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Phylogeny of Southeast Asian *Mapania* (Cyperaceae: Mapanioideae) using chloroplast sequence data

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ABSTRACT

Mapania (Cyperaceae) is a pantropical genus associated with the forest understorey. Its evolutionary history and species delimitation are poorly known in Southeast Asia. To address this lack of knowledge, DNA sequence data from four chloroplast regions (*trn*L-F, *atp*H-F, *psb*A-*trn*H, and *trn*K-*mat*K) were generated for a number of populations of 15 species of *Mapania*. Bayesian and maximum likelihood analyses of the concatenated regions showed a better-resolved phylogeny than previous analyses based on morphological data alone. *Mapania bancana* was resolved as the sister to the other species of *Mapania* included in the study. Moreover, this study highlights the need for further investigation of the species limits in this genus. For instance, *Mapania cuspidata* is retrieved as polyphyletic, and a tentative new species has been detected closely related to *Mapania debilis*. This study also infers the cradle of the Southeast Asian Mapanias in Borneo, which also holds the largest diversity of the genus in the region. *Mapania* is still a poorly understood genus that requires further local taxonomic work and more comprehensive fieldwork records to better assess and protect these species.

Keywords: ancestral area reconstruction; phylogenetics; sedges; systematics; tropics

INTRODUCTION

Cyperaceae (sedges) are the third-largest monocot family with >5600 species in 95 genera (Larridon 2022). Two subfamilies are recognized, Mapanioideae and Cyperoideae (Muasya *et al.* 2009, Larridon *et al.* 2021). Subfamily Mapanioideae (two tribes, 10 genera, ~185 species) is the relatively species-poor sister lineage to subfamily Cyperoideae (two tribes, 85 genera, ~5400 species; Larridon *et al.* 2021). Tribe Hypolytreae comprises four genera of mostly forest-dwelling sedges and is widely distributed throughout the tropics: *Hypolytrum* Pers., *Mapania* Aubl., *Paramapania* Uittien, and *Scirpodendron* Zipp. & Kurz. *Mapania*, the most biodiverse, is a pantropical genus of ~100 species which occurs in rainforests, mainly at low elevation, a habitat that is globally threatened (Bowler *et al.* 2020, Larridon *et al.* 2021). Many species of *Mapania* are regionally endemic, narrowly distributed, and of conservation concern (Shabdin *et al.* 2013a, b). Several species of *Mapania* are used in basket- and mat-making, while others are utilized by local people for

medicinal purposes, including as a fever remedy (Simpson and Inglis 2001).

The greatest diversity in the genus occurs in Borneo with 39 species (Fig. 1), of which 26 are endemic (POWO 2023). Recent work in Borneo, especially Sarawak, has highlighted this diversity, with 16 new species, and a new variety of *Mapania cuspidata* (Miq.) Uittien described since 2013 (Shabdin *et al.* 2013a, b, 2016, Miraadila and Shabdin 2016, Miraadila *et al.* 2016a, b, Melana *et al.* 2023). Melana *et al.* (2023) suggested that up to 60 species may be present in Borneo. Nevertheless, our overall knowledge of the genus is still limited due to a lack of detailed systematic studies shedding light on complex species delimitation. On the other hand, Peninsular Malaysia has more limited diversity, with only 18 documented species, of which only three are not present in Borneo (POWO 2023): *Mapania holttumii* J.Kern, *M. kurzii* C.B.Clarke, and *M. micropandanus* Holttum.

