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Plastomes resolve generic limits within tribe Clusieae (Clusiaceae) and reveal the new genus *Arawakia*

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ABSTRACT

Clusieae is an exclusively Neotropical tribe in the family Clusiaceae *sensu stricto*. Although tribes within Clusiaceae are morphologically and phylogenetically well-delimited, resolution among genera within these tribes remains elusive. The tribe Clusieae includes an estimated ~500 species distributed among five genera: *Chrysochlamys*, *Clusia*, *Dystovomita*, *Tovomita*, and *Tovomitopsis*. In this study, we used nearly complete plastid genomes from 30 exemplar Clusieae species representing all genera recognized, plus two outgroups to infer the phylogeny of the tribe using Maximum Likelihood and Bayesian Inference. For comparison, we also inferred a phylogeny from the nuclear Internal Transcribed Spacer (ITS) region using the same methods. Our study corroborates earlier findings that *Clusia* is monophyletic while *Tovomita* is not. It also provides additional support to the hypothesis that *Chrysochlamys* and *Tovomitopsis* are not closely related despite gross morphological similarity. *Tovomita* is divided into three distantly related clades: (i) core *Tovomita* (including the type *T. guianensis*), (ii) *T. croatii*, and (iii) the *T. weddelliana* species complex. Members of the *T. weddelliana* complex are isolated from the core *Tovomita*, and placed in a well-supported clade that is sister to a clade composed of *Chrysochlamys* plus *Clusia*. *Tovomita croatii* is nested within *Chrysochlamys*. We propose taxonomic revisions to accommodate our phylogenetic findings, including the description of the new genus *Arawakia*, which includes the 18 species formerly recognized in the *T. weddelliana* species complex. Lectotypes are also designated for nine species (i.e., *Arawakia angustata*, *A. lanceolata*, *A. lingulata*, *A. longicuneata*, *A. macrocarpa*, *A. oblanceolata*, *A. pithecobia*, *A. rhizophoroides*, and *A. weddelliana*), and a taxonomic key for the identification of the six genera of Clusieae recognized is presented.

1. Introduction

The tribe Clusieae is a large subclade within the family Clusiaceae *sensu stricto* (Wurdack and Davis, 2009; Ruhfel et al., 2011, 2013; Xi et al., 2012), and includes ca. 65% of the 800 species recognized within the family (Stevens, 2001 onwards). Species of Clusieae are easily delimited from other members of the family by their prevalent dioecy, absence of bud scales, non-fasciculate androecium, and fleshy capsules bearing arillate seeds (Stevens, 2007). The ~500 species recognized within the tribe are distributed among five genera: *Chrysochlamys* Poepp. (~35 spp.; Fig. 1A), *Clusia* L. (350–400 spp.; Fig. 1B), *Dystovomita* (Engl.) D'Arcy (two spp.; Fig. 1C), *Tovomita* Aubl. (~70 spp.; Fig. 1D–E), and *Tovomitopsis* Planch. & Triana (two spp.; Fig. 1F) (Stevens, 2001 onwards). These genera are exclusively Neotropical and distributed from southern Mexico and the Caribbean Islands to southeastern Brazil, with most species occurring in the Amazon and Brazilian Atlantic rainforests (Stevens, 2001 onwards). Members of the tribe are very diverse in some South American biomes, especially the Amazon (Cardoso et al., 2017).

Although tribes of Clusiaceae are well circumscribed (Gustafsson et al., 2002; Ruhfel et al., 2011, 2013), relationships among genera within each tribe remain elusive. Historically, circumscriptions of

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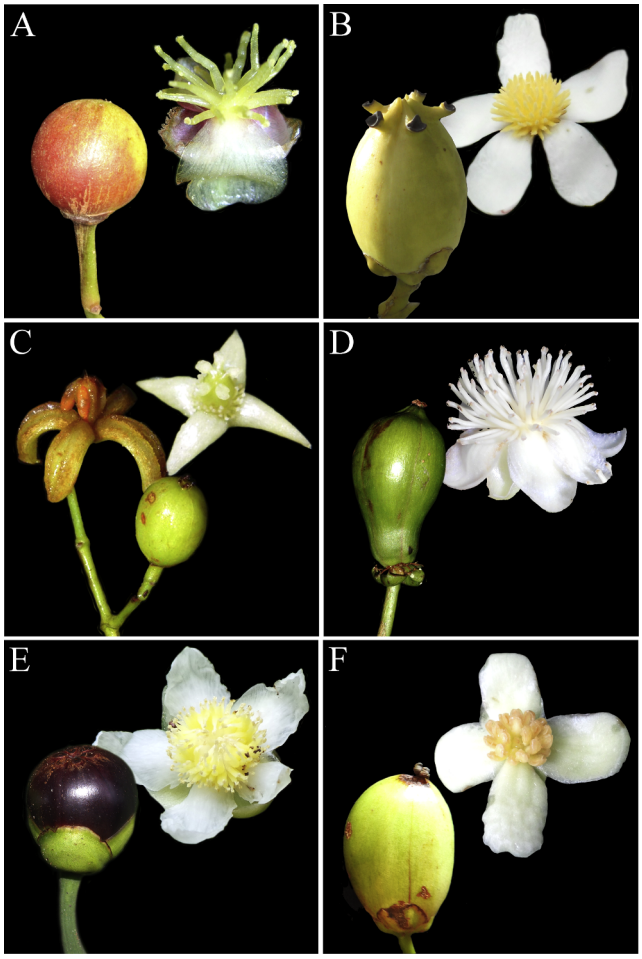

Fig. 1. Representative flowers and fruits of Clusieae genera. A. *Chrysochlamys* spp., staminate flower and fruit; B. *Clusia* spp., staminate flower and fruit; C. *Dystovomita paniculata*, pistillate flower and fruit; D. *Tovomita* spp., staminate flower and fruit; E. *Tovomita weddelliana* complex, staminate flower and fruit; F. *Tovomitopsis paniculata*, staminate flower and fruit. Photos by A. Vicentini and the *Florula Digital de La Selva* (A); C. Martins and L. Marinho (B); A. Monro and *Florula Digital de La Selva* (C); L. Marinho and M. Engels (D); C. Galdames and M. Luján (E); M. Mig and R. Penati (F).

Clusieae genera have been controversial. For example, *Clusia* was divided into several small genera in the past (Planchon and Triana, 1860), although this classification is not adopted today (Gustafsson et al., 2002, 2007). Similarly, *Tovomitidium* Ducke, once segregated from *Tovomita*, is now treated as a member of the latter genus (Stevens, 2007; Marinho et al., 2018). *Dystovomita* was once considered as a section of *Tovomita*, with species floating between these two genera, is now recognized as a separate genus (D'Arcy, 1978; Bittrich and Marinho, 2016). Finally, *Chrysochlamys* and *Tovomitopsis* have often been treated as synonyms owing to their gross morphological similarity (D'Arcy, 1980; Hammel, 1999), but have also been treated as separate genera in the most recent treatments of the family (Stevens, 2007; BFG, 2015).

The earliest molecular phylogenetic studies in the tribe focused on *Clusia* and raised interesting questions about relationships among other Clusieae genera (Gustafsson and Bittrich, 2002; Gehrig et al., 2003; Gustafsson et al., 2007). Using nuclear rDNA Internal Transcribed Spacer (ITS) data, Gustafsson et al. (2007) identified a monophyletic *Clusia*, a non-monophyletic *Tovomita*, and discovered that *Chrysochlamys* and *Tovomitopsis* were not closely related. In addition, Gustafsson et al. (2007) identified morphological synapomorphies for *Clusia*, including seeds < 5 mm in length, and a non-vascularized aril. However, the topology of Gustafsson et al. (2007) was not well supported and taxon sampling was insufficient to fully evaluate generic limits and relationships among genera.

