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INVITED SPECIAL ARTICLE

For the Special Issue: Exploring Angiosperms353: a Universal Toolkit for Flowering Plant Phylogenomics

Phylogenomics and biogeography of Cunoniaceae (Oxalidales) with complete generic sampling and taxonomic realignments

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PREMISE: Cunoniaceae are a family of shrubs and trees with 27 genera and ca. 335 species, mostly confined to tropical and wet temperate zones of the southern hemisphere. There are several known issues regarding generic limits, and the family also displays a number of intriguing long-range disjunctions.

METHODS: We performed a phylogenomic study using the universal Angiosperms353 probe set for targeted sequence capture. We sampled 37 species covering all genera in the Cunoniaceae, and those in the three closely related families of the crown Oxalidales (Brunelliaceae, Cephalotaceae, and Elaeocarpaceae). We also performed analyses for molecular dating and ancestral area reconstruction.

RESULTS: We recovered the topology (Cunoniaceae, (Cephalotaceae, (Brunelliaceae, Elaeocarpaceae))) and a well-resolved genus-level phylogeny of Cunoniaceae with strongly supported clades corresponding to all previously recognized tribes. As previously suspected, the genera *Ackama* and *Weinmannia* were recovered as paraphyletic. Australasia was inferred as the likely ancestral area for the family.

CONCLUSIONS: The current distribution of Cunoniaceae is best explained by long-distance dispersal with a few possible cases of Australasian–American vicariance events. Extinctions may have been important in determining the mostly Oceanian distribution of this family while some genera in the tribe Cunonieae and in New Caledonia have undergone recent bursts of diversification. New generic diagnoses, 80 new combinations, and one new name are provided for a recircumscribed *Ackama* (including *Spiraeopsis*), a much smaller *Weinmannia* (mostly New World), and a resurrected *Pterophylla* to accommodate Old World taxa previously in *Weinmannia*.

KEY WORDS Antarctica; Australia; *Caldcluvia*; Gondwana; Madagascar; relicts.

Cunoniaceae are a medium-sized family of flowering plants with 27 genera and ca. 335 species (Bradford et al., 2004) of shrubs and trees mostly confined to tropical (including montane) and wet temperate zones of the southern hemisphere. The greatest diversity of species and genera is found in Oceania, particularly New

Guinea, eastern Australia, and New Caledonia. The family has a rich fossil record, especially in Australia (Barnes et al., 2001), but also in other areas where it is no longer extant, such as Antarctica (Poole et al., 2003), Sweden (Schönenberger et al., 2001), and Burma (Chambers et al., 2010). Cunoniaceae are now placed

in the order Oxalidales (APG IV, 2016), along with six other families (Fig. 1). Huaceae (2 genera and 3 spp., tropical Africa) appears to be sister to the rest of the order (Soltis et al., 2011), which is composed of two well-supported clades: Connaraceae + Oxalidaceae, and Brunelliaceae + Cephalotaceae + Cunoniaceae + Elaeocarpaceae (Wang et al., 2009; Soltis et al., 2011). The relationships within the latter clade, which could be referred to as crown Oxalidales or Elaeocarpaceae Engler (1898, p. 148), remain unresolved, and therefore the sister group of Cunoniaceae is uncertain.

Hufford and Dickison (1992) conducted the first cladistic analysis of the family, using morphological and anatomical characters. A molecular phylogenetic analysis, based on plastid *trnL* and *rbcL* sequences, was later published, including 23 of the currently accepted genera in the family (Bradford and Barnes, 2001). This study confirmed the placement of *Bauera* Banks ex Andrews, *Davidsonia* F.Muell., and *Eucryphia* Cav. within Cunoniaceae, three genera that have often been placed in their own monotypic families. This study also enabled the delimitation of several monophyletic tribes: Caldcluvieae, Codieae, Cunonieae, Geissoeae, Schizomerieae, and Spiraeanthemeae, although the position of some other genera (e.g., *Eucryphia*, *Acrophyllum* Benth.) remained unresolved. This phylogenetic framework paved the way for subsequent, more narrowly targeted studies. In a phylogenetic analysis of the tribe Cunonieae (*Cunonia* L., *Pancheria* Brongn. & Gris, *Vesselowskyia* Pamp., *Weinmannia* L.), Bradford (2002) found support for the division of *Weinmannia*, the largest genus of the family (ca. 150 species), into five monophyletic sections, while only recovering weak support for the monophyly of the entire genus. A new, monotypic genus from New Caledonia, *Hooglandia* McPherson & Lowry, was later discovered and described (McPherson and Lowry, 2004), with molecular phylogenetics indicating that it occupied an isolated position (Sweeney et al., 2004). A phylogenetic analysis of Spiraeanthemeae (Pillon et al., 2009a) suggested that two genera, *Acsmithia* Hoogland and *Spiraeanthemum* A.Gray, were not monophyletic and were therefore reunited. A later study of Geissoeae (Hopkins et al., 2013), including *Geissois* Labill., *Pseudoweinmannia* Engl., and the first published molecular data for *Lamanonia* Vell., led to the placement of the two Australian species of *Geissois* in the newly described *Karrabina* Rozefelds & H.C.Hopkins. Before the present work was initiated, no molecular data were available for the New Guinean endemics *Aistopetalum* Schltr. (2 spp.) and *Opocunonia* Schltr. (1 sp.), and in addition, questions regarding the monophyly and, hence, the limits of *Ackama* A.Cunn. and *Weinmannia* remained unclear (Y. Pillon, unpublished data).

Most phylogenetic studies of Cunoniaceae have been conducted with a handful of plastid (Bradford and Barnes, 2001) or nuclear (Pillon et al., 2009b) genes that lacked the power to resolve recalcitrant nodes. High-throughput DNA sequencing permits data gathering from a large number of loci, thereby increasing significantly the resolution of phylogenetic studies. Plastome phylogenomic

studies (e.g., Givnish et al., 2010; Drew et al., 2014; Li et al., 2019) have become common, but they rely on a number of loci that are tightly linked. Cytoplasmic gene flow implies that such approaches could be misleading (Rieseberg and Soltis, 1991), particularly between closely related species, but also even at higher ranks, e.g., between orders (Sun et al., 2015). Therefore, approaches using many unlinked nuclear loci are expected to yield more robust phylogenies. One such approach, targeted sequence capture, has now been made accessible to all angiosperm researchers through the development of a universal probe set, known as Angiosperms353 (Johnson et al., 2019). Also, targeted sequence capture employs short-read sequencing, which permits the use of degraded genomic DNA, such as that typically found in and extracted from herbarium specimens, i.e., museomics (e.g., Zedane et al., 2016), which can be a good substitute for fresh material for species that are extinct or difficult to procure. The efficacy of target sequence capture using Angiosperms353 on DNA from herbarium specimens has been well demonstrated (Brewer et al., 2019).

The primary aims of this study were to (1) clarify the relationships between Cunoniaceae and its closest relatives in the crown Oxalidales (viz Brunelliaceae, Cephalotaceae, and Elaeocarpaceae), (2) produce a phylogenetic tree of Cunoniaceae based on a sampling of every genus, (3) investigate the limits of two particularly problematic genera: *Ackama* and *Weinmannia*, and (4) investigate the biogeographical history of this predominantly southern hemisphere group. Secondary goals were to ensure that Cunoniaceae genera for which we sampled several species were monophyletic and to make the necessary taxonomic and nomenclatural adjustments to genera and species on the basis of a strongly supported phylogeny that was further supported by morphological characters whenever possible.

MATERIALS AND METHODS

Sampling

The sampling included all 27 genera currently recognized within Cunoniaceae (following Bradford et al., 2004; Pillon et al., 2009a; Hopkins et al., 2013), as well as all of the genera of the related families: Brunelliaceae (monogeneric, Kubitzki, 2004), Cephalotaceae (monogeneric, Conran, 2004), and Elaeocarpaceae (12 genera, Coode, 2004), except *Sloanea* L. in the last family, for which sequencing was not successful (Appendix S1). Within Cunoniaceae, we sampled all five sections within *Weinmannia* (sect. *Weinmannia*, *Fasciculatae*, *Inspersae*, *Leiospermum*, *Spicatae*; sensu Bradford, 1998). To test generic monophyly and for biogeographic analysis, one species from each geographical area for those taxa with a disjunct distribution was included in the sampling: *Cunonia* (southern Africa and New Caledonia), *Eucryphia* (South America and Australia), *Ackama* (Australia and New Zealand), and *Weinmannia* sect. *Weinmannia* (Americas and Mascarenes). Two species of

FIGURE 1. One representative of each of the four crown families of Oxalidales, clockwise from top left: *Cunonia capensis* L. (Cunoniaceae), drawn by Matilda Smith and reproduced from Curtis' Bot. Mag. vol. 139, tab. 8504 (1913); *Cephalotus follicularis* Labill. (Cephalotaceae), drawn by Louis-Constantin Stroobant and reproduced from L. B. van Hootte, Flore des serres et des jardins de l'Europe, vol. 3, tab. 8 (1847); *Brunellia sibundoya* Cuatrec. (Brunelliaceae), artist unknown. Reproduced from the Project to digitize the drawings of the Royal Botanical Expedition of the New Kingdom of Granada (1783–1816), directed by José Celestino Mutis: www.rjb.csic.es/icones/mutis. Royal Botanic Garden-CSIC; *Elaeocarpus grandiflorus* Sm. (Elaeocarpaceae), drawn by Walter Hood Fitch and reproduced from Curtis' Bot. Mag. vol. 78, tab. 4680 (1852).



Connaraceae, *Manotes expansa* Sol. ex Planch. and *Rourea calophylla* (Gilg ex G. Schellenb.) Jongkind, and one of Oxalidaceae, *Sarcotheca macrophylla* Blume, were chosen as outgroup taxa. Accessions were sourced from the DNA & Tissue Bank at the Royal Botanic Gardens, Kew, or were selected from herbarium specimens.

DNA extraction, library preparation, hybridization, and sequencing

DNA was extracted using a modified CTAB protocol (Doyle and Doyle, 1987) and purified using Mag-Bind TotalPure NGS (Omega Bio-tek, Norcross, GA, USA). The quality and concentration of the DNA extracts were assessed using a 1.5% agarose gel (to evaluate average fragment size) and a Qubit 3.0 fluorometer (Life Technologies, Carlsbad, CA, USA). DNA extracts with fragment sizes above 350 bp were sheared using a Covaris M220 Focused-ultrasonicator™ with Covaris microTUBES AFA Fiber Pre-Slit Snap-Cap (Covaris, Woburn, MA, USA). Dual-indexed libraries for Illumina sequencing were prepared using the DNA NEBNext Ultra™ II Library Prep Kit using half the recommended volume, with Dual Index Primers Set 1, NEBNext Multiplex Oligos for Illumina (New England BioLabs, Ipswich, MA, USA). The quality of the resulting libraries was evaluated on an Agilent Technologies 4200 TapeStation System using High Sensitivity D1000 ScreenTape (Agilent Technologies, Santa Clara, CA, USA). Libraries were pooled (equimolar 1 µg per pool) and enriched using the Angiosperms353 probe kit (Catalog #308196; Johnson et al., 2019) following the manufacturer's protocol v4 (4.0; <http://www.arborbiosci.com/mybait-manual>). Hybridizations were performed at 65°C for 28–32 h in a Hybex Microsample Incubator (SciGene, Sunnyvale, CA, USA) and using red Chill-out Liquid Wax (Bio-Rad, Hercules, California, USA) to prevent evaporation. Enriched products were amplified with KAPA HiFi 2X HotStart ReadyMix PCR Kit (Roche, Basel, Switzerland) for 10 cycles. PCR products were then cleaned using the QIAquick PCR purification kit (Qiagen, Hilden, Germany). Products were quantified with a Qubit 3.0 fluorometer, in some cases, reamplified a second time between 3 and 8 cycles. Final products were run on an Agilent Technologies 4200 TapeStation System using High Sensitivity D1000 ScreenTape to assess quality and average fragment size. Several pooled libraries were multiplexed, and sequencing was performed at the Royal Botanic Gardens, Kew on an Illumina MiSeq (Illumina San Diego, CA, USA) with v 3 reagent chemistry (2 × 300-bp paired-end reads) or at Macrogen (Takeley, UK) on an Illumina HiSeq to produce 2 × 150-bp paired-end reads.

