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RESEARCH ARTICLE

Molecular phylogeny of *Atractocarpus* (Rubiaceae): taxonomic implications for several New Caledonian Gardenieae species

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Background and aims – New Caledonia is a hotspot of biodiversity in the world. Among the most diverse New Caledonian plant families is Rubiaceae, which consist of 30 genera containing 220 species, with a level of endemism of 93%. The tribe Gardenieae is represented by four genera, *Gardenia* (8 species), *Aidia* (2 species), *Randia* (7 species), and *Atractocarpus* (10 species). As *Randia* has now been restricted to the Neotropics, the New Caledonian *Randia* species remain unplaced within the tribe. *Atractocarpus* is a Pacific genus, easily characterized by long imbricated stipules, a feature also present in the *Randia* species and in several *Gardenia* species in New Caledonia. The aims of the present study are to test the monophyly of *Atractocarpus* and to assess the phylogenetic placement of the *Randia* and *Gardenia* species with long imbricated stipules within Gardenieae and specifically their relationships with taxa of the *Porterandia* group to which *Atractocarpus* belongs.
Material and methods – We investigated 63 species of Pacific Gardenieae, with a focus on the *Porterandia* group, in a Bayesian phylogenetic reconstruction (cpDNA: *trnTF* and *rpl32*, and nrDNA: ITS).
Key results – Our study provides a mostly supported consensus tree topology of the *Porterandia* group. Five *Gardenia* and seven *Randia* species fall within a clade that comprises the New Caledonian *Atractocarpus* species, rendering both *Atractocarpus* and *Gardenia* polyphyletic.
Conclusion – We enlarge the delimitation of *Atractocarpus* to include 12 New Caledonian *Randia* and *Gardenia* species. New Caledonia is consequently confirmed as the centre of diversity for *Atractocarpus* with 31 species. According to our study, three genera of Gardenieae occur in the archipelago: *Aidia*, *Gardenia*, and *Atractocarpus*.

Keywords – *Atractocarpus*; centre of diversity; *Gardenia*; New Caledonia; Pacific Islands; *Porterandia* group; *Randia*; Rubiaceae.

INTRODUCTION

New Caledonia is a hotspot of biodiversity isolated in the west Pacific Ocean. The exceptional flora of this archipelago mainly originated from relatively recent colonisation events from surrounding islands and the Asian and Australian continents after the emersion of the New Caledonian island group about 37 Mya (Pillon 2012). Several plant families have undergone a large diversification. Rubiaceae is among the largest New Caledonian plant families, with ca 220 species (Munzinger et al. 2020). The largest rubiaceous genus is *Psychotria* L. with ca 80 species (Barrabé et al. 2014), followed by *Ixora* L., and *Cyclophyllum* Hook.f with 19 species each. Like *Cyclophyllum* Hook.f., *Atractocarpus* Schltr. & K.Krause has its centre of species diversity in New Caledonia (Mouly & Jeanson 2015).

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The tribe Gardenieae was recently studied using molecular phylogeny and several main lineages were identified (Mouly et al. 2014). Different monophyletic groups were resolved and recognized: an *Aidia* group, a *Gardenia* group, a *Porterandia* group, a *Randia* group, and a *Rothmannia* group, plus the genus *Schumanniophyton* Harms as a basal lineage in the tribe. Currently, the named New Caledonian Gardenieae species belong to four genera: *Aidia* Lour. (2 spp.), *Gardenia* J.Ellis (8 spp.), *Randia* L. (7 spp.), and *Atractocarpus* (14 spp.).

Atractocarpus is a member of the *Porterandia* group Mouly et al. (2014), together with the Asian genera *Bungarimba* K.M.Wong, *Catunaregam* Wolf (also African), *Deccania* Tirveng, *Duperrea* Pierre ex. Pit., *Porterandia* Ridl., *Rubovietnamia* Tirveng., *Tamilnadia* Tirveng. & Sastre, *Tarennoidea* Tirveng. & Sastre, *Vidalasia* Tirveng, plus the two genera *Brachytome* Hook.f. and *Dioecrescis* Tirveng. *Atractocarpus* was initially described for a single New Caledonian species (Schlechter & Krause 1908) and took its name (atraktos: a spindle, carpos: a fruit) from the fusiform berry fruit of the type species *A. bracteatus* Schltr. & K.Krause (Mouly 2012). Then, 13 species restricted to the New Caledonian archipelago were described in or transferred to *Atractocarpus* (Guillaumin & Beauvisage 1913; Guillaumin 1930) based on the shared character of numerous seeds merged within the entire placentas (fig. 1G). Some of these do not have the fusiform fruit of the type species (e.g. spherical as fig. 1C, obpyriform as fig. 1D, or ovoid) but have fruits with a somewhat hard endocarp (fig. 1H). These "*Gardenia*-like fruits" (Eriksson & Bremer 1991) are berry-like drupes, often large, with a very fibrous mesocarp and/or endocarp and a pulpy placenta when mature. Later on, Green (1990) included an Australian species from Lord Howe Island, *Atractocarpus stipularis* (F.Muell.) Puttock ex. P.S.Green, because of the elongated and imbricated stipules common to all species of the genus and the fruit structure. As a result, the genus *Atractocarpus* was no longer a New Caledonian endemic. After a phylogenetic study of the Australian and Pacific Gardenieae (Puttock 1999; Puttock & Quinn 1999) broadened the circumscription of *Atractocarpus* to include the genera *Neofranciella* Guillaumin, *Sukunia* A.C.Sm., *Sulitia* Merr., and *Trukia* Kaneh., plus several Australian *Randia* and *Gardenia* species. From Puttock's circumscription of the genus *Atractocarpus*, the newly accepted diagnostic features were elongated imbricated stipules lacking yellow wax (fig. 1B; a product secreted by colleters on the inside of the stipules), unisexual flowers (individuals dioecious or gynodioecious), and fruits with a woody endocarp. Following Puttock's (1999) circumscription, *Atractocarpus* consists of 29 species.

