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Expanded generic concepts for *Kermadecia* and *Persoonia*, Proteaceae of New Caledonia and neighboring islands

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Abstract

Proteaceae, the Macadamia nut family, are diverse in New Caledonia with c. 50 species distributed in nine genera in tribes Embothrieae, Macadamieae, Persoonieae, Roupaleae, where they represent an important component of the rainforest and particularly the maquis. The family is also represented by a few species in the neighboring archipelagos of Vanuatu and Fiji, which marks the eastern limit of its distribution in the Pacific. Here we address some issues regarding generic limits within Pacific Proteaceae, using new molecular data and a review of morphology. The generic limits within the tribe Macadamieae have long been problematic, particularly amongst *Kermadecia, Sleumerodendron* and *Turrillia*, which are part of subtribe Gevuininae. Molecular phylogenetics show that they form a monophyletic group while morphological data indicate that they are only weakly differentiated. We conclude that they are better treated as a single genus, *Kermadecia*, as has been done previously, with eight species. *Kermadecia elliptica* is placed in synonymy under *K. rotundifolia* for the first time and several names in the genus are lectotypified. As previously observed, we found that the New Caledonian endemic *Garnieria spathulifolia* is nested in *Persoonia* (tribe Persoonieae) from which it differs only by the number of ovules, and is therefore transferred to it and a lectotype is designated.

Key Words: endemic, Fiji, New Caledonia, systematics, Vanuatu.

Introduction

Proteaceae are represented in New Caledonia by a rich and unique assemblage of 9 genera and c. 50 species that are all endemic to the archipelago (Jaffré et al. 2001; Morat et al. 2012). Until recently, few alterations to the list of species had been made since their last complete revision published as volume two of the series Flore de la Nouvelle-Calédonie (Virot 1968). Subsequent taxonomic work included the transfer of the endemic species of *Macadamia* F.Muell. to the new endemic genus *Virotia* L.A.S.Johnson & B.G.Briggs (Johnson and Briggs 1975; Mast et al. 2008). Work has recently been initiated to refresh the taxonomy of the family to prepare its evaluation for the IUCN red list. This work has included the description of a new species in *Kermadecia* Brongn. & Gris (Hopkins and Pillon 2019), another in *Virotia* (Hopkins and Pillon 2020), and a reappraisal of the New Caledonian *Grevillea* R.Br., with ten species recognised instead of three (Majourau and Pillon 2020). In addition, two New Caledonian species of *Knightia* R.Br. have been transferred to a newly reinstated endemic genus, *Eucarpha* (R.Br.) Spach (Mabberley and Moore 2022). In Fiji and Vanuatu, the family is represented by two species in each archipelago, which have had varying generic placements, sometimes associated to New Caledonian taxa.

The three south-western Pacific genera, *Kermadecia* (5 spp., New Caledonia), *Sleumerodendron* Virot (1 sp., New Caledonia) and *Turrillia* A.C.Sm. (3 spp., Vanuatu and Fiji) are closely related members of the Proteaceae, tribe Macadamieae, subtribe Gevuininae (Weston and Barker 2006; Weston 2007). The Gevuininae contains eight genera: *Bleasdalea* F.Muell. ex Domin, *Cardwellia* F.Muell., *Euplassa* Salisb., *Gevuina* Molina, *Hicksbeachia* F.Muell., as well as *Kermadecia*, *Sleumerodendron* Virot, and *Turrillia* A.C.Sm., and according to Weston and Barker (2006) and Sauquet et al. (2009) it is strongly supported as monophyletic. It can be defined within the Macadamieae by the following combination of characters: Plants bisexual with adult leaves alternate. Flower pairs subtended by a scale-like bract, common peduncle of each flower-pair present or absent and flowers pedicellate or sessile, floral bract absent. Perianth zygomorphic (actinomorphic in *Hicksbeachia*), staminal filaments adnate to tepals, hypogynous disc variable. Fruit drupaceous with a hard inner mesocarp and succulent outer mesocarp with radially oriented fibres (dry, follicular in *Cardwellia*). Seed globose to compressed-ellipsoid, not winged (flat, elliptical, winged in *Cardwellia*) (Weston and Barker 2006; Weston 2007).

In the past, the limits of some genera in the Gevuininae have been quite fluid; for example, the Australian species now known as *Bleasdalea bleasdalei* (F.Muell.) A.C.Sm. & J.E.Haas has been placed in no fewer than six other genera at various times, including both *Kermadecia* and *Turrillia*. Because of their similarities, *Kermadecia, Sleumerodendron* and *Turrillia* have quite a complex and intertwined taxonomic history, which is outlined below and summarised in Table 1, with a synopsis

of names, authors, types and synonyms given in the final section. The main part of this paper presents novel molecular data and a review of morphology based on both our own observations and the existing literature for these three genera in order to determine whether the current taxonomy is satisfactory and to clarify generic limits. In the results and discussion, *Kermadecia* s.s. refers to the five species regarded as belonging to this genus at the start of our study, i.e. *K. brinonieae* H.C.Hopkins & Pillon, *K. elliptica* Brongn. & Gris, *K. pronyensis* (Guillaumin) Guillaumin, *K. rotundifolia* Brongn. & Gris and *K. sinuata* Brongn. & Gris; and *Kermadecia* s.s. plus *Sleumerodendron* (*S. austrocaledonica* (Brongn. & Gris) Virot) and *Turrillia* (*T. lutea* (Guillaumin) A.C.Sm. (Vanuatu), *T. ferruginea* (A.C.Sm.) A.C.Sm. (Fiji), *T. vitiensis* (Turrill) A.C.Sm. (Fiji)). Occasionally the term *Kermadecia* p.p. is used to refer to *Kermadecia* s.s. minus *K. pronyensis*.

Another debate regarding generic concepts in Pacific Proteaceae involves *Garnieria* Brongn. & Gris in the tribe Persoonieae and whose taxonomic history is also outlined below. According to Weston and Barker (2006) and Weston (2007), members of Persoonieae are characterised as follows: Bisexual trees or shrubs. Cotyledons elliptic to linear, sessile, semi-circular to triangular in cross-section. Leaves entire. Inflorescence a raceme or spike. Stamens usually monomorphic. Carpel shortly stipitate, ovules 1 - 7. Fruit a drupe, the stony endocarp penetrating between the seeds. Seeds ovoid, not winged. A second aim of the current paper is to present molecular data for *Persoonia* and the related genera *Garnieria, Acidonia* and *Toronia*, with a much shorter discussion of morphology (see Discussion), leading to the formal synonymising of *Garnieria* under *Persoonia* in the Taxonomic section.

Taxonomic history of Kermadecia, Turrillia and Sleumerodendron

Kermadecia was established by Brongniart and Gris (1863) to accommodate their three new species, *K. elliptica, K. rotundifolia,* and *K. sinuata.* In the same publication, they also described *Adenostephanus austrocaledonicus* Brongn. & Gris, which was subsequently transferred to *Kermadecia* by Jackson (1894), based on Bentham and Hooker (1880, see Turner 2016), a move supported by Guillaumin (1935), though he noted that the flowers were still unknown, implying some uncertainty about its generic placement. One reason why Brongniart and Gris (1863) considered that the species they described in *Adenostephanus* and their new genus *Kermadecia* did not fit into genera already known from New Caledonia was the form of the ovules: in each ovary two orthotropous (rather than anatropous) ovules were pendulous from the summit of the locule, with the micropyle oriented downwards.

Kermadecia pronyensis Guillaumin was described in Guillaumin (1922). Initially he placed it in *Grevillea*, transferring it to *Kermadecia* when he recognised that the ovules were pendulous rather than attached to the side of the ovary wall (Guillaumin 1935). In his synoptic flora for New Caledonia, he recognised seven species within *Kermadecia* (Guillaumin 1948), including the four listed above, *K. austrocaledonica* (Brongn. & Gris) Benth. & Hook.f. ex B.D.Jacks. and two taxa (*K. leptophylla* Guillaumin and *K. neurophylla* Guillaumin) that Virot (1968) subsequently placed in *Macadamia* and that are now in *Virotia* (Johnson and Briggs 1975; Mast et al. 2008).

In his treatment for New Caledonia, Virot (1968) regarded *Kermadecia* as consisting of seven species: four from that archipelago (*K. elliptica, K. pronyensis, K. rotundifolia, K. sinuata*) plus the three from Vanuatu and Fiji. These three were originally described in *Kermadecia*, as *K.* vitiensis (Turrill 1915), *K. lutea* (Guillaumin 1932)and *K. ferruginea* (Smith 1936), before being transferred first to *Bleasdalea* by Smith and Haas (1975) and then to *Turrillia* (Smith 1985). Virot (1968) also established the monotypic genus *Sleumerodendron* to accommodate the plant known previously as either *Adenostephanus austrocaledonicus* or *K. austrocaledonica*. He remarked on the similarities of *S. austrocaledonicum* to *Euplassa* and *Gevuina* but did not discuss differences from *Kermadecia* except in the keys to the genera. *Adenostephanus* Klotzsch is now a synonym of the South American genus *Euplassa* (Plana and Prance 2004).

As mentioned above, Smith and Haas (1975) took the three species from Vanuatu and Fiji out of *Kermadecia* and placed them in *Bleasdalea*, alongside *B. papuana* (Diels) Domin from New Guinea, and *B. bleasdalei* from north-east Australia. *Kermadecia* now contained only four species, all from New Caledonia, and *Sleumerodendron* continued to comprise just one.

