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Phylogenomics of the Palm Tribe Lepidocaryeae (Calamoideae: Arecaceae) and Description of a New Species of *Mauritiella*

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Abstract—The palm tribe Lepidocaryeae (Arecaceae) comprises seven genera and 51 currently accepted species that are distributed in lowland tropical forests and savannas across Africa and the Americas. Subtribal relationships within Lepidocaryeae have been a persistent challenge, limiting our understanding of its systematics, morphology, and biogeography. Several aspects make the tribe an ideal system to study plant evolution and diversity: it is well-represented in the fossil record as a prolific pollen producer, its continental diversity contradicts common biodiversity patterns of lower species richness in Africa in comparison to South America, and it contains one of the most abundant Amazonian tree species, *Mauritia flexuosa*. Here, we investigated the systematics of the tribe by sampling 122 individuals representing 42 species (82% of the tribe), using target sequence capture. We recovered nearly 10,000 single nucleotide polymorphisms from nuclear and plastid DNA across 146 target sequences to separately infer a phylogenomic tree. Our results strongly support inter-generic and inter-specific relationships, where a majority of nodes were resolved with over 90% bootstrap support. We also identify strong phylogenetic support for the recognition of a new species from central and south Amazonia, ***Mauritiella disticha***. The distichous phyllotaxy is diagnostic of the species within the genus. Rare and currently only known from the middle-lower Madeira River basin in the state of Amazonas, Brazil, *M. disticha* is restricted to open vegetation and forest edges growing in white sand habitats with saturated or well-drained soils. Our preliminary red list assessment suggests its threatened status to be vulnerable (VU). We use our phylogenomic inference to define and contextualize systematic relationships in the tribe, and present a formal species description.

Keywords—Africa, Amazonia, Palmae, phylogenomics

Resumo—As palmeiras Lepidocaryeae compreendem sete gêneros e 51 espécies aceitas actualmente, distribuídas em florestas tropicais de baixa altitude e savanas da África e América do Sul. As relações subtribais têm sido um problema taxonômico persistente no grupo, limitando sua compreensão sistemática, morfológica e biogeográfica. Vários fatores fazem da tribo Lepidocaryeae um sistema ideal para estudos de evolução e diversidade vegetal: a tribo é bem representada no registro fóssil como produtora prolífica de pólen, ela contradiz os padrões de biodiversidade comuns entre a África e a América do Sul e contém uma das espécies amazônicas mais abundantes, *Mauritia flexuosa*. Aqui, investigamos a sistemática da tribo amostrando 122 indivíduos representando 42 espécies (86% da tribo), usando o método de captura de sequência alvo (target sequence capture). Produzimos aproximadamente 10.000 polimorfismos de nucleotídeo único en 146 genes para inferir árvores filogenômicas. Nossos resultados suportam fortemente as relações intergenéricas e interespecíficas, nas quais a maioria dos nós foi resolvida com mais de 90% de suporte. Também identificamos um forte suporte filogenético para o reconhecimento de uma nova espécie da Amazônia central e sul, *Mauritiella disticha*. A espécie apresenta filotaxia dística, um caráter diagnóstico da espécie. Atualmente conhecida apenas para a bacia do médio-baixo rio Madeira, no estado do Amazonas, Brasil, *M. disticha* é restrita à vegetação aberta e bordas de florestas baixas em habitats de areia branca com solos saturados ou bem drenados. Nossa avaliação preliminar indica que esta espécie é vulnerável (VU) em relação ao nível de ameaça. Usamos nossa inferência filogenômica para definir e contextualizar as relações sistemáticas na tribo e apresentamos a descrição formal da nova espécie.

Palavras-chave—África, Amazônia, Palmae, filogenômica

Palms are tropical ecosystem indicators. As silica-rich plants with high pollen production, palms have a well-preserved fossil record, indicating their presence in tropical ecosystems since at least 100 million years ago (Dransfield et al. 2008). Since the first occurrence of the analogues of modern tropical forest in the Americas ca. 58 Ma, palms have been present (Wing et al. 2009). Palms are also abundant elements in tropical forests (Muscarella et al. 2020). For example, eight of the top twenty most common tree species in Amazonia are palms (Ter Steege et al. 2013). The ecological representation of palms in tropical forests, combined with a comprehensive understanding of taxonomy, distribution, phylogeny, and natural history, make them a model plant family for understanding the formation and change through time of the tropical forest biome.

The Lepidocaryeae are of special relevance for the American and African tropical forests since they comprise the majority of the palm species on mainland Africa (Stauffer et al. 2017; Cosiaux et al. 2018) and harbor one of the most widespread and abundant palms in South America, *Mauritia flexuosa* (Ter Steege et al. 2013; Melo et al. 2018). In South America, the subtribe Mauritiinae encompasses seven species, primarily distributed in lowland (flooded and non-flooded) forests and open, white sand areas in Amazonia. Co-distributed with some of the Mauritiinae species, *Raphia taedigera* is the only representative of the Raphiinae subtribe in South America (Dransfield et al. 2008; Mogue Kamga et al. 2020). The remaining 42 species of Raphiinae are distributed in Africa (Sunderland 2012; Mogue Kamga et al. 2020), with 21 species in *Raphia* and the rest in the Ancistrophyllinae subtribe (which includes the three genera *Eremospatha, Laccosperma*, and *Oncocalamus*). With this, the Lepidocaryeae present an interesting anomaly to the common biogeographic pattern of higher species richness in tropical America (the Neotropics) in comparison to Africa (Richards 1973; Couvreur 2015; Zizka 2019). Indeed, there are many more species in Africa (42 species) than in the Neotropics (nine species including *R. taedigera* and *M. disticha*). However, the study of the evolutionary drivers of this pattern, the evolutionary success of *Mauritia flexuosa* (Melo et al. 2020), and the use of Lepidocaryeae as model for rainforest evolution have been hampered by the lack of a robust and well-sampled molecular phylogeny.

A molecular phylogeny of the Lepidocaryeae is also fundamental to defining taxonomic relationships. First, the relationships of the subtribes that comprise Lepidocaryeae have been a persistent taxonomic challenge. From morphological data, Baker et al. (1999) resolved the Ancistrophyllinae and Raphiinae as more closely related than either are to the Mauritiinae, a relationship strongly supported by phylogenomic data of Kuhnhäuser et al. (2021). However, molecular data also supported Mauritiinae and Raphiinae as sister clades, but with low statistical support (Baker et al. 2000b; Asmussen et al. 2006; Helmstetter et al. 2020). Based on combined morphological and molecular data, Baker et al. (2000a) resolved Mauritiinae and Raphiinae as sister subtribes, who together are sister to Ancistrophyllinae, but with poor statistical support. In contrast, Faye et al. (2016) resolved Ancistrophyllinae as sister to Mauritiinae as strongly supported (>90% branch support), albeit with poor sampling within the subfamily. An additional issue with these unclear systematic relationships is the inconsistent placement of *Eugeissona* (the sole genus of Eugeissoneae) inside Lepidocaryeae and even as data representation for taxa and genes has increased, it has been resolved as sister to Raphiinae, which together have been resolved as sister to Mauritiinae (Baker et al. 2009). Recently, Eugeissoneae has been placed with strong support as sister to Calameae, and Lepidocaryeae as sister to both (Kuhnhäuser et al. 2021).