Recently, when describing the genus *Bungarimba* K.M.Wong, Wong (2004) questioned the monophyly of *Atractocarpus* based on morphological comparison of taxa and phylogenetic data. Indeed, this author showed that *Atractocarpus* sensu Puttock was paraphyletic, with *Porterandia* nested within it (Wong 2004: fig. 2), and *Bungarimba* distinct from the *Atractocarpus*-*Porterandia* clade, though without branch support. The results of Mouly et al. (2014) also questioned the circumscription of *Atractocarpus* proposed by Puttock (1999), showing a close relationship of the three genera *Sukunia*, *Trukia*, and *Bungarimba* to *Catunaregam* and *Deccania*, rather than to *Atractocarpus* and *Neofranciella*. However, very few of the internal *Porterandia* group relationships received high posterior probabilities in Mouly et al. (2014), meaning that it was preferable to consider the relationships unresolved. More recently, Kainulainen et al. (2017) included one species of *Atractocarpus* and one of *Sukunia* in a biogeographical study of Indian Ocean Rubiaceae. These two representatives were not closely related, but no support for branching was provided. Therefore, there is no strong evidence so far that Puttock's concept of *Atractocarpus* is not reliable.

The New Caledonian *Randia* and *Gardenia* species were not studied by Puttock (1999), and their phylogenetic positions in Gardenieae remain problematic. Indeed, *Randia* in its old circumscription was shown to be polyphyletic (Persson 2000; Andreasen & Bremer 2000) and is now restricted to the Neotropics (Gustafsson & Persson 2002), leaving several New Caledonian *Randia* species unplaced within the Gardenieae. Within the New Caledonian *Gardenia*, only *Gardenia aubryi* Vieill., *G. oudiepe* Vieill., and *G. urvillei* Montrouz. have stipules covered by yellow wax, a typical feature in *Gardenia*. Among the other New Caledonian *Gardenia* species, at least one has a monocaulous habit and is dioecious (*Gardenia conferta* Guillaumin), two common features in *Atractocarpus* (Puttock 1999) but not in *Gardenia*, and another one has elongated fruits (*Gardenia colnettiana* Guillaumin), which are more common in *Atractocarpus* than in *Gardenia*. On the other hand, *G. conferta* differs from *Atractocarpus* sensu Puttock (1999) by corolla lobes shorter than the corolla tube. Kainulainen et al. (2017) included seven of the New Caledonian *Gardenia*; they found that the three species with stipules covered by yellow wax were embedded within the *Gardenia* group, whereas the four other species (e.g. *G. conferta* and *G. colnettiana*) were associated with *Atractocarpus heterophyllus* (Montrouz.) Guillaumin & Beauvis. These findings clearly show that the taxonomic position of the New Caledonian *Randia* and *Gardenia* need to be investigated thoroughly.

As New Caledonian Gardenieae species relationships are still problematic, we decided to dedicate a study in order to obtain a well-defined molecular phylogenetic structure for relationships within the *Porterandia* group, with a focus on *Atractocarpus* and New Caledonian Gardenieae. The present study aims at 1) testing the monophyly of the genus *Atractocarpus* as delimited by Puttock; 2) assessing the phylogenetic positions and relationships of the New Caledonian *Atractocarpus*, *Gardenia*, and *Randia*; and 3) providing taxonomic treatments for supported relationships, when necessary.

MATERIAL AND METHODS

Material

To cover the diversity in Gardenieae as much as possible, and thus be able to place New Caledonian species with unknown affinities more accurately, we sampled 13 genera and 63 species from both silica and herbarium material (K, NOU, P, UPS, S; acronyms follow the Index Herbariorum;