A morphology-based cladogram by Simpson (1992) provided the first phylogenetic hypothesis for the genus. Definition
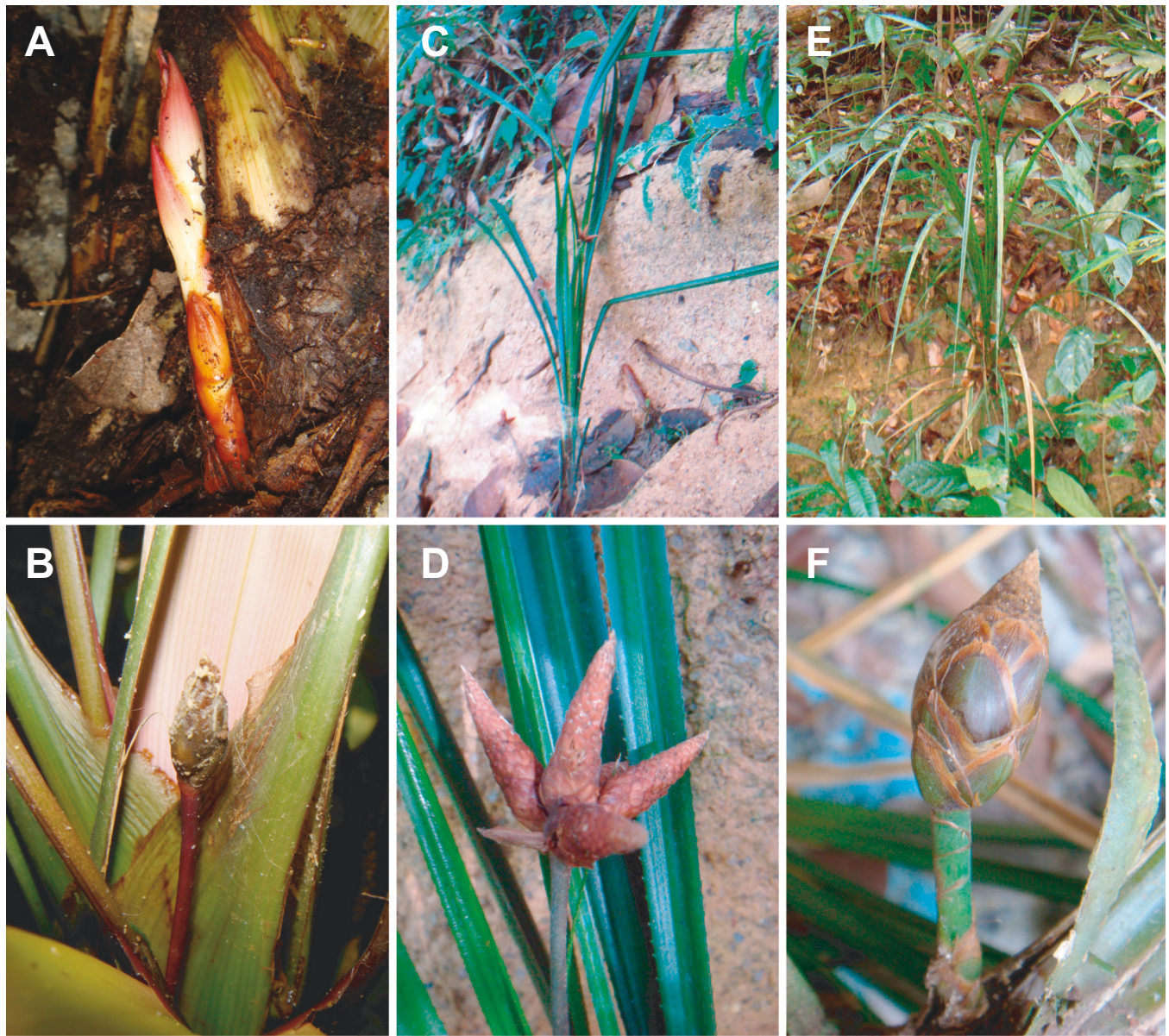
Figure 1. Morphological diversity of *Mapania* in Southeast Asia. A, young lateral shoot with the characteristic salmon-pink colour of *Mapania cuspidata* var. *petiolata*. B, inconspicuous unispicate inflorescence of *Mapania cuspidata* var. *petiolata*. C, habit of *Mapania* cf. *palustris*. D, capitate multispicate inflorescence of *Mapania* cf. *palustris*. E, habit of *Mapania wallichii*. F, unispicate inflorescence with large spicoid bracts of *Mapania wallichii*. A–B, coll. number ZINN 68. C–D, coll. number ZINN 75. E–F, coll. number ZINN 97.

of species within *Mapania* remains challenging due to insufficient discontinuous morphological attributes. The Southeast Asian specimens are particularly difficult in this respect, with some species comprising several morphologically complex infraspecific taxa. This was shown by Simpson (1992: 117), where a principal coordinates analysis of the varieties of *M. cuspidata* was carried out, demonstrating the morphologically ill-defined nature of these varieties, except for var. *pumila* (Uittien) Uittien which was recognized as a separate species.

Molecular phylogenetic studies of Cyperaceae, including species of the subfamily Mapanioideae, were initiated based on plastid DNA utilizing *rbc*L gene sequences to examine higher-level relationships in the family (Muasya *et al.* 1998, Simpson *et al.* 2003). Other studies followed using more rapidly evolving markers such as *ndh*F, *trn*L-F and ITS (Starr *et al.* 2003, Hirahara *et al.* 2007, Jung and Choi 2010, Mesterházy *et al.* 2022), with the most recent phylogenomic framework established by Larridon *et al.* (2021). Meanwhile, studies at tribal and generic level for the subfamily Mapanioideae have, to date, used plastid markers such as *rps*16 and *trn*L (Muasya *et al.* 2009). Although these studies have provided a better understanding of within- and between-tribe relationships, resolution and sampling within *Mapania* remain low.