Here, we present a target sequence capture dataset of all seven genera and 42 of the 51 species of Lepidocaryeae and determine systematic relationships in the tribe. We use these data together with new morphological information to formally describe *Mauritiella disticha*, from the Madeira River basin in the state of Amazonas, Brazil. These data contribute to increasingly available target sequence capture and highlight their power to elucidate relationships across taxonomic scales. Because taxonomy is fundamental to conservation, we stress the importance of field and laboratory work to continue our cataloging of biodiversity to identify areas and lineages of societal and scientific importance and greatest need of protection.

Materials and Methods

Taxon Sampling—We used the species nomenclature of the Royal Botanic Gardens, Kew Checklist of Selected Plant Families for Arecaceae (last retrieved on Feb 25, 2020; Govaerts et al. 2020). We obtained leaf tissue from silica dried samples collected in the field (65 samples) and herbarium specimens from the Kew herbarium (K, 22 samples) and the Instituto Nacional de Pesquisas da Amazônia herbarium (INPA, 7 samples), and obtained three samples from freshly collected leaf material at Montgomery Botanical Center (*Calamus australis*, *Raphia australis*, and *Raphia regalis*). Two species from Calaminae (*C. australis* and *C. concinnus*), a subtribe closely related to Lepidocaryeae, were sampled as outgroups. Voucher information is given in Supplementary Appendix S1, available from Dryad (Torres Jiménez et al. 2021), and sequence data are available from the PRJNA705684 BioProject on NCBI. Additional phylogenies with support annotations, congruence information, and maps (Appendices S2–S7) are available in Torres Jiménez et al. (2021).

We used 10–25 mg tissue to extract DNA using a modified CTAB protocol (see Appendix S3; Doyle and Doyle 1987; Štorchová et al. 2000). Extracts were cleaned using AMPure XP magnetic beads (Beckman Coulter, High Wycombe, UK). DNA quantity and quality were assessed with a 1% agarose gel. Additional DNA quantification and fragment size were quantified using a screentape assay (TapeStation, Agilent Technologies, UK). Additional sequences from *Raphia* species from Helmstetter et al. (2020) were mined from the Sequence Read Archive database (SRA) using the fastq-dump tool from the SRA toolkit v. 2.9.4. (SRA Toolkit Development Team http://ncbi.github.io/sra-tools/; Accession numbers SRX8011613 to SRX8011674).

Target Sequence Capture—DNA was prepared for target sequence capture using a NEBNext Ultra II library kit (New England BioLabs Ltd, Hitchin, UK). Extracts with DNA fragment sizes larger than 1000 bp were sheared using a Covaris ME220 focused ultrasonicator (Covaris Ltd, Brighton, UK) to attain fragments of 300–400 bp. Libraries were prepared with 200 ng input DNA, size selection using magnetic beads, dual indexing with NEBNext Multiplex Oligos for Illumina (New England BioLabs Ltd, Hitchin, UK), and 10–12 PCR cycles. DNA concentration of prepared libraries was measured using a Quantus fluorometer and distribution of DNA fragment lengths were assessed using a TapeStation. Equal amounts of DNA from 16 to 38 indexed libraries of similar DNA fragment length distribution were pooled to a total of 300–1500 ng DNA.

The pooled DNA was hybridized for 24 h at 65°C to the Heyduk (Heyduk et al. 2016) or PhyloPalm probes (Loiseau et al. 2019) using a myBaits hybridization capture kit (Arbor Biosciences, Ann Arbor, Michigan, USA). The 971 PhyloPalm targets is a broader set that includes the 176 targets from the Heyduk set. The hybridized DNA was amplified using 10–12 PCR cycles. Sequencing was conducted in different rounds either at Macrogen Inc. on an Illumina HiSeq X Ten Platform (Seoul, Korea), or at RapidGenomics (Miami, USA) or SciLifeLab (Uppsala, Sweden) on an Illumina HiSeq 2500 sequencing platform (Illumina, San Diego, California, USA), generating 150 bp paired-end reads.

Phylogenomics—Reads were trimmed and adapters were removed from paired reads using Trimmomatic with a sliding window option

(Bolger et al. 2014), with a minimum sequence length of 25, a window size of 4, and minimum quality of 20. The quality of the reads before and after trimming was visually assessed using FastQC (Andrews 2010). Before marking duplicates, reads were sorted and the coordinates of paired reads fixed when missing using samtools v. 1.9 sort and fixmate utilities, respectively (Li et al. 2009). Duplicate reads were marked using samtools v. 1.9 markup (Li et al. 2009). To extract the SNPs from the sequences, variant calling was performed using GATK v. 3.5 tools following GATK's best practices (DePristo et al. 2011). We used the exon sequences targeted by Heyduk et al. (2016) as the reference for variant calling in order to standardize the regions called across all samples regardless of which bait set they were hybridized to during sequence hybridization (see Target Sequence Capture section above). UnifiedGenotyper was used for the initial variant calling per sample. Indels were called and realigned with SelectVariants, RealignerTargetCreator, and IndelRealigner. In order to recalibrate the base quality scores for all samples, two recalibration rounds were run using BaseRecalibrator. A final variant call for all samples was performed on the realigned and calibrated bam files with UnifiedGenotyper. SNPs with minimum quality 30, present in 99% of the samples, and minimum allele count of one, were filtered from the final VCF using vcftools v. 0.1.16 (Danecek et al. 2011). Filtered On-target SNPs were re-aligned with MUSCLE v. 3.8 (Edgar 2004) and a phylogeny was estimated using IQ-TREE II v. 2.1.2 (Minh et al. 2020) with a GTR substitution model and ascertainment bias correction (+ASC), combined with an ultrafast bootstrap (UFBoot) with 1000 replicates (Hoang et al. 2018).

To estimate a species tree phylogeny from individual gene trees, trimmed and marked reads were processed with the SECAPR pipeline and default values (Andermann et al. 2018). De novo contig assembly was done with SPAdes (Bankevich et al. 2012). For the target extraction steps, we used the longest exon sequence for every gene targeted by Heyduk et al. (2016). Extracted target sequences were individually aligned with MUSCLE v. 3.8 (Edgar 2004) and the gene tree estimated with IQ-TREE II v. 2.1.2 (Minh et al. 2020), automatized model selection (Kalyaanamoorthy et al. 2017), and UFBoot with 1000 replicates (Hoang et al. 2018). A summary species tree and the proportion of gene congruence for each branch were estimated using ASTRAL III (Zhang et al. 2018). We used baltic (https://github.com/evogytis/baltic) to visualize the phylogenies.