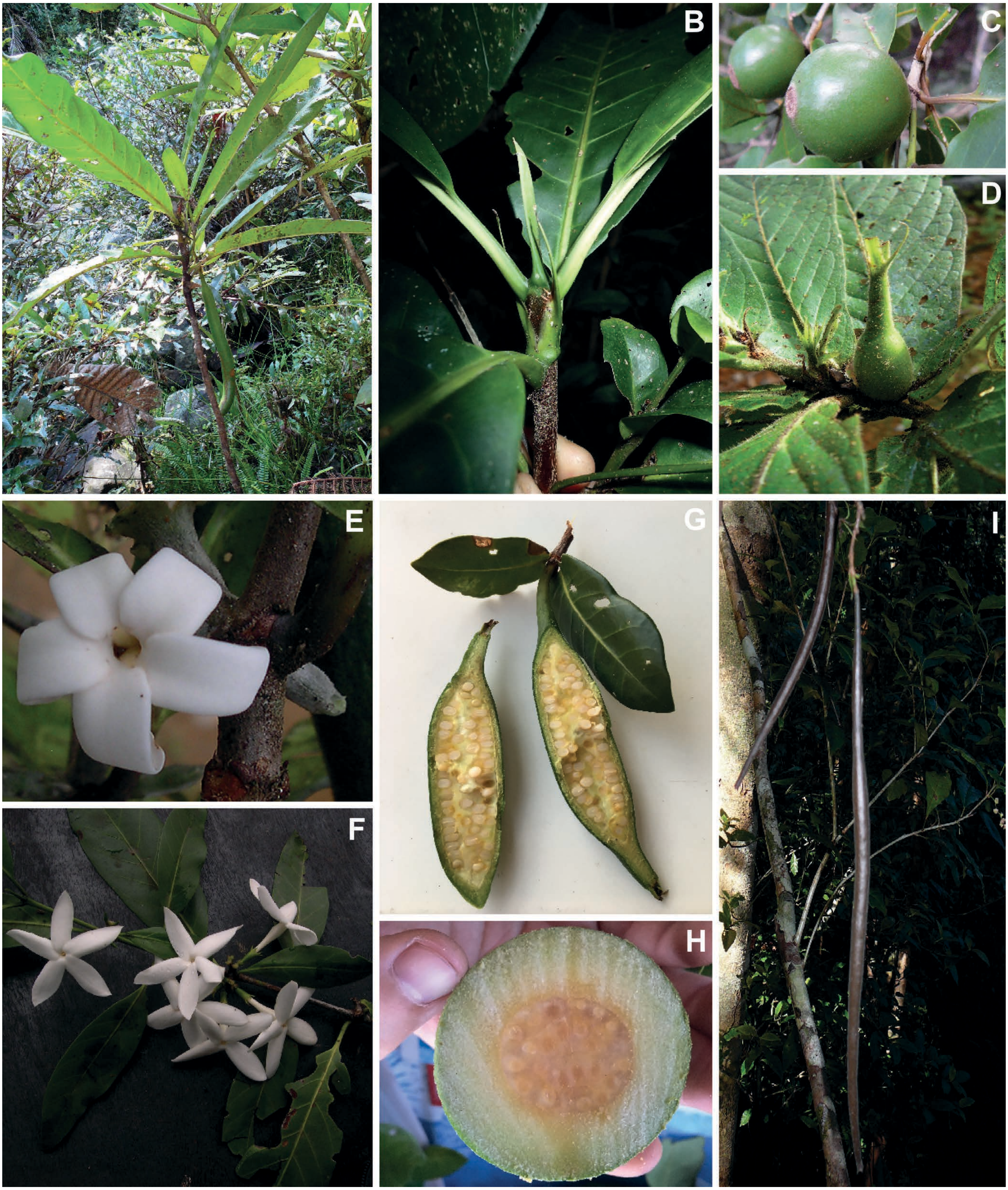

Figure 1 – Selected New Caledonian *Atractocarpus* species showing characters of interest. **A**. *A.* sp. 5, fruiting treelet. **B**. *A. bracteatus*, treelet apex showing the characteristic stipules. **C**. *A. pancherianus*, round fruits. **D**. *A. mollis*, obpyriform fruit on a branch apex. **E**. *A.* sp. 2, female flower showing the constricted corolla throat with emerging stigma lobes. **F**. *A. ngoyensis*, flowering branch of a male individual. **G**. *A. heterophyllus*, young fusiform fruit in longitudinal section showing seeds embedded within the placental pulp. **H**. *A. vaginatus*, detail of an immature fruit in transversal section showing the thick fruit walls. **I**. *A. longistipitatus*, thin-walled elongated berries. Photographs: A, C–I by Arnaud Mouly; B by Laure Barrabé.

Thiers continuously updated). We were, however, unable to obtain material or sequences for *Sulitia* species from the Philippines.

The taxa represent a quite exhaustive sampling of New Caledonian Gardenieae, including 11 undescribed new species (*Atractocarpus* sp. 2 to *A.* sp. 12*)*, with a special emphasis on *Atractocarpus*, *Randia*, and *Gardenia*, plus two New Caledonian *Aidia* species. We included several available Pacific and South-East Asian Gardenieae species (including another undescribed species of *Atractocarpus* from Tahiti; *A.* sp. 1) and other Gardenieae representatives from the different groups recognized by Mouly et al. (2014). Taxa of the Octotropideae s.l. (Mouly et al. 2014) clade were selected to root the tree. The list of sequenced material is available as supplementary file 1. The 12 undescribed species cited here will be published in a complete revision of the genus *Atractocarpus* for New Caledonia by the first author of the present publication.

Laboratory procedures

We utilized information from two chloroplast regions (*trnTF* and *rps32*) and a nuclear ribosomal region (ITS). DNA was extracted, amplified, and sequenced using standard procedures as outlined in Kårehed & Bremer (2007) and Rydin et al. (2008).

Alignment and phylogenetic reconstruction

Sequences were aligned using the software Se-Al v.2.0 (Rambaut 1996). Insertion/deletion events were inferred by eye. Gaps were treated as missing data in the alignment and were added as binominal characters (absent or present) at the end of the matrix.