In this study, we use four molecular markers, *trn*L-F, *atp*H-F, *psb*A-*trn*H, and *trn*K-*mat*K, to infer the phylogenetic relationships among the species of *Mapania* that have been described under two sections in the genus, section *Pandanophyllum* (Hassk.) Benth. & Hook.f. and section *Thoracostachyum* (Kurz)

T.Koyama. We use these molecular data as a foundation to better understand species delimitation and biogeographical history of *Mapania* in Southeast Asia.

MATERIALS AND METHODS

Taxon sampling

Ninety-one accessions representing 19 species of subfamily Mapanioideae [*Mapania*, *Paramapania radians* (C.B.Clarke) Uittien, and *Hypolytrum nemorum* (Vahl) Spreng.] were collected in the field from Malaysia. *Mapania* sect. *Thoracostachyum* is only represented by *M. bancana* (Miq.) Ridl. in the study, whereas the rest are assigned to sect. *Pandanophyllum*. Voucher specimens were obtained for every species from each population encountered and deposited in K, RNG, and SAR herbaria (Thiers 2024). Fresh leaves (5–10 g) were harvested per accession and dried in a zip-locked plastic bag containing ~80 g silica gel. Detailed information about the accessions is given in Supporting Information Appendix S1. One accession of *Carex microglochin* Wahlenb. (subfamily Cyperoideae, tribe Cariceae Dumort.) from GenBank was used as the outgroup.

DNA extraction and amplification

Total DNA was extracted from material collected in silica gel (Supporting Information Appendix S1). The modified CTAB method of Doyle and Doyle (1987) was used but extractions were precipitated in isopropanol for 1 week, before proceeding with the next extraction steps.

Selection of markers was based on previous phylogenetic studies in the family that have proven suitable for species delimitation (e.g. Starr *et al.* 2003, Hirahara *et al.* 2007, Jung and Choi 2010). The markers *trn*L-F, *psb*A-*trn*H, *atp*H-F, and *trn*K-*mat*K were each amplified using the following forward and reverse primers: *trn*L-F (Taberlet *et al.* 1991), *psb*A-*trn*H (Sang *et al.* 1997), *atp*H-F (Lahaye *et al.* 2008), and *trn*K-*mat*K (designed for this study, Table 1). The polymerase chain reaction (PCR) was carried out in 50-µL volumes for bidirectional sequencing and 25 µL for unidirectional sequencing. After some experimentation, optimum results were achieved using 2 µL of template DNA, 1× NH4 buffer (Bioline), 2 mM MgCl$_2$, 0.2 mM dNTPs, 0.2 mg/mL BSA, 0.35 µM of each primer and 1.5 units of *Taq* DNA polymerase per 50-µL reaction. Amplification was

done on an Applied Biosystems GeneAmp 2700 thermal cycler (Applied Biosystems, Foster City, CA, USA) using the following programme for *atp*H-*atp*F, *trn*L-*trn*F, *psb*A-*trn*H, and *trn*K-*mat*K primers: an initial denaturation of 2 min at 94°C, 30 cycles of 30 s denaturation at 94°C, 1 min annealing at 48°C, and an extension of 1.3 min at 72°C. A final extension of 7 min at 72°C was also included.

PCR products were loaded onto 1% agarose gels containing ethidium bromide and subjected to electrophoresis at 5 V/cm for 45 min. Bands were visualized under UV light. Size and approximate concentration were estimated by comparison with a known concentration of Hyperladder1 (Bioline™) size markers. For taxa that amplified poorly, several reactions were pooled prior to cleaning in order to concentrate the PCR products.

PCR products were sent to Macrogen (Korea) for purification and sequencing. Sequences were edited and aligned using Muscle v.3.8.425 (Edgar 2004). The alignments were then optimized manually in Geneious v.11.1.2 (Biomatters, Auckland, New Zealand).

