WEBBIA Journal of Plant Taxonomy and Geography

Firenze University Press
www.fupress.com/webbia

OPEN ACCESS

Citation: Frans J. Breteler, Floris C. Breman, Di Lei, Freek T. Bakker (2022) *Wrong flowers*? The evolutionary puzzle of *Jongkindia* (Passifloraceae s.l.), a new monotypic genus and tribe from Liberia, West Africa. *Webbia. Journal of Plant Taxonomy and Geography* 77(2): 229-246. doi: 10.36253/jopt-13470

Received: July 29, 2022

Accepted: November 7, 2022

Published: December 15, 2022

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Competing Interests: The Author(s) declare(s) no conflict of interest.

Editor: Riccardo M. Baldini

ORCID
FCB: 0000-0002-9722-7564
FTB: 0000-0003-0227-6687

Wrong flowers? The evolutionary puzzle of *Jongkindia* (Passifloraceae s.l.), a new monotypic genus and tribe from Liberia, West Africa

Frans J. Breteler[1], Floris C. Breman[2], Di Lei[2], Freek T. Bakker[2,*]

[1] *Grintweg 303, 6704 AR Wageningen, The Netherlands (previously Herbarium Vadense, Wageningen), fransbreteler@xs4all.nl*
[2] *Biosystematics Group, Wageningen University & Research, Postbus 647, NL-6700 AP, Wageningen, The Netherlands*
*Corresponding author. E-mail: freek.bakker@wur.nl

Abstract. *Jongkindia*, a small tree species endemic to a local area in southeast Liberia, is described as a new monotypic genus of Passifloraceae sens. lat. Its only species *Jongkindia mulbahii* combines floral characteristics of the Turneraceae and fruit characteristics of the Passifloraceae s.s. (or subfamily Passifloroideae in APG) and can therefore be regarded to occupy an isolated morphological position. This is confirmed here by DNA sequence-based phylogenetic analyses including most Passifloracean genera, which places it as sister to Passifloroideae. We delineate 16 morphological characters and their states and optimise them on our reconstructed phylogenetic tree. Based on these results we consider the Passifloraceae fruit characteristics (berries with arilled seeds) as synapomorphic for Passifloroideae. The monotypic *Pibiria* and *Jongkindia* are predominantly characterised by autapomorphies. On the other hand, the *Adenia*/*Passiflora* clade is characterised by polymorphisms. We place *Jongkindia* in a new tribe Jongkindieae Breteler & F.T.Bakker. A draft plastome sequence for *Jongkindia mulbahii* is presented and evidence for two mitome to plastome (mtpt) fragment transfers is discussed. Structurally the *Jongkindia* plastome appears similar to that of *Populus*, *Adenia*, *Mitostemma*, *Dilkea*, and *Passiflora pittieri*, but not to contain the previously-described major inversions within other, more derived, *Passiflora* plastomes.

Keywords: Passifloraceae, Passifloroideae, Turneroideae, plastome, floral evolution, West Africa.

INTRODUCTION

Ongoing botanical exploration of Liberia (Breteler 2020; Jongkind 2012, 2015a, b, c; 2016; 2017; 2019; Jongkind and Breteler 2020) revealed the presence of a thus far undescribed species of Passifloraceae s.l., near Sapo National park (Sinoe County, Liberia; see Figure 1) which contains "the second-largest area of primary tropical rainforest in West Africa." (Freeman et

Figure 1. Collection site of *Jongkindia mulbahii*, indicated by the red marker. Green area indicates boundaries of the Sapo National Park.

al. 2019). The undescribed species presented here appears somewhat of a conundrum: in spite of its 4- instead of 5-merous flowers it is best placed in Turneraceae (now Turneroideae sensu APG III (2009) and IV (2016)) because of its tubular calyx with the petals insterted on it and because of the absence of a corona (see Figure 10). However, Turneroideae have capsular fruits (Arbo 2007) whereas the new species presented here has an indehiscent fleshy fruit (see Figure 2), common in *Passiflora* (in Passifloroideae sensu APG).

Wurdack et al. (2009) maintained Turneraceae and Malesherbiaceae as separate under Passifloraceae s.l. but Takuoka (2012), based on comparison of rbcL, atpB, matK, and 18S rDNA sequences, considered a well-supported monophyletic Passifloraceae ss. and Turneraceae as (well-supported) sister groups. Both Xi et al. (2012), based on concatenated analysis of 82 plastid genes from 58 species, and Cai et al. (2021), based on multi-species coalescent analysis of 423 single-copy nuclear loci from 64 taxa, support a 'Parietal clade' in which Turneraceae and Passifloraceae are sister groups, with Malesherbiaceae sister to them. The two latter studies differ in the placement of Achariaceae, which is sister to the remainder of the Parietal clade (Xi et al. 2012) or in a derived position within it (Cai et al. 2021). Within the Parietal clade, the two studies differ with regards monophyly of the salicoids sensu Xi et al. (2012), which is supported by the concatenated analysis but not in any of the coalescent methods (Cai et al. 2021).

Within Passifloraceae s.s., Takuoka (2012) recognises monophyletic tribes Passifloreae and Paropsieae, wich is also adopted by APG. The first is distributed in the Old and New World and the second only in Old World (mainly Africa; Table 1). Maas et al. (2019) described the enigmatic 'unknown yellow' *Pibiria* as a lineage sister to Turneroidea and chose to place it at subfamily-level, which brings the number of recognised subfamilies in Passifloraceae to four, i.e. Passifloroideae, Turneroideae, Pibirioideae and Malesherbioideae

Given the remarkable combination of *Turnera*-like floral morphology and *Passiflora*-like fruits in the new species presented here it will be interesting to infer its phylogenetic position within this part of Malpighiales, known to present major challenges (such as incomplete lineage sorting, gene tree error and horizontal gene transfer) to phylogenetic reconstruction (Xi et al. 2012; Cai et al. 2020; APG IV). Therefore, we generated DNA sequences for this species, both Sanger and Illumina HiSeq, and compared it with publicly available sequence data for Passifloraceae s.l. We find our new species, which we refer to as *Jongkindia mulbahii* (see below), to be in an isolated position on a relatively short branch between, on the one hand, the Parietal clade (or Passifloroideae, to which it is sister) including a *Barteria*/*Paropsia* clade (both genera of small trees; Breteler 1999; 2003; de Vos and Breteler 2009), and the Turneroideae clade on the other. It is described and illustrated here as a new monotypic genus, and its draft plastome is compared with plastomes from *Adenia*, *Passiflora*, *Dilkea*, *Mitostemma* and allies.

Figure 2. *Jongkindia mulbahii* morphology. Abaxial surface glandular leaf tip (a), fruiting branch (b, c), with one fruit in longitudinal section (b) and sterile branch (d).

MATERIALS AND METHODS

Morphology

We delineated morphological characters and states in order to describe floral, fruit and vegetative morphology for our new species (see below under 'taxonomy') and its inferred allied genera (see below and Table 2). Characters were based on published taxonomic descriptions for the different genera (e.g. Feuillet and MacDougal 2007; Arbo 2007) plus our own observations (see the isotype specimen, Figure S1). We also included 'ecology' and habit in the descriptions in order to obtain a broad characterisation of all groups involved, within a phylogenetic framework.

DNA & Sanger sequencing

A few mgs of leaf tissue was used to extract DNA from, using standard CTAB protocols, including incubation with CTAB at 65°C, isopropanol precipitation at –20°C, followed by washing the DNA pellets with 70% EtOH. The DNA was dissolved in water and subjected to purification using the Promega clean-up system protocol. Cleaned DNA was then shipped to BGI HongKong, for library preparation and paired-end sequencing at the Illumina HiSeq2050 platform, using a read-length of 100bp. Part of the cleaned DNA sample was used for PCR amplification and Sanger sequencing of chloroplast rbcL, trnL-F as well as rDNA ITS regions, using standard protocols, and CodonCodeAligner (CodonCode Corporation, www.codoncode.com) for editing of sequence tracers.

Plastome assembly

Plastome contigs were assembled using GetOrganelle v20150226 (Jin et al., 2020) and IOGA (Bakker et al. 2016), the latter shown to be outperformed by the former (Freudenthal et al. 2019), but both having useful analytical aspects. For GetOrganelle we used default settings, for filtering plastid-like reads, conducting de novo assembly, purifying the assembly graph, and generating the plastome contigs. k-mer gradients were set as '-k 21,31,41,51,61,71,81,85,87,95,99'. For IOGA we used *Passiflora edulis* (NC_034285.1) as reference, and using only one instead of both Inverted Repeat (IR) regions in order to avoid possible artefacts related to assembling a linear sequence from a circular chloroplast genome. Typically, IOGA returns a full short single copy (SSC) region and full 'consensus IR', but the large single copy region (LSC) is usually recovered only in large parts, and compartments are rarely assembled together. Resulting contigs were assessed using nBLAST (www.ncbi.nlm.nih.gov, Altschul et al. 1990) in GenBank and then concatenated, along with the scaffolds from GetOrganelle, according to their position relative to the *Mitostemma brevilis* plastome. In GetOrganelle, contigs were automatically annotated as part of the post-assembly pipeline. Final assembly graphs, with connections between contigs, were visualized in Bandage (Wick et al. 2015). All data is available from the corresponding author on request, in addition all sequences will be available in GenBank.

Plastome structural analysis

Concatenated contigs were visualised using dotplots, generated at MAFFT on-line, in order to check plastome integrity and structure. Using the progressive Mauve algorithm, they were then aligned and visualised as Local Colinear Blocks (LCB's), relative to the *Populus trichocarpa*, *Adenia mannii*, *Mitostemma*, *Dilkea* and *Malesherbia* (partial) plastomes, in Mauve v2.3.1 (Darling et al. 2004) with default settings. One of the Inverted Repeats (B) was removed from all sequences (including the *Jongkindia* contigs) in order to not confound the alignment and allow for an optimal homology assessment (see Wicke et al. 2013). Strand orientation of the (numbered) LCBs was identified by progressiveMauve.

