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RESEARCH ARTICLE

Phylogenetic position and reinstatement of *Gayella* (Sapotaceae), a monotypic genus endemic to Chile with an Eocene origin in continental Australia

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Abstract *Pouteria splendens* is the only native species of Sapotaceae in Chile, a species once placed in the monotypic genus *Gayella* and known as *G. valparadisaea*, but for a long time treated as a *Pouteria*. In a phylogenetic analysis, this species was placed in an Australasian clade, not with its presumed relatives in South America. We used Bayesian inference under a relaxed molecular clock in BEAST, nuclear ribosomal DNA (ETS, ITS), the nuclear gene *RPB2*, indel information, and 201 terminals to find the closest relative of *P. splendens* and to estimate the age of the disjunction between Australasia and South America. The taxon has an isolated phylogenetic position, being part of the clade's backbone, and is placed with weak support as sister to *Van-royena*, another monotypic genus, but endemic to Australia. Our results justify reinstatement of *Gayella* with its single species *G. valparadisaea*. *Gayella* has a unique combination of morphological features including alternate, opposite or 3-whorled leaves, often on the same plant, a usually 6-lobed, rotate corolla with revolute corolla lobes giving the flower a star-like appearance, lacerate to dentate staminodes, and yellow-orange-red fruit with plano-convex cotyledons and an exserted radicle below the cotyledon commissure. The split between *Gayella* and *Van-royena* is estimated to the late Eocene at about 40.0 Ma (50.5–25.3 Ma). The hypothesis that the presence of *Gayella* in South America is a result of vicariance is consistent with the timing of the geological splits of southern Gondwana, as well as with evidence from fossil pollen, but long-distance dispersal is an alternative explanation that cannot be excluded. *Gayella* is restricted to an area with a Mediterranean-type climate in coastal central Chile, where it occurs in rocky places, ravines, and gullies, usually below 100 m altitude within reach of sea mist. *Gayella valparadisaea* is a rare plant, listed as Endangered (EN) in Chile, but it does not occur in any protected area. Considering the isolated phylogenetic position of this old lineage, we urge the Chilean authorities to increase the efforts towards protection of this species.

Keywords Bayesian inference; Chrysophylloideae; dated phylogeny; molecular data; taxonomy

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

Sapotaceae is a pantropical family comprising some 1300 species of shrubs, understorey and canopy trees. Various systems based on morphology alone have adopted between 53 (Pennington, 1991) and 125 genera (Aubréville, 1964). However, molecular phylogenetics, often with support from morphology, have identified natural lineages in this family (Anderberg & Swenson, 2003; Bartish & al., 2005; Swenson & Anderberg, 2005; Swenson & al., 2008a, 2013; Faria & al., 2017; Borg & al., 2019), and 72 genera are currently accepted, of which 20 have been reinstated from Pennington's broad concepts (Swenson & al., 2023). This number will inevitably increase with further research.

Chrysophylloideae is one of three subfamilies of Sapotaceae, distributed in all tropical parts of the world, and including some 650–700 species in 43+ genera (Swenson & al., 2023). A recent phylogenetic study of New World Chrysophylloideae, including 123 terminals of which 40 have been (or still are) placed in *Pouteria* Aubl. (Pennington, 1990), was designed to test generic limits in the presumed monophyletic group of Neotropical species (Swenson & al., 2023). Sampling of Australasian taxa was therefore not an issue and instead limited to one species each of the recognized genera, i.e., eight type

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species and *Magodendron mennyae* Vink. However, surprisingly, the Chilean endemic *Pouteria splendens* (A.DC.) Kuntze was nested with strong support in the Australasian clade. Phylogenetic affinity of a South American species with taxa from the other side of the Pacific was so astounding that leaf material was sequenced again from scratch, only to yield identical molecular sequences. Discovery of *P. splendens* being part of the Australasian clade raises several interesting questions such as: (1) which taxon is its closest relative, (2) how should it be handled taxonomically, and (3) how old is this trans-Pacific disjunction?

