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Drift in the tropics: Phylogenetics and biogeographical patterns in Combretaceae

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Abstract

Aim: The aim of this study was to further advance our understanding of the species-rich, and ecologically important angiosperm family Combretaceae to provide new insights into their evolutionary history. We assessed phylogenetic relationships in the family using target capture data and produced a dated phylogenetic tree to assess fruit dispersal modes and patterns of distribution.

Location: Tropical and subtropical regions.

Time Period: Cretaceous to present.

Major Taxa Studied: Family Combretaceae is a member of the rosid clade and comprises 10 genera and more than 500 species, predominantly assigned to genera *Combretum* and *Terminalia*, and occurring on all continents and in a wide range of ecosystems.

Methods: We use a target capture approach and the Angiosperms353 universal probes to reconstruct a robust dated phylogenetic tree for the family. This phylogenetic framework, combined with seed dispersal traits, biome data and biogeographic ranges, allows the reconstruction of the biogeographical history of the group.

Results: Ancestral range reconstructions suggest a Gondwanan origin (Africa/South America), with several intercontinental dispersals within the family and few transitions between biomes. Relative abundance of fruit dispersal types differed by both continent and biome. However, intercontinental colonizations were only significantly enhanced by water dispersal (drift fruit), and there was no evidence that seed dispersal modes influenced biome shifts.

Main Conclusions: Our analysis reveals a paradox as drift fruit greatly enhanced dispersal distances at intercontinental scale but did not affect the strong biome conservatism observed.

KEYWORDS

Angiosperms353, biogeography, Combretaceae, dispersal mode, drift fruits, niche and biome conservatism, phylogenomics, systematics

Olivier Maurin, Artemis Anest, Félix Forest and Ian Turner contributed equally to this work.

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1 | INTRODUCTION

The family Combretaceae (Myrtales) comprises 10 genera and 568 species of trees, shrubs and lianas, widely distributed in the tropics and subtropics (POWO, 2022). Although the systematics of the family was revised several times in recent decades (Jongkind, 1990, 1995, 1999; Maurin et al., 2010, 2017, 2020; Stace, 2002, 2010; Tan et al., 2002), several key relationships remain unclear, notably (1) relationships within tribe Laguncularieae; (2) the monophyly of subtribe Terminaliinae and the relationships between *Conocarpus*, *Terminalia* and all recently subsumed genera (*Anogeissus*, *Bucida*, *Buchenavia* and *Pteleopsis*); (3) relationships within subtribe Combretinae, in particular the identity of the sister taxon to *Combretum*, and the position of the previously accepted genera *Meiostemon*, *Quisqualis* and *Thilsea*; and (4) relationships between subgenera of *Combretum* (*Apetalanthum*, *Cacoucia* and *Combretum*; Figure 1). A detailed review of the current accepted classification is presented in Notes S1 and S2.

Biogeographical patterns within Combretaceae have received only limited attention despite the pan-tropical distribution and the reasonably detailed fossil record of the family (reviewed by Friis et al. (1992); recent fossil discoveries are summarized

in Table S1). The wealth of fossils assigned to the family indicates a worldwide distribution of Combretaceae by the end of the Cretaceous. Fossilized woods dated to Late Cretaceous have been assigned to 40 different species from Africa, South America and Asia, suggesting the prevalence of woodiness in the family early in Combretaceae evolutionary history (Mädel-Angeliwewa & Müller-Stoll, 1973; Prasad, 1988). Fossil flowers dating from the late Cretaceous (Coniacian; Barbosa, 1981) assigned to genus *Esgueiria* have been found in Japan (Takahashi et al., 1999a,b) and in Portugal (Teixeira & Zbyszewski, 1976). Fossil fruits also confirm the presence of Combretaceae in North America in the mid-Cretaceous (*Dilcherocarpon*; Manchester & O'Leary, 2010) and in Asia in the Late Cretaceous (*Gyrocarpusocarpon*; Mistri & Kapgate, 1990). Despite the extensive fossil record and the strong support it could provide for the inference of ancestral range in the family, few attempts to analyse the past distribution of Combretaceae have been performed. Gere et al. (2015) suggested that Combretaceae originated in Africa, and Berger et al. (2016) proposed South America and/or Africa as the ancestral range for order Myrtales, suggesting that the separation of South America and Africa preceded the divergence of Combretaceae.

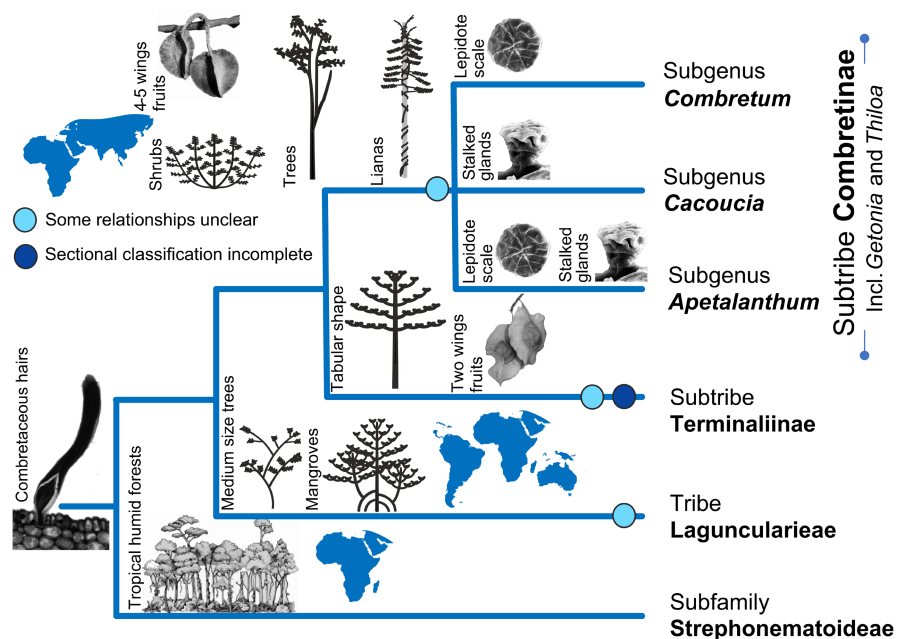


FIGURE 1 Schematic tree presenting the relationships among major groups within Combretaceae, with key morphological characteristics for each group, distribution and habitat. Clades with incomplete sectional classification or unclear relationships are highlighted. Leaf anatomy illustration from Tilney (2002).