Phylogenetic analysis

Using *Populus alba* (Salicaceae) as outgroup, the Sanger sequences generated for our new species were used in nBLAST searches in GenBank and compiled into rDNA ITS, rbcL and trnL-F alignments using MAFFT (Katoh & Standley, 2013) with standard settings, apart from rDNA ITS where we used the 'Q-INS-I' iterative setting which considers secondary structure of RNA. In addition, an atpB alignment was compiled using one of the *Jongkindia* contigs as source and query for BLASTn searches. Alignments were then subjected to phylogenetic analysis using either IQ-TREE (Nguyen et al., 2015) for maximum likelihood based reconstruction (at the Vienna server), with the ultrafast bootstrap (Hoang et al. 2018) implemented in IQ-TREE, or MrBayes v3.2 (Ronquist et al., 2012) at a (local) laptop. For both, a partitioned analysis was set-up in which one partition contained codon positions 1+2 and the other partition contained codon position 3. A 10M generations Markov Chain was set-up using 'nst=mixed,

rates=gamma and temp=0.05' for mcmc settings. The MrBayes consensus tree was visualised using FigTree, whereas the last two-third of trees sampled in the MCMCMC were converted into a Consensus Network with conflict threshold of 5% using SplitsTree. Resulting consensus trees were compared and, as taxonomic sampling for each gene sequence had been independent and non-overlapping, a majority consensus topology was inferred by visual inspection. That topology was then imported into TNT, after which the 'Optimise synapomorphies' and 'Optimise characters' commands were used to optimise (under parsimony as criterion) the non-DNA characters listed in Table 2. We used Mesquite to visualise the optimizations on the overall consensus tree topology.

RESULTS

For a general description of biogeographic distribution of Passifloraceae genera and species see Table 1. For morphological characters and their state delimitation in representative genera of Passifloraceae see Table 2. We distinguished 16 morphological characters, predominantly describing floral structures. Some of these we treated as (unordered) multi-state with, for instance, character 8 (stigma shape) having states 0, 1, 2 and 3 and no á priori assumed plesiomorphic state.

DNA extraction and purification of our leaf sample yielded <100 ng of DNA, most of which was used for library construction and sequencing at BGI HongKong, where seven million read pairs (forward and reversed) were generated. The rest of the DNA extract was used

Table 1. Passifloraceae, number of genera and species (according to Stevens, P.F. (2001 onwards).

Passifloraceae	genera/species	Distribution
Turneroideae Eaton	12/227	Tropical to warm temperate America and Africa (incl. Madagascar and Rodriguez Island)
Passifloroideae Burnett	16/775	Tropics to warm temperate, especially Africa and America
Paropsieae de Candolle	6/22	Tropical Africa, Madagascar, Malay Peninsula
Passifloreae de Candolle	10/705	Tropics to warm temperate, especially Africa and America
Malesherbioideae Burnett	1/24	South America from Peru southwards, esp. N. Chile
Pibirioideae Chase & Christenh.	1/1	South America, Guyana

Table 2. Passifloraceae s.l. selected floral morphological characters and states, as well as vegetative characters, habit and ecology; *or nearly so.

	Character	States			
		0	1	2	3
1	Flowers	pedicellate	sessile		
2	Flowers per inflorescence	one	several		
3	4/5-merous	four	five		
4	Anther shape	non-sagittate	sagittate		
5	Nr. of stamens	four	five	many	
6	Nr. of coronas	absent	one	two	
7	Extrafloral nectaries	absent	present		
8	Stigmas	punctate	disc-shaped	capitate	lobate-penicillate
9	Ovules	few	many		
10	Androgynophore	absent	present		
11	Calyx	tubular	sepals free*		
12	Indumentum flower buds	non-resinous	covered in resin		
13	Fruits	berry	capsule		
14	Number of arils	zero	one	two	
15	Stipules	absent	present		
16	Indumentum	absent	present		
17	Habit	herb	shrub	tree	climber
18	Ecology	forest	open, scrubby vegetation		

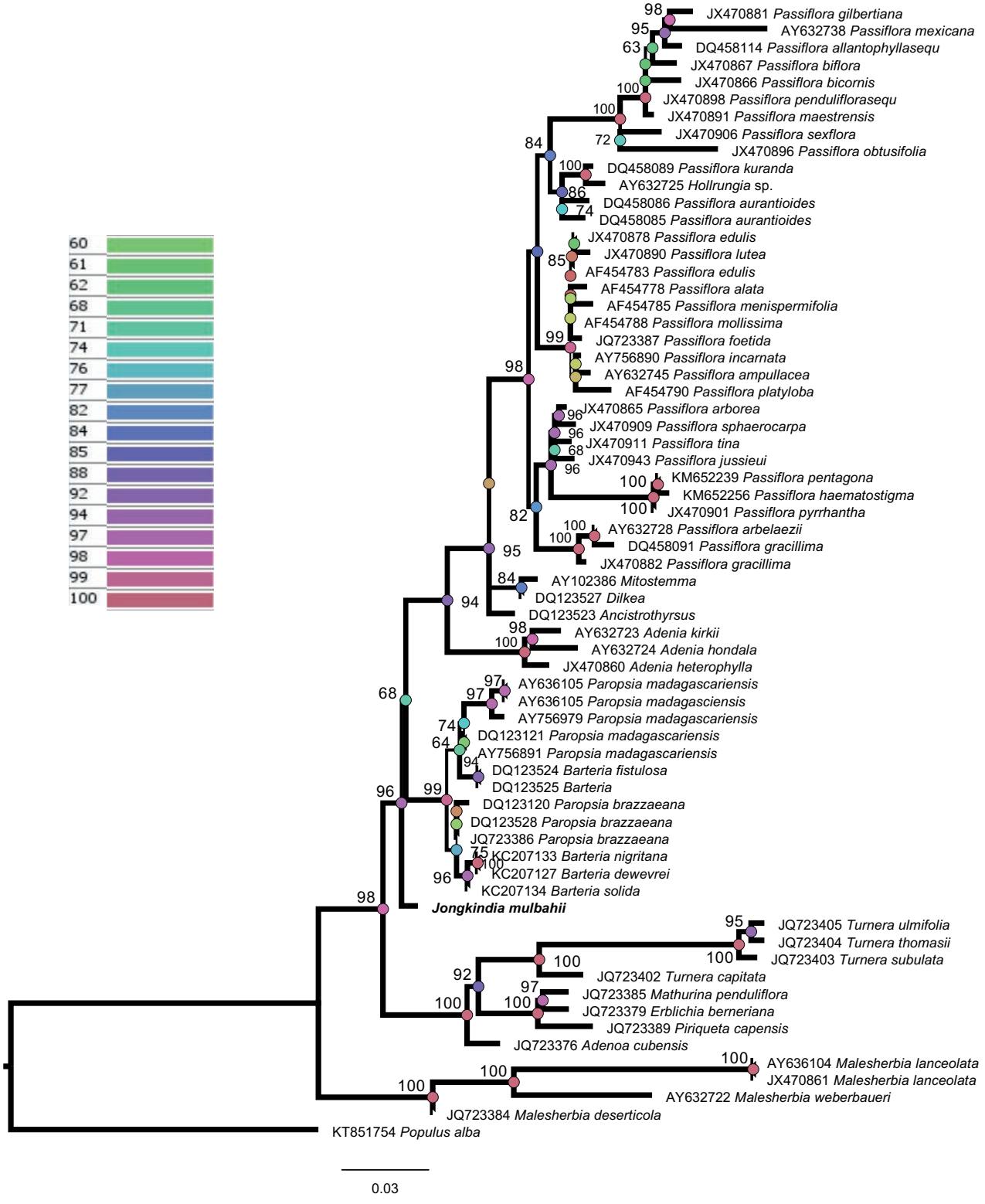

Figure 3. Maximum likelihood IQ-TREE analysis of trnL-F sequences, and rooted on *Populus alba*. *Jongkindia mulbahii* is shown in a well-supported position in between Turneroideae and Passifloroideae, but more closely related to the latter. Nodes without bootstrap frequencies indicate bootstrap values <60%. The colour coding indicates a range from green (no support) to red (100% support).