Molecular Species Identification—PCAngsd (Meisner and Albrechtsen 2018) was used to calculate a covariance matrix between *Mauritiella* species. A principal component analysis of the covariances (PCA) was fit with the Python library sklearn (Pedregosa et al. 2011) and results were plotted with custom Python scripts. Per site Weir and Cockerham's F_{ST} between *M. disticha* and *M. armata* were calculated with vcftools from biallelic sites only (Danecek et al. 2011). F_{ST} values were estimated only between *M. disticha* and *M. armata* because only one individual was sampled from the other *Mauritiella* species (*M. macroclada* and *M. aculeata*). Negative F_{ST} values were considered as zero for the calculations of the mean per-site F_{ST}.

Results

DNA Sequencing—After realigning, recalibrating and calling variants, we retained 10,568 on-target polymorphic SNPs of the 51,051 possible SNPs for the phylogenetic reconstruction (minimum two and maximum four alleles). Sequencing depth across all samples had a mean = 89.2 and SD = 78.1 (Appendix S2). Retained SNPs had a mean depth of 89.3 and a standard deviation of 22.8. Within the nine *Mauritiella* samples and after applying the same filters to recover SNPs, we retained 26,337 biallelic SNPs. Retained SNPs had a mean depth of 74.5 and a standard deviation of 59.4.

Phylogenomic Inference—The phylogeny inferred from the 10,568 retained SNPs from 122 samples had a strong ultrafast bootstrap (UFBoot) support for all branches except for the branch between *Laccosperma* and *Eremospatha* (82%) and some branches within *Raphia* (64–97%, Fig. 1). Of all branches, 67% had an UFBoot support higher than 98%, 11% between 90–98, and 22% had support lower than 90. Mauritiinae was recovered as sister of Ancistrophyllinae + Raphiniiae with UFBoot of 100% (Appendix S1). Within Mauritiinae, all samples of *Mauritiella disticha* group together in a single clade with the highest possible support (with lowest zero and highest 100).

The ASTRAL species phylogeny inferred from 154 exon sequences extracted with SECAPR shows local posterior probabilities (lpp) higher than 0.9 in most branches. Of all branches, 45.8% had lpp > 0.9 and 44.2% have lpp below 0.7 (Appendix S2). The species tree showed a similar topology at generic and subtribal levels to the phylogeny inferred with SNPs. Only 31 genes supported the branch Mauritiinae + Ancistrophyllinae (Node 104 in Appendix S3) whereas the two alternative topologies at that branch, Mauritiinae + Raphiniiae and Mauritiinae + (Ancistrophyllinae + Raphiniiae) were supported by 25 and 35 genes, respectively. The second alternative topology was congruent with the topology recovered from the SNP data. Within Ancistrophyllinae and unlike the SNP phylogeny, *Eremospatha* was recovered as sister to *Oncocalamus* + *Laccosperma* and the three alternative topologies at this branch were supported by similar numbers of genes (between 37 and 42 genes). Within *Mauritiella, M. disticha* was recovered as a single clade strongly supported by the exon data (lpp = 1)

We examined the position of *M. disticha* samples within *Mauritiella* using SNP data to assess its identity as a species previously unknown to science. Within the nine *Mauritiella* samples, 7005 variable SNPs were retained and used to estimate the covariance matrix and its PCA. The first PCA axis explains 74.2% of the variation between *M. disticha* and other *Mauritiella* species whereas the second PCA axis explains 7.4% (Fig. 2). The genome-wide weighted Weir and Cockerham's F_{ST} was estimated as 0.23 using 26,337 biallelic SNPs retained between *M. disticha* and *M. armata* (Appendix S4).

Discussion

In order to determine evolutionary relationships of tribe Lepidocaryeae, we inferred a phylogenomic tree using SNPs and exon sequence data of 82% of the species in the tribe. Based on our results, we determined inter- and intra-generic relationships at an unprecedented level due to dense sampling within most species. Most systematic relationships resolved are supported in both analyses but also revealed topological conflicts at short branches where diversification likely occurred rapidly. Our finding on a previously unrecognized conspicuous species of *Mauritiella*, in one of the taxonomically best studied plant families, highlights the high diversity in Amazonia. This diversity is yet to be included in biodiversity analyses, but faces an increasingly high risk of loss to habit change (Hansen et al. 2013; Barlow et al. 2019; Stropp et al. 2020).

Mauritiinae—*Lepidocaryum* was unequivocally supported as monophyletic and sister to the clade of *Mauritia* and *Mauritiella*, both of which were also unequivocally supported as monophyletic genera (Fig. 1; Appendices S1–S2). These intergeneric relationships have long been recognized and have consistently been well-supported in phylogenetic studies (Baker et al. 2000a, 2000b, 2009; Faye et al. 2016). We suggest this monophyletic species represents an interesting future study system in phylogeography, considering its high morphological diversity (Henderson 1995; Henderson et al. 1995; Galeano and Bernal 2010), and its fundamental importance to Amazonian people through its uses for roof thatching and tools related to fishing and hunting (Navarro et al. 2011).