Understanding how the family spread from its geographical origin requires understanding of which adaptations facilitated dispersal and shifts across biomes. Combretaceae is an ideal family to investigate how seed dispersal strategies could influence large-scale migrations as it possesses a variety of fruit types and dispersal modes, and an extensive distribution across the tropics (Stace, 1965b, 2010; Figure 2). Dispersal strategies may also have been involved in the colonization of the numerous types of biomes currently occupied by the family. Here, we investigated whether fruit morphology and associated dispersal modes could explain the intra- and intercontinental disjunctions observed within the family and discussed by Barrett (2015), Berger et al. (2016) and Gere et al. (2013, 2015). Combretaceae display an array of strikingly different dispersal modes such as water, animal and wind. Studies in other families revealed the important roles of dispersal modes in both inter- and intracontinental dispersal. For example, Fajardo et al. (2019) found that water-dispersed fruits significantly influenced the connection between the floras of the Galápagos Islands and the Central and South America landmasses. Onstein et al. (2019) concluded that fruit traits involved in frugivory likely contributed to the dispersal of Annonaceae to disconnected biogeographical areas in the tropics. Guimarães et al. (2008) suggested that megafauna extinctions have reduced geographic ranges of species with fruits thought to be dispersed by large animals. As shown by Klaus and Matzke (2020), the inclusion of dispersal-related fruit traits may improve accuracy of ancestral range reconstructions, but this method has not been widely used to infer ancestral ranges in Angiosperms and not at all in Combretaceae.

Here, we hypothesized that contrasted seed dispersal strategies may be responsible for intercontinental disjunctions and the occupation of contrasted vegetations in Combretaceae. More specifically, we searched whether each fruit type and its associated seed dispersal syndrome improved the dispersal rates between the different continents and the different biomes. We also searched whether fruit morphological innovations impacted the evolutionary history of the family through the colonization of new environments. Testing for these hypotheses should improve the understanding of both range expansion and species maintenance in any worldwide distributed plant clade.

For this purpose, we reconstructed a robust dated phylogenetic tree for Combretaceae using a target capture approach and the Angiosperms353 bait set (Johnson et al., 2019) and used this tree to interpret phylogenetic relationships within the family and its biogeographical history. This phylogenetic tree allows us to evaluate, update and revise the classification at lower taxonomic level within the family, to resolve several of the systematic problems outlined above. The resulting chronogram allows us to develop a more comprehensive understanding of the evolutionary history and biogeography of Combretaceae, including explaining the disjunct distributions observed today in many groups such as *Getonia/Guiera* and *Conocarpus*. We tested whether different dispersal modes have positively impacted dispersal rates between continents and islands, and between biomes, as well as infer ancestral ranges across Combretaceae.

2 | METHODS

2.1 | Sampling

We selected samples from 200 taxa (30% of the family, Table S2) including all the 11 recognized genera. For the two largest genera, *Combretum* and *Terminalia*, we maximized the representation of the recognized subgenera and sections, and geographic distribution and characteristic trait diversity. We also included taxa from the related families Lythraceae, Onagraceae and two outgroups from Francoaceae and Geraniaceae. We sourced our material from silica gel dried samples and herbarium specimens (see Voucher Information in Table S2). The final selection of samples included in this study was based on the best available DNA quality, with a minimum of 100–200ng of DNA with fragment sizes ≥ 350 bp following the library preparation kit manufacturer's recommendation (New England BioLabs). The full protocol from DNA extraction to sequencing is provided in Note S3.

2.2 | Phylogenomic inference workflow and tree reconstruction

A species tree was first inferred by analysing the individual supercontigs (i.e. exons and their flanking regions) and alignments concatenated using FASconCAT-G v1.0 (Kück & Meusemann, 2010). This species tree was generated using RAxML (Stamatakis, 2014) referred to hereafter as the maximum likelihood (ML) approach. We applied a multispecies coalescent approach, in which gene trees were generated for each trimmed locus alignment using IQ-TREE v2.0 (Minh et al., 2020), selecting the ultrafast bootstrap (1000 replicates, UFBoot2; Chernomor et al., 2016) and the model selection option (-m MFP). Branches with support values below 10% (Mirarab, 2019) were collapsed in each gene tree using Newick Utilities v1.6 (Junier & Zdobnov, 2010). We performed a first coalescent analysis using ASTRAL-III (Mirarab & Warnow, 2015) with extensive branch annotations (-t 2 flag). These annotations allowed recovery of both normalized quartet score (QS) values and local posterior probabilities (LPP). We evaluated this set of gene trees using TreeShrink (Mai & Mirarab, 2018) to identify taxa that increased the diameter of each gene tree (i.e. the maximum distance between any two tips of the tree) by more than 20%, using centroid re-rooting (-b 20 -c). The TreeShrink output allowed us to remove the outlier taxa and then realigned, trimmed, and analysed using IQ-TREE as described above. A final coalescent analysis was conducted on this second set of gene trees, as described above, but after excluding genes with <25% of the taxonomic sampling from the second set of gene trees and alignments shorter than 100bp. We finally conducted a quartet-based polytomy test using ASTRAL-III as described by Sayyari and Mirarab (2018) to evaluate gene tree discordance in the data set and identify potential hard polytomies. The phylogenetic results presented follow the phylogenomic reconstructions shown in Figure S1. QS



FIGURE 2 Variation of habit and habitat in Combretaceae. (a) *Combretum mossambicense* a scrambling shrub to liana, Niassa, Mozambique. (b) *Combretum imberbe* a large tree, Ngamiland, Botswana. (c) *Lumnitzera racemosa* a mangrove, in Kwazulu-Natal, South Africa. (d) *Combretum platypetalum* subsp. *oatesii* a suffrutex, Mashonaland West, Zimbabwe. (Olivier Maurin; OM; $\times 4$). Variation of inflorescences and flowers in Combretaceae. (e) *Strephonema sericeum* (David Harris). (f) *Laguncularia racemosa* (Rafael Govaerts). (g) *Lumnitzera racemosa* (OM). (h) *Dansiea elliptica* (Lui Weber). (i) *Macropteranthes montana* (CSIRO). (j) *Conocarpus lancifolius* (Helen Pickering; HP). (k) *Pteleopsis myrtifolia* (Bev Ocroft). (l) *Anogeissus leiocarpa* (Marco Schmidt; MS). (m) *Terminalia buceras* (OM). (n) *Terminalia tetraphylla* (Alex Popovkin). (o) *Terminalia phanerophlebia* (OM). (p) *Guiera senegalensis* (MS). (q) *Getonia floribunda* (V.R.Vinayaraj). (r) *Combretum apetalum* (Jie Cai). (s) *Combretum paniculatum* (OM). (t): *Combretum kraussii* (OM). Different fruit types observed in family Combretaceae based on floras and image databases. (u) cypselas of *Laguncularia racemosa* (Reinaldo Aguilar). (v) large-sized drupes of *Terminalia bellirica* (Himesh Dilruwan Jayasinghe; HJD). (w) small-sized drupes of *Terminalia chebula* (HDJ). (x) almonds of *Terminalia catappa* (HJD). (y) pyrenes of *Guiera senegalensis* (Michel Chauvet). (z) samaras of *Combretum kraussii* (Ori Fragman-Sapir). (aa) capsules of *Combretum pisoniiflorum* (Hyde et al., 2022). (ab) Achenocnium of *Conocarpus lancifolius* (HP).