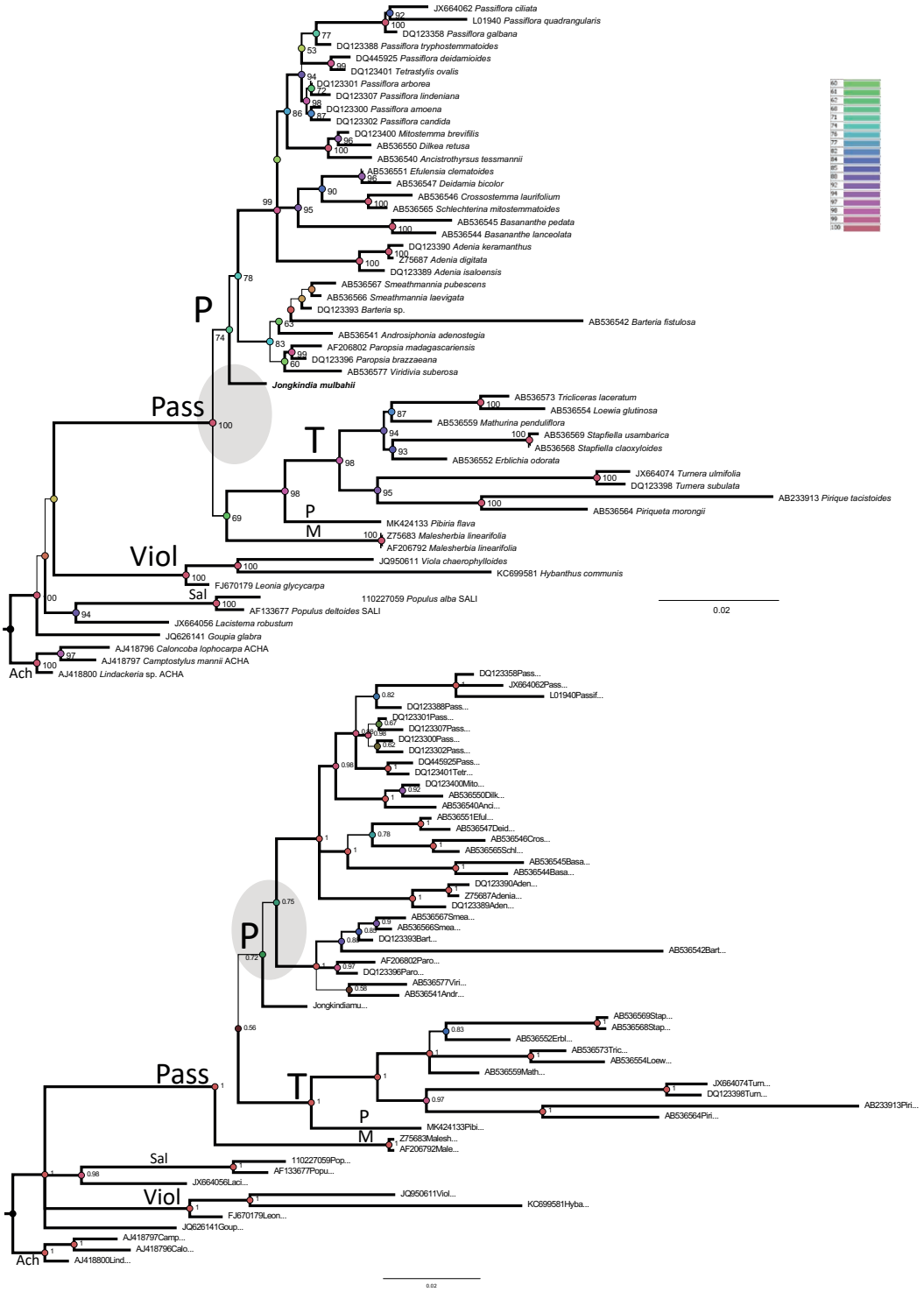

Figure 4. Passifloraceae phylogeny based on rbcL comparison, and rooted on Achariaceae; Maximum likelihood IQ-TREE analysis (top), using a partition according to codon position (1st +2nd versus 3rd); nodes without bootstrap frequencies indicate values <60%. And Bayesian Inference Markov Chain analysis (bottom) using the same data set and partitioning, with posterior probabilities indicated at the nodes. The colour coding indicates a range from green (no support) to red (100% support). Position of subfamilies Passifloroideae (P), Turneroideae (T), Pibirioideae (P), Malesherbioideae (M), as well as of Passifloraceae (Pass), Violaceae (Viol), Salicaceae (Sal) and Achariaceae (Ach) are indicated. In both analyses *Jongkindia mulbahii* is shown in a weakly-supported position, indicated with grey ellipses, in between Turneraceae and Passifloraceae, more closely related to the latter.

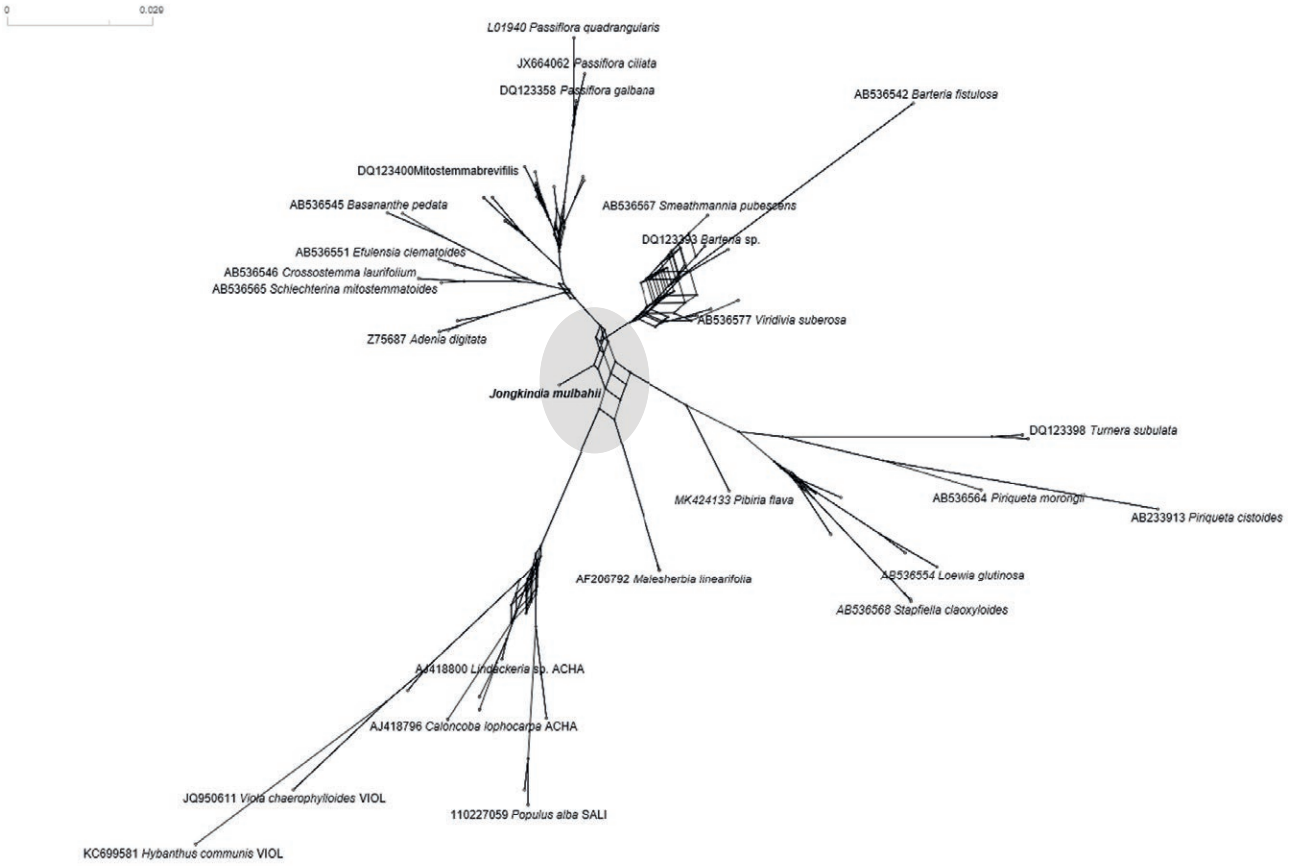

Figure 5. Passifloraceae phylogeny based on rbcL comparison, and rooted on Achariaceae; MrBayes analysis as in figure 5, summarised here as Consensus Network of the last 750 trees from one of the Markov Chains, using a splits-conflict threshold of 5% (NB in order to maintain readability not all terminal names are shown). The position of *Jongkindia mulbahii*, indicated with grey ellips, is shown in a relatively isolated position and connected with multiple splits to Turneraceae and *Barteria*/*Paropsia*.

for PCR and Sanger sequencing, aimed at phylogenetic reconstruction.

Phylogenetic analysis using chloroplast DNA as well as rDNA ITS sequences revealed that *Jongkindia mulbahii* has a relatively isolated position in between a Turneroideae clade and one containing Passifloroideae. Our new species is resolved as sister with low to medium support to a Passifloroideae clade containing *Barteria*, *Paropsia*, *Adenia*, *Mitostemma*, *Dilkea*, *Ancistrothyrsus* and *Passiflora*, supported by bootstrap values ranging between 68 and 99 (see Figures 3 and 4 for comparisons based on trnL-F and rbcL sequences) and 0.74 – 0.78 posterior probability (Bayesian rbcL, Figure 4 and 5). For rbcL comparisons we found a different tree topology and nodal support when comparing IQ-TREE ML and MrBayes tree inference (see Figure 4). Visualising among-tree conflict among the MrBayes Markov Chain tree sample of 751 trees with a Consensus Network (Figure 5) reveals that *Jongkindia mulbahii* is connected with multiple splits to (the outgroup) Achariaceae and Malesherbia and then to the other main clades. This could indicate that its rbcL sequence contains different, possibly conflicting, phylogenetic signals, whereas all other rbcL sequences in this analysis, apart from the *Barteria* clade and Achariaceae, show more 'tree-like' behaviour. For instance, *Pibiria flava* clearly groups with Turneroideae, without any extra splits separating its position. Phylogenetic relationships based on atpB were similar to those in the other trees with regards the placement of *Jongkindia mulbahii* (Fig S2) but indicated an incongruent placement of the Malesherbia clade, grouping as sister to Passifloroideae. This may be due to the fact that for atpB many more sequences were available in GenBank (stemming from Tokuoka 2012) and included in our alignment, as compared with the other marker regions. In any case is the (incongruent) position of Malesherbia clade not well-supported in our analyses, which is also apparent from the rbcL Consensus

Network (Figure 5). Phylogenetic relationships based on nrDNA ITS sequences (Figure S6) were congruent with those based on plastome sequences. Our four gene tree topologies then (trnL-F, rbcL, atpB and rDNA ITS) were overall congruent with regards the placement of *J. mulbahii*. A summary tree, placing *Malesherbia* as sister to