Phylogenetic analyses

We reconstructed the phylogenetic relationships of the species by concatenating all amplified region alignments. We used ultrafast bootstrapping (UFBoot) and Shimodaira–Hasegawa approximate likelihood ratio test (SH-aLRT), and Bayesian inference. We ran IQ-TREE v.1.6.11 (Nguyen *et al.* 2015) setting the parameters to 1000 replicates of UFBoot and SH-aLRT, also checking for the overestimation of the UFBoot branch support through the hill-climbing nearest-neighbour interchange search (NNI; Hoang *et al.* 2018). Best-fitting substitution models were given by the ModelFinder option implemented in IQ-TREE (Kalyaanamoorthy *et al.* 2017). These substitution models were used in the Bayesian inference analysis in MrBayes v.3.2.6 (Ronquist *et al.* 2012). Since some of the models were not allowed in that software, we used GTR as suggested by the manual. We ran four Markov chain Monte Carlo (MCMC) simulations for 5 million generations, sampling every 1000 generations and with 20% as the burn-in parameter. The runs were examined in Tracer v.1.7.1 (Rambaut *et al.* 2018) to check for convergence and a high effective sample size (ESS). A consensus 50% majority rule tree was generated for all the matrices.

Table 1. List of primers used for amplification of chloroplast DNA regions and intergenic spacer of *Mapania* samples.

Marker	Primer	Direction	Sequence 5′–3′	Citation
*atp*H-F	*atp*H	F	GCTTTTATGGAAGCTTTAACAAT	Lahaye *et al.* (2008)
	*atp*F	R	ACTCGCACACACTCCCTTTCC	Lahaye *et al.* (2008)
*trn*H-*psb*A	*psb*AF	F	GTTATGCATGAACGTAATGCTC	Sang *et al.* (1997)
	*trn*HR	R	CGCGCATGGTGGATTCACAAATC	Sang *et al.* (1997)
*trn*L-F	c	F	CGAAATCGGTAGACGCTACG	Taberlet *et al.* (1991)
	f	R	ATTTGAACTGGTGACACGAG	Taberlet *et al.* (1991)
*mat*K	*mat*K F1	F	TTGGTTCAAATCCTTCAATGC	This study
	*mat*K F2	F	TCTTTGCATTTATTGCGATTC	This study
	*mat*K R1	R	GAAAGGATCCGTGAAGAACC	This study
	*mat*K R4	R	TCGAACATAATGCATGAAAGG	This study

Divergence time estimation

We generated an alignment with one tip per taxon, selecting those specimens with longer sequences and less uncertain positions in the DNA matrix (Supporting Information Appendix S2). Specimens belonging to polyphyletic species were selected based on their morphological proximity to their respective type specimen. The analyses were configured on Beauti v.2.6.2 and carried out using BEAST v.2.6.2 (Bouckaert *et al.* 2019) set with a lognormal clock and Yule speciation process. One secondary calibration was used at the crown node of the family based on previous results from Spalink *et al.* (2016) and Larridon *et al.* (2021). Those studies showed a similar estimation for the crown of the Cyperaceae with an estimate of 85.99 Mya vs. 85 Mya (95% Highest Posterior Density = 77–89 Mya), respectively. Therefore, we used a secondary calibration following a normal distribution with a mean of 85 Mya and a standard deviation of 5 Mya to include the uncertainty range in Spalink *et al.* (2016).

We conducted additional analysis sampling only from the priors to check whether the data might be overriding the set information. Moreover, we also tested exponential clock and birth–death process models to assess for any difference in the estimations. Every analysis was configured to run four MCMC simulations of 500 million generations, sampling the parameters every 5000 generations.

The output was examined in Tracer v.1.7.1 (Rambaut *et al.* 2018), which showed the chains reached the stationary plateau after around 100 million generations. Therefore, the burn-in parameter was set to 20%. The files from the different runs were joined into one using LogCombiner v.2.6.2 (Bouckaert *et al.* 2019) and a consensus of the trees was calculated using TreeAnnotator v.2.6.2 (Bouckaert *et al.* 2019) selecting the median values for node heights.

Biogeographical analyses

Species distributions were obtained from the Plants of the World Online database (POWO 2023). Since the ingroup is mainly distributed in Southeast Asia, which has undergone extensive geological changes and complex land bridge systems through time (e.g. de Bruyn *et al.* 2014), we coded the region in nine areas: Indochina plus Indian subcontinent, tropical China, Borneo, Java, the Malay Peninsula, the Philippines, Sulawesi plus the Maluku islands, Sumatra, and Papuasia plus Australia. We estimated the ancestral areas using the package BioGeoBEARS (Matzke 2014) as implemented in R (R Core Team 2023). We tested DEC (dispersal–extinction–cladogenesis; Ree and Smith 2008) and DIVA (dispersal–vicariance analysis; Yu *et al.* 2010) models for the analysis, and added a free *j* parameter in two additional models to test for founder speciation events. We did not consider any temporal stratification model or distance matrix between the areas (i.e. *x* parameter) as the Sunda shelf has undergone multiple sinking and emerging events over time (Hall 2013, Morley 2018).