values are interpreted as follows: if $Q1 \geq 0.75$ congruence is high; if $75 > Q1 \geq 0.5$ congruence is moderate; and if $Q1 < 0.5$ congruence is low. When interpreting LPP values: if $LPP > 0.95$ support is strong; if $0.5 < LPP < 0.95$ support is moderate; and if $LPP < 0.5$ support is low. When interpreting BS values: if $BS \geq 95$ support is strong; and if $BS < 95$ support is weak (low). The polytomy test of Sayyari and Mirarab (2018) evaluates the null hypothesis that a given branch is a polytomy. The test's ability to reject the null hypothesis is influenced by the length of a given branch and the number of genes available; the shorter the branch, the more genes are required for the null hypothesis to be rejected. This explains why, in some instances, the null hypothesis is maintained on short branches although they are supported with high LPP in the ASTRAL analysis.

2.3 | Divergence time estimates

To obtain a calibrated ultrametric phylogenetic tree, we used the penalized likelihood method (Sanderson, 2002) as implemented in the programme treePL (Smith & O'Meara, 2012). We applied this approach to the best maximum likelihood phylogenetic tree obtained from the concatenated, partitioned phylogenetic analysis of all genes produced using RAxML (version 8.2.12; Stamatakis, 2014) with the GTRCAT model assigned to each partition (1000 bootstrap replicates). We used three calibration points: the stem node of tribe Combretae (crown node of Combretaceae) was assigned a minimum age of 93.9 Ma based on the mid-Cretaceous macrofossil *Dilcherocarpon combretoides* (Manchester & O'Leary, 2010); the crown node of *Terminalia* comprising nine species was assigned a minimum age of 5 Ma from the oldest known *Terminalia* fossil (Mehrotra et al., 2003). Finally, the root node of the tree (i.e. crown node of Myrtales) was assigned a minimum age of 104.4 Ma and a maximum age of 128.7 Ma, according to estimates obtained for this node by Ramírez-Barahona et al. (2020) using BEAST and their relaxed calibration dating strategy with a complete fossil set. Following the use of the prime option to determine the best optimization parameters, we performed a cross-validation to select the most appropriate smoothing parameter (in this case 0.0000001). The penalized likelihood analyses were performed on the set of 1000 trees from bootstrap replicates produced by RAxML to estimate error on the divergence times. Resulting trees were compiled in TreeAnnotator (Suchard et al., 2018) to produce a 95% confidence interval on the divergence time estimates using the best maximum likelihood tree from the RAxML analysis as the target tree.

2.4 | Distribution, environmental and fruit data acquisition and treatment

We attributed each species to its preferred biome using climate and soil data, and geographical occurrence from GBIF (GBIF.

org, 27 October 2022, GBIF Occurrence Download <https://doi.org/10.15468/dl.7p2kpa>) and BIEN (the Botanical Information and Ecology Network, <https://bien.nceas.ucsb.edu/bien>). The fruit morphology of each species was scored from photographic records of living specimens having a voucher or herbarium plates, and the types of seed dispersal mode from literature (Table S4). We further investigated whether the distribution of traits in Combretaceae is associated with abiotic driver variations in tropical regions, including aridity, moisture seasonality and soil fertility using a principal component analysis (PCA) on the [occurrences \times environmental variables] matrix. The detailed protocol for the acquisition of distribution, environmental and fruit data and the treatment of environmental variables and biome identification is provided in Notes S4 and S5.

2.4.1 | Ranges, biomes and fruit ancestral state reconstructions

We reconstructed ancestral geographic range using the BioGeoBEARS package (Matzke, 2013), following the method of Klaus & Matzke (2020) (Table S5) and using the dated phylogenetic tree of Combretaceae (see Note S6 for our step-by-step model selection methods). We reconstructed the ancestral states of the fruit types using the 'make.simmap' function ('phytools' package; Revell, 2012) performing stochastic mapping and summarizing character state probabilities at each node and computed 1000 simulations for each of the trees according to the best-fitting model (Table S4).

3 | RESULTS

We will primarily discuss inferred phylogenetic relationships based on the ASTRAL tree (Figure 2a,b). The ASTRAL tree is also compared to the ML concatenated analysis (Figures S2 and S3).

3.1 | Phylogenetic relationships

Subfamily Strephonematoideae, represented only by genus *Strephonema*, is found to be sister to subfamily Combretoideae, with high QS, LPP and BS support (Figure 2b, Figure S1). All species of the genus form a strongly supported clade, with *Strephonema polybotryum* sister to the rest of the genus, while relationships between *S. pseudocola*, *S. sericeum* and *S. mannii* vary between the ASTRAL (moderate QS/LPP) and ML (high BP) analyses.

Within subfamily Combretoideae, tribe Laguncularieae is strongly supported as sister to tribe Combretae in both ASTRAL and ML trees, and forms a highly supported clade (high QS, LPP and BP). Within Laguncularieae, *Laguncularia racemosa* is sister to the rest of the clade, while *Lumnitzera* forms a strongly supported monophyletic clade (high QS, LPP and BP). *Dansiea* and *Macropteranthes* species also form a strongly supported group (high QS, BP and LPP).

However, *Macropteranthes* is not monophyletic in either the ASTRAL or ML trees, due to the nested position of *Dansiea*.