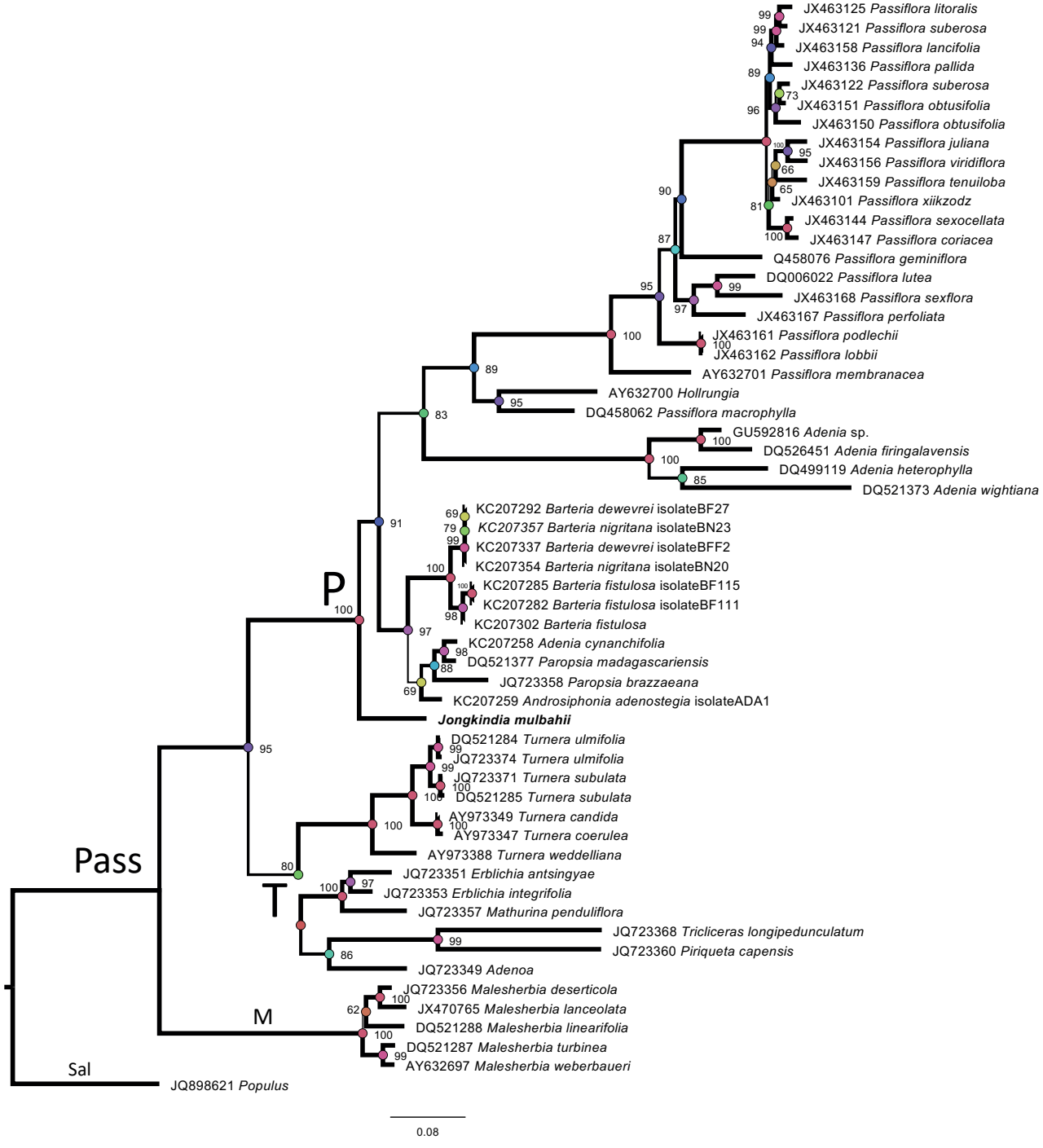

Figure 6. Passifloraceae phylogeny. Maximum likelihood IQ-TREE analysis of rDNA ITS sequences. *Jongkindia mulbahii* is shown in a well-supported position in between Turneroideae and Passifloroideae. Nodes without bootstrap frequencies indicate values <60%. The colour coding indicates a range from green (no support) to red (100% support). NB *Adenia* appears polyphyletic, however we suspect this could be due to mis-identification of the *Adenia cynanchifolia* KC207258 specimen.

Table 3. Scoring of characters in Table 2 for selected terminals in Passifloraceae. Question marks indicate unknown state.

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.
Adenia	0	1	0/1	0	0/1	0/1	1	3	1	0	0/1	0	0/1	1	1	1	0/1/3	0/1
Barteria	1	1	1	0	2	2	1	2	1	0	0	0	0	1	0	1	2	0
Erblichia	0	0	1	0	1	1	1	3	0	0	1	0	1	1	1	1	1/2	1
Jongkindia	1	0	0	0	0	0	1	1	1	0	0	1	0	2	1	0	2	0
Malesherbia	0	0	1	0	1	1	0	0	1	0	1	0	1	0	0	1	0/1	1
Paropsia	0	1	1	0	1	1	1	1	0	1	1	0	0	1	1	1	1/2	0/ 1
Passiflora	0	1	1	0	1	1	1	1/2	1	1/2	1	0	0	2	1	0/1	3	0/ 1
Pibiria	0	1	1	1	1	0	0	0	0	0	0	0	?	?	0	1	1	0
Piriqueta	0	0/1	1	0	1	1	0/1	3	1	0	0	0	1	1	0/1	1	0/1/2	1
Turnera	0	0/1	1	0	1	0	1	3	1	0	0	0	1	1	1	1	0/1/2	0/1

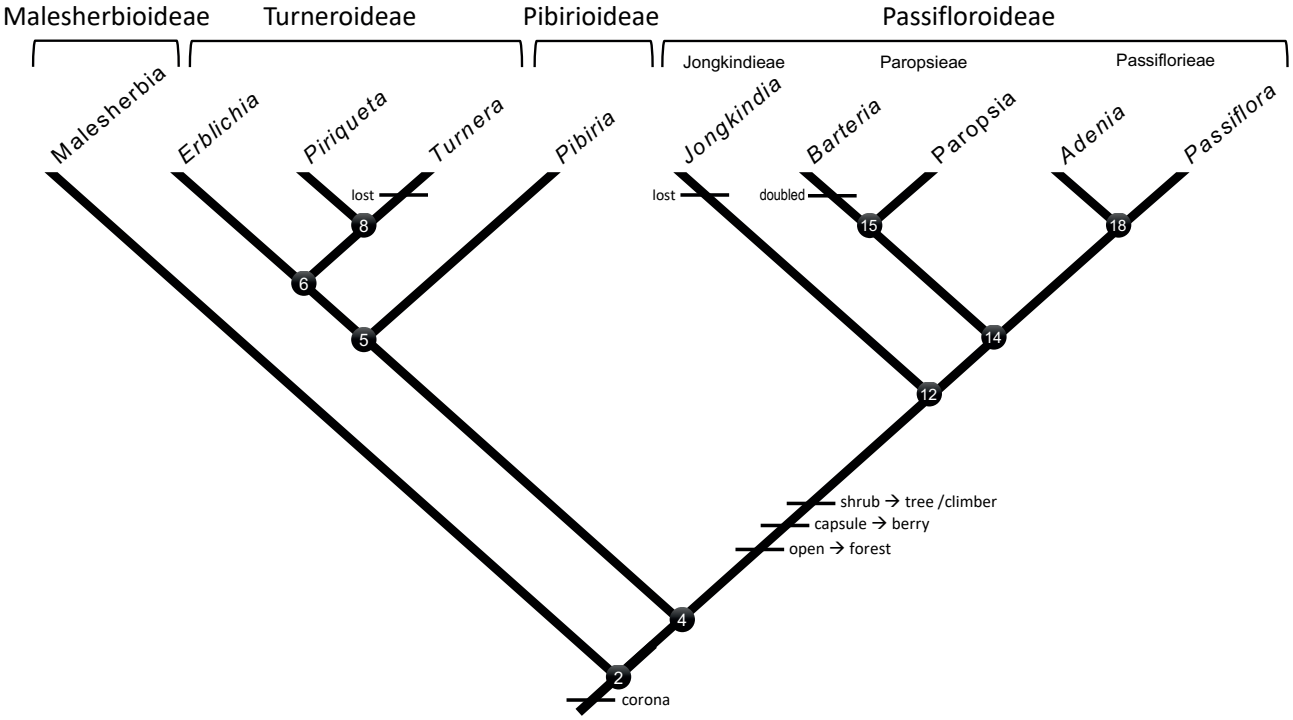

Figure 7. Summary tree depicting phylogenetic relationships in Passifloraceae s.l. based on chloroplast and rDNA sequence comparisons (see Figures 3-6), using exemplar genera to represent the clades. Note that Paropsieae also includes the African genera *Viridivia*, *Paropsiopsis* and *Smeathmannia* and that Passiflorieae also includes *Deidamia*, *Basananthe*, and *Ancistrothyrsus*. Node numbers and (selected) character state changes are indicated; 'lost' and 'double' refer to corona. For individual character optimizations see suppl. figure S4.

all other lineages, was inferred 'by eye' (Figure 7) and used to optimise the non-DNA characters inferred for the entire ingroup, using TNT. This topology was also found by Xi et al. 2012, based on plastome comparisons across Malpighiales.

Results from the morphological character optimisation (Figures 7, S3 and S4) indicate that i) Turneroideae and Passifloroideae are distinguished mainly by fruit type (capsular versus berry) and ii) that coronas have been lost in both *Turnera* and *Jongkindia*, but doubled in *Barteria*. Furthermore, we observe that whereas *Jongkindia* and *Pibiria* are characterised by significantly higher amounts of apomorphies than all other lineages, *Adenia* and *Passiflora* on the other hand show almost predominantly polymorphisms (see Fig. S3). No other lineage in our sampling exhibits such a level of polymorphism and

could perhaps indicate their relatively recent origin or the occurrence of hybrids among these species. When looking at the ancestral states (Table S1) we see that for the most recent common ancestor of the Passifloroideae clade (node 12 in Figure 7) our reconstruction would imply a forest-dwelling tree with single, pedicellate, 5-merous flowers, a corona, extrafloral nectaries but no androgynophore. Its flowers would have many ovules and its fruits would be berries with single-arilled seeds; vegetatively, it would have stipules as well as indumentum on its leaves.

It took GetOrganelle only a few iterations to complete the plastome assembly process. This yielded 78 contigs (nodes) and 48 connections (edges) between them with a total length of 168.577 bp (163.172 without overlaps). This is slightly longer than the *Passiflora edulis* plastome length of 151,406bp (KX290855.1, Cauz-Santos et al. 2017). Nodes had an N50 of 3.985 bp and the longest node was 14,535 bp. The median read depth across all nodes was 18,7x and nodes were connected by Bandage into 33 'components' (see Fig. 8), the largest of which was 70,320 bp long. Total length of unconnected ('orphaned') nodes was 93,826 bp. It took IOGA >75 iterations to complete the assembly process which was stopped when no apparent N50 increase was observed. This yielded many contigs >1000bp with N50 =14,796. nBLAST analysis of the obtained contigs revealed that both plastome and mitome fragments had been assembled (with comparable read coverages each) and that *Jongkindia* IRs, SSC and LSC compartments had been partly assembled. Contigs from GetOrganelle and the IOGA analyses were mixed and mapped to the *Mitostemma brevilis* plastome (Fig. S6) which was covered by appr. 90%.