RESULTS

Chloroplast analysis

The consensus tree based on all four chloroplast DNA regions produced a well-supported phylogeny, providing a better resolution compared with the single-region tree. The results of the combined analysis show *Mapania* as monophyletic, with *M. bancana* as an early diverging species in Southeast Asian Mapanias (Fig. 2). However, the support for that clade relative to the other specimens included in our study is only poorly recovered [0.90 posterior probability (pp), 74% SH-aLRT, and 74% UFBoot]. Nevertheless, this lineage is moderately supported (0.95 pp) in the one tip per taxon phylogeny (BEAST analysis, Supporting Information Appendix S2). Other lineages with unclear relationships in the phylogeny are the following clades: *Mapania sapuaniana* Shabdin plus *M. sessilis* Merr. with 0.94 pp, 75.3% SH-aLRT, and 61% UFBoot support, *M. cuspidata* var. *angustifolia* (Uittien) Uittien (1 pp, 90% SH-aLRT, 94% UFBoot), and *M. enodis* (Miq.) C.B.Clarke plus *M. cuspidata* var. *cuspidata* (0.93 pp, 22.8% SH-aLRT, 50% UFBoot). This last pair of taxa are not inferred as sisters in the one tip per taxon phylogeny (Appendix S2).

Biogeography and divergence time

The Southeast Asian *Mapania* lineage was inferred to have originated in the Miocene, around 17.76 Mya (95% Highest Posterior Density: 9.07–32.75 Mya, Supporting Information Appendix S2). Overall, the region corresponding to current Borneo is the most probable ancestral area of this clade in all the biogeographical models (Fig. 3). We detected the Malay Peninsula and Sumatra, or an extension of the region with Borneo (former Sunda) as another subcentre of diversification within the lineage. The analysis in BioGeoBEARS (Table 2) suggests DEC as the best-fitting model, with and without considering the founder effect parameter *j*. As the founder effect was inferred to be extremely low in those models ($j = 1 \times 10^{-5}$), we selected the simplest DEC model as the most suitable and will be used for the discussion hereafter.

DISCUSSION

Systematic implications

The species *M. bancana* (sect. *Thoracostachyum*) is sister to the rest of the species of *Mapania* included here, holding a similar position to the one inferred in the phylogeny constructed using only morphological data by Simpson (1992). Morphologically, the characters that separate section *Thoracostachyum* from section *Pandanophyllum* are the paniculate inflorescence and hard, non-fleshy fruits (Koyama 1959, 1961, Kern 1974, Goetghebeur 1986). *Thoracostachyum* has been treated as a genus by some authors (e.g. Kern 1974, Goetghebeur 1986) but others have treated is as infrageneric taxon within *Mapania* (e.g. Koyama 1959, 1961, Simpson 1992). The phylogeny in Simpson (1992) showed it to be a paraphyletic group but DNA sampling of more species needs to be carried out to obtain a better understanding of its taxonomic status.

