

# An updated infrageneric classification of the pantropical species-rich genus *Garcinia* L. (Clusiaceae) and some insights into the systematics of New Caledonian species, based on molecular and morphological evidence

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## Abstract

*Garcinia* L. is a pantropically distributed genus comprised of at least 250 species of shrubs and trees and has centers of diversity located in Africa/Madagascar, Australasia, and Southeast Asia. The genus is notable due to its extreme diversity of floral form, common presence in lowland tropical rainforests worldwide, and potential pharmacological value. Across its entire geographic range, *Garcinia* lacks a recent taxonomic revision, with the last genus-level taxonomic treatment of *Garcinia* conducted over 40 years ago. In order to provide an evolutionary-based framework for a revised infrageneric classification of the genus and to investigate in more detail the systematics of New Caledonian species, we conducted molecular phylogenetic analyses using DNA sequence data for the nuclear ITS region on all samples, and for three chloroplast intergenic spacers (*psbM-trnD*, *trnQ-rps16* and *rps16-trnK*) on a subset of our overall sampling. Our phylogenetic analyses are the most comprehensive to date for the genus, containing 111 biogeographically and morphologically diverse *Garcinia* species. The analyses support a broad circumscription of *Garcinia*, including several previously segregated genera (e.g. *Allanblackia*, *Clusianthemum*, *Ochrocarpos* p.p., *Pentaphalangium*, *Rheedia*, and *Tripetalum*). We recovered nine major clades falling within two major lineages, and we delimit 11 sections. We discuss each of the clades, assign them sectional names, discuss their distinguishing morphological features, compare our taxonomic treatment with the most recent sectional treatment, list representative species, note geographic distribution, and highlight some questions that deserve future investigations. We propose nine new nomenclatural combinations, four new names, and three new lectotypes. In New Caledonia (NC), a total of ten, all endemic, species are recognized and were included in our phylogenetic analyses, with several replicates per species (with the exception of *G. virgata* and *G. urceolata*, represented by a single accession each). New Caledonian species were retrieved within three separate clades, respectively including 1) *G. balansae*; 2) *G. comptonii*, *G. neglecta*, *G. urceolata*, *G. virgata*; and 3) *G. amplexicaulis*, *G. densiflora*, *G. pedicellata*, *G. puat*, *G. vieillardii*. Within NC, the phylogenies did not support the distinction between a putative undescribed species and *G. balansae*. However, it confirmed the distinction between NC species and both *G. vitiensis* (found in Fiji and Vanuatu) and *G. adinantha* (found in Fiji), suggesting that all NC species should be considered as endemics.



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**Key words:** Androecium, floral diversity, *Garcinia*, infrageneric classification, molecular phylogeny, morphological characters, New Caledonia, taxonomy

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## Introduction

Species rich, morphologically diverse genera can benefit from the delimitation of natural infrageneric groups, which can help to facilitate future monographic work, ecological and evolutionary research, and conservation efforts (van Welzen et al. 2009; Moonlight et al. 2018; Atkins et al. 2021). *Garcinia* L. is a large genus with centers of species diversity located in Africa/Madagascar, Australasia, and Southeast Asia. The genus exhibits extreme diversity of floral morphology, particularly in the androecium and is of high ecological significance with many species forming an important component of the lower strata of lowland tropical forests worldwide. *Garcinia* is also of high economic significance since many species have edible fruits (especially *G. mangostana*) and/or possible medicinal properties (e.g., Pedraza-Chaverri et al. 2008; Espirito Santo et al. 2020).

Recent phylogenetic and biogeographic studies (e.g. Sweeney 2008; Ruhfel et al. 2011; Ruhfel et al. 2016) support a broad circumscription of *Garcinia* that justifies the inclusion of several previously segregated genera (e.g. *Ochrocarpos* Thouars p.p., *Pentaphalangium* Warb., *Rheedia* L., and *Tripetalum* K. Schum.). When broadly circumscribed, the genus contains at least 250 species (Stevens 2007) and maybe as many as ca. 400 (POWO 2023). While some of these molecular studies (Sweeney 2008) revealed major clades with suites of shared morphological characters, no recent genus-wide infrageneric classification of the genus has been attempted.

## Infrageneric taxonomy and classification of *Garcinia*

The taxonomy and systematics of *Garcinia* is made challenging due to several factors including the large number of species, dioecy, extreme floral diversity in the paleotropics (particularly in the androecium), poor preservation state of some features (e.g. fruits and flowers) on herbarium specimens, and numerous geographic sites harboring sympatric species. Several valuable efforts have been made to bring taxonomic order to the genus, at various geographic and taxonomic scales.

Previous taxonomic treatments over the past 200 years have resulted in more than 50 infrageneric taxa (Jones 1980). In the most recent worldwide taxonomic treatment of the genus and the benchmark against which more recent genus-level taxonomic work has been evaluated, Jones (1980) recognized 14 sections (Table 1). This treatment relied heavily on staminate flower and pollen morphology to classify upwards of 345 named species. Prior to Jones (1980), the most recent taxonomic treatment of the genus was that of Engler (1894, 1925), which recognized 34 sections. That work was an elaboration of Pierre (1883), who produced the first monograph of *Garcinia* (excluding *Ochrocarpos* and *Rheedia*) and used largely flower and inflorescence characters to classify 149 species into 37 sections that were organized into six groups. The only other monograph of the genus is that of Vesque (1893) who used floral morphology and leaf anatomy to classify 180 species (excluding *Rheedia*) into three

subgenera and nine sections. The first major, global treatment of *Garcinia* (but narrowly circumscribed and not including the segregate genera *Discostigma*, *Ochrocarpos*, *Rheedia*, and *Xanthochymus*) was that of Planchon and Triana (1860), who used mostly floral characters to group 32 species into six sections.

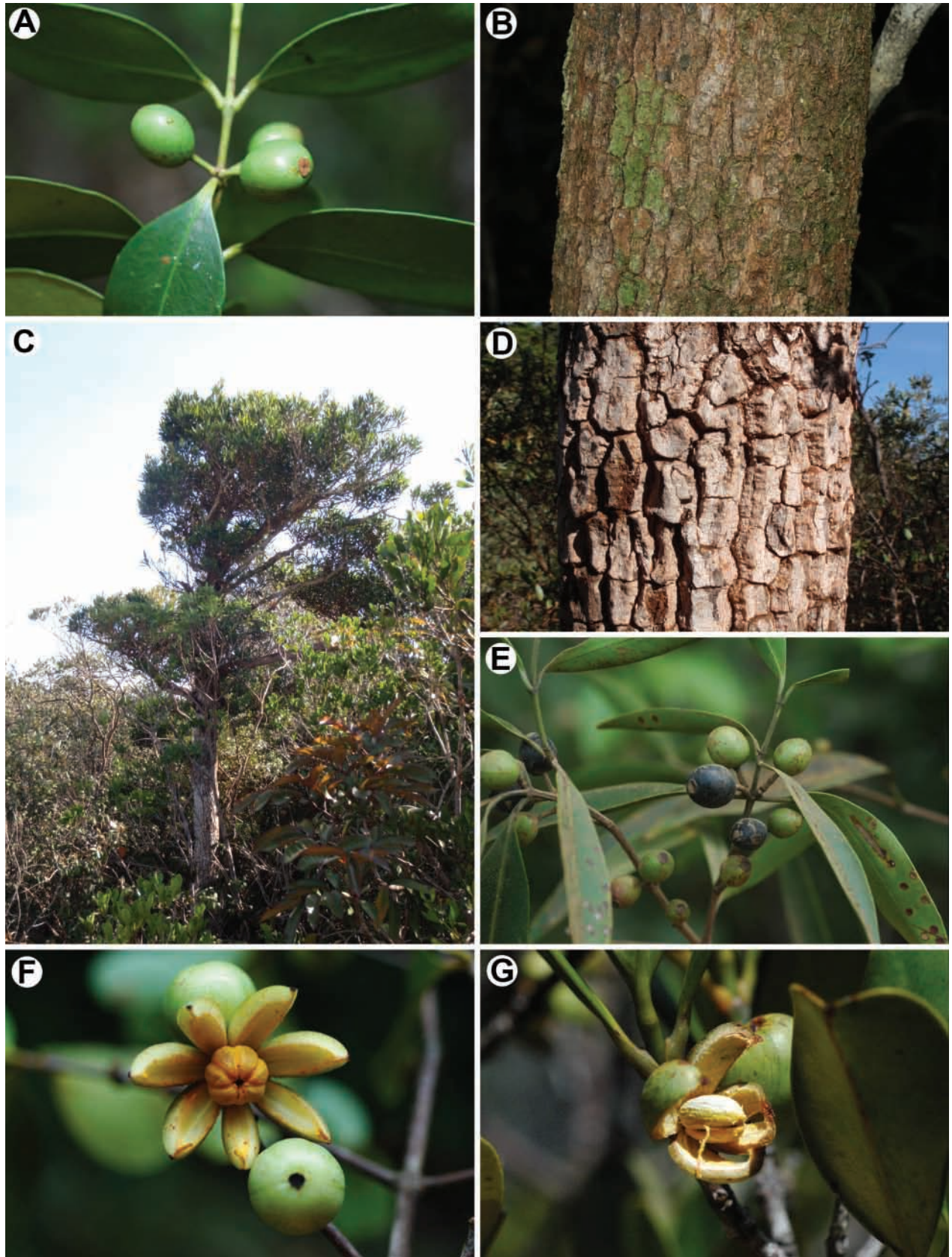
In addition to the above-mentioned works that are global in scope, there have been several noteworthy publications that have dealt with the genus at narrower geographic or taxonomic scales. These studies include work on species in Africa (Sosef and Dauby 2012), Australia (Cooper 2013), Brazil (Mouzinho et al. 2022), China (Li et al. 2007), Colombia (Medellín Zabala 2015), India (Maheshwari 1964; Singh 1993; Mohanan et al. 2023), and Madagascar (Sweeney and Rogers 2008; Rogers et al. 2011).

Two notable recently published works dealing with the infrageneric classification of *Garcinia* are that of Nazre et al. (2018), who provided a monograph for section *Garcinia* and the molecular phylogenetic study of Sweeney (2008) who evaluated Jones' (1980) classification in relation to phylogeny and morphology. Some major findings of Sweeney (2008) were that some segregated genera should be included within *Garcinia*, and while partly congruent with phylogeny, the infrageneric sectional classification of Jones (1980) needs revision.

### Taxonomy of New Caledonian *Garcinia* species

In contrast to other regions cited above, and in spite of the observed diversity within *Garcinia* in New Caledonia (NC), an archipelago that is well-known for its high overall levels of botanical diversity and endemism (Morat et al. 2012; Munzinger et al. 2023), the genus has not been recently and thoroughly studied in this territory. Only one species (*G. amplexicaulis*) was included in the phylogeny of Sweeney (2008). One species was recently described (Munzinger et al. 2021), leading to a total of ten –all presumed endemic– species, but the circumscription of some species is unclear and some questions remain about the conspecificity or, at least, the close evolutionary relationships between some non-NC and NC species that appear morphologically similar.

A taxon resembling *G. balansae* grows on the ultramafic massifs in the northwest of NC, but it displays linear, erect leaves and a very cracked greyish bark compared to the brownish and smoother bark of *G. balansae* (Fig. 1). This putative new taxon (*G. sp.* “JT814”) is restricted to three massifs (Boulinda, Koniambo and Tiébaghi) and should be considered as Endangered (Lowry and Munzinger 2015), but its taxonomic rank remains unresolved. In addition, the Fijian *G. vitiensis* (A. Gray) Seem. is cited in NC by Sebert and Pancher (1874), but the material of this species is then assigned by Pierre to his endemic species: *G. balansae* Pierre. Strangely, Pierre (1883: XXXVI) states “that he has never seen material of *G. vitiensis*, appearing close to *G. balansae*” (our translation). The conspecificity or non conspecificity between the two taxa remains to be tested. The presence of *G. sessilis* Seem. in NC is also mentioned at the end of the 19<sup>th</sup> and in the early 20<sup>th</sup> century (Sebert and Pancher 1874; Hemsley 1895), while subsequent authors considered this species as a Fijian endemic (Smith and Darwin 1974; Smith 1981) without discussion about its potential occurrence in NC. *Garcinia sessilis* was later split into two species, with the description of *G. adinantha* A.C.Sm. & S.P.Darwin (Smith and Darwin 1974), but the evolutionary relationship between the New Caledonian and these two Fijian species remains unknown.



