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Delimitation of the new tribe *Parartocarpeae* (Moraceae) is supported by a 333-gene phylogeny and resolves tribal level Moraceae taxonomy

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Abstract

Here we describe the new tribe, Parartocarpeae, within the Moraceae (mulberry family). The tribe comprises two small Malesian genera, *Parartocarpus* and *Hullettia*, and brings the total number of Moraceae tribes to seven. Evidence for this new designation comes from a phylogeny based on 333 nuclear genes sequenced using target enrichment via hybridization (hybseq). Morphological characters that set Parartocarpeae apart from other Moraceae tribes include the combination of the following characters: lateral nonamplexicaul stipules, spirally arranged leaves without annulate stipule scars, the presence of a single layer of involucral inflorescence bracts, and the lack of perianth tissue, wherein flowers are embedded in cavities of the receptacle. With the designation of Parartocarpeae, the tribe-level circumscription of Moraceae is now well-supported by phylogenetic methods. Because the phylogenetic markers employed here work well throughout Moraceae, they can facilitate much needed work at the genus level in the family.

Keywords: hybridization sequencing, *Hullettia*, inflexed stamens, Malesia, *Parartocarpus*

Introduction

The mulberry family (Moraceae), with approximately 1,100 species in 39 genera, includes several economically and ecologically important species such as breadfruit (*Artocarpus altilis* (Parkinson 1773: 45) Fosberg 1941: 95), paper mulberry (*Broussonetia papyrifera* (Linnaeus 1753: 986) Ventenat 1799: 547), and figs (*Ficus*) (Berg 2001, 2005, Clement & Weiblen 2009, Zerega *et al.* 2010).The family is characterized by the presence of laticifers producing a milky exudate, tiny unisexual flowers usually condensed on a thickened inflorescence axis, and multiple accessory fruits that develop either from the inflorescence axis or perianth tissue. Moraceae are distributed throughout tropical and temperate regions worldwide, but their diversity is centered in the tropics.

There is strong support for the monophyly of Moraceae (Datwyler & Weiblen 2004, Zerega *et al.* 2005, Clement & Weiblen 2009, Williams *et al.* 2017), but an amazing diversity of complex inflorescence structures, pollination syndromes, breeding systems, and growth forms in the family have historically complicated its taxonomy at the tribal level and below (Corner 1962, Berg 1977ab, Rohwer 1993, Berg 2001, Datwyler & Weiblen 2004, Zerega *et al.* 2005, Berg *et al.* 2006, Clement &Weiblen 2009, Gardner *et al.* 2017). In the most recent family-wide phylogenetic study, Clement and Weiblen (2009) recognized six tribes based on molecular and morphological evidence (Artocarpeae, Castilleae, Dorstenieae, Ficeae, Maclureae, and Moreae). They circumscribed tribe Artocarpeae to include seven genera: *Artocarpus, Prainea, Batocarpus, Clarisia, Parartocarpus*, *Hullettia,* and *Treculia*. However, only a single *Parartocarpus* exemplar was included, and no samples of *Hullettia* or *Treculia* were included in the analysis. Additionally, the position of *Parartocarpus* differed between the molecular and the morphological data sets. Accordingly, they maintained the traditional placement of *Parartocarpus* in Artocarpeae. More recently, based on molecular data from two gene regions, Zerega *et al.* (2010) recircumscribed tribe Artocarpeae to include only three genera: *Artocarpus* (with *Prainea* reduced to a subgenus within *Artocarpus*)*, Batocarpus,* and *Clarisia.* They also proposed the transfer of *Treculia* to tribe Dorstenieae*,* and removed *Parartocarpus* and *Hullettia* from Artocarpeae as unplaced, pending further study.

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TABLE 1. Samples used in this study. All sequences used in alignments were assembled from Illumina reads using HybPiper, except for *Morus notabilis* and *Cannabis sativa*, for which the sequences were extracted from publicly available whole-genome assemblies. All HybPiper assemblies were on target-enriched reads except for *Broussonetia papyrifera* (whole transcriptome) and *Ficus racemosa* (whole genome).

Species	Collection	Herbarium	Total reads (% on target)	Genes recovered	NCBI acc.	Citation
Antiaropsis decipiens	N. Zerega 281	CHIC	1,915,667 (5%)	245	BioProject PRJNA301299	Johnson et al., 2016
Artocarpus camansi	E. Gardner 149	SAN (duplicates at F)	–	333	BioProject PRJNA301299	Gardner et al., 2016
Artocarpus heterophyllus	E. Gardner 98	SAN (duplicates at F)	1,113,542 (67%)	332	BioProject PRJNA301299	Johnson et al., 2016
Artocarpus limpato	N. Zerega 609	SAN (duplicates at F)	993,661 (66%)	331	BioProject PRJNA301299	Johnson et al., 2016
Artocarpus nitidus ssp. lingnanensis	N. Zerega 911	SAN (duplicates at F)	720,786 (65%)	331	BioProject PRJNA301299	Johnson et al., 2016
Bagassa guianensis	G. Weiblen 1677	MIN	689,135 (82%)	333	BioProject PRJNA301299	This study
Batocarpus costaricensis	G. Weiblen 1463	MIN	2,049,622 (81%)	327	BioProject PRJNA301299	This study
Brosimum alicastrum	E. Gardner 23	SAN (duplicates at F)	265,816 (58%)	289	BioProject PRJNA301299	This study
Broussonetia papyrifera	–	–	57,431,597 (0.8%)	277	SRR1477753	Xianjun et al., 2014
Cannabis sativa	–	–	–	332	PRJNA73819	van Bakel et al., 2011
Clarisia biflora	G. Weiblen 1460	MIN	180,075 (70%)	304	BioProject PRJNA301299	This study
Dorstenia hildebrandtii	N. Zerega 311	CHIC	183,239 (26%)	195	BioProject PRJNA301299	Johnson et al., 2016
Ficus macrophylla	E. Gardner 30	SAN (duplicates at F)	2,370,860 (62%)	326	BioProject PRJNA301299	Johnson et al., 2016
Ficus racemosa	–	–	119,328,883 (0.06%)	196	SRR1405699	Fan et al., 2015
Hullettia dumosa	N. Zerega 242	NY	242,318 (45%)	195	BioProject PRJNA301299	This study
Hullettia griffithiana	A.F.G. Kew 16886	US	522,296 (41%)	278	BioProject PRJNA301299	This study
Maclura cochinchinensis	N. Zerega 757	SAN (duplicates at F)	112,466 (52%)	277	BioProject PRJNA301299	This study
Maclura pomifera	E. Gardner 139	SAN (duplicates at F)	554,270 (52%)	307	BioProject PRJNA301299	Johnson et al., 2016
Malaisia scandens	E. Gardner 122	SAN (duplicates at F)	547,924 (60%)	311	BioProject PRJNA301299	This study
Milicia excelsa	McPherson 16087	US	4,374,668 (84%)	332	BioProject PRJNA301299	This study
Morus notabilis	–	–	–	333	PRJNA202089	He et al., 2013
Parartocarpus bracteatus	N. Zerega 730	SAN (duplicates at F)	158,592 (33%)	220	BioProject PRJNA301299	This study
Parartocarpus venenosus	N. Zerega 874	SAN (duplicates at F)	95,607 (29%)	202	BioProject PRJNA301299	Johnson et al., 2016
Sorocea steinbachii	G. Weiblen 1501	MIN	1,133,920 (74%)	332	BioProject PRJNA301299	This study
Streblus glaber	E. Gardner 78	SAN (duplicates at F)	679,968 (23%)	309	BioProject PRJNA301299	Johnson et al., 2016
Trophis montana	Andrianantoanina 1023	F	433,273 (80%)	330	BioProject PRJNA301299	This study