Morphologically, *M. multiflora* Shabdin shares characters in common with both sections under study: a paniculate inflorescence and seven floral bracts as reported in section *Thoracostachyum* and linear-oblong leaf-blades with a
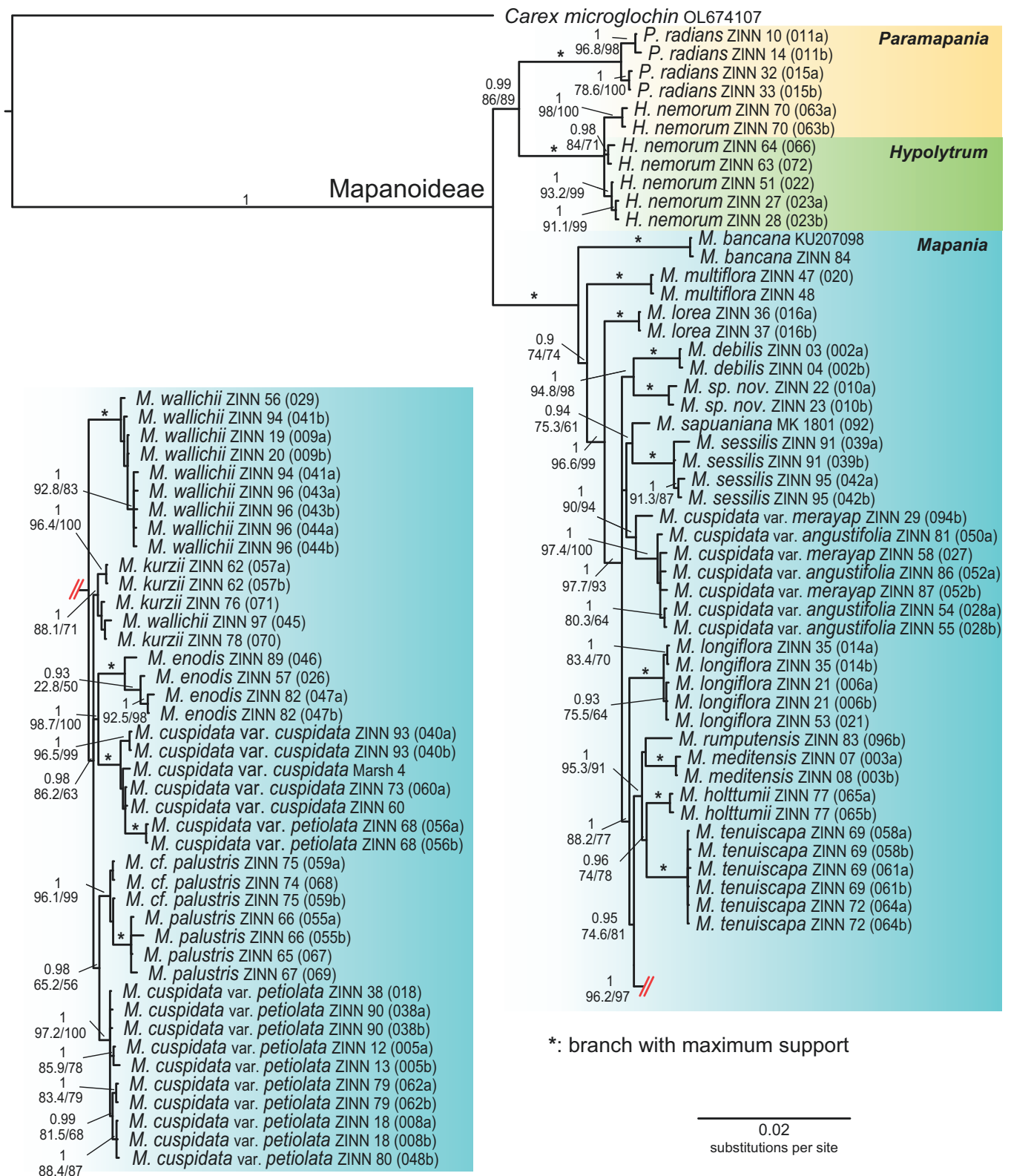
Figure 2. Phylogenetic tree using *trn*L-F, *atp*H-F, *psb*A-*trn*H, and *trn*K-*mat*K chloroplast markers. Branch support is indicated by posterior probability (pp), Shimodaira-Hasegawa approximate likelihood ratio (SH-aLRT), and ultrafast bootstrapping (UFBoot).

pseudopetiole found in some species of section *Pandanophyllum*. This could point to an apomorphic change of floral bract characteristics in *Pandanophyllum* and multiple origins of

pseudopetioles in the genus. Further sampling of section *Thoracostachyum* is needed to test sectional classification and allow assessment of character evolution.

The lineage comprising *M. sapuaniana*, *M. sessilis*, and *M. cuspidata* var. *angustifolia* has not been resolved in the phylogeny (Fig. 2). Although further studies will be required to improve the phylogenetic placement of these species, they are placed within sect. *Pandanophyllum*.

Mapania tenuiscapa C.B.Clarke formed a monophyletic group and shared the most recent ancestor with *M. holttumii*. Some specimens previously identified as *M. tenuiscapa* (ZINN 22 and ZINN 23) were recovered in another clade, sister to *M. debilis* C.B.Clarke (Fig. 2), despite being morphologically similar. The unknown species has shorter leaves than those of *M. tenuiscapa* when compared a posteriori. The fruit is ellipsoid, with a conical stipitate base that resembled *M. tenuiscapa*, but smaller in size. The included specimens are separated by relatively minor morphological characters. However, the specimens did not belong to the same group as *M. tenuiscapa*. Therefore, these samples might represent a new species, but the decision requires further study of morphological characters, especially when the inner part of the inflorescence has already matured into fruit, providing less information on the floral bracts, stigma, and anther size.