The large tribe Combreteae, which includes the majority of species in the family, is divided into subtribes Combretinae and Terminaliinae, both strongly supported (strong QS, high LPP and BP). In subtribe Terminaliinae, *Conocarpus* form a strongly supported clade sister to the large genus *Terminalia*, which includes the previously recognized genera *Anogeissus*, *Buchenavia*, *Bucida* and *Pteleopsis*. Within *Terminalia*, both analyses support similar topologies with seven major clades containing taxa that broadly reflect geographic patterns (Figure 5, Figure S1b). In subtribe Combretinae, the monotypic genera *Getonia* and *Guiera* are confirmed as closely related and together strongly supported as sister to the large genus *Combretum*. Within *Combretum*, subgenus *Apetalanthum* is nested within subgenus *Cacoucia* in both analyses, the pair forming a clade with moderate QS but with strong LPP and BP. Furthermore, *C. apetalum*, the sole taxon from subgenus *Apetalanthum* included here, is fully supported as closely related to *C. roxburgii* and *C. trifoliatum*, both considered as being part of subgenus *Cacoucia*, from sections *Decandrae* and *Kaloedendron* respectively. The next well-supported clade comprised *C. obovatum* and *C. zenkeri*, from sections *Lasiopetala* and *Caputilliformia*, respectively, together fully supported as sister to a large clade comprising all remaining species of subgenus *Cacoucia*, itself divided into two clades. The first strongly supported clade comprises sections *Calopyxis*, *Grandiflora* (previously included in *Poivreia*), *Poivreia*, *Quisqualis* and *Trichopetalae*. Within this clade, the topologies slightly differ between analyses, with relationships only fully supported in the ML tree. The second clade in subgenus *Cacoucia* presents similar topologies in both analyses and overall strong to full support on all branches. The *Cacoucia* subgenus clade includes sections *Cacoucia*, *Conniventia*, *Kaloedendron*, *Megalantherum*, *Oxystachya*, *Poivreia*, *Racemosa* and *Spinosae*.

Subgenus *Combretum*, the largest of the three subgenera, is strongly supported as monophyletic in all analyses with two major clades, both strongly supported in the ASTRAL and ML trees, although with poor QS support. The first comprises sections *Combretum*, *Hypocrateropsis*, *Leptosae*, *Mellifluae*, *Monetariae*, *Ovalifoliae* and *Quisqualoides* as well as the previously accepted genera *Meiostemon* and *Thiloea*, both now reduced to sections within subgenus *Combretum*. Within this clade, most relationships are strongly supported in the ML tree, but generally more moderate in the ASTRAL tree. The second large clade within subgenus *Combretum* comprises seven clades which are mostly strongly supported in both analyses: (1) sections *Plumbea*, *Quisqualoides* and *Tetragonocarpus*; (2) sections *Paucinervis* and *Paradoxae*; (3) sections *Chionanthoidea* and *Combretastrum*; (4) sections *Breviramea*, *Campestris*, *Mettalicum* and *Micrantha*; (5) section *Macrostigmatea*; (6) sections *Glabripetala* and *Angustimarginata*; (7) section *Ciliatipetala*.

3.2 | Biomes, fruit and dispersal type

Species of Combreteae are assigned to seven pedoclimatic envelopes for biomes: Dry savannas (A), dystrophic humid savannas (B),

eutrophic monsoonal forests (C), eutrophic woodlands (D), mesotrophic rainforests (E), dystrophic rainforests (F) and eutrophic rainforests (G). A few species in our sample are mangrove specialists but did not cluster together as a separate unit (likely due to the absence of coastal environmental variables). Those species were reassigned to a separate mangrove biome based on literature. The eight resulting pedoclimatic envelopes (Figure 3, Figure S4) separate into an open canopy group (A, B, C and D with an average tree cover below 50%) and a closed canopy group (E, F and G with a cover above 50%).

Dispersal modes differ significantly between continents and biomes (Figure 5b): Wind-dispersed seeds are more common in Africa and in savannas (biomes A, B) and dystrophic rainforests (F). Animal-dispersed seeds are more common in the Austro-Pacific and significantly less common in Africa and are more prevalent in eutrophic woodlands and rainforests (biomes D, G). Water-dispersed seeds are more common in the Austro-Pacific area and in mesotrophic monsoonal woodlands (biome C) and mangroves.

3.3 | Ancestral ranges, biomes and fruit inferences

All the results of model selection are available in Tables S5 and S6. The parameters for the best-fitting models are provided in Table S7. The best-fitting model for ancestral range distribution is the trait-dependent model DEC+j+x+t12+t21+m2 with water dispersal and constant geography (Figure 4, AIC of 256.5009 and an estimated m^2 of 0.108, the second best-fitting model is the trait-independent model DEC+j+x+t12+t21 with water dispersal and constant geography (AIC of 256.5037)). The Combretaceae ancestor likely occupied the Gondwanan fragment containing both Africa and South America (Figure 4, Figures S5 and S6), from where the inferences suggest range shifts to Africa between 128 (128.8–127.6) and 94.0 (95.2–93.9)Mya along the stem lineage of the family. From Africa, there was a range shift to Australia, while remaining in Africa (A+C) on the branch subtending *Macropteranthes* at 61 (64–24.8) and 17.8 (21–4.2)Mya. A second major shift to Australia is suggested 23 (31.6–2.8)Mya and seems also to be preceded by a range composed of both Africa and Australia (A+C) ca. 4 Mya earlier. From Africa, three major range shifts to South America are inferred: two occurred ca. 44.5 (52.1–11.1)Mya, one in *Terminalia* and another in *Combretum*, and a third occurred within the latter genus ca. 27 (32.8–5.8)Mya. All three shifts seem to have been preceded by a range composed of both Africa and South America (A+D). About 60.1 (64.2–52.2)Mya, inferences suggest a major shift from Africa to Africa-Asia range (A+B) in *Combretum*. From this ancestor, two major Asia-exclusive lineages appeared ca. 45.5 (50.1–18.5) and 41 (45.6–25)Mya.