Read mapping and sequence alignments

The reads of the sequencing output (.fastq) were trimmed using Trimmomatic (Bolger et al., 2014) to remove reads with a quality score below 30 and reads that had any 4-bp window below 30, retaining reads with at least 36 bp (LEADING: 30 TRAILING: 230 SLIDING WINDOW:4:30 MINLEN:36). The MINLENGTH setting was also used with length set to 36 to remove shorter reads that might not be uniquely positionable against other sequences. Paired reads and combined unpaired reads were used to recover target sequences using HybPiper version 1.3 (Johnson et al., 2016) using a target file available at <https://github.com/mossmatters/Angiosperms353>. Reads were mapped to de-gapped me-doid sequences using BLASTX (Camacho et al., 2009), each gene was assembled de novo using SPAdes (Bankevich et al., 2012),

and coding sequences were extracted using Exonerate (Slater and Birney, 2005). HybPiper was run using the BLAST option (Altschul et al., 1990) because it has been found to produce longer sequences (Murphy et al., 2020). Noncoding sequences (i.e., introns and untranslated regions [UTRs]) flanking the coding sequences were recovered using the script intronerate.py available with HybPiper. Gene matrices were aligned separately using MAFFT V7 (mafft-7.419-gcc_fc6.x86), with accuracy-oriented methods (--localpair --maxiterate 1000) and the option to generate reverse complement sequences to align them together with the remaining sequences based on 6-mer counting (--adjustdirectionaccurately). Matrices were subsequently trimmed using phyutility (<https://github.com/blackrim/phyutility>) to delete sites that were missing 80% data (-clean 0.8). Gene trees from trimmed matrices were generated using IQtree V1.6.12 (Minh et al., 2020), using ultrafast bootstrap with partition models (Chernomor et al., 2016). In a first iteration, generated gene trees were evaluated using TreeShrink 1.3.1 (Mai and Mirarab, 2018) to identify and exclude branches that increased the diameter of each gene tree by more than 20% using centroid re-rooting (-b 20 -c). Each locus was then realigned, trimmed, and analyzed using IQtree with bipartition support assessed with 1000 UFBoot2 (Hoang et al., 2018) bootstrap replicates (-bb 1000), while collapsing branches with support values below 10% (Mirarab, 2019 [Preprint]) using Newick Utilities 1.6 (Junier and Zdobnov, 2010). We additionally excluded genes that contained data for fewer than 25% of species. A species tree was constructed from the set of trees produced based on the supercontigs (exons + introns) individually produced with IQ-Tree. Tree and extensive branch annotations were generated using ASTRAL-II (Mirarab and Warnow, 2015) using alternative quartet topologies (-t 2): indicating the local posterior probabilities of the percentage of quartets in gene.

Divergence time estimates

To limit the effects of rate and topology heterogeneity between genes on divergence time estimations and the computational times required for such analysis, we first selected a set of genes using Sortadata (Smith et al., 2018). Genes chosen were those that were at least 10% concordant (bipartition >0.1) with the species tree produced with ASTRAL, had a root-to-tip variation less than 0.003, and had a tree length exceeding 2.1. The threshold for the agreement with the species tree was based on those used in previous studies (e.g., Shee et al., 2020), while those for the root-to-tip variation and tree length were determined using the median of the values obtained with Sortadata for all gene trees.

Divergence times were estimated using the Bayesian approach implemented in BEAST v1.10.4 (Suchard et al., 2018) on the CIPRES Science Gateway V. 3.3 (<https://www.phylo.org/>). We used the selected genes as independent partitions with their specific DNA substitution models and clock models, both unlinked. The topology of the tree was constrained to the relationships retrieved in the ASTRAL analysis. We used an uncorrelated relaxed clock with a lognormal distribution prior and a Yule process tree prior. Six fossil taxa were used for calibration using a normal distribution prior (Table 1). Five independent runs were conducted with 100 million generations, sampled every 2000 generations. Parameter convergence and appropriate effective sample sizes were verified in Tracer v1.7 (Rambaut et al., 2018). Tree files were combined in

LogCombiner with a burnin of 25% (based on results visualized in Tracer), while the maximum credibility tree and associated posterior probabilities were computed in TreeAnnotator (Suchard et al., 2018). Diversification rates were calculated using equation 4 of Magallón and Sanderson (2001).

Biogeographical patterns

Ancestral range estimation for Cunoniaceae was performed using the dispersal–extinction cladogenesis (DEC) (Ree and Smith, 2008) and DEC+J models as implemented in the R package BIOGEOBEARS (Matzke, 2013). Geographic areas, as defined by Buerki et al. (2011), were used with the addition of Antarctica as one of the available regions because of its potential role in the past as a dispersal route for plants and animals (de la Estrella et al., 2017, 2019). The adopted area of delimitation approximates that of Buerki et al. (2009) and de la Estrella et al. (2019) with some modifications as follows: A, Africa; B, Madagascar (including Comoro and Mascarene Islands); C, Australia/New Guinea; D, New Caledonia; E, New Zealand; F, Americas; G, West Malesia (including India and Sri Lanka); H, Pacific Islands; I, Antarctica (see Appendix S2 for detailed definition). India and Sri Lanka were included within West Malesia to reduce the number of areas in our analysis, as only one sampled genus occurs in India (*Elaeocarpus*). Area assignments for each terminal are listed in Appendix S3. The biogeographical models proposed by Buerki et al. (2011) and de la Estrella et al. (2019) with five time slices reflecting the probability of area connectivity through time served as the basis for the development of a model tailored for Cunoniaceae (Appendix S2). Four of the time slices from de la Estrella et al. (2019) were employed here because the oldest one, 160–125 Ma, is older than the time spanned by the current analysis (i.e., 100.2 Ma). We performed these biogeographical analyses including and excluding Antarctica as an area to ascertain its impact on the estimation of the biogeographical patterns. The outgroup taxa were removed before these analyses.

RESULTS

Cunoniaceae were recovered as the sister group of a clade comprising (Brunelliaceae, (Cephalotaceae, Elaeocarpaceae)) (Fig. 2). The sister relationship of Cephalotaceae to the Brunelliaceae + Elaeocarpaceae clade is only moderately supported (local posterior probability, LPP = 0.97; quartet values $q_1 = 0.45$, $q_2 = 0.31$, $q_3 = 0.24$). Within Cunoniaceae, most nodes are strongly supported (i.e., LPP = 1) with a few exceptions. *Spiraanthemum*, *Hooglandia*, *Aistopetalum*, and *Bauera* were the successive sister groups to the rest of the

Cunoniaceae, although the placement of *Bauera* is only weakly supported (LPP = 0.36; $q_1 = 0.51$, $q_2 = 0.27$, $q_3 = 0.22$).

The tribes Caldcluvieae (*Ackama*, *Caldcluvia* D. Don, *Opocunonia*, *Spiraeopsis* Miq.), Codieae (*Callicoma* Andrews, *Codia* J.R. Forst. & G. Forst., *Pullea* Schltr.), Cunonieae (*Cunonia*, *Pancheria*, *Vesselowskyia*, *Weinmannia*), Geissoieae (*Geissois*, *Karrabina*, *Lamanonia*, *Pseudoweinmannia*), Schizomerieae (*Anodopetalum* A. Cunn. ex Endl., *Ceratopetalum* Sm., *Platylophus* D. Don, *Schizomeria* D. Don) were all recovered as monophyletic with strong support (LPP = 1; except for tribe Codieae, LPP = 0.95). *Davidsonia* was the sister of tribe Schizomerieae, but this relationship was only moderately supported (LPP = 0.92; $q_1 = 0.42$, $q_2 = 0.33$, $q_3 = 0.26$). Within tribe Schizomerieae, the relationships between the genera differed from the published studies based on two plastid genes. For instance, *Anodopetalum* was previously recovered as the sister group to *Platylophus* with strong support (Bradford and Barnes, 2001; Hopkins et al., 2013), while here *Ceratopetalum* is the sister group to *Platylophus* with strong support (LPP = 1).

A strongly supported (LPP = 1) “core Cunoniaceae” (sensu Bradford et al., 2004), including *Acrophyllum*, *Eucryphia*, *Gillbeea* F. Muell., and the tribes Caldcluvieae, Codieae, Cunonieae, and Geissoieae, was recovered as in previous studies (Bradford and Barnes, 2001; Hopkins et al., 2013). Relationships resolved within tribe Codieae agree with previous studies (Bradford and Barnes, 2001; Hopkins et al., 2013). The relationships between the four genera of tribe Geissoieae were here only moderately supported (Fig. 2), with *Lamanonia* and *Geissois* as sister groups (LPP = 0.86), and *Karrabina* and *Pseudoweinmannia* as sister groups (LPP = 0.70). *Opocunonia* was recovered in the tribe Caldcluvieae as the sister group to *Caldcluvia* (LPP = 0.93). In this tribe, the genus *Ackama* was paraphyletic with respect to *Spiraeopsis* Miq., with the Australian and New Zealand species of *Ackama* forming separate subclades, based on our sampling.

In Cunonieae, *Weinmannia* formed two distinct clades (Fig. 2). The species belonging to the four Old World sections (sect. *Fasciculatae*, *Inspersae*, *Spicatae*, and *Leiospermum*) formed a monophyletic group (LPP = 1) sister to *Cunonia* + *Pancheria* (LPP = 1). The fifth section, composed of taxa from the Americas and the Mascarenes (sect. *Weinmannia*), was sister to this assemblage. The two sections of *Weinmannia* endemic to Madagascar and the Comoros (*Inspersae* and *Spicatae*) formed a monophyletic group sister to section *Leiospermum* from the Pacific Islands. Several groups showing major geographic disjunctions were also recovered: *Cunonia* (southern Africa, New Caledonia), *Eucryphia* (South America, Australia), and *Weinmannia* sect. *Weinmannia* (Americas, Mascarenes) were all monophyletic. The other genera endemic to America (*Caldcluvia*, 1 sp., *Lamanonia*, 6 spp.) and South Africa (*Platylophus*, 1 sp.) all have their closest relatives in Oceania.

A set of 41 gene trees were selected based on their concordance, which was further reduced to include only those that comprised at

TABLE 1. List of the six fossil taxa used as calibration points in the molecular dating analysis of Cunoniaceae and relatives. Ages are reported in millions of years. SD, standard deviation.