**Figure 1.** Some *Garcinia* New Caledonian species (except E from Fiji) and morphological features **A** *G. balansae* (Munzinger 4916), fruiting branch **B** *G. balansae* (Munzinger 4916), bark **C** *G. sp.* "JT814" (Munzinger 7282), habit **D** *G. sp.* "JT814" (Munzinger 7282), bark **E** *G. vitiensis* (Munzinger 7377), fruiting branch **F** *G. neglecta* (Munzinger 2690), fruit **G** *G. comptonii* (sin voucher), fruit.

Based on an enlarged taxonomic sampling compared to Sweeney (2008), and an important sampling effort in the Pacific Ocean region and NC in particular (including several samples per morphologically delimited species), our goal is to provide an updated molecular phylogeny of the genus in order: 1) to offer a way forward on a revised infrageneric classification of *Garcinia* considering both morphological and molecular evidence; and 2) to provide insight into the systematics of NC species.

## Materials and methods

### Taxonomic sampling

This study was based on both published and newly generated sequences, leading to a total of 160 samples representing 121 species (including ten outgroups) and two putative new species (*G. sp.* “JT814” from NC and *G. sp.* Munzinger 7380 from Fiji; Suppl. material 1). Published sequences included sequences from Sweeney (2008; 57 sequences), in addition to 25 sequences downloaded from Genbank and three sequences taken from Nazre (2006). New ITS sequences were generated from both herbarium and silica-dried leaf material collected in the field. They included a total of 72 samples representing 39 species and two unidentified taxa, among which were 32 samples representing 10 species and one unidentified taxon from NC (Suppl. material 1). The sampling comprised representatives of all major *Garcinia* clades based on Sweeney (2008) and *Allanblackia*, and covered both the morphological diversity and biogeographic range of *Garcinia*. The outgroup included seven genera: *Lorostemon* Ducke, *Montrouziera* Pancher ex Planch. & Triana, *Moronobea* Aubl., *Pentadesma* Sabine and *Symphonia* L.f. from the Symphonieae tribe, and *Arawakia* L.Marinho and *Clusia* L. from the Clusieae tribe. A subset of this sampling was used to generate a fully original chloroplast DNA dataset: it comprised 67 samples representing 45 species (among which was one outgroup) and two putative new species (see above), covering all *Garcinia* clades based on Sweeney (2008) and including nine out of the ten NC *Garcinia* species.

### DNA sequencing

DNA extraction was performed with the DNeasy Plant Mini Kit (QIAGEN, Courtaboeuf, France), following the manufacturer’s protocol except for a slight modification: we added 30 µL CTAB and 30 µL proteinase K for the initial digestion, which lasted 24h at 42 °C. The nuclear ribosomal ITS region included the two transcribed intergenic spacers ITS1 and ITS2, separated by the 5.8S gene. It was sequenced using either the primers ITS4 and ITS5 (White et al. 1990) or the newly designed primers ITS4Garci (5'-CCTGACCTGGGGTCGC-3') and ITS5Garci (5'-AACCTGCGGAAGGATCATTG-3') that were more specific to *Garcinia* or at least to angiosperms, minimizing the risk of false positive due to fungi amplification when the amount of plant DNA was too low as a PCR template. Three chloroplast intergenic spacers were also sequenced: *psbM-trnD*, *trnQ-rps16* and *rps16-trnK*. PCR primers were *psbM* and *trnD*<sup>GUCR</sup> for *psbM-trnD* (Shaw et al. 2005), *trnQ*<sup>UUG</sup> and *rps16*x1 for *trnQ-rps16* (Shaw et al. 2007) and *rpS16*x2F2 and *trnK*<sup>UUU</sup>x1 for *rps16-trnK* (Shaw et al. 2007). All PCRs

were performed in 25  $\mu$ L including 1X Taq Buffer, 2.5 mM MgCl<sub>2</sub>, 1M betaine, 0.25 mM of each dNTP, 0.4  $\mu$ M of each primer, 0.6U Taq polymerase and 1  $\mu$ L template DNA. PCR conditions were: 94 °C for 5 min, followed by 40 cycles of: 94 °C 30 sec, Tm 45 sec, 72 °C 1 min, and a final extension step of 10 min at 72 °C. Tm was 48 °C for ITS and *psbM-trnD*, 44 °C for *trnQ-rps16*, and 46 °C for *rps16-trnK*. PCR products were sequenced in both directions by Eurofins (Evry, France), using the same primers as for the PCRs. Sequences were automatically aligned in MUSCLE v3.6 (Edgar 2004) before the alignments were manually revised in BioEdit v.7.2.5 (Hall 1999). Indels were coded following the simple coding method of Simmons and Ochoterena (2000) implemented in SeqState (Müller 2005). Vouchers details are listed in Suppl. material 1.

### Phylogenetic reconstructions

First, individual analyses were carried out on each DNA region. Bayesian inferences (BI) were performed using MrBayes v.3.1.2 (Ronquist et al. 2011). For each region, the best-fitting model of nucleotide substitution was identified under the Akaike information criterion in MrModelTest v.2.3 (Nylander 2004): GTR + I +  $\Gamma$  for the ITS region and *psbM-trnD* intergenic spacer, and GTR +  $\Gamma$  for the *trnQ-rps16* and *rps16-trnK* intergenic spacers (using distinct models for ITS1, ITS2 and 5.8S did not make any difference in the resulting tree). For indels, we used the restriction site (binary) model, with the option Iset coding = variable. Two independent but parallel analyses were conducted using flat priors, starting from random trees and consisting of four chains each. The analyses were run for 6 million generations, sampling every 1000 generations and with a 25% burn-in. Analysis of output parameters, in Tracer v.1.6 (Rambaut et al. 2014), confirmed the convergence of chains and adequate burn-in length. Post-burn-in trees were pooled and a 50% majority-rule consensus tree was computed with posterior probability (PP) estimates for all nodes. Maximum likelihood (ML) was also used to estimate phylogenetic relationships. The ML analysis was performed in raxmlGUI 1.5.1 (Silvestro and Michalak 2012; Stamatakis 2014), using the same partitions and models of nucleotide evolution as for the BI. We performed 1000 rapid bootstrap (BS) replicates and searched for the best-scoring ML tree. The topologies inferred by BI analyses from each chloroplast marker were visually compared to identify potential incongruence among them (Suppl. materials 2–4). Since no major incongruence was highly supported, the three chloroplast sequences for each sample were then combined to maximise the number of characters analysed in the BI and ML analyses. Also, a BI analysis was performed by merging the nuclear and chloroplast datasets on the reduced sampling (Suppl. material 5).

## Results

### Large-scale infrageneric phylogeny

The ITS alignment was 773 base pairs (bp) long and 91 indels were coded, whereas the cpDNA alignment was 2484 bp long (795 bp for *psbM-trnD*, 674 bp for *trnQ-rps16* and 1015 bp for *rps16-trnK*) and 167 indels were coded. Only minor differences were identified among trees using BI and ML, and no conflict

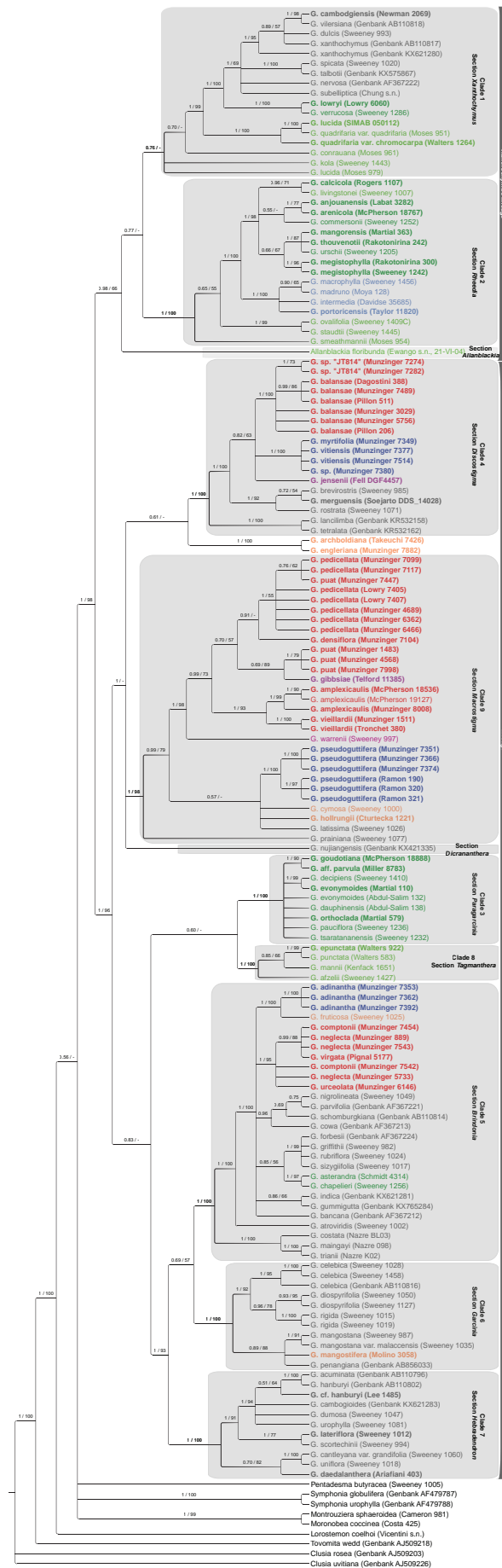
was supported. Because both resolution and support were higher using BI, we chose to present the resulting BI topologies, on which we also indicated the support values obtained from the ML analyses (Figs 2, 3).

Based on ITS, we recovered mostly the same two major lineages and nine clades as Sweeney (2008). The allied genera *Allanblackia*, *Ochrocarpos*, *Pentaphalangium*, *Rheedia*, and *Tripetalum* were again retrieved within *Garcinia*. We retrieved a clade containing clade 1 and clade 2, which corresponds to Lineage A in Sweeney (2008). Its support was PP = 0.77 (vs. 0.99 in Sweeney 2008) and it was not retrieved in ML. Nevertheless, the clade consisting of lineage A of Sweeney (2008) and *Allanblackia floribunda* was more strongly supported (PP = 0.98, BS = 66). Clade 1 was not highly supported in BI (PP = 0.76 vs. 0.98 in Sweeney 2008) and not fully retrieved in ML. This was due to three species: *G. conrauana*, *G. kola* and *G. lucida*. The support of clade 1 excluding these three species reached PP = 1 and BS = 99. Compared to Sweeney (2008), nine new species were assigned to this clade (five downloaded from Genbank, three newly sequenced and *G. conrauana*). Clade 2 was strongly supported (PP = 1, BS = 100). Seven newly sequenced species were assigned to this clade. A clade corresponding to Lineage B of Sweeney (2008) consisted of clades 3 to 9 and three additional species, *G. engleriana*, *G. archboldiana* and *G. nujiangensis*, which were not included in any major clade. The Lineage B clade was highly supported (PP = 1, BS = 96) and all major subclades also received strong support (all PP = 1 and all BS = 100 except for clade 9, BS = 98). They included one (in clade 8) to 15 (in clade 5) additional species each compared to Sweeney (2008). Relationships between clades remained largely unresolved. No grouping was supported except the one including clades 5, 6 and 7 (PP = 1, BS = 93), as was observed by Sweeney (2008).