The best-fitting model for biome inferences is the trait-independent model BAYAREALIKE+j+x+t12+t21 model with time-stratified biome states and continuous geography (Figure 5, AIC of 1148.97). The second best-fitting model is the trait-dependent model BAYAREALIKE+j+x+t12+t21+m2 model with time-stratified biome states, water dispersal trait and continuous geography (AIC of 1150.89). Ancestral biome inferences suggest

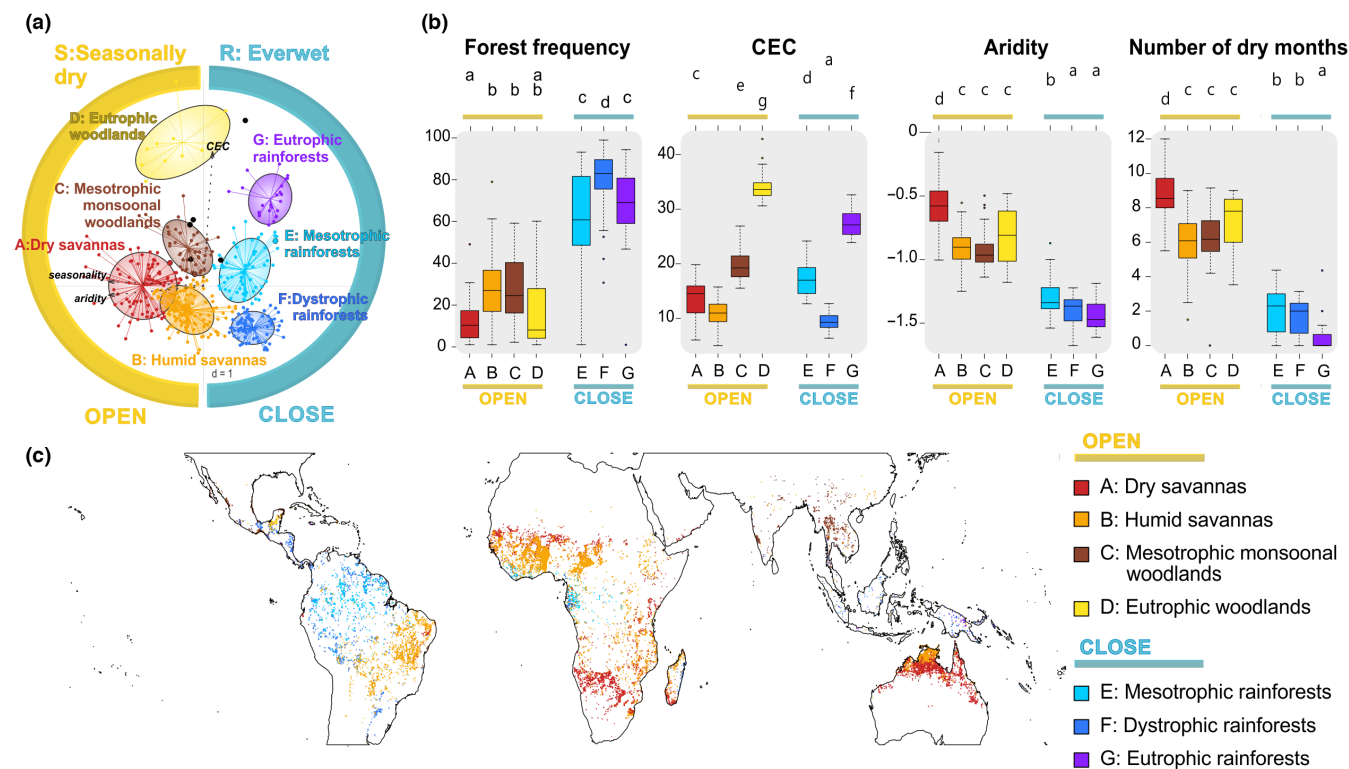


FIGURE 3 Biome clustering according to the structuring of the distribution data of 46 Combretaceae species. (a) Clustering of biome types; black filled points show mangrove exclusive species, points rounded in black are species which also grow in mangroves. (b) Relative contribution of each abiotic variable: forest frequency (according to Hansen et al., 2013); Cation Exchange Capacity (CEC); aridity; and number of dry months per year. Lowercase letters above each boxplot panel indicate pairwise comparisons (Tukey's HSD tests). (c) Map of retained Combretaceae occurrences and biomes attributed by species.

the ancestral biome for Combretaceae was likely a tropical seasonally dry and likely open-canopy biome (Figure 5, Figures S7 and S8), from which a biome shift to tropical everwet, and likely closed-canopy biome occurred along the stem lineage of *Strephonema*. Between 94 and 66 Mya, six major switches are suggested from tropical seasonally dry and open-canopy to tropical everwet and closed-canopy biomes. Finally, very few shifts are suggested after 23 Mya, and likely mainly occurred from dry savannas (A) to humid savannas (B) and between mesotrophic (E) and dystrophic rainforests (F).

A samara is inferred to be the likely ancestral fruit type in Combretaceae (Figure 5a, Table S8, Figure S9).

4 | DISCUSSION

This study confirms previously inferred generic relationships within Combretaceae based on a much denser sampling of taxa and greatly enlarged set of molecular markers (Figure 2a,b; Maurin et al., 2010, 2017, 2021; Tan et al., 2002). It provides first insights into biome shifts and evolution of seed dispersal strategies in Combretaceae. Using fruit types in ancestral range and biome modelling, it highlights a positive impact of drift fruits on dispersal rates between continents and a strong biome conservatism in the family.

4.1 | Taxonomy and relationships within Combretaceae

Subfamily Strephonematoideae (all described species were sampled) is fully supported as monophyletic and as sister to the rest of the family. Despite atypical morphology (Note S1), the presence of combretaceous hairs identifies this clade as closely related to Combretoideae (Stace, 1965a, 1965b). The divergence of Strephonematoideae is marked by the acquisition of large-sized drupes together with a biome shift from seasonally dry to everwet habitat.

The second subfamily, Combretoideae, and its two tribes (Laguncularieae and Combreteae) are all strongly supported as monophyletic. Laguncularieae comprises mangrove genera (*Laguncularia* and *Lumnitzera*) and two non-mangrove genera (*Dansiea* and *Macropteranthes*). The topology retrieved here confirms the position of *Laguncularia* as sister to the remainder of the tribe with two fully supported clades, the first comprising *Lumnitzera* and the second the two non-mangrove genera, both endemic to Australia, and differing from its two mangrove sister clades by having only dry fruits, no cypselas and occupying seasonally dry habitats. However, the relationship between these two genera remains unclear in both ASTRAL and ML analyses, with *Dansiea* embedded within *Macropteranthes*. We suggest that