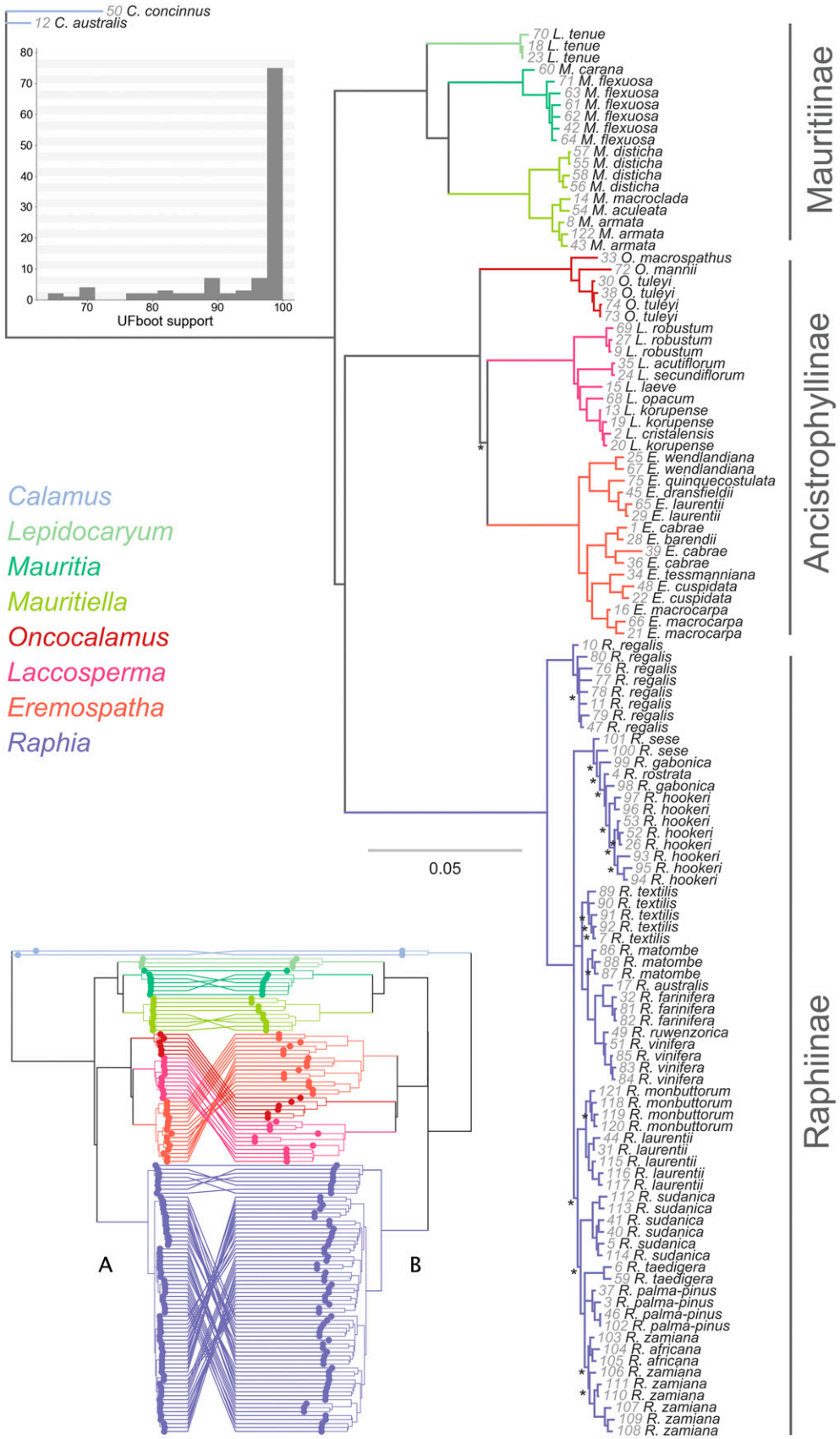

FIG. 1. Maximum likelihood phylogeny highlighting the relationships between genera within Lepidocaryeae and *Mauritiella*. Tips on the tree represent samples, and a fully annotated phylogeny is available in Appendix S1 (Torres Jiménez et al. 2021). Branches with UFboot branch support values < 70% are collapsed, UFboot between 70% and 90% are marked with an asterisk. UFboot > 90% are not shown, except in the histogram. The histogram in the upper part of the figure shows the distribution of UFBoot values across all branches throughout the phylogeny. The tanglegram in the lower part of the figure compares the topological incongruence between the phylogeny from SNP data (A) and the ASTRAL species tree from gene sequences (B). The numbers before the species are unique identifiers across all figures.

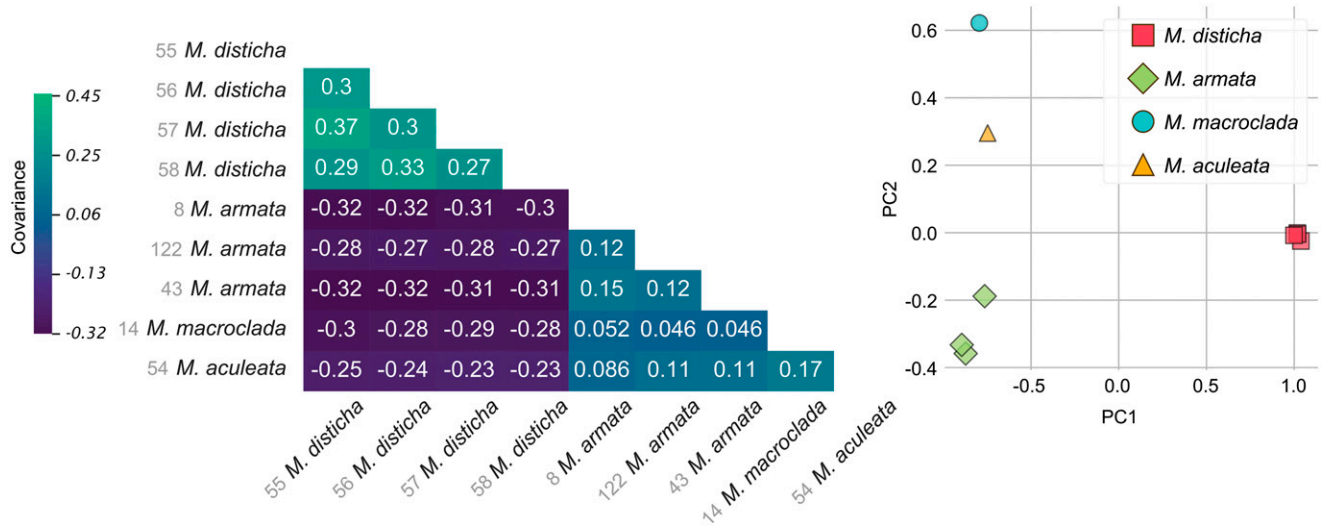

FIG. 2. Left: Covariance matrix estimated from 7005 variable SNPs between sequences within *Mauritiella*. The color bar indicates the population covariance. Right: Principal Component Analysis from the covariance matrix showing the genetic distances between *Mauritiella* species based on 7005 variable SNPs. Explained variation per principal component: PC1 explains 74.2% of the variance and PC2 explains 7.41% of the remaining variance. The numbers before the species are unique identifiers across all figures.

Mauritia flexuosa was resolved as sister to the more narrowly distributed species, *M. carana*. The success of *M. flexuosa* is attributed to its highly structured genetic diversity (Melo et al. 2018) and persistence through climate change and genomic adaptation to environmental stress (Melo et al. 2020). Sampling of *Mauritiella pumila* and multiple individuals for all species is essential for complete understanding of the genus, especially since *M. armata* was not resolved as monophyletic in the ASTRAL tree (Appendices S2, S3). Here, we also identified a formally undescribed species in the genus, *M. disticha*. The species was previously mentioned in the book of Brazilian palms (Lorenzi et al. 2010) but not described, and is treated here. Both sources of data (SNPs and gene sequences) strongly support the branch grouping all *M. disticha* samples with minimal topological incongruence, only observed in a short branch within the species possibly explained by incomplete lineage sorting (see N62 in Appendix S3).