Bayesian analyses were performed using MrBayes v.3.1.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003). For each single gene data set, the best performing evolutionary model was identified under three different model selection criteria: Akaike information criterion (AIC) (Akaike 1973), AICc (a second order AIC, necessary for small samples), and the Bayesian information criterion (BIC) (Schwartz 1978). We performed these calculations using MrModeltest v.2.4 (Nylander 2004). Ambiguous alignments and insertions-deletions were excluded from the data sets for analyses. For single gene analyses, the best performing model under the AICc criterion was selected, 10^7 generations were run, with a sample frequency of 1000 and four parallel chains. A flat dirichlet prior probability (all values are 1.0) was selected for the substitution rates (revmatpr) and the nucleotide frequencies (statefreqpr). The prior probability for the shape parameter of the gamma distribution of rate variation (shapepr) was uniformly distributed over the interval (0.1, 50.0). For analyses using a gamma distribution with a proportion of invariable sites, we specified a prior probability for this proportion (pinvarpr), uniformly distributed over the interval (0.0, 1.0). For the combined analyses, model selection and settings were selected in the same way as for single gene analyses, in order to ensure that the analyses represented an adequate sample of the posterior distribution, five million generations were run. Partitions were unlinked so that each partition was allowed to have its own set of parameters.

RESULTS

Separate analyses of all markers resulted in more or less resolved tree topologies, with low to high support for clades. Relationships of the main clades highlighted on the tree (fig. 2) were often not resolved or if so, poorly supported. However, these main clades were retrieved in most of the analyses. The combined data from the three markers resulted in a much more resolved topology, where the main clades were well-supported and their relationships received strong support (fig. 2).

In the combined phylogeny, the ingroup forming the Gardenieae was monophyletic (PP = 1.00). The earliest divergent lineage consisted of *Gardenia* species (PP = 1.00) and included the type species of the genus, *G. jasminoides* J.Ellis, and the New Caledonian species *G. aubryi*, *G. oudiepe*, and *G. urvillei*. They represented the *Gardenia* group sensu Mouly et al. (2014). The second lineage represented the *Randia* group sensu Mouly et al. (2014) and comprised two specimens of *Randia aculeata* L. (PP = 1.00), the neotropical type species of *Randia*. The third clade consisted of *Aidia abeidii* S.E.Dawson & Gereau from East Africa and *A. racemosa* (Cav.) Tirveng. from Asia. The last lineage (PP = 0.88) represented the *Porterandia* group (Mouly et al. 2014) and included representatives of the genera *Atractocarpus*, *Brachytome*, *Bungarimba*, *Catunaregam*, *Deccania*, *Dioecrescis*, *Duperrea*, *Porterandia*, *Rubovietnamia*, *Tamilnadia*, *Tarennoidea*, *Vidalasia*, and several New Caledonian *Gardenia* and *Randia* species, two New Caledonian *Aidia* species (*A. congesta* and *A. viellardii*), plus two Australian *Randia* species.

Within the ingroup, the genera *Aidia*, *Atractocarpus*, *Gardenia*, and *Randia* were not monophyletic when including the New Caledonian native species. First, the two New Caledonian native *Aidia* species formed a clade with the genera *Tamilnadia*, *Brachytome*, and *Dioecrescis* (not supported; PP = 0.60), but not with the other *Aidia* species from Africa and Asia.

Within the lineage that included most of the *Atractocarpus* species (hereafter called *Atractocarpus* s.l.; fig. 2), a first basal clade (PP = 1.00) occurred with *A. carolinensis* (Valeton) Puttock, *A.* sp. 1, and *A. pentagonioides* (Seem.) Puttock from the Caroline Islands, French Polynesia, and Fiji Islands, respectively. The second clade to appear was the Australian and Lord Howe Island species of *Atractocarpus*, here represented by *A. fitzalanii* (F.Muell.) Puttock, *A. hirtus* (F.Muell.) Puttock, *A. merikin* (F.M.Bailley) Puttock, and *A. stipularis* (F.Muell.) Puttock ex P.S.Green (PP = 1.00), plus the Tongan species *A. crosbyi* (Burkill) Puttock as sister to the Australian group (PP = 0.86). The third clade (NC clade; PP = 1.00) grouped all the included New Caledonian species of *Atractocarpus*, plus all the New Caledonian *Randia*, and five New Caledonian *Gardenia*. The NC clade splits into two well-supported subclades (NC subclades 1 and 2) of 17 (PP = 1.00) and 14 species (PP = 0.83), respectively.