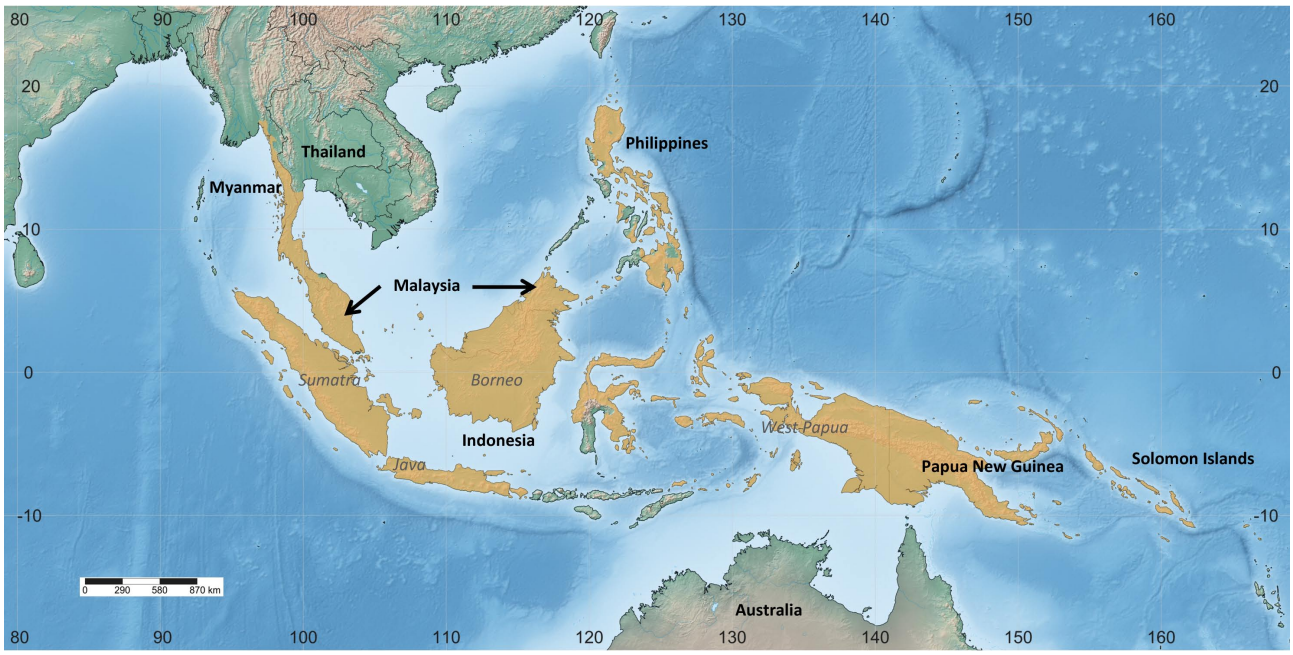

FIGURE 1. Map of distribution of tribe Parartocarpeae. Map created with SimpleMappr, http://www.simplemappr.net.

FIGURE 2. *Parartocarpus venenosus.* (a) shoot showing spiral arrangement of leaves, late-stage carpellate inflorescences, and the inflorescence involucre (arrow); (b) bark with pustular lenticels; (c) buttressed tree trunk; (d) submature syncarp; (e) young carpellate inflorescence with inflorescence involucre (arrow); and (f) staminate inflorescence with inflorescence involucre (arrow). a, f: *Gardner 224,* Tambunan, Sabah, Malaysia (SAN); b–d: Kebun Raya Bogor living collection VIII.B.1, Bogor, Indonesia; e: N. Zerega 877 (SAN). Beaufort, Sabah, Malaysia; photos: N. Zerega).