This Chilean plant was one of five species originally described in the genus *Lucuma* Molina (Molina, 1782). Juan Ignacio Molina (1740–1829), born in Chile when this was part of the Spanish Empire, was educated within Jesuit establishments (Thulin & al., 2021). However, by decree of Charles III of Spain, all Jesuits were expelled from Chile and other Spanish territories (Ronan, 2002). Molina had to leave Chile for Italy in 1768 and all his notes and other materials were confiscated, although most of his notes and papers were later returned to him in Italy. Molina's species of *Lucuma* have later been shown to be members of three unrelated families: Fabaceae, Gomortegaceae and Sapotaceae (Thulin & al., 2021). Two of these species were *L. bifera* Molina and *L. valparadisaea* Molina, of which the former was selected as the type of *Lucuma* (Britton & Millspaugh, 1920) and the generic name became attributed to Sapotaceae. These two and many other species originally described in *Lucuma* have for decades been included in *Pouteria* (Baehni, 1942, 1965; Pennington, 1990, 1991), but phylogenetic studies have identified a clade, including *L. bifera*, as distantly related to *Pouteria*, meriting resurrection of *Lucuma* with 17 species (Faria & al., 2017; Swenson & al., 2023).

Lucuma valparadisaea was said by Molina (1782) to grow in large quantities in the surroundings of Valparaíso, a seaport 120 km northwest of Santiago, but no original material has ever been located. Therefore, Candolle (1844) described *L. splendens* A.DC., based on material collected by Bertero in 1830, also from the vicinity of Valparaíso. This material was studied by Pierre (1890) when he established the genus *Gayella*, with the single species *G. valparadisaea* (Molina) Pierre, with *L. splendens* in synonymy. Pierre stated that it was a very isolated genus, distinct by its flowers and seeds, as well as by anatomical characters. Indeed, Kukachka (1981), in a series of wood anatomical studies of Neotropical Sapotaceae, concluded that *Gayella* shows little, if any, similarity with the wood anatomy of *Pouteria*. However, Pennington (1990) cited *L. valparadisaea* with a query as a synonym of *P. splendens*, noting that a type had not been designated for the name. Still, Pennington (1990) established *P.* sect. *Gayella* (Pierre) T.D.Penn., possibly based on the rotate flower, with eight species and with *G. valparadisaea* as type. Since then, four of Molina's species of *Lucuma* have been neotypified, including *L. bifera* and *L. valparadisaea* (Thulin & al., 2021).

Gayella valparadisaea, the name here adopted, is the only native species of Sapotaceae in Chile (Fig. 1). It is limited to ravines and gullies near the coast of the provinces of Choapa (Coquimbo Region) and San Antonio (Valparaíso Region) in central Chile (Sotes & al., 2013). It was first assessed as Near Threatened (NT) by the IUCN in 1998 (iucnredlist.org), then as Critically Endangered (CR) (Hechenleitner & al., 2005), and it is currently listed as Endangered (EN) (especies.mma.gob.cl). The purpose of this paper is to find the closest relatives of *G. valparadisaea*, to test whether *Gayella* merits generic recognition, to estimate the age of the trans-Pacific disjunction, and to expand the description of this intriguing Chilean species.

■ MATERIALS AND METHODS

Taxonomy and sampling strategy. — We follow the concept of Chrysophylloideae sensu Swenson & Anderberg (2005) and the classification of Australasian genera proposed by Swenson & al. (2013), including the recently described monotypic genus *Sahulia* Swenson (Swenson & Kearey, 2020). All species with available nrDNA were selected of *Amorphospermum* F.Muell. (1 of 1 sp.), *Gayella* (1 of 1 sp.), *Magodendron* (1 of 2 spp.), *Niemeyera* F.Muell. (4 of 4 spp.), *Pichonia* Pierre (9 of 13 spp.), *Pleioluma* (Baill.) Baehni (28 of 40 spp.), *Pycnandra* Benth. (58 of 62 spp.), *Sahulia* (1 of 1 sp.), *Sersalisia* R.Br. (3 of 5 spp.), and *Van-royena* Aubrév. (1 of 1 sp.). *Planchonella* Pierre is a genus of approximately 110 species of which 83 were included, partly because an extensive sampling is necessary for node calibration (see below). In total, 201 terminals representing 190 ingroup species (79% of all described species), including all genera, were sampled.

