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Journal of Plant Taxonomy and Geography (Webbia) is a peer-reviewed journal on Plant Taxonomy, Nomenclature, Phylogeny, Phytogeography and Palaeobotany of the Vascular Plants.

The journal aims to allow research in botanical topics such as taxonomy, systematics, nomenclature, molecular phylogeny, conservation, biogeography, and history of botany, and botanical collections.

It was founded in **1905** in Florence by **Ugolino Martelli** (1860-1934), a botanist well known for his studies of and contributions to the systematics of the tropical genus *Pandanus* and on the Flora of Sardinia.

In the 19th century Florence represented one of the most important European centres in Plant Taxonomy and Phytogeography with several notable Italian botanists worth mentioning such as Filippo Parlatore, Teodoro Caruel, Eugenio Baroni, Stefano Sommier, Odoardo Beccari and Ugolino Martelli himself. In 1842 **Filippo Parlatore** (1817-1877) founded in Florence the *Herbarium Centrale Italicum (FI)*, which soon became one of the most important herbaria in the world. Most of the specimens described and/or cited in *Webbia* are still kept in it.

In 1905, and as a consequence of this multitude of activities in Plant Systematics and Phytogeography, Ugolino Martelli established the journal *Webbia-Raccolta di Scritti Botanici*, firstly published annually in a single issue, and later twice a year. *Webbia* also began to be a place of publication of contributions from Tropical Botany, especially after the Royal Colonial Herbarium founded in 1904 in Rome was moved to Florence in 1914, currently named Tropical Herbarium Study Center (Centro Studi Erbario Tropicale - Herbarium FT) belonging to the Department of Biology of the University of Florence.

Webbia had been created in honor of **Philip Barker Webb** (1793-1845), a close friend of Filippo Parlatore, who before passing away entrusted his personal herbarium and a library rich of old botanical books and publications to the then Botanical Museum in Florence.

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Cover images: Group of individuals of *Attalea crassipatha* (Mart.) Burret growing in habitat in Kasosent, Sud Department, Haiti. This is a Critically Endangered palm (*sensu* IUCN) endemic in southern Haiti. Photo by Brett Jestrow. Background shows drawing of this species made by Plumier (1703, Plate 1) that is part of the illustrations that he published after he travelled to Haiti between 1689 and 1693. Plate courtesy of the Linnean Society of London.

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The Critically Endangered Haitian endemic palm *Attalea crassipatha* (Arecaceae) and its living collections in Fairchild Tropical Botanic Garden: Perspectives from conservation surveys and DNA microsatellite (SSR) data

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Abstract. With only 24 plants located in the wild in 2017, the Haitian endemic *Attalea crassipatha* (Mart.) Burret (Arecaceae) is one of the major priorities for palm conservation in the Caribbean Island Biodiversity Hotspot and is the only member of the genus (~ 30 species) that occurs in the region. A project of ex situ conservation and field surveys published in 1994 involved Fairchild Tropical Botanic Garden (FTBG) as a major distributor of wild collected germplasm with other botanic gardens/institutions from South Florida and the tropics in 1989 and 1991. Part of this material was also grown in FTBG. Over 25 years after this conservation initiative was established, new field surveys were made in 2017 where the species occurs in Peninsula de Tiburon, southern Haiti. The number of living plants recorded in this new inventory was 24 (vs 25 reported in 1994). DNA microsatellite data (SSRs) were used to compare levels of genetic variation in the FTBG ex situ conservation collections and the wild. We found that the FTBG genotypes did not capture most of the already limited genetic diversity found in the wild. Cluster analyses based on Bayesian statistics recognized three major genetic groups in the wild, and three of them were found in plants occurring mostly in the northern slopes of Peninsula de Tiburon; in contrast, only two of the genetic clusters were predominant in the southern portion of this peninsula mostly in the Cavailon area. Our results concur with those recently published based on Single-nucleotide polymorphisms (SNPs) molecular markers for ex situ collections of this palm species conserved in five botanic gardens/research institutes.

Keywords: Conservation genetics, Greater Antilles, Tropical islands, Biodiversity Hotspots.

INTRODUCTION

Almost 30 years ago the first-known work focusing on an ex situ conservation program for a Critically Endangered plant species endemic in Haiti was published by Timyan and Reep (1994). The study concerned one of the most threatened palms of the Caribbean Islands, *Attalea crassispatha* (Mart.) Burret, and it provided an account on the status of this species in the wild as well as a germplasm collection initiative that had two aims: (1) introducing the species in private gardens of Haiti and (2) developing ex situ conservation collection of living plants in botanic gardens and horticulture stations.

The target species is restricted to southern Haiti (departments of Sud and Nippes at Peninsula de Tiburon) and it is the only Caribbean Island endemic in the Neotropical genus *Attalea* (~30 species; Henderson 2020). In 1994 only 25 plants (19 adults— including a senescent plant, and six juveniles) were found in eleven sites, but none of these localities had more than ten individuals (Figure 1A, Table 1). A more recent survey made by Timyan (2001) reported 18 seedlings, six juveniles, and 24 adults along the distribution range of the species.

Based on the age of the original description, this suggests that this palm was more abundant in the late 17th century (Martius 1844: 110–112, as *Maximiliana crassispatha* Mart.), and even Charles Plumier (1646–1697) drew and published a plate and a description of

this species (Plumier 1703: 2, Plate 1; Figure 2). This pre-Linnean French botanist and monk traveled twice to Haiti between 1689 and 1693 (Mottram 2002).

Based on our own field observations and palm conservation work conducted in the Caribbean with other species, reasons for its decline are unsustainable harvesting of seeds for human consumption, introduced herbivores, and clearance of land for agriculture (Timyan and Reep 1994; Jestrow et al. 2018; Freitas et al. 2019).

As part of this ex situ conservation program implemented in the late 1980s and early 1990s, seeds were sent to 16 botanic gardens or agricultural research stations in South America, Central America, Germany, Australia, and Asia (Timyan and Reep 1994). According to Timyan and Reep (1994), two main shipments of seeds were distributed. The first happened in 1989, and was the most extensive one, having Fairchild Tropical Botanic Garden (FTBG), Miami, Florida as the hub for germplasm distribution. It involved sending seeds that were collected from five different mother plants from four places (localities A, D, G, and J; Figure 1A). Germplasm was sent to 13 botanic gardens and five other sites (Timyan and Reep 1994: Table 4). These seeds were also sent to Tropical Research and Education Center (TREC) and resulted in the plants currently cultivated in this research station of the University of Florida. The second consignment (harvested in 1991) was more limited in number of germplasm samples; and seeds were shipped only to botanic gardens in Australia, St. Vincent (Lesser Antilles), and Guyana (Timyan and Reep 1994), with samples received by FTBG as well. This second batch had the progeny of nine different mother plants from nine different places (localities A–H and J, Figure 1A); however, FTBG successfully cultivated plants from only A, B, and D (Fond-des-Nègres region, in the northeastern area of the species distribution range, Figure 1A). It is worth mentioning that Timyan and Reep (1994) found only six plants in these three localities. Regarding material distributed in Haiti, a total of 117 seedlings were sent to private gardens and non-government organizations between 1990 and 1991. Fairchild Tropical Botanic Garden received a third shipment of seeds in 2001 (also from Fond-des-Nègres region), as the ex situ conservation project continued.

The contribution here presented has two main objectives. The first one concerned revisiting the localities reported by Timyan and Reep (1994) to determine if there have been any changes regarding the *Attalea crassispatha* population demographics of these sites. This is particularly relevant in Haiti, a country that it is considered to have one of the highest deforestation rates of the Americas, and has experienced major socio-political turmoils in the last 50 years. In addition, this Carib-

Table 1. Localities of *Attalea crassispatha* reported by Timyan and Reep (1994: Table 1).

Population code	Locality	Coordinates	Number of individuals (adults/ juveniles)
A	Rivière Seche	73°14' 18°22'	2/0
B	Baron – Le Blanc	73°23' 18°22'; 73°15' 18°23'	2/0
C	Pemel	73°12' 18°22'	1/0
D	Grande Savanne	73°12' 18°23'; 73°13' 18°22'	2/0
E	Dipa	73°07' 18°22'	1/0
F	Perine	73°07' 18°17'	1/1
G	Rousseau	73°35' 18°22'	2/0
H	Bonne Fin	73°37' 18°23'	2/0
I	Christine	73°41' 18°17'	1/0
J	Dumay, Bois Nègre and Desvarine	73°42' 18°16'; 73°16' 18°16'	4/5
K	Boulier	73°43' 18°16'	1 ^a /0
Total individuals in the wild			19/6

^a Senescent individual.

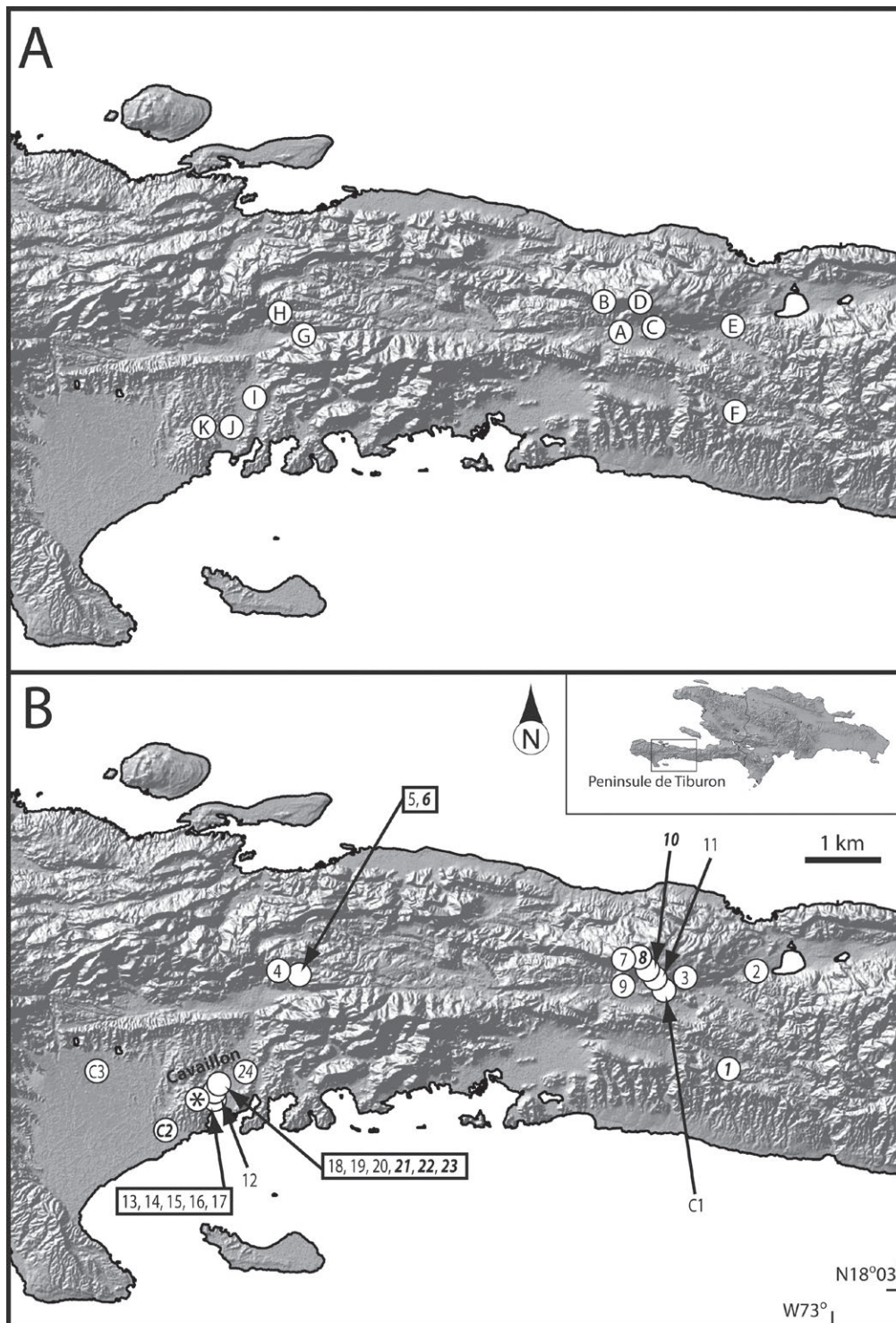


Figure 1. (A) The eleven localities where Timyan and Reep (1994) found wild plants of *Attalea crassispatha* in Peninsule de Tiburon. Locations plotted based on the geographical coordinates published by Timyan and Reep (1994). Number of individuals found in each of these eleven sites are reported in Table 2. Localities are coded as A: Rivière Sèche; B: Baron - Le Blanc; C: Pemel; D: Grande Savanne; E: Dipa; F: Perine; G: Rousseau; H: Bonne Fin; I: Christine; J: Dumay; Bois Nègre and Desvarine; and K: Boulier. (B) The geographical location of the individuals found during the 2017 field surveys conducted for this study in Peninsule de Tiburon. SSR profiles were obtained for all of the plants except for those indicated in bold-italic font (individuals 1, 6, 8, 10, 21–23, and C2). Individuals C1–C3 were found in cultivation. Locality where dead individual was located is coded with an asterisk (*). See Table 2 with geographical coordinates and names of the collecting sites

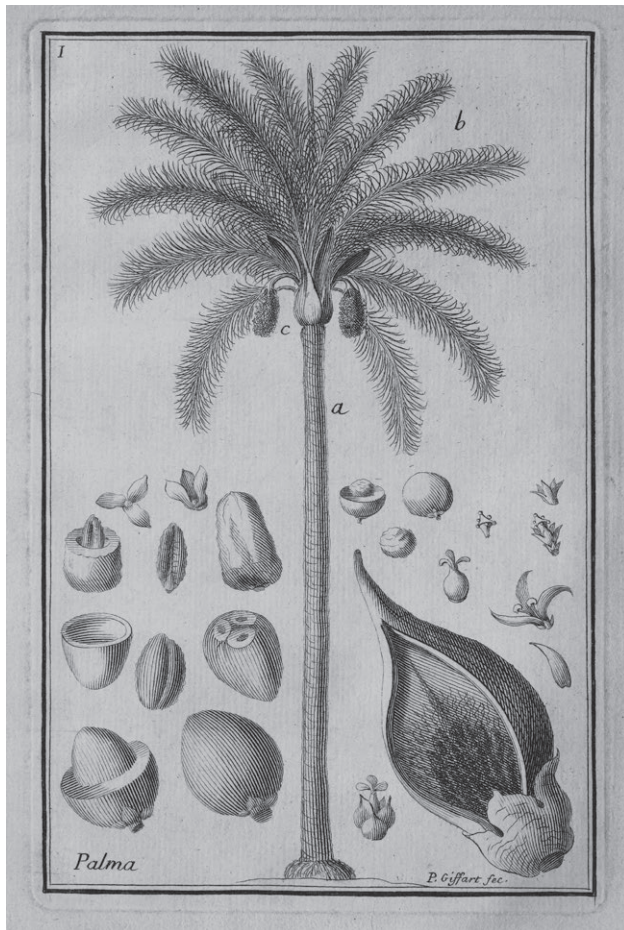


Figure 2. Pre-Linnean illustration of *Attalea crassispatha* as drawn and published by Plumier (1703) based on observations made during his botanical expeditions to Haiti between 1689 and 1693. Courtesy of the Linnean Society of London.

bean country has been affected by major environmental disasters such as the catastrophic 2010 and 2021 earthquakes and six devastating hurricanes (*Georges* in 1998, *Dennis* in 2005, *Gustav* in 2008, *Tomas* in 2010, *Matthew* in 2016, and *Laura* in 2020) that hit the area where this palm occurs. We wanted to assess the conservation status of one of the most threatened Caribbean palms since the last field conservation-oriented actions were taken in the 1990s by Timyan and Reep (1994) and Timyan (2001). The results of this first objective could provide some insights regarding long-term conservation goals performed in situations in which external detrimental conditions can evolve.