In his account for Fiji, Smith (1985) established the genus *Turrillia* to replace the name *Bleasdalea*, which he considered was invalidly published. He transferred the five species that he had previously placed in *Bleasdalea* to *Turrillia* but was aware of the lack of clarity at the generic level in this part of the family and discussed several scenarios, including whether the taxa from Australia and New Guinea (*T. bleasdalei* (F. Muell.) A.C.Sm. and *T. papuana* (Diels) A.C.Sm.) might belong to the otherwise South American genus *Gevuina*. In their new classification for the family, Weston and Barker (2006) and Weston (2007) recognised *Kermadecia* and *Sleumerodendron*, with four and one species respectively, as endemic to New Caledonia, and *Turrillia* now comprised only the three species from Vanuatu and Fiji. The Australian and New Guinean taxa that Smith (1985) had placed in *Turrillia* were returned to *Bleasdalea* as the only members of this genus, with *Gevuina* being confirmed as endemic to South America. Recently, a new species of *Kermadecia* was described from New Caledonia (Hopkins and Pillon 2019).

Taxonomic history and phylogenetic background of Garnieria

Labillardière (1804) described the genus *Cenarrhenes* Labill., which initially included only a single species from Tasmania, *C. nitida* Labill. Brongniart & Gris (1865) later described two New Caledonian species in this genus: *C. spathulæfolia* Brongn. & Gris (spelling to be corrected to *C. spathulifolia*, see (article 60.10, Turland et al. 2018) and *C. paniculata* Brongn. & Gris. With additional material, they considered that the first was misplaced and created the new genus *Garnieria* Brongn. & Gris (Brongniart and Gris 1872) to accommodate it. Virot (1968) transferred the second one to another new genus, *Beaupreopsis* Virot. *Beaupreopsis, Cenarrhenes* and *Garnieria* are currently all treated as monotypic genera (Weston 2007).

In his treatment for the flora of New Caledonia, Virot (1968) placed *Beaupreopsis, Beauprea* Brongn. & Gris (12 spp., New Caledonia) and *Garnieria* together in the subfamily Persoonioideae, without mentioning any genera outside New Caledonia, particularly *Persoonia* Sm. Later Johnson and Briggs (1975) moved *Beaupreopsis* and *Beauprea* to subfamily Proteoideae and placed *Garnieria* in subfamily Persoonioideae, tribe Persoonieae, subtribe Persooniinae, along with *Persoonia* and three novel monotypic genera segregated from it: *Acidonia* L.A.S.Johnson & Briggs, *Pycnonia* L.A.S.Johnson & Briggs, and *Toronia* L.A.S.Johnson & Briggs. Weston (1994; 1995a) subsumed *Pycnonia* back into *Persoonia* but retained *Acidonia* as distinct. Thus, according to the taxonomic scheme of Weston (2007), the tribe Persoonieae includes the widespread Australian genus *Persoonia* (c. 100 species) and three monotypic genera: *Acidonia* (south-western Australia), *Garnieria* (New Caledonia), and *Toronia* (New Zealand).

The molecular phylogenetic analysis by Sauquet et al. (2009) recovered a monophyletic group in which *Placospermum* C.T.White & W.D.Francis (1 sp., Australia), in subfamily Persoonioideae, tribe Placospermeae (Weston 2007) is sister to *Toronia* (*Persoonia* (*Acidonia* + *Garnieria*)) (=tribe Persoonieae). However, in a well-sampled molecular phylogenetic analysis of *Persoonia* (93 out of 101 species), Holmes et al. (2018) found that it was paraphyletic, with *Toronia*, as well as *Acidonia* and *Garnieria* nested within it. They nevertheless refrained from subsuming these three monotypic genera into *Persoonia*, although acknowledging *Persoonia* would be a "highly corroborated, easily identified clade" if these three were included.

Material and Methods

Molecular phylogenetics

DNA extraction, amplification, cloning and sequencing

We collected samples of *Kermadecia sinuata, K. rotundifolia* and *Garnieria spathulifolia* (Brongn. & Gris) Brongn. & Gris from the field and from the Herbarium of New Caledonia (NOU, Bruy et al. 2022). We extracted total genomic DNA from silica-dried leaves following a modified cetyltrimethylammonium bromide (CTAB) protocol (Doyle and Doyle 1987).

We amplified four plastid genes and three nuclear regions for *Kermadecia* species with the following primers: ATP synthase subunit beta (*atpB*) with the primers rbcL1pro and S766RProt (Mast et al. 2005) and the internal primers S611 and S1494R (Hoot et al. 1995); NADH dehydrogenase F (*ndhF*) with -52pro, 972Rpro, 972Fgre, and 2100Rgre from Mast et al. (2008); maturase K (*matK*) with matK1F from Sang et al. (1997) and trnK2R from Hu et al. (2000); ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (*rbcL*) with rbcL1F, rbcL724R, rbcL636F (Fay et al. 1997) and rbcL1460R (Olmstead et al. 1992); phytochrome A-like (*PHYA*) with PHYA_34F and PHYA_1159R from Mast et al. (2008); the internal transcribed spacer 1, 5.8S ribosomal RNA gene and internal transcribed spacer 2 (ITS region) with ITSP1L and ITSP2R from Barker et al. (2002); and the exons 7 through 10 at the *waxy* loci with waxy_7bFpro and waxy_10Rpro from Mast et al. (2005).

For *Garnieria spathulifolia*, we amplified two molecular markers: the nuclear DNA internal transcribed spacer (ITS) region including ITS-1, 5.8S and ITS2 and the chloroplast *trn*L-F region including the *trn*L intron , *trn*L (UAA) 3' exon and the *trn*L-*trn*F intergenic spacer using the primers P1L/P2R designed by Barker et al. (2002) and the primers c/d and e/f designed by Taberlet et al. (1991) respectively.

The PCR amplification program consisted of 5 min of initial denaturation at 80 °C, followed by 30 cycles of 1 min denaturation at 95 °C, 1 min of annealing at 50 °C, 1 min 30 elongation at 65 °C; and a final hold of 4 min at 65 °C. We separated the *waxy* PCR product by electrophoresis on 2% (w/v) agarose gel and excised the resulting band. We cleaned it up with QIAquick [®]Gel Extraction Kit (Qiagen) and we cloned the purified fragment in pGEM[®]-T Easy vector (Promega Corp.) according to the manufacturer's instructions.

Purification and bidirectional sequencing were carried out by an external service (Genoscreen, Lille, France) on an automated sequencer using BigDye Terminator V3.1 reagents. In ITS PCR product of *Garnieria*, we coded as per the IUPAC nucleotide ambiguity scheme (Cornish-Bowden 1985) for the sites which had double peaks. The sequences were edited in MEGA X (Kumar et al. 2018), aligned using MUSCLE (Edgar 2004) and cleaned from problematic alignment blocks using Gblocks 0.91 (Castresana 2000) using the less stringent options set.

The list of accessions with voucher information and Genbank accession numbers for the Gevuininae dataset is provided in supplemental data online. A collection (*Weston 1639*), with a sequence previously published under the name *K. elliptica* is here re-identified as *K*. cf. brinoniae.

These two species were previously confused and *K. brinoniae* was described several years after the Weston collection was first identified (Hopkins and Pillon 2019). The four sheets of *Weston 1639* from Mont Koghis at NSW are all juvenile foliage and do not allow a firm identification at species-level, but *K. brinoniae* is the only species of *Kermadecia* s.s. that has previously been collected in this area. Our sampling of Gevuininae contains all the species we currently recognise (see taxonomic section) in New Caledonia and Vanuatu, but neither of the two Fijian species. *Virotia* and *Athertonia* L.A.S.Johnson & B.G.Briggs (subtribe Virotiinae) were used as outgroups. For the Persoonieae, a single new accession (*Garnieria spathulifolia, Pillon & Isnard 1505*, ITS: OP942404, *trnL*-F region: OP933395) was added to the dataset of Holmes et al. (2018). *Bellendena* R.Br. (subfamily Bellendenoideae) and *Placospermum* (subfamily Persoonioideae tribe Placospermeae) were used as outgroups.

Phylogenetic analysis

We conducted phylogenetic analyses using Bayesian inference. The best substitution models for each DNA regions were determined using jModelTest version 2.1.6 (Darriba et al. 2012) setting *Akaike's information criterion (AIC)*. Then, we combined these models in Mr Bayes v. 3.2.7 (Ronquist and Huelsenbeck 2003) linking the branch lengths but not the sampling of character-state frequencies, substitution rates, the gamma shape parameter and the proportion of invariant sites. We performed Markov chain Monte Carlo (MCMC) analysis for 5 million generations with eight chains, sampling every 1000th generation. We assessed convergence of runs by examining the ESS of parameters under Tracer v.1.7 (Rambaut et al. 2018), using the recommended threshold of 200 (Drummond et al. 2006). We generated majority-rule consensus trees discarding a burn-in fraction of 25%.

Morphological observations

All material of *Kermadecia* s.l. at P (Le Bras et al. 2017) and K was seen by us, plus some at NOU (Bruy et al. 2022) and BM. Images of types in other herbaria were studied using Jstor Global Plants (2023) and databases for some individual herbaria, located using Index Herbariorum (Thiers et al. continuously updated). In the morphological section, characters for *K. elliptica* are included in *K. rotundifolia* and the reasons for this are discussed in the Taxonomic section. In the synopsis of names, authors, synonyms and types for *Kermadecia* s.s., *Sleumerodendron* and *Turrillia*, publication details for species names were taken initially from the International Plant Names Index (IPNI 2022) and the Australian Plant Names Index (APNI 2022) and verified by us.