More recently, Ruhfel et al. (2011) greatly increased character and taxon sampling by incorporating plastid (*matK*, *ndhF*, and *rbcL*) and mitochondrial (*matR*) sequences into a phylogeny of the tribe. This study provided additional support for the non-monophyly of *Tovomita,* as well as corroborated the distant relationship between *Chrysochlamys* and *Tovomitopsis*. Despite the improved taxon and character sampling, however, phylogenetic resolution was still insufficient to draw firm conclusions for most generic limits and intergeneric relationships in Clusieae. Furthermore, although sampling of *Clusia* itself was extensive enough for a broad circumscription of the genus to be adopted (Gustafsson and Bittrich, 2002; Gustafsson et al., 2007), it did not adequately sample morphologically unusual species such as *Tovomita croatii* Maguire and *T. gazelii* Poncy & Offroy.

Here, we reconstruct phylogenetic relationships among genera in tribe Clusieae using a nearly complete plastid (plastome) dataset that reflects the broad taxonomic, biogeographic, and morphological breadth of the tribe. Our analyses, combined with an independent nuclear ITS dataset, provide insights on: (i) the phylogenetic placement of *Tovomita croatii*; (ii) the delimitation of *Tovomita sensu lato* and; (iii) the relationship between *Chrysochlamys* and *Tovomitopsis*.

2. Materials and methods

2.1. Taxon sampling

Our dataset includes 32 accessions of which 30 species belong to Clusieae, and two are outgroups, *Garcinia gardneriana* (Planch. & Triana) Zappi (Garcinieae) and *Symphonia globulifera* L.f., (Symphonieae) (Appendix A). Few *Clusia* species (eight spp.) were sampled since the monophyly of this genus has been well established (Gustafsson et al., 2002, 2007). Our sampling also included five spp. of *Chrysochlamys*, one sp. of *Dystovomita*, two spp. of *Tovomitopsis*, and 14 spp. of *Tovomita*, including four spp. of the *T. weddelliana* complex, and the two morphologically unusual species *T. croatii* and *T. gazelii*. Plant materials were largely collected in the field. Specimens were deposited in CEPEC and HUEFS (herbarium acronyms follow Thiers, 2018 continuously updated), and silica-dried leaves were stored at −20 °C in the laboratory. Additional DNAs were extracted from herbarium materials deposited at A, CEPEC, GH, HUEFS, INPA, MG, NY, P, and RB.

2.2. DNA isolation, amplification, and sequencing

We isolated total genomic DNA from 0.01 g of silica dried leaf material using the Maxwell® 16 Tissue DBA Purification Kit (Promega Corporation, Inc., Madison, WI, USA). DNA from herbarium specimens was extracted using the CTAB method (Doyle and Doyle, 1987). Genomic libraries were prepared using ca. 70 ng of genomic DNA. The libraries were prepared using quarter reactions and indexed for Illumina multiplex sequencing by using the Kapa HyperPlus library prep (Kapa Biosystems, Inc., MA, USA) with Nextflex-Ht barcodes (Bioo Scientific Corporation, TX, USA). Libraries were fragmented to 350–400 base pairs (bp). The library quality, expected size and concentration, were verified with the Agilent TapeStation 2200 (Agilent Technologies, Inc., Waldbronn, Germany) and the Qubit dsDNA HS Assay Kit on a Qubit 2.0 Fluorometer (Invitrogen, Carlsbad, CA, USA). All 32 libraries were diluted into 0.7 nM, pooled and sequenced with the Illumina HiSeq 2x125 on the Genome Analyzer II (Illumina, Inc., San Diego, CA, USA) at the Faculty of Arts and Sciences (FAS) Center for Systems Biology at Harvard University, MA, USA. The raw data were deposited at NCBI (SAMN09652111–SAMN09652142).

2.3. Plastid genome assembly and annotation

We applied a reference-assisted strategy for plastid genome assembly using Geneious 9.0.5 (Kearse et al., 2012). The multiplexed Illumina reads were mapped to the reference plastid genome of *Manihot esculenta* Crantz (Euphorbiaceae, NCBI's Reference Sequence: NC_009143.1), including both inverted repeat regions. Regions with more than 5% error probability were trimmed before assembly. Consensus sequences of aligned reads were called to match at least 50% of the aligned reads. For example, "Y" was called for a site composed of 45% aligned C, 30% T, and 25% A. Regions with read coverage of less than 2x were masked. Consensus sequences with less than 5000 bp unambiguous sites were removed from subsequent analyses, except from sequences of five taxa, i.e., *Chrysochlamys nicaraguensis* (Oerst., Planch. & Triana) Hemsl., *Tovomita caputmonsia* Gahagen, *T. gazelii*, *T. guianensis* Aubl., and *T. panamaea* Gahagen. Although sequence quality for these species was lower than others, they were deemed essential for the study. Sequences were annotated against *Manihot esculenta* using the BLAST-like "transfer annotations" tool in Geneious with identity cut-off of 60%. We also applied the successive reference approach for obtaining higher quality assemblies as specified in Zhang et al. (2015) using the assembly of *T. acutifolia* M.S. Barros & G. Mariz as a reference. We used similar genus-specific references to assemble the ITS regions due to its high rate of evolution (Baldwin et al., 1995). Seven ITS reference sequences were downloaded from Genbank: *Chrysochlamys glauca* (Oerst., Planch. & Triana) Hemsl. (AJ509213.1), *Clusia burle-marxii* Bittrich (MF871656.1), *Dystovomita paniculata* (Donn. Sm.) Hammel (AJ509216.1), *Garcinia macrophylla* Mart. (EU128439.1), *Symphonia globulifera* (AF479782.1), *Tovomita weddelliana* (AJ509219.1), and *Tovomitopsis saldanhae* Engl. (AY145240.1).

2.4. Plastid genome alignment and phylogenetic inference

Sequence alignment of our assembled consensus sequences was implemented in MAFFT 7.245 (Katoh and Standley, 2013) using the fast Fourier transformation approximation option, a partition size of 1000, and three iterative refinements. The aligned sequences were prepared for phylogenetic analyses by removing sites with > 70% missing data using trimAL 1.4.rev15 (Capella-Gutiérrez et al., 2009). The coding regions (CDS) were defined using the *Manihot esculenta* annotation. The best partition scheme for Maximum Likelihood (ML) analyses applying the GTRGAMMA model was selected by PartitionFinder 2 using the heuristic search algorithm 'rcluster' (Lanfear et al., 2012). We inferred an ML phylogeny of the 32 species using RAxML 8.2.4 (Stamatakis, 2014) with 1000 rapid bootstrap replications followed by a thorough ML search (-f a –N 1000). A second ML analysis was conducted excluding *Tovomita gazelii* and *T. guianensis* to verify support values without accessions with relatively low sequence coverage. A Bayesian inference (BI) was performed using PhyloBayes MPI 1.7a (Lartillot et al., 2013) under the CAT–GTR model (Lartillot and Philippe, 2004), which accounts for across-site rate heterogeneity using an infinite mixture model. Two independent Markov chain Monte Carlo (MCMC) analyses were conducted for each concatenated nucleotide matrix. Stationarity from both MCMC analyses were determined using Tracer 1.5. We ran each MCMC analysis until the minimum effective sampling size estimated by Tracer exceeded 200 for all parameters in each chain. This yielded 73,241 and 37,293 sampled trees for each run. The largest discrepancy observed across all bipartitions was 0.10, indicating convergence of the two independent runs. Bayesian posterior consensus trees and parameter estimates were calculated using the 'bpcomp' option in PhyloBayes using a burn-in of 2000, and sub-sampling every 10 trees.