The second objective was to investigate the current ex situ genetic conservation status of the collected material at FTBG. Our results are complementary to those recently published in an exhaustive and comprehensive

genetic conservation study of populations of this species in (1) ex situ living collections of Montgomery Botanical Center, FTBG, Singapore Botanic Garden, USDA Chapman Field Station at Miami, and the Tropical Research and Education Center (TREC) of the University of Florida at Homestead, Florida, and (2) eight wild sites of Haiti. This work was published by Diaz-Martin et al. (2023) based on 6093 single nucleotide polymorphisms (SNPs) and to identify optimal breeding pairs for future ex situ conservation actions.

In many instances ex situ conservation goals concern sample strategies in small populations in order to maximize the amount of genetic diversity that can be preserved in living individual germplasm banks. This is relevant in the tropics where the vast majority of species have recalcitrant seeds and cannot be massively stored in seed banks (Normah et al. 2019). Therefore, living plant germplasm banks with a very limited number of individuals is in many cases the only feasible alternative to ex situ conservation. The use of highly variable co-dominant molecular markers known as SSR microsatellites provide cost-effective quick tools to determine levels of genetic variation both in the natural populations and in those that are ex situ conserved (Griffith et al. 2017, 2020). These co-dominant markers were not so commonly available in 1994 when conservation activities targeting *Attalea crassispatha* were implemented. The strategy for ex-situ conservation established by Timyan and Reep (1994) was based on seeds collected from a limited number of mother plants across the distribution range of the species. Because in its natural environment this species has very few individuals it was assumed that this sampling strategy would not result in a major genetic bottleneck between the original populations and those established in the ex situ collections. Therefore, our genetic conservation goal at FTBG was to use SSRs to investigate the success of establishing genetic conservation in an ex situ living collection of a Critically Endangered species when the available germplasm comes from a very reduced number of individuals.

METHODS

Field surveys

Field work was conducted during January 2017 including authors BJ, WC, and AF. The geographic coordinates provided by Timyan and Reep (1994) were not recorded with GPS devices but were based on geographical maps; furthermore, they were reported using only degree and minute digits. The eleven populations that were identified by Timyan and Reep (1994) were

Table 2. Localities of *Attalea crassipatha* found during the 2017 surveys.

Palm number	Locality	Coordinates		Number of individuals (adults/ juveniles)
1	Perine	18.283183	-73.108383	1/0
2	Dipa	18.3626	-73.10645	1/0
3	Pemel	18.364517	-73.195	1/3 ^a
4	Demoulin	18.396867	-73.6146	1/0
5	Carré-1	18.3905	-73.604633	0/1
6	Carré-2	18.390317	-73.60505	1/0
7	Baron	18.385333	-73.248917	1/0
8	Poitié	18.3853	-73.239917	1/0
9	Le Blanc	18.367683	-73.24855	1/0
10	Ca Michaud	18.373267	-73.23035	1/0
11	Fond-des-Nègres	18.368683	-73.224433	1/0
12	Kasosent-1	18.258083	-73.698033	1/0
13-17	Kasosent-2	18.256917	-73.697783	5/0
18-23	Desravine	18.260967	-73.6964	6/0
24	Nan Guildiv	18.291133	-73.671833	1/0
C1	Riviere Sèche	18.36415	-73.22	1 ^b /0
C2	Charpentier	18.2123	-73.753633	1 ^b /0
C3	Levy	18.303417	-73.854383	1 ^b /0
Total individuals in the wild				23/1
Total individuals in cultivated sites				3/3 ^a

^a Seedlings in cultivation.

^b Adult individuals found in cultivation.

labeled with a letter system from “A” to “K” as shown in Figure 1A. These localities represent two different watersheds involving the rivers Côtes-de-Fer (sites A–F) and Cavaillon (sites G–K). Therefore, one of the main challenges that we had during our field studies was to locate the actual places that were sampled by Timyan and Reep (1994); their geographic data were used as the initial framework for our own field surveys. In each of the sites we made demographic inventories and recorded the number of adults and juveniles.

Sampling

We obtained SSR genetic profiles of samples from 18 of the 23 wild plants collected in Haiti during our field studies (Figure 3). We were unable to obtain DNA data for seven of the wild collected individuals (plants 1, 6, 8, 10, 21, 22, 23; Table 2, Figure 3). Also, we obtained genetic data for the two of three individuals that were cultivated in this country (plants C1 and C3). Fairchild Tropical Botanic Garden currently has a total of 38 liv-

ing individuals of *Attalea crassipatha*, and 30 of these were included in the molecular study (Figure 3). Two are from historical collections, the first one, plant F22 (recently died), confirmed as received from USDA in 1938 (accession number PI 129884), from germplasm originally collected by botanist and palm taxonomist Orator F. Cook (1867–1949) when he was working in Haiti in agriculture development projects (Todd 2009; Francisco-Ortega et al. 2018). The other early accession, represented by three living palms with F23 included, was received in 1940 of questionable source but most likely via the USDA as well, either with USDA accession number PI 129884, PI 138962, or PI 138963. Thirty-two of the 38 individuals found in FTBG belong to the material that reached FTBG in 1991 and 2001. As the living collections of FTBG developed, three young plants (one included, individual F31) were the progeny of palms already present in this garden, and considered part of the living collections.

Microsatellite protocols

DNA was isolated from fragments of leaflets that were fast-dried using Drierite (W. A. Hammond Drierite Co. Ltd). Liquid nitrogen was used to disrupt the leaf tissues, and this was followed by the actual DNA isolation using DNeasy Plant Mini Kit (Qiagen). Ten of the 14 microsatellite loci, originally developed for *Attalea phalerata* Spreng. (Choo et al. 2010), were used as molecular markers for our study (Table 2). First, the regions were amplified and sequenced to verify both the presence of microsatellite loci in the amplicon and the repeat motifs as described in Choo et al. (2010). We used PuReTaq Ready-To-Go PCR Beads (GE Healthcare Life Sciences, Piscataway, NJ, USA) for the polymerase chain reaction (PCR) amplification reaction mix. For all regions, the PCR conditions were 94°C for 2 min, 30 cycles at 94°C for 45 s, 55°C for 45 s, 72°C for 30 s, and a final extension of 72°C for 10 min. We ran PCR products on a 2% agarose gel stained with SYBR safe (Invitrogen, Carlsbad, CA) and used UV light to visualize them and confirm amplicon lengths. Cycle sequencing was performed in both directions with the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA) following the manufacturer’s instructions. The primers used for PCR amplification were also utilized for the cycle sequencing reactions. Nucleotide sequences were visualized on an ABI PRISM 377 DNA Sequencer (Applied Biosystems) at the Florida International University (FIU) DNA Core Facility. All sequences were assembled and visually aligned, using Geneious 11.1.5 (<https://www.geneious.com>).

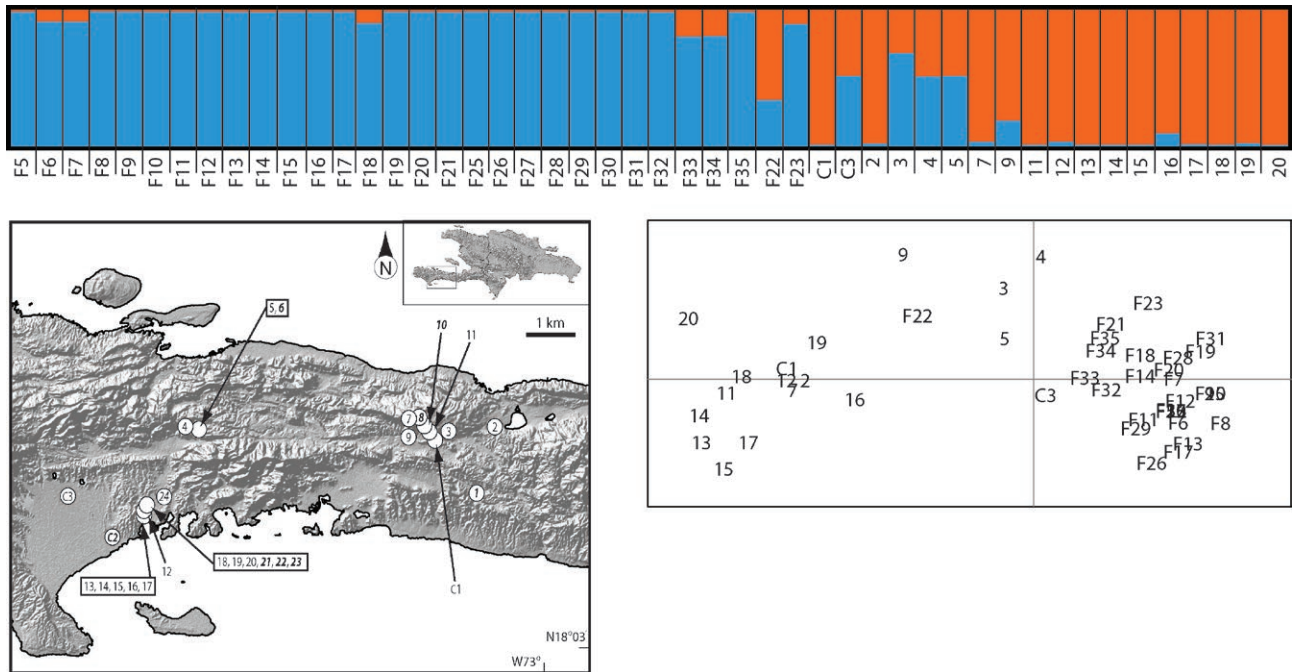


Figure 3. Genetic profiling results of the wild and cultivated populations of *Attalea crassispatha* included in this study. Top diagram shows results of the STRUCTURE analysis for $K = 2$. Bottom-right scatter diagram shows results of the Principal Coordinate Analyses. Geographic provenances of material collected in Haiti is shown in the map. SSR profiles were obtained for all of the plants except for those indicated in bold-italic font (individuals 1, 6, 8, 10, 21–23, and C2). Individuals C1–C3 were found in cultivated stands from Haiti. Plants from Fairchild Tropical Botanic Garden are coded with the letter “F” followed by individual number.

Once confirmed, samples for fragment analysis were prepared using the following PCR reactions of 10 μL volumes containing, 6.25 μL Apex Master Mix, 1.75 μL ddH₂O, 2.50 μL TBT-PAR [prepared as indicated by Samarakoon et al. (2013)], 0.75 μL of 10 μM fluorescent primer, 0.75 of 10 μM unlabeled primer, and 0.5 μL DNA extract. The PCR conditions were the same, but changed the annealing temperature to 56° C, and occasionally increased to 32 cycles to improve the signal. The samples were then sent to the DNA Core Facility at FIU for fragment analysis. The PCR fragments were separated using an ABI 3100 Genetic Analyzer and visualized with GeneMapper (Applied Biosystems).

Genetic analyses

Percentage of polymorphic loci (P), average number of alleles per locus (A), observed heterozygosity (H_o), expected heterozygosity (H_e), number of loci that deviate significantly from HWE (nd_s ; $p < 0.05$), estimates of genetic differentiation (F_{st}), and percentage of paired loci showing linkage disequilibrium (LDL; $p < 0.05$) were calculated with ARLEQUIN v. 3.5.2.2 (Excoffier and Lischer, 2010). Inbreeding coefficients (F_{is}) were

estimated using GDA (Weir, 1996). GenAlEx v. 6.5 (Peakall and Smouse 2006, 2012) was used to estimate the number of private alleles (n_p) and of identical genotype pairs per population. GenAlEx was also used to perform a principal coordinate analysis (PCA) among all the individuals included in the study. STRUCTURE v. 2.3.4 (Pritchard et al. 2000), a program based on Bayesian searches was utilized to reveal the genetic structure among populations. K values (1 to 10) were estimated through 20 replicate runs of 1,000,000 iterations with burn-in of 100,000. The Dk method of Evanno et al. (2005) as implemented in CLUMPAK (Kopelman et al. 2015) was performed to determine the optimal value of K across samples. CUMPLAK was also used to obtain a consensus Q-matrix from the 20 runs of each k value and to visualize the final consensus cluster diagrams.

RESULTS AND DISCUSSION

Field surveys

The geographical data found in Timyan and Reep (1994) were used as the initial framework for our own field surveys. Furthermore, Ossin Jean helped relocate

these palms as he was with Timyan and Reep during their original search. We located 24 living plants in 15 wild sites (Table 2, Figure 1B). We also found cultivated mature individuals in three different places (Figure 1B). Interestingly the three plants grown in Pemel were small seedlings propagated in pots for future cultivation because of the ethnobotanical value of this palm, particularly for seed consumption.

One site (marked with an asterisk in Figure 1B) had a single dead individual, deceased in 2016 from Hurricane *Matthew*, likely the same individual listed as “Senescent” by Timyan (1991). The vast majority of the visited sites had a single individual except the Kasosent-2 and Desravine localities that had five and six adult plants, respectively. A comparison can be made between the 1994 and 2017 surveys, the number of adult individuals increased from 19 to 23; however, the number of juveniles decreased from six to one; this suggests that there has been a recruitment crisis (cf. Griffith et al. 2019). We hypothesize that the increase of adult plants is because individuals that were reported as juveniles in 1994 became adults prior to our 2017 field work. Plants were located in different environments but mostly in secondary forest or areas with severe deforestation (Figures 4–5).

Genetic analyses

Because of the scattered distribution of the few wild individuals and the very reduced number of plants encountered in each site, the population genetic statistics considered all the wild plants as belonging to a single population. Genetic diversity statistics show that the living collection of FTBG harbors much less diversity than that from Haiti. For instance, only 40% of loci (e.g., A106_2, B101_4, B102_8, B121_4) were polymorphic in FTBG (vs 100% in the wild). Other genetic diversity indicators also revealed that the FTBG individuals do not capture most of the genetic diversity found in the wild [e.g., number of private alleles (2 vs 20), average number of alleles per locus (2.7 vs 3.5), number of identical genotypes (7 vs 0), and percentage of loci showing linkage disequilibrium (15.56 vs 0)]. Concerning the FTBG ex situ collection, its values of expected heterozygosity almost double those of the observed one (0.464 vs 0.293). In contrast these two population genetic estimators were very similar in the wild population ($H_e = 0.302$ vs. $H_o = 0.464$). However, unexpectedly the wild population exhibited a much higher degree of inbreeding (F_{is}) than that from FTBG (0.310 vs 0.026)

Our genetic diversity data match those obtained by Diaz Martin et al. (2023) based on SNPs, as they found

that plants grown in FTBG, Montgomery Botanical Center, Singapore Botanic Garden, USDA Chapman Field Station, and the TREC of the University of Florida do not capture most of the genetic diversity found in the wild. The broad study of germplasm genetic diversity conducted by Diaz Martin et al. (2023) has relevant conservation implications as they resulted in the identification of optimal breeding pairs in collections from different sites (including FTBG) and showed cases in which plants were likely mislabeled as accessions were moved between institutions.

Results yielded by the PCA and the Cluster Analyses based on Bayesian methods were concordant with those displayed by the genetic diversity statistic data (Figure 3). The PCA scatter diagram showed all genotypes from FTBG to have positive values along the first coordinate (38.2% of the multivariate variation vs 11.25% along the second coordinate), except for plant F22, which is the oldest plant found in this botanic garden (introduced in 1938). The narrow range of values along this coordinate shown by the FTBG individual provides evidence for the genetic bottleneck that happened when populations were sampled in the wild prior to their introduction in Miami. It suggests that few in situ individuals were the source of the living collections and matches the fact that only four loci were polymorphic.