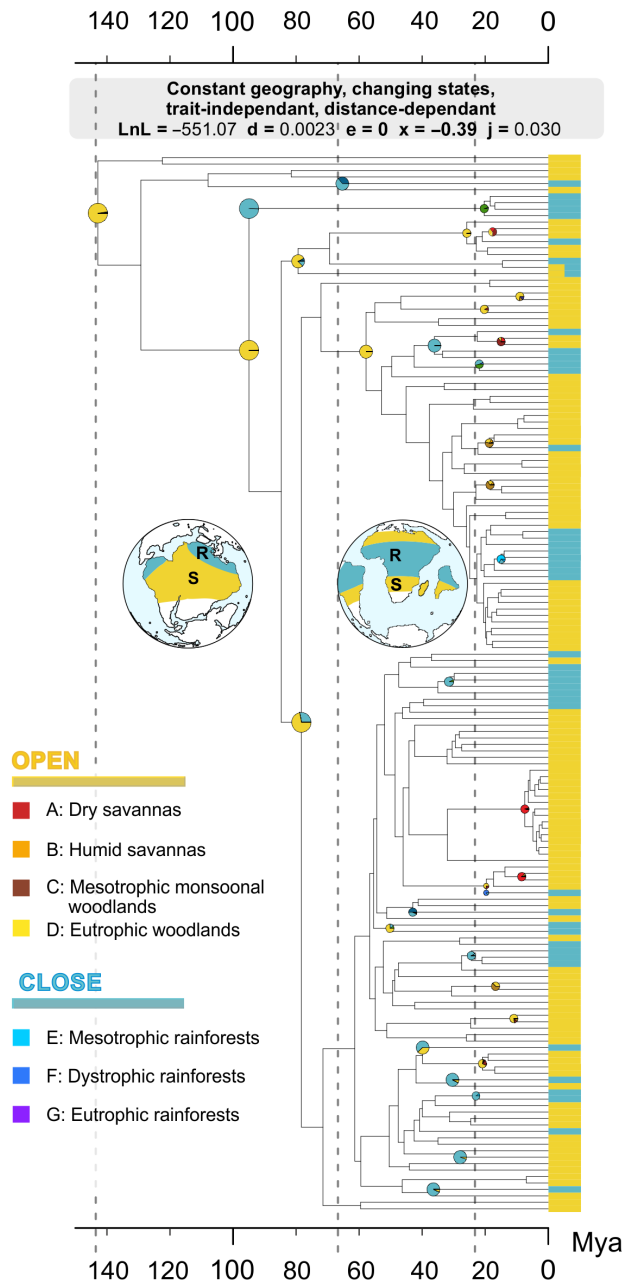


FIGURE 4 Reconstruction of ancestral biome for the 164 Combretaceae species according to the best-fitting model. Retained topology used to map the ancestral biomes with the best-fitting model DEC+j (see more detail in [Figures S7](#) and [S8](#)) with constant geography, trait-independent dispersal rates, distance dependent and time stratification applied to states: Dotted lines indicated the three dates of time stratification; from 142 to 66 Mya, only seasonally dry (open) and everwet (close) biomes are allowed; from 66 to 23 Mya, intermediate states open/close and present biomes are allowed, after 23 all present biomes are allowed.

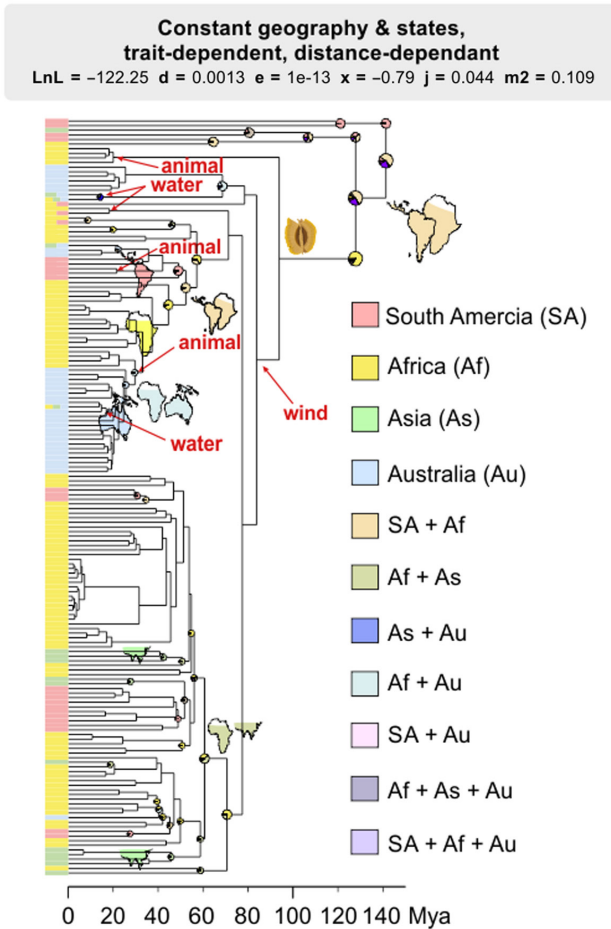
it may be appropriate to include the three recognized *Dansiea* species within an already variable *Macropteranthes* (Note [S1](#); Byrnes, [1981](#); Pedley, [1990](#)).

In Combreteae, the expanded species sampling compared to Maurin et al. ([2021](#)) enables the reassessment of taxonomic and biogeographic relationships within the group. Despite its divergent leaf morphology (considered an anomaly by Stace, [1965a](#); Note [S1](#)), the genus *Conocarpus* (subtribe Terminaliinae) is consistently retrieved (fully supported) as the sister group to the rest of the subtribe, even though it possesses a specific fruit type, characterized by an infructescence containing small samaras, and capable of both anemochory and floating dispersal. This genus also remarkably occupies different biomes, specifically mangroves and savannas. Sister to *Conocarpus*, we retrieved a monophyletic *Terminalia*, where the relationships differ notably in this study from the one presented in Maurin et al. ([2017](#)). Clade 1 (moderate in QS, but strongly in LPP and BP) comprises three clades, the first two include taxa from the former African genera *Pteleopsis* and Afro-Asian *Anogeissus*, while the third includes two taxa from South East Asia and Australia which likely obtained, first, a drupe-type fruit and later, almond-type fruit As suggested, taxa previously placed in *Anogeissus* are closely related to *Conocarpus* and share fruits borne in a cone-like infructescence (Stace, [1980](#)). Clade 2 (moderate QS and LPP, and strong BP) comprises taxa from Central to Southern America previously included in *Bucida* (*Terminalia buceras*) and *Buchenavia* (*T. pulcherrima* (Exell & Stace) Gere & Boatwr., and *T. oxycarpa*), with several taxa from South East Asia and Australia, including the former *Myrobalanus* (*T. australis* and *T. oblongata*), which is sister to a clade comprising mostly Asian species (including *T. bellirica*, *T. calamansanai*, *T. oblongata* and *T. platyptera*). Clades 3, 4 and 5 include taxa from Southern Africa, the first comprising two taxa from Madagascar (*T. gracilipes* and *T. ulexoides*), the second including taxa all belonging to section *Platycarpae* (sensu Griffiths, [1959](#); *T. prunioides*, *T. randii* and *T. stuhlmanni*) with a wide distribution range from Eastern and Southern Africa, and the last comprising African taxa with a wide distribution and diversity of habits, but with some restricted to Southern Africa or West Tropical Africa. Clade 6, like Clade 3, is endemic to Madagascar, while Clade 7 is a large clade of Asian, South East Asian, Australian and Pacific Islands species, including the coastal *T. catappa*, one of the species with the largest distributions in the family, from the Indian Ocean (Madagascar) to the Pacific.