Fossil taxa	Period	Position	Mean age, Myr (SD)	Reference
1. <i>Tropidogyne</i>	Early Cretaceous (Upper Albian)	Crown node of Oxalidales	100.5 (1.0)	Chambers et al. (2010)
2. <i>Lacinipetalum</i>	Early Paleocene	Stem node of tribe Schizomerieae	66.0 (1.0)	Jud et al. (2021)
3. <i>Eucryphia</i>	Late Paleocene	Stem node of <i>Eucryphia</i>	66.0 (1.0)	Barnes et al. (2001)
4. <i>Codia</i>	Middle Eocene-Oligocene	Crown node of <i>Codia</i> and <i>Callicoma</i>	47.8 (1.0)	Barnes et al. (2001)
5. <i>Vesselowskyia</i>	Early Oligocene	Stem node of <i>Vesselowskyia</i>	33.9 (1.0)	Barnes et al. (2001)
6. <i>Elaeocarpus</i>	Early Oligocene	Crown node of <i>Elaeocarpus</i>	33.9 (1.0)	Crayn et al. (2006)

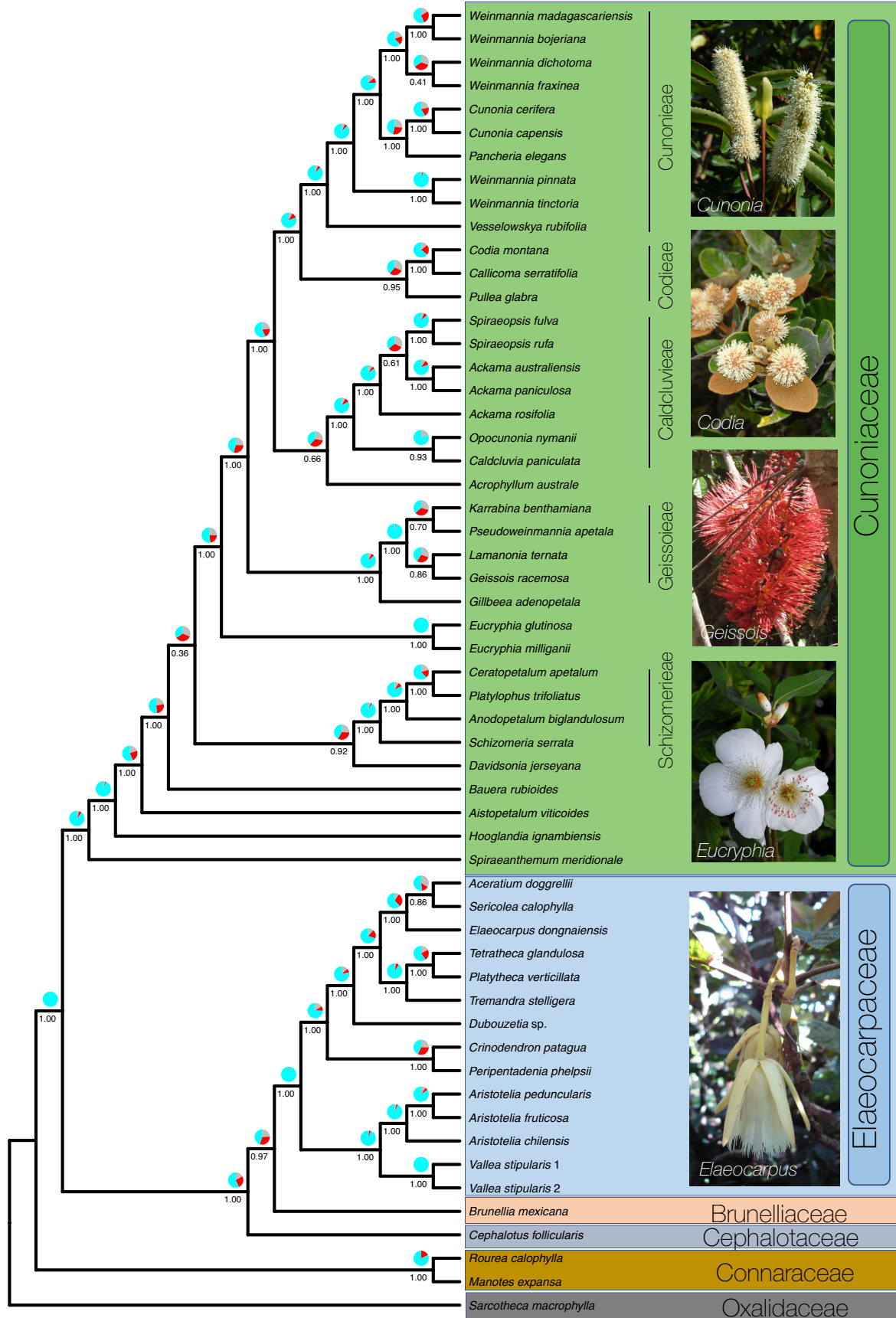


FIGURE 2. Genus-level phylogenetic tree of Cunoniaceae and its relationships with the closely related families Brunelliaceae, Cephalotaceae, and Elaeocarpaceae. Tree based on the universal Angiosperms353 probe set for targeted sequence capture. Numbers below branches represent local posterior probability values, and pie charts indicate quartet support.

least 48 of the 56 taxa (86%) included in this study. This resulted in the set of 14 genes totalling 51,614 characters that were used in the molecular dating analyses.

All parameters from the combined BEAST analyses reached convergence, except for a few for which the effective sample size was slightly under the generally accepted threshold of 100. Most age estimates have relatively small confidence intervals (Appendix S4), including the estimate for the crown node of Elaeocarpaceae (66.7 Ma) and the crown node of Cunoniaceae (88.6 Ma; Appendix S4). The DEC+J model was favored over the DEC model ($p < 0.01$), which is indicative of a greater role of vicariance in explaining the biogeographical patterns observed in the study group. The analyses with Antarctica included or not as an available area produced very similar results; only the results including Antarctica are presented hereafter (Fig. 3). The most likely ancestral area for the crown node of Cunoniaceae is a combination of Australia/New Guinea (area C) + New Caledonia (area D); the same ancestral area is assigned to the subsequent node in Cunoniaceae. The remainder of the earliest-diverging nodes in Cunoniaceae are reconstructed as occurring in Australia/New Guinea with dispersal to other regions later in the history of the group. For Elaeocarpaceae, America is the most likely area assigned to the crown node of the family, with Australia/New Guinea the second most likely reconstruction. In the clade comprising the genera *Vallea* Mutis ex L.f. and *Aristotelia* L'Hér., America is the most likely ancestral area, while for the clade comprising the remainder of the family, Australia/New Guinea is favored.

DISCUSSION

This study resolved the phylogenetic relationships amongst the largest clade within Oxalidales as follows: (Cunoniaceae, (Cephalotaceae, (Brunelliaceae, Elaeocarpaceae))). It also confirmed that the monospecific Cephalotaceae (Albany pitcher plant) from southwestern Australia is nested in an otherwise entirely woody and mostly tropical clade. No obvious floral characters support this particular arrangement amongst the four families (Matthews and Endress, 2002). All four are predominantly found in the southern hemisphere, although Elaeocarpaceae (Hably et al., 2007; Manchester and Kvaček, 2009), like Cunoniaceae, has credible fossils in several regions of the northern hemisphere where it no longer occurs.

The monophyly of Cunoniaceae with its current limits is confirmed, and our analysis supports the inclusion of the families Baueraceae, Davidsoniaceae, and Eucryphiaceae within it (Angiosperm Phylogeny Group, 1998). We found support for the monophyly of all six of the tribes delineated by Bradford and Barnes (2001): Caldcluvieae, Codieae, Cunonieae, Geissoieae, Schizomerieae, and Spiraeanthemeae, the last being now monogeneric (Pillon, et al., 2009a). Assigning all genera to tribes would require the description of several new tribes (mostly monotypic) and will be dealt with elsewhere. The generic relationships recovered within Elaeocarpaceae agree with those of Crayn et al. (2006).

The Caldcluvieae currently comprises four genera: *Ackama*, *Caldcluvia*, *Opocunonia*, and *Spiraeopsis* (Bradford et al., 2004). Although this tribe contains only 12 species, seven generic names have been published for them. The last complete species-level revision was by Hoogland (1979), who treated the entire group as a single genus, *Caldcluvia*, but this broad generic concept has not been followed in most subsequent works (de Lange et al., 2002; Hopkins and Hoogland, 2002; Bradford et al., 2004; Heslewood and Wilson, 2013). Here we found that *Ackama* was paraphyletic with *Spiraeopsis* nested inside it, and so we sink *Spiraeopsis* into *Ackama*, while *Opocunonia* and *Caldcluvia* s.s. remain as distinct, monotypic genera (see Appendix 1: Taxonomic treatment). Characters that unite *Ackama* s.l. and distinguish it from *Caldcluvia* s.s. and *Opocunonia* are the size and shape of the inflorescence, the size of the flowers and length of their pedicels, and the number and arrangement of the stipules.

Our data supported the paraphyly of the genus *Weinmannia* that was suspected by Bradford (2002) and Y. Pillon (unpublished data). The species of *Weinmannia* fell into two clades. The first, comprising sect. *Weinmannia*, was represented in our analysis by one species from the Americas (*W. pinnata* L., the type of the genus) and one from the Mascarenes (*W. tinctoria* Sm.). The second clade includes the remaining species in our analysis, all from the Old World, representing sections *Fasciculatae* (Malesia and Pacific), *Inspersae* (Madagascar), *Leiospermum* (Pacific), and *Spicatae* (Madagascar + Comoros). We therefore propose splitting *Weinmannia* into two genera, *Weinmannia* s.s., which equates to sect. *Weinmannia*, and *Pterophylla* D.Don, which we re-establish for the clade including the four other sections (see Appendix 1: Taxonomic treatment). These two groups differ in inflorescence architecture, corolla, and seeds.

This phylogenomic study provides insights into the enigmatic biogeography of Cunoniaceae, traditionally considered a “Gondwanan” family (Raven and Axelrod, 1974). Our ancestral area reconstruction indicates a combination of Australia/New Guinea (area C) + New Caledonia (area D) as the likely ancestral area for the family (Fig. 3). Indeed, the greatest number of extant species and genera are found in Oceania, and particularly in eastern Australia, New Guinea, and New Caledonia (Fig. 4). The three lineages in the basal grade (*Spiraeanthemum*, *Hooglandia*, *Aistopetalum*) are all restricted to Oceania. Few lineages are found outside Oceania and nearby Southeast Asia (Malesia), and they are all phylogenetically distantly related to one another. The divergence of the southern African *Cunonia capensis* L. (24.5 Ma), the South American *Lamanonia* (20.8 Ma) and *Eucryphia* (14.5 Ma), and the Malagasy *Pterophylla* (25.6 Ma) from their Oceanian relatives postdate land connections between Australia and their current ranges. Their distributions may therefore be explained by long-distance dispersal. It is worth noting that the only major difference between the reconstructions including and excluding Antarctica concerns the ancestral area of the node subtending *Platylophus* and *Ceratopetalum* (27.9 Ma). It is reconstructed as Australia/New Guinea when Antarctica is not accounted for and as a combination of Africa and Australia/New Guinea when Antarctica is included (Fig. 3). This scenario could suggest that the ancestor of *Platylophus*

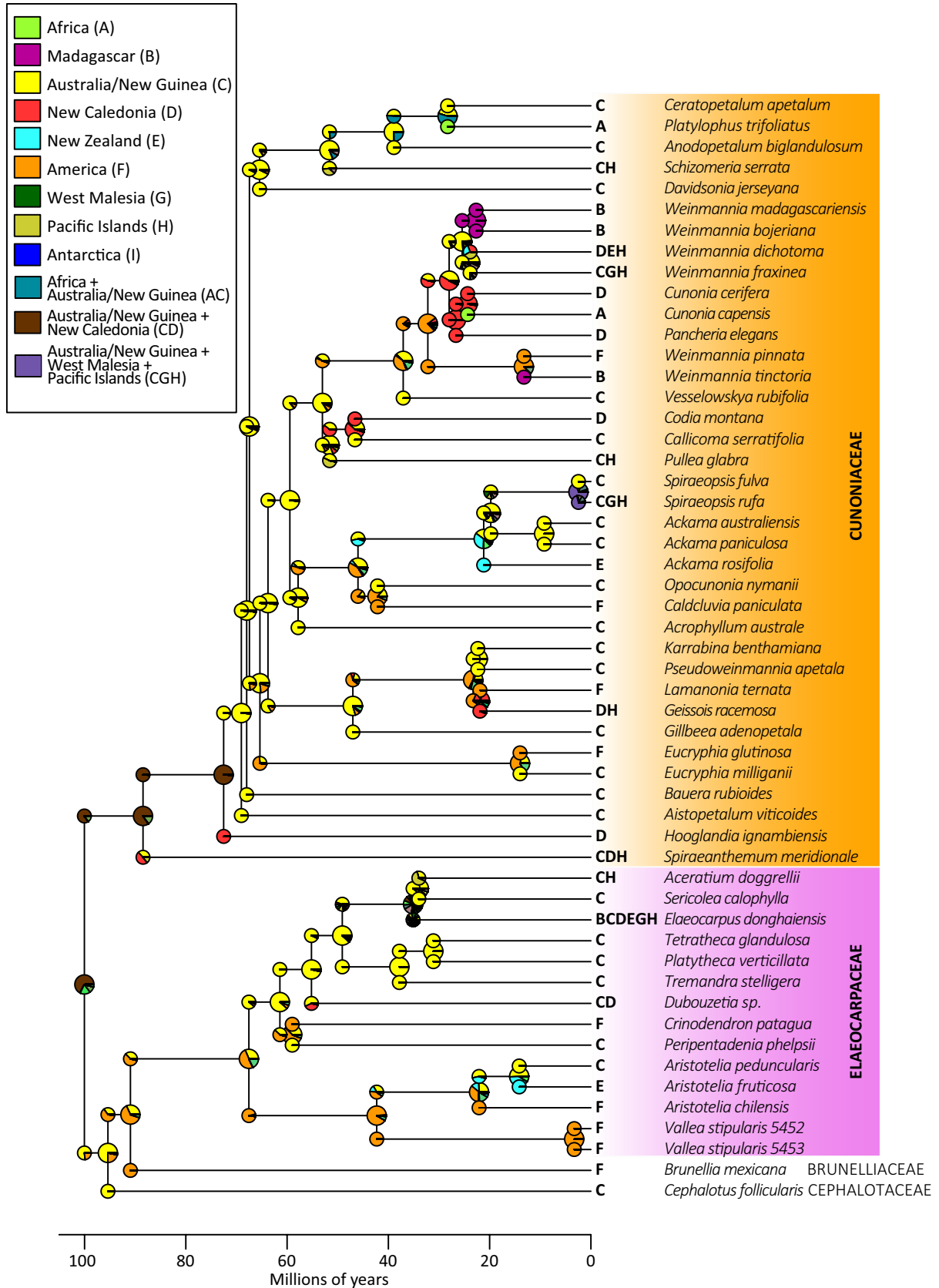


FIGURE 3. Ancestral area reconstruction in Cunoniaceae and related families using the DEC-J model.