These PCA findings were supported by the STRUCTURE analyses (optimal $K = 2$, the two obtained genetic groups are shown in orange and blue colors in Figure 3). Individuals from Fairchild that resulted from germplasm introduced in 1991 and 2001, showed virtually no admixture and were dominated by the Blue Genetic Cluster. There were only seven exceptions in which admixture was clearly detected for the ex situ collection. They concerned genetic profiles from five (F6, F7, F18, F33 and F34) of the 27 plants introduced 1991 and 2001 (17% of them); and from the two oldest trees planted in the Garden prior 1991 (F23– introduced in 1940, and the already mentioned F22). Regarding the two Haitian cultivated adult plants, one of them (C1) only grouped with the Orange Genetic Cluster; however, the second one (C2) showed admixture for the two genetic groups. Five of the 16 wild-collected (31%) plants (individuals 3–5, 9, and 16) also had admixture for the two genetic groups with the Blue Genetic Cluster mostly found in these plants. These individuals are mostly found in northern areas of the species range. In contrast, most of the plants growing on southern regions of this peninsula, particularly in the Cavaillon area, did not show admixture and were dominated by the Orange Genetic Cluster. The Blue Genetic Cluster was widespread among the 1991 and 2001 plants at FTBG, confirming that the germplasm



Figure 4. Examples of the isolated palms from the northern distribution. (A) A cultivated palm from the collection of Timyan growing at the tomb of a relative of Ossin Jean. (B) Ossin Jean holding an inflorescence of Palm 1. (C) Palm 7 used for storing corn, no longer flowers. (D) Palm 8 was among the tallest found.



Figure 5. Palms from the Southwest populations of the Cavaillon area. (A) Collecting leaf material from palm 12. (B) Palm cluster of individuals 13–17. (C) Palm cluster of individuals 18–23.

Table 3. The ten SSR loci included in this study. Based on Choo et al. (2010).

Locus	Primer (5'-3') sequence	Repeat motif	Number of alleles
A103_3	F: CAATGCAAGAGACAAGCATA R: GCACACTTGATGACATTTTATG	GT ₉	2
A106_2	F: CATTGGCATTCTTACACATTC R: CTTGGGGTGAAGTACTTTAC	CA ₁₁	3
B101_4	F: CCTGGTCATCCGATTATTCA R: TGTCGCCATCTTTTCGTTTAT	TC ₁₉	5
B102_8	F: AGCACTAATGTGCATGTATGTG R: CCATTCCCTCTACAAGGATAAC	GA ₂₁	4
B103_3	F: ATGCTGCTTGGCGTGTAG R: GAGGTATTGATGGGAGGAAGAC	TC ₁₇	2
B121_4	F: CCTGGAGCATCAATGGAC R: TCCGAGAACCCTAAACCTG	TC ₁₂	4
C5_4	F: AAGATGACCGTAGCATTAAACAG R: TCCCATGTTTTCTTTAGTCTTC	GTT ₉	2
C11_7	F: AGTCGTGAAGTCTACCACTTTC R: TGTGCCCCTTCAGATATAGATC	CAA ₉	2
D106_3	F: ACCACCCATCACAAAAG R: GGACCATTCAGCCAGAG	AGAT ₇	5
D124_5	F: GGTGGTGATTGAACTGAACTC R: GCTGATGCTTGCTGACAG	ATCT ₁₀	5

originated from the northern region of the peninsula, specifically the Fond-des-Nègres area.

In a subsequent STRUCTURE exploratory analysis, we noticed that for the wild population the optimal *K* value was 3 (shown as clusters in orange, red, and dark purple in Figure 6). The PCA scatter diagram (20.8% of variation along the first axis, and 16.07% along the second one) for the wild population is also presented in Figure 6. The results agreed with those yielded by STRUCTURE when the wild and cultivated populations were run together. Genotypes found in the northern area of Peninsula de Tiburon mostly displayed positive values along the first component, whereas those from the Cavillon area exhibited negatives values along this axis. These multivariate ordination results agreed with the STRUCTURE outcome. Plants occurring in northern Peninsula de Tiburon were the only ones with admixture for Orange, Blue and Dark Purple Clusters. In contrast the Dark Purple Cluster was very uncommon in individuals found in the Cavillon area (Figure 6).

Recommendations

Our study demonstrates that even when source populations have very few individuals, genetic bottlenecks can happen when ex situ conservation collections

Table 4. Population genetic statistics for the wild collected plants and for those grown in Fairchild Tropical Botanic Garden (FTBG). P = percentage of polymorphic loci, np = number of private alleles, A = average number of alleles per locus, Ho = observed heterozygosity, He = expected heterozygosity, nds = number of loci that deviate significantly from HWE ($p < 0.05$), Fis=inbreeding coefficient, #id= number of identical genotype pairs, LDL = percentage of paired loci showing linkage disequilibrium ($p < 0.05$)

	P	np	A	Ho	He	nds	Fis	#id	LDL
Wild	100	20	3.5	0.295	0.302	4	0.310	0	0
FTBG	40	2	2.7	0.293	0.464	1	0.026	7 ^a	15.56

^a One of these seven genotypes was shared by six individuals and another one was shared by three individuals.

are established. We are aware that there is limited time for field exploration and collection of germplasm, and that in many instances not all individuals of the original population are fruiting or have mature seeds to be collected during field surveys. For example, no seed was collected in 1990 since the same mother palms that were harvested in 1989 either failed to produce fruits or fruited poorly (Timyan & Reep, 1994). In this case, collecting more seed from the south Cavillon population is recommended as germplasm from this area did not reach FTBG. The use of molecular markers are opening new horizons on the management of ex situ collections of living plants, particularly of Critically Endangered species.

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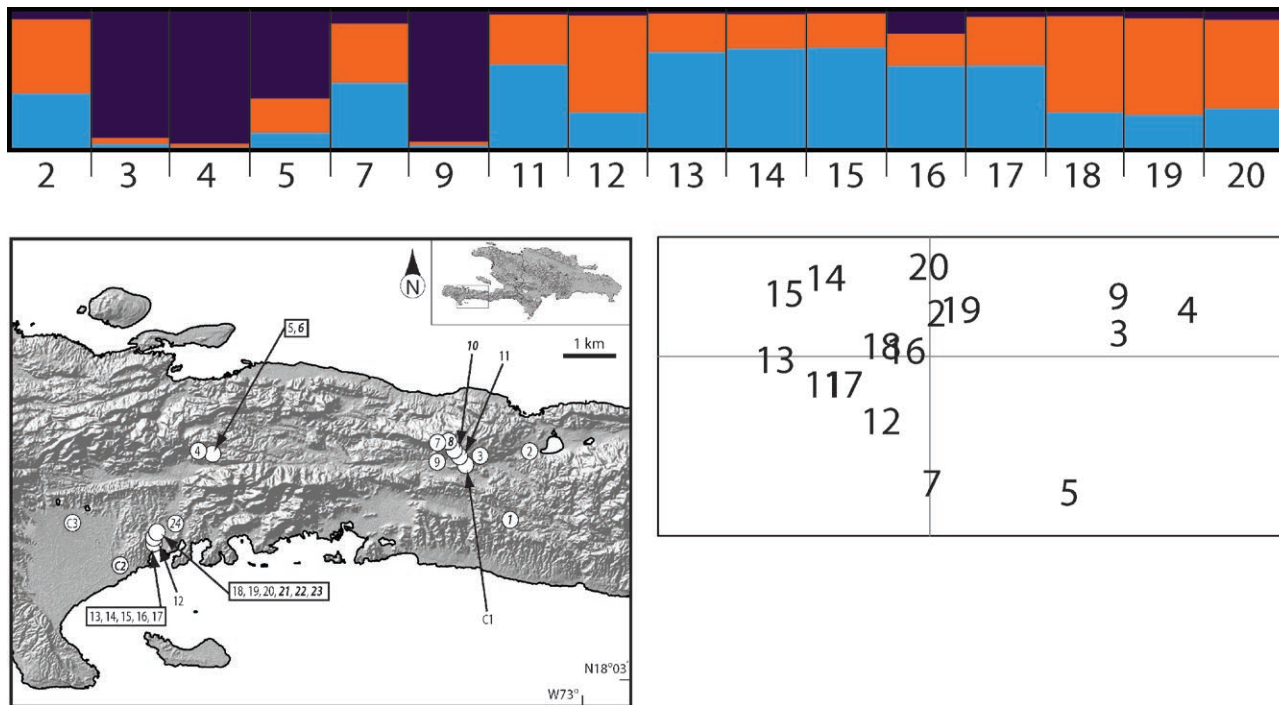


Figure 6. Genetic profiling results of the wild populations of *Attalea crassispatha* included in this study. Top diagram shows results of the STRUCTURE analysis for $K = 3$. Bottom-right scatter diagram shows results of the Principal Coordinate Analyses. Geographical provenances of material collected in Haiti is shown in the map. SSR profiles were obtained for all of the plants except for those indicated in bold-italic font (individuals 1, 6, 8, 10, 21–23, and C2). Individuals C1–C3 were found in cultivated stands and were not included in the analysis.

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Homalomeneae (Araceae) of Borneo XXVIII – *Homalomena bengohensis* [Chamaecladon Clade] a new species endemic to the Bengoh Range, Sarawak

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Abstract. A new species of *Homalomena* Chamaecladon Clade is described from the Bengoh Range, Kuching Division, Sarawak, and compared with the two most similar described species from Kuching: *H. paucinervia* from the Matang Massif, and *H. santubongensis* from Gunung Santubong. The three species are illustrated from living plants and differentiated in an identification key.

Keywords: Araceae, Borneo, Chamaecladon clade, *Homalomena*, Kuching Division, Malaysia, Palaeogene sandstones.

INTRODUCTION

Homalomena Chamaecladon Clade (*sensu* Wong et al. 2013) with major centres of species diversity in Peninsular Malaysia and especially Sumatera is relatively poorly represented on Borneo. The first species described for NW Borneo was *Homalomena paucinervia* Ridl. (Ridley 1905). Since then, species names for the clade on Borneo have been comprehensively misapplied and only recently has the taxonomy begun to be addressed (Boyce et al. 2010; Wong & Boyce 2020, 2021; Wong et al. 2020). Problems stem partly from the species tending to be outwardly rather similar in appearance, especially as preserved specimens, and partly from most of the key diagnostic data present in the usually tiny blooms being lost in herbarium specimens. A further factor is that wild plants are most often encountered sterile or with the blooms post-anthesis, by which time the staminate florets and the staminodes associated with the pistillate florets, the most useful diagnostic portions of the spadix, have rotted. Consequently, the only practicable means to study these plants is by a combination of fieldwork and maintaining living plants.

At present we recognize four described species for the Chamaecladon Clade in NW Borneo, two mesophytes in humid forest belonging to the Griffithii complex — *Homalomena acuminata* (Ridl.) S.Y.Wong & P.C.Boyce and *H. ridleyi* S.Y.Wong & P.C.Boyce (Wong & Boyce 2020); and two rheophytes: *H. paucinervia* and *H. santubongensis* S.Y.Wong & P.C.Boyce (Wong & Boyce 2021). Here we describe a novelty for NW Sarawak, *Homalomena bengohensis*, that most closely resembles *H. paucinervia* and *H. santubongensis* in the form of the blooms but differs by characteristics of the leaf blades and spadix as well as by occurring on earth banks along small streams although not as a rheophyte. Geology in this paper is specified based on Hutchinson (1989, 2005) and Tate (2001).

**Key to differentiate *Homalomena bengohensis*,
H. paucinervia and *H. santubongensis***

1. Leaf blades oblong-spathulate; base of spathe truncate. Muddy streamlet banks. Bengoh.....
.....*Homalomena bengohensis*
- Leaf blades lanceolate to obanceolate; base of spathe not truncate. Bare rocks.....2
2. Spathe opening wide to reveal the pistillate florets; spadix 4 mm × 19 mm [diam.:length ratio 1:4.5]; stigma about half as wide as the ovary; pistillate florets each with an oblong staminode, petioles entirely green; leaf blades abaxially semi-glossy pale green. Palaeogene sandstones. Santubong.....
.....*Homalomena santubongensis*
- Spathe not opening wide enough to reveal the pistillate florets; spadix 3 mm × 19.5 mm [1:6.5], stigma equalling the ovary in width, pistillate florets lacking staminodes, petioles stained deep red in the lower half, leaf blades abaxially slightly glaucous. Cretaceous sandstones. Matang Massif.....
.....*Homalomena paucinervia*

***Homalomena bengohensis* S.Y.Wong & P.C.Boyce, sp. nov.**

Type: Malaysian Borneo. Sarawak, Kuching, Padawan, Bengoh Dam reservoir, hills along the lake, 1°14'54.9"N 110°10'12.5"E, 85 m asl. 27 Jan 2021, *Wong Sin Yeng & P.C.Boyce AR-3452* (holotype SAR!; isotype SAR - spirit!). (Figures 1 & 2A).

Diagnosis

Homalomena bengohensis is unique among Bornean Chamaecladon Clade species in the broadly elliptic, oblong-spathulate or spathulate leaf blades. The spadix most closely resembles that of *H. santubongensis* in the

presence of well-developed staminodes but differs by the truncate base to the spathe and fully sessile spadix.

Description

Small aromatic (terpenoids) terrestrial mesophytes up to c. 15 cm tall. Stem epigeal, erect with internodes somewhat elongated, rooting from the lower-most nodes and through the petiole bases; roots c. 1–3 mm diam., tough, flexuous, medium brown, velvety. Leaves up to c. 10 together per shoot, petioles erect to spreading; petiole 4–10 cm long, c. 2 mm diam. midway, dorsally very narrowly channelled, dull medium green, glabrous; petiolar sheath 1.5–3 cm long, extending c. 1/4 length of the petiole, clasping at the base, width between both margins c. 1 mm, wings persistent; leaf blade broadly elliptic, oblong-spathulate or spathulate, 6–12 cm long by 2–3 cm wide, thinly coriaceous, semi-glossy, glabrous, medium green adaxially, abaxially paler matte green with the higher order veins darker-translucent, base cuneate, apex acute to acuminate with a brief (c. 2 mm long) tubular mucro, margins smooth; midrib adaxially slightly impressed, abaxially prominent; primary lateral veins 5–7 on each side of midrib, adaxially slightly impressed, abaxially alternating with much fainter much more numerous interprimaries, diverging at c. 40°–60° from the midrib; secondary and tertiary venation obscure; all veins running into a very slightly thickened intramarginal vein. Blooms up to 3 together, produced sequentially in a simple synflorescence; peduncle terete, slender, 4–5 cm long by c. 1 mm diam., coloured as for petiole; spathe ca 1.5 cm long, ca 5 mm wide across the truncate-gibbous base, limb dorsally incurved towards the tip, ventrally straight, not constricted, ventrally semiglossy pale green, dorsally medium green, interior shiny pale green, apex with a terminal short brown mucro to 1.5 mm long, spathe inflating at anthesis and opening by a broad slit with the margins recurving and hyaline, later closing and enclosing the spadix, persisting until basal dehiscence at fruit dispersal. Spadix slightly exceeding spathe limb opening at anthesis, c. 1.6 cm long by c. 5 mm diam., sessile and obliquely inserted onto spathe; pistillate florets in two spirals, ovaries compressed-globose very slightly narrowed below the stigma; stigmas about half as wide as ovary, ca. 0.3 mm diam., disc-like, sessile; associated staminodes globose on a very slender stipe, sessile, cream, less than half as tall as the pistil; staminate zone c. 1 cm long, closely resembling the outline of the spathe with a straight ventral side and a curved dorsal side, apex acute; staminate florets each consisting of two stamens, anthers rounded, c. 0.5 mm tall, 1–1.5 mm long by 0.5–0.8 mm wide, creamy white with white tips; post anthesis blooms pendulous by bending of the peduncle. Infructescence



Figure 1. *Homalomena bengohensis* S.Y.Wong & P.C.Boyce. A. Plants in habitat. B–D. Bloom at onset of pistillate anthesis. E. Bloom at pistillate anthesis (nearside spathe artificially removed). All from Wong Sin Yeng & P.C. Boyce AR-3452. Refer to description for dimensions.