Relationships in subtribe Combretinae are consistent with previous studies. Fruits and biomes seem very stable in this group which mostly possess samaras and predominantly grow in seasonally dry biomes (both ancestral in the family). The position of *Guiera* and *Getonia* combined as a strongly supported and monophyletic clade sister to the remainder of the subtribe is also supported. Sister to this pair is the genus *Combretum*, with the notable inclusion of subgenus *Apetalanthum*. This monospecific subgenus has consistently been separated from subgenera *Combretum* and *Cacoucia* as it bears both scales and glandular trichomes. Maurin et al. ([2021](#)) and the current study indicate that *Apetalanthum* is closely related to subgenus *Cacoucia*, forming a clade with members of sections *Decandrae* and *Kalodendron*, both assigned to subgenus *Cacoucia*.

[Correction added on 27 July 2023, after first online publication: captions for figures 4 and 5 have been corrected in this version.]

(a) Ancestral range inference (continents)



(b) Fruits dispersals and their geographical dependencies

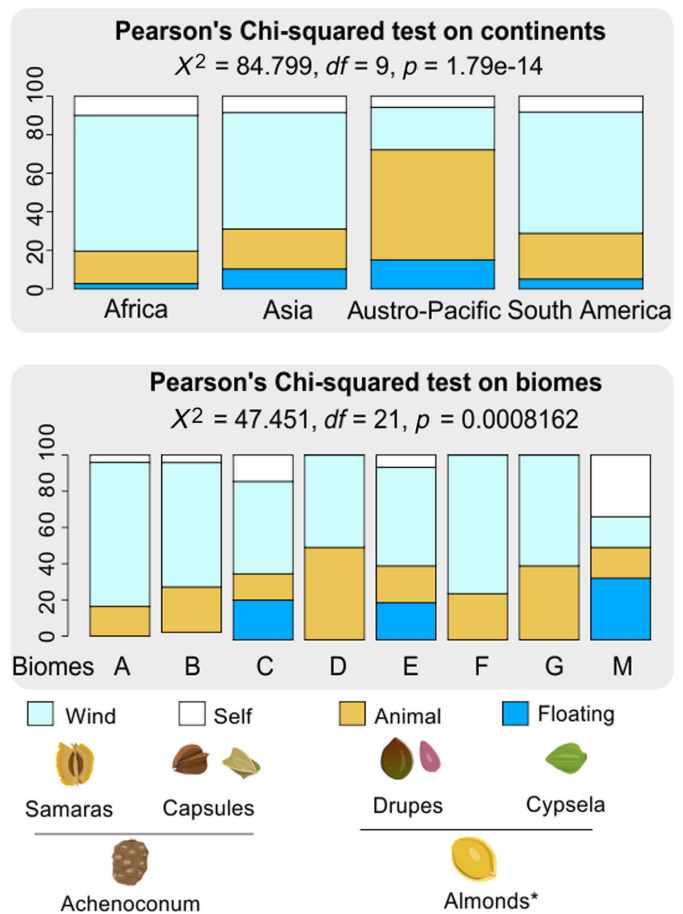


FIGURE 5 Ancestral range reconstruction according to the best-fitting model in BioGeoBEARS. (a) Inference according to the best-fitting model (trait-dependent and distance-dependent DEC+J+x+t12+t21+m2) and summary of the innovation of seed dispersal (see more detail in Figures S5, S6, S9). The map shows the legend of the pie's colours. (b) Fruit types and associated dispersal modes in Combretaceae used in the inference model (a) with distribution within the different continent and biomes, and their associated Pearson's chi-squared test.

The remaining *Combretum* species included in this study are assigned to sections not represented in previous studies (Maurin et al., 2010, 2017). The remaining species of subgenus *Cacoucia* form a fully supported clade with both low QS and LPP and characterized by the absence of scales and the presence of clavate stalked glands on the leaf surface mainly along the midrib and veins (Stace, 1980). Species of subgenus *Combretum* form two main clades, both poorly supported by QS but strongly supported by LPP. The first contains the sections *Haplostemon* (previously genus *Meiostemon*) and *Thiloo* (previously genus *Thiloo*), which is a novel relationship for those former genera, both previously poorly supported as sister to genus *Combretum* (Maurin et al., 2010, 2017). Section *Hypocrateropsis* is also noted as a member of this clade as it was also unplaced due to poor support in previous analyses (Maurin et al., 2010, 2017). The second large clade within subgenus *Combretum* is essentially composed of African taxa, except for the first clade containing three Asian taxa and the Southern African *Combretum imberbe*. Our current research provides a broad sectional-level sampling for the subgenera, but given the size of the genus, additional

sampling will be required before sectional relationships can be appropriately revised.

4.2 | Dispersal mode paradox: Move further but only to a similar environment

Current fruit-type distribution significantly varies over biomes (Figure 5b), for example, animal-dispersed seeds are more common in eutrophic biomes (D and G) which is consistent with mammalian mixed feeders being more common in fertile areas of open biomes (Sitters et al., 2020). Inferences on ancestral fruit type for the family suggest a samara, other fruit types seem to appear only once or twice each starting from 40Mya (Table S8). The earliest known fossil fruit assigned to Combretaceae is a samara (*Gyrocarpusocarpon*), dated to Late Cretaceous–Early Tertiary (Mistri & Kapgate, 1990) and the earliest fossils of other fruit types are in the Miocene ('infructescence fragment' assigned to *Conocarpus tertaria*; Menzel, 1913) and the Pliocene ('common drift-fruit' assigned to *Terminalia catappa*; Jurd & Pole, 2017). The

absence of fossils of non-winged fruits before the Miocene is coherent with our inferences which suggest that other fruit types evolved between 40 and 20 Mya in the family.