Typification

Several names are lectotypified below, in accordance with the International Code of Nomenclature (article 9, Turland et al. 2018) if the original author(s) of a name did not specify a holotype in the protologue. In these cases, the details of the type as cited in the protologue are quoted although this is not done for names already lectotypified or with a holotype. In three cases where the original author mentioned a single collection in the protologue, or mentioned a single gathering as the "typus", Smith and Haas (1975) stated that the holotype of the name was at a particular herbarium and referred to the duplicates at other herbaria as isotypes. Under ICN Art. 9.10, on the correction of a misused term, we have changed the status of their "holotypes" to lectotypes. In one instance, a second step lectotypification is required because the material designated as the holotype by Smith and Haas consists of two sheets.

Five of the names discussed in the taxonomic section were published by Brongniart and Gris based on material collected by Eugène Vieillard in New Caledonia between 1855 and 1860. The numbering and labelling of Vieillard's collections are notoriously complex as each of his numbers generally refers to what he thought was a species rather than to an individual gathering, and so material he collected from different localities and on different dates can all have the same number. Furthermore, when duplicates were distributed, material from different gatherings may sometimes have become muddled and handwritten data were not always copied accurately nor completely. This applies particularly to Vieillard's later collections (1861 – 1867) rather than to those dated 1855 – 1860. While it is usually clear which material at P was used by Brongniart and Gris for their descriptions of the species discussed here, comparison between specimens housed in different herbaria is not straightforward and many sheets outside P that were labelled as isotypes during the 20th century are unlikely to be part of the original material. Barcodes are given here for sheets that are known or thought likely to be part of the type and most but not all remaining sheets with the same number are mentioned by herbarium abbreviation only, although a few may eventually prove to be isolectotypes.

Results

Molecular phylogenetics

No major conflicts were observed between tree topologies (i.e. no strongly supported conflicting nodes) recovered in individual gene analyses. We obtained a combined matrix of 14 terminals and 9,942 sites for the Gevuininae (with 18% of gaps) and a combined matrix of 85 terminals and 1,405 sites for the Persoonieae. In our Bayesian phylogenetic analyses, convergence of runs is obtained

with all parameters ESS values \geq 200. In the majority-rule consensus tree of Gevuininae (Figure 1) inferred from *atpB*, ITS, *matK*, *ndhF*, *PHYA*, *rbcL* and *waxy*, *Kermadecia* s.s. is a strongly supported (PP=1) monophyletic clade, with *Turrillia*, *Sleumerodendron* and *Euplassa* each recovered as successive sister taxon with strong support.

In the majority-rule consensus tree of Persoonieae (Figure 2) inferred from DNA ITS and *trn*L-F sequences, this subfamily is recovered as a strongly supported monophyletic clade (PP=1). The genus *Persoonia* is paraphyletic with the monotypic *Acidonia, Garnieria,* and *Toronia* nested in it. *Toronia toru* (A.Cunn.) L.A.S.Johnson & B.G.Briggs is recovered as sister to the Rufiflora group (sensu Weston 1995a) with moderate support (PP=0.94) whereas *Acidonia microcarpa* (R.Br.) L.A.S.Johnson & B.G.Briggs is placed as sister to the Quinquenervis group with weak support (PP=0.83). The intraindividual polymorphism in the ITS sequence of *Garnieria* (represented by several terminals, labelled A1, A2, and A3 for one accession) affects the phylogenetic placement of our sample (PP=0.84). *Garnieria* is unresolved at a basal node along with *Persoonia* species (PP=0.86).

Morphology in Kermadecia, Turrillia and Sleumerodendron

The results of the literature review and our own observations are summarised in Table 2 and a selection of specimens that demonstrate these characters given in Appendix 2. Some of the characters described below were illustrated in Smith and Haas (1975, figs. 1–12 & 36–51) and Figure 3.

1. Leaves and indumentum. Leaves of mature plants are simple in all species except *T. vitiensis* and sometimes *T. lutea*, in which they are imparipinnate. In *Kermadecia* s.s. and *T. ferruginea* the blades are relatively broad and the margins not or rarely toothed (*T. vitiensis*), though frequently slightly sinuate, misshapen or damaged. The leaves of *Sleumerodendron* have comparatively narrow blades and entire margins, and those of *T. lutea* are narrowly ovate and entire or rarely coarsely toothed. Juvenile leaves of *Sleumerodendron* and *Kermadecia* are apparently difficult to distinguish (Virot 1968).

Ferruginous indumentum is characteristic in several species, and white or grey indumentum in others. The trichomes vary from minute, curled structures to longer, straight or curved ones. Indumentum is commonly but not universally present on the leaves and young vegetative axes, on the inflorescence axes and outer surface of the perianth, and on the ovary.

2. Inflorescences and flowers. Inflorescences are raminascent (i.e. borne on the branches, proximal to the leaves), axillary or in pseudo-terminal groups. Although many appear axillary when mature,

they probably, at least sometimes, originate from supra-axillary buds. In *Turrillia ferruginea*, occasionally several axes arise in series in a single leaf axil. When the inflorescence is a pseudo-terminal group, a number of lateral axes are borne towards the end of a shoot, distal to the leaves, and the shoot's apical bud is dormant; each axis has a scar at the base from a fugacious bract, except for the most proximal axes that may be in leaf axils.

In all species, the flowers are arranged in pairs (or very exceptionally singly) along almost the full length of the main inflorescence axis; flower-pairs are organised irregularly or are sometimes opposite. Each main axis is usually unbranched except for the flower-pairs, and racemose (most species) or forming a panicle of racemes in *K. rotundifolia* and occasionally in *K. sinuata* and *T. lutea*. Weston (2007) used the term conflorescence (i.e. a compound inflorescence consisting of two or more unit inflorescences, in which the main axis does not end in a flower but the axes of the branches do so, McCusker 2007). In Table 2, the main axis of each inflorescence is classified as either robust or slender according to species.

Floral characters were outlined in the keys and descriptions of Virot (1968), Smith (1975; 1985) and Weston (2007). In the species of *Kermadecia* s.s. except *K. pronyensis*, (i.e. *Kermadecia* p.p.) each flower is borne on a comparatively long, slender, free pedicel (rarely a few flowers are single or the pedicels are fused in pairs). These pedicels are arranged in collateral pairs (Figure 3a), each subtended by a small free bract, or the bracts are fused into a single structure that may have a bifurcate tip. The apex of each pedicel is unequal so the base of the flower is oblique. The hypogynous disc at the base of the ovary is semi-circular to crescent-shaped, well developed on the anterior side where pedicel is shorter and absent on the posterior side (Figure 3b – d). All four tepals are either curved back or rolled up at, or soon after, anthesis. In *K. sinuata* the stiffness of the perianth appears to prevent the tepals from rolling up.

In *Turrillia, Sleumerodendron* and *K. pronynensis*, the flowers are sessile in pairs on a comparatively short, broad peduncle (especially short in *K. pronyensis*) (Figure 3g, I, q), which is sometimes grooved down the centre (very rarely a few flowers per inflorescence are borne on free pedicels). Each peduncle has a small, fugacious bract or its scar at the base. The apex of the peduncle is acute, with one flower inserted on either side, attached obliquely on its asymmetric base. Plotting whether the flowers are sessile or pedicellate onto the phylogeny for the clade formed by *Kermadecia* s.s., *Sleumerodendron, Turrillia*, and *Euplassa*, suggests that sessile flowers on short peduncles is plesiomorphic, with the longer, free pedicels in *Kermadecia* p.p. derived from this arrangement. In *Turrillia* and *K. pronyensis*, the disc is also a shield-like or crescent-shaped structure on the anterior side of the flower, extending $\frac{1}{2}$ ($\frac{3}{4}$) way round the base of the ovary (Figure 3h – j, m – o). In contrast, in *Sleumerodendron*, the disc consists of four minute, free lobes (Figure 3r).

Rao (1967) described the disc of "*Kermadecia* sp." as having the two anterior (sic) lobes suppressed and the two posterior ones connate to form a two-lobed, crescent-like gland, with no vestigial remnant of the suppressed parts. However, anterior and posterior are reversed in his description compared with their use here. According to Smith and Haas (1975), the disc of *Kermadecia* s.s. is formed of three fused glands and that of *Turrillia* (as *Bleasdalea*) by only two, although they included additional taxa in *Bleasdalea*. At \times 10, the discs of *Kermadecia* s.s. and *Turrillia* appear quite similar in our observations. The number of lobes forming the disc in *Kermadecia* p.p. needs confirmation from developmental studies.

In *Turrillia, Sleumerodendron* and *K. pronyensis*, two adjacent tepals, one from each flower of a pair (the dorsal perianth segment according to Smith and Haas 1975), have a tendency to remain erect at or immediately post anthesis, while the remaining three tepals per flower are recurved or rolled back, though this is more apparent in some specimens than others.