Based on the combined chloroplast dataset, the same nine clades were retrieved with high support (all PP = 1 and BS from 93 to 100). The only allied genus included in the analysis was *Pentaphalangium*, which was retrieved within *Garcinia* in agreement with the ITS phylogeny. *Garcinia archboldiana* and *G. engleriana* were again sister species, and not included in any major clade. Clades 1 and 2 grouped together (PP = 1, BS = 81), as did clades 3 and 8 (PP = 0.99, BS = 81), which were sister to clade 4 (PP = 1, BS = 95). Clades 5, 6 and 7 grouped together (PP = 1, BS = 78) and this clade grouped with clade 9 and *G. archboldiana* and *G. engleriana* (PP = 1, BS = 99).

### Focus on the New Caledonian species

New Caledonian species were retrieved within three distinct clades: *G. balansae* and *G. sp.* “JT814” were recovered in clade 4; *G. comptonii*, *G. neglecta*, *G. urceolata* and *G. virgata* were placed in clade 5, within which they formed a highly supported subclade (PP = 1 and BS = 95 in the more densely sampled ITS phylogeny); and *G. amplexicaulis*, *G. densiflora*, *G. pedicellata*, *G. puat* and *G. vieillardii* were recovered in clade 9, grouped in a subclade that also included the Australian *G. gibbsiae* (PP = 0.99, BS = 73 in the ITS phylogeny). Together with *G. warrenii*, they formed a strongly supported clade (PP = 1, BS = 98). Within clade 4, the two accessions of *G. sp.* “JT814” formed a subclade based on ITS, but were scattered among the *G. balansae* accessions based on cpDNA. Similarly, the NC species grouped within clades 5 and 9 did not appear reciprocally





monophyletic, neither in the ITS nor in the cpDNA trees (combined analyses, including both ITS and cpDNA data, did not allow a better discrimination). The only exceptions were *G. vieillardii* (two samples from the same locality; PP = 1 and BS = 100 both based on ITS and on cpDNA) and *G. amplexicaulis* (three samples, PP = 1 and BS = 99 based on ITS; only one sample in cpDNA). *Garcinia vieillardii* and *G. amplexicaulis* were also sister species with high support based on ITS (PP = 1 and BS = 93), but not based on cpDNA. Both the ITS and (to a lesser extent) the cpDNA trees show that *G. vitiensis* from Fiji, although belonging to clade 4, was distinct from any of the NC taxa and more related to others Fijian species and to the *G. vitiensis* accession from Vanuatu. In clade 5, *Garcinia adinantha* was also closer to *G. fruticosa* (based on the ITS phylogeny, which was more densely sampled) than to NC species.

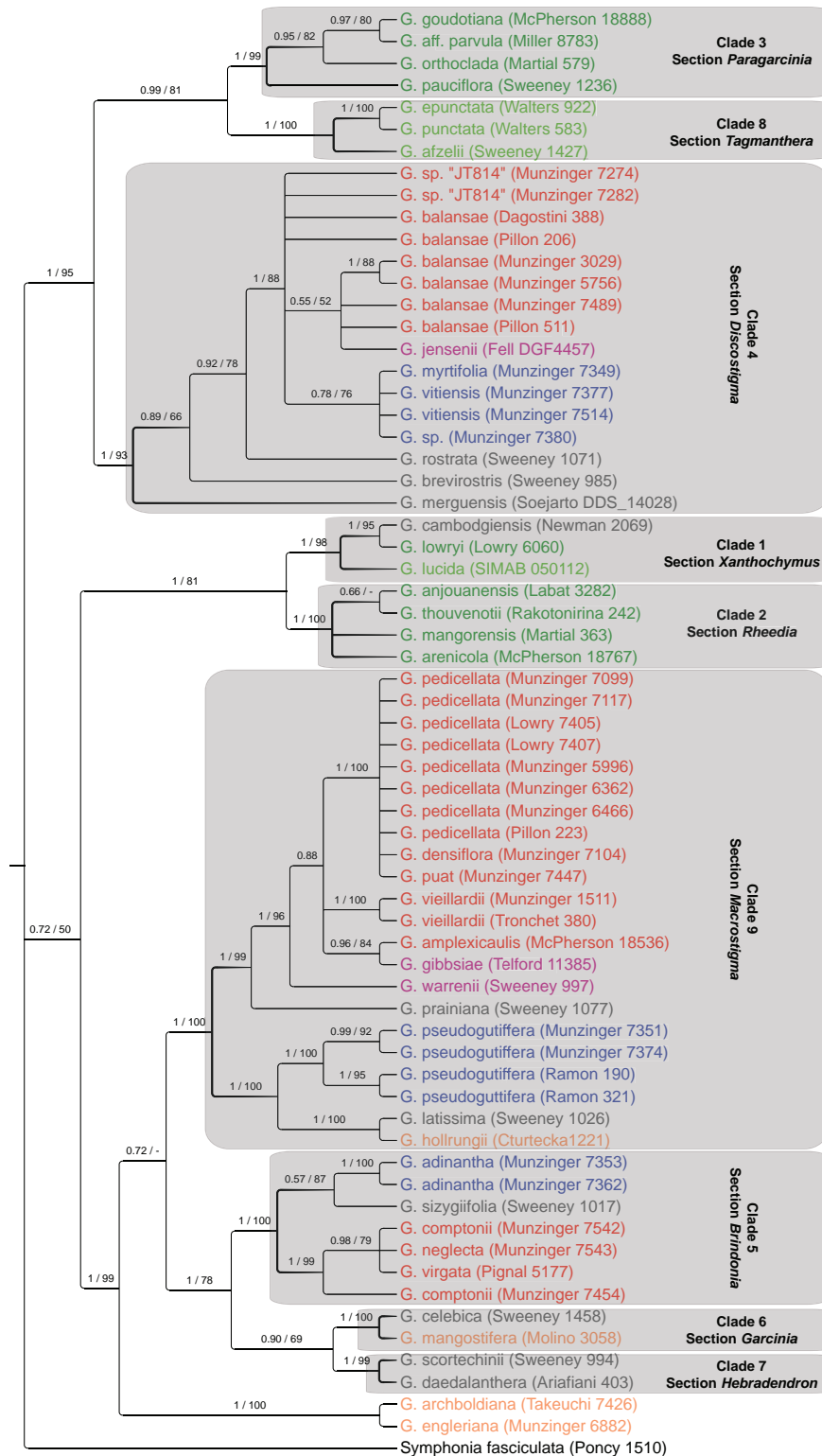
## Discussion

The previous most comprehensive phylogeny for *Garcinia* (*sensu lato*) included 53 species (Sweeney 2008), and the present study increases this number to 111 and includes a biogeographically and morphologically diverse set of species. This more dense and diverse sampling allows for a robust evaluation of the infrageneric classification of the genus, in relation to the morphology-based sections delineated by Jones (1980). Additionally, the inclusion of 32 samples representing the ten species endemic to New Caledonia provides an opportunity to explore in more depth the evolution and taxonomy of New Caledonian *Garcinia*.

## Taxonomy: proposal for an updated infrageneric classification of *Garcinia*

This study, like others (e.g. Sweeney 2008; Ruhfel et al. 2011; Ruhfel et al. 2016), supports a broad circumscription of *Garcinia* that justifies the inclusion of several previously segregated genera (e.g. *Allanblackia*, *Ochrocarpos* p.p., *Pentapetalangium*, *Rheedia*, and *Tripetalum*). The phylogenetic analyses in this paper and in Sweeney (2008) reveal nine major clades falling within two major lineages and provide a framework for a revised sectional classification of the genus. Seven of the major clades roughly correspond to sections recognized by Jones (1980; Table 1. Of the two remaining major clades, one (clade 2) is a morphologically cohesive group that is comprised chiefly of species that Jones (1980) placed into sections *Rheedia*, *Rheediopsis*, and *Teracentrum*. The other remaining major clade (clade 9) contains primarily species that were placed by Jones (1980)

**Figure 2.** Molecular phylogeny of *Garcinia* L. based on ITS sequences and Bayesian inference. Posterior probabilities (PP) and bootstrap support values (BS), obtained respectively by the Bayesian inference and Maximum Likelihood (ML) analysis, are indicated at each node of the cladogram. Nodes were collapsed when PP < 0.50. The lineages/sections discussed in the text are highlighted, and species names appear in colors depending on their native distribution areas: light blue, Central and South America; light green, Tropical Africa; dark green, Madagascar and Western Indian Ocean islands; grey, Southeast Asia; purple, Australia; orange, New Guinea; red, New Caledonia; dark blue, Southwest Pacific islands. Distribution information was taken from the Plants of the World Online website (POWO 2023; also see the table of vouchers). A few species occur in several regions, and the color of the main (largest) geographic region was used. Accessions in bold were newly sequenced in this study.



**Figure 3.** Molecular phylogeny of *Garcinia* L. based on a combined chloroplast DNA dataset and Bayesian inference. Posterior probabilities (PP) and bootstrap support values (BS), obtained respectively by the Bayesian inference and Maximum Likelihood (ML) analysis, are indicated at each node of the cladogram. Nodes were collapsed when PP < 0.50. The lineages/sections discussed in the text are highlighted, and species names appear in colors depending on their native distribution areas: light green, Tropical Africa; dark green, Madagascar and Western Indian Ocean islands; grey, Southeast Asia; purple, Australia; orange, New Guinea; red, New Caledonia; dark blue, Southwest Pacific islands. Distribution information was taken from the Plants of the World Online website (POWO 2023; also see the table of vouchers). A few species occur in several regions, and the color of the main (largest) region was used. All accessions were newly sequenced in this study.

**Table 1.** Sections and numbers of species recognized by Jones (1980) and their correspondence to sections and clades recognized in this study. *Allanblackia* was treated as separate from *Garcinia* by Jones (1980).

Section sensu Jones (1980)	No. spp. (sensu Jones 1980)	Clade	Section in this study
<i>Xanthochymus</i> (Roxb.) Pierre	42	1	<i>Xanthochymus</i> (Roxb.) Pierre
<i>Tetraphalangium</i> Engl.	2		
<i>Rheediopsis</i> Pierre	20	2	<i>Rheedia</i> (L.) S.W.Jones ex P.W.Sweeney
<i>Rheedia</i> (L.) S.W.Jones, <i>nom. inval.</i>	21		
<i>Teracentrum</i> Pierre	4		
<i>Paragarcinia</i> (Baillon) Vesque	10	3	<i>Paragarcinia</i> (Baillon) Vesque
<i>Discostigma</i> (Haask.) Hook.f. subsection <i>Discostigma</i>	53	4	<i>Discostigma</i> (Haask.) Hook.f.
<i>Brindonia</i> (Thouars) Choisy	78	5	<i>Brindonia</i> (Thouars) Choisy
<i>Garcinia</i> L.	46	6	<i>Garcinia</i> L.
<i>Hebradendron</i> (Graham) Planch. & Triana	35	7	<i>Hebradendron</i> (Graham) Planch. & Triana
<i>Tagmanthera</i> Pierre	18	8	<i>Tagmanthera</i> Pierre
<i>Mungotia</i> Pierre	9	9	<i>Macrostigma</i> Pierre
<i>Tripetalum</i> (K. Schum.) S.W.Jones, 1980, <i>nom. inval.</i>	1		
<i>Macrostigma</i> Pierre	7		
<i>Discostigma</i> subsection <i>Dicrananthera</i> (Pierre) S.W.Jones, <i>nom. inval.</i>	2	–	<i>Dicrananthera</i> Pierre

into sections *Macrostigma*, *Mungotia*, and *Tripetalum*. Below we discuss each of these clades, providing their distinguishing characteristics and assigning them sectional names, with the aim of laying the foundation for a phylogenetically informed infrageneric classification of *Garcinia*. The distinguishing sectional characters below are taken from the literature and from examination of physical and digitized herbarium specimens (A, BO, CNS, G, GH, K, KEP, KLU, L, MEL, MO, NY, P, PE, SCA, SING, TAN, TEF, US, YU) and plants in the field. We refer readers to Jones (1980) for a detailed account of previous infrageneric classifications of *Garcinia*, along with sectional synonymy. Informed by an examination of specimens, protologues, and Jones' (1980) sectional assignments, we assign accepted species to sections. In cases where protologue descriptions or specimens were insufficient for determining sectional assignment, species were unplaced.