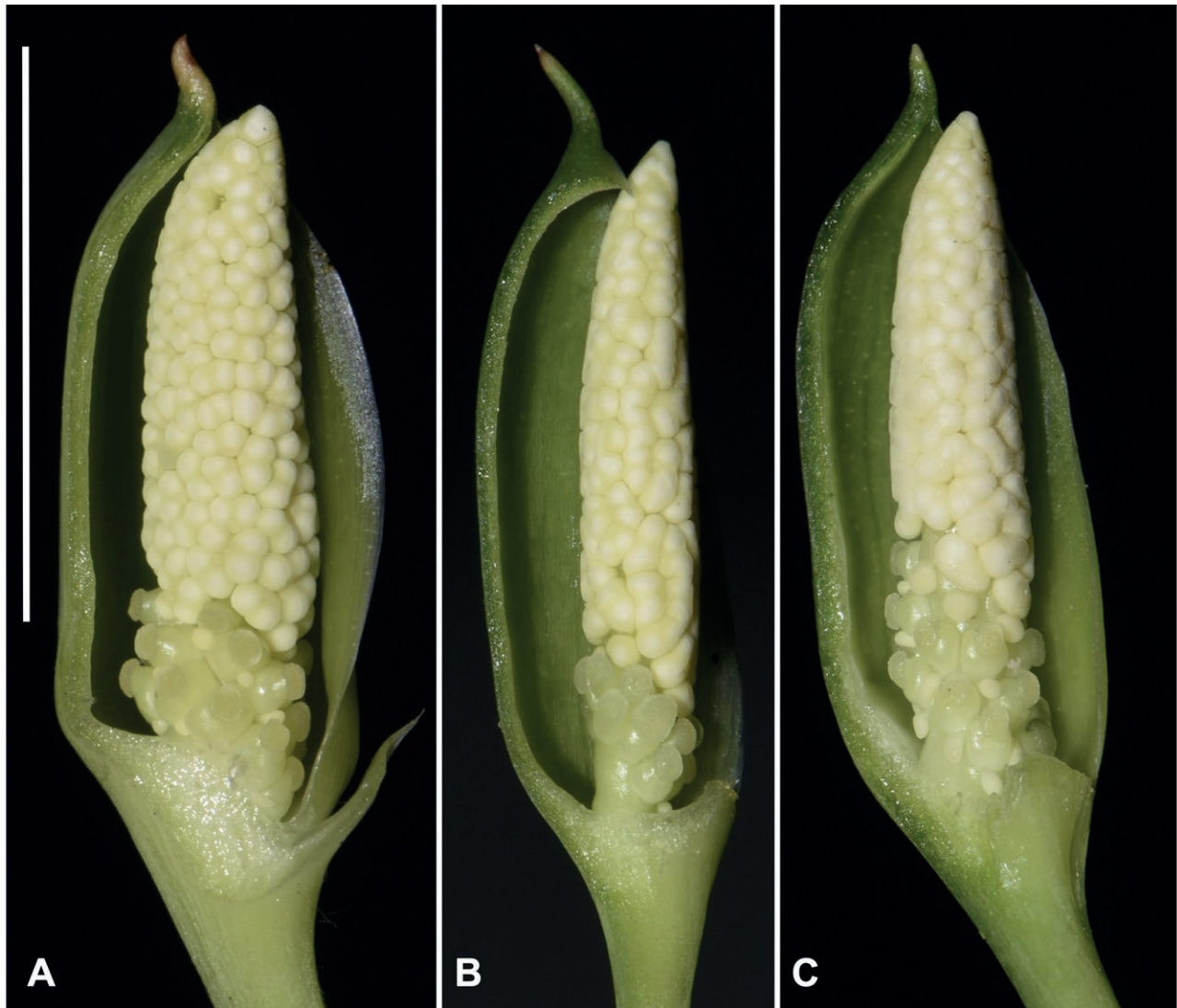


Figure 2. Spadix comparisons A. *Homalomena bengohensis*. B. *Homalomena santubongensis*. C. *Homalomena paucinervia*. Scale bar = 1.5 cm.

ripening within the persistent spathe, ripe fruit and seed not observed.

Etymology

From Bengoh, plus Latin *-ensis*, to indicate originating from.

Distribution

Known only from the type locality where populations are scattered.

Ecology

Banks of muddy streamlets leading into larger streams in rather open perhumid riverine forest on Palaeogene sandstones.

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A new diminutive species of *Schismatoglottis* (Araceae) from Samar Island, Philippines

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Abstract. *Schismatoglottis minuta* (Araceae) is described as a new species and illustrated based on accessions collected from Samar Island, Philippines. The new species, belonging to the Calyptrata clade *sensu* Hay and Yuzammi is distinct from previously reported taxa. Due to its habitat preferences and low (<100) estimated number of mature individuals, we recommend that this noteworthy species should be considered as critically endangered.

Keywords: Araceae, *Schismatoglottis*, Calyptrata Clade, endemic species, Samar Island Natural Park.

INTRODUCTION

The aroid genus *Schismatoglottis* Zoll. & Moritzi (1846: 83) comprises about 139 species distributed across the Malay Archipelago, with extensions towards the Pacific Islands (e.g., Vanatu), Indo-China, and tropical to subtropical China (Hay 1996; Hay and Yuzami 2000; Wong et al. 2016; Wong et al. 2018). The islands of the Philippines host about 9% of its diversity, with most species restricted to one or few islands (Wong et al. 2010; Pelsner

et al. 2011 onwards; Boyce et al. 2015). *Schismatoglottis* in Samar Island is represented by four species: *S. calyptrata* (Roxb.) Zoll. & Moritz (1846:590), *S. edanoi* A.Hay (2000: 121), *S. plurivenia* Alderw. (1922: 209), and *S. samarensis* A.Hay (2000:143), of which two species (*S. edanoi* and *S. samarensis*) are endemic. Given the recent descriptions of many new species of *Schismatoglottis* from Borneo and the Malay Peninsula (Boyce and Wong 2015; Wong 2012; Wong et al. 2020; Wong and Boyce 2021; Wong et al. 2022), it is plausible that the diversity of this numerous genus has not been fully assessed in the Philippines, especially at remote biological hotspots such as Samar Island.

While exploring Samar Island Natural Park at Paranas, Samar Island, the second author photographed a *Schismatoglottis* whose morphological characteristics did not fully match with any of the currently known Philippines species. The most notable features were its remarkably diminutive habit of about 3–6 cm tall and 21 cm wide, the cordate base of its leaves, and the size, slender shape, sharp tip, and white color of its inflorescences. Examinations of vegetative and floral characters suggest that this taxon belongs to the Calyptrata informal species group (*sensu* Hay and Yuzammi, 2000), which is characterized by having a long and persistent leaf sheath fully attached to stems, deciduous spathe limb, minute sessile stigmas, and inflorescences bearing an appendix of sterile male flowers that demarcate the pistillate and staminate sections (Hay and Yuzammi, 2000).

Further expeditions in Samar Island located a second population between Can-avid and Taft, and examinations of herbarium specimens revealed a third one at Matuguinao. Given the unique combination of characters that do not fit within the variation reported from conspecifics in the Philippines and the centralized location of Samar Island at the eastern edge of the Philippine Archipelago (Figure 1), we consider that this taxon represents an undescribed member of *Schismatoglottis*. Hence, here we propose considering it as a new species, which appears to be restricted to Samar Island.

MATERIALS AND METHODS

Fieldwork conducted in March 2016, between June and October 2021, and in October 2022 aimed to document the occurrence of native and introduced species to prepare an updated floristic account for the Samar province.

Initial taxonomic descriptions and photo-documentation of key plant structures from collected specimens were done *in situ* at the type locality. Type specimens

were kept in a field press treated with denatured alcohol prior to being transported to the Systematics Laboratory at the Institute of Biological Sciences, College of Arts and Sciences, University of the Philippines Los Baños, where they were pressed and dried. Some ripe inflorescences were preserved in alcohol vials to conserve the delicate structures of flowers at anthesis. Living plants were collected and cultivated by the first author (M.D.D.A.) to further observe developmental stages of structures, especially inflorescences. Morphological and microscopic characters of fresh specimens were carefully examined using a stereomicroscope and a compound translucent microscope. Measurements of large structures were taken using a ruler and a digital caliper (Tactix: 150 mm). Images of structures were analyzed using the software ImageJ (version 1.53o). After examinations, specimens were dried and mounted into herbarium sheets using standard procedures. Scientific illustrations were based on photos taken in the field using a Nikon D3400 camera or from material preserved in spirit collections. The terminology used in the description section concords with the one used by Hay and Yuzammi (2000) for descriptions of *Schismatoglottis* species. The holotype specimen was deposited at the Philippine National Herbarium (PNH), while isotypes were sent to the College of Agriculture Herbarium at the University of the Philippines Los Baños (CAHUP) and to the Forest Herbarium and Wood Collection (LBC). Herbarium acronyms follow Thiers (2021).

Besides our bibliographic survey, we studied the *Schismatoglottis* collection at the University of the Philippines Los Baños (LBC), PNH, CAHUP, and CMUH herbaria to search for previous collections of the putative new species. We were not able to locate any voucher matching the combination of morphological characteristics defining *S. minuta* except at CAHUP, where we identified two vouchers from the Province of Western Samar collected by M. Price and B.F. Hernaez in July 1975. It is worthy to note that the species delimitation concept being applied here is based on phenetics, which assumes that all operational taxonomic units sharing a set of morphological characters form a cohesive evolutionary assemblage (De Queiroz 2007). Based on the consistency in the range of the morphological characters observed among all known localities of the species here described and the fact that they are phenetically distinguishable from other members of the genus reported for the Philippines, we assume that they represent an independent evolutionary lineage distinct enough to merit recognition as a new species. However, this hypothesis is open to debate when biological and phylogenetic data become available and we can resolve relationships within

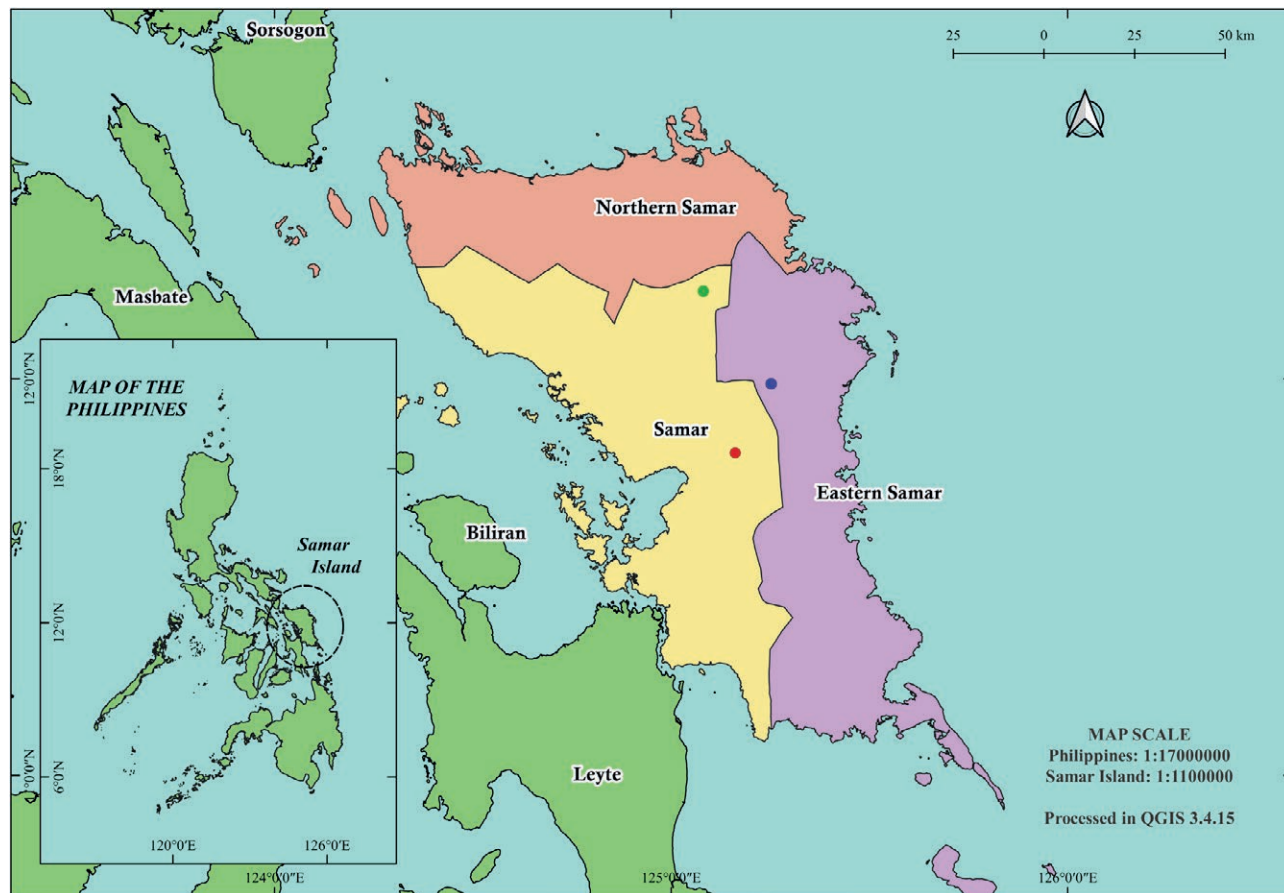


Figure 1. Distribution of *Schismatoglottis minuta* Tandang & M.D.Angeles within Samar Island, Philippines. Localities are as follows: Samar Island Natural Park, Paranas (red circle); Can-avid, Taft (blue circle); Matuguinao (green circle). Map generated by Ren Divien Obeña using QGIS.

Schismatoglottis and delimit species under the framework of a unified species concept (De Queiroz 2007).

TAXONOMIC TREATMENT

Schismatoglottis minuta Tandang & M.D.Angeles, **sp. nov.** (Figure 2)

Type: Philippines, Visayas region, Samar Island, Province of Samar, Municipality of Paranas, Barangay Tenani, Samar Island Natural Park, forest over limestone, 11.814056°, 125.160820°, 132 m, 2 June 2021, *M.D. delos Angeles 274* (holotype PNH!; isotypes CAHUP!, LBC!), CMUH!.

Diagnosis

Schismatoglottis minuta can be distinguished from *S. prietoi* by its longer petioles 5–7 cm (*vs* 3–5 (–9) cm

long); narrowly lanceolate to narrowly cordate or rarely cordate leaf outline (*vs* ovate to oblong-ovate to narrowly elliptic leaf outline); leaf apex acute (*vs* leaf apex acuminate); leaf base rounded with posterior lobes sometimes overlapping (*vs* leaf base cuneate); spathe white below the constriction and whitish green at the upper portion (*vs* lower spathe light green and white with orange tip above); and limb with one constriction (*vs* limb with two weak constrictions).