In all three genera the ovary is relatively narrow; according to Virot (1968) it is quadrangulartrapezoid in section in *Kermadecia* p.p. but not angular in *K. pronyensis* and *Sleumerodendron*. In all species it narrows gradually but only slightly into a long style, which is either straight and erect or curved away from the mid-line of the flower-pair. The style is stiff and straight in *K. sinuata*, which has the largest flowers, and most curved in *Sleumerodendron*, in which the flowers are relatively small and delicate, but whereas some variation is species specific, some may be due to the age of the flower or the speed of drying. Smith and Haas (1975) reported the orientation of the ovary as diagonal in *Kermadecia* s.s. and antero-posterior in *Sleumerodendron* and *Turrillia* (as *Bleasdalea*), but this is difficult to confirm and again anatomical studies are required.

The distal 1 – 2 mm of the style forms a pollen presenter that is usually papillose, often expanded and either barrel-shaped or slightly splayed on the downward-facing surface (not expanded in *K. sinuata* and scarcely expanded in *T. vitiensis*, though this may depend on the floral stage). According to Ladd (1994), the pollen presenter is of the same type in *Turrillia* and *Kermadecia* s.s. In *T. lutea* at least, the stigma appears to be a minute pore at the very tip of the style though some species have lateral or ventral stigmas (Weston 2007). The structure and functioning of the pollen presenters and the position of the stigmas in the related genera *Gevuina* and *Euplassa* were described in Prance et al. (2007).

The flowers of several species are brown or brownish on the outer surface, from the dense indumentum, and commonly yellowish, cream-colored or sometimes pale green on the inner surface, with the style often green. *Turrillia lutea* and *T. vitiensis* both have bright yellow flowers. *S. austrocaledonicum* is the only species in this group in which the tepals are dark purple or violet on the outer surface, with yellow-green tips and purple on the inner surface, though again style is

green; this coloration suggests a different pollinator from that of *Kermadecia* s.s. In Fiji, *T. lutea* is reported to be visited by birds (field notes of *Wheatley 767*).

3. Fruits. In all three genera, the fruits are woody, indehiscent and drupaceous, and scarcely to moderately laterally compressed. Weston and Crisp (1996) suggested they were likely to be dispersed by bats. Although the ovaries of several species have dense indumentum, mature fruits are glabrous. Probably all fruits contain a single seed: see Virot (1968) for *Kermadecia* s.s., Smith and Haas (1975) for *Turrillia* (as *Bleasdalea*). Small differences in fruit shape and degree of fissuring of the fruit-wall occur. The species of *Kermadecia* p.p. have similar fruits that are inequilateral in lateral view, somewhat ellipsoidal, obovoid or gibbous, with the dorsal side more developed than the ventral one (Figure 3e – f). The dorsal margin is either slightly angled distally or rounded (*K. sinuata*), and the base is cuneate with the attachment scar central or somewhat lateral. Towards the apex the fruit is blunt or obtuse and the style base forms a small mucro positioned slightly towards the ventral margin. In ventral view the fruits are elliptic and in cross-section, somewhat trullate and slightly angled, especially along the dorsal line (see fig. 4 in Smith and Haas (1975), *K. brinoniae*, as *K. elliptica*, based on *MacKee 16339*). In dry fruits of this species the fruit-wall has a tendency to be corrugated and occasional fissures can develop; in the other species of *Kermadecia* p.p., the fruit-wall is almost smooth when mature.

In *Sleumerodendron*, the fruits are sub-circular lateral view, slightly inequilateral and better developed on the dorsal side (Figure 3 s – t). Young fruits can be \pm globose, but most mature fruits are slightly flattened laterally so that in ventral view they are elliptic to \pm broadly elliptic, and in cross-section, oblong-elliptic to almost circular and not angled along the dorsal line. The basal attachment scar is at the lowest point and slightly asymmetrically placed. The apex is \pm round with the mucro small or absent. In dry fruits, the fruit-wall has numerous deep fissures, revealing that the outer layer of the mesocarp is composed of short fibres perpendicular to the surface (Smith and Haas 1975, fig. 8).

The fruits of *Turrillia* are more variable. In lateral view they are \pm rhomboidal, almost circular but slightly gibbous, obovate/obtrullate, or turbinate (see illustration for *T. vitiensis* in Gillespie 1932) and often inequilateral (Figure 3p). Distally, many have an umbo positioned either centrally or towards the dorsal margin, with the style-base at its apex. The base is cuneate to broadly cuneate and the attachment scar \pm oblique or not. In ventral view they are ovate, broadly ovate or obovate and in transverse section elliptic or broadly elliptic, and not especially angled along the dorsal line. In dry fruit, the fruit-wall is stony-woody and its surface is \pm smooth, usually without fissures, though occasionally old fruits have a few cracks that may be the result of the drying process (e.g. perhaps in

F.D. 1031, T. vitiensis). Exceptionally the fruit-wall starts to develop cracks that resemble those of *Sleumerodendron*, as in *Raynal RSNH 16338* (*T. lutea*).

The fruits of *K. pronyensis*, based on *Franc 1912a* (P00607473), *Veillon 5223* (P02363771) and *Dumontet et al. 686* (P02785695), are ovate-rhomboidal in lateral view and thus somewhat resemble those of *T. ferruginea* (e.g. *Smith 8227, Smith 8797*) (Figure 3k).

Smith and Haas (1975) described the endocarps as follows: *Kermadecia*: 4 angled, 1 - 4 mm thick; *Sleumerodendron*: bony, 6 mm thick; *Turrillia* (as *Bleasdalea*): bony, 1.5 - 3.5 (-5) mm thick.

Discussion

Kermadecia, Turrillia and Sleumerodendron – how many genera should be recognised?

Comparisons of *Kermadecia* s.s., *Sleumerodendron* and *Turrillia* (sometimes as *Bleasdalea*) based on the generic descriptions of Virot (1968), Smith and Haas (1975) and Weston (2007), on characters from the keys in these publications, and on our observations, show that *Kermadecia* s.s. overlaps with the other two in significant characters, especially of the flowers and their arrangement. Because of the heterogeneity in floral arrangement in *Kermadecia* s.s., the genus keys out twice in Weston (2007) and having sessile flowers in pairs on short peduncles places *K. pronyensis* with *Turrillia* and *Sleumerodendron*. Although little fruiting material of *K. pronyensis* is available (none at K and only three sheets at P), as noted above, the fruits of this species are markedly similar to those of *T. ferruginea* and differ somewhat from those of the remaining species of *Kermadecia* s.s. If *K. pronyensis* remains in *Kermadecia* s.s. then *Turrillia* must also be included because no characters would strongly differentiate between them (Tables 2 & 3). The phylogeny also supports this conclusion because *K. pronyensis* is sister to the other species of *Kermadecia* s.s.

The position of *Sleumerodendron*, as sister to the subclade formed by *Kermadecia* s.s. + *Turrillia lutea* (Figure 1), is somewhat different because it has several distinctive characters, including its floral disc (4 small, free lobes), the deep fissuring of the fruit wall, and its purple, more delicate flowers. A case could be made either for uniting it with *Kermadecia* s.s. + *Turrillia*, which would make the resulting genus more heteromorphic, or for maintaining it as a monotypic genus. One factor to consider in deciding the fate of *Sleumerodendron* must be how narrowly or broadly other genera in the Gevuininae are circumscribed and whether *Kermadecia* s.l., including both *Turrillia* and *Sleumerodendron*, would be markedly more heteromorphic than the remaining genera in the subtribe. A second factor is what morphological characters would define an expanded *Kermadecia* s.s. + *Turrillia* if *Sleumerodendron* was also included.

The distinguishing characters of the genera in Gevuininae are compared in Table 3 and illustrations of all can be found in Flora of Australia (Hyland 1995; Weston 1995b; Weston 1995c),

Flora Neotropica (Pennington 2007; Plana 2007), Flore de la Nouvelle-Calédonie (Virot 1968), Smith and Haas (1975), and Smith (1985). Common characters throughout the subtribe include the gynoecium containing two, pendulous or ± pendulous, orthotropous ovules, the pollen presenter developed, and the carpel orientation anterior-posterior (or perhaps diagonal in *Kermadecia* s.s.) (Weston and Barker 2006; Weston 2007).

The two Australian endemics, *Cardwellia* and *Hicksbeachia*, are both narrowly defined and distinctive. The first differs from all other members of the subtribe by its numerous ovules, winged seeds and follicular fruits. Members of the second are small unbranched trees or multi-stemmed from the ground, with actinomorphic flowers and inflorescences borne on the stems proximal to the leaves (caulinascent). In Figure 1, *Hicksbeachia pinnatifolia* F.Muell. is sister to *Bleasdalea bleasdalei*, also from Australia, and the two differ in floral symmetry and the structure of the floral disc. The two South American genera, *Gevuina* (imparipinnate leaves with relatively small, toothed leaflets) and *Euplassa* (paripinnate leaves with toothed or entire margins), also differ in their floral discs and leaf rachises (see key in Prance et al. 2007). With 20 species, *Euplassa* shows a wider range of variation than any other genus, notably in the form of the floral disc (see Plana 2007, fig. 14).

As noted above, *Sleumerodendron* shares with most species in *Kermadecia* s.s. + *Turrillia* its simple leaves with entire margins and comparatively large globular fruits with fibrous fruit walls. Although its inclusion in a broader *Kermadecia* make the resulting genus more heteromorphic, on balance, we consider it is preferable to include it in *Kermadecia* s.l., and the resulting genus would not encompass a wider range of variation than does *Euplassa*. *Kermadecia* s.l. can be distinguished from other genera of the Gevuininae by the adult foliage consisting largely of simple, entire leaves (or imparipinnate and/or leaflets sparsely serrate in *T. vitiensis* and occasionally in *T. lutea*). *Kermadecia* is the oldest of the three generic names and all the necessary combinations within it already exist.