## Taxonomic account

### Genus *Garcinia* L. Sp. Pl. 1: 443 (1753).

**Type.** *Garcinia mangostana* L., Sp. Pl. 1: 443 (1753).

**Synonyms.** *Rheedia* L., Sp. Pl. 2: 1193 (1753). Type. *Rheedia lateriflora* L. [= *Garcinia humilis* (Vahl.) C.D.Adams, Phytologia 20(5): 312 (1970); non *Garcinia lateriflora* Blume, Bijdr. Fl. Ned. Ind. 5: 214 (1825)].

*Cambogia* L., Gen. Pl., ed. 5: 225 (1754). Type. *Cambogia gummi-gutta* L., Gen. Pl., ed. 5: 225 (1754) [≡ *Garcinia gummi-gutta* (L.) N.Robson, Brittonia 20: 103 (1968)].

*Coddampuli* Adans., Fam. Pl. (Adanson) 2: 445 (1763), *nom. illeg. superfl.* Type: *Cambogia gummi-gutta* L., Gen. Pl., ed. 5: 225 (1754) [≡ *Garcinia gummi-gutta* (L.) N.Robson, Brittonia 20: 103 (1968)].

*Mangostan* Garcin ex Adans., Fam. Pl. (Adanson) 2: 445 (1763), *nom. illeg. superfl.* Type. *Garcinia mangostana* L., Sp. Pl. 1: 443 (1753).

*Biwaldia* Scop., Intr. Hist. Nat. 232 (1777), *nom. illeg. superfl.* Type. *Garcinia mangostana* L., Sp. Pl. 1: 443 (1753).

*Stalagmitis* Murray, Commentat. Soc. Regiae Sci. Gott. 9: 173 (1789). Type. *Stalagmitis cambogioides* Murray, Commentat. Soc. Regiae Sci. Gott. 9: 173 (1789) [= *Garcinia cambogioides* (Murray) Headland, Man. Mater. Med. Therap. [Royle], ed. 3. 339 (1856)].

*Oxycarpus* Lour., Fl. Cochinch. 2: 647 (1790). Type. *Oxycarpus cochinchinensis* Lour., Fl. Cochinch. 2: 648 (1790) [= *Garcinia cochinchinensis* (Lour.) Choisy, Prodr. [A. P. de Candolle] 1: 561 (1824)].

*Mangostana* Rumph. ex Gaertn., Fruct. Sem. Pl. ii. 105. t. 105. (1791), *nom. illeg. superfl.* Type. *Garcinia mangostana* L., Sp. Pl. 1: 443 (1753).

*Verticillaria* Ruiz & Pav., Fl. Peruv. Prodr. 81, t. 15 (1794). Type. *Verticillaria acuminata* Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil. 1: 140 (1798) [= *Garcinia madruno* (Kunth) Hammel, Ann. Missouri Bot. Gard. 76: 928 (1989)].

*Ochrocarpos* Noronha ex Thouars, Gen. Nov. Madagasc. 15 (1805). Type. *Ochrocarpos madagascarensis* Choisy, Prodr. [A. P. de Candolle] 1: 560 (1824) [non *Ochrocarpos madagascariensis* Planchon & Triana, Ann. Sci. Nat. Bot., sér. 4, 14: 364 (1860)], see Sprague (1934) and Sweeney and Rogers (2008) for discussions about original material of *Ochrocarpos madagascarensis* and the type species of *Ochrocarpos*.

*Xanthochymus* Roxb., Pl. Coromandel 2(4): 51, t. 196 (1805). Type. *Xanthochymus pictorius* Roxb. [= *Garcinia xanthochymus* Hook.f. ex T. Anderson Fl. Brit. India [J. D. Hooker] 1(2): 269 (1874)].

*Brindonia* Thouars, Dict. Sci. Nat. [F. Cuvier] 5: 339 (1806). Type. *Brindonia oxycarpa* Thouars, Hist. Veg. Isles Austr. Afr. ed. 2 t. 27 (1805) [= *Garcinia oxycarpa* (Thouars) P.W.Sweeney comb. nov.]. See commentary under Section *Brindonia* for details about the status of *B. oxycarpa*.

*Chloromyron* Pers., Syn. Pl. [Persoon] 2(1): 73 (1806). Type. *Chloromyron verticillatum* Pers., Syn. Pl. [Persoon] 2(1): 73 (1806) [= *Verticillaria acuminata* Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil. 1: 140 (1798); = *Garcinia madruno* (Kunth) Hammel, Ann. Missouri Bot. Gard. 76: 928 (1989)].

*Hebradendron* Graham, Companion Bot. Mag. 2: 199 (1837), *nom. illeg. superfl.* (Art. 58.1). Type. *Stalagmitis cambogioides* Murray, Commentat. Soc. Regiae Sci. Gott. ix. 1787-88 (1789) 173. [= *Garcinia cambogioides* (Murray) Headland, Man. Mater. Med. Therap. [Royle], ed. 3. 339 (1856); = *Hebradendron cambogioides* (Murray) Graham, Companion Bot. Mag. 2: 199, t. 27 (1837)].

*Discostigma* Hassk., Flora 25(2, Beibl.): 33 (1842). Type. *Discostigma rostratum* Hassk., Flora 25(2, Beibl.): 33 (1842) [= *Garcinia rostrata* (Hassk.) Miq., Ann. Mus. Bot. Lugduno-Batavi 1(7): 209 (1864)].

*Terpnophyllum* Thwaites, Hooker's J. Bot. Kew Gard. Misc. 6: 70, t. 2 C (1854). Type. *Terpnophyllum zeylanicum* Thwaites, Hooker's J. Bot. Kew Gard. Misc. 6: 70, t. 2. F. 1 (1854) [= *Garcinia terpnophylla* Thwaites, Enum. Pl. Zeyl. [Thwaites] 406 (1864)].

*Rhinostigma* Miq., Fl. Ned. Ind., Eerste Bijv. Pt. 3: 495 (1861). Type. *Rhinostigma parvifolium* Miq., Fl. Ned. Ind., Eerste Bijv. Pt. 3: 495 (1861) (lectotype, designated here) [= *Garcinia parvifolia* (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 1(7): 208 (1864)].

*Clusianthemum* Vieill., Bull. Soc. Linn. Normandie 9: 338 (1865). Type. *Clusianthemum pedicellatum* Vieill., Bull. Soc. Linn. Normandie 9: 339 (1865).

*Allanblackia* Oliv., Gen. Pl. [Benth. & Hook.f.] 1(3): 980 (1867), J. Linn. Soc., Bot. 10: 43 (1867). Type. *Allanblackia floribunda* Oliv., J. Linn. Soc., Bot. 10: 43 (1867).

*Pentaphalangium* Warb., Bot. Jahrb. Syst. 13(3–4): 382 (1891). Type. *Pentaphalangium crassinerve* Warb., Bot. Jahrb. Syst. 13(3–4): 382 (1891) [= *Garcinia crassinervis* (Warb.) Kosterm., Ceylon J. Sci., Biol. Sci. 12(1): 68 (1976)].

*Tripetalum* K.Schum., Fl. Kais. Wilh. Land [K.M. Schumann & M.U. Hollrung] 51 (1889). Type. *Tripetalum cymosum* K.Schum., Fl. Kais. Wilh. Land [K.M. Schumann & M.U. Hollrung] 51 (1889) [= *Garcinia cymosa* (K.Schum.) I.M. Turner & P.F. Stevens, Gard. Bull. Singapore 51(2): 176 (1999)].

*Tsimatimia* Jum. & H. Perrier, Ann. Sci. Nat., Bot. sér. 9, 11: 256 (1910). Type. *Tsimatimia pedicellata* Jum. & H. Perrier, Ann. Sci. Nat., Bot. sér. 9, 11: 265 (1910) (lectotype, designated here) [= *Garcinia tsimatimia* P.W. Sweeney & Z.S. Rogers, Novon 18(4): 535 (2008)].

*Septogarcinia* Kosterm., Reinwardtia 6: 167 (1962). Type. *Septogarcinia sumbawaensis* Kosterm., Reinwardtia 6: 167 (1962) [= *Garcinia septogarcinia* I.M. Turner & L.V.S. Jenn; non *Garcinia sumbawensis* Lauterb., Bot. Jahrb. Syst. 58(1): 26 (1922)].

### *Xanthochymus* Lineage

**Leaves** with prismatic crystals in the mesophyll (this character is unstudied in *Allanblackia*) (Vesque 1889, 1893). **Flowers** with nectariferous antesealous appendages or intrastaminal rings and disks (sometimes manifested as lobe-like antesealous appendages that alternate with staminodes) (Sweeney 2008, 2010; Mathew et al. 2009, Fig. 1). Staminate flowers lacking pistillodes (rarely present and then rudimentary) and anthers with globose to widely elliptic thecae.

The *Xanthochymus* lineage is comprised of Lineage A in Sweeney (2008) and *Allanblackia*. It contains three sections as circumscribed below.

#### **1. *Garcinia* section *Xanthochymus* (Roxb.) Pierre, Fl. Forest. Cochin. 1, Fasc. 5, 3 (1883). Clade 1**

Figs 2, 3

**Basionym.** *Xanthochymus* Roxb., Pl. Coromandel 2(4): 51, t. 196 (1805).

**Type.** *Xanthochymus pictorius* Roxb. [= *Garcinia xanthochymus* Hook.f. ex T. Anderson Fl. Brit. India [J. D. Hooker] 1(2): 269 (1874)].

**Distinguishing sectional characters.** **Flowers** usually five-merous (rarely four-merous). Staminate flowers with stamens united into fascicles with filaments united for at least  $\frac{1}{2}$  (usually considerably more) of their length. Pollen five- to seven-colporate (Jones 1980). Ovaries with five (rarely four) locules and a single ovule per locule, placentation axile. Afrotropics, Indomalaya, and tropical Australasia.

This section largely corresponds section *Xanthochymus* sensu Jones (1980); however, based on molecular data [this study and Sweeney (2008)] and morphology, we exclude *G. hollrungii* Lauterb. and *G. prainiana* King (and the closely allied *G. phuongmaiensis* V.S. Dang, H. Toyama & D.L.A. Tuan). We also include

here *G. conrauana* Engl. and *G. giadidii* De Wild. [=*G. kola* Heckel] – the only two species that Jones (1980) placed into section *Tetraphalangium* Engl., Bot. Jahrb. Syst. 40(4): 562 (1908), Type. *Garcinia conrauana* Engl.

**Species.** *Garcinia cambodgiensis* Vesque; *G. capuronii* Z.S.Rogers & P.W.Sweeney; *G. conrauana* Engl.; *G. densivenia* Engl.; *G. dulcis* (Roxb.) Kurz; *G. gamblei* Shameer, T.Sabu & N.Mohanan; *G. gerrardii* Harv. ex Sim; *G. kola* Heckel; *G. letestui* Pellegr.; *G. longifolia* Blume; *G. lowryi* Z.S.Rogers & P.W.Sweeney; *G. lucida* Vesque; *G. nervosa* (Miq.) Miq.; *G. petiolaris* Pierre; *G. pushpan-gadaniana* T.Sabu, N.Mohanan, Krishnaraj & Shareef; *G. quadrifaria* (Oliv.) Baill. ex Pierre; *G. spectabilis* Pierre; *G. spicata* (Wight & Arn.) Hook.f.; *G. subelliptica* Merr.; *G. talbotii* Raizada ex Santapau; *G. thwaitesii* Pierre; *G. verrucosa* Jum. & H.Perrier; *G. vidalii* Merr.; *G. vilersiana* Pierre; *G. volkensii* Engl.; *G. vriesiana* Pierre; *G. warburgiana* A.C.Sm.; *G. xanthochymus* Hook.f. ex T.Anderson.

