001	<i>mesocarpa</i>	MK830986, MK825769
<i>P. henryana</i>	Cult., Fiji	voucher 1988-2933 (Kew)	<i>mesocarpa</i>	AJ831321, AJ830135
<i>P. mesocarpa</i>	Cult., Fiji	NTBG 800426.001	<i>mesocarpa</i>	MK830989, MK825772
<i>P. mesocarpa</i>	Cult., Fiji	FP-1	<i>mesocarpa</i>	MK830990, MK825773
<i>P. mesocarpa</i>	Cult., Fiji	FP-2	<i>mesocarpa</i>	MK830991, MK825774
<i>P. mesocarpa</i>	Cult., Fiji	FP-3	<i>mesocarpa</i>	MK830992, MK825775
<i>P. mesocarpa</i>	Cult., Fiji	FP-4	<i>mesocarpa</i>	MK830993, MK825776

For additional photographs and other supporting data for this article, go to the e-journal *PalmArbor* at <https://ucanr.edu/sites/HodelPalmsTrees/PalmArbor/> and click on 2019.

Hugh Harries 1940–2019

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Hugh Harries, doyen of the world of coconuts, passed away on 7th February 2019, after a short illness. He was preeminent in the field of natural history, origin and dissemination of the coconut and held many stimulating ideas.

After graduation in 1962 (BSc Horticulture, London University) he worked for the UK Agricultural Research Council as a plant breeder for five years before taking up a career as a tropical agriculturalist in the Caribbean in 1968. There he spent over ten years as a botanist/plant breeder for the Coconut Industry Board in Jamaica. In 1983 he moved

to Southeast Asia where he spent five years as a technical cooperation officer for the UK Overseas Development Administration (ODA) in Thailand. In the Pacific he spent five years as chief agronomist to New Britain Palm Oil Development in Papua New Guinea. Six years were spent in Africa with both the German Agency for Technical Cooperation (GTZ) and

ODA, on coconut and cashew projects in Tanzania. He moved back to Latin America for four years as Researcher at Centro de Investigación Científica (CICY), Merida, Yucatan in Mexico. Between appointments he undertook short-term consultancies in a further 20 countries for national, bilateral, international, commercial or environmental organizations concerned with smallholder and plantation tree crops. Since 1978, when he wrote the seminal "The evolution, dissemination and classification of *Cocos nucifera*" in Botanical Review (44: 265–320), his goal was to illuminate the exceptional importance of the coconut palm since earliest times. Among his many lasting achievements are the development of a commercial method to breed lethal yellowing resistant, wind-storm tolerant F1 hybrid coconuts in Jamaica. He also coordinated the FAO coconut breeders' consultative committee and published an hypothesis on coconut evolution. Latterly he expanded his specialist knowledge in production of disease resistant and improved coconut planting material by breeding and tissue culture to include date and oil palm, cashew and even frankincense.

In 1999, he set up the Centre for Information on Coconut Lethal Yellowing (CICLY) that acted as a clearing-house for information about lethal yellowing and similar diseases of coconuts and other palms. The CICLY website was discontinued in 2011.

Since 2001, he was the Moderator of The Coconut Time Line, an internet message board devoted to all aspects of coconut. He was an Honorary Research Associate at the Herbarium, Royal Botanic Gardens, Kew (Herbarium) and also a Volunteer Guide in the Gardens.

For the last ten years or so of his life, Hugh was afflicted with Parkinson's disease, yet he continued to moderate the Coconut Time Line and think about coconut evolution and publish. His spirit seemed indomitable. The world of coconuts has lost a titan and he will be much missed.

Hugh C. Harries Bibliography

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Photo Feature

Acanthophoenix crinita



Acanthophoenix crinita is found in La Réunion, the site of the 2020 IPS Biennial. Gîte de Bélouve, La Réunion (Photo: J.Dransfield).

Palm News, continued from p. 108...

***Ceroxylon* at the San Francisco Botanical Garden has begun flowering.** The two large palms were grown from seeds collected by Garrin Fullington in Colombia in 1983. They were accessioned as *C. quindiuense* but *Ceroxylon* expert Maria José Sanín suspects that the plant may be *C. ventricosum*. Now that it is flowering (and perhaps fruiting), a definitive identification will be possible. Late word from SFBG is that the second of the two individuals has also initiated an inflorescence. The palms at SFBG are not the first *Ceroxylon* to flower in California: Garrin Fullington planted two palms of *C. vogelianum* at the Lakeside Palmetum in Oakland, and these have produced fertile seeds, which have been distributed to local growers.



A new species of *Coccothrinax* has been described by a team from Montgomery Botanical Center. *Coccothrinax viridescens* is described by L. Noblick, A. Street and M. Barros in an open-access paper in the journal *Phytotaxa* (413: 001–010. 2019). The palm is known only from material in cultivation but may have its origins in Cuba. It distinguished by its compact crown, short-petiole leaves with green undersides and very short costas and tiny seeds. The PDF can be downloaded here: <<https://doi.org/10.11646/phytotaxa.413.1.1>>

A new species of *Aiphanes* from Colombia was recently described by R. Bernal, F. Castaño and M.J. Sanín. The species, christened *Aiphanes suaita*, is already assessed as Endangered. It is known from only two, small populations that are separated by about 56 km. The publication of this new species is Bernal et al. 2019. A new, overlooked species of *Aiphanes* (Arecaceae) from Santander, Colombia. *Phytotaxa* 405: 101–105. <<https://doi.org/10.11646/phytotaxa.405.2.5>> A second paper by Bernal et al. was also published recently in *Phytotaxa* entitled “A revision of the *Aiphanes parviflora* complex (Arecaceae).” The findings are based on new collections. The authors recognize seven species in the complex, five of them new, including *A. gloria*, shown at right. *Phytotaxa* 411: 275–292. <<https://doi.org/10.11646/phytotaxa.411.4.3>>



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