The circumscription of Persoonia

All combinations for Persoonieae species already exist in the genus *Persoonia*, except for *Garnieria spathulifolia*. This genus has never been critically compared to *Persoonia*, and the only character that appears to distinguish them is the number of ovules (see key in Weston 2007). Virot (1968) wrote that *Garnieria* has 3 - 7 ovules and up to seven seeds per fruit, and Weston (1995a) indicated two ovules in *Acidonia*, and 1 - 2 in *Persoonia*. Otherwise *G. spathulifolia* fits within the variation described for the genus *Persoonia* in Australia (Weston 1995a). A broader concept of *Persoonia*, which would be strongly supported as monophyletic (Figure 2) and that equates to the tribe

Persoonieae seems preferable. A new combination in *Persoonia* is therefore provided below for the species currently in *Garnieria*.

TAXONOMY

KERMADECIA Brongn. & Gris, Bull. Soc. Bot. France 10: 228. 1863.
Lectotype (designated by Brongniart and Gris 1868, see Wilson 1985): K. rotundifolia Brongn. & Gris Sleumerodendron Virot, Fl. Nouv.-Calédonie & Dépend. 2: 101. 1968, syn. nov.
Type: Sleumerodendron austrocaledonicum (Brongn. & Gris) Virot
Turrillia A.C.Sm., Fl. Vit. Nova 3: 753. 1985, syn. nov.
Type (designated by Smith 1985): Turrillia vitiensis (Turrill) A.C.Sm.

Trees. Adult leaves petiolate, simple or imparipinnate (K. vitiensis, sometimes K. lutea), leaf or leaflet margins entire or somewhat sinuous, or occasionally with a few distal teeth (K. vitiensis). Inflorescence (conflorescence fide Weston 2007) lateral (axillary or raminascent) or "terminal" (i.e. distal to the apical leaves), the main axis simple (producing a raceme of flower pairs) or occasionally branched (a panicle of racemes). Flowers in pairs, either borne on free, slender pedicels or sessile on a short, broader peduncle; each pedicel subtended by a bract or bracts of adjacent flowers fused; each peduncle subtended by a fugacious bract. Pedicels unequal at the apex or peduncles acute at the apex and flowers asymmetric at the base; perianth lobes 4, all recurved or curled at or post anthesis or the posterior lobe remaining erect; hypogynous disc semi-annular, crescentic or shieldshaped, well developed on the anterior side of flower where the pedicel or peduncle is shorter and lacking on the posterior side, or of 4 free lobes (K. austrocaledonica); carpel orientation anterioposterior or perhaps sometimes diagonal (fide Smith and Haas 1975); staminal filaments adnate to the tepals; ovules 2 per ovary, pendulous; style straight or curved post anthesis, the distal 2 mm swollen or not, commonly bent over, papillose, forming a pollen presenter; stigma terminal(?), ventral or lateral. Fruits drupaceous, indehiscent, somewhat laterally flattened, in side-view inequilateral, turbinate to ± circular, dorsal margin sometimes slightly to markedly angled, sometimes widest in the distal half, base cuneate with the attachment scar central or slightly oblique, remnant of style-base often persistent as a mucro, located towards the ventral margin; pericarp entire, slightly to deeply fissured (K. austrocaledonica), mesocarp thick and woody, endocarp woody or bony. Seed 1, not winged.

Kermadecia austrocaledonica (Brongn. & Gris) Benth. & Hook.f. ex B.D.Jacks., Index Kew. 2(1): 5. 1894.

(≡) Adenostephanus austrocaledonicus Brongn. & Gris, Bull. Soc. Bot. France 10: 229. 1863.

(≡) *Sleumerodendron austrocaledonicum* (Brongn. & Gris) Virot, Fl. Nouv.-Calédonie & Dépend. 2: 102. 1968.

Type as given in the protologue: "crescit in montibus Novae Caledoniae *Poila* dictis (Vieillard, n° 1109)".

Lectotype (designated here): NEW CALEDONIA, montagne de Poila, 1855 – 1860, *Vieillard 1109* (P00645322!; iso-: P00645323!).

The sheet stated here to be an isolectotype at P (P00645323) resembles the lectotype in both its leaves and phenological state (flowers). Sheets at B (B10 0295559!, *Vieillard s.n.*, 1861 – 1867) and K (K00073959!, *Vieillard 1109*, s. loc., s.dat.) both have mature fruits and lack flowers. They are potentially from the same gathering as each other but they do not match the protologue and so are excluded from being isolectotypes.

Kermadecia brinoniae H.C.Hopkins & Pillon, Candollea 74(1): 86. 2019.

Type: NEW CALEDONIA, Thy River Valley, c. 12 air-km NE of Nouméa [22°14'S 166°32'E], 200 m, 12 Oct. 1979, *McPherson 1945* (holo: P02363286!; iso-: MO, NOU035963!, NOU105020! NSW666095! NSW666097!).

Kermadecia ferruginea A.C.Sm., Bull. Bernice P. Bishop Mus. 141: 48. 1936.

(≡) Bleasdalea ferruginea (A.C.Sm.) A.C.Sm. & Haas, Amer. J. Bot. 62(2): 143. 1975.

(=) *Turrillia ferruginea* (A.C.Sm.) A.C.Sm., Fl. Vit. Nova 3: 757. 1985.

Lectotype (designated by Smith and Haas 1975): FIJI, Taveuni, Mt Manuka, 18 Dec. 1933, *Smith 788* (BISH; iso-: GH00035385!, K000736962!, NY00284768!, P00750555!, S07-11560!, UC, US00107253!, WIS00000249-MAD!).

Kermadecia lutea Guillaumin, J. Arnold Arbor. 13: 86. 1932.

(≡) Bleasdalea lutea (Guillaumin) A.C.Sm. & J. Haas, Amer. J. Bot. 62(2): 147. 1975.

(=) *Turrillia lutea* (Guillaumin) A.C.Sm., Fl. Vit. Nova 3: 754. 1985.

Lectotype (designated by Smith and Haas 1975): [VANUATU], Tanna, Mt Tokosh Meru, 15 March 1928, *Kajewski 167* (A00035386!; iso-: B10 0295483!, BISH, BRI-AQ0317478!, MEL2515330, NY00284769!, P00750567!, US00107254!).

Kermadecia pronyensis (Guillaumin) Guillaumin, Bull. Soc. Bot. France 82: 277. 1935.
(≡) Grevillea pronyensis Guillaumin, Bull. Mus. Natl. Hist. Nat. 28: 104. 1922.
Type as given in the protologue: "[Franc]. Prony, terrains ferrugineux (1921^a)".
Lectotype (designated here): NEW CALEDONIA, Prony, Jan. 1915, Franc 1912a (P00607474!; iso-: BM000915583!, G00341850!, P00607472!, P00607473!).

Kermadecia rotundifolia Brongn. & Gris, Bull. Soc. Bot. France 10: 228. 1863.

Type as given in the protologue: "crescit in silvis montium Novae Caledoniae prope *Balade* (Vieillard, n° 1105)".

Lectotype (designated here): NEW CALEDONIA, Balade, 1855 – 1860, *Vieillard 1105* (P00645098!; iso-: P00645099!, P00645100!; likely isolectotypes: A00035492! HBG-508308!, K000736970!, K000736971!, K001235631!).

(=) *Kermadecia elliptica* Brongn. & Gris, Bull. Soc. Bot. France 10: 228. 1863. **syn. nov.** Lectotype (designated by Hopkins and Pillon 2019): NEW CALEDONIA, Balade, 1855 – 1860, *Vieillard 1104* (P00607467!; iso-: P00607468!).

The only character that distinguishes between *K. elliptica* and *K. rotundifolia* is their inflorescence structure (a simple raceme of flower-pairs vs. a trident of flower-pairs). However, field observations and photographs show that individuals of *K. rotundifolia* can bear both unbranched and branched inflorescences. Branched inflorescences can also be found occasionally in *K. sinuata*. Branching of the main inflorescence axis is therefore not a reliable character on its own to distinguish between *Kermadecia* species. Furthermore, we were unable to find any characters of the foliage that differ consistently between *K. elliptica* and *K. rotundifolia* and so we put the former into the synonymy of the latter here.

It is unlikely that all of the specimens we have seen with the number *Vieillard 1105* belong to the same gathering. The lectotype, with the locality Balade and the date 1855 – 1860, would have been part of the material available to Brongniart and Gris in their publication of 1863 and two of the sheets have Brongniart's writing on them. Amongst the material of *Vieillard 1105* seen at K and online (via Jstor Global Plants), sheets A00035492 and HBG-508308 have the same label data as the lectotype and resemble it morphologically; K000736970 and K000736971 lack original label data but may also be part of this gathering. However, localities given on sheets in various other herbaria include "prope Wagap" or "Wagap – Balade", or they have no locality, and the dates given are 1864 or 1861 – 1865, or they have no date. While some that lack a locality or date may prove to be

isolectotypes, most of these specimens, at B, E, K, G, GH, KFTA, L, MEL, MPU and NY, are unlikely to be so, although close comparison with the sheets at P is required to be certain.

For the name *K. elliptica*, the lectotype and isolectotype at P have labels with the locality Balade and the date 1855 – 1860. Sheets at various other herbaria that are labelled *Vieillard 1104* but which are unlikely to be part of the original material were discussed in Hopkins and Pillon (2019).