## 2. *Garcinia* section *Rheedia* (L.) S.W.Jones ex P.W.Sweeney, comb. & stat. nov. Clade 2

[urn:lsid:ipni.org:names:77338399-1](https://nomenclature.ipni.org/names/77338399-1)

Figs 2, 3

**Basionym.** *Rheedia* L., Sp. Pl. 2: 1193 (1753).

**Type.** *Rheedia lateriflora* L. [=*Garcinia humilis* (Vahl.) C.D.Adams, Phytologia 20(5): 312 (1970); non *Garcinia lateriflora* Blume, Bijdr. Fl. Ned. Ind. 5: 214 (1825)].

**Distinguishing sectional characters.** **Flowers** usually with four petals (sepal number varies from two to five). Staminate flowers with stamens free or united into fascicles with filaments united up to  $\frac{1}{2}$  (rarely up to  $\frac{2}{3}$ ) of their length. Pollen tri-colporate with long ectoapertures and endocolpi (Jones 1980). Ovaries with two to four locules and a single ovule per locule, placentation axile. Vesque (1893:288) noted that the leaves of species included in this section (i.e., species placed in the genus *Rheedia* and *Garcinia* subgenus *Rheediopsis* in his monograph) have sunken stomata with raised papilla-like protuberances arising from the accessory cells and partially covering the stomatal opening. Neotropics and Afrotropics.

This section includes species placed by Jones (1980) into sections *Rheedia* (L.) S.W.Jones *nom. inval.* (Art. 30.9, Turland et al. 2018); *Rheediopsis* Pierre, Fl. Forest. Cochinch. 1, Fasc. 5, 2 (1883), Type. *G. smeathmannii* (Planch. & Triana) N.Robson ex Spirl. (lectotype, designated here); and *Teracentrum* Pierre, Fl. Forest. Cochinch. 1, Fasc. 5, 1 (1883), Type. *G. livingstonei* T. Anderson. This section includes species that were formerly placed into the genus *Rheedia* L.

**Species.** *Garcinia albuquerquei* (M.E.Berg) Bittrich; *G. ambrensis* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. anjouanensis* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. aphanophlebia* Baker; *G. apostoloi* Mouzinho; *G. arenicola* (Jum. & H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. aristata* (Griseb.) Borhidi; *G. bakeriana* (Urb.) Borhidi; *G. barkeriana* (Urb. & Ekman) Alain; *G. benthamiana* (Planch. & Triana) Pipoly; *G. brasiliensis* Mart.; *G. calcicola* (Jum. & H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. cincta* (Urb.) Borhidi; *G. clarensis* Borhidi; *G. commersonii* (Planch. & Triana) Vesque; *G. cubensis* (Borhidi) Borhidi; *G. dalleizettei* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. decussata* C.D.Adams; *G. floribunda* Miq.;

*G. fluviatilis* Mouzinho & L.Marinho; *G. gabonensis* Sosef & Dauby; *G. gardneriana* (Planch. & Triana) Zappi; *G. × guacopary* (S.Moore) M.Nee; *G. hessii* (Britton) Alain; *G. humilis* (Vahl) C.D.Adams; *G. intermedia* (Pittier) Hammel; *G. kingaensis* Engl.; *G. leptophylla* Bittrich; *G. livingstonei* T.Anderson; *G. macrophylla* Mart.; *G. madruno* (Kunth) Hammel; *G. magnifolia* (Pittier) Hammel; *G. magnophylla* (Cuatrec.) Hammel; *G. mangorensis* (R.Vig. & Humbert) P.W.Sweeney & Z.S.Rogers; *G. martinii* (Maguire) Govaerts; *G. megistophylla* P.W.Sweeney & Z.S.Rogers; *G. moaensis* (Bisse) Borhidi; *G. obliqua* Sosef & Dauby; *G. ophiticola* (Borhidi) Borhidi; *G. ovalifolia* Oliv.; *G. pachyclada* N.Robson; *G. parviflora* Benth.; *G. pervillei* (Planch. & Triana) Vesque; *G. polyneura* (Urb.) Borhidi; *G. portoricensis* (Urb.) Alain; *G. pulvinata* (Planch. & Triana) Hammel; *G. pungens* Borhidi; *G. revoluta* (Urb.) Borhidi; *G. robsoniana* Bamps; *G. ruscifolia* (Griseb.) Borhidi; *G. semseii* Verdc.; *G. serpentini* Borhidi; *G. smeathmannii* (Planch. & Triana) Oliv.; *G. spruceana* (Engl.) Mouzinho; *G. staudtii* Engl.; *G. thouvenotii* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. tsimatimia* P.W.Sweeney & Z.S.Rogers; *G. urschii* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. verticillata* Alain.

### 3. *Garcinia* section *Allanblackia* (Oliv.) P.W. Sweeney, comb. & stat. nov.

urn:lsid:ipni.org:names:77338400-1

**Basionym.** *Allanblackia* Oliv., Gen. Pl. [Benth. & Hook.f.] 1(3): 980 (1867), J. Linn. Soc., Bot. 10: 43 (1867).

**Type.** *Allanblackia floribunda* Oliv., J. Linn. Soc., Bot. 10: 43 (1867) [= *Garcinia oleosperma* P.W. Sweeney, nom. nov.; non *Garcinia floribunda* Miq., Stip. Surin. Sel. 39, non *Garcinia floribunda* Mast. ex Vesque, Monogr. Phan. [A.DC. & C.DC.] 8: 488 (1893)]

**Distinguishing sectional characters.** **Flowers** five-merous. Staminate flowers with stamens united into five phalanges, anthers subsessile, two-theous. Pollen 4-colporate (Jones 1980). Ovaries incompletely five-locular containing multiple ovules per carpel/locule, placentation parietal. Afrotropics.

**Note.** There are nine currently accepted species in the genus *Allanblackia* Oliv., all native to Africa (Bamps 1969; Stevens 2007; POWO 2023). Here we create the section *Allanblackia* (Oliv.) P.W. Sweeney for these species when they are treated as *Garcinia* and below provide names for them in *Garcinia*.

#### Species:

##### *Garcinia guineensis* P.W.Sweeney, nom. nov.

urn:lsid:ipni.org:names:77338401-1

*Allanblackia parviflora* A.Chev., Vég. Ut. Afr. Trop. Franç. 5: 163 (1909). Type. Côte d'Ivoire: Alépé, *Chevalier* 16239.

**Note.** A replacement name ("nom. nov."), *Garcinia guineensis*, is created here for *Allanblackia parviflora*, because the epithet *parviflora* was used previously in *Garcinia* for a different species. The epithet *guineensis* is chosen to reflect the distribution of this species in the Upper Guinean Forest region of West Africa.

***Garcinia kisonghi* (Vermoesen) P.W.Sweeney, comb. nov.**

urn:lsid:ipni.org:names:77338402-1

*Allanblackia kisonghi* Vermoesen, Man. Ess. Forest. Congo: 11 (1923). Type. Democratic Republic of the Congo: Mpse, *Van Naemen in Gillet s.n.*

***Garcinia kimbiliensis* (Spirlet) P.W.Sweeney, comb. nov.**

urn:lsid:ipni.org:names:77338403-1

*Allanblackia kimbiliensis* Spirlet, Bull. Jard. Bot. État Bruxelles 29: 357 (1959). Type. Democratic Republic of the Congo: Kimbili, *Michelson 766*.

***Garcinia marienii* (Staner) P.W.Sweeney, comb. nov.**

urn:lsid:ipni.org:names:77338404-1

*Allanblackia marienii* Staner, Bull. Jard. Bot. État Bruxelles 13: 110 (1934). Type. Democratic Republic of the Congo: Haute Nsele, *De Groof s.n.*

***Garcinia ngouniensis* P.W.Sweeney, nom. nov.**

urn:lsid:ipni.org:names:77338405-1

*Allanblackia gabonensis* (Pellegr.) Bamps, Bull. Jard. Bot. Natl. Belg. 39: 356 (1969). Type. Gabon: between Moubighou and Nzoundou, *Le Testu 6001*.

**Note.** A replacement name, *Garcinia ngouniensis*, is created here for *Allanblackia gabonensis*, because the epithet *gabonensis* was used previously in *Garcinia* for a different species. The epithet *ngouniensis* is in reference to Gabon's Ngounié province, an area where many specimens of this species have been collected.

***Garcinia oleosperma* P.W.Sweeney, nom. nov.**

urn:lsid:ipni.org:names:77338406-1

*Allanblackia floribunda* Oliv., J. Linn. Soc., Bot. 10: 43 (1867). Type. Cameroon: Cameroon River, *Mann 2193*.

**Note.** A replacement name, *Garcinia oleosperma*, is created here for the type species (*A. floribunda*) of the genus *Allanblackia*, because the epithet *floribunda* was used previously in *Garcinia* for a different species. The epithet *oleosperma* is in reference to the seeds that have a high oil content and are an important source of vegetable oil in tropical western Africa (Crockett 2015).



***Garcinia staneriana* (Exell & Mendonça) P.W.Sweeney, comb. nov.**

urn:lsid:ipni.org:names:77338407-1

*Allanblackia staneriana* Exell & Mendonça, J. Bot. 74(Suppl.): 20 (1936). Type. Angola: Belize, Grossweiler 8221.

***Garcinia stuhlmannii* (Engl.) P.W.Sweeney, comb. nov.**

urn:lsid:ipni.org:names:77338408-1

*Allanblackia stuhlmannii* (Engl.) Engl., H.G.A.Engler & K.A.E.Prantl, Nat. Pflanzenfam., Nachtr. 1: 249 (1897). Type. Tanzania: Usambara, Holst 2296.

***Garcinia ulugurensis* (Engl.) P.W.Sweeney, comb. nov.**

urn:lsid:ipni.org:names:77338409-1

*Allanblackia ulugurensis* Engl., Bot. Jahrb. Syst. 28: 435 (1900). Type. Tanzania: Sudost Uluguru, Stuhlmann 8773.

### *Garcinia* Lineage

**Leaves** with druse crystals in the mesophyll (Vesque 1889, 1893). **Flowers** without nectariferous antesealous appendages or intrastaminal rings and disks (Sweeney 2010). Staminate flowers in many sections with pistillodes (but usually absent in sections *Brindonia*, *Hebradendron*, and *Macrostigma*) and anthers of various shapes.

The *Garcinia* lineage contains eight sections as circumscribed below and corresponds to Lineage B in Sweeney (2008).

#### **4. *Garcinia* section *Paragarcinia* (Baillon) Vesque, Monogr. Phan. [A. DC. & C. DC.] 8: 254 (1893). Clade 3**

Figs 2, 3

**Type.** *Ochrocarpos decipiens* Baill., Adansonia 11: 370 (1876) [≡*Garcinia decipiens* (Baill.) Vesque, Monogr. Phan. [A.DC. & C.DC.] 8: 482 (1893)].

**Distinguishing sectional characters.** **Flowers** with two (usually) sepals, fused in bud. Staminate flowers with a pistillode, stamens arranged into four (up to eight) fascicles with sessile to subsessile, two-thecous anthers. Ovaries four locular, stigmas weakly lobed. **Fruits** with smooth walls. **Inflorescences** terminal or axillary with few to many flowers. Afrotropics (Madagascar and Comoros).

This section contains the *Garcinia* species that were formerly placed into the segregate genus *Ochrocarpos*. The twelve species in this section are endemic to Madagascar and Comoros (Sweeney and Rogers 2008).

**Species.** *Garcinia cerasifer* (H.Perrier) P.F.Stevens; *G. dauphinensis* P.W.Sweeney & Z.S.Rogers; *G. decipiens* Vesque; *G. evonymoides* (Planch. & Triana)

P.W.Sweeney & Z.S.Rogers; *G. goudotiana* (Planch. & Triana) P.W.Sweeney & Z.S.Rogers; *G. madagascariensis* (Planch. & Triana) Pierre; *G. multifida* (H. Perrier) P.W.Sweeney & Z.S.Rogers; *G. orthoclada* Baker; *G. parvula* (H. Perrier) P.W.Sweeney & Z.S.Rogers; *G. pauciflora* Baker; *G. tsaratananensis* (H. Perrier) P.W.Sweeney & Z.S.Rogers.