Mapania cuspidata is a species with four varieties [vars *cuspidata*, *angustifolia*, *petiolata* (C.B.Clarke) Uittien and *merayap* Miraadila, Shabdin & Meekiong]. Three of these appeared in different lineages of section *Pandanophyllum*, while vars *angustifolia* and *merayap* were resolved in the same clade. *Mapania cuspidata* is a highly variable species and has been proven to be difficult to differentiate due to the overlapping morphological variability in characters commonly used to separate the varieties (e.g. leaf length and width). Such a striking result highlights the need for further investigation into this and other taxa in the section, as the diversity of species of *Mapania* has been underestimated. These results could point to the need of elevating to species rank some of those varieties, but such a conclusion requires further taxonomic and genetic work. Since this study used chloroplast DNA, some of those varieties could be hybrids, being placed within the clades of the plastid donor. For instance, some samples of *M. cuspidata* var. *petiolata* are clustered with *M. cuspidata* var. *cuspidata* and not with the rest of the samples from that variety.

Biogeographical history of the lineage

We detected the centre of biodiversity and the origin of the Southeast Asian sections of *Mapania* in present-day Borneo, and a secondary region that includes the Malay Peninsula (Fig. 3). This suggests a Sunda origin for most of the species and continued diversification after the posterior sinking event of the Sunda shelf (Hall 2013, Morley 2018), pointing to what may be considered two subcentres of diversification in Southeast Asia: east Sunda (Borneo) and west Sunda (mostly Sumatra and the Malay Peninsula). Such an inference is compatible with a scenario of lowland forests connecting both areas, which has been estimated for those periods, including the Miocene (Morley 2018 and references therein). Therefore, *Mapania* could have inhabited larger areas of the Sunda ancestral forest and diversified under local conditions (e.g. within mountain ranges) or through vicariance to later expand their distribution as the Sunda shelf partially emerged or submerged over time (Hall 2013).

However, this study is focused on the Malay Peninsula species, and the addition of more species and further systematic work for the genus may show new subcentres of diversity that could add relevant information about the natural history of the lineage and elucidate dispersal routes out of Sunda into the Sahul region through Wallacea. For instance, a northern Sunda subcentre may be possible, as Vietnam hosts several endemic species that have not been included in this study [*M. balansae* (E.G.Camus) T.Koyama, *M. nudispica* T.Koyama, *M. tamdaoensis* N.K.Khoi, and *M. tonkinensis* (E.G.Camus) T.Koyama; POWO 2023].

Conservation priorities

There is an urgent need for biodiversity conservation, especially in tropical areas, due to a combination of climate change, deforestation, and lack of legal protection (Bowler *et al.* 2020). Only three species of *Mapania* from Southeast Asia have been included in the IUCN red list (IUCN 2023): *M. enodis*, *M. longiflora* C.B.Clarke, and *M. tonkinensis*. *Mapania tonkinensis* is evaluated as Data Deficient (DD), while the other two are considered Least Concern (LC). However, there is no curated georeferenced information about the distribution of these species, with all three taxa being considered to have similar threats, and only *M. enodis* is considered to have a declining population trend. Thus, this information is highly deficient and in need of an urgent, more detailed evaluation to accurately assess the future of species of *Mapania* so that they can be included in conservation programmes.

This work highlights undescribed diversity within *Mapania* and the further need to continue with systematic studies in Southeast Asian sedges. Only after extensive additional fieldwork to complete the gaps in knowledge will it be possible to obtain a comprehensive understanding of the diversity and distribution of and threats to *Mapania* in Southeast Asia.