Kermadecia sinuata Brongn. & Gris, Bull. Soc. Bot. France 10: 228. 1863.

Type as given in the protologue: "crescit in monte Novae Caledoniae Diane dicto (Vieillard, n° 1103)". Lectotype (designated here): NEW CALEDONIA, montagnes de Diaoué, 1855 – 1860, *Vieillard 1103* (P00645302!; possible iso-: P00645303!, P00645304!).

Three sheets at P have labels with the locality of Diaoué and are dated 1855 – 1860 (lectotype and isolectotypes). Most of the sheets labelled *Vieillard 1103* at A, B, HBG, K, L, MEL, MPU and NY have the date 1861 – 1867 and the locality Wagap; a few lack a locality, or a date, or both; it is doubtful that any of them are part of the original material.

Kermadecia vitiensis Turrill, Hooker's Icon. Pl. 31: t. 3022. 1915; J. Linn. Soc., Bot. 43: 36. 1915.

(≡) Bleasdalea vitiensis (Turrill) A.C.Sm. & J.E.Haas, Amer. J. Bot. 62(2): 144. 1975.

(=) *Turrillia vitiensis* (Turrill) A.C.Sm., Fl. Vit. Nova 3: 755. 1985.

Lectotype (first step lectotypification designated by Smith & Haas (1975: 146), who cited material at K as the holotype; second step designated here): FIJI, [Viti Levu], Nandarivatu, 14 March 1906, *im Thurn 149* (K000736963!, with drawings attached; iso-: B10 0295480!, BM000915584!, K000736964!).

PERSOONIA

PERSOONIA Sm., Trans. Linn. Soc. London 4: 215. 1798.
Type = Persoonia lanceolata Andrews
Linkia Cav., Icon. iv: 61. 1797. nom. rej.
Pentadactylon C.F.Gaertn., Suppl. Carp. 3: 219. 1807.
Type: Pentadactylon angustifolium C.F.Gaertn.
Garnieria Brongn. & Gris, Bull. Soc. Bot. France 18: 189. 1871, syn. nov.
Type: Garnieria spathulifolia (Brongn. & Gris) Brongn. & Gris
Acidonia L.A.S.Johnson & B.G. Briggs, Bot. J. Linn. Soc. 70: 175.1975.
Type: Acidonia microcarpa (R.Br.) L.A.S.Johnson & B.G.Briggs

Pycnonia L.A.S.Johnson & B.G.Briggs, Bot. J. Linn. Soc. 70: 175. 1975.
Type: Pycnonia teretifolia (R.Br.) L.A.S.Johnson & B.G.Briggs
Toronia L.A.S.Johnson & B.G.Briggs, Bot. J. Linn. Soc. 70: 174. 1975.
Type: Toronia toru (A.Cunn.) L.A.S.Johnson & B.G.Briggs

Persoonia spathulifolia (Brongn. & Gris) Pillon, comb. nov. urn:lsid:ipni.org:names:77313102-1
Basionym: Cenarrhenes spathulifolia Brongn. & Gris, Bull. Soc. Bot. France 12: 41. 1865.
Type as given in the protologue: "in montibus prope Kanala (Vieillard, n° 1120)".
Lectotype (designated here): NEW CALEDONIA, Canala, 1855 – 1860, Vieillard 1120 (P00645047!).
Garnieria spathulifolia (Brongn. & Gris) Brongn. & Gris, Bull. Soc. Bot. France 18: 189. 1871.
Cenarrhenes spathulata Pancher & Sebert, Not. Bois Nouv. Caled. 180. 1874. orth. var.

Sheets labelled *Vieillard 1120* at BM, K, MEL, MPU and P (P00645046!, P00645048!) and *Deplanche 1120* (P00645049!) are unlikely to be part of the same gathering as the type material.

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Data availability statement

Novel DNA sequences were submitted to Genbank and full lists of accessions used for the phylogenetic and the morphological studies are provided in the supplemental online material.

Author contributions

KG produced the DNA sequences. YP, HFH and KG wrote the paper.

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Table 1. Generic placement of epithets associated with the name *Kermadecia* according to various authors. ¹Some names are placed in these genera by implication. ²This species was originally described as *Grevillea pronyensis* Guillaumin (Guillaumin 1922). ³This epithet has also been placed in *Adenostephanus, Euplassa, Grevillea, Gevuina, Kermadecia* and *Roupala* Aubl. by various authors. ⁴This epithet has also been placed in *Euplassa* and *Gevuina* by some authors (IPNI 2022) and no combination exists in *Kermadecia. Kermadecia pinnatifida* F.M.Bailey from Australia is not shown here and is a synonym of *Grevillea baileyana* McGill. (Makinson 1999).

epithet	distribution	Brongniart & Gris (1863)	Guillaumin (1935; 1948)	Virot (1968)	Smith & Haas (1975)	Smith (1985)	Weston & Barker (2006); Weston	this study
brinoniae	New Caledonia							Kermadecia
elliptica	New Caledonia	Kermadecia	Kermadecia	Kermadecia	Kermadecia		Kermadecia	Kermadecia
pronyensis ²	New Caledonia		Kermadecia	Kermadecia	Kermadecia		Kermadecia	Kermadecia
sinuata	New Caledonia	Kermadecia	Kermadecia	Kermadecia	Kermadecia		Kermadecia	Kermadecia
rotundifolia	New Caledonia	Kermadecia	Kermadecia	Kermadecia	Kermadecia		Kermadecia	Kermadecia
austrocaledonica	New Caledonia	Adenostephanus	Kermadecia	Sleumerodendron	Sleumerodendron	Sleumerodendron	Sleumerodendron	Kermadecia
lutea	Vanuatu			Kermadecia	Bleasdalea	Turrillia	Turrillia	Kermadecia
ferruginea	Fiji			Kermadecia	Bleasdalea	Turrillia	Turrillia	Kermadecia
vitiensis	Fiji			Kermadecia	Bleasdalea	Turrillia	Turrillia	Kermadecia
bleasdalei ³	Australia				Bleasdalea	Turrillia	Bleasdalea	
papuana ⁴	New Guinea				Bleasdalea	Turrillia	Bleasdalea	
leptophylla	New Caledonia		Kermadecia	Macadamia			Virotia	
neurophylla	New Caledonia		Kermadecia	Macadamia			Virotia	

Table 2. Comparative morphology of the species of Kermadecia s.s., Sleumerodendron and Turrillia. Note that K. elliptica is included in K. rotundifolia.

	adult leaves (near	trichomes ¹	position of	inflorescence structure	flower color	flowers	disc	fruits
	inflorescences)		inflorescence	(main axis)				
K. brinoniae	simple, broadly ovate, entire	small, curled, ferruginous	axillary or raminascent	robust, unbranched	tepals brown or brown-yellow outside, pale yellow inside, style greenish yellow	pedicellate	semi-annular, crescent-shaped	obovate or ± elliptic (inequilateral) in side view, angled distally on dorsal margin, slightly angled in cross-section, style-base towards ventral margin; fruit-wall sometimes with a few irregular fissures; 4.5 – 4.8 x 2 x 2.5 cm
K. rotundifolia	simple, ovate to broadly ovate, sinuate or entire	curled and ferruginous on infl. axes, narrow and ferruginous on ovary	raminascent	robust, unbranched or branched (panicle of racemes)	tepals yellow, ovary pink	pedicellate	semi-annular, crescent-shaped	 elliptic (gibbous to almost semi-circular, inequilateral) in side view, circular to slightly elliptical, sometimes with four angles in cross- section, style-base towards ventral margin; fruit-wall not fissured; 3.3 – 5 x 1.6 x 1.7 – 2.5 cm
K. sinuata	simple, ovate, entire	minute, ferruginous	raminascent	robust, unbranched	tepals pale brown ferruginous outside, gynoecium dull yellow with brown hairs on ovary	pedicellate	semi-annular, crescent-shaped	 ± elliptic (gibbous, inequilateral) in side view, broadest in distal half, ± angular along dorsal line, style-base towards ventral margin; fruit-wall not fissured; 3.6 - 5 x 1.7 - 2 x 1.9 - 2.8 cm
K. pronyensis	simple, ovate, entire	small, curled, ferruginous and some longer, narrow, straw-colored to orange trichomes	axillary	± slender, unbranched	tepals whitish to pale yellow with white pubescence, ovary violet, style green,	sessile	difficult to observe because of hairs on ovary; probably 2 semi- fused anterior glands	 ± rhombic (equilateral) in side view, rostrate at either end, circular or laterally flattened in cross section, style-base ± central; fruit-wall not fissured; 3.8 - 4 x 1.8 - 2 x 2.4 - 3 cm
T. lutea	simple, ovate, or sometimes compound, margins entire or sparsely toothed distally	straight, narrow and ferruginous	axillary or in pseudo- terminal group	± slender, unbranched or occasionally branched	bright yellow, with light green stigma	sessile	2 glands fused into a n anterior 'shield' below the ovary	 ± ovate to circular or inequilateral in side view, almost circular cross-section, style-base ± central; fruit-wall not fissured; 2.5 – 3 x 1.5 – 2 x 2 – 2.6 cm
T. ferruginea	simple, broadly ovate, margins rather irregular, not toothed	curled, ferruginous	axillary or in pseudo- terminal group	± slender, unbranched	brownish outside, pale green inside	sessile	2 glands fused into an anterior 'shield' below the ovary	 ± rhombic (equilateral) in side view, rostrate at either end, elliptic in cross-section, style-base ± central; fruit-wall not fissured; 3 – 3.6 x 1.5 – 1.8 x 2.3 cm
T. vitiensis	imparipinnate, margins entire (rarely coarsely toothed)	small, curved, ferruginous	in pseudo-terminal group	slender, unbranched	bright yellow	sessile	2 glands fused into an anterior 'shield' below the ovary	 turbinate (almost equilateral or inequilateral) in side view, with a small, terminal umbo, elliptic in cross-section, style-base ± central; fruit-wall not fissured; 2.6 - 3.3 x 1.1 - 1.6 x 2.4 - 2.8 cm
S. austrocaledonicum	simple, narrowly ovate, entire	small, straight, grey to almost white	axillary	slender, unbranched	tepals dark blue or purple with dirty yellow tips outside; purple inside, style green	sessile	4 small free lobes	subglobose (slightly inequilateral) in side view, oblong-elliptic to almost circular in cross-section, style-base ± central or absent; fruit-wall with numerous deep fissures; 3.5 x 2.3 x 2.7 cm