##### 5. *Garcinia* section *Discostigma* (Haask.) Hook.f., Gen. Pl. [Benth. & Hook.f.] 1: 174 (1862). Clade 4

Figs 2, 3

**Basionym.** *Discostigma* Hassk., Flora 25(2, Beibl.): 33 (1842).

**Type.** *Discostigma rostratum* Hassk., Flora 25(2, Beibl.): 33 (1842) [= *Garcinia rostrata* (Hassk.) Miq., Ann. Mus. Bot. Lugduno-Batavi 1(7): 209 (1864)].

**Distinguishing sectional characters.** **Flowers** with four sepals and petals. Staminate flowers with a pistillode, stamens arranged into four fascicles that are distally covered with sessile to subsessile, two-theous anthers. Ovaries bilocular (or unilocular; four-locular in *G. yunnanensis*), stigmas unlobed and smooth. **Fruits** with a smooth surface and capped with a conspicuous discoid stigma, sepals caducous in fruits. **Inflorescences** terminal or axillary with few to many flowers. Indomalaya, tropical Australasia, and Oceania.

Sweeney (2008) noted that there were two groups of species placed into section *Discostigma* by Jones (1980) that differed from typical members of the section by their androecial morphology. One group of species differs by having their stamens fused to the petals and includes *G. balansae*, *G. lanessanii* Pierre, *G. terpnophylla* Thwaites, and *G. warrenii* F.Muell. The position of *G. warrenii* in the trees presented here and in Sweeney (2008) suggests that some of these species may be better placed within section *Macrostigma* (clade 9); however, our molecular analyses find strong support for placement of *G. balansae* within *Discostigma*. The second group of species is restricted to New Guinea, the Philippines, and Taiwan and includes *G. dives* Pierre, *G. hunsteinii* Lauterb., *G. linii* C. E. Chang, *G. luzoniensis* Merrill, and *G. palawanensis* Elmer (Jones 1980). This latter group is reported to have peltate anthers, like species of section *Hebradendron* (sensu Jones 1980); however, Jones (1980) placed them into section *Discostigma* because they share the same stamen arrangement and pollen apertures as typical members of the section. Species representing the *G. dives* group have not yet been included in molecular phylogenetic analyses. *Garcinia anomala* was placed into Section *Garcinia* by Jones (1980), but excluded from that section by Nazre et al. (2018), due to its possession of axillary inflorescences in thyrses and stamens being united into an unlobed annular mass. Fruit characters suggest that this species belongs to Section *Discostigma*; however, the stamens are arranged into a ring.

In our ITS phylogeny, two species not treated by Jones (1980), *G. archboldiana* A.C. Sm. and *G. engleriana* A.C.Sm., are weakly supported as sister to section *Discostigma*; however, in the chloroplast phylogeny these two species are shown as sister to a larger clade comprised of sections *Brindonia*, *Garcinia*, *Hebradendron*, and *Macrostigma*. The staminate flowers of *G. archboldiana* and *G. engleriana* lack pistillodes and they have deeply branched fascicles with numerous subpeltate anthers (Smith 1941). We leave these species unplaced.

Future molecular and morphological work may warrant the placement of these species into their own section.

**Species.** *Garcinia apetala* Pierre; *G. balansae* Pierre; *G. balica* Miq.; *G. binendijkii* Pierre; *G. boerlagii* Pierre; *G. brevirostris* Scheff.; *G. cadelliana* King; *G. calophylla* Pierre; *G. calophyllifolia* Ridl.; *G. caudiculata* Ridl.; *G. cordata* Merr.; *G. cuneifolia* Pierre; *G. cuspidata* King; *G. diversifolia* King; *G. dives* Pierre; *G. dryobalanoides* Pierre; *G. enthaematoeides* Lauterb.; *G. gitingensis* Elmer; *G. grandifolia* (Choisy) Pierre; *G. hasskarlii* Pierre; *G. havilandii* Stapf; *G. holtumii* Ridl.; *G. hunsteinii* Lauterb.; *G. jensenii* W.E.Cooper; *G. keenania* Pierre; *G. kwangsiensis* Merr. ex F.N.Wei; *G. lanceola* Ridl.; *G. lancilimba* C.Y.Wu ex Y.H.Li; *G. lanessanii* Pierre; *G. linearis* Pierre; *G. linii* C.E. Chang; *G. luzoniensis* Merr.; *G. memecyloides* Ridl.; *G. merguensis* Wight; *G. microphylla* Merr.; *G. minimiflora* Ridl.; *G. minutiflora* Ridl.; *G. monantha* Ridl.; *G. multiflora* Champ. ex Benth.; *G. murtonii* Whitmore; *G. myrtifolia* A.C.Sm.; *G. novoguineensis* Vesque; *G. picrorhiza* Miq.; *G. rostrata* (Hassk.) Miq.; *G. salakensis* Pierre; *G. sampitana* Diels; *G. santisukiana* Ngerns. & Suddee; *G. sarawhensis* Pierre; *G. scaphopetala* B.L.Burt; *G. tauensis* Lauterb.; *G. terpnophylla* Thwaites; *G. tetralata* C.Y.Wu ex Y.H.Li; *G. travancorica* Bedd.; *G. treubii* Pierre; *G. umbonata* Lauterb.; *G. versteegii* Lauterb.; *G. vitiensis* (A. Gray) Seem.; *G. wollastonii* Ridl.; *G. zichii* W.E.Cooper.

## 6. *Garcinia* section *Brindonia* (Thouars) Choisy, Mém. Soc. Hist. Nat. Paris 1: 230 (1823). Clade 5

Figs 2, 3

**Basionym.** *Brindonia* Thouars, Dict. Sci. Nat. [F. Cuvier] 5: 339 (1806).

**Type.** *Brindonia oxycarpa* Thouars, Hist. Veg. Isles Austr. Afr. Ed. 2 t. 27 (1805) [= *Garcinia oxycarpa* (Thouars) P.W.Sweeney, comb. nov.; *Garcinia indica* (Thouars) Choisy Mém. syn. nov.]. The copy of *Histoire des végétaux recueillis dans les isles australes d'Afrique* ed. 2 at Kew bears the date 1805 (Baker 1894) and contains six plates (25–30) that do not have accompanying text in the main body of the publication (see also Hiern 1900). Plate 27 is labeled "*Brindonia oxycarpa*" and it depicts two flowering branches, fruit, and dissected flowers (pers. obs). This suffices as an illustration with analysis and thus *Brindonia oxycarpa* is validly published as per Articles 38.1, 38.7, and 38.8 of the ICN (Turland et al. 2018). Some (e.g. Hiern 1900) have considered *B. oxycarpa* a synonym of *Garcinia indica* (Thouars) Choisy Mém. Soc. Hist. Nat. Paris 1: 230 (1823) [= *Brindonia indica* Thouars, Dict. Sci. Nat. [F. Cuvier] 5: 340 (1806)]; however, if these two taxa are considered synonymous, the epithet *oxycarpa* would have priority.

**Distinguishing sectional characters.** **Flowers** with four sepals and petals. Staminate flowers without a pistillode (usually), stamens united into a single central bundle (or ring when pistillode present), anthers four-thecous (but in some species two-thecous). Ovaries multilocular, stigmas divided into distinct rays and usually papillate. **Fruits** in many species with furrows or grooves along the septal radii. **Inflorescences** terminal or axillary with one to many flowers. Afrotropics (Madagascar), Indomalaya, tropical Australasia, and Oceania.

Three species treated as section *Garcinia* by Jones (1980) (i.e., *G. costata* Hemsl. ex King, *G. maingayi* Hook.f., and *G. trianaii* Pierre) form a clade sister to

clade 5, the latter largely corresponding to section *Brindonia* sensu Jones (1980). While they share some features (e.g. tendency to have furrowed/grooved (very shallow in *G. maingayi* and *G. trianaii*), multilocular fruits) with *Brindonia* sensu Jones (1980), they have other features (i.e., pistillodes, stamens arranged into a ring, and two-theous anthers) that are not typical of the section. While it would be tempting to recognize a separate section for these species, pistillodes and stamens arranged into a ring are also shared by *G. atroviridis* Griff. ex T.Anderson and *G. pedunculata* Roxb. ex Buch.-Ham., two species that were included in section *Brindonia* by Jones (1980). It is noteworthy that *G. atroviridis* is the first branching lineage within clade 5, which together with the *G. costata*/*G. maingayi*/*G. trianaii* clade form a basal grade within section *Brindonia* (as circumscribed here).

*Garcinia* usually has an indehiscent drupe or berry (Stevens 2007). The genus *Clusianthemum* Vieill. was established by Vieillard for a new Caledonian species having a capsular fruit (*C. pedicellatum* Vieill.). Later, another capsular genus, *Septogarcinia* was established by Kostermans (1962) for *S. sumbawaensis* Kosterm., from Sumbawa (Indonesia), obviously not knowing about Vieillard's *Clusianthemum*. Notably, several species of NC *Garcinia*, viz. *G. virgata* Vieill. ex Guillaumin, *G. neglecta* Vieill. and *G. comptonii* Baker f. have capsular fruits (Fig. 1). Jones (1980) did not mention *Clusianthemum* in her treatment but included *Septogarcinia* in *Garcinia* sect. *Brindonia*. Jones (1980) does not cite any NC capsular species. The newly described *G. urceolata* is also suspected of having dehiscent fruits (Munzinger et al. 2021). All these species are morphologically similar and could result from *in situ* (within NC) diversification, and all sampled species with dehiscent fruit are found in a strongly supported subclade within clade 5. We do not have sequence material of *G. septogarcinia* I.M. Turner & L.V.S. Jenn. to determine whether that character is an autapomorphy of a dehiscent fruit clade, or if it evolved at least twice, in New Caledonia and Sumbawa. Staminate floral morphology supports placement of *G. septogarcinia* I.M. Turner & L.V.S. Jenn. into section *Brindonia* (Medellín-Zabala and Marinho 2015).

**Species.** *Garcinia adinantha* A.C.Sm. & S.P.Darwin; *G. amabilis* Kaneh. & Hatus.; *G. amboinensis* Spreng.; *G. angustifolia* A.C. Sm.; *G. assamica* J.Sarma, Shameer & N.Mohanan; *G. assugu* Lauterb.; *G. asterandra* Jum. & H.Perrier; *G. atroviridis* Griff. ex T.Anderson; *G. balimensis* A.C. Sm.; *G. bancana* Miq.; *G. beccarii* Pierre; *G. bicolorata* Elmer; *G. binucao* (Blanco) Choisy; *G. borneensis* Pierre; *G. chapelieri* (Planch. & Triana) H.Perrier; *G. cochinchinensis* (Lour.) Choisy; *G. comptonii* Baker f.; *G. conicarpa* Wight; *G. corallina* Vieill.; *G. costata* Hemsl. ex King; *G. cowa* Roxb. ex DC.; *G. crassiflora* Jum. & H.Perrier; *G. dallmannensis* Kaneh. & Hatus.; *G. delpyana* Pierre; *G. dhanikhariensis* S.K.Srivast.; *G. dioica* Blume; *G. emarginata* Lauterb.; *G. erythrosepala* Y.H.Li; *G. esculenta* Y.H.Li; *G. fruticosa* Lauterb.; *G. fusca* Pierre; *G. griffithii* T.Anderson; *G. gummi-gutta* (L.) N.Robson; *G. horsfieldiana* Pierre; *G. hygrophila* Lauterb.; *G. indica* (Thouars) Choisy; *G. klinkii* Lauterb.; *G. korthalsii* Pierre; *G. lanceifolia* Roxb.; *G. lauterbachiana* A.C.Sm.; *G. ledermannii* Lauterb.; *G. leggeae* W.E.Cooper; *G. loheri* Merr.; *G. macgregorii* Merr.; *G. macrantha* A.C.Sm.; *G. maingayi* Hook. f.; *G. maluensis* Lauterb.; *G. mestonii* F.M.Bailey; *G. microstigma* Kurz; *G. minahassensis* Pierre; *G. miquelii* Pierre; *G. myristicifolia* Pierre; *G. nigrolineata* Planch. ex T.Anderson; *G. oblongifolia* Champ. ex Benth.; *G. oligophlebia* Merr.; *G. oliveri* Pierre; *G. oreophila* Lauterb.; *G. oxycarpa* (Thours) P.W.Sweeney; *G. pachyantha* A.C.Sm.; *G. pachypetala* Lauterb.; *G. pallida* Lauterb.; *G. parvifolia* (Miq.) Miq.; *G. pedunculata* Roxb.

ex Buch.-Ham.; *G. ponapensis* Lauterb.; *G. quaesita* Pierre; *G. ramosii* Merr.; *G. riparia* A.C.Sm.; *G. rubra* Merr.; *G. rubriflora* Boerl.; *G. sabangensis* Lauterb.; *G. samarensis* Merr.; *G. schomburgkiana* Pierre; *G. segmentata* Kosterm.; *G. septogarcinia* I.M.Turner & L.V.S.Jenn.; *G. siripatanadilokii* Ngerns., Meeprom, Boonth., Chamch. & Sinbumr.; *G. solomonensis* A.C.Sm.; *G. sopsopia* (Buch.-Ham.) Mabb.; *G. stigmacantha* Pierre; *G. succifolia* Kurz; *G. sulphurea* Elmer; *G. tetrandra* Pierre; *G. teysmanniana* Scheff.; *G. trianaii* Pierre; *G. urceolata* Munzinger, Bruy & M.Pignal; *G. valetoniana* Lauterb.; *G. vidua* Ridl.; *G. virgata* Vieill. ex Guillaumin; *G. viridiflora* Ridl.; *G. wallichii* Choisy; *G. xishuanbannaensis* Y.H.Li; *G. zeylanica* Roxb.