Parartocarpus includes two species of medium to large trees found primarily in lowland rainforests from the Malay peninsula east to the Solomon Islands (Jarrett 1960, Berg *et al.* 2006) (fig. 1). *Parartocarpus bracteatus* (King 1888: 540) Beccari (1902: 632) is found in peninsular Malaysia, Sumatra, and Borneo, while *P. venenosus* (Zollinger & Moritzi 1845: 213) Beccari (1902: 632) (with four subspecies sensu Jarrett 1960 and no subspecies sensu Berg *et al.* 2006) (fig. 2) ranges from southern Thailand to, Malaysia, Singapore, Indonesia, Papua New Guinea, and the Solomon Islands. Both *Parartocarpus* species produce a poisonous exudate that is used as an arrow poison, have valuable

timber, and while the ripe fruits are said to be edible, the seeds are considered poisonous (Jarrett 1960). The *Tree Flora of Sabah and Sarawak* recognized two additional species, *P. spinulosus* Go (1998: 2) and *P. microcarpus* Corner (1976: 184) (Kochummen 2000), but the more recent *Flora Malesiana* treatment—which we leave unchanged here as species delimitation was not the focus of the study—included those taxa within *P. venenosus* and *P. bracteatus*, respectively (Berg *et al.* 2006). *Hullettia* comprises two species of shrubs to small trees. The multiple fruits of *H. dumosa* King (1888: 547) are said to have sweet, edible pulp (i.e. fleshy receptacular tissue), and some medicinal uses of the leaves and bark are reported (Burkhill & Haniff 1930). *Hullettia griffithiana* (Kurz 1873: 104) King (1888: 547) is known only from peninsular Myanmar and peninsular Thailand, while *H. dumosa* is found in peninsular Malaysia, Singapore, and Sumatra.

The placement of *Parartocarpus* and *Hullettia* has long been a source of confusion (King 1888, Renner 1907, Corner 1962, Berg 1977). While taxonomists long recognized an affinity between *Parartocarpus* and *Artocarpus* (Jarrett 1959, 1960, Corner 1962), *Hullettia* was originally placed in Conocephaleae (=Cercropiaceae) due to an erroneous interpretation of the position of its ovule attachment—King (1888) stated basal attachment when it is in fact apical. It was later determined to be of uncertain affinity within Moraceae (Renner 1907). Jarrett (1959, 1960) proposed for the first time a close affinity between *Hullettia* and *Parartocarpus* based on the shared presence of an inflorescence involucre (absent in *Artocarpus*), 2–3 stamens per flower (compared to a single stamen in *Artocarpus*), and the shared absence of a perianth (present in *Artocarpus*), with flowers instead embedded in receptacular cavities. Although Jarrett (1959) considered *Partocarpus* and *Hullettia* to be part of tribe Artocarpeae, she stated "…it must be realized that there is nothing except general similarity to justify the classification of .... *Artocarpus* with ... *Parartocarpus* and *Hullettia;* the superficial resemblance of the syncarp in *Artocarpus* and *Paratocarpus* is due to parallel evolution." Since then, phylogenetic analyses have strongly supported *Hullettia* and *Parartocarpus* as a monophyletic lineage, but their position within Moraceae has been uncertain (Zerega *et al.* 2010, Williams *et al.* 2017, Gardner *et al.* 2017), leaving them the last genera of Moraceae to be understood at the tribal level.

Here we utilize high throughput target enrichment sequencing (HybSeq) to investigate the affinities of *Parartocarpus* and *Hullettia*. Previous phylogenetic analyses of Moraceae that include at least one of these genera have been based on one to eight gene regions (Datwyler & Weiblen 2004, Zerega *et al.* 2006, Clement & Weiblen 2009, Zerega *et al.* 2010, Williams *et al.* 2017, Gardner *et al.* 2017). Recently, 333 low-copy phylogenetic markers for Moraceae were developed from a draft genome of *Artocarpus camansi* Blanco (1837: 670) (Gardner *et al.* 2016), and they were successfully sequenced in several genera using target enrichment: an efficient, cost-effective method for generating phylogenomic data sets for nonmodel organisms (Johnson *et al.* 2016). Here, we employed these same markers for phylogenetic analysis of 25 Moraceae species (Table 1), including all species of *Parartocarpus* and *Hullettia* (Jarrett 1960, Berg *et al.* 2006), all genera in the tribes Moreae, Artocarpeae, Ficeae, and Maclureae, and representative genera in Dorstenieae and Castilleae, which are well established as monophyletic tribes (Clement & Weiblen, 2009, Zerega *et al.* 2010), plus one outgroup taxon. The aim was to achieve a clear picture of the tribal affinities throughout Moraceae in order to facilitate future studies on taxonomy, character evolution, and biogeography within the family.

Materials and methods

Sampling and DNA preparation

We sampled 25 species throughout Moraceae (Table 1), including all four species of *Parartocarpus* and *Hullettia* recognized by Berg *et al.* (2006), all genera in the tribes Moreae (six genera), Artocarpeae (three genera), Ficeae (monotypic), and Maclureae (monotypic), and representative genera of Dorstenieae (four of 13 genera) and Castilleae (one of 11 genera) (Clement & Weiblen, 2009). *Cannabis sativa* Linnaeus (1753: 1027) (Cannabaceae) was used as the outgroup (van Bakel *et al.*, 2011). Twelve new sequencing libraries were prepared for this study, and the reads have been deposited in the National Center for Biotechnology Information (NCBI) Sequence Read Archive (BioProject PRJNA301299). Leaf material was collected either on silica gel or in three cases (*Hullettia griffithiana, Milicia excelsa* (Welwitsch 1869: 69.) Berg (1982: 227), and *Trophis montana* (Leandri 1948: 25) Berg (1988: 355), from herbarium sheets. DNA was extracted using the Qiagen DNeasy Plant Mini Kit (Qiagen, Valencia, California, USA) following the manufacturer's protocol, except that for herbarium specimens the protocol was modified with longer incubation times (Williams *et al.* 2017). DNA was sonicated to a mean insert size of 550 bp using a Covaris M220 (Covaris, Wobum, Massachussetts, USA). Libraries were prepared with the Illumina TruSeq Nano HT DNA Library Preparation Kit (Illumina, San Diego, California, USA) following the manufacturer's protocol, except that reactions were performed

in half-volumes to save reagent costs. Libraries were enriched for 333 phylogenetic markers (Gardner *et al.* 2016) with a MYbaits kit (Arbor Biosciences, Ann Arbor, Michigan, USA) following the MYbaits manufacturer's protocol. Hybridization took place alongside samples for another study in pools of 6–24 libraries, followed by PCR amplification with 14 cycles using the conditions specified in the manufacturer's protocol. Pools of enriched libraries were sequenced on an Illumina MiSeq (2 x 300bp, version 3 chemistry) at the Field Museum of Natural History alongside samples for other studies in three multiplexed runs each containing 30–70 samples.