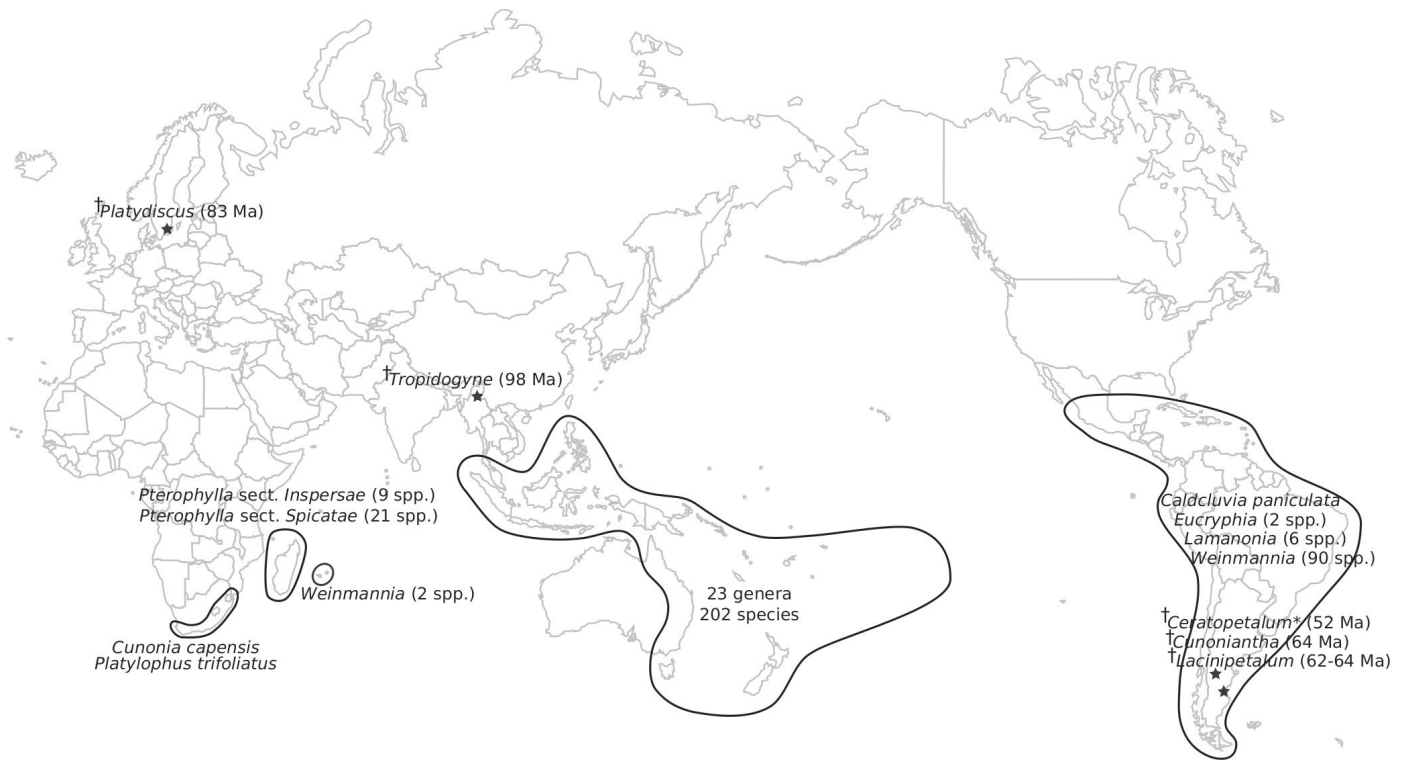


FIGURE 4. Distribution and diversity of Cunoniaceae according to the new taxonomic framework presented here. **Ceratopetalum* is still extant in Australia, New Guinea, and New Britain. †Extinct genera (age of fossil deposit).

would have dispersed to Africa from Australia/New Guinea via Antarctica. The older timing of divergence of the mostly American *Weinmannia* s.s. (32.3 Ma) and the American *Caldcluvia* (41.2 Ma) from their Oceanian relatives may also be compatible with colonization through Antarctica. Indeed, until the Eocene, Antarctica was either directly connected to, or separated by relatively narrow seas from, both South America and Australia (Scotese, 2004; Müller et al., 2016), increasing the possibility of biotic exchange between these two now distant landmasses. It is not precisely clear when these landmasses became irreversibly separated by sea barriers, but it was probably sometime in the Eocene, ca. 35–41 Ma (Stickley et al., 2004; Scher and Martin, 2006). The same “via-Antarctica” scenario might also apply to two Elaeocarpaceae genera confined to South America: *Crinodendron* Molina (58.1 Ma) and *Vallea* (41.8 Ma). Nevertheless, the ancestral area reconstruction using the models proposed by de la Estrella et al. (2019) did not suggest Antarctica as an ancestral area for Cunoniaceae, although the family has a substantial fossil record there (Cantrill and Poole, 2012).

The parsimonious scenario of an Oceanian origin of the extant diversity of Cunoniaceae with repeated dispersal events to Africa, the Americas, and Madagascar, may however, be in conflict with the fossil record. Firstly, Cretaceous fossils from Sweden (Schönenberger et al., 2001) and Burma (Chambers et al., 2010; Poinar and Chambers, 2017, 2019) have been attributed to this predominantly southern hemisphere family although some authors have recently considered the fossil evidence for Cunoniaceae in the northern hemisphere to be equivocal (Carpenter and Rozefelds, 2021). However, the attribution of fossils from Greenland and North America (Manchester and Kvaček, 2009) and Italy (Hably et al.,

2007) to the extant genus *Sloanea* (Elaeocarpaceae) is more difficult to challenge, and the two closely related families have very similar present-day distributions. Secondly, the Southern Cone of South America appears to have been another significant center of diversity for the Cunoniaceae, with fossils described from the Paleocene and Eocene of Argentina. These comprise two extinct genera, *Lacinipetalum* Jud, Gandolfo, Iglesias & Wilf (Jud et al., 2018) and *Cunoniantha* Jud & Gandolfo (Jud and Gandolfo, 2021), as well as an extinct species of *Ceratopetalum* (Gandolfo and Hermsen, 2017), a genus now composed of nine extant species in Australia and New Guinea. In addition, fossils from the Oligocene of Tasmania have been placed in the genera *Acsmithia* Hoogland (= *Spiraeanthemum*), *Callicoma*, *Schizomeria*, and *Vesselowskya*, although these genera no longer occur on this island (Carpenter and Buchanan, 1993), and a fossil assigned to *Codia* was described from the middle Eocene to Oligocene of Western Australia (Barnes and Hill, 1999), although this genus is now confined to New Caledonia. Extinction has clearly been important in the history of the Cunoniaceae and this family has other features of relictual groups. Most genera have few species with a median of only three. Furthermore, the family is similar to several small families of the ANA grade (Amborellales, Nymphaeales, Austrobaileyales), Chloranthales and Magnoliids in being over-represented in eastern Asia and Oceania, where supposed climatic stability may have played a key role in the survival of these ancient lineages (Morley, 2001; Buerki et al., 2014; Pouteau et al., 2015). Thus, the Australia/New Guinea + New Caledonia origin inferred here for Cunoniaceae may be the result of their greater persistence in these regions, compared to areas such as South America (Kooyman et al., 2014; Barreda et al., 2021).

TABLE 2. The 27 genera recognized within Cunoniaceae in this study, their tribal placement, number of species, distribution, and selected taxonomic references.

Genus	Tribe	No. of species	Distribution	Selected taxonomic references
<i>Ackama</i>	Caldcluvieae	10	Australia, New Zealand, Malesia, Solomon Islands	Hopkins and Hoogland (2002); de Lange et al. (2002); Schönenberger et al. (2020); APNI (2020)
<i>Acrophyllum</i>	unplaced	1	Australia	Hoogland (1960, 1981)
<i>Aistopetalum</i>	unplaced	2	New Guinea	Hopkins and Hoogland (2002)
<i>Anodopetalum</i>	Schizomerieae	1	Tasmania	Barnes and Rozefelds (2000)
<i>Bauera</i>	unplaced	4	Australia	APNI (2020)
<i>Caldcluvia</i>	Caldcluvieae	1	South America	Hoogland (1979); Rodriguez et al. (2018)
<i>Callicoma</i>	Codieae	1	Australia	APNI (2020)
<i>Ceratopetalum</i>	Schizomerieae	9	Australia, New Guinea	Rozefelds and Barnes (2002)
<i>Codia</i>	Codieae	15	New Caledonia	Hopkins et al. (2014)
<i>Cunonia</i>	Cunonieae	24 + 1	New Caledonia + South Africa	Hopkins et al. (2014); Goldblatt and Manning (2000)
<i>Davidsonia</i>	unplaced	3	Australia	Harden and Williams (2000)
<i>Eucryphia</i>	unplaced	5 + 2	Australia + South America	Taylor and Hill (1996); Rodriguez et al. (2018)
<i>Geissois</i>	Geissoieae	19	New Caledonia, Fiji, Vanuatu, Solomon Islands	Hopkins (2006); Hopkins et al. (2014)
<i>Gillbeea</i>	unplaced	3	Australia, New Guinea	Rozefelds and Pellow (2000); Hopkins and Hoogland (2002)
<i>Hooglandia</i>	unplaced	1	New Caledonia	McPherson and Lowry (2004)
<i>Karrabina</i>	Geissoieae	2	Australia	Schimanski and Rozefelds (2002, as <i>Geissois</i>); Hopkins et al. (2013)
<i>Lamanonia</i>	Geissoieae	6	South America	Zickel and Leitão Filho (1993); Hopkins (2018a)
<i>Opocunonia</i>	Caldcluvieae	1	New Guinea	Hopkins and Hoogland (2002)
<i>Pancheria</i>	Cunonieae	27	New Caledonia	Hopkins et al. (2014)
<i>Platylophus</i>	Schizomerieae	1	South Africa	Goldblatt and Manning (2000)
<i>Pseudoweinmannia</i>	Geissoieae	2	Australia	Rozefelds and Pellow (2011)
<i>Pterophylla</i>	Cunonieae	68	Madagascar, Comoros, Malesia, Pacific Islands	Madagascar and Comoros: Bradford (2001); Bradford and Miller (2001); Rogers (2017). Malesia and Pacific: Hopkins (1998); Hopkins and Bradford (1998); Hopkins and Florence (1998); Hopkins et al. (1998)
<i>Pullea</i>	Codieae	3	Australia, Malesia, Fiji	Hoogland (1979); Hopkins and Hoogland (2002)
<i>Schizomeria</i>	Schizomerieae	9	Australia, Malesia, Solomon Islands	Hopkins (2018b)
<i>Spiraeanthemum</i>	Spiraeanthemeae	19	Australia, New Guinea, Moluccas, Pacific Islands	Pillon et al. (2009a)
<i>Vesselowskyia</i>	Cunonieae	2	Australia	Rozefelds et al. (2001)
<i>Weinmannia</i>	Cunonieae	90 + 2	Americas, Caribbean + Mascarenes	America: Bernardi (1961, 1963). No recent checklist available for all American taxa, but several regional treatments ^a . Mascarenes: Scott and Bosser (1997)

^aRegional treatments for American *Weinmannia* include: Central America and Mexico (Morales, 2010, 2011), Venezuela (Bradford and Berry, 1998), Ecuador (Bradford, 1999; Harling, 1999), Peru (Zarucchi, 1993), Bolivia (Harling and Fuentes, 2014), Chile (Rodriguez et al., 2018), Southern Cone (Hopkins, 2008).