Future directions

This study posits future lines of study on the genus *Mapania*. The inclusion of Southeast Asian species has allowed a better understanding of systematics of the genus and has also shown the need for including additional species of *Mapania* into more comprehensive molecular work. Moreover, it highlights aspects of what is known about these species, as reconsiderations are required in the concept of some taxa due to their polyphyletic placement. *Mapania cuspidata* demonstrates the importance of including specimens from different populations and infraspecific taxa to enhance our knowledge about possible cryptic species. Future studies will have to address the reasons underlying the reported taxonomic complexity. For instance, genomic traits, such as polyploidy, can be followed by an increase in the species distribution range or 'invasiveness', as they can develop pre-adaptations to new environments (Ellstrand and Schierenbeck 2000). Thus, a thorough investigation of the traits defining species and their evolutionary history would be immensely insightful for this ecologically and economically important genus. The need for further taxonomic and evolutionary studies is reinforced by the number of species that have been recently described for the region (Shabdin *et al.* 2013a, b, Miraadila and
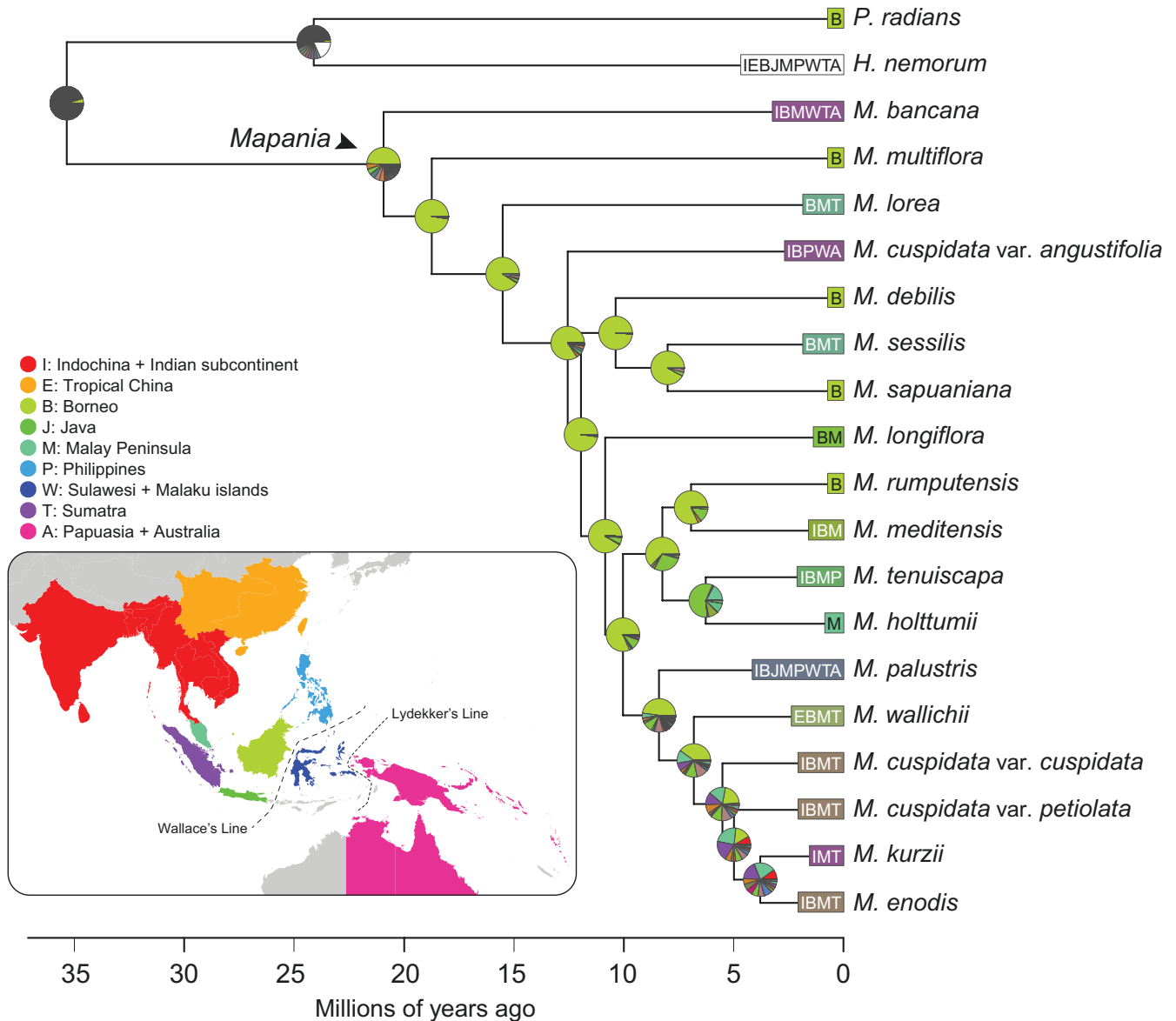
Figure 3. Ancestral area reconstruction inferred by the DEC model in BioGeoBears. Labels at the branch tips represent the regions where the species occur.

Table 2. Statistics from the biogeographical models (BioGeoBEARS) for the dated phylogeny of the subfamily Mapanioideae.

Model	Likelihood	Number of parameters	Dispersal (d)	Extinction (e)	Founder effect (j)	AICc
DEC	**−92.136**	**2**	**0.019**	**1×10^{-12}**	**0**	**189.02**
DEC+j	−92.137	3	0.019	1×10^{-12}	1×10^{-05}	191.87
DIVA-like	−96.065	2	0.024	0.031	0	196.88
DIVA-like+j	−96.065	3	0.024	0.032	1×10^{-05}	199.73

The best models are in bold type. AICc, corrected Akaike information criterion.

Shabdin 2016, Miraadila *et al.* 2016a, b) and the results of this study, where a few putative new species have been detected.

SUPPLEMENTARY DATA

Supplementary data are available at *Botanical Journal of the Linnean Society* online.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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