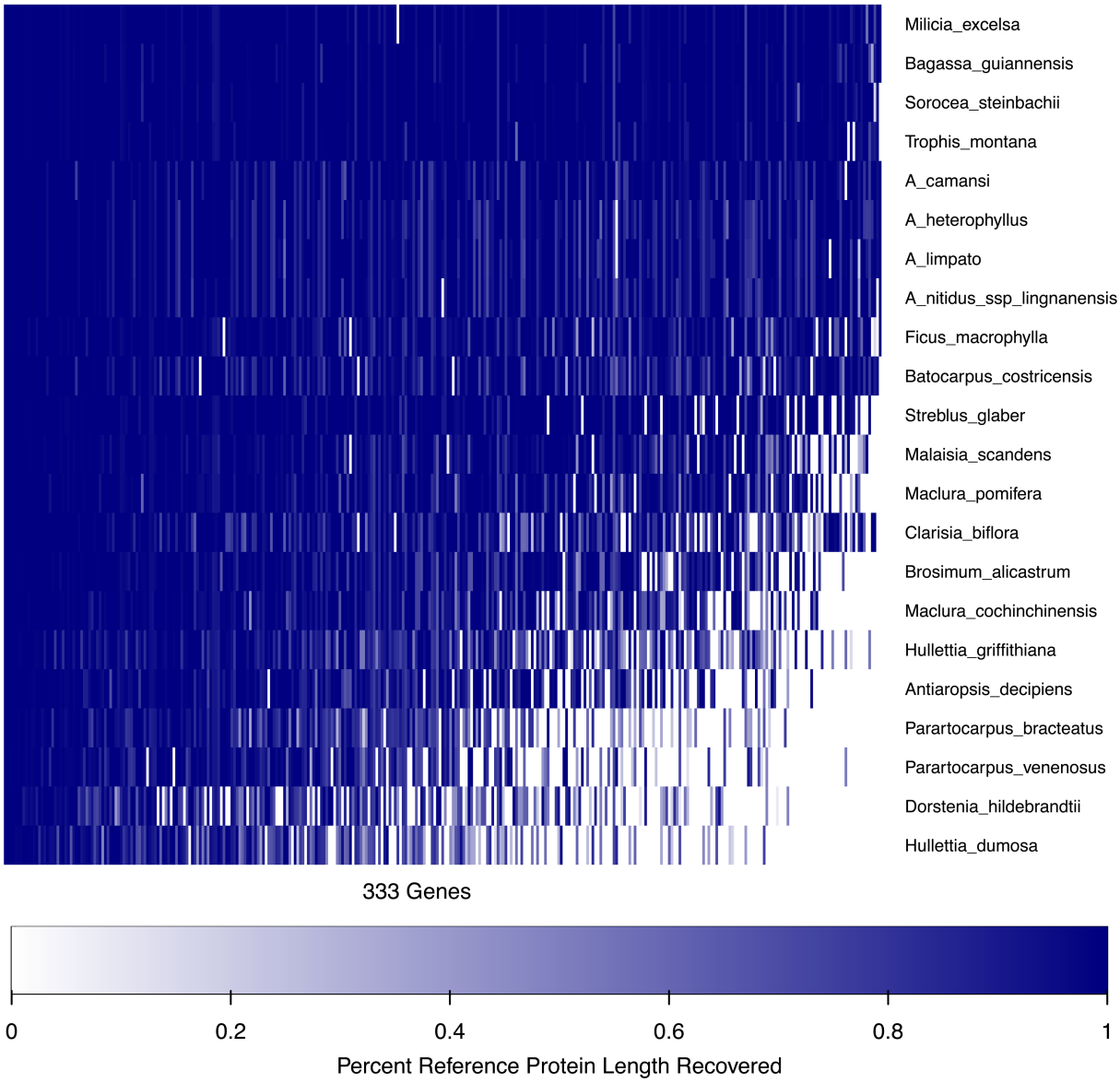

FIGURE 3. Heat map showing recovery efficiency for 333 genes. Each column is a gene, and each row is one sample. The intensity of color in each cell is determined by the length of sequence recovered divided by the length of the reference gene (maximum of 1.0).

Sequence assembly and phylogenetic analysis

Demultiplexing and adapter trimming took place automatically through Illumina BaseSpace (basespace.illumina.com). Reads were then quality trimmed using Trimmomatic (Bolger *et al.* 2014), with a quality cutoff of 20 in a 4-bp sliding window, discarding any reads trimmed to under 30 bp. In addition to the 12 samples sequenced for this study, reads used for assemblies included 10 samples sequenced in Johnson *et al.* (2016), as well as unenriched reads for *Broussonetia papyrifera* and *Ficus racemosa* Linnaeus (1753: 1060) downloaded from NCBI's Sequence Read Archive (Fan *et al.*, 2015; Peng *et al.*, 2014). We used HybPiper to carry out localized *de novo* assemblies of targets for 24 samples guided by reference targets from *Artocarpus camansi* and *Morus notabilis* C.K. Schneider (1916: 293) (Johnson *et al.* 2016). In samples with multiple homologous sequences for a single target, HybPiper retained the sequence with the highest identity to the reference as the best ortholog, flagging others as paralogs (Johnson *et al.* 2016), which were not used

in this analysis. The final HybPiper output used here was the predicted coding sequence for each target gene. To the HybPiper output, we added orthologs from the *Morus notabilis* and *Cannabis sativa* genomes (Gardner *et al.*, 2016, He *et al.*, 2013, van Bakel *et al.*, 2011), for a total of 26 samples.