One tribe, nevertheless, is remarkably successful at the present time: Cunonieae. It comprises two thirds of the species in the family and contains the four largest genera (*Weinmannia* s.s., *Pterophylla*, *Pancheria*, *Cunonia*). Crown Cunonieae (i.e., excluding *Vesselowskyia* Pamp.) has a diversification rate of 0.316, 2.2 times higher than the rate for the entire family (0.144). The tribe also has the largest distribution, with major radiations in the Andes, Madagascar, and New Caledonia. The genus *Pterophylla* is widespread in the Pacific and has reached the remote islands of the Marquesas and Rapa Iti. *Weinmannia* s.s. has itself an enigmatic distribution, divided between the Americas and the Mascarenes. Although the present study included only a single species from each of these two areas, for which divergence is estimated at 13.4 Ma, the previous study by Bradford (2002) included two additional ones in a phylogenetic analysis and numerous others in

his morphological study. He found that the temperate *W. trichosperma* Cav. (Southern Cone of South America) was resolved as sister to a tropical clade (Americas + Mascarenes), suggesting a dispersal from the Americas to the Mascarenes. This may be one of the most intriguing dispersal events known, and the disjunction is similar to one in the palm tribe Chamaedoreae, which comprises four genera in the neotropics and *Hyophorbe* in the Mascarenes (Baker and Couvreur, 2013). The disjunction in *Cunonia* between South Africa and New Caledonia is similar to that in *Dietes* Salisb. ex Klatt (Iridaceae), which is found in Africa, including southern Africa, and on Lord Howe Island (Goldblatt, 1981), and is also probably due to transoceanic dispersal. It is not clear why Cunonieae diversified and dispersed more than other tribes. It has small winged or hairy seeds, features found in several other genera of the family.

TABLE 3. Comparison of selected morphological features of *Ackama*, *Opocunonia*, *Spiraeopsis*, and *Caldcluvia* s.s.

Characters	<i>Ackama</i> (New Zealand)	<i>Ackama</i> (Australia)	<i>Spiraeopsis</i>	<i>Opocunonia</i>	<i>Caldcluvia</i> s.s.
Number of species	2	2	5	1	1
Leaf type	imparipinnate	imparipinnate	imparipinnate	imparipinnate or trifoliolate	simple
Venation	semi-craspedodromous	semi-craspedodromous	semi-craspedodromous	semi-craspedodromous to craspedodromous	craspedodromous
Stipule position, number, margin	interpetiolar, 1 pair per node, toothed in <i>A. rosifolia</i>	interpetiolar, 1 pair per node, not toothed	interpetiolar, 1 pair per node, not toothed	interpetiolar, 1 pair per node, usually stalked and bilobed, sometimes toothed	lateral, 4 per node, sometimes asymmetric, toothed
Trichome type	simple	simple	simple and stellate	simple	simple
Presence of raised glands, peltate scales, or orbicular glands	yes	yes	yes	no (yes?)	no
Inflorescence size, shape ^a	large, triangular in outline	large, triangular in outline	large, triangular in outline	small, rounded or flattish in outline	small, rounded in outline
Pedicels (length)	± absent	± absent	1–2.5 mm	3–5 mm	4–8 mm
Flower size ^b (length)	small (1.5 mm)	small (1–1.5 mm)	small (1.5–2 mm)	large (2–4 mm)	large (3–4 mm)
Petals	(4–) 5, oblanceolate-elliptic	4–6, oblanceolate-elliptic	4–5, oblanceolate-elliptic	5–6 (–7), ovate	4 (–5), oblanceolate-elliptic
Carpel number	2 (–3)	2–4	2–5	2	2
Replum in fruit	absent	absent	present	absent	present
Sepals in fruit	persistent	persistent	persistent	persistent	caducous
Seed shape, pubescence	ovoid, pubescent all over	ovoid, pubescent all over	spindle-shaped, glabrous	spindle-shaped, glabrous	spindle-shaped, glabrous

Observations based on herbarium material at K and supplemented with data taken from literature: Godley (1979); Webb and Simson (1991); de Lange et al. (2002); Hopkins and Hoogland (2002).

^aInflorescence size – large: typically 25–50 cm long though sometimes smaller in *S. clemensiae* L.M.Perry; small: typically 10–15 cm long.

^bFlower size – length measured from the base of the calyx to the tips of the lobes.

Outside Cunoniaceae, all genera with more than 10 species occur in New Caledonia. The remarkable success of Cunoniaceae on this archipelago (particularly *Geissois*: 13 species, *Codia*: 15 spp., *Cunonia*: 24 spp., *Pancheria* 27 spp.) mirrors that of the relictual conifer family Araucariaceae, in which the largest (and recent, <20 Ma) radiations of *Agathis* Salis. and *Araucaria* Henkel & W.Hochst. are also in New Caledonia (Setoguchi et al., 1998; Kranitz et al., 2014). Both families have a marked bias toward ultramafic substrates, an important feature of New Caledonia, and one that has probably had major effects on the survival (or not) of immigrant taxa and their diversification on the island (Pillon et al., 2010; Isnard et al., 2016).

CONCLUSIONS

The phylogenomic approach using Angiosperms353 has allowed us to resolve relationships across Cunoniaceae and neighboring families of Oxalidales, as well as issues of generic delimitation relating to *Ackama* and *Weinmannia*. It is hoped that the classification obtained in this study will be stable in the future, requiring few changes in generic concepts. The resulting Cunoniaceae have a total of 27 genera and ca. 335 species (Table 2). This phylogenetic framework for Cunoniaceae and the related families Brunelliaceae, Cephalotaceae, and Elaeocarpaceae was used to produce a linear sequence of genera for herbarium arrangement (Appendix S5) following the rules of Trias-Blais et al. (2015). Cunoniaceae has a mixture of relict features and recent radiations that will be better understood with further research on fossils and through species-level phylogenies.

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AUTHOR CONTRIBUTIONS

Conceptualization: F.F., O.M., Y.P., W.J.B.; data curation: H.C.F.H., O.M., N.E.; formal analysis: F.F., O.M.; funding acquisition: F.F., W.J.B.; investigation: Z.R.; methodology: W.J.B.; project administration: F.F., W.J.B.; supervision: Y.P., W.J.B.; validation: J.B., Z.R.; visualization: F.F., O.M., Y.P.; writing original draft: F.F., O.M., Y.P., H.C.F.H., Z.R.; writing review, and editing: F.F., H.C.F.H., J.B., O.M., Y.P., W.J.B., Z.R.

DATA AVAILABILITY STATEMENT

DNA sequences produced for this study are available in European Nucleotide Archive under umbrella project PRJEB35285; accession numbers are provided in Appendix S1.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. List of sequenced material with full information on herbarium vouchers and data quality.

APPENDIX S2. Biogeographical model.

APPENDIX S3. Geographical area assignments for each terminal included in the biogeographical analysis.

APPENDIX S4. Dated tree of crown Oxalidales.

APPENDIX S5. Linear sequences of families and genera in the crown clade of Oxalidales for use in herbarium curation.

APPENDIX S6. The 12 currently recognized species in the Caldcluvieae, showing their distribution and historical and current generic placements.

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APPENDIX 1. TAXONOMIC TREATMENT

Here, we present a summary of the taxonomic history and morphology of the two groups of taxa whose re-circumscription is justified above, plus conspectuses for *Ackama* and *Pterophylla*, which include the new combinations that are necessary. In these conspectuses, accepted taxa are listed with their homotypic synonyms, except for ca. 70 combinations in *Windmannia* P.Brown (nom. rej.) made by Kuntze (1891). Relevant heterotypic synonyms are provided for a few generic and sectional names. The year of publication is given for each name, but full publication details

appear only with the basionym or replaced name in the case of a new combination or nomen novum, respectively.

Taxonomic history of the genera in *Caldcluvieae*

Because the genera and species in the *Caldcluvieae* have a convoluted taxonomic history, the generic placement of the species currently recognized here and in previous studies is compared in Appendix S6.

Caldcluvia was established in 1830, when it contained a single species, *C. paniculata* (Cav.) D. Don, from South America (Don, 1830). No other species have basionyms in this genus, which was not equated with any other genera until Hoogland (1979), who included all the species now in the tribe *Caldcluvieae* within this genus. *Ackama* was established by Cunningham (1839), based on a single species from New Zealand (*A. rosifolia* A. Cunn.), but others were subsequently added from Australia and New Zealand.

Miquel (1856) established *Spiraeopsis*, which initially included only *S. celebica* (Blume) Miq., based on the basionym *Cunonia celebica* Blume, from Sulawesi. This name also served as the basionym of *Dirhynchosis celebica* (Blume) Blume, the sole species in *Dirhynchosis* Blume, described in his privately published "Mélanges botaniques" (Blume, 1855). Due to the extremely rare print run of apparently only two copies, Stafleu and Cowan (1976) erroneously concluded that "Mélanges" had never in fact been printed, and until van Steenis (1986), it was generally accepted that the name *Dirhynchosis* was effectively published in a volume of *Flora* edited by Fühner (1858). The fact that *Dirhynchosis* had been effectively published in 1855, the year before *Spiraeopsis*, was overlooked by Bradford and Barnes (2001), Bradford et al. (2004), and Hopkins and Hoogland (2002), which led to illegitimate combinations being made in *Spiraeopsis*.

Opocunonia and *Stollaea* Schltr. were described by Schlechter (1914) based on material from New Guinea; *Stollaea* contained one species (*S. papuana* Schltr.), whereas *Opocunonia* had three (*O. nymanii* (K. Schum.) Schltr., *O. kanaiensis* Schltr., *O. trifoliata* Schltr.), but all four names now apply to a single variable taxon, *O. nymanii* (Hopkins and Hoogland, 2002). Since Schlechter's work, *Opocunonia* has never been considered to be synonymous with *Ackama* or *Spiraeopsis*, nor with *Caldcluvia* (except by Hoogland [1979]), although the basionym of *O. nymanii* was originally published in *Ackama* (Schumann and Lauterbach, 1905). In our study, *Caldcluvia* and *Opocunonia* are sister groups and together they are sister to *Ackama* + *Spiraeopsis* (all well-supported clades).

The distinction between *Ackama* and *Spiraeopsis* (including *Betchea*) has not always been clear. Both Schlechter (1914) and Engler (1928) placed one of the Australian taxa in *Ackama* and the other in *Betchea*, and the basionym of *S. papuana* (Pulle) L.M. Perry is in *Ackama*. The synonymy of *Betchea* and *Spiraeopsis* is demonstrated by Engler's (1928) placement of *S. rufa* (Schltr.) L.M. Perry and *S. papuana*, and/or some of their synonyms, in both genera simultaneously. Perry (1949) subsequently accepted *Betchea* as a synonym of *Spiraeopsis*. In summary, *Ackama* and *Spiraeopsis* have not always been clearly distinguished from each other but they have not generally been confused with either *Opocunonia* or *Caldcluvia* s.s.

Since our analysis shows *Spiraeopsis* is nested within *Ackama*, the options were to: (1) maintain *Spiraeopsis* as distinct and split *Ackama* into two, creating five genera in the *Caldcluvieae*; (2) include *Spiraeopsis* within *Ackama*, which would result in three genera in the tribe; or (3) combine *Ackama* and *Spiraeopsis* with *Opocunonia* and perhaps also with *Caldcluvia* s.s., further reducing the number of genera. We have chosen the second option, although this makes *Ackama* more heterogeneous than before, especially in its indumentum, fruits, and seeds (Table 3 and see below).