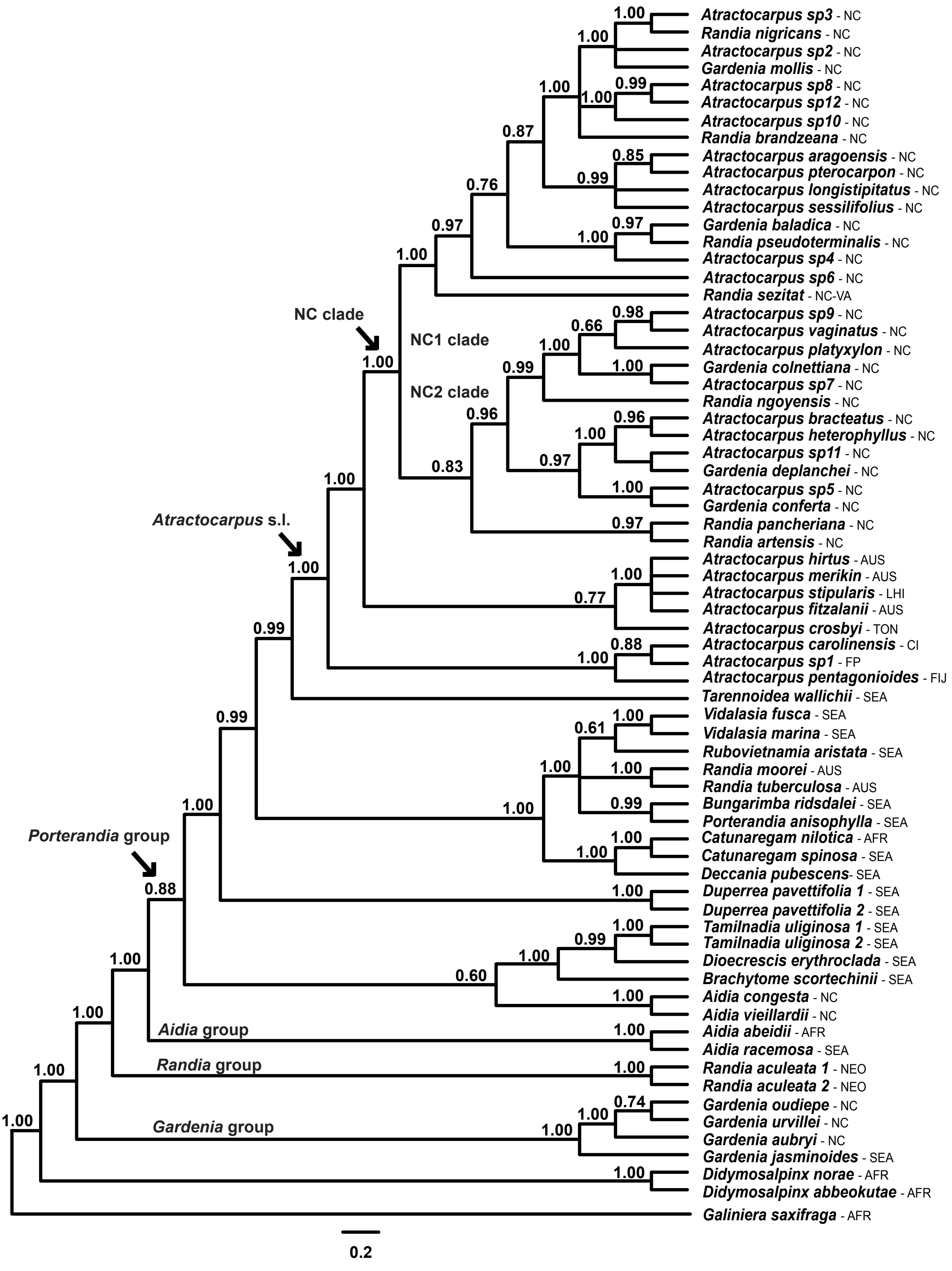

Figure 2 – Phylogenetic tree of the *Porterandia* group obtained from the combined analysis of cpDNA (*trnTF* and *rpl32*) and nrDNA (ITS). Numbers indicate Bayesian posterior probabilities. Areas of distribution are indicated after species names: AFR = Africa; AUS = Australia; CI = Caroline Islands; FIJ = Fiji; FP = French Polynesia; LHI = Lord Howe Islands; NEO = Neotropics; NC = New Caledonia; SEA = South-East Asia; TON = Tonga; VA = Vanuatu.

DISCUSSION

When redefining *Atractocarpus*, a century after its original description, Puttock (1999) and Puttock & Quinn (1999) did not extensively treat the New Caledonian species. The inclusion in our phylogenetic study of a large number of species of *Atractocarpus* and several uncertainly placed New Caledonian *Randia* and *Gardenia* demonstrates the paraphyly of *Atractocarpus* sensu Puttock and the need for a new circumscription of New Caledonian Gardenieae species associated to it in the phylogeny.

Paraphyly of *Atractocarpus* sensu Puttock and consequences

Most of the Gardenieae species restricted to New Caledonia grouped with the New Caledonian *Atractocarpus* species in a NC clade sister to a Lord Howe Island and Australian *Atractocarpus* clade. Several of these species bear an elongated pendulous fruit, the initial characteristic feature for the genus *Atractocarpus*. Most of the *Randia* and *Gardenia* species here placed within the NC clade have unisexual flowers, common in *Atractocarpus*. All have elongated imbricated stipules lacking yellow wax that constitute a diagnostic character of *Atractocarpus* (Guillaumin 1930; Puttock 1999; Mouly 2012).