For each target gene, sequences were aligned using MAFFT (Katoh & Standley 2013) and trimmed with Trimal using the "automated1" method (Capella-Gutiérrez *et al.* 2009). Single-gene phylogenies for each of 333 genes were calculated using RAxML under the GTR+GAMMA model, with 700 rapid bootstrap replicates (Stamatakis 2006). Bootstrap results for each gene were summarized in a majority-rule tree using SumTrees (Sukumaran & Holder 2010). These 333 gene majority-rule trees were used to estimate a species tree with a coalescent-based approach implemented in ASTRAL-II (Mirarab & Warnow 2015, Zhang *et al.* 2018). Bootstrap support for each node was calculated by resampling within and across the 333 bootstrap files, with 500 replicates. A maximum likelihood tree was also calculated with RAxML based on a concatenated supermatrix of all 333 genes using a mixed-partition GTR+GAMMA model, with 1,000 rapid bootstrap replicates. We also repeated these analyses on a reduced data set including only those genes with at least one *Parartocarpus* or *Hullettia* sequence.

To investigate the effectiveness of the capture baits at various phylogenetic distances, we used the "cophenetic.phylo" function in the R package APE (Paradis *et al.* 2004). This allowed us to calculate the distance between each hybridized sample and *Morus notabilis* or *Artocarpus camansi,* whichever was closer, in branch length units on the maximum likelihood tree (substitutions per site). These two taxa were chosen because the bait sequences originated from *M. notabilis* and *A. camansi*. We then tested a linear model based on percent target recovery (out of 333) as a function of distance.

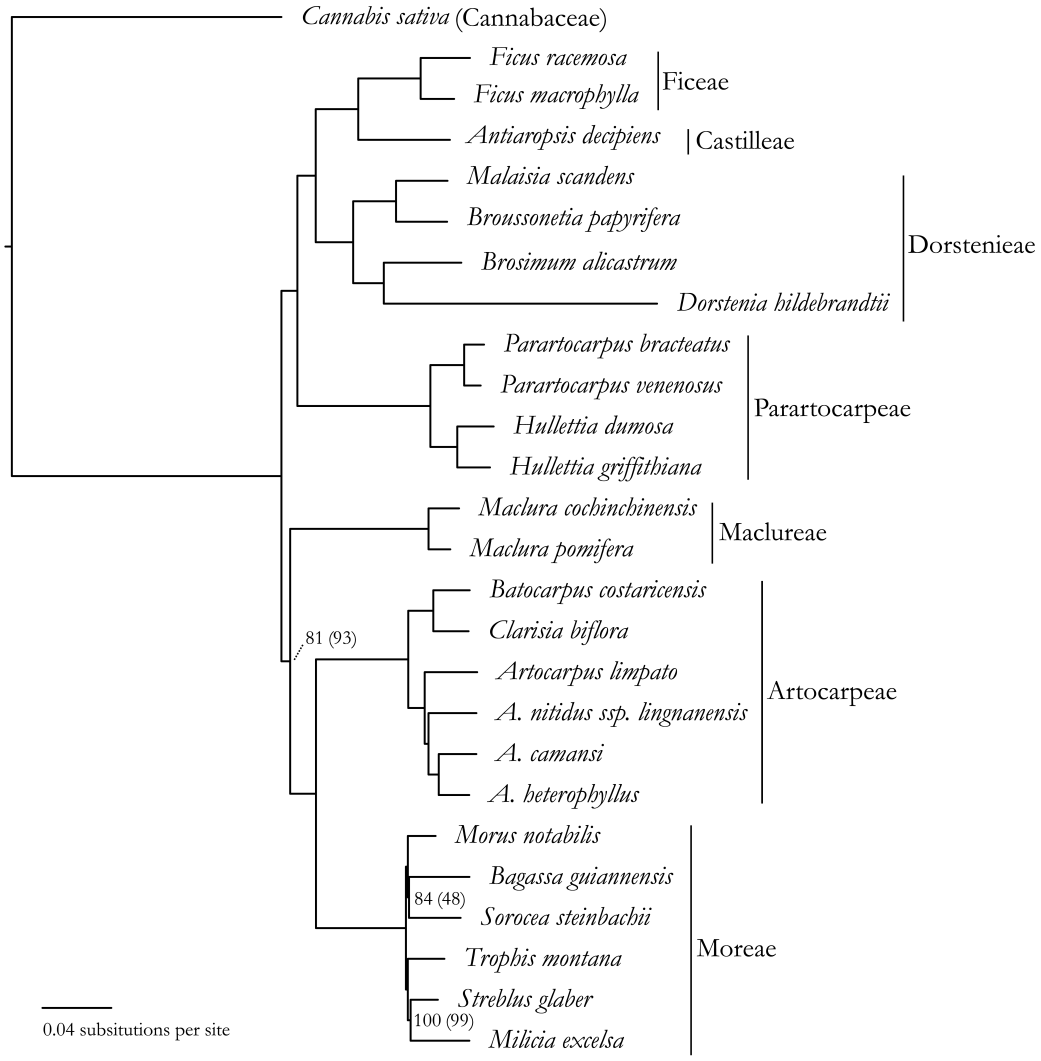

FIGURE 4. Maximum likelihood tree showing the seven Moraceae tribes. Unlabeled nodes had 100% bootstrap support in both analyses. Labeled nodes show support from maximum likelihood analysis, with support from the ASTRAL species tree reconciliation in parentheses.