2.5. ITS alignment and phylogenetic inference

Nuclear ribosomal ITS sequences were assembled and extracted from our genomic libraries for a parallel comparative analysis. Sequences were aligned using MAFFT 7.245 (Katoh and Standley, 2013), with subsequent manual adjustments. The ITS dataset was partitioned (18S, ITS1, 5.8S, ITS2, and 26S) and the evolutionary models for each partition were selected using MrModelTest and AIC (Posada and Buckley, 2004): 18S = SYM + I; ITS1 = GTR + G; 5.8S = SYM + I; ITS2 = K80 + G; and 26S = HKY + G; BI was performed using MrBayes 3.1.2. (Ronquist et al., 2012). We conducted 10^6 generations in two runs with four chains, with one tree sampled every 1000 generations. To evaluate convergence, we used Tracer 1.5. The posterior probabilities (PP) were determined by calculating the majority rule consensus topology after excluding the burn-in from 10% of the initial trees. The ML analyses were conducted with RAxML 8.2.4 (Stamatakis, 2014) following the same standards that were adopted above for the plastid genome, but without partitions specified. All newly generated sequences were deposited at NCBI (MH198326–MH198357).

3. Results

Our dataset includes 180,903 bp of plastid genomic data, and 874 bp of ITS data for 32 species. The final plastid genome assemblies ranged from 149,040 to 165,463 bp per accession. The GC content varied from 35.8% to 39.1%, with the exception of *Tovomita caputmonsia* and *T. guianensis*, which had 42.6% and 41.3%, respectively, likely due to low sequence coverage (Appendix A).

Results from ML and BI analyses of the plastid genome dataset are presented in Fig. 2. The plastid genome tree recovered three main clades, one of which includes a nested series of well-supported clades here labeled as clades A (99 BP/0.86 PP), B (85 BP/0.66 PP), and C (100 BP/0.85 PP). *Dystovomita*, *Tovomitopsis*, and the remainder of Clusieae form a polytomy at the base of the tribe. The branching order of *Dystovomita* and *Tovomitopsis* is unclear (Fig. 2). Clade A (99 BP/0.86 PP), corresponds to core *Tovomita* (86 BP/0.51 PP) plus its sister group, clade B (85 BP/0.66 PP). Clade B is moderately supported (85 BP/0.66 PP) and includes species of the *T. weddelliana* complex plus the well supported clade C (100 BP/85 PP). Clade C is composed of two subclades. One sub-clade includes *Tovomita croatii* plus *Chrysochlamys* (100 BP/0.96 PP), which is well supported as sister (100 BP/0.85 PP) to a monophyletic *Clusia* (100 BP/0.91 PP). As currently circumscribed, *Tovomita* is not monophyletic, with the *T. weddelliana* complex appearing as distantly related to core *Tovomita*. Moreover, *Tovomita croatii* appears as sister to *Chrysochlamys* (100 BP/0.96 PP), or embedded within *Chrysochlamys* (trees A, B, C and E, Appendix B). In both ITS analyses, *T. croatii* was placed as sister to *C. skutchii* Hammel (60 BP/0.99 PP; Appendix B).

The topology inferred from the analyses of the ITS dataset are in agreement with those from the plastome analyses (Fig. 2). However, no resolution was recovered for intergeneric relationships, despite the high overall support for generic-level clades (BP ≥ 93 and PP = 1.0). These analyses suggest that the nuclear and plastid genomes are not in conflict.

The plastid ML tree with *Tovomita guianensis* and *T. gazelii* removed (tree E, Appendix B) increased the overall BP support values, but did not change the overall topology. This tree without *Tovomita guianensis* and *T. gazelii* (tree E, Appendix B) presented higher BP support values for core *Tovomita* (100 vs. 86), and for all species relationships within core *Tovomita*, with the exception of the relationship between *T. acutiflora* and *T. choisyana* (62 vs. 58). Moreover, *Tovomita croatii* was