Ancistrophyllinae—Consistent with most previous works (Baker et al. 2000a, 2009; Faye et al. 2016), the inter-generic relationships from the SNP data of the subtribe Ancistrophyllinae were well-supported with *Oncocalamus* as the sister to *Eremospatha* and *Laccosperma* (82% UFboot support; Fig. 1; Appendix S1), all three of which were unequivocally supported as monophyletic groups. These relationships are further supported by floral morphology, yet contradicted by life history states within Lepidocaryeae, as *Laccosperma* species are hapaxanthic and die after flowering, whereas both *Eremospatha* and *Oncocalamus* are pleonanthic (continuously flowering; Sunderland 2012). However, our exon data recovered *Eremospatha* as sister to *Oncocalamus* and *Laccosperma* (node 102, Appendix S3). This topology was also resolved by Kuhnhäuser et al. (2021). The presence of sequence gaps on the exon alignments, the exclusion of introns and off-target regions during variant calling, and incomplete lineage sorting could explain the topological incongruence between exon and SNP data. On one hand, the SNPs used to infer the IQ-TREE phylogeny are sites present in 99% of our samples. On the other hand, ASTRAL accounts for incomplete lineage sorting and can accommodate gene-topology incongruence better (Zhang et al. 2018). A closer examination of the topology at this node is needed to assess the effect of missing data and gene-tree congruence in the species tree under a multispecies coalescent model.

Within *Oncocalamus*, we resolved *O. macrospathus* as sister to *O. mannii* and *O. tuleyii* with unequivocal support (Fig. 2; Appendix S1), in contrast to Faye et al. (2016) which identified *O. macrospathus* and *O. mannii* as sister species, albeit with low support. Without samples of *O. djodu* and *O. wrightianus* it is impossible to interpret interspecific relationships further, but Sunderland (2012) points to a third potential relationship defined by shared morphological traits in *O. macrospathus* and *O. tuleyii* that are different from *O. mannii*, including the length of the leaf sheaths, the number of leaflets on each side of the rachis, and the nature of the seed surface.

We resolved two main clades in *Eremospatha* (Fig. 1; Appendices S1–S2), neither of which are consistent with results from Faye et al. (2016), some of which is attributed to differential sampling. We did not reconstruct the sister relationship between *E. cabrae* and *E. dransfieldii*, identified in previous works (Faye et al. 2014, 2016). Sunderland (2012) pointed to strong plasticity in leaf form, which has caused taxonomic confusion in the genus. Here, we sampled nine of the 11 species recognized, five of which are sampled with more than one individual, allowing for robust inference of species monophyly. *Eremospatha cuspidata*, *E. laurentii*, *E. macrocarpa*, and *E. wendlandiana* all were unequivocally supported as reciprocally monophyletic species. The three *Eremospatha cabrae* individuals were not monophyletic and *E. barendii* was jointly resolved in the clade, likely due to *E. barendii*'s low mean sequencing depth (Appendix S2). *Eremospatha barendii*, *E. dransfieldii*, *E. quinquecostulata*, and *E. tessmanniana* were represented by single individuals in our work and further understanding of genomic and morphological variation in these species is required to define relationships.

With complete sampling in the genus *Laccosperma*, we corroborated relationships found in Faye et al. (2016), where *Laccosperma acutiflorum*, *L. robustum*, and *L. secundiflorum* were closely related (Fig. 1; Appendices S1–S2). Those authors

resolved a non-monophyletic *L. secundiflorum,* but we only sampled a single individual. Sunderland (2012) suggests that the name *L. secundiflorum* has been too widely applied to three distinct species. Our results reconstructed *L. korupensis* as non-monophyletic, with *L. cristalensis* being nested within our three samples with unequivocal support. Couvreur and Niangadouma (2016) recently described *L. cristalensis* as resembling *L. korupensis* because of a lack of acanthophylls on the cirrus and sigmoid pinnae, yet is distinct in its fewer pinnae that are sigmoid in shape and lack spines on the margins, as well as in their short, truncated ocrea. These species should be further studied in detail to assure their taxonomic validity.

Raphiinae—The subtribe is composed of a single genus, *Raphia*, which has 21 species and is the most diverse in Africa (Stauffer et al. 2014; Helmstetter et al. 2020; Mogue Kamga et al. 2020). Almost all species are found in tropical Africa, with one species reaching Madagascar (*R. farinifera*) and another endemic in Central and South America (*R. taedigera*; Dransfield et al. 2008). In the last revision of the genus, Otedoh (1982) recognized five sections based on inflorescence structure. Some of these sections were, however, not recovered as monophyletic clades in the phylogenetic inference of the genus by Helmstetter et al. (2020) based on molecular data that were incorporated here. Our study, based on a larger sampling for the tribe, recovered similar, but not identical relationships within *Raphia*. First, the delimitation of the five sections as proposed by Helmstetter et al. (2020) is also recovered here to a certain extent (Appendix S2). Similar to Helmstetter et al. (2020), we recovered the section Erectae as sister to the rest of the genus, with maximal support. The single species comprising this section, *R. regalis,* here sampled with eight individuals, formed an unequivocally supported monophyletic clade. We also recovered the sections Moniliformes and Temulentae as monophyletic. Relationships between species within the Monoliformes are also consistent with Helmstetter et al. (2020).

Our study recovered some phylogenetic inconsistencies, mainly within and between species. In the concatenated analysis using IQ-TREE, the section Obclavatae (consisting of the sole species *R. sudanica*) is nested within the Raphiate section, with moderate support. This, however, is not supported in the ASTRAL analysis where this section is sister to the Raphiate section, also with moderate support, as in Helmstetter et al. (2020). These differences might be related to the different assumptions behind concatenation and gene tree analyses or to the moderate support of the Raphiate section in general.

Relationships between species within the Raphiate and Temulentae sections remain difficult to resolve (Helmstetter et al. 2020), even within an extended sampling of the tribe. These sections comprise species that are very similar morphologically (Otedoh 1982; Tuley 1995), but which show consistent morphological differences useful for species identification, such as habit, morphology of the fibers surrounding the stipe, and inflorescence position (Couvreur and Sunderland 2019; Helmstetter et al. 2020). For example, *R. hookeri* (a widespread and economically important species) and *R. gabonica* (an endangered species endemic to Gabon) are suggested to be paraphyletic in the present study; however the former is restricted to periodically inundated soils along river systems and generally occurs in high density, while the latter occurs in non-inundated soils in low density populations (Couvreur and Sunderland 2019; Mogue Kamga et al. 2020). Species delimitation suggested that species with the Temulentae section could be considered as a single widespread and morphologically diverse species or belong to a complex with seven different species, depending on the stringency of the analysis (Helmstetter et al. 2020). In addition, relationships within the Raphiate section as inferred here suggest paraphyletic species, which contrasts to Helmstetter et al. (2020), where species were recovered as monophyletic based on field morphological identification of species. When species were resolved as non-monophyletic (e.g. *R. zamiana*), individuals clustered according to geographic distribution, suggesting potentially cryptic species (Helmstetter et al. 2020). The present study supports the view that a deeper look into population dynamics within the genus, together with fine-scale morphological analyses of these sections, are needed to get a clearer picture of species delimitation.