Description

A hapaxanthic stoloniferous diminutive evergreen herbaceous plant usually 3.33–6.23 mm tall when flowering, individual plants forming small clusters (colonial). *Juvenile plants* terrestrial, emerging from seeds, from the tip of stolons, and from clonal buds present at the connection point between leaf blade and petiole. *Stems* epigeal, decumbent, terete, light yellow on older part becoming pale green on apical part, glabrous;

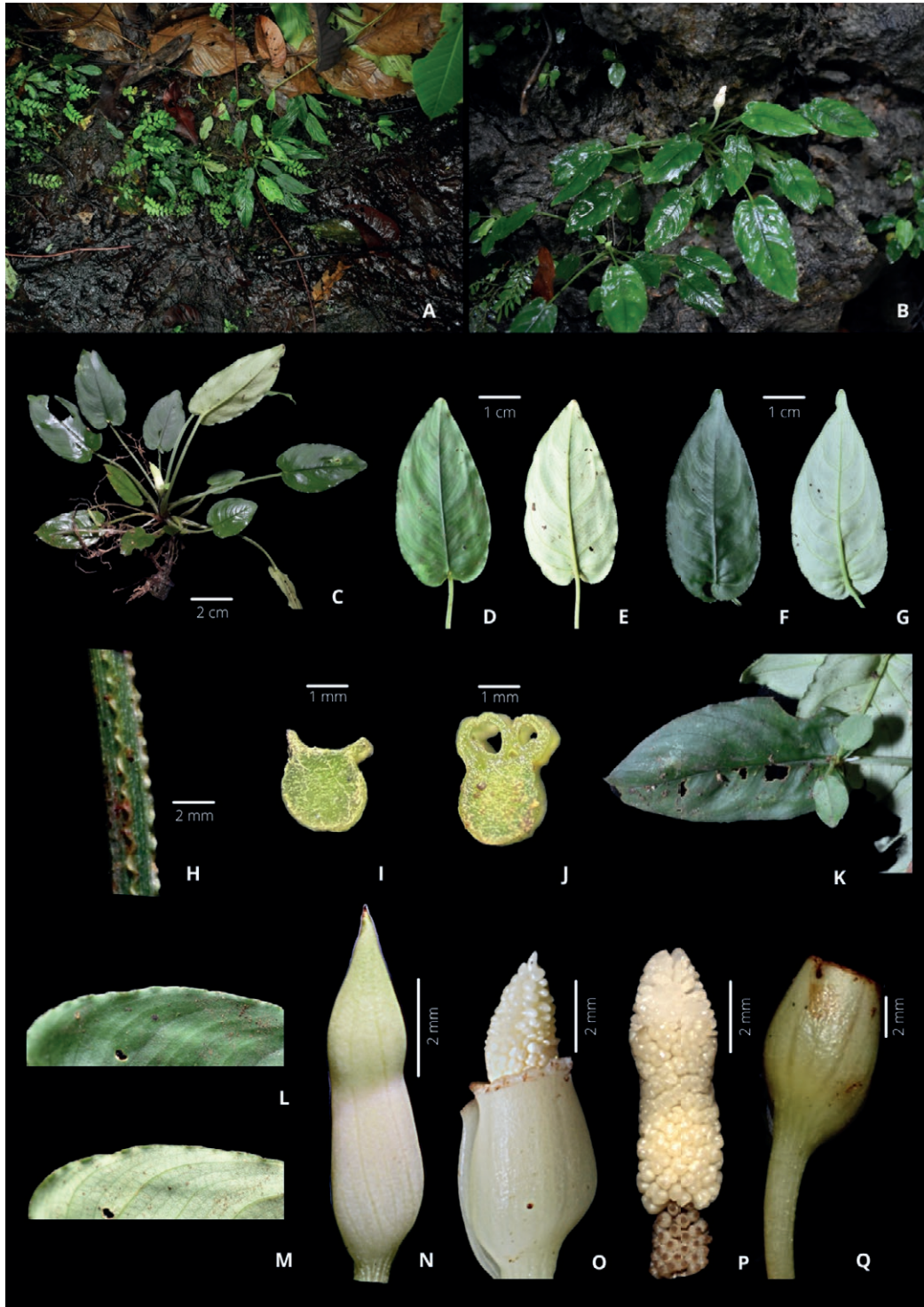


Figure 2. *Schismatoglottis minuta* Tandang & M.D.Angeles— A. Humid habitat along river edges habitat B. Rocky habitat on crevices of Forests over limestone habitat C. Habit D. Leaf with non-overlapping posterior lobes (adaxial view) E. Leaf with non-overlapping posterior lobes (abaxial view) F. Leaf with overlapping posterior lobes (adaxial view) G. Leaf with overlapping posterior lobes (abaxial view) H. Petiole margin I. Cross section of petiole J. Leaf sheath of petiole showing incurved margins K. Viviparous plant emerging from the base a leaf blade L. Leaf margin (adaxial view) M. Leaf margin (abaxial view) N. Mature inflorescence O. Inflorescence with flowers at staminate anthesis (spathe partially removed to show upper portion of spadix) P. Spadix (spathe artificially removed) Q. Unripe infructescence showing an enlarged spathe (Photo credits: D.N. Tandang: A; M.D. delos Angeles: B–Q).

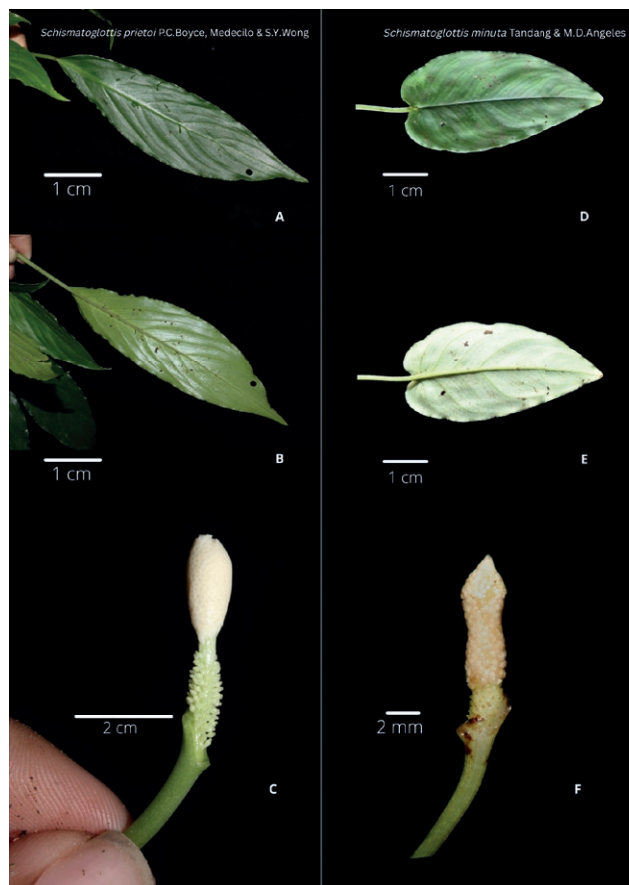


Figure 3. Differences of leaf shape and spadix between *Schismatoglottis minuta* and *S. prietoi*. A–C. *Schismatoglottis prietoi*. D–F. *Schismatoglottis minuta*. (Photos credits: J.R. Callado: A–C; M.D. delos Angeles: D–F).

individuals with short stem showing a very condensed internode obscured by fully attached overlapping petiole sheaths which becomes distinct in plants with long naked stems; stem 2.2–7.1 × 2.5–3.6 mm, not branching, bearing numerous long light-yellow stolons along its length, 42.7–98.8 × 1.1–1.3 mm. *Leaves* spirally arranged, 8–12, crowded at tip of the stem; petioles dark green turning light green towards the stem, fleshy, slender, 5.3–6.9 cm long (including petiole leaf sheath) × 2.9–3.4 mm wide at base, becoming narrow at the middle, 1.8–2.1 mm, and towards near the base of the leaf 1.5–1.6 mm, glabrous, dorsally channeled with persistent slightly undulating minute keels along the edges, “U” shaped in cross section, sheathed at base for 1.8–2.0 cm in length, the petiole sheath margin involute slightly enrolled, entire to rugulose, 2.3–2.5 mm wide when expanded. Blades dark green adaxially, dull and paler green to whitish-green abaxially, variable in shapes from lanceolate or narrowly cordate to rarely cordate



Figure 4. Morphological differences of leaf shape between *Schismatoglottis minuta* and *S. prietoi*. A–B. *Schismatoglottis minuta* from Samar Island C–D. *Schismatoglottis prietoi* from Iloilo, Visayas E–F. *Schismatoglottis prietoi* from Catanduanes, Luzon. (Photos credits: M.D. delos Angeles: A–B; D.N. Tandang: C–F).

when young, glabrous on both sides, rugulose at base, length from point of attachment to, 21.1–34.8 (–54.7) mm, basal lobes to apex 25.1–37.4 (–59.0) mm, at widest point 15.2–23.4 (–26.5) mm; leaf base deep to swallow cordate with rounded posterior lobes 2.8–3.9 (–4.5) × 6.3–7.2 (–8.7) mm, sometimes overlapping 1.1–2.3 (–2.8) mm, margin minutely undulated, acute at the apex, acumen 5.3–6.0 mm, young clonal plants emerging from the leaf blade base; midrib adaxially inconspicuous, abaxially prominent with 6–7 primary lateral veins on each side, diverging at 40°–42°, arching and connecting near the margin; secondary and tertiary venation conspicuous on abaxial side. *Inflorescences* single, no odor; peduncles white, erect, glabrous, very short during bud stage and gradually elongating to a slender shape and a sharp tip as the spathe become fully opened 30.4–42.4 mm long, with longitudinal striations that are decurrent on the urceolate base spathe, tightly clasped at base by

the sheath wings of the minuscule cataphyll, the cataphyll has reduced petiole ca. 6.5×0.7 mm and small light-green cordate foliage ca. 6.1×3.4 mm. *Spathe* erect, white below the constricted part becoming whitish-green at the upper portion; spathe in mature bud, 15.6 mm long, unopened upper part conical; spathe in opened stage 19.6 mm long, the white urceolate-shaped spathe at base oblique, 11.2×6.2 mm, spathe constriction ca. 4.4 mm, blade of the spathe (limb) cucullate, ca. 9.6 mm long, apex acute, caducous; *Spadix* erect, sessile, 9.5–11.6 mm long; sterile section absent; pistillate flower zone oblong, 2.2×2.2 – 2.4 mm, 1/4 of its length adnate at base to the spathe; pistil subglobose, loosely arranged, glabrous, 0.4 – 0.5×0.3 – 0.4 mm; stigma sessile, circular, papillae, 0.1×0.1 – 0.2 mm; style not distinct; sterile interstice separating male and female zones absent; staminate flower zone 3.5 – 6.7×2.3 – 3.7 mm, adjoining directly with female zone, oblong, longer than the female and terminal appendix; staminate flowers cream white, joined, each with 2 stamens, dumbbell-shaped with slightly sunken connective clearly separating pairs of thecae; thecae domed, 0.4 – 0.9 mm in length and 0.3 – 0.6 mm across, opening by a short terminal slit; weak constriction near the tip; appendix at the terminal section white, conical, much shorter than the male and female zones, 1.4 – 2.0×1.8 – 2.2 mm, apex flat-topped at mature bud becoming conoid in open flower; appendix staminodes obovoid to globose. *Fruiting spathe* asymmetrical urceolate, 8.4×5.7 mm. *Fruits* not observed.

Etymology

The specific epithet “*minuta*” refers to the overall small habit of this new species when compared to conspecifics.

Phenology

Observed to bear flowers during the months of March, September, and October.

Distribution and Ecology

Schismatoglottis minuta is so far only known from Samar Island, Philippines. The species is currently known from three localities in Samar, at the “Samar Island Natural Park, Municipality of Paranas”, “Canavid, Municipality of Taft”, and “Municipality of Matuguinao”. The sites are rocky habitats with moist substrate under tropical lowland evergreen rainforest dominated by towering dipterocarp trees. The species grows as a terrestrial herbaceous lithophyte on low vertical cliffs along creeks with shallow running water and on rock crevices under full shade in forests over limestone.

Conservation status

This new species, thus far, is found only at three fragmented localities. All sites contain clustered populations of less than 100 mature individuals in total, mainly in forested habitats (D.N.T., pers. obs.). Two of the known localities where *S. minuta* has been observed are not within the protected land (i.e. Canavid and Matuguinao), and we expect that there will be a reduction in population size in more than ten years. Thus, following the IUCN Standards and Petitions Committee (2019), this noteworthy species is proposed to be categorized as critically endangered under criteria A4, B2a, C2a, and D1.

Additional specimens examined (paratypes)

PHILIPPINES: Samar Island: Province of Western Samar, Municipality of Matuguinao, primary forest on limestone and limestone-derived soils, $12^{\circ}09'$ – $12^{\circ}10'N$, $124^{\circ}54'$ – $124^{\circ}56'E$ [12.15° – 12.17° , 124.90° – 124.93°], [243–523 m], 8–9 July 1975, M.G. Price and B.F. Hernaes 418 (CAHUP [two sheets: accession numbers 40237 and 40238]).

DISCUSSION

The addition of *S. minuta* raises to 13 total number of *Schismatoglottis* species reported for the Philippines (Pelser et al. 2011–onwards). *Schismatoglottis minuta* is one of the smallest species in the genus, especially if compared to the rest of congeners occurring in the Philippines (Hay and Yuzammi 2000; Boyce et al. 2015). The only two other Philippine species of *Schismatoglottis* with relatively small size are *S. prietoi* P.C.Boyce, Medecilo & S.Y.Wong (2015: 407) and *S. mindanaoana* Engler (1912: 103). The former occur in Cebu and Luzon, while the latter is endemic to Mindanao. Of these, the taxon with closest morphological resemblance is *S. prietoi*.

Despite sharing an overall miniature size, *S. minuta* and *S. prietoi* can be differentiated by the shape of their leaves (blades with cordate base vs cuneate base; Figures 2 and 3), inflorescences with staminate to female zones contiguous vs very short sterile interstice (Figure 3), and flowers with two stamens vs 3–4 stamens. Furthermore, *S. minuta* has a white urceolate-shaped spathe vs pale green to white cylindrical. Additional characters separating both species include cross sections of their leaf petioles (“U” vs “D” shapes), number and angle of primary lateral veins (6–7 diverging at 40° – 42° vs 3–5 diverging at 30° – 60°), and diameter of floral stigma (0.1 – 0.2 vs 0.3 mm).

The shallow to deeply cordate leaf base shape of *S. minuta* appears to be consistent among individuals in

the three sites where the species has been found (Figures 1 and 5). In fact, this is the most noticeable character to differentiate it from *S. prietoi*, whose all known populations have leaves with cuneate leaf and has not been reported for Samar Island.

The new species is further compared with *S. mindanaoana* because both share characteristics such as stem diameter and acute leaf apex. However, *S. minuta* can be distinguished by its lanceolate or narrowly cordate to rarely cordate leaf blades (*vs* oblong elliptic to slightly obovate leaf blades), shorter leaf length (2.1–3.5 (–5.5) cm *vs.* 3–4 (–7.5 cm), wider leaf diameter (2.5–3.7 (–5.9) *vs* 1.5–3 cm), and by having more primary veins (6–7 *vs* 2–4).

The forests of Samar Island are highly diverse but have been poorly studied, as reflected by the many species of flowering plants described from there in recent years (e.g., Adorador et al. 2021; delos Angeles et al. 2022; Tandang et al. 2022). These high levels of endemism are mainly concentrated in forests over limestone, as discussed in Tolentino et al. (2020). Future field expeditions in highly threatened habitats outside protected areas should emphasize not only collections of voucher specimens, but also samples for genomic studies and germplasm for ex-situ conservation efforts in national and international botanic gardens.

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AUTHOR CONTRIBUTIONS

MDDA collected the species from the field. MDDA and DNT took photographs of the species on site.

MDDA prepared a first draft of the manuscript and revised herbaria. All authors contributed to the manuscript and approved the final version.