To recognize only monophyletic lineages, the well-supported tree topology forces us to split *Atractocarpus* sensu Puttock or to lump the New Caledonian *Randia* and four *Gardenia* within it. The internal position of the type species *A. bracteatus* and the relative homogeneity of the representatives included in the lineage, with an available diagnostic feature for the lineage (linear imbricated stipules), support the recognition of a broad concept for the genus *Atractocarpus* (*Atractocarpus* s.l.; fig. 2). This necessitates maintaining the name *Atractocarpus*, the oldest available name, and extending the generic limits to include 12 additional species and 12 novelties. The species newly included under *Atractocarpus* generate few changes in its previous circumscription (see Puttock 1999), such as the corolla lobes possibly shorter than the tube (e.g. in *Gardenia conferta*) and the presence of monoecy or hermaphroditism (e.g. in *Randia pseudoterminalis* Guillaumin).

A broad circumscription of *Atractocarpus* also has the advantage of maintaining the concept of *Atractocarpus* provided by Puttock (1999), including the previously separated genera *Neofranciella*, *Trukia*, and *Sukunia*. Indeed, our new phylogenetic study, using other molecular markers than previous analyses (e.g. Mouly et al. 2014 and Kainulainen et al. 2017) ended in a significantly structured and supported tree topology for *Atractocarpus* and its relatives. Here, we find no support for a closer relationship of *Sukunia* (represented by *A. pentagonioides* on fig. 2) to *Bungarimba* (as in Kainulainen et al. 2017) or of *Sukunia* and *Trukia* (represented by *A. carolinensis* on fig. 2) to *Bungarimba* (as in Mouly et al. 2014).

To split *Atractocarpus* and to delimit several narrow genera makes no sense, as the internal morphological variability of *Atractocarpus* s.l. subclades (clades NC1, NC2 and Australian *Atractocarpus*; fig. 2) is almost similar to the morphological diversity between the subclades. Plus, we have been unable to find morphological synapomorphies to diagnose the different subclades within *Atractocarpus* s.l. (fig. 2). Consequently, we favour the recognition of the lineage called *Atractocarpus* s.l. (fig. 2) enlarged to include several New Caledonian *Randia* and *Gardenia* species.

The tree topology for *Atractocarpus* s.l. is congruent with the geographical distribution and may be a frame for an infra-generic classification. However, the present sampling of species from outside New Caledonia is not sufficient to give a comprehensive view of the morphological variability within the genus. A possible infra-generic delimitation of *Atractocarpus* should be addressed in a further study, due to missing species from Australia, Fiji, and Papua-New Guinea in our phylogenetic sampling.

Emended generic description of *Atractocarpus* s.l.

Accepting a broad concept of *Atractocarpus*, in order to render the taxonomic concept monophyletic, results in a well-diversified lineage with 53 species in the genus (39 included in our phylogeny) and 31 species indigenous to New Caledonia when including the undescribed novelties. *Atractocarpus* becomes the second most species-diverse genus of Rubiaceae in New Caledonia (Munzinger et al. 2020) and one of the most species-rich genera in the tribe Gardenieae in general (Mouly et al. 2014). New Caledonia remains the centre of diversity for *Atractocarpus*, with ca 60% of the species. Following our results, an emended description of *Atractocarpus* is provided and 12 New Caledonian *Randia* and *Gardenia* species are transferred to it.

Atractocarpus Schltr. & K.Krause (Schlechter & Krause 1908); Guillaumin (1930); Puttock (1999); Mouly (2012).

Neofranciella Guillaumin (Guillaumin 1925: 481).

Sulitia Merr. (Merrill 1926: 494).

Trukia Kaneh. (Kanehira 1935: 278).

Sukunia A.C.Sm. (Smith 1936: 136).

Description – Monoecious, dioecious or gynodioecious, thornless, slender, strictly monocaulous, monocaulous with weak reproductive secondary axes or well-branched treelets, sometimes small robust trees. Bark furrowed or smooth; branchlets with irregular, circular to horizontal lenticel protrusions; subrhytidome light- to mid-green. Stipules connate into a long sheath with terminal, intrapetiolar limbs, or intermediately or completely divided into two discrete long imbricate stipules, deciduous in older nodes. Colleters lanceolate or linear, laterally compressed or cylindrical, numerous between the basal part of the stipule and the stem, producing a small quantity of viscid resin. Leaves opposite or 3–4-nate, usually isophyllous, sessile or petiolate; lamina entire, coriaceous to chartaceous; secondary venation brochidodromous, eucamptodromous or cladodromous, occasionally with intersecondary veins; tertiary veins, sometimes irregularly percurrent; tuft, pocket, pit or crypt domatia in primary (and rarely secondary) vein angles or absent. Flowers functionally male and female and dimorphic, or hermaphroditic, pentamerous, pedicellate or sessile, borne in many-flowered thyrsoids, dichasial cymes or triads, rarely solitary, terminal at inception (appearing pseudoaxillary) on main axis or terminal on (occasionally paired) long spindly lateral branches bearing numerous reduced leaves. Hypanthium globular to elongated-inflated, usually smooth or sometimes with ridges continuous with the calyx lobes. Calyx coriaceous or chartaceous; tube cylindrical or tubiform, truncate, or with triangular or linear lobes (rarely spathulate). Corolla pale green in the bud, generally pure white, rarely cream to pale salmon at anthesis, turning brown with age; tube short to elongated, slightly to strongly constricted (urceolate) and thickened at the throat; lobes patent, narrowly ovate to lanceolate, shorter, equalling or longer than the tube. Anthers sessile or on short filaments, linear, more or less medifixed, included in the corolla tube; fertile anthers slightly longer than sterile anthers. Pollen grains single, radially symmetrical, isopolar, 3- to 5-porate; exine reticulate. Style clavate; stigma lobes 2, connate, emarginate, not exserted beyond the throat of the corolla tube. Disc annular. Ovary bilocular with axile placentation; ovules numerous, partially embedded in the placenta. Fruit drupaceous or berry-like drupe, spherical, oblong, fusiform or elongated and cylindrical, crowned by the usually persistent calyx; mesocarp parenchymatous or fibrous; endocarp membranous (drupe berry-like) or bony (drupe). Seeds few to many, lenticular to almost spherical, embedded in a firm placental mass, dark brown. Seed coat with a thin margin around the hilum, dark brown; exotestal cells unthickened or thickened at the inner tangential wall base.