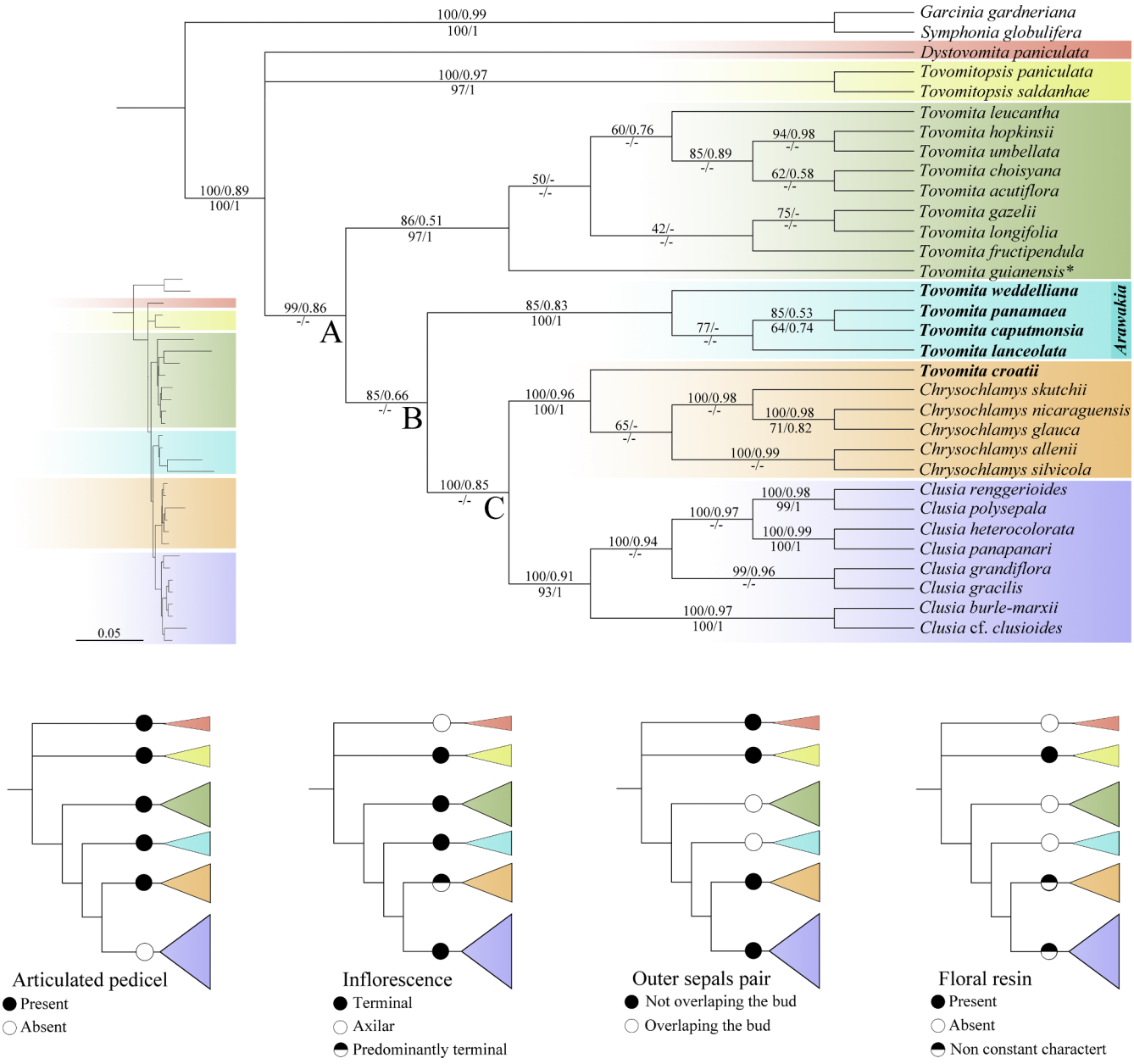

Fig. 2. Maximum likelihood plastid genome phylogeny of Clusieae. Asterisk indicates the type species of *Tovomita*. Numbers above branches represent support values inferred from the plastid genome data; numbers below branches represent support values obtained from the analyses of the ITS dataset, as follows: ML bootstrap percentage (BP)/BI posterior probabilities (PP). A hyphen indicates that the node was not recovered > 50% BP/ > 0.50 PP. Clades designated A–C are used to orient discussion in the main text. Phylogram with associated clade colorations inset to left. Diagrams illustrate the distribution of morphological characters among generic-level clades. See Appendix B for results from individual analyses.

placed as sister to the clade formed by *Chrysochlamys allenii* (Maguire) Hammel and *C. silvicola* (Hammel) Hammel (59 BP). The removal of *Tovomita guianensis* and *T. gazelii* also increased BP support for clade B from 85 BP to 98.

4. Discussion

Our study presents a significantly improved phylogeny of tribe Clusieae, which we utilize as the basis for important taxonomic updates within the clade. Here, we inferred the phylogeny of Clusieae using nearly complete plastomes and a companion nuclear ITS dataset. Since there were no well supported conflicting nodes (BP > 70%) between topologies derived from these datasets, the more well-resolved topology inferred from our plastid dataset is discussed below. This phylogeny provides a foundation for future phylogenetic and biogeographic investigations in this group.

4.1. Molecular phylogeny of tribe Clusieae

Our study confirmed the monophyly of *Clusia* and provided additional support for the non-monophyly of *Tovomita*, as well as shed new light on the affinities among *Chrysochlamys*, *Tovomitopsis*, and other members of the tribe. Species traditionally assigned to *Tovomita* fall into three distantly related subclades: (i) core *Tovomita*, which includes the type species *T. guianensis*, and the bulk of *Tovomita* diversity (52 of 70 species); (ii) species from the *Tovomita weddelliana* complex (18 spp.),

which form a clade (85 BP/0.83 PP, Fig. 2) that is sister to *Chrysochlamys* plus *Clusia* (100 BP/0.85 PP, Fig. 2), and; (iii) *Tovomita croatii*, which was confidently placed as sister (Fig. 2, and tree D, Appendix B) or nested within *Chrysochlamys* (trees A, B C and E, Appendix B). Increased taxon and gene sampling is necessary to further investigate the precise placement of *T. croatii* relative to *Chrysochlamys*.

4.2. Morphological and taxonomic implications

The *Tovomita weddelliana* complex was recently revised using morphologically quantifiable characters and multivariate statistics (Gahagen et al., 2015). This research resurrected eight species previously synonymized under *T. weddelliana*, and proposed five new species. In this complex, staminate and pistillate plants of the same species display morphological variation that must be taken into consideration while proposing the recognition of additional taxa. Careful morphometric analyses including specimens distributed across the range of the *T. weddelliana* complex (from Nicaragua to Bolivia) are necessary to evaluate the variation and informativeness of this character. Additional characters such as pedicel length, floral bud shape and size also require further investigation (Marinho, pers obs.).

The *Tovomita weddelliana* complex differs from core *Tovomita* by the exudate color (white in the *T. weddelliana* complex vs. yellowish to orange in core *Tovomita*), leaf blade shape (spatulate and gradually narrowed towards the base, becoming truncate to abruptly rounded in members of the *T. weddelliana* complex vs. acute or cuneate to attenuate in core *Tovomita*), leaf base (not excavated in the *T. weddelliana* complex vs. often shortly excavated in core *Tovomita*), and epicarp color (purplish red when mature in the *T. weddelliana* complex vs. green in core *Tovomita*). Owing to our phylogenetic findings and these morphological differences, we circumscribe species of the former *T. weddelliana* complex as the newly described genus, *Arawakia* (see Taxonomic treatment below). This circumscription largely follows Gahagen et al. (2015), but is here expanded to also include *Clusia oblanceolata* Rusby and *Tovomita glossophylla* Cuatrec., species previously included in the *T. weddelliana* complex by Maguire (1977).

The morphological affinities of *Tovomita croatii* have been complicated since its description (Maguire, 1977). Hammel (1999) placed this species as morphologically intermediate between *Chrysochlamys* and *Tovomita*. The species exhibits numerous traits linking it with *Tovomita*, including long axillary internodes and leaves clustered at the apex, leaves with numerous secondary veins, and outer sepals similar in size to the inner ones (Fig. 3A). At the same time, the genus shares other features with *Chrysochlamys* such as intramarginal veins (Fig. 3A), lack of dark purplish red placentas and inner fruit walls, presence of resin in the flower (diagram IV, Fig. 2), and outer sepals that do not enclose the floral bud (diagram III, Fig. 2). Furthermore, the reddish inflorescence, bracts, sepals, and fruits of *T. croatii* (Fig. 3B) are shared with *Chrysochlamys* but uncommon in *Tovomita*. *Tovomita croatii* had been previously associated with *Chrysochlamys-Tovomitopsis* (D'Arcy, 1980). D'Arcy (1980) synonymized *Chrysochlamys* under *Tovomitopsis*, and proposed the combination *Tovomitopsis croatii* (Maguire) D'Arcy. Our phylogenetic findings indicate that *T. croatii* is more closely related to *Chrysochlamys* and the appropriate taxonomic changes are proposed (see Taxonomic treatment below). Specifically, we synonymize *T. croatii* as a member of the genus *Chrysochlamys*.

5. Taxonomic treatment

***Chrysochlamys croatii* (Maguire) L. Marinho & Hammel, comb. nov.** ≡ *Tovomita croatii* Maguire, Phytologia 36(4): 404. 1977. Type: PANAMA. Coclé: El Valle, behind Club Campestre, 12 Apr 1971, *T. B. Croat 14268A* (holotype: MO barcode MO194883 photo!).

≡ *Tovomitopsis croatii* (Maguire) D'Arcy, Ann. Missouri Bot. Gard. 67(4): 1031. 1980 [1981].

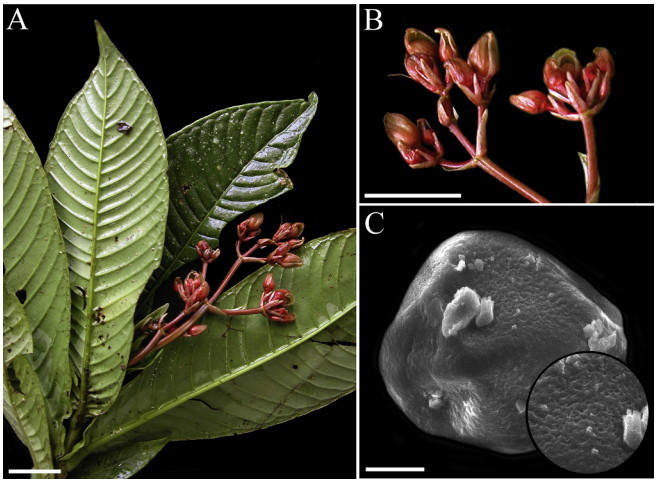

Fig. 3. General morphology of *Chrysochlamys croatii*. A. Branch with inflorescence; B. Inflorescence detail (scale bar: 2.5 cm); C. Scanning electron micrograph of pollen, detail of the rugulate-foveolate exine in 2× magnification (scale bar: 2.5 μm, from *Mori 6725* [NY]). Photos by C. Galdames.