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Studies on Homalomeneae (Araceae) of Borneo XXIX — *Homalomena latisinus*, a new species for the Borneensis Complex from Brunei

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Abstract. *Homalomena latisinus* is described and illustrated as a new Bruneian species of the *Homalomena* Borneensis Complex from shaded damp kerangas. It is compared with the five species previously described for the complex.

Keywords: Borneo, Brunei, *Homalomena*, kerangas, Palaeogene sandstones.

INTRODUCTION

The *Homalomena* Borneensis Complex of the *Homalomena* Cyrtocladon Clade (Ng et al. 2011: 26; Wong et al. 2013a; Wong et al. 2013b: 10) currently comprises five described species, all restricted to Borneo: *Homalomena borneensis* Ridl. (Ridley 1905: 173), *H. clandestina* P.C.Boyce, S.Y.Wong & Fasih. (Boyce et al. 2010: 277), *H. ibanorum* S.Y.Wong & P.C.Boyce (Wong et al. 2013: 18), *H. ovata* Engl. (Engler 1879: 296), and *H. tirtae* Asih, Kurniawan & P.C.Boyce, (Asih et al. 2012: 241). Here we describe a sixth species from damp kerangas in Brunei which is highly distinctive in the complex by the glossy deep green leaf blades with well-developed posterior lobes separated by a wide parabolic sinus. Hitherto only *H. ibanorum* has glossy leaf blades, but differs from the species described here by, among other characteristic, a weakly cordate to almost truncate base to the leaf blades.

Geology in this paper is specified based on Hutchinson (1989, 2005) and Tate (2001).

Key to species of the *Homalomena* Borneensis Complex

1. Pistillate floret zone accounting for nearly 1/2 of the spadix; staminate and pistillate floret zones contiguous, not separated by a naked interstice.....2

- Pistillate floret zone accounting for 1/3 or less of the spadix; staminate and pistillate floret zones separated by a naked interstice 3
- 2. Spathe green at anthesis; pistils somewhat lax, stigma clearly 3-lobed, wider than pistil; interpistillar staminodes shorter than pistils. Kalimantan Timur; volcanic-derived clays.....
..... *H. tirtae*
- Spathe white at anthesis; pistils very dense with stigma not 3-lobed, narrower than pistil; interpistillar staminodes equalling or slightly longer than pistils. Matang Massif, Kuching; Palaeogene sandstone-derived soils *H. ovata*
- 4. Leaf blades adaxially glossy 5
- Leaf blades adaxially matte 6
- 5. Leaf blades adaxially medium green with red margins; blade base weakly cordate to almost truncate; spathe limb internally white with a red margin, exterior glossy pale green with margins and the distal part of the spathe limb stained red; C-NE Sarawak, SW Brunei; lowland mixed dipterocarp forest on alluvial soils..... *H. ibanorum*
- Leaf blades adaxially deep green without red margins; blade base with well-developed posterior lobes separated by a wide parabolic sinus; spathe without any red colouration. Brunei; damp kerangas..... *H. latisinus*
- 6. Pistils yellowish, directed outwards; interpistillar staminodes with the clavate portion papillate; pistillate floret zone weakly fusiform; spadix somewhat sinuous; leaf blade abaxially glaucous. NW Borneo; Karst limestone.....
..... *H. borneensis*
- Pistils white with grey stigmas, directed upwards; interpistillar staminodes with the clavate portion smooth; pistillate flower zone markedly fusiform; spadix straight; leaf blade not abaxially glaucous; Ai drainages; shales.....
..... *H. clandestina*

***Homalomena latisinus* S.Y.Wong & P.C.Boyce, sp. nov.**

Type: Brunei. Belait, Ulu Ingei, Bukit Batu Patam, 4°05'N 114°42'E, 180 m asl., 8 June 1989, P.C. Boyce 276 (holotype BRUN!; isotypes K!, L!). (Figures 1–3).

Diagnosis

Homalomena latisinus differs from all described species of the Borneensis Complex by the glossy deep green leaf blades with well-developed posterior lobes separated by a wide parabolic sinus. In the glossy leaf blades *H. latisinus* most resembles *H. ibanorum*, from which it differs by the leaf blades with well-developed posterior lobes (vs blade base weakly cordate to almost truncate), the blades, prophylls and cataphylls lacking a red margin, and spathes without any red staining. *Hom-*



Figure 1. *Homalomena latisinus* S.Y.Wong & P.C.Boyce. A & B Plants in habitat. C. Leaf blade abaxial view. Photographed unvouchered. Refer to description for dimensions.

Homalomena latisinus is unique in the Borneensis Complex by occurring in damp kerangas.

Description

Mesophytic herb to c. 50 cm tall, vegetative tissues strongly aromatic (terpenoids). Stem erect to decumbent with the tip ascending, c. 2.5 cm thick, dark green; internodes to c. 2 cm long. Leaves up to 12 together, erect, the older ones spreading; each shoot module subtended by a single prophyll, c. 7 cm long, green, its margins membranous marcescent; petiole 28–35 cm long × c. 5 mm in diameter, terete, adaxially narrowly flattened, glossy medium green; petiolar sheath closed with one wing incurved upon the other, 7–8 cm long, c. 1/5 length of petiole, the wings long-persistent with the margins marcescent; leaf blade broadly cordate, 15–24 cm long × 12–14 cm wide, coriaceous, glossy dark green adaxially, semi-glossy medium green abaxially with very numerous minute darker punctations, apex acuminate and

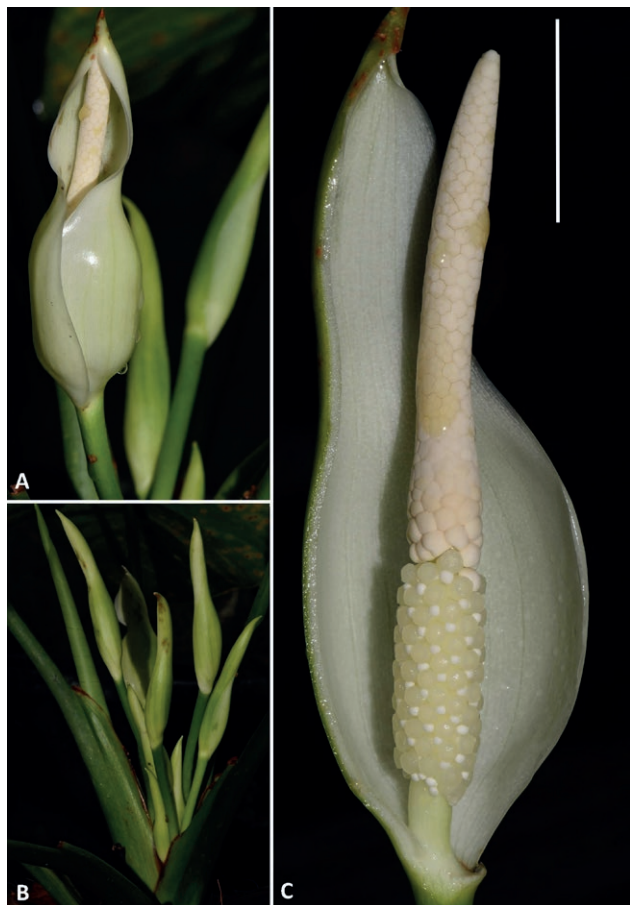


Figure 2. *Homalomena latisinus* S.Y.Wong & P.C.Boyce. A. Bloom at late pistillate anthesis. Note the resin that has been secreted ahead of pollen release. B. Emerging blooms. C. Spadix at pistillate anthesis, spathe artificially removed. Scale bar = 2 cm.

then mucronate for c. 4 mm, base cordate, lobes rounded, c. 6 cm long, separated by a parabolic sinus; midrib rounded-raised abaxially, adaxially somewhat impressed, up to 4 mm wide; primary lateral veins about 8 on each side, diverging at 40° (distal one) to 60° (proximal ones) from the midrib, abaxially raised and somewhat darker than blade; interprimary veins c. 1/2 width of the primary lateral veins, irregularly interspersed, flush with the lamina adaxially, abaxially faintly darker and prominent; secondary venation somewhat conspicuous to weakly flush with the lamina on both sides; tertiary venation invisible; all veins running into a thickened intramarginal vein; intramarginal vein somewhat inconspicuous abaxially, adaxially almost invisible. Blooms up to 12 together in a simple synflorescence, each subtended by a small narrowly triangular prophyll and one or two cataphylls, suberect at anthesis, later declinate; peduncle to c. 9 cm long × c. 4 mm in diameter, medium green.



Figure 3. *Homalomena latisinus* – Holotype. P.C.Boyce 276. [BRUN B 008 035]. Image used with permission.

Spathe stiff, fleshy, tightly furled prior to anthesis, c. 8 cm long × c. 1.5 cm wide, glossy white at anthesis; lower spathe ovoid to broadly ovoid, c. 4.5 cm long, exceeding the limb in length; limb c. 3.5 cm long, narrowly ovoid with a terminal mucro 4–5 mm long; lower spathe inflating and spathe limb gaping at pistillate anthesis, spathe limb opening wide at staminate anthesis and spadix extending; spathe later closing around spadix. Spadix c. 8 cm long × c. 5 mm in diameter, stipitate, stipe c. 3 mm, creamy white to very pale green; pistillate floret zone cylindrical, about 1/3 the length of the spadix, c. 2 cm long; pistils densely arranged, globose, c. 1.5 mm tall × c. 1 mm in diameter, greenish white, stigma convex-topped, much wider than the pistil, c. 1 mm tall × 1.5 mm in diameter, mostly 3-lobed, semitranslucent, glossy grey; most florets associated to a single interpistillar staminode (rarely two staminodes in basal-most florets); interpistillar staminodes globose-headed, on a very slender stalk with an expanded top, c. 0.5 mm long, ivory; sterile interstice c. 1 cm long, densely packed with rhombohexagonal-round-topped white staminodes; staminate floret zone narrowly conic, c. 4 cm long, about half

the length of the spadix, 1/4 held within lower spathe chamber, apex acute, ivory; staminate florets densely arranged, mostly hexagonal in plan view, each floret consisting of 4 stamens, lowermost 1 – 2 rows of florets sterile, staminate florets zone producing abundant pale amber coloured resin just prior to pollen release. Fruiting spathe dull pinkish green; fruits not observed.

Etymology

From Latin *latus*, (Genitive *lati*) – broad, and *sinus*, a hollow or bay, referring to the space between the posterior lobes of the leaf blade.

Distribution

Brunei, known from two populations approximately 100 km distant. The type locality is almost on the border with Sarawak, such that *H. latisinus* is fully expected to occur in Malaysia. The second population occurs at Tasek Lama, on the trail to Bukit Sarang Helang, Brunei-Muara.

Ecology

Shady damp kerangas on steep banks overlying Belait (Miocene) series sandstones, 100–180 m asl.

Notes

The production of resin from the staminate florets zone in the Borneensis Complex (among others) was detailed by Hoe et al. (2016).

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Homalomeneae (Araceae) of Borneo XXX — *Homalomena atlas* [Hanneae Complex] a new species from the Rejang Basin, Sarawak

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Abstract. *Homalomena atlas* is described and illustrated as a new species from the western Rejang Basin and assigned to the Hanneae Complex of the Cyrtocladon Clade, taking the complex to 12 described species on Borneo.

Keywords: Araceae, Borneo, Cyrtocladon Clade, Hanneae Complex, *Homalomena* Sarawak, Shales.

INTRODUCTION

The *Homalomena* Hanneae Complex (Ng et al. 2011: 26) of the Cyrtocladon Clade (Wong et al. 2013) is a highly distinctive group of species notable for leaf blades with conspicuous extrafloral nectaries, amber-coloured resin secreted from between the staminate florets shortly before staminate anthesis (Hoe et al. 2011, 2016; Wong & Boyce 2017), and spathes white at anthesis with the persistent post-anthesis spathe turning deep pink to red as the fruits develop. Until recognition of *Homalomena electra* P.C.Boyce & S.Y.Wong (Boyce & Wong 2017) from Peninsular Malaysia the Hanneae Complex was considered to be entirely Bornean (but see Wong et al. 2013: 592). Including that described here, the complex comprises 13 described species, all except *H. electra* restricted to Borneo, and with most species localized. Based on field observations and in particular the huge amount of undeterminable material deposited in herbaria the Hanneae Complex is most probably contains well in excess of 100 species

Geology in this paper is specified based on Hutchinson (1989, 2005) and Tate (2001).

***Homalomena atlas* S.Y.Wong & P.C.Boyce, sp. nov.**

Type: Malaysian Borneo. Sarawak, Kapit, Taman Rekreasi Seabai, 1°56'39.2"N 112°54'21.5"E, 76 m asl., 22 Sep 2017, *Wong Sin Yeng & P.C.Boyce AR-3640* (holotype SAR! + spirit; isotype BO + spirit!). (Figures 1–3).

Diagnosis

Homalomena atlas is immediately distinguished in the Hanneae Complex by the matte brick-red peduncles with dense pale grey broken longitudinal striations, glossy scarlet petiole bases and dark red petiolar sheath, and by the lower spathe inflating to almost globular during anthesis. *Homalomena atlas* most nearly approaches *H. mutans* (with which it co-occurs at the type locality – see Boyce & Wong 2014: 66) and from which it further differs by the interstice between the zones of staminate and pistillate florets being narrower than the adjacent parts of the respective zones (vs interstice markedly swollen to exceed the width of the fertile zones), and by the glossy broadly ovate-cordate (vs matte triangular-cordate) leaf blades

Description

Medium-sized, rather robust, evergreen, glabrous clumping herb to c. 1 m tall. Crushed tissues strongly aromatic of turpentine. Stem initially erect, decumbent with age with the active tip ascending, 3–3.5 cm thick, semi-glossy medium green; older parts brown; adventitious roots copious, conspicuous, penetrating petiole bases; internodes 1.5–2.5 cm long. Leaves up to ca 20; individual shoot modules beginning with a conspicuous 2-keeled semi-persistent scarlet prophyll; petiole 60–70 cm long × 9–12 mm wide, erect, older leaves with the petiole spreading or procumbent, pulvinate ca 2/3 way along from base, weakly D-shaped in cross-section with angles rounded, distally shallowly canaliculate with the angles bluntly rounded, medium green with broken paler longitudinal striae, lower fifth (about half equal to the length of the sheathing portion), glossy scarlet; petiolar sheath 10–15 cm long, c. 1/5 of petiole length, with wings up to 1 cm wide proximally, tapering distally, open, weakly decurrent at apex, their margins slightly incurved; wings initially deep red brown, soon marcescent along margin, eventually whole sheath marcescent; blade broadly ovato-sagittate or ovato-cordate, 35–45 cm long × 25–35 cm wide, thinly leathery; somewhat quilted between impressed primary veins, with scattered punctate extrafloral nectaries, semi-glossy dark green adaxially, slightly paler abaxially, sagittate at base with sinus narrowly triangular; posterior lobes subtriangular with the outer margin rather abruptly curved, and the



Figure 1. *Homalomena atlas* S.Y.Wong & P.C.Boyce. A. Plant in habitat. See description for dimensions.

inner margin straight to very slightly incurved, obtuse at apex; anterior lobe broadly triangular, acute; mid-rib raised abaxially, c. 8 mm wide at base, 4 mm wide at centre, adaxially impressed; primary lateral veins c. 20 on each side, diverging at 30–70° from midrib, adaxially impressed, abaxially sharply raised, curved towards apex when near margin; interprimary veins slightly impressed adaxially, slightly raised abaxially, alternating irregularly with primaries, posterior lobes each with 4–6 primary veins; secondary venation abaxially raised, arising from mid-rib and primary and interprimary veins; tertiary venation invisible, all veins running into a slightly thickened intramarginal vein. Blooms usually up to 10 together in a simple synflorescence, erect, smelling of anethole at anthesis, post-anthesis and into fruiting declinate; first bloom subtended by a red prophyll, c. 5 cm long × 1 cm wide; subsequent blooms subtended by slightly shorter red prophylls; peduncle 15–18 cm long × 5.0–7.5 mm wide, matte brick red with very numerous pale grey broken longitudinal striae. Spathe c. 11 cm