With regard to Puttock's delimitation (1999) of *Atractocarpus*, the main emended characteristics are the sexual system with inclusion of monoecy with hermaphroditic flowers, monocaulous treelets (see Bruy et al. 2018), the corolla lobes shorter than the corolla tube, and the elongated thin cylindrical fruits with fleshy and soft endocarp. Accordingly, there is no clear diagnostic character for the genus within the *Porterandia* group, but the combination of the elongated stipules imbricated in early stages (even fused; fig. 1B) and the corolla tube urceolate (short to elongated) with a constriction at the mouth (fig. 1E) seems sufficient to place a species within the genus as circumscribed here.

New combinations in *Atractocarpus* s.l.

Atractocarpus artensis (Montrouz.) Mouly, **comb. nov.**

Gardenia artensis Montrouz., *Mémoires de l'Académie royale des sciences, belles-lettres et arts de Lyon, section des Sciences* 10: 215. 1860 (Montrouzier 1860) – Type: NEW CALEDONIA • Ile Mack; *Montrouzier 63*; lectotype: P[P00486813], **designated here**; isolectotype: LYJB†.

Atractocarpus baladicus (Montrouz. ex Guillaumin & Beauvis.) Mouly, **comb. nov.**

Gardenia baladica Montrouz. ex Guillaumin & Beauvis., *Annales de la Société Botanique de Lyon* 38: 95. 1914 (Guillaumin & Beauvisage 1914). (replacing name for *Gardenia edulis* Montrouz., *Mémoires de l'Académie royale des sciences, belles-lettres et arts de Lyon, section des Sciences* 10: 215. 1860 (Montrouzier 1860, nom. illeg.)) – Type: NEW CALEDONIA • Ile Art, propre rivulos; Montrouzier *180*; lectotype: MPU[MPU012291], **designated here**.

Atractocarpus brandzeanus (Baill.) Mouly, **comb. nov.**

Randia brandzeana Baill., *Adansonia* 12: 244. 1879 (Baillon 1879) – Type: NEW CALEDONIA • Forêts situées au-dessus de Daaoui de Cro, près de Bourail; 11 Apr. 1869; fr.; *Balansa 1145*; lectotype: P[P00495525], **designated here**; isolectotypes: P[P00645355, P00495526].

Atractocarpus colnettianus (Guillaumin) Mouly, **comb. nov.**

Gardenia colnettiana Guillaumin, *Mémoires du Muséum national d'Histoire naturelle, Nouvelle série, Série B, Botanique* 8: 93. 1957 (Guillaumin 1957) – Type: NEW CALEDONIA • Mt Colnett, forêt mésophile; 1400 m; 13 Sep. 1951; fl.; *Hürlimann 1980*; lectotype: G[G00436232], **designated here**; isolectotypes: L[L0000360], P[P00498773].

Atractocarpus confertus (Guillaumin) Mouly, **comb. nov.**

Gardenia conferta Guillaumin, *Archives botaniques de Caen, Mémoires* 3(5): 5. 1930 (Guillaumin 1930) – Type: NEW CALEDONIA • Port des Batigardendrum (Boulari), Morari; 1870; *Pancher 624*; lectotype: P[P00645356], **designated here**; isolectotypes: P[P00645357, P00645358].

Atractocarpus deplanchei (Vieill. ex Guillaumin) Mouly, **comb. nov.**

Gardenia deplanchei Vieill. ex Guillaumin, *Archives botaniques de Caen, Mémoires* 3(5): 6. 1930 (Guillaumin 1930) – Type: NEW CALEDONIA • Mt Poume, dans les terrains éruptifs; May 1871; *Balansa 3208*; lectotype: P[P00495542], **designated here**; isolectotypes P[P00495540, P00495541].

Atractocarpus mollis (Schltr.) Mouly, **comb. nov.**

Gardenia mollis Schltr., *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Plflanzengeographie* 39: 256. 1906 (Schlechter 1906) – Type: NEW CALEDONIA • Auf den Bergen bei Oubatche; 700 m; 19 Nov. 1902; fl.; *Schlechter 15504*; lectotype: P[P00495530], **designated here**; isolectotypes: B†, BR[BR0000005306718], E[E00438328], HBG[HBG521621], K[K000742999], L[L0057935], LE[LE00017341].