***Arawakia* L. Marinho, gen. nov.**

Type: *Arawakia weddelliana* (Planch. & Triana) L. Marinho

Diagnosis: *Arawakia* is distinguished from the other genera of tribe Clusieae, except *Tovomita*, by the floral buds enclosed by the outer sepals. *Arawakia* differs from *Tovomita* by the presence of white exudate (vs. yellowish), a dark raised line joining the petiole bases which remains after apex rupture (vs. dark raised line absent, petiole bases separate), leaf base gradually narrowed, ultimately shortly truncate or abruptly rounded (vs. leaf base acute or cuneate to attenuate), fruit epicarp red when mature (vs. green or brownish), and sepals adpressed to the fruit (vs. not adpressed).

Description: Trees or shrubs; exudate white; leaves clustered at the apex of the branches; petiole bases united by a dark raised line. Leaf blades fleshy, base not excavated. Inflorescence terminal; pedicels with distal portions not thickened. Flowers with buds enclosed by the outer sepals; petals white to yellowish; stamens free; pollen exine rugulate-perforate to perforate; ovary 4–6-carpellate, one ovule per locule. Capsules purplish-red when mature, mesocarp red to purplish red; petals and staminodes caducous, sepals persistent and adpressed to the fruit; seeds one per locule, arillate, the aril orange. Fig. 4.

Etymology: The genus honors the *Arawak*, a group of American Indians originally from the Greater Antilles to South America, in the Amazon and the slopes of the Andean mountain ranges (Schmidt, 1917; Encyclopedia Britannica, 2017), whose distribution is similar to that of species in the *T. weddelliana* complex (Gahagen et al., 2015).

Distribution and habitat: Species in the genus occur from southern Nicaragua to Bolivia, and range in elevation from 100 to 1700 m a. s. l. (Hammel, 2001; Gahagen et al., 2015). The species usually grow in highlands in the Andes and the Guianan Shield (Funk et al., 2007), although some species reach lowlands in Central America and Colombia.

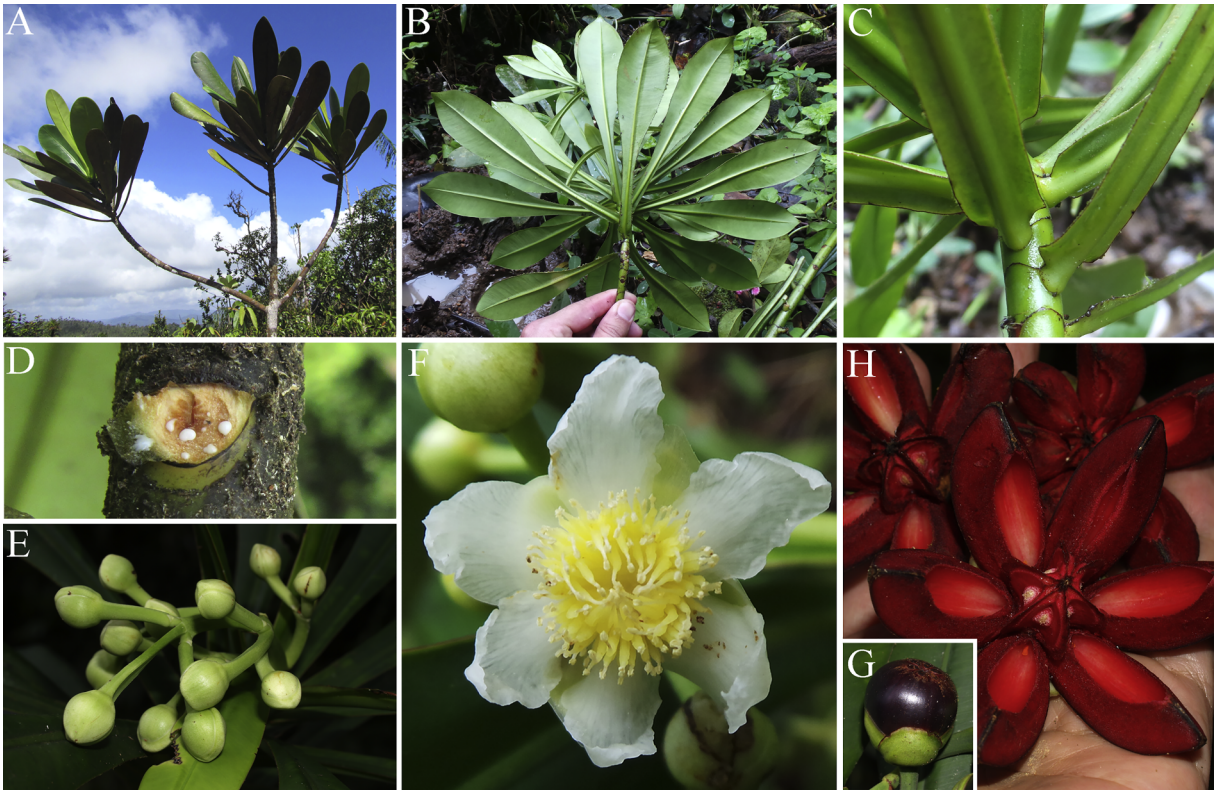

Fig. 4. General morphology of *Arawakia*. A. Branch of *A. panamaea*; B. Abaxial view of *A. lanceolata* leaves; C. Internode detail and leaf bases of *A. lanceolata*; D. Detail of white exudate of *A. caputmonsia*; E. Inflorescence of *A. panamaea*; F. Staminate flower of *A. panamaea*; G. Mature fruit of *A. panamaea*; H. Seedless open fruits of *A. panamaea*. Photos by J. Carrión (A, D); M. Luján (B-C, F) and C. Galdames (E, G-H).

Arawakia angustata **(Steyerm.) L. Marinho, comb. nov.** ≡ *Tovomita angustata* Steyerm., Fieldiana, Bot. 28: 399. 1952. Type: VENEZUELA. Bolívar: along mesa escarpment between Santa Teresita de Kavanayén and wooded quebrada about 8 km northwest of Kavanayén, 1220 m, 23 November 1944, *J. A. Steyermark 60,475* (lectotype, designated here: F barcode F0054532F photo!; isolectotypes: NY barcode NY00073947!, US barcode US00114288 photo!).

Arawakia caputmonsia **(Gahagen) L. Marinho, comb. nov.** ≡ *Tovomita caputmonsia* Gahagen, Syst. Bot. 40(4): 975–978, f. 6A. 2015. Type: PANAMA. Panamá: in forest, about one mile upstream from Frizzel's Vinca Indio, on slopes of Cerro Jefe, 9 September 1970, *R. Foster & H. Kennedy 1832* (holotype: F barcode F1770665 photo!; isotype: CAS No. 668457!, US No. 3542808).