Table 3. Comparison of genera in the subtribe Gevuininae (Proteaceae). Data from pers. obs. at K and P plus Hyland (1995 – *Cardwellia*), Pennington (2007 – *Gevuina*), Plana (2007) and Plana & Prance (2004 – *Euplassa*), Smith (1985 – *Turrillia*), Smith & Haas (1975 – *Bleasdalea*, *Turrillia* [as *Bleasdalea*]), Virot (1968 – *Kermadecia* s.s., *Sleumerodendron*), (Weston 1995b – Bleasdalea [as Gevuina]), Weston (1995c – Hicksbeachia), Weston (2007 – all).

	Cardwellia	Gevuina Euplassa		Bleasdalea	Hicksbeachia	Kermadecia s.s.	Turrillia	Sleumerodendron
# species	1	1	20	2	2	4	3	1
geographic	NE Australia	temperate South	tropical and	NE Australia and	E Australia	New Caledonia	Vanuatu and Fiji	New Caledonia
distribution		America	subtropical South America	New Guinea				
growth form	large trees	multi-stemmed	trees or shrubs	trees	monopodial or multi-	trees	trees	tree
		small trees or shrubs			stemmed small trees			
adult leaves	paripinnate; rachis	mostly	paripinnate, rachis	imparipinnate	imparipinnate (rachis	simple	simple or	simple
	not winged	imparipinnate;	with a terminal	(sometimes	not winged) or		imparipinnate but	
		rachis frequently	extension (rarely	simple); rachis	imparipinnately lobed		then rachis not	
		winged	winged	sometimes winged	with rachis winged		winged	
margins of leaf	entire	serrate	entire to remotely	serrate	dentate	entire or sometimes	entire, ± irregular or	entire
or leaflets			serrate			sinuate	sparsely toothed distally	
position of	"terminal"	lateral	lateral (rarely	lateral or	lateral, caulinascent	lateral or "terminal"	lateral or "terminal"	"terminal" or
inflorescence			"terminal")	"terminal"				lateral
flowers sessile or	sessile	sessile	pedicellate or sessile	sessile	sessile	pedicellate (most) or	sessile	sessile
pedicellate?						sessile (K. pronyensis)		
perianth	zygomorphic	zygomorphic	zygomorphic	zygomorphic	actinomorphic	zygomorphic	zygomorphic	zygomorphic
floral disc	4 free lobes	2 free anterior lobes	4 lobes, free or variously fused, often forming a disc	1 or 2 free lobes	4 free lobes	2? lobes fused anteriorly	2 lobes fused anteriorly	4 free lobes
floral color	cream-white	white, yellowish-	whitish	ferruginous-hairy	maroon outside,	whitish yellow or	pale to golden yellow	purple
		white or greenish		outside, cream	cream to maroon	yellow, sometimes	or ferruginous-hairy	
		white		inside	inside, or pale to dark	brownish outside	outside and green	
		-	-	-	purple	-	inside	-
# ovules	10 - 14	2	2	2	2	2	2	2
fruit	follicular (and seeds winged)	slightly fleshy drupe	nut (rarely drupe)	drupaceous	drupaceous	drupaceous	drupaceous	drupaceous
fruit shape		± spherical to	subglobose to ovoid	globose,	ellipsoidal to ovoid	inequilaterally	inequilaterally	subglobose
		ellipsoid, umbonate		sometimes		obovoid, ventrally	obovoid to globose,	
				umbonate		rounded or	ventrally subacutely	
						subacutely ridged	ridged	
fruit wall deeply fissured?		no	no	no	no	occasionally	no (rarely?)	yes

Figure 1. Majority-rule consensus tree of Gevuininae resulting from Bayesian analysis of DNA *atpB*, *ITS*, *matK*, *ndhF*, *PHYA*, *rbcL* and *waxy* regions. Support values at nodes refer to posterior probabilities (PP).



Figure 2. Majority-rule consensus tree of Persoonieae resulting from Bayesian analysis of DNA ITS and *trn*L-F regions. Support values at nodes refer to posterior probabilities (PP).



Figure 3. Flowers and fruits in *Kermadecia* s.s., *Turrillia* and *Sleumerodendron*. (a – f) *Kermadecia rotundifolia*: (a) a pair of flowers in bud, each on a free pedicel, (b) base of a flower with 1 tepal remaining, retracted to show the disc, (c - d) face and side view of disc, (e - f) fruit in lateral and end views. (g - k) *Kermadecia pronyensis*: (g) a pair of flowers in bud, each sessile on a short common peduncle, (h) flower pair with a tepal removed to show position of the disc, (i - j) face and side view of disc, (k) fruit in lateral view. (I - p) *Turrillia vitiensis*: (l) a pair of flowers in bud, each sessile on a common peduncle, (m) base of a flower after removal of anterior tepal to show the disc, (n - o) detail of face and side view of disc, (p) fruit in lateral view. (q - t) *Sleumerodendron austrocaledonicum*: (q) a pair of flowers in bud, each sessile on a common peduncle, (r) base of a flowers in bud, each sessile on a common peduncle, (t) fruit in L.S. showing fibres in outer layer and seed. (c, i - j, m - o) tepal scar is indicated by cross hatching, (a, g, l, q) note bases of all flowers are oblique. Voucher material: (a - d) *MacKee 33465*, (e - f) *MacKee 19980*, (g - j) *Weston 1661*, (k) *Veillon 1270*, (l - o) Im *Thurn* s.n., K000736963, (p) Berry L14069, (q - r) *McPherson* 6357, (s - t) *Balansa* 3296. Drawn by Andrew Brown.



Supplemental online material

List of taxa, voucher specimen (herbarium), and GenBank accession numbers for *matK*, *atpB*, *ndhF*, *rbcL*, *PHYA*, *waxy1*, *waxy* 2 and ITS for Gevuininae.

Athertonia diversifolia, P.H. Weston 2760 (NSW), EU642699, EU642729, EU642668, ,EU642760, EU649765, EU649735; _. P.H. Weston 1859 (NSW), _, _, EU676108, _, _, EU642793. Bleasdalea bleasdalei, P. H. Weston 891 (NSW), EU642693, EU642723, EU642662, EU676050, EU642754, EU649759, EU649729, EU642786. Cardwellia sublimis, P. H. Weston 1824 (NSW), EU642688, EU642718, EU642657, DQ875851, EU642749, EU649754, EU649724, EU642777. Euplassa inaequalis, B. Walter 2741 (NY), EU642689, EU642719, EU642658, EU642750, EU649755, EU649725, EU642778; PER029 (PER),____ KX640856,____. Gevuina avellana, E. E. Reed s.n. (UC), EU642694, EU642724, EU642663,_, EU642755, EU649760, EU649730, EU642787; NSW 397516 (NSW), ___, DQ875852, ___, Hicksbeachia pinnatifolia, P. H. Weston 2761 (NSW), EU169636, EU642727, EU642666,_, EU642758, EU649763, EU649733, . Ρ. Η. Weston 2015 (NSW),_,_,EU676115,_,_, EU642790. Ρ. Kermadecia brinoniae, Н. Weston 1639 (NSW), ____, EU642784. Kermadecia pronyensis, P. H. Weston 1661 (NSW), EU642692, EU642722, EU642661,_, EU642753, EU649758, EU649728,_; NSW 232275 (NSW),_,_, EU676116, ____. P. H. Weston 1844 (NSW), ____, EU642783. Kermadecia rotundifolia, Pillon 1171 (NOU), __, OP795727, _, _, OP806851. Kermadecia rotundifolia, Pillon 1500 (NOU), OP675564, OP675562, OP795728, OP795730, OP933393,_,_,OP806852; Kermadecia sinuata, Pillon 1503 (NOU), OP675565,OP675563, OP795729, OP795731, OP933394,_,OP902605,OP806853. Sleumerodendron austrocaledonicum, P. H. Weston 2505 (NSW),EU642690, EU642720, EU642659,_, EU642751, EU649756, EU649726, EU642781. Turrillia lutea, E. A. Brown s.n. (NSW), EU642691, EU642721, EU642660, , EU642752, EU649757, EU649727, EU642782. Virotia neurophylla, P. Kater s.n. (NSW), EU642698, EU642728, EU642667, , EU642759, EU649764, EU649734, EU642791.