Morphology of *Caldcluvieae*

Characters shared by all members of the *Caldcluvieae* include valvate sepals, apparently bisexual flowers that are strongly protandrous in some,

and loosely connate carpels that separate when dehiscent via a ventral split (Hoogland, 1979); axile placentae often thickened in fruit (Bradford, 1998) that either remain attached to the margins of the valves after dehiscence or result in the formation of a replum, i.e., strands of tissue that extend between the valves; tuft domatia on the underside of the leaves, usually in the axils of the secondary veins (more common in some species than others), and axillary, paniculate inflorescences (thyrses). However, other characters show a checkerboard pattern of occurrence amongst the species in the tribe (see Table 3).

One character that distinguished the species previously treated as *Spiraeopsis* from *Ackama* s.s. is the presence of stellate trichomes in the former, although both it and *Ackama* s.s. have structures that vary from raised "glands" (especially on the lower leaf surface in *Ackama* s.s.), to sessile, red or orange orbicular structures (often on the inflorescence axes), to peltate scales (on the leaves in *Spiraeopsis*).

Godley (1983) questioned Hoogland's (1979) placement of *Ackama rosifolia* (New Zealand) in the same genus as *Caldcluvia paniculata* (Chile and Argentina) because the fruits of the latter have strands of tissue extending between the valves of the capsule after dehiscence. This structure is absent in *A. rosifolia* and the Australian species of *Ackama*, although Bradford (1998: 590, character 14) noted the underlying similarity of the thickened placentae in *Caldcluvia* s.s. and *Ackama*. A replum is often present in the fruits of the species previously in *Spiraeopsis*. Webb and Simpson (1991) noted that the seeds of *A. rosifolia* are ellipsoid and pubescent, whereas those of *C. paniculata* are spindle-shaped and glabrous (as are those of species in *Spiraeopsis*).

Characters that support the inclusion of *Spiraeopsis* in *Ackama* and distinguish it from *Caldcluvia* s.s. are the size and shape of the inflorescence, the size of the flowers and length of their pedicels, and the number and arrangement of the stipules (Table 3). *Opocunonia* and *Caldcluvia* s.s. resemble each other in their inflorescence shape, the size of the flowers, and length of the pedicels, but are distinct in their inflorescences and stipules.

***Ackama* A.Cunn.** in *Ann. Nat. Hist.* 2: 358 (1839). Type: *Ackama rosifolia* A. Cunn., as '*rosaeifolia*'.

= *Betchea* Schltr. in *Bot. Jahrb. Syst.* 52: 146 (1914). Lectotype (Hutchinson, 1967): *B. rufa* Schltr.

= *Dirhynchosis* Blume in *Mélanges Bot.*: 6 (1855). Type: *D. celebica* (Blume) Blume.

= *Spiraeopsis* Miq. in *Fl. Ned. Ind.* 1: 719 (1856) syn. nov. Type: *S. celebica* (Blume) Miq.

Trees. Indumentum of simple hairs (all) and other structures varying from raised gland dots (especially on underside of foliage in some) to sessile, orbicular, red or orange structures (in some, especially on inflorescence axes) to peltate scales; stellate hairs sometimes present (spp. formerly in *Spiraeopsis* only, Malesia and Solomon Isl.). Stipules interpetiolar, one pair per node, margins toothed or entire. Leaves opposite and decussate, compound, imparipinnate, petiolate, rachis not winged; leaflet margins toothed; tuft domatia often present in axils of secondary veins. Inflorescence a many-flowered, axillary, cone-shaped thyrses, sometimes inserted in series, the lower axes opposite; floral maturation synchronous; flowers borne singly or in small fascicles. Flowers apparently bisexual but sometimes (often?) protandrous, small (calyx 1–2 mm from base to apex) and usually almost sessile; calyx lobes 4–5 (–6), valvate in bud; petals 4–5 (–6), oblanceolate-elliptic; stamens 8 or 10 (12); disc annular and erect to almost lobed, the indentations corresponding to the bases of the filaments; ovary of 2–5 carpels, these fused or almost free (*A. nubicola*), each bearing a free styloidium. Capsule basipetally and septically dehiscent into 2–5 valves, margins of valves (remains of axile placentae) partly or entirely thickened, sometimes forming a replum (Malesia and Solomon Isl.); seeds ca. 4–16 per capsule, either spindle-shaped and glabrous (Malesia and Solomon Isl.) or ellipsoid and pubescent (Australia and New Zealand).

Heterotypic synonymy for the taxa in *Ackama* can be found in Hoogland (1979, all taxa, including details of types), Hopkins and Hoogland (2002,

Malesian taxa), and in the Australian Plant Name Index (APNI, 2020, Australian taxa).

Conspectus of *Ackama*

1. *Ackama australiensis* (Schltr.) C.T.White (1936) ≡ *Betchea australiensis* Schltr. (1914) ≡ *Caldcluvia australiensis* (Schltr.) Hoogland (1979).
2. *Ackama brassii* (L.M.Perry) Pillon & H.C.Hopkins comb. nov. ≡ *Spiraeopsis brassii* L.M.Perry in *J. Arnold Arbor.* 30: 147 (1949) ≡ *Caldcluvia brassii* (L.M.Perry) Hoogland (1979).
3. *Ackama celebica* (Blume) Pillon & H.C.Hopkins comb. nov. ≡ *Cunonia celebica* Blume in *Bijdr. Fl. Ned. Ind.*: 868 (1826) ≡ *Dirhynchosisa celebica* (Blume) Blume (1855) ≡ *Spiraeopsis celebica* (Blume) Miq. (1856) ≡ *Caldcluvia celebica* (Blume) Hoogland (1979).
4. *Ackama clemensiae* (L.M.Perry) Pillon & H.C.Hopkins comb. nov. ≡ *Spiraeopsis clemensiae* L.M.Perry in *J. Arnold Arbor.* 30: 149 (1949) ≡ *Caldcluvia clemensiae* (L.M.Perry) Hoogland (1979).
5. *Ackama fulva* (Schltr.) Pillon & H.C.Hopkins comb. nov. ≡ *Betchea fulva* Schltr. in *Bot. Jahrb. Syst.* 52: 148 (1914) ≡ *Spiraeopsis fulva* (Schltr.) L.M.Perry (1949) ≡ *Caldcluvia fulva* (Schltr.) Hoogland (1979).
6. *Ackama nubicola* de Lange (2002).
7. *Ackama paniculosa* (F.Muell.) Heslewood (2013) ≡ *Weinmannia paniculata* F.Muell. (1860), *nom. illeg. hom.*, non Cav. (1801) ≡ *Weinmannia paniculosa* F.Muell. (1861) ≡ *Caldcluvia paniculosa* (F.Muell.) Hoogland (1979).
8. *Ackama papuana* Pulle (1912) ≡ *Betchea papuana* (Pulle) Schltr. (1914) ≡ *Spiraeopsis papuana* (Pulle) L.M.Perry (1949) ≡ *Caldcluvia papuana* (Pulle) Hoogland (1979).
9. *Ackama rosifolia* A.Cunn. (1839) as '*rosaefolia*' ≡ *Caldcluvia rosifolia* (A. Cunn.) Hoogland (1979).
10. *Ackama rufa* (Schltr.) Pillon & H.C.Hopkins comb. nov. ≡ *Betchea rufa* Schltr. in *Bot. Jahrb. Syst.* 52: 148 (1914) ≡ *Spiraeopsis rufa* (Schltr.) L.M.Perry (1949) ≡ *Caldcluvia rufa* (Schltr.) Hoogland (1979).

Taxonomy of *Weinmannia* s.l.

Among the genera in tribe Cunoniaceae, *Cunonia* and *Weinmannia* were both described by Linnaeus and have always been considered quite distinct from each other. Although superficially similar, they differ by a number of characters (Hopkins et al., 2014): stipules (spoon-shaped vs. triangular, or reniform vs. salverform), hairs on the seeds (absent/present), seed wing (present/absent), floral disk (adnate to/free from ovary), fruit dehiscence (acropetal/basipetal). The genera *Vesselowskyia* and *Pancheria* were described later and differ from each other and from *Weinmannia* and *Cunonia* in characters such as digitate leaves, dioecy (considered derived within *Weinmannia*) and trimerous flowers in *Vesselowskyia* (Rozefelds et al., 2001), and whorled simple, trifoliolate or imparipinnate leaves, dioecy, and 3–4-merous flowers in capitate inflorescences in *Pancheria* (Hopkins et al., 2009). As mentioned above, the species of *Weinmannia* in its traditional sense fall into two clades. The first clade, sect. *Weinmannia*, includes the species from the Americas and the Mascarenes. The second clade includes the remaining species, all from the Old World: sections *Fasciculatae* (Malesia and Pacific), *Inspersae* (Madagascar), *Leiospermum* (Pacific), and *Spicatae* (Madagascar + Comoros).

Three names must be considered when seeking a new generic name for Old World *Weinmannia*: *Arnoldia* Blume (1826), *Leiospermum* D.Don (1830), and *Pterophylla* D.Don (1830). *Arnoldia* Blume (1826) is a later homonym of *Arnoldia* Cass. (1824), which is itself a synonym of *Dimorphotheca* Vaill. ex Moench (Asteraceae). *Leiospermum* and *Pterophylla* were published simultaneously and so have equal priority. However, *Leiospermum* D.Don has a later illegitimate homonym, *Leiospermum* Wall. (1832). We therefore choose the generic name *Pterophylla* D.Don for the species of *Weinmannia* from the Old World (excluding the Mascarenes) to avoid unnecessary homonymic confusion.

Morphology of *Weinmannia* s.l.

Comparison of the descriptions for *Weinmannia* sect. *Weinmannia* (hereafter *Weinmannia* s.s.) and the clade formed by the four other sections (hereafter *Pterophylla*) shows that their similarities are quite marked and several characters that define each genus are not entirely diagnostic (see character matrix in Bradford, 1998). The most obvious difference between the two groups is the architecture of the inflorescence. In *Weinmannia* s.s., each inflorescence is formed by two opposite racemes or sometimes spikes (sometimes referred to as pseudoracemes and pseudospikes because the flowers are borne in fascicles), which are inserted directly in the axils of the most distal pair of leaves on a stem; lower pairs of leaves do not subtend racemes or spikes. This morphology contrasts with *Pterophylla* (and other genera in Cunoniaceae such as *Cunonia* or *Pancheria*), in which the inflorescence is usually composed of complex units, termed inflorescence modules (IMs) by Bradford (1998, 2002), each consisting of a number of racemes or spikes, the internode to which they are attached, and any associated buds. These IMs can be either axillary at the distal end of a shoot (usually with an apical bud between them), or terminal, or a combination of the two states. A few exceptions occur in sect. *Spicatae* (see diagnosis) where the inflorescence consists of simple spikes, similar to those in *Weinmannia* s.s., but usually in the taxa in sect. *Spicatae*, the spikes are inserted at several nodes along a stem and are not confined to the most distal leaf axils, and thus what Bradford (1998) termed the total inflorescence (TI) encompasses multiple nodes of the stem in these taxa. The architecture of the inflorescence in *Weinmannia* s.l. was analyzed in detail by Bradford (1998, 2001), and this approach was extended to include all genera in the tribe Cunoniaceae by Bradford (2002). When looking at the evolution of the inflorescence architecture for the entire tribe, it appears that the structure of *Weinmannia* s.s. has a unique, derived set of traits that is diagnostic on most herbarium specimens; namely, the TI is reduced to a single node with racemes (not IMs) born directly in the axils of leaves or of reduced leaves.