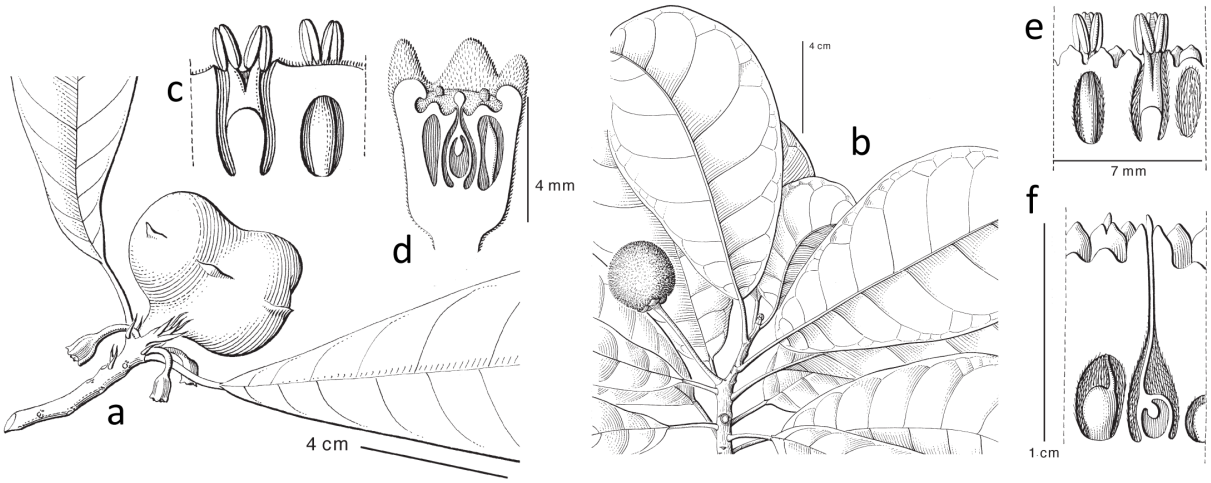

FIGURE 5. Characters of tribe Parartocarpeae as seen in its two genera, *Hullettia* and *Parartocarpus.* Inflorescence involucres and spirally arranged leaves of *Hullettia* (a) and *Parartocarpus* (b); flowers lacking perianth tissue and embedded in the receptacle in *Hullettia* staminate (c) and carpellate (d) flowers, and *Parartocarpus* staminate (e) and carpellate (f) flowers in longitudinal sections. a: *Alvins 3290*; b: *Sinclair 39426*; c: *Robinson s.n.* 20-III-1913; d: *Ridley s.n.* II1921; e: *Corner SFN 28145; f: Corner SFN 28145.* Illustrations are reproduced here from *Flora Malesiana* v. 17: 1, with permission from the Flora Malesiana Secretariat. *Parartocarpus* images come from fig. 22, p. 132; *Hullettia* images come from fig. 21, p. 127.

Characteristics for taxonomic keys

In order to develop taxonomic keys to diagnose the tribes, a range of family level treatments were consulted (Corner 1962, Berg *et al.* 2001, Berg *et al.* 2006, Clement & Weiblen 2009), as well as some specific tribal level treatments (Artocarpeae: Jarrett 1959, Zerega *et al.* 2010, Dorstenieae: Berg & Hijman 1999, Ficeae: Berg & Corner 2005, Maclureae: Gardner *et al.* 2017, Parartocarpeae: Jarrett 1960). Additionally, key specimens of *Hullettia* and *Parartocarpus* were consulted and are listed under the treatment of Parartocarpeae. Some useful characters at the tribal level include monoecy vs. dioecy, unisexual inflorescences vs. bisexual inflorescences, involucral bracts, habit, armature, and stamen number. Botanical terms used are defined in Harris and Harris (2009)

Results

The target-enriched libraries generated in this study and Johnson *et al.* (2016) had a median read count of 617,119, with a median of 61% reads on target (Table 1). Median gene recovery was 310/333 for all samples; for the ingroup, it ranged from 195 to 333 (Table 1, fig. 3). The final supermatrix had 385,454 characters, with 17% gaps or missing data. The maximum likelihood tree based on the supermatrix (fig. 4) was well supported, with 100% bootstrap support for most nodes. *Parartocarpus* and *Hullettia* formed a clade sister to Dorsteniae+Castilleae+Ficeae, with 100% bootstrap support. The ASTRAL species tree recovered the identical topology, with similar support, including 100% support for the position of *Parartocarpus* and *Hullettia* (fig. 4). The reduced data set excluding the genes without *Parartocarpus* and *Hullettia* sequences contained 285 genes. In these analyses, both the supermatrix and species-tree again had the same topology, again with 100% bootstrap support for the position of *Partartocarpus* and *Hullettia*. For the ASTRAL species-tree analyses, the final normalized quartet score was 0.96, indicating little gene tree conflict. The local posterior probability, representing quartet-tree support, for the position of *Parartocarpus* and *Hullettia* was 88%, again indicating little discordance between gene trees as to this relationship. All alignments and trees are deposited in the Dryad Digital Repository (doi:10.5061/dryad.3jn4gs8).

Model testing indicated phylogenetic distance was a major determiner of hybridization sequence capture success (slope = –1.44±0.25, adjusted R^2 = .63, F = 32.62 on 1 and 19 d.f., P < 0.0001). Gene recovery showed substantial drop off at divergences from the target sequences of greater than 0.18 substitutions per site. However, over half of the targets were recovered even at a divergence of greater than 0.30 (*Dorstenia hildebrandtii* Engler 1894: 146).

Discussion

Our analysis of 333 nuclear loci supports the conclusion that *Parartocarpus* and *Hullettia* form a well-supported clade that is not closely allied with Artocarpeae, but is instead sister to Dorstenieae+Castilleae+Ficeae. This phylogenetic position makes it impossible to transfer *Parartocarpus* and *Hullettia* to another tribe if the monophyly of those tribes is to be maintained. In addition, these two genera share unique shared morphological characters: the absence of perianth tissue, flowers embedded in receptacular cavities, and extrorse anthers (typically introrse to latrorse in the rest of the family). The molecular and morphological evidence therefore warrant the designation of the new tribe Parartocarpeae (description below).

The Moraceae family is nested within the "Urticalean" clade (including Urticaceae, Ulmaceae, Cannabaceae, and Moraceae), for which the ancestral trait of "urticaceous" stamens is considered distinctive for the group. "Urticaceous" stamens are inflexed in bud and bend outward suddenly at anthesis, allowing for an "explosive" dehiscence of pollen, which is often associated with wind pollination (i.e. *Morus*). Thus, it is interesting to consider this trait and what it might mean for pollination in the new Parartocarpeae tribe. Parartocarpeae does not have inflexed stamens, and is part of a larger clade (Dorstenieae, Ficeae, Castilleae) in which inflexed stamens have been largely lost (except in these genera: *Bleekrodea, Broussonetia, Alleanthus, Fatoua*).