Arawakia coriacea **(Maguire) L. Marinho, comb. nov.** ≡ *Tovomita coriacea* Maguire, Phytologia 36(4): 406. 1977. Type: VENEZUELA. Sucre: Península de Paria, Cerro de Humo, bosque nublado virgen en la cumbre, noroeste de Irapa, entre Roma y Santa Isabel, 12 km norte del pueblo de Río Grande arriba, 1273 m, 2 March 1966, *J. A. Steyermark 94,884* (holotype: NY barcode NY00579004!; isotypes: F No. 1666274, VEN barcode VEN112401 photo!).

Arawakia divesora **(Gahagen) L. Marinho, comb. nov.** ≡ *Tovomita divesora* Gahagen, Syst. Bot. 40(4): 980, f. 6B. 2015. Type: COSTA RICA. Cartago: mountain slopes east of Tuis and north of Platanillo, 2 September 1968, *R. L. Wilbur & D. E. Stone 10,670* (holotype: F No. 1925103; isotypes: CAS No. 700389!, GH!, US No. 3522729).

Arawakia glossophylla **(Cuatrec.) L. Marinho, comb. nov.** ≡ *Tovomita glossophylla* Cuatrec., Revista Acad. Colomb. Ci. Exact. 8: 62. 1950. Type: COLOMBIA. Caquetá: Cordillera Oriental, Sucre, quebrada de la Calaña 1000–1100 m alt., 6 May 1940, *J. Cuatrecasas 9194* (holotype: US barcode US00114292 photo!; isotypes: COL barcode COL000002840 photo!, F barcode F0054537F photo!).

Arawakia lanceolata **(Cuatrec.) L. Marinho, comb. nov.** ≡ *Tovomita lanceolata* Cuatrec., Anales Inst. Biol. Univ. Nac. México 20: 102. 1949. Type: COLOMBIA. Valle del Cauca: río Calima, Quebrada de la Brea, 20–40 m, 24 May 1946, *J. Cuatrecasas 21,278* (lectotype, designated here: COL barcode COL000002842 photo!; isolectotypes: F barcode F0054541F photo!; F barcode F0054542F photo!, NY barcode NY00076046!, P barcode P00093857!, US barcode US00114294 photo!).

Arawakia lingulata **(Cuatrec.) L. Marinho, comb. nov.** ≡ *Tovomita lingulata* Cuatrec., Anales Inst. Biol. Univ. Nac. México 20: 99. 1949. Type: COLOMBIA. Valle del Cauca: Cordillera Occidental, vertiente occidental, Hoya del Rio Digua, lado izquierdo, Piedra de Moler, bisques, 900–1180 m, 19–28 August 1943, *J. Cuatrecasas 14,949* (lectotype, designated here: F barcode F0054544F photo!; isolectotypes: COL 3-sheets barcodes COL000002843 photo!, COL000002844 photo!, COL000002845 photo!, F barcode F0054543F photo!, P 2-sheets barcodes P00093897!, P00093898!, U barcode U0002437 photo!, US barcode US00114295 photo!, WIS barcode WIS00000755MAD photo!).

Arawakia longicuneata **(Engl.) L. Marinho, comb. nov.** ≡ *Tovomita longicuneata* Engl. Bot. Jahrb. Syst. 58: 7. 1923. Type: PERU.

Huanuco: Huamalies, Manzon, 900–1000 m, April 1904, *A. Weberbauer 3446* (holotype: B †; lectotype, designated here: G barcode G00386352 photo!).

Arawakia macrocarpa **(Cuatrec.) L. Marinho, comb. nov.** ≡ *Tovomita macrocarpa* Cuatrec. Anales Inst. Biol. Univ. Nac. México 20: 100. 1949. Type: COLOMBIA. Valle del Cauca: Cordillera Occidental, western slope, Hoya del Río Digua, left side, Piedra de Moler, forest, 900–1180 m, 19–28 August 1943, *J. Cuatrecasas 15,094* (lectotype, designated here: F barcode F0054547F photo!; isolectotypes: COL 2-sheets barcodes COL000002846 photo!, COL000002847 photo!, F barcode F0054546F photo!, US barcode US00114296 photo!).

Arawakia manchamancha **(Gahagen) L. Marinho, comb. nov.** ≡ *Tovomita manchamancha* Gahagen, Syst. Bot. 40(4): 982. 2015. Type: COLOMBIA. Chocó: Cabo Corrientes, Río Parguera, at the foot of Janano Mountain, 50–100 m, 27 May 1974, *R. H. Warner 290* (holotype: MO barcode MO1581721; isotypes: COL barcode COL000118273 photo!, F No. 1793789, No. 1791855, US No. 2770626).

Arawakia oblanceolata **(Rusby) L. Marinho, comb. nov.** ≡ *Clusia oblanceolata* Rusby, Descr. S. Amer. Pl. 58. 1920. Type: COLOMBIA. cf. Magdalena: Santa Marta, Valparaiso, 5500 feet, 20 March 1898–1899, *H. H. Smith 1880* (lectotype, designated here: GH barcode GH00067430!; isolectotypes: MO barcode MO279807, NY barcode NY00072442!, US barcode US00114235 photo!).

Arawakia panamaea **(Gahagen) L. Marinho, comb. nov.** ≡ *Tovomita panamaea* Gahagen, Syst. Bot. 40(4): 983, f. 8E. 2015. Type: PANAMA. San Blas Islands: El Llano-Cartí Road, km 19.1, 09°10′N, 78°55′W, 350 m, 13 March 1985, *G. N. de Nevers & H. Herrera 5166* (holotype: MO barcode MO916517; isotypes: GH!, US No. 3123120).

Arawakia parvifolia **(Gahagen) L. Marinho, comb. nov.** ≡ *Tovomita parvifolia* Gahagen, Syst. Bot. 40(4): 983. 2015. Type: COLOMBIA. Antioquia: Urrao Municipality, Vereda Calles, Natural National Park "Orchids", permanent inventory of montane rain forest; right bank of Río Calles, NW on the edge of the cabin street, G plot, subplot G-1, 06°32'N, 76°14'W, 1450 m, 13 August 1993, *A. Cogollo et al. 6358* (holotype: MO barcode MO1581828; isotype: F No. 2214226).

Arawakia pithecobia **(Standl. & L.O. Williams) L. Marinho, comb. nov.** ≡ *Clusia pithecobia* Standl. & L.O. Williams, Ceiba 1(4): 244. 1951. Type: COSTA RICA. Puntarenas: forested hills along the upper Río Piedras Blancas, vicinity Río Esquinas, 30 m, 3 August 1950, *P. H. Allen 5592* (lectotype, designated here: US barcode US00027111 photo!; isolectotypes: EAP barcode EAP42039 photo!, F No. 1402880, NY barcode NY00072375!).

≡ *Tovomita pithecobia* (Standl. & L.O. Williams) Gahagen, Syst. Bot. 40(4): 985. 2015.

Arawakia rhizophoroides **(Cuatrec.) L. Marinho, comb. nov.** ≡ *Tovomita rhizophoroides* Cuatrec. Anales Inst. Biol. Univ. Nac. México 20: 101. 1949. Type: COLOMBIA. Valle del Cauca: Pacific Coast, Río Naya, Aji branch, right bank on Calle Larga, 28 February 1943, *J. Cuatrecasas 14,280* (lectotype, designated here: F No. 1321908; isolectotypes: COL barcode COL000002851 photo!, F No. 1321907), NY barcode NY00076048!, P barcode P00093896!, US barcode US00114301 photo!, WIS barcode WIS00000757MAD photo!).