Given the fact that that several *Jongkindia* mitome sequences were assembled using a plastome reference,

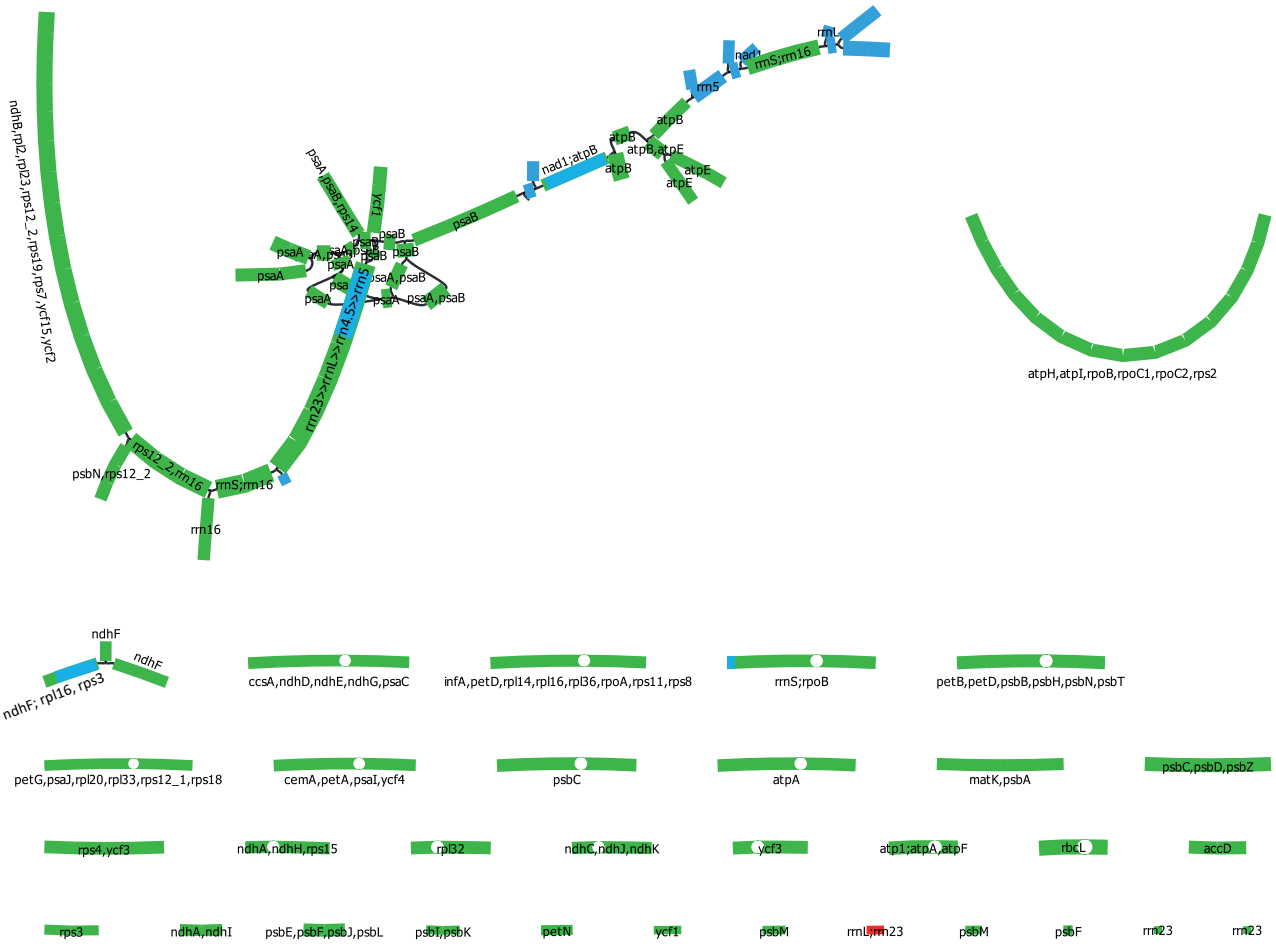

Figure 8. *Jongkindia mulbahii* mitome (blue) and plastome (green) assembly scaffolds sorted by size (kb) and resulting from GetOrganelle assembly using plastome reference sequences. Relative position and BLASTn hits of main contigs as reconstructed in GetOrganelle (see text) is indicated.

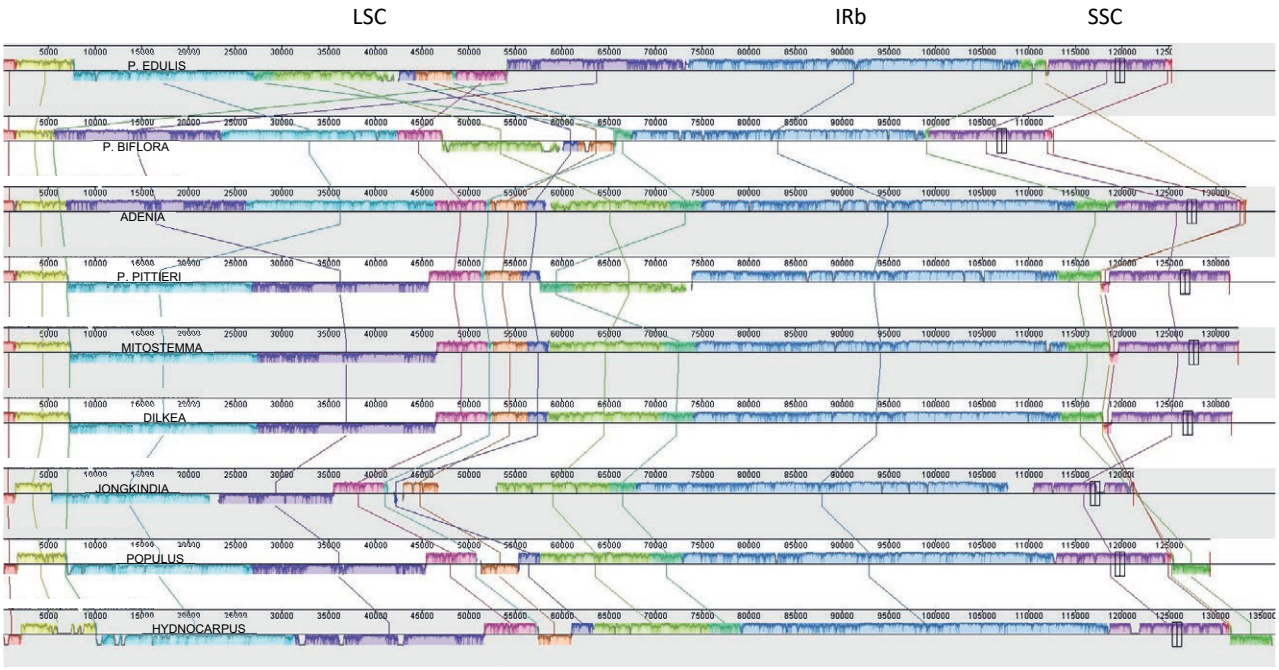

Figure 9. Mauve plastome alignments comprising the large single copy region (LSC), one of two inverted repeats (IRb) and the short single copy region (SSC). Shown are (from top to bottom, and approximately in phylogenetic arrangement) *Passiflora edulis* NC034285 (length 151,286), *P. biflora* NC038120, *Adenia mannii* NC043791 (length 165,364), *P. pittieri* NC 038125, *Mitostemma brevifilis* MT525867 (length 163,032), *P. edulis* MF807938, *Dilkea retusa* NC053302, *Jongkindia mulbahii*, *Populus trichocarpa* NC_009143.1 (length 157,033) and *Hydnocarpus hainanensis* (Achariaceae) NC_042720.1 (length 163,330). NB for *Malesherbia* only the IRb is available in GenBank and was therefore not included here. Colours indicate different Local Colinear Blocks and their relative position is indicated by coloured lines. Position of scaffolds indicates directionality relative to the reference, i.e. above the line is same orientation, below the line is in reverse orientation.

we interpret this as plastome fragments having, at some stage in the evolution of this lineage, been transferred to mitomes. This process, yielding so-called *mtpts*, has been documented as fairly frequently occurring among angiosperm organelle genomes (Jansen & Ruhlman 2012; Wang et al. 2007; 2017). Gandini and Sanchez (2018) estimate that "one out of five plant mtDNAs received plastid sequences by HGT". In case such a mtpt is still present in the reference plastome, it could prime the assembly process, extending the iterative assemblies into neighbouring mitome sequence. We found one scaffold consisting of both plastome and mitome associated contigs of 400-600bp, which means that read pairs had been found with one read being plastome-derived and the other stemming from the mitome, indicating the two sequences had been in linear order. We found the presumed *Jongkindia* mtpts to correspond to the consecutive atpB—atpE—ndhC intron region in *P. edulis*, which is part of the LSC. This region was found to comprise the smaller of two reversals found in *Passiflora* when compared across 12 Malpighialan plastomes (Cauz-Santos et al. 2017). The same region was also found to represent a mtpt in *Geranium brycei* (Adams et al. 2000), and for atpB in *Sapria himalayana* (Rafflesiaceae; Bock 2010).

The plastome structural analysis (Figure 9) indicated overall good alignability among the *Jongkindia* draft plastome with the other plastomes included. The dotplots (Figure S5) showed that *Jongkindia* contains, apart from the two Inverted Repeats, two small inversions which are present in all other plastomes too. It also clearly shows that with regards *Passiflora pittieri* there is a main inversion stretching from positions 20–65kb. This is also visible in the Mauve structural alignment in Figure 9, around 7–47kb. The implication is that *Jongkindia* has a *Paropsieae*/*Adenia* – like plastome structurally, and the elevated structural rearrangements known to have occurred in *Passiflora* plastomes (Cauz-Santos et al. 2017) occurred later within the *Passiflora* clade.