Lepidocaryeae Systematics—The relationships of the subtribes that comprise Lepidocaryeeae have been a persistent taxonomic issue since the advent of palm phylogenetics. Most molecular phylogenetic studies supported Mauritiinae and Raphiinae as sister clades (Baker et al. 2000a, 2000b; Asmussen et al. 2006; Helmstetter et al. 2020). In contrast, Faye et al. (2016) resolved Ancistrophyllinae as sister to Mauritiinae and as strongly supported (>90% branch support), a relationship that is also indicated by the main topology in our exon data analysis (Appendix S3), albeit with low support (lpp 0.3; Appendix S2).

Here, we present new evidence for the third possible relationship between the three subtribes: our analyses of SNP data resolve with maximal support a monophyletic clade of Ancistrophyllinae and Raphiinae, with Mauritiinae as sister to that clade (Fig. 1; Appendix S1), a relationship supported by morphological data (Fig. 1 in Baker et al. 2000b) and a recent study of higher-level relationships of the Calamoideae (Kuhnhäuser et al. 2021). Of note, this relationship also coincides with the biogeographic disjunction between the American Mauritiinae and the predominantly African Ancistrophyllinae and Raphiinae. Further research is needed to unravel the causes for the substantial discrepancy of inferred subtribal relationships between different analytical approaches.

The Power of Phylogenomics in Elucidating Palm Taxonomy—Molecular systematics has been transformed with the advent of phylogenomic tools such as target sequence capture (Andermann et al. 2020) and it has significantly improved palm classification at lower taxonomic levels (Heyduk et al. 2016; Loiseau et al. 2019; Helmstetter et al. 2020; Bacon et al. 2021). In this study, we show the power to resolve relationships across taxonomic scales, from subtribe to interspecific relationships, with strong support for most clades. Indeed, we recovered high branch support at all hierarchical levels, from inter-generic to inter-specific. The biological processes driving persistent challenges in systematics, such as hybridization, paralogy, and incomplete lineage sorting (Doyle 1992), are not eradicated with increased amounts of data or sampling (Bravo et al. 2019). However, target sequence capture is a reasonable alternative for palm taxonomy and for systematics in general, especially for overcoming the limitations of analyzing large genomes (Andermann et al. 2020).

Taxonomic Treatment

Mauritiella disticha Prata, Oliveira, Cohn-Haft, Emilio and Bacon, sp. nov. Type: Brazil. Amazonas: Apuí

FIG. 3. *Mauritiella disticha* sp. nov. A. Pistillate flowering plant. B. Inflorescence with pistillate flowers. C. Staminate flowering plants. D. Staminate flowers grouped in the rachillae. E. Fruits. F. Staminate flowers grouped in the rachillae. G. Bract in the base of the rachilla in the inflorescence. H. Bracts in the peduncle of the inflorescence. I. Stems with root spines. J. Two flowering individuals. Images from E. Prata (A–D, F–J) and A. V. G. Oliveira (E).

municipality, Rodovia Transamazônica (Apuí-Humaitá), 7°42'53" S, 61°04'36" W, 14 September 2011, *E.M.B. Prata & M. Cohn-Haft 1085* (holotype INPA [259235]).

Diagnosis—*Mauritiella disticha* differs from all other species of the genus by its distichous phyllotaxy. *M. disticha* co-occurs with and resembles *M. armata* in shape, size and color of the fruits (Appendix S5). The new species can be distinguished from *M. armata* by its shorter stature (2–7 m tall vs. up to 20 m tall in *M. armata*), by the leaves with little or no waxiness on the abaxial surface (vs. pronounced waxy coating) and by the smaller scales in the fruit (1.2–1.7 × 2.1–2.5 mm vs. 2–2.2 × 3.1–3.8 mm), in addition to the distichous leaf arrangement.

Description—Dioecious tree palm. Stem 2–7 m tall, 5–15 cm in diameter, solitary or cespitose, covered with brown spines, the top of the stem with persistent dead leaf sheaths, the stem brownish. **Leaves** 2–12, distichous, costapalmate