Our results suggest water-dispersed seeds enhance the probability of migration between continents (90% higher for water-dispersed lineages; Tables S5 and S7). This is consistent with the fact that several transitions between continents are suggested by the best-fitting inferences in water-dispersed lineages. Studies from other families also revealed that possessing 'drift-fruits' (water-dispersed seeds) allow species to cross long distances by floating, facilitating the colonization of new areas (Andrade Pereira et al., 2020; Guja et al., 2010; Lesko & Walker, 1969). However, probably due to a low number of water-dispersed species compared to other dispersal modes, including dispersal modes into the model did not improve it compared to a trait-independent model ($\Delta\text{AIC}=0.01\%$). A more exhaustive sampling would be needed to conclude the net effect of water-dispersed fruits on dispersal rates in Combretaceae. From a Gondwanan origin (supported by two best-fitting models), Combretaceae shifted its range between Africa and South America (Figure 4a). This node however shows an ambiguity, suggesting that Australia might have also been included in this ancestral range (Figure 4a). The range shift to Africa exclusively happened between 128 (128.8–127.6) and 94 (95.2–93.9) Mya indicating that the ancestral range of Combretaceae was Africa, as suggested by Gere et al. (2015). According to Takhtajan (1978), at least 19 plant families show a similar pantropical distribution, for example, Anacardiaceae, Myrtaceae and Sapindaceae, which also show a variety of seed dispersal strategies (Levey et al., 2002). In these three families, several studies have reported multiple intercontinental disjunctions (Gao et al., 2020; Thornhill et al., 2015; Weeks et al., 2014) and, while causes remain uncertain, dispersal strategies are often proposed as a major factor explaining those distributions (C ortes et al., 2009). Thus, studying biogeography of panglobal plant clades should always consider the benefit of including dispersal strategies to provide a more comprehensive view of a clade's present and past distribution and the relative importance of their dispersal strategies on the biogeographical patterns observed today.

Ancestral range reconstructions suggest that the ancestral biome of Combretaceae was a tropical seasonally dry and open-canopy biome (Figure 4) which corresponds to the Central African climate during the Cretaceous (Iglesias et al., 2011; Smith et al., 1994; Wilford & Brown, 1994). The colonization of less seasonal, and likely more closed habitats occurred a few times after 50 Mya which might be either due to the colonization of new habitats, or a progressive closing of the habitat over time. As stated by Matzke (in the BioGeoBEARS package), 'traits-based dispersal has been implemented for time-stratified analyses but is still experimental'. Our best-fitting model for ancestral range inferences is a trait-independent model which shows similar results to the trait-dependent model for the oldest nodes. This study thus brings a new contribution to the evaluation of the very recently

implemented traits-based dispersal in time-stratified models. Interestingly, the evolutionary history of the family is characterized by very few biome shifts and no link between dispersal mode and transition between biomes, suggesting a very strong niche and biome conservatism (Swenson, 2011) in Combretaceae. This suggests that fruit type might be strongly constrained by environmental factors associated with each biome (e.g. mammal-dispersed seeds in mammal-rich savannas, Figure 4b) and restrict dispersal events between biomes (Crisp & Cook, 2012). Some antagonistic interactions might be critical for explaining this biome conservatism, which is specific type of niche conservatism: for example, floating fruits cannot disperse out of mangroves and coastal systems, or else wind-dispersed seeds can hardly disperse in the absence of wind within closed-canopy forests.

Our study therefore suggests a dispersal mode paradox: While having the potential of dispersing more easily between continents, the acquisition of a specialized dispersal mode can also have the disadvantage of making species harder to disperse outside their biome, and thus colonize new environments. A specialized interaction may increase sympatric speciation in a suitable habitat, leading to the diversification of lineages with an optimal dispersal mode. This also suggests critical outcomes for species maintenance in biomes exposed to environmental changes where the disperser might be affected (e.g. closing open savannas by suppressing fire). As the equatorial area is likely to experience a strong warming in the future (Stuecker et al., 2020), numerous tropical plant clades could be affected by disperser loss.

4.3 | Further steps

Our study, improving both resolution and sampling in the large genera *Terminalia* and *Combretum*, highlights the need to further expand the sampling in these two genera to clarify the phylogenetic relationships of these ecologically dominant species. Increased sampling provides greater definition on transitions between open and closed habitats, suggesting how important the impact of potential environmental changes might be, for example, rising sea level, canopy closure or canopy opening, on species conservation through dispersal efficiency. Many pantropical distributed clades require further ecological studies considering both historical and future perspectives. In other plant clades, we can speculate whether alternative seed dispersal strategies absent in Combretaceae (e.g. bursting of the fruit, synzoochory) may have improved the colonization of new biomes and species maintenance. Further studies should investigate other strategies, such as vegetative propagation or extremely specialized dispersal strategies (e.g. myrmecochory), to estimate species ability to colonize new biomes. Understanding the present and historical association between plants and their dispersal strategies could enhance the conservation effort of any vegetation type through protecting their interactions with their dispersers.

AUTHOR CONTRIBUTIONS

Olivier Maurin, Artemis Anest, Félix Forest, Kyle W. Tomlinson and Tristan Charles-Dominique designed the project; Olivier Maurin, Artemis Anest, Robyn C. Cowan, Lijia Wang conducted data collection and processing; Olivier Maurin, Artemis Anest, Félix Forest and Kyle W. Tomlinson performed the analyses; Olivier Maurin, Artemis Anest, Ian Turner, Félix Forest, Russell L. Barrett, Kyle W. Tomlinson and Tristan Charles-Dominique wrote the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors whose names are listed immediately below report the following details of affiliation or involvement in an organization or entity with a financial or non-financial interest in the subject matter or materials discussed in this manuscript.

DATA AVAILABILITY STATEMENT

All Sequences files (fastq) generated for this study are deposited in the European Nucleotide Archive (ENA accession PRJEB56667 and PRJEB35285; Table S2). All alignments, Newick tree files generated are available at Zenodo ([10.5281/zenodo.6524742](https://doi.org/10.5281/zenodo.6524742)). All fruit type descriptions and assigned biomes are available in supporting information.

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BIOSKETCH

The research team leading this work is composed of phylogeneticists and ecologists from various institutions. Olivier Maurin has a longstanding interest in the taxonomy and phylogenetics of the family Combretaceae, while Artemis Anest has been studying the evolutionary ecology of the morphology and biogeography of this family as part of her PhD work.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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