DISCUSSION

Jongkindia mulbahii as described here presents an interesting case evolutionarily as it combines a typical *Passiflora* (Passifloroideae) fruit syndrome with a Turneroideae floral syndrome. Assuming our summary tree reflects phylogenetic relationships accurately, *Jongkindia*

mulbahii is in an isolated position phylogenetically, but not quite divergent from all other species groups in Passifloroideae, as judged from its moderate DNA-based branch lengths. This could indicate there having been other Jongkindia species now extinct, but probably no substitution rates increase in *J. mulbahii* after it split off from its common ancestor with the rest of Passifloroideae.

The fleshy fruits (berries) of *J. mulbahii* should be considered synapomorphic for Passifloroideae (Figure 7, S3 and S4) and this would imply that the 'genomic wiring' of *J. mulbahii* with regards to fruit formation and structure was already in place in the most recent common ancestor (MRCA) of this clade. In contrast, floral morphology for *J. mulbahii* appears to be less straightforward to interpret: its 4-merous flower seems to be, along with *Viridivia*, the only cases in Passifloraceae s.l. and can probably be considered independent autapomorphies. The absence of a corona in *J. mulbahii* should probably be interpreted as a secondary loss, as coronas are known from Turneroidea as well (but not *Turnera*, Figure 7, S3 and S4). For instance, the Neotropical *Piriqueta* is known to have coronas developed from calyx and a corolla not unlike that of *Passiflora* (Bernhard 1999). This could point to homology between the two clades with regards to their coronas, and possibly *Jongkindia* may have lost a corona 'secondarily' whereas in *Barteria* it got doubled (as well as in its sister group *Paropsiopsis*). Nevertheless, whether Turneroideae and Malesherbiodeae coronas are truly homologous with that what got lost in *Jongkindia* could be assessed based on, for instance, developmental studies, such as carried out by Bernhardt (1999). He concluded that the ancestral androecium for Passifloroidea would have been a single whorl. In our ancestral state analysis we reconstructed the MRCA of Passifloroidea (node 12 in Figure 7) to be a forest-dwelling tree with single, pedicellate, 4-merous flowers, a corona, extrafloral nectaries but no androgynophore, many ovules and berries with single-arilled seeds. It can be argued that this reconstruction might change upon the inclusion of additional Passofloracean lineages but nevertheless, we interpret our inferred pattern as indicative of conserved fruit morphology combined with unstable /labile floral morphology. *Jongkindia* would then have developed maintaining the Passifloracean fruit morphological syndrome but developing a new autapomorphic floral syndrome that could perhaps reflect adaptation to new environmental conditions in Miocene tropical Africa. To what extend pollinator-use may have played a role here is not known, but probably floral evolution was more 'adaptive' or under selective pressure (at least exerted by pollinators) then fruit morphology, for which the genomic wiring was probably already in place in the proto-*Jongkindia* lineage.

In the *Adenia*/*Passiflora* clade, we reconstructed predominantly polymorphic characters (see Figure S3) and interpret this as reflecting the possible young age of these clades, the occurrence of hybridization(?), biparental inheritance of plastids in *Passiflora* (Hansen et al. 2007) and possibly the occurrence of dioecy in *Adenia*. In such a scenario, with transitions in breeding system, evolutionary stasis or dead ends have been suggested but evidence is accumulating that this does not need to be the case (e.g. Muyle et al. 2020; Takahashi et al. 2022). Moreover, the genetic consequences of dioecy at the population level, for instance effective population size, are not yet fully understood, but may be relevant to the occurrence of (morphological) polymorphism.

Plastomics

For *Jongkindia mulbahii* we assembled appr. 90% of its plastome sequence as compared with *Passiflora edulis* and *Mitostemma*, currently the most closely-related plastomes available to date. Direction of our scaffolds relative to *Populus trichocarpa* and *Hydnocarpus hainanensis* (Achariaceae) was straightforward to determine and within the scaffolds itself we infer only a few rearrangements, especially within SSC and LSC. This leads us to conclude that the *Jongkindia* plastome looks rather similar in terms of genome structure to that in *Adenia*, *Mitostemma*, *Dilkea* and parts of *Passiflora*, especially the early-branching *P. pittieri* (see Cauz Santos et al. 2017). 'Downstream' in the Passiflora clade several inversions have occurred, sometimes overlapping but this has to be confirmed by *Malesherbia* plastome data (currently, only *Malesherbia* IRb plastome sequence is available in GenBank). In any case, plastome structural rearrangements in *Jongkindia* appear not to be present at the scale as seen in some other plants groups, e.g. in *Silene* (Sloan et al. 2014) and in *Pelargonium* (Weng et al. 2017). We argue that *Jongkindia* will be a suitable outgroup for future plastome evolution studies in Passifloraceae.

We found a possible *Jongkindia* mtpt to be in exactly the same atpB—atpE—ndhC region as where in Passiflora a reversion was reconstructed (and confirmed with PCR and Sanger sequencing) when compared across 12 Malpighialan plastomes by Cauz-Santos & al. (2017). It is interesting to find this same region to have probably moved to the *Jongkindia* mitome, and in addition in *Geranium brycei* (Adams et al. 2000), and for atpB in *Sapria himalayana* (Rafflesiaceae; Bock 2010). Whether this pattern is co-incidence or a structural factor or mechanism is involved remains to be investigated. In terms of mechanisms, whether inversions and transfers are related is not

known yet. Rice et al. (2013) proposed a 'fusion-compatibility' model in which a foreign mitochondrion is captured, with subsequent fusion and genomic recombination of donor and recipient mitochondria. Gandini and Sanchez (2018) estimate that in most observed cases (i.e. 65%) mtpts are the result of mt—mt HGT following pt—mt transfer, rather than direct pt—mt transfer, although the amount of angiosperm mitome sequence data is still not sufficient in order to substantiate this further. It is not known to what extent *Jongkindia mulbahii*, like *Passiflora*, has biparental inheritance too and if so, whether it could explain the conspicuous mtpts found in our study.

In conclusion, we describe a new monotypic genus of Passifloraceae sens. lat., with the only species *Jongkindia mulbahii* combining floral characteristics of the Turneraceae and fruit characteristics of the Passifloraceae s.s. (or subfamily Passifloroideae). Phylogenetic analysis based on plastome-derived sequence comparisons places *Jongkindia* 'in between' the Passifloroidea and Turneroideae clades, but clearly more closely related to the former. We present evidence for two mitome-plastome fragment transfers in this species which correlate with transfers for the same region in other lineages. As a possible explanation for the 'chimaeric' morphological syndrome in *Jongkindia mulbahii* with its 'wrong flowers' we consider the following historical scenario: An ancestral polymorph proto-Passifloracean lineage in Africa, at the population-level and possibly driven by late Miocene/Pliocene climatic changes, as well as the earlier, Eocene Whole Genome Duplication events reconstructed in Malpighiales (Cai et al. 2019), would have undergone fixation, development and splitting into two lineages with either the Turneroideae or the Passifloroidean syndrome. Subsequent 'canalisation' and sorting of the genomic wiring of either syndromes would have fixed the capsule and berry syndromes that we still recognise today. Subsequently, and possibly by jump dispersal, *Passiflora* will have ended-up in Neotropics, and perhaps it was in Africa too but went extinct. In any case, the radiation of 600+ species of *Passiflora* in the Neotropics indicate that selection and pollinator pressures there must have been quite different from what was experienced in Africa, where *Jongkindia* did not undergo extensive floral morphological changes, keeping a more symplesiomorphic floral appearance. As such the Passifloroideae biogeographic pattern supports the more general pattern (e.g. Good 1964, Slik et al. 2015) of higher generic but lower species-diversity in Africa as compared with Neotropics.

TAXONOMY

Jongkindieae Breteler & F.T.Bakker, **trib. nov.**

Diagnosis

Small trees with *Turnera*-like, 4-merous flowers without corona and *Passiflora*-like, baccate fruits with arillate seeds. The phylogenetic position of this tribe as sister to Passifloreae plus Paropsieae is confirmed by chloroplast and rDNA sequence comparisons. Type: *Jongkindia* Breteler & F.T. Bakker

Jongkindia Breteler & F.T.Bakker, **gen. nov.**

Diagnosis

Glabrous treelet with alternate, glandular-dentate, simple, stipulate leaves and single, axillary, shortly pedicellate, bisexual flowers. Calyx tubular in lower half and with free petals inserted on rim of the calyx tube. Flowers *Turnera*-like, differing by being 4-merous. Fruits fleshy, many-seeded, indehiscent, typical *Passiflora*-like. Species: one. Type species: *Jongkindia mulbahii*.

Jongkindia mulbahii Breteler & F.T.Bakker, **sp. nov.** (Fig. 1, 10).

Type: LIBERIA. Sino, c. 50 km E of Greenville, riverbank forest, 5°05.09'N, 8°32.02'W, Alt. 56 m, 13 Mar. 2014 (fl., fr.), *Jongkind, Mulbah, Harris, Chaleson & Forkpah 12424* (holotype BR!, two sheets numbered BR 0000014915833 and BR 0000014915826); isotypes B!, COI!, G!, K!, LISC!, MA!, MO!, NY!, PRE!, WAG!).