Corner (1962) observed that the presence of inflexed stamens is quite variable within Moraceae. The repeated loss of inflexed stamens raises the possibility of multiple transitions from wind to animal pollination in Moraceae—a rare character shift in angiosperms (Culley *et al.*, 2002). Although, little is known about pollination in Dorstenieae and Parartocarpeae, fascinating insect brood site pollination mutualisms occur in both Ficeae and Castilleae (Weiblen 2002, Sakai 2001, Zerega *et al.* 2004, Machado *et al.*, 2005), and possibly *Dorstenia* as well (Thorgood *et al.* 2018). These pollination modes are characterized by tiny insects that use inflorescences as a brood site for their young but also provide pollination services. In figs, the relationship is an obligate mutualism, but it is not yet known if the pollinating insects and the plants are entirely interdependent on one another for reproduction in other groups. Inflexed stamens appear to have also been independently lost at least three other times in Moraceae—within the tribe Artocarpeae (which also has known brood site pollination mutualisms (Sakai *et al.* 2000, Gardner *et al.* 2018), the genera *Bagassa* and *Sorocea* (in Moreae), which have been speculated to have brood site pollination (Berg 2001), and in *Maclura* section *Cudrania* (Maclureae) (Gardner *et al.* 2018). In brood site pollination mutualisms in *Ficus* and some *Artocarpus* species, volatile cues from inflorescences are known to be involved in attracting pollinators (Ware *et al.* 1993, Grison-Pige *et al.* 2002, Hossaert-McKey *et al.* 2010, Gardner *et al.* 2018). Male inflorescences of *Parartocarpus venenosus* are fragrant (Gardner pers. obs.), and it would be of interest to study pollination in the Parartocarpeae tribe.

Conclusion

With the designation of Parartocarpeae, the Moraceae family appears to be well circumscribed at the tribal level, and this evolutionary framework will be valuable for considering character evolution, such as shifts in pollination. There is still much to be sorted out at the generic level, especially within the Moreae and Dorstenieae tribes. The phylogenetic markers employed here may facilitate that work. Sampling across Moraceae illustrated the utility of the capture baits described by Gardner *et al.* (2016) at substantial phylogenetic distances.

Taxonomy

Parartocarpeae Zerega & Gardner, *trib. nov*.

Type:—*Parartocarpus* Baillon

Diagnosis:—Parartocarpeae superficially resembles the genus *Artocarpus* in having carpellate inflorescences made up of numerous small flowers condensed on capitate heads that develop into large syncarp structures. However, it differs from *Artocarpus* in the combination of lateral nonamplexicaul stipules and spirally-arranged leaves (never occurring together in *Artocarpus*), the presence of involucral inflorescence bracts (absent in *Artocarpus*), and the lack of perianth tissue (present in *Artocarpus*). In Parartocarpeae, flowers are embedded in cavities of the receptacle. Thus, whereas the fleshy pulp of *Artocarpus* syncarps is derived from perianth tissue, the fleshy pulp in the syncarps of *Hullettia* and *Parartocarpus* species is derived from receptacular tissue.

Description:—Shrubs to large trees; abundant white exudate. *Leaves* spirally arranged; simple; entire; pinnately veined; thin to thick coriaceous; glabrous, pubescent, scabrid, or hispid pubescent. *Stipules* axillary, simple or paired, nonamplexicaul. *Inflorescences* unisexual. capitate pedunculate, solitary or paired in leaf axils; stamens or ovaries sunken into the receptacle, perianths absent; involucre of 3–8 bracts. *Staminate inflorescences* with numerous flowers, anthers exserted through perforations in the upper surface of the receptacle, 1–3 stamens in each cavity, filaments free or united. *Carpellate inflorescences* (sub)globose; ovaries solitary in each cavity, unilocular, the style apical with a short exserted stigma. *Syncarp* formed by the enlargement of the entire female head, with 1 to many flowers forming fruit and filling the fleshy receptacle.

Distribution: Thailand to the Solomon Islands (fig. 1)

List of genera: *Hullettia* King ex Hook.*, Parartocarpus* Baill. (fig. 5)

Specimens Examined:—***Hulletia dumosa*** King: MALAYSIA. Perak, March 1883, *Dr. King's Collector 3959* (syntype K); INDONESIA. Riau, Sumatra, Tigapulu Mountains, 102º 32'E 0º 46'S, 3 December 1988, *J.S. Burly et al 1840* (Arnold A); MALAYSIA. Pahang, 16 April 1967, *T.C. Whitmore FRI3574* (L); MALAYSIA. Kuala Lumpur, Kepong, Forest Institute of Malaysia, 4 March 2002, *N. Zerega et al. 242* (CHIC!). ***Hullettia griffithiana*** (Kurz) King: MYANMAR. No date. *W. Griffith 929* (lectotype K); THAILAND. Ranong, 9º20'N 98º25'E, 25 April 1974, *K. Larsen et al. 33349* (L!); THAILAND. Ranawng, Klawng Kampuam, 30 January 1929, *A.F.G. Kerr 16886* (US). ***Parartocarpus bracteatus*** (King) Beccari. MALAYSIA. No date. *A.C. Maingay 1476* (isosyntype GH); INDONESIA. Kalimantan: 50m elev, 117E 1S, 7 September 1991, *M.M.J. Van Balgooy 6099* (L); MALAYSIA. Sabah, Papar: primary forest, 7 September 2002 S. *Dolois et al. SP17164* (SNP); MALAYSIA. Sabah, Telupid, Institut Perhutanan, 05º36.176'N 117º05.846'E, 18 June 2013, *N. Zerega et al. 730* (CHIC, SAN). ***Parartocarpus venenosus*** (Zollinger & Moritzi) Beccari. INDONESIA. No date. *H. Zollinger 2371* (isosyntype BM!); INDONESIA. Moluccas, Aroe Islands, primary forest, 26 June 1938, *P. Buwalda 5420* (L); INDONESIA. North Sulawesi, primary lowland forest, 350m elev., 0º41'N 123º40'E, 6 March 1990, *J.S, Burley et al. 3686* (L); MALAYSIA. Sabah, Beaufort, 05º10.145'N 115º36.710'E, 24 June 2013, *N. Zerega et al. 874* (CHIC, SAN).