### 7. *Garcinia* L. section *Garcinia*. Clade 6

Figs 2, 3

**Type.** *Garcinia mangostana* L., Sp. Pl. 1: 443 (1753).

**Distinguishing sectional characters.** **Flowers** with four sepals and four petals. Staminate flowers often with a pistillode, stamens united into a single four-lobed or four-angled bundle, anthers two-theous. Ovaries multilocular and stigmas with or without lobes and smooth or corrugated. **Fruits** with a smooth surface. **Inflorescences** terminal and comprised of simple cymes (Nazre et al. 2018). Indomalaya and tropical Australasia.

This section was recently monographed by Nazre et al. (2018) who recognized 13 species in the section and noted that species in the section share terminal inflorescences of simple cymes, stamens united into a single four-lobed or four-angled bundle, and fruits with a smooth surface. Based on morphological and molecular data he excluded several species that were included in this section by Jones (1980); our molecular results fully support his decisions (see discussion under clade 5).

**Species.** *Garcinia acuticosta* Nazre; *G. celebica* L.; *G. diospyrifolia* Pierre; *G. discoidea* Nazre; *G. exigua* Nazre; *G. harmandii* Pierre; *G. mangostana* L.; *G. mangostifera* Kaneh. & Hatus.; *G. nitida* Pierre; *G. ochracea* Nazre; *G. penangiana* Pierre; *G. rigida* Miq.; *G. sangudsangud* Nazre; *G. sibeswarii* Shameer, J.Sarma, N.Mohanan & A.Begum; *G. venulosa* (Blanco) Choisy.

### 8. *Garcinia* section *Hebradendron* Planch. & Triana, Ann. Sci. Nat., Bot. sér. 4, 14: 349 (1860). Clade 7

Figs 2, 3

**Basionym.** *Hebradendron* Graham, Companion Bot. Mag. 2: 199 (1837), *nom. illeg. superfl.* The genus name *Hebradendron* is illegitimate (superfluous as per Article 52.1, Turland et al. 2018) because Graham (1837) included within it *Stalagmitis cambogioides* Murray, Commentat. Soc. Regiae Sci. Gott. ix. 1787-88 (1789) 173 [= *Hebradendron cambogioides* (Murray) Graham, Companion Bot. Mag. 2: 199, t. 27 (1837)], the type of *Stalagmitis* Murray, Commentat. Soc. Regiae Sci. Gott. 9: 173 (1789). Later, Planchon and Triana (1860) published *Garcinia* section *Hebradendron* Planch. & Triana, Ann. Sci. Nat., Bot. sér. 4, 14: 349 (1860), which according to Article 58.1 (Turland et al. 2018) can be considered a replacement name.

**Type.** *Stalagmitis cambogioides* Murray, Commentat. Soc. Regiae Sci. Gott. 9: 173 (1789) [= *Garcinia cambogioides* (Murray) Headland, Man. Mater. Med. Therap. [Royle], ed. 3. 339 (1856); = *Hebradendron cambogioides* (Murray) Graham, Companion Bot. Mag. 2: 199, t. 27 (1837)]. See Shameer and Mohanan (2020) for a discussion about the priority of *G. cambogioides* (Murray) Headland over *G. morella* (Gaertn.) Desr.

**Distinguishing sectional characters.** **Flowers** sessile to subsessile and with four sepals and four petals. Staminate flowers without a pistillode, stamens united into a single central bundle, anthers unilocular and peltate with circumscissile dehiscence or with multiple chambers that dehisce via pores. Ovaries multilocular, stigmas lobed and variously ornamented, often papillate. **Fruits** with smooth surface, pedicels thick in fruit. **Inflorescences** axillary with one to a few flowers. Indomalaya and tropical Australasia.

**Species.** *Garcinia acuminata* Planch. & Triana; *G. blumei* Pierre; *G. bonii* Pit.; *G. burkillii* Whitmore; *G. calycina* Kurz; *G. cambogioides* (Murray) Headland; *G. cantleyana* Whitmore; *G. choisyana* (Choisy) Wall. ex Planch. & Triana; *G. daedalanthera* Pierre; *G. desrousseauxii* Pierre; *G. dumosa* King; *G. fuscopetiolata* Lauterb.; *G. garciae* Elmer; *G. gaudichaudii* Planch. & Triana; *G. gjellerupii* Lauterb.; *G. grahamii* Pierre; *G. hanburyi* Hook.f.; *G. hendersoniana* Whitmore; *G. heterandra* Wall. ex Planch. & Triana; *G. hopii* H.Toyama & V.S.Dang; *G. idenburgensis* A.C.Sm.; *G. imberti* Bourd.; *G. jaweri* Lauterb.; *G. lateriflora* Blume; *G. microcarpa* Pierre; *G. microtropidiiformis* Kaneh. & Hatus.; *G. mindanaensis* Merr.; *G. murdochii* Ridl.; *G. oligantha* Merr.; *G. poilanei* Gagnep.; *G. pullei* Lauterb.; *G. rheedei* Pierre; *G. schlechteri* Lauterb.; *G. scortechinii* King; *G. subtilinervis* F.Muell.; *G. timorensis* Zipp. ex Span.; *G. uniflora* King; *G. urophylla* Scort. ex King; *G. wightii* T.Anderson.

#### 9. *Garcinia* section *Tagmanthera* Pierre, Fl. Forest. Cochinch. Vol. 1, Fasc. 6, 17 (1883). Clade 8

Figs 2, 3

**Type.** *Garcinia punctata* Oliv., Fl. Trop. Afr. 1: 167 (1868).

**Distinguishing sectional characters.** **Staminate flowers** with a pistillode, stamens arranged into four (rarely two) strap-shaped fascicles each with a single row of sessile, recurved, and sometimes multilocellate anthers at the end. Ovaries four locular, stigmas weakly lobed. **Fruits** with smooth surface. **Inflorescences** terminal or axillary with one to a few flowers. Afrotropics.

**Species.** *Garcinia acutifolia* N.Robson; *G. afzelii* Engl.; *G. bifasciculata* N.Robson; *G. buechananii* Baker; *G. buchneri* Engl.; *G. elliotii* Engl.; *G. epunctata* Stapf; *G. huillensis* Welw. ex Oliv.; *G. lujae* de Wild.; *G. mannii* Oliv.; *G. preussii* Engl.; *G. punctata* Oliv.; *G. tanzaniensis* Verdc.

#### 10. *Garcinia* section *Macrostigma* Pierre, Fl. Forest. Cochinch. Vol. 1, Fasc. 6, 36 (1883). Clade 9

Figs 2, 3

**Type.** *Garcinia latissima* Miq., Ann. Mus. Bot. Lugduno-Batavi 1: 209 (1864).

**Distinguishing sectional characters.** **Staminate flowers** lacking pistillode (usually, but rudimentary or well-developed pistillode present in some species), stamens united into central column (sometimes lobed with lobes equaling number of petals) or into completely separate antepetalous fascicles, androecium often adnate to the petals to varying degrees, anthers two-theous. Ovaries four (three) to eight locular, stigmas unlobed and smooth or divided and papillose. **Fruits** with smooth walls or faintly to deeply furrowed/grooved. **Inflorescences** axillary or terminal with one to many flowers. Indomalaya, tropical Australasia, and Oceania.

This section includes chiefly species that were included in Jones' (1980) sections *Macrostigma*, *Mungotia*, and *Tripetalum*. This is perhaps the most heterogenous of the sections recognized here and it is difficult to point to a single character shared by all of the species in the section. Many species, especially those that were placed into sections *Macrostigma* and *Tripetalum*, often have stamen bundles adnate to the petals. It has been suggested that highly branched, anastomosing exudate-containing canals on the adaxial leaf surface may be a synapomorphy for this clade (Sweeney 2008); however, this has not been comprehensively studied across the genus and may not be a reliable character for determining sectional placement (see Cooper 2013). Many species possess leaves with elliptic, elliptic-obovate, or obovate leaves with thin, closely spaced (ca. <5 mm) secondary veins. Other possible features uniting species in the group include the presence of an exotegmen and non-garcinioid type seed germination (see Brandza 1908; Stevens 2007). Further study is needed to confirm the distribution/presence of these characters.

In the phylogeny, this clade includes three species that have been variously placed into other sections by other authors (Lauterbach 1922; Jones 1980): *G. hollrungii*, *G. prainiana*, and *G. warrenii*. In addition to molecular data, these species have morphology that supports their placement into section *Macrostigma*.

**Species.** *Garcinia amplexicaulis* Vieill. ex Pierre; *G. branderhorstii* Lauterb.; *G. brasii* C.T.White; *G. carolinensis* (Lauterb.) Kosterm.; *G. crassifolia* Seeth.; *G. crassinervis* (Warb.) Kosterm.; *G. cymosa* (K.Schum.) I.M.Turner & P.F.Stevens; *G. densiflora* Pierre; *G. gibbsiae* S.Moore; *G. hollrungii* Lauterb.; *G. latissima* Miq.; *G. moselleyna* Pierre; *G. multibracteolata* Merr.; *G. mungotia* Planch. ex Pierre; *G. nuntasaenii* Ngerns. & Suddee; *G. pachycarpa* (A.C.Sm.) Kosterm.; *G. pancheri* Pierre; *G. pedicellata* (G.Forst.) Seem.; *G. phuongmaiensis* V.S.Dang, H.Toyama & D.L.A.Tuan; *G. platyphylla* A.C.Sm.; *G. prainiana* King; *G. pseudoguttifera* Seem.; *G. puat* (Moutrouz.) Guillaumin; *G. quadrilocularis* Seeth.; *G. russellii* W.E.Cooper; *G. sessilis* (G. Forst.) Seem.; *G. smithii* Kosterm.; *G. vieillardii* Pierre; *G. warrenii* F.Muell.

#### 11. *Garcinia* section *Dicrananthera* Pierre, Fl. Forest. Cochinch. 1, Fasc. 6, 8 (1883).

**Type.** *Garcinia thorelii* Pierre, Fl. Forest. Cochinch. t. 62.

**Distinguishing sectional characters.** **Leaves** with prominent stipuliform structures. Staminate flowers with a pistillode, stamens united into an annular mass encircling and attached to the pistillode, anthers two-theous. Ovaries one to two locular, stigmas unlobed and smooth. **Fruits** with smooth walls. **Inflorescences** axillary or terminal with three to many flowers. Indomalaya.