Seed characters are only partly diagnostic. The seeds are straight (i.e., ellipsoid) and typically comose in the sections that now form *Pterophylla*, whereas in *Weinmannia* s.s. (as sect. *Weinmannia*) they are curved (reniform) with the hairs sparsely and widely distributed (Bradford, 1998). However, species descriptions for some New World taxa state that the seeds are ellipsoid, and the hairs are dispersed in a few species of *Pterophylla*. Another largely diagnostic character is the corolla, which commonly but not universally falls off as a "cap" of four petals soon after anthesis in the New World species (*Weinmannia* s.s.), whereas in *Pterophylla*, it appears never to be caducous.

Bradford's (1998) morphological data matrix, based on examination of both Mascarenes species of *Weinmannia* and numerous American ones, also demonstrated that these two geographically separated groups within *Weinmannia* s.s. are not identical in all major characters, although overall, a greater range of variation occurs in *Pterophylla* than in *Weinmannia* s.s.

***Pterophylla* D.Don** in *Edinburgh New Philos. J.* 9: 93 (1830). Type: *Pterophylla fraxinea* D.Don

Trees or shrubs, hermaphroditic, dioecious or polygamodioecious. Indumentum of simple hairs. Stipules interpetiolar, one pair per node. Leaves opposite and decussate (rarely whorled, *P. commersonii*, Madagascar), simple, trifoliolate or imparipinnate (rarely unifoliolate), petiolate or ± sessile (especially in some simple-leaves spp.); in compound leaves, petiole and rachis unwinged or narrowly winged; leaflet margins toothed (rarely ± entire, e.g., *P. mammea*, Madagascar); domatia in axils of secondary veins absent. Inflorescence of racemes or sometimes spikes (pseudoracemes and pseudospikes when flowers in fascicles), these usually arranged in complex groups with a sterile basal peduncular segment, the groups either axillary or terminal or a combination (rarely spikes borne singly, directly in leaf axils, often of several successive pairs of leaves, e.g., *P. comorensis*, Comoros; *P. baehniiana*, *P. lucens*, *P. minutiflora*, all Madagascar, sect. *Spicatae*); flowers inserted on axes either singly or in fascicles, each flower or fascicle subtended by a bract; floral maturation synchronous. Flowers bisexual or

unisexual by early suppression of one sex, pedicellate or sometimes sessile; calyx lobes 4–5 (mostly 5 in Madagascar and New Caledonia, mostly 4 in the remaining species), imbricate in bud; petals 4–5, ± elliptic, membranous, persistent; stamens 8 or 10 (5 in *P. sanguisugarum*, Madagascar); disc segmented, ribbed or membranous; ovary of 2 (–3) fused carpels, each with a free styloidium. Capsule basipetally and septically dehiscent into 2 (–3) valves, central column often present, calyx persistent or caducous; seeds numerous, ellipsoid, usually comose or occasionally hairs widely distributed, either densely or sparsely so.

Conspectus of *Pterophylla*

Pterophylla* sect. *Pterophylla ≡ *Weinmannia* sect. *Fasciculatae* Bernardi ex Hoogland & H.C.Hopkins in *Adansonia*, sér. 3, 20: 21 (1998), as 'Fasciculata'.

= *Arnoldia* Blume in *Bijdr. Fl. Ned. Ind.* 15: 868 (1826), nom. illeg. hom., non Cass. (1824). Lectotype (Hopkins and Hoogland, 2002): *A. heterophylla* Blume.

This section was treated as *Weinmannia* sect. *Fasciculatae* in Hopkins and Bradford (1998), Hopkins (1998), and Hopkins et al. (1998), where a description of the section and details of types and heterotypic synonyms can be found (see also Hopkins and Hoogland, 2002).

- Pterophylla aphanoneura* (Airy Shaw) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia aphanoneura* Airy Shaw in *Bull. Misc. Inform. Kew* 1940: 260 (1940).
- Pterophylla celebica* (Koord.) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia celebica* Koord. in *Meded. Lands Plantentuin* 19: 640 [450] (1898).
- Pterophylla clemensiae* (Steenis) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia clemensiae* Steenis in *J. Bot.* 72: 3 (1934).
- Pterophylla coodei* (H.C.Hopkins) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia coodei* H.C.Hopkins in *Adansonia*, sér. 3, 20: 52, f. 4A–D (1998).
- Pterophylla descombesiana* (Bernardi) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia descombesiana* Bernardi in *Bot. Jahrb. Syst.* 83: 186 in key, 190, f. 33 (1964).
- Pterophylla devogelii* (H.C.Hopkins) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia devogelii* H.C.Hopkins in *Adansonia*, sér. 3, 20: 48, f. 1 (1998).
- Pterophylla exigua* (A.C.Sm.) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia exigua* A.C.Sm. in *J. Arnold Arb.* 33: 137 (1952).
- Pterophylla eymana* (H.C.Hopkins) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia eymana* H.C.Hopkins in *Adansonia*, sér. 3, 20: 50, f. 3E–H, J (1998), as 'eymaena'.
- Pterophylla fraxinea* D.Don (1830) ≡ *Weinmannia fraxinea* (D.Don) Miq. (1856).** The type of the genus and thus also the autonymic section.
- Pterophylla furfuracea* (H.C.Hopkins) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia furfuracea* H.C.Hopkins in *Adansonia*, sér. 3, 20: 49, f. 3A–D (1998).
- Pterophylla hooglandii* (H.C.Hopkins & J.Bradford) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia hooglandii* H.C.Hopkins & J.Bradford in *Adansonia*, sér. 3, 20: 37, f. 11 (1998).
- Pterophylla hutchinsonii* (Merr.) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia hutchinsonii* Merr. in *Philipp. J. Sci.*, C. 2: 275 (1907).
- Pterophylla lucida* (Merr.) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia lucida* Merr. in *Philipp. J. Sci.*, C. 10: 7 (1915).
- Pterophylla luzoniensis* (S.Vidal) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia luzoniensis* S.Vidal in *Révis. Pl. Vasc. Filip.*: 125 (1886).
- Pterophylla macgillivrayi* (Seem.) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia macgillivrayi* Seem. in *Fl. Vit.* [Seemann] 1: 109 (1866).
- Pterophylla negrosensis* (Elmer) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia negrosensis* Elmer in *Leaf. Philipp. Bot.* 2: 577 (1909).
- Pterophylla pullei* (Schltr.) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia pullei* Schltr. in *Bot. Jahrb. Syst.* 52: 164 (1914).
- Pterophylla richii* (A.Gray) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia richii* A.Gray in *U.S. Expl. Exped., Phan.* 15: 675, Atlas t. 85 (1854).

19. ***Pterophylla urdanetensis* (Elmer) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia urdanetensis* Elmer in *Leaf. Philipp. Bot.* 7: 2608 (1915).

20. ***Pterophylla ysabelensis* (L.M.Perry) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia ysabelensis* L.M.Perry in *J. Arnold Arb.* 30: 162 (1949).

***Pterophylla* sect. *Leiospermum* (D.Don) Pillon & H.C.Hopkins comb. nov.** ≡ *Leiospermum* D.Don in *Edinburgh New Philos. J.* 9: 91 (1830) ≡ *Weinmannia* sect. *Leiospermum* (D.Don) Engl. in *Nat. Pflanzenfam.* III, 2a: 101 (1891). Lectotype (Hopkins and Bradford, 1998): *Leiospermum racemosum* (L.f.) D.Don.

= *Weinmannia* sect. *Racemosae* Bernardi in *Bot. Jahrb. Syst.* 83: 132, 185 (1964).

With the exception of species from Samoa, Rarotonga, and New Zealand, this section was revised as *Weinmannia* sect. *Leiospermum* in Hopkins and Bradford (1998), Hopkins et al. (1998), and Hopkins and Florence (1998), where a description of the section and details of types and heterotypic synonyms can be found. Minor updates including new taxa have been published by Hopkins and Pillon (2011, New Caledonia), Lorence and Wagner (2011, Marquesas Isl.); see also Hopkins and Hoogland (2002, Malesia), Hopkins et al. (2014, New Caledonia), and Sykes (2016, Cook Isl.) for regional treatments.

New combinations are unnecessary for *Weinmannia manuana* Christoph. and *W. rarotongensis* Hemsl. because they are considered to be synonyms of *W. samoensis* A.Gray (Hopkins et al., 1998; Sykes, 2016), and *W. spiraeoides* A.Gray is omitted on account of its doubtful status (Bernardi, 1964). Names of accepted taxa in New Zealand are taken from Schönberger et al. (2020).

1. ***Pterophylla affinis* (A.Gray) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia affinis* A.Gray, *U.S. Expl. Exped., Phan.* 15: 674 (1854).

2. ***Pterophylla croftii* (H.C.Hopkins) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia croftii* H.C.Hopkins, *Adansonia*, sér. 3, 20: 76, f. 4 (1998).

3. ***Pterophylla denhamii* (Seem.) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia denhamii* Seem., *Fl. Vit.* [Seemann] 1: 109 (1866), as 'denhami'.

4a. ***Pterophylla dichotoma* (Brongn. & Gris) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia dichotoma* Brongn. & Gris, *Bull. Soc. Bot. France* 9: 73 (1862).

4b. ***Pterophylla dichotoma* var. *monticola* (Däniker) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia monticola* Däniker, *Vierteljahrsschr. Naturf. Ges. Zürich* 76: 165 (1931) ≡ *Weinmannia dichotoma* var. *monticola* (Däniker) H.C.Hopkins & Pillon (2012).

5a. ***Pterophylla marquesana* (F.Br.) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia marquesana* F.Br., *Bull. Bernice P. Bishop Mus.* 130: 99 (1935).

5b. ***Pterophylla marquesana* var. *angustifolia* (Lorence & W.L. Wagner) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia marquesana* var. *angustifolia* Lorence & W.L.Wagner, *PhytoKeys* 4: 62 (2011).

5c. ***Pterophylla marquesana* var. *myrsinites* (Fosberg & Sacht) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia parviflora* var. *myrsinites* Fosberg & Sacht, *Micronesica* 8: 45 (1972) ≡ *Weinmannia marquesana* var. *myrsinites* (Fosberg & Sacht) H.C.Hopkins & J.Florence (1998).

6. ***Pterophylla ouaiemensis* (Guillaumin & Viro) Pillon & H.C.Hopkins comb. nov.** ≡ *Cunonia ouaiemensis* Guillaumin & Viro, *Mem. Mus. Natl. Hist. Nat., B. Bot.* 4: 28 (1953) ≡ *Weinmannia ouaiemensis* (Guillaumin & Viro) Hoogland (1998).

7. ***Pterophylla paitensis* (Schltr.) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia paitensis* Schltr., *Bot. Jahrb. Syst.* 39: 124 (1906).

8. ***Pterophylla parviflora* (G.Forst.) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia parviflora* G.Forst., *Fl. Ins. Austr.*: 29 (1786), as 'parviflora'.

9. ***Pterophylla purpurea* (L.M.Perry) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia purpurea* L.M.Perry, *J. Arnold Arb.* 30: 159 (1949).

10. ***Pterophylla racemosa* (L.f.) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia racemosa* L.f., *Suppl. Pl.*: 227 (1782) ≡ *Leiospermum racemosum* D.Don (1830).

11. ***Pterophylla raiateensis* (J.W.Moore) Pillon & H.C.Hopkins comb. nov.** ≡ *Weinmannia raiateensis* J.W.Moore, *Bull. Bernice P. Bishop Mus.* 102: 28 (1933).

12. *Pterophylla rapensis* (F.Br.) Pillon & H.C.Hopkins comb. nov. ≡ *Weinmannia rapensis* F.Br., *Bull. Bernice P. Bishop Mus.* 130: 100 (1935).

13. *Pterophylla samoensis* (A.Gray) Pillon & H.C.Hopkins comb. nov. ≡ *Weinmannia samoensis* A.Gray, *U.S. Expl. Exped., Phan.* 15: 677 (1854).

14. *Pterophylla serrata* (Brongn. & Gris) Pillon & H.C.Hopkins comb. nov. ≡ *Weinmannia serrata* Brongn. & Gris, *Bull. Soc. Bot. France* 9: 73 (1862).

15a. *Pterophylla sylvicola* (Sol. ex A.Cunn.) Pillon & H.C.Hopkins comb. nov. ≡ *Weinmannia sylvicola* Sol. ex A.Cunn., *Ann. Nat. Hist.* 2: 357 (1839).