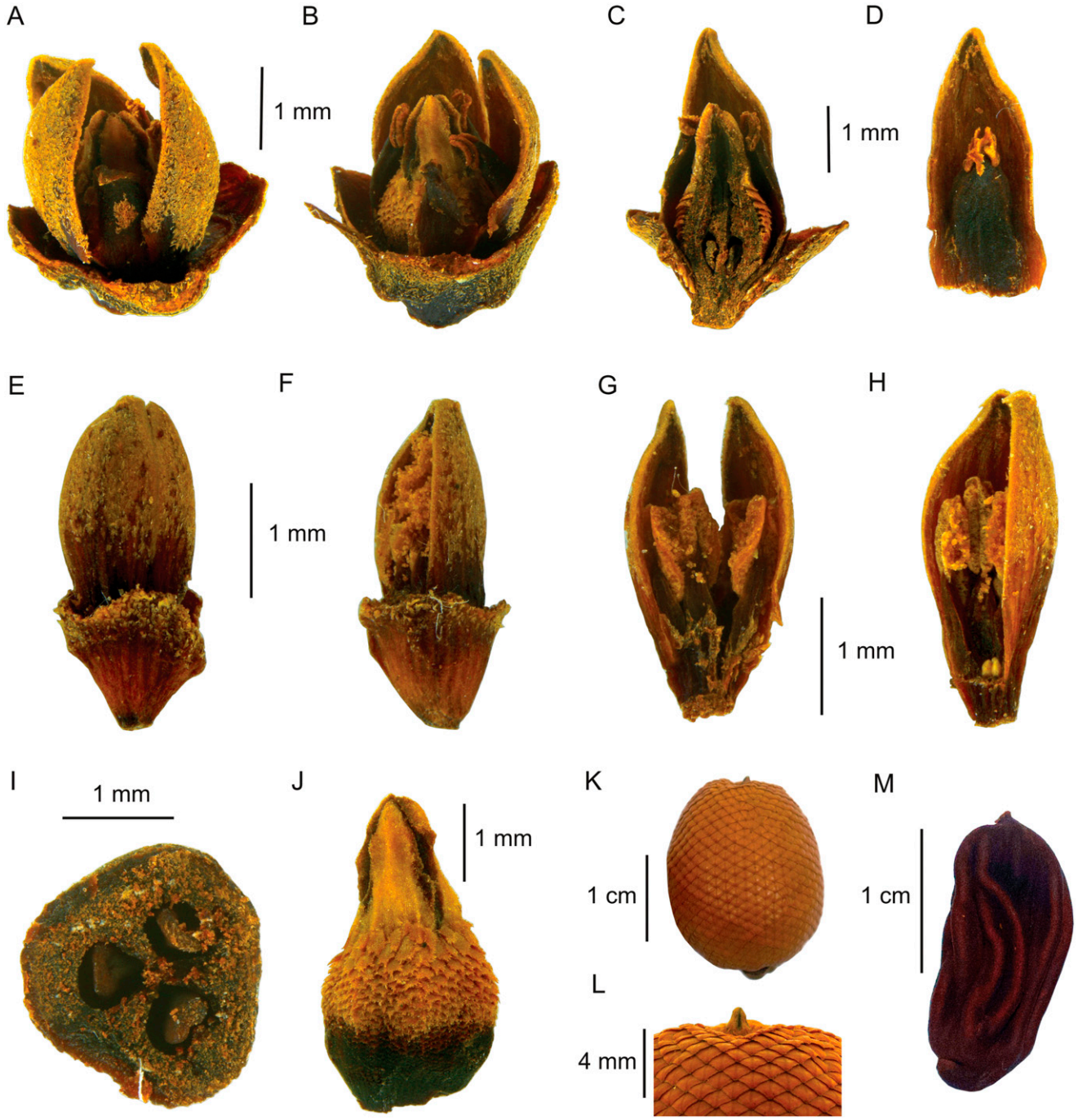

FIG. 4. *Mauritiella disticha* sp. nov. A, B. Pistillate flower showing the puberulous sepals and petals, the ovary and stigma, and the staminodes. C. Longitudinal section of a pistillate flower, with details for the ovules and the scales in the ovary. D. Staminode inserted at the base of the petal. E, F. Staminate flowers showing the puberulous sepals and petals. G, H. Staminate flowers with stamens showing the anthers with pollen grains, and the pistillode (H). I. Transverse section of the 3-locular and 3-ovulate ovary. J. Ovary with small scales and stigma with 3 lobes. K. Fruit. L. Detail of the scales and the apical remaining stigma in the fruit. M. Immature and dried seed. All images from E. Prata and F. Farroñay.

with reduplicate segments, sheath 40–50 cm long, 5–16 cm wide basally; petiole 150–185 cm (166.2 ± 15.64, N = 5) long, 2.1–3.4 cm (2.7 ± 0.6, N = 4) wide basally, cylindric; rachis 40–69 cm (54.4 ± 11.1, N = 5) long, segments 20–40, erect or arching downwards towards the apex, 90–136 cm (115.3 ± 18.6, N = 6) long, 2.2–4 (3.07 ± 0.52, N = 3) cm wide, adaxial surface light green, abaxial surface pale green with little or no wax, no spines in the margin. **Inflorescences** interfoliar, similar between male and female individuals: erect at base, arching downwards towards the apex, 62–100 cm (80.4 ± 13.9, N = 5) long, sparsely to densely pubescent, light green (young) to brown (mature); peduncle 19.5–31 cm (24.3 ± 4.9, N = 4) long, 1–1.8 cm (1.56 ± 0.33, N = 4) in diameter, cylindrical, light brown adaxially, light green abaxially; peduncular bracts 5–6, alternate, tubular, with an acute triangular apex in one of the sides, light brown adaxially, light green abaxially; rachis 40–69 cm (54.4 ± 11.1, N = 4) long, cylindrical, 11–32 (18.6 ± 8.14, N = 4) rachilla, alternate, light green.

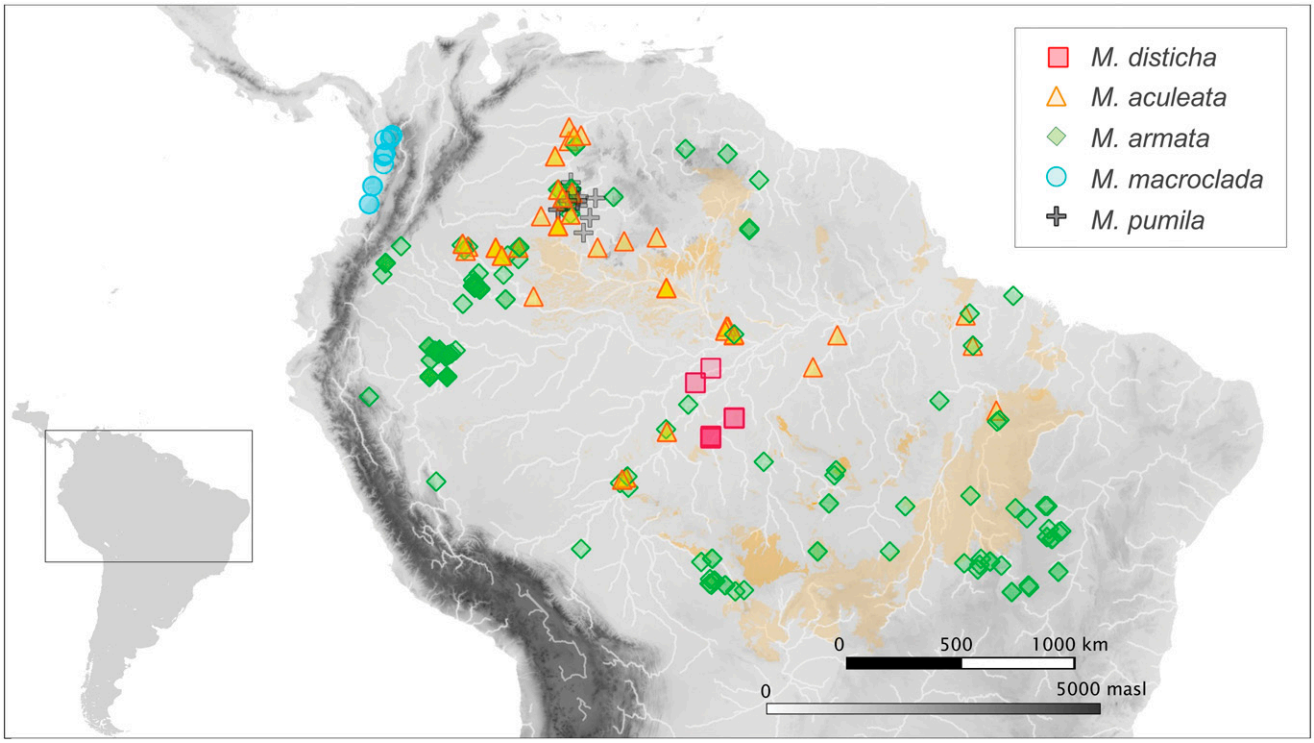

FIG. 5. Map of the geographic distribution of all species of *Mauritiella*, including the here formally described species *M. disticha*. Data were downloaded from virtual collections (from www.splink.org.br) and GBIF (March 2021, https://doi.org/10.15468/dl.pqvthv), and only specimens with clean geographic coordinates and "identifyBy" information were included. GBIF coordinates were cleaned using CoordinateCleaner (Zizka et al. 2019) and subsequently examined for geographic flags. The parameters for cleaning the coordinates, as well as the filters used for manual cleaning are in Appendix S3 and GitHub (https://git.io/JOgOm; Torres Jiménez et al. 2021). The orange shades mark the distribution of white sand habitats (where *M. disticha* is found) and other open areas (Adeney et al. 2016; downloaded on November 26, 2020 from http://www.botanicaamazonica.wiki.br/labotam/doku.php?id = projetos:campinas:mapas:inicio).