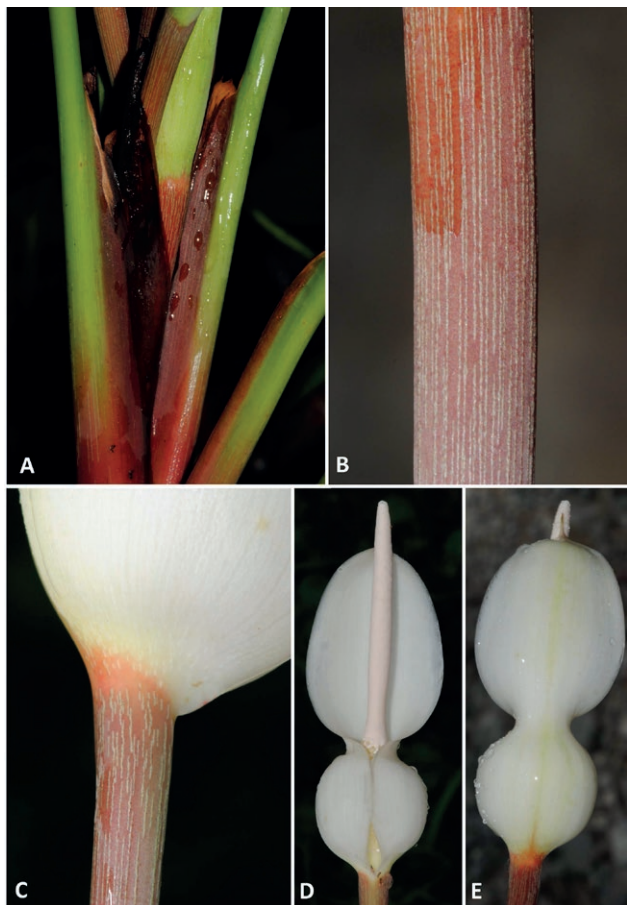


Figure 2. *Homalomena atlas* S.Y.Wong & P.C.Boyce. A. Emerging blooms B. Detail of peduncle. C. Junction of peduncle and lower spathe. D & E. Front and rear views of a bloom at late pistillate anthesis. See description for dimensions.

long \times ca 4 cm wide; lower spathe inflating globose and spathe limb loosening at pistillate anthesis, spathe limb opening widely cucullate at staminate anthesis, white, dorsally with a yellow-pale green median band corresponding to mid-keel and flanked by two paler similarly coloured bands, middle band becoming brick red where it runs into the peduncle, 2.5 cm long \times c. 2.5 cm wide, spathe strongly constricted with constriction coinciding with the base of the staminate floret zone; spathe limb c. 7 cm long \times c. 4 cm wide at pistillate anthesis, ovato-triangular, with greenish red-tipped terminal mucro to c. 3 mm. Spadix 12–12.5 cm long at anthesis, stipitate, spadix shorter than spathe at onset of anthesis, then rapidly extending and bending forwards during pistillate anthesis until exceeding spathe limb by c. 1 cm; stipe c. 10 mm long \times c. 53 mm wide, cylindrical, inserted obliquely on peduncle, waxy white; pistillate floret zone c. 4 cm long \times 1.5 cm wide, c. 1/3 length of spadix, slightly



Figure 3. *Homalomena atlas* S.Y.Wong & P.C.Boyce. A. Bloom at late pistillate anthesis. B. Bloom at late pistillate anthesis, nearside part of spathe artificially removed. Scale bar = 2 cm.

fusiform, very pale yellow; pistils 1.5–2 mm in diameter, c. 1.5 mm tall, globose-cylindrical, crowded, yellowish; infrapistillar staminodes mostly one per pistil, (rarely two or staminodes in basal-most florets); stipitate with a globose head 0.8–1 mm in diameter, not quite equalling pistils in height, waxy white; style barely differentiated; stigma globose-capitate, about as wide as ovary, dirty white, wet at anthesis; sterile interstice tapering and narrower than the adjacent fertile zones, with 2–3 rows of hardly individually distinguishable rhomboidal ivory staminodes; staminate floret zone 7–8 cm long \times c. 1 cm wide at staminate anthesis, c. 2/3 length of spadix, cylindrical, tapering basally; amber droplets of resin secreted from between staminate florets prior to onset of staminate anthesis; staminate florets polygonal in plan view, 2.0–3 mm in diameter, each comprising 4(–6) truncate stamens each overtopped by large and flat connective tissue, ivory white; pollen in short strings, white, forming a paste when mixed with resin. Infructescences up to

10 together, declinate to pendent; spathe entirely persistent, deep red; peduncle matte dark brick red conspicuous striae; fruits not observed.

Eponymy

From Atlas, a Titan in Greek mythology condemned to hold up the heavens for eternity following the conflict between the Titans and the Olympians. In artistic depictions Atlas is portrayed supporting a celestial sphere on his shoulders. The name is coined in allusion to the globose lower spathe.

Distribution

Sarawak, restricted to the western Rejang basin, with the populations occurring as far east as the confluence of the Rejang and Balleh rivers.

Ecology

Homalomena atlas forms extensive patches, occasionally intermixed with *Homalomena mutans* P.C.Boyce & S.Y.Wong and *H. ibanorum* S.Y. Wong & P.C. Boyce, on open areas of the floor of humid to per-humid lowland dipterocarp forest over shales at between 50 and 100 m.

Notes

The twelve described Bornean species of the Hanneae Complex are as follows, listed by their occurrence from west to east:

Homalomena debilicrista Y.C.Hoe from the Matang Massif, on hard Palaeogene sandstones;

H. gastrofructa Y.C.Hoe, S.Y.Wong & P.C.Boyce from the Siburan Triassic-Jurassic Karst;

H. velutipedunculata Y.C.Hoe, S.Y.Wong & P.C.Boyce from Santubong on Paleogene sandstone; *H. atlas* (described here) from Kapit Palaeogene shales and at least partly co-occurring with *H. mutans*;

H. hanneae P.C.Boyce, S.Y.Wong & Fasih., *H. vivens* P.C.Boyce, S.Y.Wong & Fasih, and *H. sengkenyang* P.C.Boyce, S.Y.Wong & Fasih. from Batang Ai on Cretaceous shales, with *H. hanneae* extending into Kalimantan Barat;

H. josefii P.C.Boyce & S.Y.Wong from Bukit Setiam on Oligocene shales;

H. lambirensis S.Y.Wong & P.C.Boyce from Lambir on Miocene sandstones;

H. ardua P.C.Boyce & S.Y.Wong and *H. striatieopetiolata* P.C.Boyce & S.Y.Wong from Mulu, the first occurring on Eocene Melinau Karst, and the second on Palaeogene Setap shales and extending into Brunei.

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Notes about *Phaseolus pallar* Molina (Leguminosae-Papilionoideae-Phaseoleae): alas but at best a synonym!

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Abstract. A name given by Molina in 1782 and again in 1810 to a new *Phaseolus* species after a food legume crop grown for millennia mostly in the western part of the Quechua realm in South America refers to that crop (in the text of his essay) as well as to a weed (in his short Latin description), thus raising taxonomical uncertainty. Obviously, a taxonomical epithet cannot refer to two different botanical entities within the same genus. An example of that uncertainty was the naming of a specimen likely of *Macroptilium lathyroides* collected in northern Colombia and kept in the negative series of Berlin-Dahlem at the Field Museum. That crop spread so widely and fast that it received several names that Molina and *a fortiori* Philippi should have considered.

Keywords: Chile, crop migration, folk taxonomy, Lima bean, nomenclature.

INTRODUCTION

The Linnean taxonomy of New World crops turned complicated by their wide and rapid adoption within the century after 1492. For instance, chili pepper was registered in Indonesia in 1540 (Andrews 1999). The success of introduction of chili peppers in warm regions of Asia was such that Nikolaus von Jacquin described a *Capsicum chinense* after its putative home, although he acknowledged having seen it cultivated in the island of Martinica, West Indies (Jacquin 1776, p. 38). Here follows one more example: the Lima bean that according to Carl Ortwin Sauer (1950, p. 501) “predominates over the common bean in the majority of the American tropics”. The purpose of this note is a clarification about *Phaseolus pallar* Molina, for which the consultation of Tropicos (2022) and the International Plant Names Index database (2022) yielded the abbreviated reference to Molina’s essay referred to hereafter. There might be an additional justification for this clarification as, and because of the presence of a specific archive kept at the Field Museum of Natural History of Chicago (see below), the consultation about the type (<https://collections-botany.fieldmuseum.org/taxonomy/58121>) indicated: “status unknown”.

RESULTS

Molina and the Phaseolus beans of Chile

The abbot Giovanni Ignazio Molina (Villa Alegre, Chile 1740 – Bologna, Italy 1829) was among the first scholars to report about the natural history of Chile. No wonder that his work raised interest – thus the various translations – among the European botanists during most of the 19th century (Charrier and Hervé 2011; Thulin et al. 2021). Molina (1782) in his essay ‘Saggio sulla Storia naturale del Chili’ indicated that the inhabitants were growing a bean (reported as “degul”; a somewhat similar name “dengüll” was reported by Ernst Wilhem de Mösbach 1992) before the arrival of the Spaniards. In addition, among the climbing varieties he mentioned the *pallari*, with seeds of about one inch in size, and then wrote the description of two new species *Phaseolus pallar* and *P. asellus* (p. 130 and p. 353). The descriptions were (and repeated as such in the second edition of 1810, p. 293):

- *Phaseolus asellus*: Phaseolus caule volubili, foliis sagittatis, seminibus globosis, and
- *Phaseolus pallar*: Phaseolus caule volubili, legum[inibus] pendulis cylindricis, torulosis.

In both publications by Molina there were no illustrations nor indications about reference specimens; these shortcomings resulted in many botanical confusions (see discussions by Lucien Hauman 1923 and Ivan Murray Johnston 1924). Efforts to track specimens of these two species at BOLO (acronyms of Herbaria according to Thiers 2023) – the likely place where Molina could have deposited specimens (Stafleu and Cowan 1981; Thulin et al. 2021) – were unsuccessful.

Several botanists mentioned these two species afterwards:

1813: Jean Louis Marie Poiret (p. 6) copied the descriptions of *P. asellus* and *P. pallar* by Molina under a subtitle “Espèces moins connues”.

1825: Augustin Pyrame de Candolle (p. 396) under a headline “species non satis notae” merely reported the two species with the same brief descriptions by Molina.

1832: George Don (p. 356) in his treatment also had a group of “Species not sufficiently known”. If his description of *P. asellus* is the translation of Molina’s Latin description into English, he added a few words about leaflets (“obliquely-oblong, villous”), peduncles (“racemose, very long”) and flowers (“small, remote”) for *P. pallar*. For both species he added “native of Chili”.

1837: George Bentham (p. 78) expressed doubts about both species mentioned at the very end of his treatment of *Phaseolus* and did not include them in any of his sections.

1841: Ernst Steudel (p. 316 and 317) mentioned the two species named by Molina. Without explanation, he related *P. pallar* with *P. pilosus* H.B.K. [= *Vigna lasiocarpa* (Mart. ex Benth.) Verdc.].

1846: Claudio Gay considered both *P. asellus* and *P. pallar* as belonging to *P. multiflorus* Willd. (= *P. coccineus* L., Piper 1926: 685). His brief descriptions of seeds (p. 207) would indicate a reference to cultivated materials. It is noteworthy that for *P. pallar* he also used the additional data given by Don but in Spanish. When he dealt with pulses and other food plants (1865, p. 103), Gay used the vernacular name ‘pallar’ for a bean grown in the northern provinces of Chile by the Amerindians before the conquest.

1847: David Dietrich (p. 1196) under “Species quoad sectiones dubiae” merely reproduced in Latin the descriptions given by Don.

1863: Rudolph Philippi (p. 703) considered *P. asellus* as a variety of common bean and *P. pallar* as a distinct species (see below). His reference to *Anales de la Universidad de Chile* 1860 page 654 for additional information is a noninformative dead-end (matters internal to the University of Chile).

1898: Karl Reiche briefly mentioned (p. 208) that *P. pallar* is from Peru (referring to Philippi, 1859) and that *P. vulgaris* coming from South America is known as a cultivated plant (‘poroto’).

1919: Edward Lewis Sturtevant indicated that both species defined by Molina were “cultivated by the natives before the Conquest”. For *P. pallar*, he added that “the beans are half an inch long” (p. 422) (Hedrick 1972).

1923: Emile Hassler (p. 470) just mentioned the two species at the end of his revision of the genus *Phaseolus* for South America.

1926: Charles Vancouver Piper did not include specimens from Chile in his revision of *Phaseolus* and did not mention the two species defined by Molina.

In taxonomic treatments of *Phaseolus lunatus*, Liberty Hyde Bailey (1923, 1940) and Glen van Eseltine (1931) did not include *P. pallar* Molina, nor did Wil-



Figure 1. Seeds of two cultivated forms of Lima bean: the small-seeded types frequent in Mesoamerica (left) and the large-seeded types frequent in Pacific Central South America (right; scale bar in cm). The seed to the left belongs to a landrace named ‘comba’ and grown in ‘Tierra caliente’ of Guerrero, Mexico (G26291 in CIAT genebank, with 100-seed weight of 50g). The seed to the right belongs to a ‘pallar’ grown on the coast of Peru in Ica (G25496, also in CIAT genebank, with 100-seed weight of 159g).

liam Wylie Mackie (1943) and Egbert Westphal (1974). Recently, in his list about Molina’s new taxa, Hugo Gunckel-Luer (2020, p. 88) indicated *Phaseolus lunaris* L. (a typographical error?) for *Phaseolus pallar* Molina; the former is considered as introduced into Chile.

It seems that the vernacular name ‘pallar’ was widely used for a large-seeded cultivated food legume or

pulse (Figure 1) in agricultural areas of the Pacific side of South America, from today central Ecuador down to central Chile (Figure 2). That crop seems to have been grown in the coastal area of Peru for five millennia (Kaplan and Lynch 1999). This name of Quechua origin (Academia 1995) and the range where constantly used seem almost matching with the expansion of the Quechua people and extension of Tawantisyuyu (Inca empire) by the early 1500s (Lumbreras 1974). The vernacular name seems not known north of Quito (CIAT 2022), where various other names are used (Figure 2), nor south of the Coquimbo region in Chile (Philippi 1859). The name *pallar* appeared early in historic documents about Peru (Navarrete 1560); it is also reported by Hipólito Ruiz for the area around Lima in May 1778, while the name Lima bean was used by English-speaking seed merchants in the second half of the 18th century. In this regard, Thomas Jefferson, the third president of the United States, reported the planting of Lima beans on his property in Virginia over many years, for example on April 19, 1777 (Jefferson 1766-1824).