Arawakia rileyi **(Cuatrec.) L. Marinho, comb. nov.** ≡ *Tovomita rileyi* Cuatrec., Brittonia 14: 52. 1962. Type: COLOMBIA. Nariño: Gorgona Island, edge of jungle above sea beach, 15 October 1924, *C. L. Collenette & H. Cullingford 594* (holotype: K barcode K000488585!; isotype: US barcode US00114302 photo!).

Arawakia sphenophylla **(Diels) L. Marinho, comb. nov.** ≡ *Tovomita sphenophylla* Diels, Notizbl. Bot. Gart. Berlin-Dahlem 14: 32. 1938. Type: ECUADOR. San Carlos de los Colorados, 150 m ü.M., im primären Regenwald, 20 October 1935, *H. Schultze-Rhonhof 1984* (holotype: B barcode B10_0003103 photo!).

Arawakia weddelliana **(Planch. & Triana) L. Marinho, comb. nov.** ≡ *Tovomita weddelliana* Planch. & Triana, Ann. Sci. Nat., Bot., sér. 4, 14: 277. 1860. Type: BOLIVIA. Bolivie septentrionale, vallée de Tipuani, province de Larecaja, 1851, *H. A. Weddell s.n.* (lectotype, designated here: P barcode P00093859!; isolectotypes: F barcode F0054555F photo!, MO No. 1680358, P barcode P00093860!).

Key for the identification of Clusieae genera

1. Inflorescence axillary or ramiflorous
   2. Leaf base excavated; distal portion of the articulated pedicels thickened; mature capsules green ..... *Dystovomita*
   2′. Leaf base not excavated; distal portion of the articulated pedicels thin; mature capsules red ..... *Chrysochlamys*
1′. Inflorescence terminal
   3. Petiole bases united by dark raised line; leaf base gradually narrowed, ultimately shortly truncate or abruptly rounded ..... *Arawakia*
3′. Petiole bases separate; leaf base acute or cuneate to attenuate
   4. Leaf blades fleshy, tertiary veins inconspicuous in fresh material; stamens free or connate; 1–∞ ovules per locule ..... *Clusia*
   4′. Leaf blades membranous to coriaceous, tertiary veins usually visible in fresh material; stamens always free; 1 ovule per locule
      5. Floral buds enclosed by the outer sepals ..... *Tovomita*
      5′. Floral buds not enclosed by the outer sepals
         6. Leaves distributed along branches; mesocarp white or pink (rarely red). Central America and Amazonia ..... *Chrysochlamys*
         6′. Leaves clustered at the apex of the branches; mesocarp always red. Atlantic Forest ..... *Tovomitopsis*

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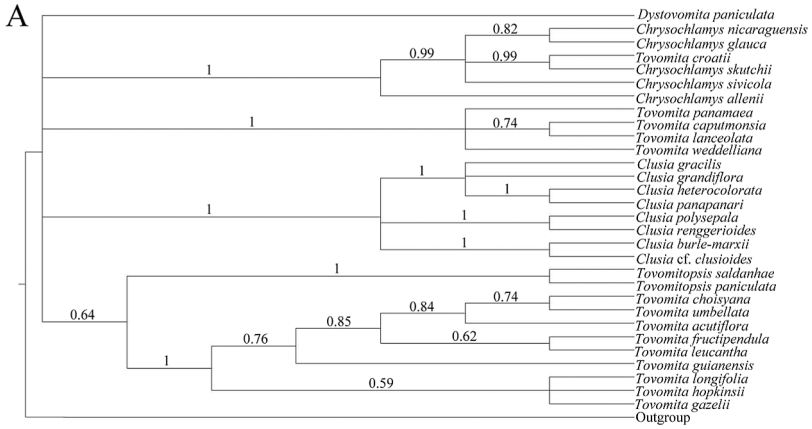
Author contributions

LCM and CCD conceived the project. LCM and XD obtained DNA sequences. LCM, LC, and CCD performed experiments. LCM analyzed the data with assistance from CCD, LC, and PF. LCM, BRR, and AMA contributed tissue samples. LCM, PF, and CCD wrote the paper, and incorporated comments from all other co-authors. LCM prepared figures and made taxonomic and nomenclatural decisions.

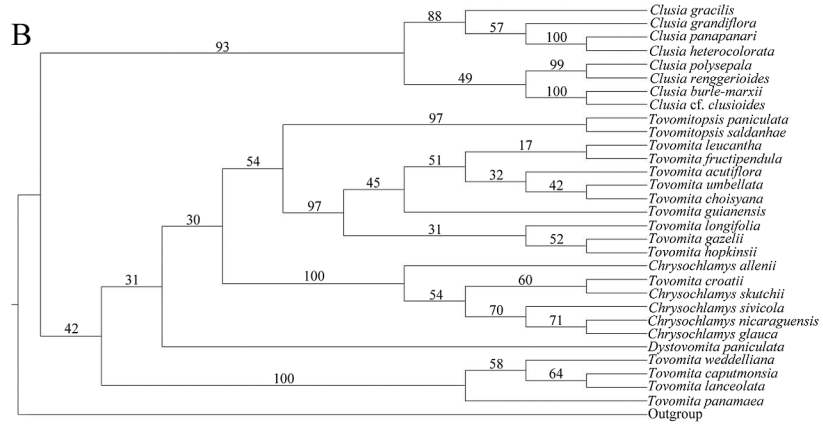
Appendix A. List of Clusiaceae taxa included in the matrix. The plastid genome was accessed for each taxon based on the assembled and annotated plastid genome of *Manihot esculenta* (bp = base pair; Chl. = chloroplast; * = species belonging to the *T. weddelliana* complex; ** = outgroup).