Description

Treelet c.5 m tall and 5 cm dbh, glabrous in all its parts. Branchlets green, bark soon becoming brown and glossy. Stipules thick, deltoid to rim-like, up to 1 mm long, sometimes gland-tipped. Leaves distichous, subsessile; lamina coriaceous, ovate-elliptic to narrowly lanceolate, 2.5–4 times as long as wide, 4–10 x (1–)1.5–2.5(–4) cm, long-cuneate at base, gradually tapering to an acute to narrowly rounded apex or slightly, 0.5–1.5 cm acuminate; margin shallowly dentate, the teeth provided with a gland beneath; midrib and the 6–8 pairs of main lateral nerves ± equally prominent both sides. Flowers bisexual, 4–merous, yellow, solitary in the leaf axil; buds covered with resin, c.8 mm long in full grown state. Bracteoles small, rim-like ≤ 0.2 mm long. Pedicel articulate, the lower part c. 1 mm long, the upper part c. 2 mm long. Sepals united into a 3 mm long funnel-shaped base (hypanthium); lobes

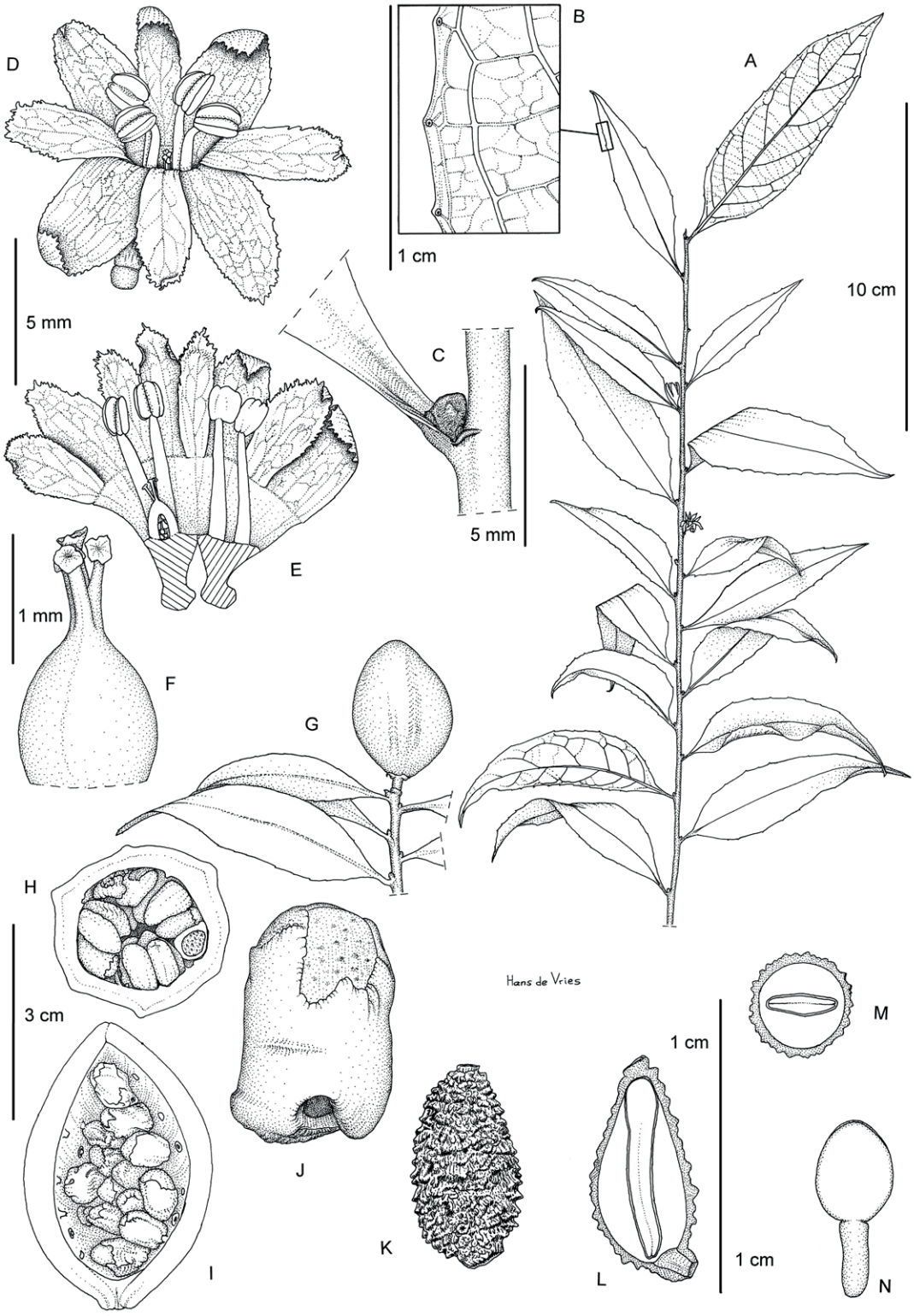

Figure 10. *Jongkindia mulbahii* morphology, with a) flowering branch zooming in b) on leaf margin at the abaxial leaf surface showing glands; c) leaf axil with resinous flower bud and stipule; d) flower; e) flower cut and laid open; f) pistil; g) branchlet with fruit; h) fruit in transverse section; i) fruit in longitudinal section; j) seed with arils; k) seed; l) seed in longitudinal section; m) seed in transverse section; n) embryo. After *Jongkind et al. 12424* (BR), see suppl. figure S1. Drawn by Hans de Vries.

imbricate, spreading at anthesis, oblong, c. 5 mm long, slightly hooded at apex, scarcely fimbriate in apical part. Petals spreading, free, valvate, inserted on the rim of the calyx tube and alternate with the calyx lobes, fimbriate in the upper half, slightly hooded at apex. Stamens 4, ± erect, alternate with the petals, free, inserted on the calyx tube near its base, c. 5 mm long; anthers exerted, c. 1.5 mm long, introrse, dorsifixed. Pistil c. 2 mm long, inserted on the bottom of the calyx tube; ovary ovoid, c. 1 mm long, with 3 multiovulate, parietal placentas; styles 3, c. 1 mm long, stigmas ± flat, ± circular in outline. Fruit indehiscent, orange, ellipsoid, (5–) 6–angled, slightly ribbed, 3–5 cm long, 2–3 cm in diameter, smooth, slightly glossy; wall 3–4 mm thick. Fruit stipe 3 mm long. Seeds numerous, black, ellipsoid, c. 7 mm long, tuberculate, with a ± thick, lobulate, free outer aril of 7–8 mm long, covering the seed for ⅔–¾ of its length, bulging over the hilum and an inner, thin, free aril, tightly covering the seed completely. Testa corrugate. Endosperm copious. Embryo straight, embedded in white, more or less soft endosperm.

Etymology

The generic name is derived from C.C.H. Jongkind, the first collector of the type specimen. He is best known as co-author of Woody Plants of Western African Forests (Hawthorn and Jongkind 2006) and continues his botanical exploration of western african forests, especially of Liberia. The specific epithet of the species is after D.M. Mulbah the second collector.

Distribution

SE Liberia (Figure 1).

Habitat and Ecology

Understorey treelet in primary riverine forest at low altitude of 56 m.

Conservation

The status of the new taxon cannot be calculated because of deficient data. Given the inconspicous habit of *Jongkindia mulbahii* it is likely that more individuals go unnoticed and therefore the area around its collecting locality needs to be further explored to establish *Jongkindia* distribution. Noticeably, the area is supposed to be rich in gold and may be exploited in the near future.

ACKNOWLEDGEMENTS

We would like to thank Hans de Vries for providing the line drawings in Figure 10. We thank an anonymous reviewer for constructive and thoughtful comments, and we thank Carel Jongkind for fruitful discussions.

REFERENCES

The Angiosperm Phylogeny Group. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society. 181: 1–20.

Adams KL, Daley DO, Qiu YL, Whelan, J. & JD Palmer. 2000. Repeated, recent and diverse transfers of a mitochondrial gene to the nucleus in flowering plants. Nature. 408, 354–357

Altschul B, Gish SF, Warren, Miller, Webb, Myers, Eugene W., and Lipman, David J. 1990. Basic local alignment search tool. Journal of Molecular Biology. 215: 403-410.

Arbo 2007. Turneraceae. In Kubitzki K, Bayer C, and Stevens, PF (eds.) The Families and Genera of Vascular Plants. Volume IX. Pp. 458-466. Springer.

Bakker FT, Lei D, Yu J, Mohammadin S, Wei Z, van de Kerke S, Gravendeel B, Nieuwenhuis M, Staats M, Alquezar-Planas DE, Holmer R. 2016. Herbarium genomics: plastome sequence assembly from a range of herbarium specimens using an Iterative Organanelle Genome Assembly pipeline. Biological Journal of the Linnaean Society. 117: 33–43.

Bankevich AS, Nurk D, Antipov AA Gurevich, M. Dvorkin, A. S. Kulikov, V. M. Lesin, S. I. Nikolenko, S. Pham, A. D. Prjibelski, A. V. Pyshkin, A. V. Sirotkin, N. Vyahhi, G. Tesler, M. A. Alekseyev and P. A. Pevzner. 2012. SPAdes: a new genome assembly algorithm and its applications to single-cell sequencing. Journal of Computational Biology. 19: 455-477.

Bock, R. 2010. The give-and-take of DNA: horizontal gene transfer in plants. Trends in Plant Science. 15: 11–22.

Breteler F.J. 1999. *Barteria* Hook. f. (Passifloraceae) revised. Adansonia. 21(2): 307-318.

Breteler F.J. 2003. Novitates Gabonenses 48. A new species of *Paropsia* (Passifloraceae) from Gabon. Adansonia. 25(2): 247-249.

Breteler F.J. 2020. *Antidesma jongkindii* (Phylanthaceae), a new species from Liberia. Plant Ecology and Evolution. 153(2): 321-324.

Cai L, Xi Z, Amorim AM, Sugumaran M, Rest JS, Liu L, CC Davis. 2019. Widespread ancient whole-genome duplications in Malpighiales coincide with Eocene global climatic upheaval. New Phytologist. 221: 565-576

Cai L, Xi Z, Moriarty Lemmon E, Lemmon AR, Mast A, Buddenhagen CE, Liu L and CC Davis. 2021. The Perfect Storm: Gene Tree Estimation Error,

Incomplete Lineage Sorting, and Ancient Gene Flow Explain the Most Recalcitrant Ancient Angiosperm Clade, Malpighiales. Systematic Biology. 70(3): 491–507, https://doi.org/10.1093/sysbio/syaa083

Camacho C, Coulouris G, Avagyan V, Ma N, Papadopoulos J, Bealer K and TL Madden. 2009. BLAST+: architecture and applications. BMC Bioinformatics. 10: 421.