15b. *Pterophylla sylvicola* var. *betulina* (A.Cunn.) Pillon & H.C.Hopkins comb. nov. ≡ *Weinmannia sylvicola* var. *betulina* (A.Cunn.) Hook.f. (1852) ≡ *Weinmannia betulina* A. Cunn., *Ann. Nat. Hist.* 2: 357 (1839).

16. *Pterophylla tremuloides* (H.C.Hopkins & J.Florence) Pillon & H.C.Hopkins comb. nov. ≡ *Weinmannia tremuloides* H.C.Hopkins & J.Florence, *Adansonia*, sér. 3, 20: 123 (1998).

17. *Pterophylla vescoi* (Drake) Pillon & H.C.Hopkins comb. nov. ≡ *Weinmannia vescoi* Drake, *Ill. Fl. Ins. Pacif.*: 35, pl. 13 (1886).

18. *Pterophylla vitiensis* (Seem.) Pillon & H.C.Hopkins comb. nov. ≡ *Weinmannia vitiensis* Seem., *Fl. Vit.* [Seemann] 1: 110 (1866).

Pterophylla sect. *Spicatae* (Bernardi ex J.Bradford) Pillon & H.C.Hopkins comb. nov. ≡ *Weinmannia* sect. *Spicatae* Bernardi ex J.Bradford in *Ann. Missouri Bot. Gard.* 89: 503 (2002). Type: *Weinmannia bojeriana* Tul.

= *Ornithophus* Bojer ex Engl. in *Linnaea* 36: 636 (1870), nom. inval.

Our placement of Malagasy taxa into sections *Spicatae* and *Inspersae* follows Bradford (2001), who subsequently provided validating types and diagnoses for both sections (Bradford, 2002), which had originally been proposed by Bernardi (1964). Information on types of older accepted names and their heterotypic synonyms can be found in Bernardi (1964, 1965). The only non-Malagasy species in either section is *Pterophylla comorensis*, a Comoran endemic (sect. *Spicatae*). Keys to species groups of both sections were provided by Bradford (2001), with some revisions as a result of new species described (see Rogers and Bradford, 2004). Taxonomic summaries of all Malagasy taxa including distributions and voucher specimens were given by Rogers (2017). New combinations are not required for two binomials that are based on material from Madagascar: *Weinmannia trigyna* Baker [= *Homalium trigynum* (Baker) Sleumer], and *W. rhodoxylon* Tul., which is a dubious name that can only be linked to two type sheets of unidentifiable juvenile material (Bernardi, 1964).

1. *Pterophylla arguta* (Bernardi) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia arguta* (Bernardi) J.Bradford (2001) ≡ *Weinmannia hildebrandtii* var. *arguta* Bernardi, *Fl. Madagasc.* Fam. 93: 30 (1965).

2. *Pterophylla baehniiana* (Bernardi) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia baehniiana* Bernardi, *Ber. Schweiz. Bot. Ges.* 74: 260, f. 1 (1964).

3. *Pterophylla bernardii* J.Bradford & Z.S.Rogers nom. nov. Replaced synonym: *Weinmannia venosa* J.Bradford, *Adansonia*, sér. 3, 23: 233, f. 6 (2001), nom. illeg. hom., non *W. venosa* Knowles & Westc. (1838) [= *Acrophyllum australe* (A.Cunn.) Hoogland]. The new epithet for this species is chosen to honor Luciano Bernardi (1920–2001), the Italian botanist who revised the genus *Weinmannia*, completely in Latin, in the 1960s while working at the Conservatoire et Jardin botaniques Genève.

4. *Pterophylla bojeriana* (Tul.) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia bojeriana* Tul., *Ann. Sci. Nat., Bot.* sér. 4, 8: 155 (1857).

5. *Pterophylla bradfordii* (I.M.Turner) Z.S.Rogers comb. nov. ≡ *Weinmannia bradfordii* I.M.Turner, *Ann. Bot. Fenn.* 51: 309 (2014) ≡ *Weinmannia integrifolia* J.Bradford, *Adansonia*, sér. 3, 23: 225, f. 2 (2001), nom. illeg. hom., non *W. integrifolia* Lesq., *Rep. U.S. Geol. Surv. Territ.* 8: 178 (1883).

6. *Pterophylla comorensis* (Tul.) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia comorensis* Tul., *Ann. Sci. Nat., Bot.* sér. 4, 8: 153 (1857).

7. *Pterophylla decora* (Tul.) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia decora* Tul., *Ann. Sci. Nat., Bot.* sér. 4, 8: 154 (1857).

8. *Pterophylla eriocarpa* (Tul.) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia eriocarpa* Tul., *Ann. Sci. Nat., Bot.* sér. 4, 8: 156 (1857).

9. *Pterophylla hildebrandtii* (Baill.) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia hildebrandtii* Baill., *Bull. Mens. Soc. Linn. Paris* 1: 475 (1885).

10. *Pterophylla humbertiana* (Bernardi) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia humbertiana* Bernardi, *Bot. Jahrb. Syst.* 83: 132 in key, 139, f. 5 (1964).

11a. *Pterophylla humblotii* (Baill.) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia humblotii* Baill., *Bull. Mens. Soc. Linn. Paris* 1: 475 (1885).

11b. *Pterophylla humblotii* var. *anceps* (Bernardi) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia humblotii* var. *anceps* Bernardi, *Fl. Madagasc. Fam.* 93: 41, f. 7 nos. 1–6 (1965).

12. *Pterophylla icacifolia* (Bernardi) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia icacifolia* (Bernardi) Bernardi (1964) ≡ *Weinmannia bojeriana* var. *icacifolia* Bernardi, *Bot. Jahrb. Syst.* 83: 134 in key, 135, f. 1 (1964).

13. *Pterophylla lucens* (Baker) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia lucens* Baker, *J. Bot.* 20: 70 (1882).

14. *Pterophylla magnifica* (J.Bradford & Z.S.Rogers) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia magnifica* J.Bradford & Z.S.Rogers, *Adansonia*, sér. 3, 26: 85, f. 1 (2004).

15. *Pterophylla mammea* (Bernardi) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia mammea* Bernardi, *Bot. Jahrb. Syst.* 83: 133 in key, 141, f. 8 (1964).

16. *Pterophylla marojejensis* (J.S.Mill. & J.Bradford) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia marojejensis* J.S.Mill. & J.Bradford, *Adansonia*, sér. 3, 23: 227, f. 3 (2001).

17. *Pterophylla minutiflora* (Baker) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia minutiflora* Baker, *J. Linn. Soc., Bot.* 21: 339 (1884).

18. *Pterophylla pauciflora* (J.Bradford) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia pauciflora* J.Bradford, *Adansonia*, sér. 3, 23: 229, f. 4 (2001).

19. *Pterophylla rakotomalazana* (J.Bradford) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia rakotomalazana* J.Bradford, *Adansonia*, sér. 3, 23: 229, f. 5 (2001).

20. *Pterophylla sanguisugarum* (Bernardi) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia sanguisugarum* Bernardi, *Candollea* 24: 85 (1969).

21. *Pterophylla stenostachya* (Baker) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia stenostachya* Baker, *Bull. Misc. Inform. Kew* 1895: 103 (1895).

Pterophylla sect. *Inspersae* (Bernardi ex J.Bradford) Pillon & H.C.Hopkins comb. nov. ≡ *Weinmannia* sect. *Inspersae* Bernardi ex J.Bradford in *Ann. Missouri Bot. Gard.* 89: 503 (2002). Type: *Weinmannia madagascariensis* DC. ex Ser.

1. *Pterophylla aggregata* (Z.S.Rogers & J.Bradford) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia aggregata* Z.S.Rogers & J.Bradford, *Adansonia*, sér. 3, 26: 86, f. 1 (2004).

2. *Pterophylla commersonii* (Bernardi) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia commersonii* Bernardi, *Bot. Jahrb. Syst.* 83: 144, f. 9 (1964).

3. *Pterophylla henricorum* (Bernardi) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia henricorum* Bernardi, *Bot. Jahrb. Syst.* 83: 144 in key, 146, f. 10 (1964).

4. *Pterophylla hepaticarum* (Bernardi) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia hepaticarum* Bernardi, *Bot. Jahrb. Syst.* 83: 143 in key, 147, f. 11 (1964).

5. *Pterophylla louveliana* (Bernardi) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia louveliana* Bernardi, *Bot. Jahrb. Syst.* 83: 143 in key, 149, f. 12 (1964).

6. *Pterophylla lowryana* (J.Bradford) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia lowryana* J.Bradford, *Adansonia*, sér. 3, 23: 223, f. 1 (2001).

7a. *Pterophylla madagascariensis* (DC. ex Ser.) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia madagascariensis* DC. ex Ser., *Prodr.* [DC.] 4: 9 (1830).

7b. *Pterophylla madagascariensis* var. *aniba* (Bernardi) J.Bradford & Z.S.Rogers comb. nov. ≡ *Weinmannia madagascariensis* var. *aniba* Bernardi, *Bot. Jahrb. Syst.* 83: 144 in key, 152 (1964).

8. *Pterophylla rutenbergii* (Engl.) J.Bradford & Z.S.Rogers comb. nov.
 ≡ *Weinmannia rutenbergii* Engl., *Abh. Naturwiss. Vereins Bremen* 7: 16 (1880).
 9. *Pterophylla venusta* (Bernardi) J.Bradford & Z.S.Rogers comb. nov.
 ≡ *Weinmannia venusta* Bernardi, *Bot. Jahrb. Syst.* 83: 156, f. 16 (1964).

Weinmannia L. in *Syst. Nat.*, ed. 10, 2: 997, 1005, 1367 (1759), nom. cons.
 Type: *Weinmannia pinnata* L.
 ≡ *Weinmannia* sect. *Weinmannia*
 = *Windmannia* P. Browne in *Civ. Nat. Hist. Jamaica*: 212 (1756), *nom. rej.*

Trees or shrubs (rarely hemi-epiphytes and strangling), hermaphroditic or dioecious—Indumentum of simple hairs. Stipules interpetiolar, one pair per node. Leaves opposite and decussate, simple (or unifoliolate?) and sometimes auriculate, trifoliolate or imparipinnate, petiolate or rarely sessile; in compound leaves, petiole and rachis commonly winged, sometimes quite broadly so (occasionally rachis not winged, e.g., *W. trianaea* Wedd.); leaflet margins toothed; domatia in axils of secondary veins absent. Inflorescence generally of simple racemes or occasionally spikes (strictly pseudoracemes and pseudospikes, see discussion), these inserted singly (not in groups on a sterile peduncular

segment) in the axils of the most distal pair of leaves on a stem only (rarely at more than one node, *W. condorensis* Z.S.Rogers) and leaves subtending racemes or spikes sometimes reduced, caducous or persistent; (rarely axis of raceme irregularly branched, *W. cogolloi* J.F.Morales; rarely racemes short and dense, umbelliform, ovoid or globular, e.g., *W. cochensis* Hieron.; rarely racemes much reduced with only 2–8 flowers, *W. bradfordiana* Z.S.Rogers, or 1–2 flowers, *W. condorensis*); flowers inserted on axes in fascicles, each fascicle subtended by a bract; floral maturation synchronous. Flowers bisexual (most) or unisexual by late suppression of one sex (Mascarenes), pedicellate or occasionally ± sessile; calyx lobes 4 (–5), imbricate in bud; petals 4 (–5), elliptic, membranous, often caducous and falling as a cap; stamens 8 (10); disc annular with an entire margin, ribbed with alternating longitudinal costae of varying thickness; ovary of 2 fused carpels, each with a free stylodium. Capsule, basipetally and septicidally dehiscent into 2 valves, central column often present, calyx persistent; seeds numerous, kidney-shaped (or sometimes ellipsoid?), pubescent, the hairs usually sparsely and widely distributed.

The circumscribed genus *Weinmannia* s.s. now comprises ca. 90 species in Central and South America and the Caribbean (see Table 2) and with two additional disjunct species in the Mascarenes.