Atractocarpus ngoyensis (Schltr.) Mouly, **comb. nov.**

Gardenia ngoyensis Schltr., *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Plflanzengeographie* 39: 257. 1906 (Schlechter 1906) – Type: NEW CALEDONIA • Auf den Bergen am Ngoye; 200 m; 11 Nov. 1902; fl.; *Schlechter 15268*; lectotype: P[P00486799], **designated here**; isolectotypes: B†, BR[BR0000005306060], HBG[HBG521620], K[K000742998], L[L0057820], LE[LE00017397], M[M0187660], NSW[NSW923246].

Atractocarpus nigricans (Schltr.) Mouly, **comb. nov.**

Randia nigricans Schltr., *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Plflanzengeographie* 39: 258. 1906 (Schlechter 1906) – Type: NEW CALEDONIA • Auf den Bergen bei Oubatche; 700 m; 23 Dec. 1902; fl.; *Schlechter 15546a*; lectotype: P[P00486800], **designated here**; isolectotypes: B†, BR[BR0000005328079], HBG[HBG521093], K[K000742964], LE[LE00017326].

Atractocarpus pancherianus (Guillaumin) Mouly, **comb. nov.**

Randia pancheriana Guillaumin, *Archives botaniques de Caen, Mémoires* 3(5): 10. 1930 (Guillaumin 1930). – Type: NEW CALEDONIA • dans les massifs; fr.; *Pancher 328*; lectotype: P[P00486798], **designated here**; isolectotypes: A[A01154769], L[L0057632], P[P00486796], P[P00486797].

Atractocarpus pseudoterminalis (Guillaumin) Mouly, **comb. nov.**

Randia pseudoterminalis Guillaumin, *Mémoires du Muséum national d'Histoire naturelle, Nouvelle Série, Série B, Botanique* 8: 96. 1957 (Guillaumin 1957). – Type: NEW CALEDONIA • Mt Tchingou; 1250 m; 18 Apr. 1951; fl.; *Hürlimann 1229*; lectotype: P[P00495527], **designated here**; isolectotype: G.

Atractocarpus sezitat (Guillaumin) Mouly, **comb. nov.**

Randia sezitat Guillaumin, *Archives botaniques de Caen, Mémoires* 3(5): 10. 1930 (Guillaumin 1930). – Type: NEW CALEDONIA • Lifou, dans les forêts; July 1869; fr.; *Balansa 2004*; lectotype: P[P00495506], **designated here**; isolectotypes: A[A01154770], HBG[HBG521096], P[P00495507, P00495508].

The tribe Gardenieae in New Caledonia

According to the database FLORICAL (Morat et al. 2012; Munzinger et al. 2020), the family Rubiaceae is represented by 220 species in New Caledonia, to which we can add the 12 undescribed *Atractocarpus* species. The tribe Gardenieae, with 31 *Atractocarpus* species (30 endemic + one native), two endemic *Aidia* species, and three endemic *Gardenia* species, covers 15.5% of the native Rubiaceae diversity of the New Caledonian islands, with 97% of endemism. *Gardenia* species are largely distributed on the main island; *G. urvillei* occurs in lowland sclerophyll forests or rarely bushes, *G. oudiepe* in forested vegetation from sea level to mountain, and *G. aubryi* is common in bushes on ultramafic substrates. The *Aidia* species, *A. congesta* and *A. vieillardii*, are dioecious, presenting sexual dimorphism. They mostly occur in forested environments on the internal mountain chains of the main island, and are both endemic to New Caledonia. These two *Aidia* species do not fall together with the two other *Aidia* species from Asia and Africa included in our study, but appear included within the *Porterandia* group (sensu Mouly et al. 2014). According to this, a specific investigation should be initiated to assess the observed polyphyly of *Aidia* with an appropriate species and geographic sampling. *Atractocarpus* in New Caledonia is adapted to a broad ecological range (Bruy et al. 2018) and occurs in most of the vegetation types, from sea level to the summit of the highest mountain. *Atractocarpus sezitat*, described from New Caledonia, is the sole species of the genus that reaches the Loyalty Islands as well as Vanuatu. All other New Caledonian *Atractocarpus* species are restricted to the archipelago, and several of them are micro-endemic to very narrow areas or specific environments, such as *A. pancherianus* in sclerophyll forests or *A. colnettianus* on the north-eastern mountains. A revision of the genus for New Caledonia is under progress by the first author of the present study.

CONCLUSION

The present study contributes to a better understanding of the genus *Atractocarpus*, based on studies initiated by Puttock & Quinn (1999) and Puttock (1999). The present molecular phylogenetic study allows the establishment of a new circumscription of the genus, with the integration of 12 previously misplaced *Randia* and *Gardenia* species from New Caledonia. Under this new circumscription, the New Caledonian *Atractocarpus* lineage is monophyletic, consisting of 20 described species (12 transferred to the genus in the present study), plus 11 species in need of description. *Atractocarpus* as a whole contains 53 species from the west to central Pacific Islands and Australia, including 11 novelties from New Caledonia and one from French Polynesia. Gardenieae are finally represented by three genera in New Caledonia: *Aidia* with two native species, *Atractocarpus*, and *Gardenia*, both with three native species.

SUPPLEMENTARY FILE

Supplementary file 1 – Specimens used for molecular sequencing.

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