Cauz-Santos LA, Munhoz CF, Rodde N, Cauet S, Santos AA, Penha HA, Dornelas MC, Varani AM, Oliveira GC, Berges H., Vieira ML. 2017. The chloroplast genome of *Passiflora edulis* (Passifloraceae) assembled from long sequence reads: Structural organization and phylogenomic studies in Malpighiales. Frontiers in Plant Science. 8, 334.

Darling ACD, Mau B, Blattner FR, Perna NT. 2004. Mauve: Multiple alignment of conserved genomic sequence with rearrangements. Genome Research. 14.7: Page 1394–1403

De Vos JM, Breteler FJ. 2009. A revision of the African genera *Paropsiopsis* and *Smeathmannia* (Passifloraceae – Paropsieae), including a new species of *Paropsiopsis* from Cameroon. Edinburgh Journal of Botany. 66(1):27—49, doi 10.1017/S0960428609005174.

Feuillet C, MacDougal JM. 2007. Passifloraceae. In Kubitzki K, Bayer C, and Stevens, PF (eds.) The Families and Genera of Vascular Plants.Volume IX. Pp. 270-281. Springer.

Freeman B, Dami FD, Molokwu-Odozi. 2019. Status of globally threatened birds of Sapo National Park, Liberia. Ostrich 90: 19-24. DOI 10.2989/00306525.2018.1502694

Gandini CL and Sanchez-Puerta MV. 2017. Foreign Plastid Sequences in Plant Mitochondria are Frequently Acquired Via Mitochondrion-to-Mitochondrion Horizontal Transfer. Sci. Rep. 7, 43402; doi: 10.1038/srep43402

Good, R. 1964. The geography of flowering plants. Longman Green & Co.

Hansen AK, Escobar LK, Gilbert LE, Jansen RK. 2007. Paternal, maternal, and biparental inheritance of the chloroplast genome in *Passiflora* (Passifloraceae): Implications for phylogenetic studies. American Journal of Botany. 94(1): 42–46.

Jansen RK and Ruhlman TA. 2012. Plastid Genomes of Seed Plants. In: Bock R and Knoop V. (eds.), Genomics of Chloroplasts and Mitochondria. Pp.103-126. Springer.

Jian-Jun Jin*, Wen-Bin Yu*, Jun-Bo Yang, Yu Song, Ting-Shuang Yi, De-Zhu Li. 2018. GetOrganelle: a fast and versatile toolkit for accurate de novo assembly of organelle genomes. bioRxiv, 256479. http://doi.org/10.1101/256479

Jongkind CCH. 2012. A new endangered species of *Jollydora* (Conneraceae) represents the first record of the genus from Upper Guinea (tropical Africa). Plant Ecology and Evolution. 145(3): 419-422. https//doi.org/10.5091/plecevo.2012.700

Jongkind CCH. 2015a. *Tragia liberica* Jongkind, (Euphorbiaceae), a new forest species from Liberia. Candollea. 70(2): 249–252. http://dx.doi.org/10.15553/c2015v702a11

Jongkind CCH. 2015b. *Rhaphiostylis minima* Jongkind, (Icacinaceae), a new liana species from Ivory Coast & Liberia. European Journal of Taxonomy. 138: 1 – 8. http://dx.doi.org/10.5852/ejt.2015.138

Jongkind CCH. 2015c. *Eugenia sapoensis* Jongkind, from Liberia and *Eugenia breteleri* Jongkind, from Gabon, two new forest species (Myrtales: Myrtaceae). European Journal of Taxonomy. 113: 1–9. http://dx.doi.org/10.5852/ejt.2015.113

Jongkind CCH. 2016. *Maesobotrya liberica* Jongkind, (Phyllanthaceae), a new forest species from Liberia. Candollea. 71(2): 275 – 279. http://dx.doi.org/10.15553/c2016v712a12

Jongkind CCH. 2017. *Bertiera sinoensis* Jongkind (Rubiaceae), a new forest liana from Liberia. Bothalia. 47(1), a2145. https://doi.org/10.4102/abc.v47i1.2145

Jongkind CCH. 2019. *Didelotia gracillima* Jongkind, sp. nov. (Leguminosae, Detarioideae), a new forest tree from Liberia and Ivory Coast. Adansonia. 41(8):69-74. https://doi.org/10.5252/adansonia2019 v 41 a 8

Jongkind CCH & FJ Breteler. 2020. *Englerodendron libassum* (Leguminosae Detarioideae - Amherstieae), a new critically endangered tree species from coastal Liberia. Plecero. 153 (3) 487-491.

Hoang DT, Chernomor O, von Haeseler A, Minh BQ, and LS Vinh. 2018. UFBoot2: Improving the ultrafast bootstrap approximation. Molecular Biology and Evolution. 35:518–522. https://doi.org/10.1093/molbev/msx281

Katoh K & Standley DM. 2013. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Molecular Biology and Evolution. 30(4), 772–780. doi:10.1093/molbev/mst010

Langmead B and SL Salzberg. 2012. Fast gapped-read alignment with Bowtie 2. Nature Methods. 9: 357-359.

Maas PJM, Baas P, Christenhusz MJM, Clarkson JJ, Koek-Noorman J, Mennega AMW, Tokuoka T, Van Der Bank M, Van Der Ham RWJM, Van Marle E-J, Westra LYTH, Chase MW. 2019. 'Unknown yellow': *Pibiria*, a new genus of Passifloraceae with a mixture of features found in Passifloroideae and Turneroideae, Botanical Journal of the Linnean Society. 189(4): 397–407, https://doi.org/10.1093/botlinnean/boz003

Miller MA, Pfeiffer W, and Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees, in Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA pp 1 - 8.

Nguyen L-T, Schmidt HA, von Haeseler A, and BQ Minh (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. Molecular Biology and Evolution. 32:268-274. https://doi.org/10.1093/molbev/msu300

Promega. 2010. Wizard® DNA Clean-Up System.

Rice DW et al. (2013). Horizontal transfer of entire genomes via mitochondrial fusion in the angiosperm *Amborella*. Science. 342, 1468–1473.

Ronquist F, Teslenko M, Van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA & Huelsenbeck JP. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Syst. Biol. 61: 539–542. http://dx.doi.org/10.1093/sysbio/sys029

Sloan DB, Triant DA, Forrester NJ, Bergner LM, WU M, Taylor DR (2014). A recurring syndrome of accelerated plastid genome evolution in the angiosperm tribe Sileneae (Carryophyllaceae). Molecular Phylogenetics and Evolution. 72: 82-89.

Slik JWF, Arroyo-Rodríguez V, Aiba S-I, Alvarez-Loayza P, Alves LF, Ashton P, et al. 2015. An estimate of the number of tropical tree species. Proceedings of the National Academy of Sciences of the United States of America. 112:7472–7.

Stevens PF. 2001 onward. Angiosperm Phylogeny Website. Version 14, July 2017 [and more or less continuously updated since].

Takahashi D, Isagi Y, Li P, Qiu Y-X, Setoguchi H, Suyama Y, Matsuo A, Tsunamoto Y and S Sakaguchi. 2022. Stable persistence of relict populations involved evolutionary shifts of reproductive characters in the genus *Tanakaea* (Saxifragaceae). Journal of Systematics and Evolution 60: 1405-1416.

Tokuoka T. 2012. Molecular phylogenetic analysis of Passifloraceae sensu lato (Malpighiales) based on plastid and nuclear DNA sequences. Journal of Plant Research. 125: 489–497. CrossRef, PubMed

Thulin M, Razafimandimbison SG, Chafe P, Heidari N, Kool A, Shore JS. 2012. Phylogeny of the Turneraceae clade (Passifloraceae s.l.): trans-Atlantic disjunctions and two new genera in Africa. Taxon. 61: 308–323.

Van der Ham RWJM. 1990. Nephelieae pollen (Sapindaceae): form, function, and evolution. Leiden botanical series, 33. Leiden: Rijksherbarium/Hortus Botanicus.

Wang D, Wu YW, Shih AC, Wu CS, Wang YN, Chaw SM. 2007. Transfer of chloroplast genomic DNA to mitochondrial genome occurred at least 300 MYA. Molecular Biology and Evolution. 24(9): 2040-8.

Wang X-C, Chen H, Yang D & C Liu. 2017. Diversity of mitochondrial plastid DNAs (MTPTs) in seed plants. Mitochondrial DNA Part A. DNA Mapping, Sequencing, and Analysis Volume 29(4).

Weng M-L, Ruhlman TA, Jansen RK. 2017. Expansion of inverted repeat does not decrease substitution rates in Pelargonium plastid genomes. New Phytologist. 214: 842-851

Wick, R. R., M. B. Schultz, J. Zobel and K. E. Holt. 2015. Bandage: interactive visualization of de novo genome assemblies. Bioinformatics. 31: 3350-3352.

Wicke S, Müller KF, de Pamphilis CW, Quandt D, Wickett NJ, Zhang Y, Renner SS and GM Schneeweiss. 2013. Mechanisms of functional and physical genome reduction in photosynthetic and nonphotosynthetic parasitic plants of the broomrape family. The Plant Cell. 25: 3711–3725; http://www.plantcell.org/cgi/doi/10.1105/tpc.113.113373

Wurdack, KJ, Davis CC. 2009. Malpighiales phylogenetics: gaining ground on one of the most recalcitrant clades in the angiosperm tree of life. American Journal of Botany. 96: 1551–1570. CrossRef, PubMed

Xi Z, Ruhfel BR, Schaefer H, Amorim AM, Sugumaran M, Wurdack KJ, Endress PK, Matthews M, Stevens PF, Mathews S, Davis CC III. 2012. Phylogenomics and a posteriori data partitioning resolve the Cretaceous angiosperm radiation in Malpighiales. Proceedings of the National Academy of Sciences of the United States of America. 109: 17519–17524.

Online Supplementary at https://oaj.fupress.net/index.php/webbia/article/view/13470/11405