Molina used twice (1782, 1810) the name *pallar* thinking of that cultivated plant (“per i loro semi di un pollice incirca di grandezza”, p. 130), without understanding that his scanty Latin description would better

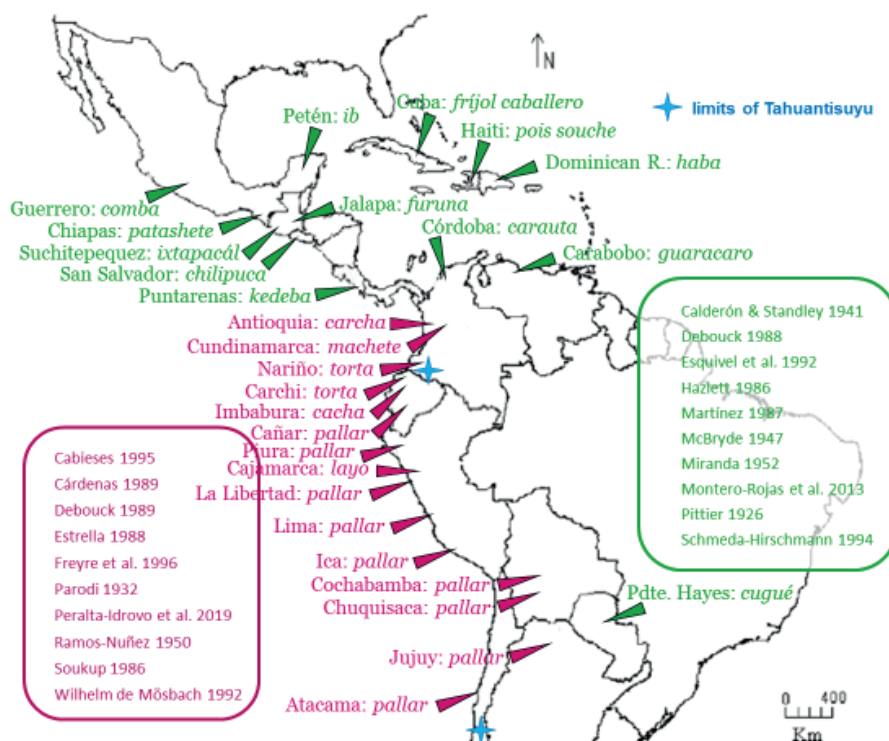


Figure 2. Some folk names given by native peoples to *P. lunatus* in the Neotropics. The names reported in purple refer to the large-seeded Lima beans, while those reported in green refer to the small-seeded Lima beans.

apply to that of a common weed of the legume family. Philippi (1859) realized that the pods of the *pallar* plant described by Molina were completely different from the ones of the plant grown by the native Chilean farmers and named by them '*pallar*'. Accordingly, he remade a description of the species (without indicating a reference specimen nor providing an illustration).

The case of 'specimen 2598'

In 1821, Carlo Giuseppe Bertero collected a legume plant (Figure 3 left) in the surroundings of Soledad, on the left bank (downstream) of the Magdalena River in Colombia. This hamlet, whose approximate coordinates would be 10° 54' lat. N, 74° 46' long. W, elev. 20 masl, is now part of the city of Barranquilla (dep. Atlántico).

Shortly after, the specimen was received by Giovanni Battista Balbis, who passed it to Kurt Polycarp Sprengel, then working at Halle (Laura Guglielmone, personal communication, April 2022). Balbis had the opportunity to affix a label to the specimen, that reads: "Phaseolus pallar, Soledad, 2598". While the specimen was kept in Halle in the late 1820s, it seems that at least one botanist had the opportunity to see it: George Don and maybe also David Dietrich, because both added data to the original description by Molina.

The Herbarium of K. Sprengel was received at the Museum botanicum Berolinense (B) in 1890, and included in the collections of B. In 1929-1933, the types kept at Berlin-Dahlem were photographed by J.F. Macbride (then Staff member of the Field Museum of Natural History of Chicago), thanks to the support of the Rockefeller Foundation (Grimé and Plowman 1987). Fortunately,

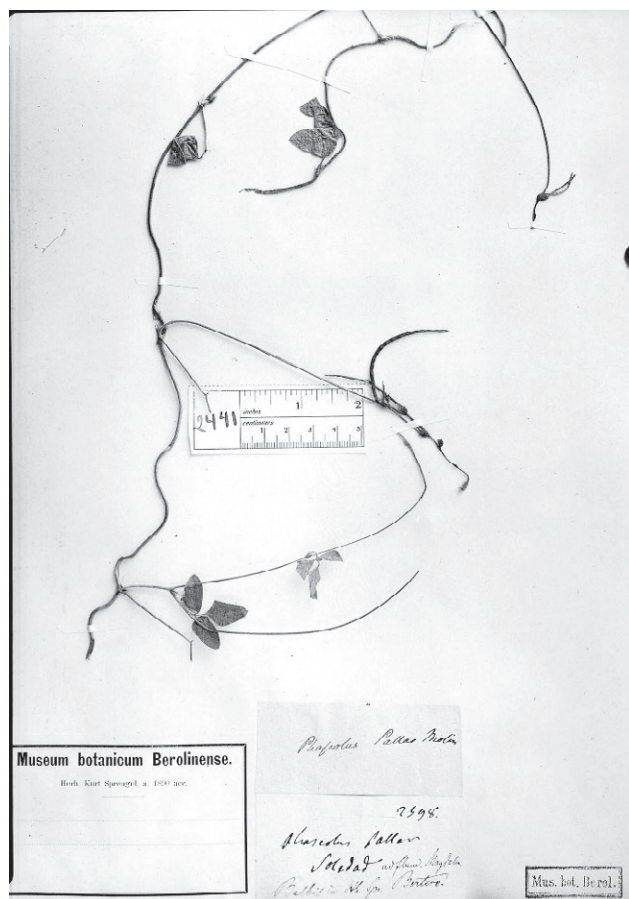


Figure 3. Left: photograph of the specimen 2598 collected by Bertero; that B/N photograph was likely taken by James Francis Macbride in 1929-1933. The lower central label is considered by the authors as the oldest label with the identification in bold face by G.B. Balbis. The upper central label has the identification possibly given by K. Sprengel. The third label in the lower left corner would have been affixed upon receipt at the Herbarium of Berlin (confirmed by the stamp in the lower right corner). Right: a young plant of *Macroptilium lathyroides* growing on a dyke at flowering (wings brick red) and early pod setting stages, a paddy field in the back (photograph taken in Palmira, Colombia, on September 24, 2022).

someone at B considering the specimen '2598' as a possible lectotype of *Phaseolus pallar* Molina (although dates do not match with the protologue) included it in the set of specimens to be photographed. By the way, the types of *Phaseolus augusti* Harms and of *Phaseolus pachyrrhizoides* Harms were included too, and these B/N photographs (numbered as 2434 and 2440, respectively) were key to solve another puzzle (Debouck 2021). The specimen '2598' was numbered '2441' in that series of B/N photographs and is currently available in the project 'Berlin negatives' at the Field website (https://collections-botany.fieldmuseum.org/list?search_fulltext=Phaseolus+pallar&family=&genus=&species=&country=&collector=&ss_ObjEcode=&type_status=&scientific_name=&ss_DarCollectorNumber=&catalog_number=&state_province=&ss_ColCollectionEventRefColSiteRef_PolPD1=&ss_ColCollectionEventRefColSiteRef_PolPD3=&collection_date=&project=&ss_EcoHabitatMicrohabitat=&ss_EcoSubstrate=&photo_neg_number=&ss_EcbUse=&sm_DesObjectName=&sort_by=solr_document&sort_order=ASC&items_per_page=25&f%5B0%5D=ss_CatCatalogSubset%3A%22Seed+Plants%22) and kindly reproduced here with permission. The specimen '2598' can be identified as *Macroptilium lathyroides* (L.) Urban (Figure 3 right). This taxon has been reported for the flora of Paraguay (Hassler 1923), many states of Brazil (Barbosa-Ferevereiro 1986-1987) and the northern provinces of Argentina (Drewes 1999); according to the later author, it is also present in Bolivia and Chile. This plant seems to have benefited directly or indirectly from humans because it has also been reported from Australia, Hawaii, Java, Thailand, Vietnam, the Philippines (Maréchal et al. 1978), and the southeastern USA (Isely 1990). Perhaps this current huge distribution may indicate that this plant was present in the area of central Chile visited by Molina (about 30-40° latitude south: Figure 4 in Charrier and Hervé 2011, p. 452) in the 1780s, thus explaining his Latin description.

DISCUSSION

From the afore-mentioned compilation and elements available in the two editions of "Saggio" (1782 p. 130 and 1810 p. 293), two points seem worth discussing, perhaps along the intention by Molina and next the consequences of his scanty description. The first point relates to a legume cultivated for its seeds ("i loro semi di un pollice incirca di grandezza", 1782 p. 130), and grown from Santiago northwards into Chile and Peru (Philippi 1859; Gay 1865). Molina usefully fixed the prevailing ver-

nacular name 'pallar' with a date and a location on the Pacific side of South America (Figure 2). Incidentally, by doing so, Molina anticipated the linguistic argument developed by Alphonse de Candolle (1883, p. 15 and following) when searching about the origin of cultivated plants. In this part of "Saggio" Molina clearly referred to the crop, likely native, but did not realize that this crop was already widely distributed into the tropics, possibly since and thanks to the crossing of the Strait of Magellan since 1520 (twelve years before the fall of the Inca empire; Moseley 1993). Charles de l'Écluse (1601) reported one variety from Ethiopia, while Johannes Bauhin and John Henry Cherlero (1651) also mentioned large-seeded types from Africa. Linnaeus (1737, p. 359) did the description of *P. inamoenus* (the epithet could be translated as 'continuously beautiful', namely because of its seeds? To note, better described in 1737 than in *Species Plantarum* of 1753 and its second edition of 1763!) on a plant grown in the Clifford Garden at Hartekamp, Holland, from seeds obtained from Africa. In this regard, Henri Perrier de la Bathie (1923) reported two groups of Lima beans present in Madagascar: one with small and toxic seeds, and one with large white seeds known as *kabaro* or *Pois du Cap* and present as early as 1620. This bean went at least as far as the Tonkin where it was described as *Phaseolus tunkinensis* Lour. (de Loureiro 1790). By 1810, Molina had recovered all his notes (Charrier and Hervé 2011) and could have anticipated that it was not a minor crop, and thus already named in the scientific literature.

The second point relates to the Latin description provided by Molina (the same in the two versions of "Saggio"), namely in relation to the pod that clearly cannot contain seeds of one inch each (and with 2-3 seeds per pod). It seems that Rudolph Philippi was the first in noting this impossibility and thus changed and completed the description of *P. pallar* (1859, p. 363) as a crop. But there was no need to redefine *P. pallar*. The evidence about its spread and adoption in warm regions had further increased since the "Saggio": at that time this pulse was grown in India (as *Phaseolus maximus* Roxb.; Roxburgh 1832), Jamaica (as *Phaseolus limensis* Macfad.; Macfadyen 1837), the Philippines (as *Phaseolus vexillatus* Blanco; Blanco 1837), and in warm parts of the United States: a cultivar named Large Lima was reported there in 1822 (Jarvis 1908). Again in 1859 the previous records of names and places were poorly surveyed. As aptly explained by van Eseltine (1931) and Mackie (1943), these species names – and others – traced back to *Phaseolus inamoenus* L., the large-seeded form of *P. lunatus* L.

That said, coming back to the original Latin description by Molina and on that basis, Balbis did in the 1820s

an identification not in contradiction with the elements provided by the abbot when he identified the specimen 2598 of Bertero as *P. pallar*, although he could have referred to *P. lathyroides* L. instead. The later taxon was described in 1763 and reported from Jamaica (Sloane 1696, p. 71; Linnaeus 1763, p. 1018).

The two parallel botanical stories, complicated by poor descriptions, lack of types or illustrations, absence of reference to specimens and incomplete studies of previous works, apparently ended up on the one hand in 1910 when Julien Costantin and Désiré Bois considered *P. pallar* as belonging to *P. lunatus*. Their conclusion is based on morphological characters of flowers and seeds, using Peruvian materials (reported to them as *pallares*, plural of *pallar*), including archaeological seeds, but with no reference to ‘specimen 2598’. On the other hand, when reassessing the reports by archaeologists such as Alphonse-Trémeau de Rochebrune (1879) and Ludwig Wittmack (1879), Hermann Harms (1922), again without referring to ‘specimen 2598’, wisely concluded: “But it is not sure at all of which species spoke Molina. It is doubtful that he really understood *Ph. Pallar* as *lunatus* because the description of the legumes does not fit. The name *Ph. Pallar* Molina has to be let away because it cannot be totally identified”.

From a nomenclatural perspective, the epithet ‘pallar’ based on the Quechuan vernacular name for the cultivated pulse was effectively published as evidenced by the numerous works afore mentioned referring to it (article 29.1 of the Shenzhen Code; Turland et al. 2018). Apparently, Molina meant the crop but made a scanty Latin description incompatible with the pods of that crop, thus raising confusion (and with no illustration nor any reference specimen to help with the taxonomic delimitation). Specimen 2598 exemplified that confusion as two botanists, G.B. Balbis and K. Sprengel, considered it as *P. pallar*, while it was more accurately attributed to *P. lathyroides* (now within *Macroptilium* after the work of Ignatz Urban of 1928). The situation of having a single name referring to two different botanical entities within the same genus (a situation that must be avoided: Article 34, de Candolle 1867, p. 22) casts doubts whether *P. pallar* was validly published. The designation ‘pallar’ has thus no status under the Code (article 12.1 of the Shenzhen Code), and cannot have a type (Turland 2013, p. 47). While one can regret the missed recognition to the Amerindians for that long and wide impacting domestication, the taxonomic use of *P. pallar* was in addition untenable because of the overlooking of so many previous records (Principle 4 of the Code).

Botanists were of different opinion about the small and the large-seeded Lima beans (as cultivated; Figure

1), some arguing about two different species (e.g. Bailey 1923, 1940), while others considered them as one species (Piper 1926; van Eseltine 1931; Mackie 1943; Maréchal et al. 1978; Freytag and Debouck 2002). The finding of wild populations in the Andes of southwestern Ecuador and northwestern Peru (Debouck et al. 1987) opened another perspective on the independent domestication of two gene pools (Motta-Aldana et al. 2010). While there are some differences between the wild forms in existence for one million years (Delgado-Salinas et al. 2006) in contrast to the cultivated forms in existence possibly for several thousands of years (Kaplan and Lynch 1999), these differences do not exceed those found between gene pools of wild forms within the common bean (Caicedo et al. 1999; Serrano-Serrano et al. 2010). Further, in spite of significant progress over the last two decades, it might be premature to inflate the naming of Lima bean variants, since another gene pool A2 has been found in wild forms in the Colombian Andes (Toro-Chica et al. 1993; Garcia et al. 2021). Given this, the best solution for nomenclatural stability at this time might still be in using *P. lunatus*.

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Table of contents

Articles

**Brett Jestrow, Michael Hass, William Cinea,
Alan R. Franck, Joel C. Timyan, M. Patrick
Griffith, Javier Francisco-Ortega**

The Critically Endangered Haitian endemic palm
Attalea crassispata (Arecaceae) and its living
collections in Fairchild Tropical Botanic Garden:
Perspectives from conservation surveys and DNA
microsatellite (SSR) data

3

Wong Sin Yeng, Peter C. Boyce

Homalomeneae (Araceae) of Borneo XXVIII –
Homalomena bengohensis [Chamaecladon Clade]
a new species endemic to the Bengoh Range,
Sarawak

15

**Marjorie D. delos Angeles, Danilo N. Tandang,
Maria Melanie P. Medecilo-Guiang, Inocencio
E. Buot, Jr., Harald Schneider, Marcos A.
Caraballo-Ortiz**

A new diminutive species of *Schismatoglottis*
(Araceae) from Samar Island, Philippines

21

Wong Sin Yeng, Peter C. Boyce

Studies on Homalomeneae (Araceae) of Borneo
XXIX — *Homalomena latisinus*, a new species for
the Borneensis Complex from Brunei

29

Wong Sin Yeng, Peter C. Boyce

Homalomeneae (Araceae) of Borneo XXX —
Homalomena atlas [Hanneae Complex] a new
species from the Rejang Basin, Sarawak

33

Daniel G. Debouck, Chiara Nepi

Notes about *Phaseolus pallar* Molina
(Leguminosae-Papilionoideae-Phaseoleae): alas
but at best a synonym!

39