Taxon	Voucher	Chl. Reads	Plastome size	GC%	HQ%	GenBank reference	
						Chl.	ITS
Chrysochlamys							
C. allenii	Kriebel, R. 2289	30,076	161,419	36.8%	91%	SAMN09652111	MH198349
C. glauca	Hammel, B. 25,292	46,103	161,409	36.6%	93.6%	SAMN09652112	MH198352
C. nicaraguensis	Hammel, B. 25,298	13,616	156,600	37.2%	40.7%	SAMN09652113	MH198328
C. silvicola	Hammel, B. 25,293	66,774	161,404	36.5%	94.8%	SAMN09652114	MH198353
C. skutchii	Aguilar, R. 12,292	18,172	161,470	36.9%	78.6%	SAMN09652115	MH198351
Clusia							
C. burle-marxii	Amorim, A. 4023	3,548	161,564	38%	40.1%	SAMN09652116	MH198340
C. cf. *clusioides*	Barclay, A.S. 3201	209,701	161,516	37.7%	77.8%	SAMN09652117	MH198341
C. heterocolorata	Marinho, L. 923	61,961	161,470	36.7%	93.4%	SAMN09652118	MH198343
C. gracilis	Ruhfel, B. 23	15,139	154,802	36.2%	80.8%	SAMN09652119	MH198327
C. grandiflora	Marinho, L. 1243	10,428	155,417	37.4%	54.4%	SAMN09652120	MH198342
C. panapanari	Marinho, L. 958	88,710	161,492	36.3%	95.6%	SAMN09652121	MH198344
C. polysepala	Marinho, L. 1305	99,260	161,297	36.3%	95.8%	SAMN09652122	MH198338
C. renggerioides	Marinho, L. 1376	44,710	161,406	36.7%	92.6%	SAMN09652123	MH198339
Dystovomita							
D. paniculata	Hammel, B. 25,295	14,987	155,664	36.1%	67.8%	SAMN09652124	MH198331
Garcinia							
*G. gardneriana***	Marinho, L. 918	5,433	156,347	36.5%	42.9%	SAMN09652125	MH198336
Symphonia							
*S. globulifera***	Ruhfel, B. 21	8,052	161,630	37.4%	55.6%	SAMN09652126	MH198335
Tovomita							
T. acutiflora	Marinho, L. 1370	22,561	157,246	36.2%	94.5%	SAMN09652127	MH198334
*T. caputmonsia**	Carrión, J. 1740	6,836	154,487	42.6%	7.9%	SAMN09652128	MH198346
T. choisyana	Marinho, L. 460	18,883	156,992	36%	82.9%	SAMN09652129	MH198329
T. croatii	Mori, S. 6725	8,300	161,451	37.9%	58.1%	SAMN09652130	MH198350
T. fructipendula	Marinho, L. 950	66,455	161,629	36.5%	94.9%	SAMN09652131	MH198332
T. gazelii	Sabatier, D. 3576	673	161,538	39.1%	11.9%	SAMN09652132	MH198356
T. guianensis	Munziger, J.K. 1360	293,273	165,463	41.3%	5.3%	SAMN09652133	MH198330
T. hopkinsii	Sothers, C. 452	28,338	161,506	36.7%	91.1%	SAMN09652134	MH198337
*T. lanceolata**	Luján, M. 650	4,698	161,409	39.5%	43%	SAMN09652135	MH198347
T. leucantha	Marinho, L. 888	17,161	161,561	36.9%	81.8%	SAMN09652136	MH198357
T. longifolia	Aguilar, R. 12,290	9,479	157,310	35.8%	59.4%	SAMN09652137	MH198333
*T. panamaea**	Carrión, J. 1741	14,552	149,040	38.4%	27.6%	SAMN09652138	MH198345
T. umbellata	Marinho, L. 1345	18,058	161,415	36.7%	79.8%	SAMN09652139	MH198355
*T. weddelliana**	Hammel, B. 25,294	39,290	161,249	36.6%	94.2%	SAMN09652140	MH198348
Tovomitopsis							
T. paniculata	Amaral, M.C. s.n.	1,073	161,694	38.7%	12.9%	SAMN09652141	MH198354
T. saldanhae	Bittrich, V. s.n.	24,108	156,062	36.7%	64.5%	SAMN09652142	MH198326

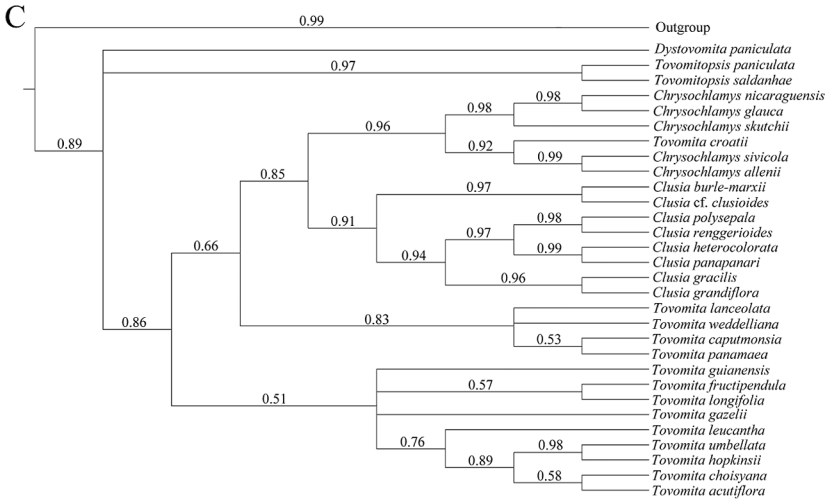
Appendix B. Individual trees of Clusieae tribe inferred from the ITS and plastid genome datasets. Support values are indicated at the nodes. *Symphonia globulifera* and *Garcinia gardneriana* were used for rooting, but have been removed for brevity. Generic names reflect the previous taxonomic placement for those species (without the new combinations proposed in this work)



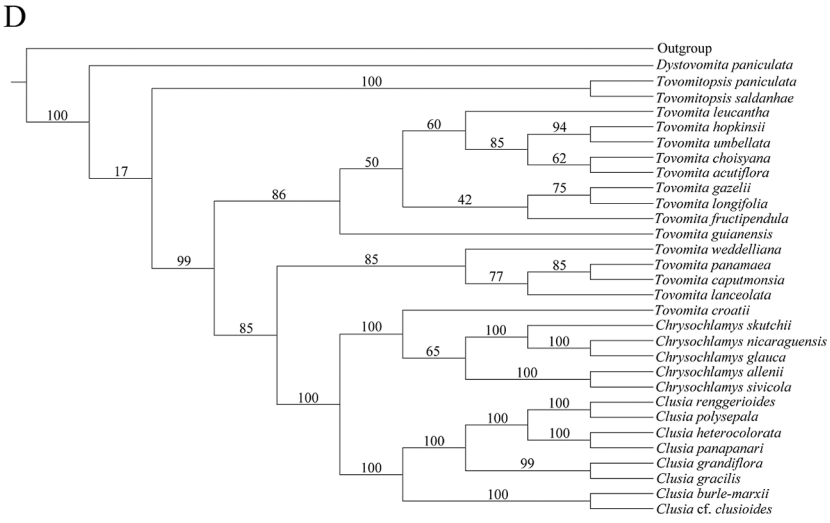
Tree A: One of the Bayesian inference (BI) topologies inferred from the ITS dataset. Numbers above the branches are BI posterior probabilities values (PP).



Tree B: Maximum likelihood (ML) topology inferred from the ITS dataset. Numbers above the branches are ML bootstrap percentage (BP).

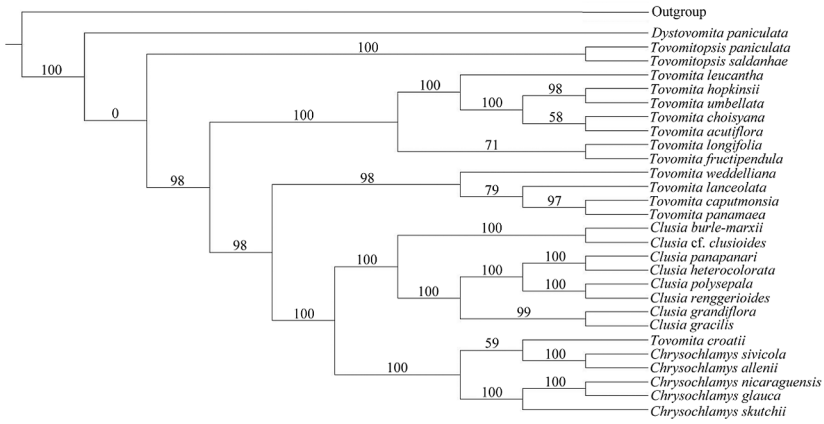


Tree C: One of the Bayesian inference (BI) topologies inferred from plastid genome dataset. Numbers above the branches are BI posterior probabilities values (PP).



Tree D: Maximum likelihood (ML) topology inferred from plastid genome dataset. Numbers above the branches are ML bootstrap percentage (BP).

E



Tree E: Maximum likelihood (ML) topology inferred from the plastid genome dataset, excluding two low quality samples: *Tovomita gazelii* and *T. guianensis*. Numbers above the branches are ML bootstrap percentage (BP).

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