Key to Genera and species of Parartocarpeae Zerega & Gardner, *trib. nov*.

The following key is provided at the species level for *Hullettia* and *Parartocarpus*. Characteristics used for the key were drawn from Jarrett (1960) and Berg *et al.* 2006. For generic and species level descriptions see Jarrett (1960) or Berg *et al.* (2006). Representative specimens of each taxa were also consulted (see Parartocarpeae description above).

1. Surface of receptacle/syncarp armored by indurated, spinous, conical, or truncate processes. Stipules fused, intrapetiolar, triangular. Stipule scars elongate. Leaves not punctate beneath. ..... *Parartocarpus*
a. Leaves having 11–15 pairs of lateral veins, rufous pubescent beneath with the intercostals distinctly prominent, 5–10 on each side of midrib; processes on the syncarp spinous, the bases +/- bulbous, on inflorescences at anthesis narrowly spinous, ca. 3 × 1 mm; involucral bracts 5–10 mm long ..... *P. bracteatus*
b. Leaves having 6–15 pairs of lateral veins, thinly pubescent to glabrous beneath with the intercostals not or shallowly prominent, fewer; processes on the syncarp truncate to spinous, the base not bulbous, on inflorescences at anthesis truncate to acute, never narrowly spinous; involucral bracts to 5 mm long ..... *P. venenosus*
1. Surface of receptacle/syncarp not armored but smooth. Stipules paired, lateral, linear. Stipule scars round. Leaves minutely punctate beneath. ..... *Hullettia*
a. Male head ca. 10 mm across, peduncle to 20 mm; syncarp with obtuse to obsolete involucral bracts, peduncle to 45 (–55) mm; leaves smooth to scabrid beneath, base cuneate to rounded, petiole to 50 mm ..... *H. dumosa*
b. Male head to 7 mm across, peduncle 25–45 mm; syncarp with lanceolate involucral bracts, peduncle ca. 75 mm, leaves hispid-pubescent to scabrid beneath, base narrowly and abruptly rounded or auriculate, petiole to 18 mm ..... *H. griffithiana*

Key to Moraceae Tribes

The key below follows the tribal circumscription of Clement & Weiblen (2009) with the creation of Parartocarpeae as presented above and modifications to Artocarpeae (sinking *Prainea* in *Artocarpus,* and excluding *Treculia* and transferring it to Dorstenieae) following Zerega *et al.* 2010, and the recognition of *Allaeanthus* within Dorstenieae (following Chung *et al.* 2017). For descriptions and generic delimitation of tribes other than the newly described Parartocarpeae, see Berg *et al.* (2001), Clement & Weiblen (2009) and Zerega *et al.* (2010).

1. Inflorescences urceolate with the opening entirely closed by ostiolar bracts (i.e. syconium) such that the flowers are enclosed at all stages of development; lamina with waxy glandular spots at the base of the midrib or in the axils of the basal lateral veins beneath. ..... **Ficeae** (*Ficus*)
1. Inflorescences capitate, spicate, discoid, or urceolate, but flowers are not entirely enclosed at all developmental stages (i.e. mature anthers or stigmas are open to the surrounding environment); lamina without waxy glandular spots. 2

2. Inflorescences with an involucre of multiple layers of imbricate bracts; with self-pruning horizontal branches (except *Poulsenia* without self-pruning branches)..... **Castilleae** (*Antiaris, Antiaropsis, Castilla, Helicostylis, Maquira, Mesogyne, Naucleopsis, Perebea, Poulsenia, Pseudolmedia, Sparattosyce*)
2. Inflorescences typically not involucrate and when an involucre is present it is a single layer of bracts; without self-pruning branches.....3
3. Trees or lianas; with the combination of both short shoots ending in spines and globose capitate pistillate inflorescences, dioecious..... **Maclureae** (*Maclura*)
3. Trees, shrubs, lianas, herbaceous, or succulent; without short shoots ending in spines or if with spines then pistillate inflorescences are either uniflorous or racemose but not globose capitate; dioecious or monoecious.....4
4. Trees or shrubs; unisexual inflorescences; staminate flowers with one (rarely two in *Batocarpus, Clarisia,* and *Artocarpus annulatus*) stamens; monoecious..... **Artocarpeae** (*Artocarpus, Batocarpus, Clarisia*)
4. Trees, shrubs, lianas, herbaceous, or succulent; unisexual or bisexual inflorescences; staminate flowers with more than one stamen (or if one stamen then dioecious); monoecious or dioecious.....5
5. Trees or shrubs; always with the combination of unisexual inflorescences, stamens straight in bud, and monoecious..... .....**Parartocarpeae** (*Hullettia, Parartocarpus*)
5. Trees, shrubs, lianas, herbaceous, or succulent; bisexual or unisexual inflorescences, stamens straight or inflexed in bud; monecious or dioecious, but never with the combination listed above.....6
6. Trees, shrubs, lianas, herbaceous, or succulent; bisexual inflorescences (or if unisexual then a climber or herbaceous)..... ..... **Dorstenieae** (*Allaeanthus* in part*, Bleekrodea, Bosqueiopsis, Brosimum, Broussonetia* in part, *Dorstenia, Fatoua, Helianthostylis, Malaisia, Scyphosyce, Sloetia, Treculia, Trilepsium, Trymatococcus, Utsetela*)
6. Trees or shrubs; unisexual inflorescence.....7
7. Trees; stipules membranous; syncarp globose with thickly set slender stalked interfloral bracts of various shapes more or less covering the drupes..... **Dorstenieae** (*Allaeanthus* in part*, Broussonetia* in part)
7. Trees or shrubs; stipules not membranous; syncarp not as above..... ..... **Moreae** (*Bagassa, Milicia, Morus, Sorocea, Streblus, Trophis*)

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