*Garcinia nujiangensis* C.Y.Wu & Y.H.Li occupies an isolated position in the phylogeny, in a polytomy with clades 4 and 9. We resurrect Pierre's section *Dicrananthera* for a morphologically coherent group of species that was designated the "*Garcinia stipulata*" group in Sweeney et al. (2022). Jones (1980) treated this group, using Pierre's sectional name, as a subsection of *Discostigma* (*Garcinia* section *Discostigma* subsection *Dicrananthera* (Pierre) S.W.Jones *nom. inval.* Art. 30.9, Turland et al. 2018). Species in this group collectively range from eastern India and Bhutan, east to southwest China, and south to Myanmar and Laos. In addition to *G. nujiangensis*, the section contains *G. yaatapsap* K. Armstr. & P.W. Sweeney, *G. paucinervis* Chun & F.C.How (1956: 12), *G. stipulata* T.Anderson, and *G. thorelii* Pierre (1882: t. [plate] 62). These species all share prominent stipuliform structures (rare in Clusiaceae, Stevens 2007), leaves with prominent, widely spaced, curved secondary veins and percurrent tertiaries, staminate flowers with numerous stamens united into an annular mass encircling and attached to the pistillode (in *G. paucinervis* and *G. nujiangensis* the stamens are described as being in four bundles (Chun and How 1956; Li 1981)), and ellipsoid fruits with a discoid stigma and one to two seeds. Future molecular phylogenetic analyses will confirm if species of the 'stipulata' group are monophyletic and whether they will remain a distinct clade separate from clade 4/section *Discostigma*.

**Species.** *Garcinia nujiangensis* C.Y.Wu & Y.H.Li; *G. paucinervis* Chun & F.C.How; *G. stipulata* T.Anderson; *G. thorelii* Pierre; *G. yaatapsap* K.Armstr. & P.W.Sweeney.

#### Unplaced species

*Garcinia anomala* Planch. & Triana; *G. archboldiana* A.C.Sm.; *G. blancoi* Pierre; *G. bracteata* C.Y.Wu ex Y.H.Li; *G. busuangaensis* Merr.; *G. caloneura* Boerl.; *G. ceramica* Boerl.; *G. clusiifolia* Ridl.; *G. engleriana* A.C.Sm.; *G. erythrosperma* Lauterb.; *G. fagraeoides* A.Chev.; *G. graminea* Kosterm.; *G. ituman* Merr.; *G. jelinckii* Kurz; *G. klossii* Ridl.; *G. linearifolia* Elmer; *G. longipedicellata* Kosterm.; *G. lucens* Pierre; *G. mammeoides* Kosterm.; *G. matsudae* Kaneh.; *G. montana* Ridl.; *G. moszkowskii* Lauterb.; *G. moulmeinensis* Pierre ex Vesque; *G. nubigena* Lauterb.; *G. pacifica* Merr.; *G. pallide-sanguinea* Lauterb.; *G. plena* Craib; *G. propinqua* Craib; *G. qinzhouensis* Y.X.Liang & Z.M.Wu; *G. ramulosa* Lauterb.; *G. rhizophoroides* Elmer; *G. rumiyo* Kaneh.; *G. rupestris* Lauterb.; *G. schraderi* Lauterb.; *G. squamata* Lauterb.; *G. subfalcata* Y.H.Li & F.N.Wei; *G. torensis* Lauterb.; *G. tuberculata* Lauterb.; *G. whitfordii* Merr.; *G. wichmannii* Lauterb.

#### Taxonomy of the NC *Garcinia* species

The phylogenetic framework estimated in this study does not support the distinction between *G. sp.* "JT814" and *G. balansae* within NC, nor recover four species with multiple accessions as monophyletic (viz. *G. pedicellata*, *G. puat*, *G. comptonii*, *G. neglecta*), but confirms the distinction between NC species and both *G. vitiensis* and *G. adinantha* found in Fiji. Therefore, all NC species should still be considered as endemics. Also, *G. balansae* (belonging to clade 4/section *Discostigma*) appears more closely related to species from Fiji (*G. myrtifolia*, *G. vitiensis*), Australia (*G. jensenii*) and southeast Asia (*G. brevirostris*, *G. merguensis*, *G. rostrata*, *G. lancilimba*, *G. tetralata*) than to any other NC species.



The four species with capsular fruits (*G. comptonii*, *G. neglecta*, *G. urceolata* and *G. virgata*; retrieved in clade 5/section *Brindonia*) cannot be distinguished based on the present molecular data, but they form two pairs of species based on morphology and ecology. *Garcinia urceolata* and *G. virgata* have small leaves and were confused for a long time but differ by their flowers (green urceolate versus yellowish cup-like corolla), leaves and fruits. Both occur in dense humid forest on non-ultramafic substrates, but *G. urceolata* grows at higher elevation and in wetter conditions than *G. virgata*. *G. comptonii* appears restricted to maquis or forest edges on ultramafic substrates, while *G. neglecta* is mostly a forest tree on ultramafic and non-ultramafic substrates.

In the other NC clade (included in clade 9/section *Macrostigma*), *G. vieillardii* is restricted to the northeast dense humid forest on non-ultramafic soils, above 550 m a.s.l., while *G. densiflora* occurs in the same area and also on non-ultramafic substrates but at lower elevation. In addition, it is more a rupicolous species. The three other species can be found on both substrates (ultramafic and non-ultramafic). *Garcinia puat* is restricted to dense humid forest at low elevations, while *G. pedicellata* is a coastal (including small islands) to medium elevation tree, growing in drier conditions than the three previously cited species. Finally, *G. amplexicaulis* is the species with the widest ecological amplitude, growing in open maquis to closed humid forest, from low to 900 m a.s.l., throughout all the main island.

## Conclusions

This study offers a way forward on a revised infrageneric classification of the species-rich genus *Garcinia*, based on both evolutionary history (as informed by molecular phylogenies) and morphology. We recognize eleven sections within *Garcinia*, list representative species and document distinctive morphological features for each. This classification provides an evolutionary-based foundation for future, much needed monographic work within the genus. Although additional phylogenetic analyses are warranted, by including more species and increasing the phylogenetic resolution, our phylogenetic results are a major contribution to the understanding of the evolutionary history of the genus and they provide a starting point for more ecological and evolutionary investigations as well as conservation planning and taxonomic work. Future revisionary efforts focused on some of the more speciose sections/clades recognized here (*Brindonia*, *Discostigma*, and *Hebradendron*) will certainly result in many species being reduced to synonymy and some new species being described. This was the case with a recent revision of Section *Garcinia* (Nazre et al. 2018). And, as more detailed taxonomic work is done, some species section reassignments are inevitable as are the erection of new sections to accommodate newly discovered clades with distinct suites of morphological characters.

One area that is particularly attractive for future research concerns the biogeographic history of the genus. A more complete knowledge of the spatio-temporal history of *Garcinia* would allow for a better understanding of the events that lead to the present geographic distribution of the genus. This would contribute to a growing body of knowledge about the biogeography of pantropically distributed clades and would provide additional data for exploring hypotheses about intercontinental disjunctions (e.g. Clayton et al. 2009; Couvreur et

al. 2011; Baker and Couvreur 2013; Ruhfel et al. 2016; Torke et al. 2022). At a smaller scale, studying the origin of the ten endemic NC *Garcinia* species would also be valuable. Species diversification probably occurred after colonization of the territory by long-distance colonization and recent studies on other plant groups showed that in addition to the closest and largest landmass that is Australia, diverse geographic origins could be revealed (e.g. Duangjai et al. 2009; Del Rio et al. 2017; Samuel et al. 2019).

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

Conceptualization: PS, JM, MG. Data curation: JM, PS, MG. Formal analysis: MG, PS. Funding acquisition: MG. Investigation: PS, MG. Writing - original draft: MG, PS, JM.

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### Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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## Supplementary material 1

### List of taxa and accessions used in this study

Authors: Myriam Gaudeul, Patrick Sweeney, Jérôme Munzinger

Data type: xlsx

Explanation note: The origin of DNA sequences is indicated, together with information on the herbarium voucher and distribution area of the taxon. In cases where the accepted name that was used in this study differed from the name provided in the original study that generated a sequence or voucher, the original name is provided (under “Prior determination”) along with a reference for the taxonomic decision. Accessions that were newly sequenced in this study have boldface text. All accessions were included in the nuclear DNA phylogenetic analysis (except three samples, as indicated in the first column) and a subset was included in the chloroplast DNA phylogenetic analysis, as indicated in the corresponding column.

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Link: <https://doi.org/10.3897/phytokeys.239.112563.suppl1>

## Supplementary material 2

### Molecular phylogeny of *Garcinia* L. based on *psbM-trnD* and Bayesian inference

Authors: Myriam Gaudeul, Patrick Sweeney, Jérôme Munzinger

Data type: jpeg

Explanation note: Posterior probabilities (PP) are indicated at each node of the cladogram. Nodes were collapsed when PP < 0.50. Species names appear in colors depending on their native distribution areas: light green, Tropical Africa; dark green, Madagascar and Western Indian Ocean islands; grey, Southeast Asia; purple, Australia; orange, New Guinea; red, New Caledonia; dark blue, Southwest Pacific islands. Distribution information was taken from the Plants of the World Online website (POWO 2023; also see the table of vouchers). A few species occur in several regions, and the color of the main (largest) region was used. All accessions were newly sequenced in this study.

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Link: <https://doi.org/10.3897/phytokeys.239.112563.suppl2>

## Supplementary material 3

### Molecular phylogeny of *Garcinia* L. based on *trnQ-rps16* and Bayesian inference

Authors: Myriam Gaudeul, Patrick Sweeney, Jérôme Munzinger

Data type: jpeg

Explanation note: Posterior probabilities (PP) are indicated at each node of the cladogram. Nodes were collapsed when PP < 0.50. Species names appear in colors depending on their native distribution areas: light green, Tropical Africa; dark green, Madagascar and Western Indian Ocean islands; grey, Southeast Asia; purple, Australia; orange, New Guinea; red, New Caledonia; dark blue, Southwest Pacific islands. Distribution information was taken from the Plants of the World Online website (POWO 2023; also see the table of vouchers). A few species occur in several regions, and the color of the main (largest) region was used. All accessions were newly sequenced in this study.

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Link: <https://doi.org/10.3897/phytokeys.239.112563.suppl3>



## Supplementary material 4

### Molecular phylogeny of *Garcinia* L. based on *rps16-trnK* and Bayesian inference

Authors: Myriam Gaudeul, Patrick Sweeney, Jérôme Munzinger

Data type: jpeg

Explanation note: Posterior probabilities (PP) are indicated at each node of the cladogram. Nodes were collapsed when PP < 0.50. Species names appear in colors depending on their native distribution areas: light green, Tropical Africa; dark green, Madagascar and Western Indian Ocean islands; grey, Southeast Asia; purple, Australia; orange, New Guinea; red, New Caledonia; dark blue, Southwest Pacific islands. Distribution information was taken from the Plants of the World Online website (POWO 2023; also see the table of vouchers). A few species occur in several regions, and the color of the main (largest) region was used. All accessions were newly sequenced in this study.

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Link: <https://doi.org/10.3897/phytokeys.239.112563.suppl4>

## Supplementary material 5

### Molecular phylogeny of *Garcinia* L. based on a combined ITS and chloroplast DNA (*psbM-trnD*, *trnQ-rps16* and *rps16-trnK*) dataset and Bayesian inference

Authors: Myriam Gaudeul, Patrick Sweeney, Jérôme Munzinger

Data type: jpeg

Explanation note: Posterior probabilities (PP) are indicated at each node of the cladogram. Nodes were collapsed when PP < 0.50. Species names appear in colors depending on their native distribution areas: light green, Tropical Africa; dark green, Madagascar and Western Indian Ocean islands; grey, Southeast Asia; purple, Australia; orange, New Guinea; red, New Caledonia; dark blue, Southwest Pacific islands. Distribution information was taken from the Plants of the World Online website (POWO 2023; also see the table of vouchers). A few species occur in several regions, and the color of the main (largest) region was used.

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