List of taxa, voucher specimen (herbarium), and GenBank accession numbers for ITS and *trnL-F* region for *Persoonia* and related genera.

Acidonia microcarpa, PHW2247 (NSW), KX669270, KX669463; Bellendena montana, Duretto M.F. 869 (MEL), KX669271,KX669464; Garnieria spathulifolia, Pintaud J.-C.439b (NSW), KX669273-4 &EU676081, KX669465; Persoonia spathulifolia, Pillon & Isnard 1505 (NOU), OP942404, OP933395; Persoonia acerosa, PHW 3328 (NSW), KX669275, KX669468; P. acicularis, BGB 9479 (NSW), KX669277, KX669471; P. acuminata, DJM 507 (MEL), KX669278, KX669472; P. amaliae, Champion I.G. s.n. (NSW), KX669279, KX669474; ; P. angustiflora, PJ 5851 (NSW), KX669281, KX669475; P. arborea, Jeanes J.A. 1570 (MEL), KX669282, KX669476; P. asperula, Walsh N.G. 6624 (MEL), KX669287, KX669477; P. baeckeoides, Archer B. 2153 (MEL), KX669289, KX669479; P. bargoensis, CLP s.n. (NSW), KX669292, KX669482; P. biglandulosa, PHW 289 (NSW), KX669296, KX669484; P. bowqada, Hancock M. s.n. (NSW), KX669297, KX669485; P. brevifolia, Vaganiance J.A. 220 (MEL), KX669298, _; P. brevifolia, Albrecht D.E. 3696, _, KX669486; P. brevirhachis, PJ 5877 (NSW), KX669299, KX669487; P. comata, Hort F. 3671, KX669310, KX669492; P. chamaepeuce, NGW 6980 (MEL), KX669301, KX669488; P. chamaepitrys, PHW 3337 (MEL), KX669304, KX669491; P. chapmaniana, PHW 2155 (NSW), KX669308, KX669515; P. confertiflora, DJM 499 (MEL), KX669313, KX669495; P. coriacea, PHW 2157 (NSW), KX669314, KX669497; P. cornifolia, DJM 505 (MEL), KX669316, KX669498; P. cymbifolia, PHW 2330 (NSW), KX669319, KX669501; P. dillwynioides, PHW 2317 (NSW), KX669321, KX669502; P. elliptica, PHW 2187 (NSW), KX669322, KX669503; P. falcata, Milne J. 560 (MEL), KX669325, KX669506P. fastigiata, Copeland L.M. 3293 (NSW), KX669327, KX669508; P. filiformis, PHW 2145 (NSW), KX669328, KX669512; P. flexifolia, PHW 2323 (NSW), KX669329, KX669509; P. glaucescens, PHW 3316 (MEL), KX669330, KX669510; P. graminea, Davis R.7426 (MEL), KX669333, KX669513; P. gunnii, Jordan G.J. s.n. (NSW), KX669337, KX669519; P. hakeiformis, PHW 259 (SYD), KX669338, KX669520; P. helix, PGW 1394 (NSW), KX669340, KX669522; P. hindii, PHW 2354 (NSW), KX669341, KX669523; P. hirsuta, PHW 2415 (NSW), KX669342, KX669525; P. isophylla, PHW 2337 (NSW), KX669343, KX669527; P. juniperina, NGW 6811 (MEL), KX669346, KX669530; P. katerae, PHW 2360 (NSW), KX669351, KX669532; P. lanceolata, PHW 2420 (NSW), KX669354, KX669549; P. laurina, PHW 2355 (NSW), KX669355, KX669536; P. leucopogon, Smith B.H. 1419 (MEL), KX669360, KX669537; P. levis, PHW 2352 (NSW), KX669363, KX669539; P. linearis, PHW 2350 (NSW), KX669365, KX669541; P. longifolia, PHW 2114 (NSW), KX669366, KX669543; P. media, NSW 421833 (NSW), KX669369, KX669546; P. microphylla, PHW 1979 (NSW), KX669370, KX669547; P. mollis, PHW 3330 (MEL), KX669381, KX669559; P. muelleri, JGM 196 (NSW), KX669387, KX669563; P. myrtilloides, PHW 3332 (MEL), KX669390, KX669566; P. nutans, CLP s.n. (NSW), KX669392, KX669567; P. oblongata, PHW 2349 (NSW), KX669393, KX669569; P. oxycoccoides, PHW 177 (NSW), KX669396, KX669572; P. pauciflora, PHW 2086 (NSW), KX669397, KX669573; P. pentasticha, Smith B.H. 1085 (MEL), KX669399, KX669516; P. pinifolia, PHW 2338 (NSW), KX669402, KX669574; P. procumbens, DJM 503 (MEL), KX669404, KX669560; P. pungens, Smith B.H. 1828, KX669406, KX669575; P. auinguenervis, PJ 5890 (NSW), KX669411, KX669578; P. recedens, Davies F.E. 1701 (MEL), KX669412, KX669579; P. rigida, Green A. s.n., KX669414, KX669581; P. rufiflora, PHW 2161 (NSW), KX669424, KX669587; P. rudis, Hancock M. s.n. (NSW), KX669422, KX669584; P. saccata, PHW 2180 (NSW), KX669426, KX669588; P. saundersiana, Olde 04/315 (NSW), KX669428, KX669589; P. scabra, Archer 2152 (MEL), KX669429, KX669590; P. sericea, Forster P.J. 23712, _, KX669592; P. sericea, PIF 25162 (MEL), KX669432, _; P. silvatica, Martin D. 1 (MEL), KX669433, KX6669593; P. stradbrokensis, PHW 1070 (NSW), KX669437, KX669596; P. striata, PJ 5856 (NSW), KX669439, KX669599; P. stricta, PHW 2160 (NSW), KX669440, KX669600; P. subtilis, PHW 1558 (NSW), KX669442, KX669601; P. sulcata, PHW2182 (NSW), KX669444, KX669605; P. teretifolia, Archer B. 2366 (MEL), KX669445, KX669608; P. terminalis, PHW 1445 (NSW), , KX669612; P. trinervis, Hort F. 3670 (MEL), KX669449, KX669615; P. tropica, PHW 2112 (NSW), KX669451, KX669616; P. virgata, Forster P.J. 29030 (MEL), KX669453, KX669618; P.

volcanica, Halford D.A. Q9363 (MEL), KX669455, KX669621 *Placospermum coriaceum*, PHW2019 (NSW), KX669353, KX669462; *Toronia toru*, PHW2004 (NSW), KX669461, KX669466. Selection of the material used to score morphological characters for Table 2. NC: New Caledonia, fl.: flower, fr.: fruit.

Kermadecia austrocaledonica: Lam 7206, NC, Forêt des This (P) (fl.); McPherson 6357, NC, Mt Aoupinié (K) (fl.); Balansa 3296, NC (P) (fr.); McPherson 6366, NC, Mt Aoupinié (P) (fr.). K. brinoniae: MacKee 5284, NC, Vallée de Thy (K) (fl.); McPherson 1945, NC, Thy River Valley (P) (fl.); MacKee 16339, NC, Conception (K, P) (fr.). K. ferruginea: Berry 96, Fiji, Viti Levu, Nadaravutu (K) (buds fl.); Smith 8227 (K) (old fl.); Smith 8227, Fiji, Taveuni, Mt Manuka (K) (fr.); Smith 8797, Fiji, Viti Levu, Namosi (K) (fr.). K. lutea: MacKee RSNH 21465, Vanuatu, Santo, Mt Tabwemasana (K) (fl.); Wheatley 767, Vanuatu, Aneityum, Anelgawhat (K) (fl.); MacKee RSNH 21465 (K) (fr.); Morat 5933, Vanuatu, Tanna (P) (fr.); Raynal RSNH 16338, Vanuatu, Espiritu Santo (K) (fr.). K. pronyensis: Veillon 5896, NC, Rivière Bleue (K) (fl.); Weston 1661, NC, Ongoné (K), (fl.); Franc 1912a, NC, Prony (P) (fr.); Veillon 5223, NC, Mt Ongoné (P) (fr.); Dumontet et al. 686, NC, Mt Ongoné (P) (fr.). K. rotundifolia: MacKee 19623, NC, Haute Diahot: Tende (K) (fl.); MacKee 31855, NC, Haute Témala: Poami (P) (fl.); MacKee 40805, NC, Houailou: Neaoua (K) (fl.); Vieillard 1106, NC (K); McPherson et al. 19102, NC, Mt Colnett (P) (fr.); MacKee 19980, NC, Haute Diahot: Tende (P) (fr.); Pillon et al. 1171, NC, Col d'Amieu (NOU) (fr.); Veillon 1504, NC, Ouegoa: Le Cresson (P) (fr.). K. sinuata: Franc 779, NC (K) (fl.); MacKee 12292, NC, Col d'Amieu (K), (fl.); Weston 1673, NC, Col d'Amieu (K) (fl.); MacKee 9862, NC, Haute Poueo (K) (fr.); MacKee 17419, NC, Haute Népoui (K), (fr.); Balansa 2295, NC, Sud de Canala (P) (fr.); Weston 1673 NC (K) (fr.). K. vitiensis: Stauffer 5823, Fiji, Viti Levu, Nadarivatu (K) (fl.); Watkins 753, Fiji, Viti Levu, Nadarivatu (K) (fl.); Berry L14069, Fiji (K) (fr.); F.D. 1031, Fiji, Serua (K) (fr.).