Male inflorescences: rachilla 33.5–66 cm (49.05 ± 11.49, N = 4) long, alternate, cylindrical bract at the base of the rachilla bearing an acute triangular apex on the same side of the rachilla; rachillae 45–86 (59.5 ± 13.24, N = 4), 8.5–16 mm (10.66 ± 2.19, N = 3) long, alternate, bearing 38–64 (48.22 ± 9.87, N = 3) flowers each, light green; Flowers solitary, sessile, arranged around the rachillae, 2.9–4.1 mm long; calyx 1.2–2 mm long, cream-colored or yellowish, glabrous inside and puberulous outside; corolla 2–3 mm long, petals 3, free, valvate, yellowish or greenish, glabrous inside and puberulous outside; stamens 6, 2 mm long, yellowish, anthers 0.8–1 mm, dorsifixed, brownish; pistillode <0.2 mm long; style short, stigmatic lobes 3, closed, non-papillose, non-receptive. Female inflorescences: rachilla 40–73 cm long, alternate, cylindrical bract at the base of the rachilla bearing an acute triangular apex on the same side of the rachilla; rachillae 62–81, 3–10 mm long, alternate, bearing 3 flowers each, light green; Flowers solitary, sessile, arranged around the rachillae, 5.8–6 mm long; calyx 3–3.5 mm long, 3-lobed, cream-colored or yellowish, glabrous inside and puberulous outside; corolla 3.5–4 mm long, petals 3, free, valvate, yellowish or greenish, glabrous inside and puberulous outside; staminodes 6, 2.7–3.1 mm long, fused at the base, 3 staminodes inserted at the base of the petals and 3 inserted between the petals, anthers 0.8–0.9 mm long; ovary superior, 2.7–3.1 mm long, 1.9–2 mm in diameter, 3-locular and 3-ovulate, covered by puberulous scales that will develop into the scales in the fruit, style short, stigmatic lobes 3, open, papillose, receptive. **Fruits** 2.2–2.5 cm long, 2–2.1 cm in diameter, ellipsoid, covered with imbricate scales arranged in 20–30 rows, scales 1.2–1.7 mm long, 2.1–2.5 mm wide, the stigmatic remains apical, light green (young) to orange-brown (mature); mesocarp fleshy; seed 1, elliptic-oblong, with uncinate-acuminate apex. Figures 3, 4).

Common Names—Buritirana, buritirana-de-leque.

Distribution and Habitat—*Mauritiella disticha* is currently known from four localities, two on each side of the middle and lower Madeira River basin in the state of Amazonas, Brazil, in low altitudes around 130 m a. s. l. These populations are distant from each other for at least ca. 150 km to up to ca. 370 km (Torres Jiménez et al. 2021). The species is found in open grasslands to low forests in white sand ecosystems, including secondary forests close to roads. These white sand ecosystems, locally called "campina" or "campinarana," are characterized by their nutrient-poor, acid-sandy soils, saturated by the outcrop of the water table or well drained (Fig. 5; Appendix S6).

Flowering and Fruiting—Flowering and fruiting plants were observed in September and October.

Preliminary IUCN Conservation Assessment—The species is currently known only from four populations in the South Amazon, Brazil. The species appears to be truly rare in the landscape as it is a highly conspicuous plant that was neither described before nor registered by the extensive permanent-plot network established in the region (http://ppbio.inpa.gov.br/). Our preliminary red list assessment suggests its status to be vulnerable (VU).

Etymology—The specific epithet refers to the distichous arrangement of the leaves, a conspicuous diagnostic feature and an apomorphy of the species within the genus.

***Note*—**Distichous leaf arrangement in adult individuals is diagnostic of a small number of palm species (e.g. *Aiphanes linearis*, *Oenocarpus distichus*, *Orania disticha*, *Orania ravaka*, *Orania trispatha*, *Orania tabubilensis*, *Wallicha disticha*, *Wettinia disticha*; Dransfield et al. 2008), and is here recognized as fixed in juvenile and adult *M. disticha* (seedling was not recorded). Distichous leaves have also been recorded in *Mauritia*, the sister genus of *Mauritiella*, as single individuals in otherwise normal populations of *M. flexuosa* in Peru (Kahn 1988) and Ecuador (WJB pers. obs.). In contrast to these aberrant individuals of *M. flexuosa*, *Mauritiella disticha* forms a coherent species according to our DNA evidence, with a number of morphological correlates in addition to the distichous phyllotaxy that distinguish it from all other species in the genus. *Mauritiella disticha* also differs from *M. pumila*, the only species in the genus with no genetic data currently available to date by its distribution along the Upper Rio Negro (in Colombia and Venezuela), and by the smaller scales in the fruit (1.2–1.7 × 2.1–2.5 mm vs. 2–3 × 2.5–5 mm; see Galeano and Bernal 2010).

***Additional Specimens Examined (Paratypes)*—Brazil.** —Amazonas: Manicoré, Margem da BR-319, km 390–411 no sentido Manaus - Porto Velho, 5°11'08″S, 61°48'47″W, 21 September 2010, E.M.B. Prata, A.V.G. Oliveira, J.R.M. Ferreira & S.S. Souza 699 (NY); Apuí, Estrada Nova (Apuí-Novo Aripuanã), 6°50'34″S, 59°57'41″W, 12 September 2011, E.M.B. Prata & M. Cohn-Haft 1056 (INPA); Apuí, Estrada Nova (Apuí-Novo Aripuanã), 6°52'35″S, 59°57'46″W, 12 September 2011, E.M.B. Prata & M. Cohn-Haft 1064 (INPA); Apuí, Estrada Nova (Apuí-Novo Aripuanã), 6°51'36″S, 59°58'35″W, 12 September 2011, E.M.B. Prata & M. Cohn-Haft 1070 (INPA); Apuí, Rodovia Transamazônica (Apuí-Humaitá), 7°42'59″S, 61°04'41″W, 14 September 2011, E.M.B. Prata & M. Cohn-Haft 1086 (INPA).

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Author Contributions

AZ and CDB designed the study; AZ provided material and conducted laboratory work; TLPC conducted field work, provided funding and material, data and expertise; SMK conducted field work and provided expertise, BS provided expertise, EMBP provided material, conducted fieldwork, and wrote the species description; MCH conducted field work and provided material, TE conducted field work, provided material and expertise; ÁC conducted laboratory work; RC provided data; BGK provided data; MFTJ and NC analyzed the data; WJB and AA provided expertise, funding, and supervision; CDB conducted field work, provided funding, interpreted results and wrote the paper with MFTJ and with contributions from all co-authors.

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