The tree was rooted on the African genus *Aubregrinia* Heine and the South American genus *Ecclinusa* Mart., following the latest results by Swenson & al. (2023). Accepted names and synonyms of Sapotaceae are continuously updated online at Plants of the World Online, Royal Botanic Gardens, Kew (powo.science.kew.org). All terminals are reported with voucher information and GenBank accession numbers in Appendix 1. Morphological information was gathered from Pennington (1990) and herbarium material deposited in CONC and S.

Molecular data. — Sequence data from the nuclear ribosomal DNA (ETS, ITS) and the nuclear gene *RPB2* were used since they have proven to provide ample information for phylogenetic inference in Sapotaceae at all taxonomic levels (Swenson & al., 2013, 2019, 2020; Terra-Araujo & al., 2015; Faria & al., 2017). Also, since *Gayella* is a member of the well-known Australasian clade (Bartish & al., 2005; Swenson & al., 2008b, 2013, 2014, 2015, 2018, 2019, 2020), existing sequence data was used and assembled into matrices using AliView v.1.26 (Larsson, 2014), manually checked, adjusted and subsequently prepared in BEAUti v.1.10.4 (part of the BEAST package) to an input xml-file for Bayesian inference. Gaps for each locus were manually scored as binary characters (present/absent) in separate partitions, disregarding uninformative deletions or inserts, homopolymer regions with high variability, and regions with ambiguous alignment.

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Fig. 1. *Gayella valparadisaea* (Sapotaceae) from three different locations along the Chilean coast. **A**, Shrubland at Tototalillo (Region Coquimbo); **B**, Flower with 5 or 6 greenish corolla lobes at Los Molles (Region Valparaíso); **C**, Ripening fruits at Tototalillo; **D**, Population on steep cliff near the sea at Quebrada el Lucumo (Region Valparaíso); **E**, Flowers with 6 corolla lobes (Quebrada el Lucumo); **F**, Dry fruits from Quebrada el Lucumo. Note the thin exocarp and absence of pulp. — Photos: A–C by M.T. Eyzaguirre and D–F by P. Baxter.

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Node calibration. — Two nodes were calibrated for age estimates following Swenson & al. (2014, 2019) based on fossils representing the split between taxa in Africa/South America (the outgroup) and Australasia (the ingroup) as well as a split between species of *Planchonella* in New Zealand and Australia. The first calibration point was set with a leaf fossil from the Cerrejón Formation in Colombia dating back to the Paleocene (c. 58 Ma) and it is suggested to be of Sapotaceae origin (Wing & al., 2009). We assigned this split with an exponential decay and an offset of 58 Ma (mean 0.8; upper 97.5% credibility interval, 61 Ma). The second calibration point was set with fossils of leaf impression from Oligocene-Miocene transition strata at Landslip Hill (Campbell, 2002) and unpublished Sapotaceae microfossils, including a flower bud containing pollen from Foulden Maar near Middlemarch, Otago, New Zealand (Swenson & al., 2014, 2019). Foulden Maar once hosted a rich mesothermal Lauraceae-dominated evergreen forest, archived in a former freshwater deposit formed by basaltic volcanism, dated to 23.2 ± 0.2 Ma (Lindqvist & Lee, 2009; Bannister & al., 2012). These fossils are allied to *Planchonella costata* (Endl.) Pierre, the only extant native species of Sapotaceae in New Zealand, which is sister to the Australian species *P. eerwah* (F.M.Bailey) P.Royen (Swenson & al., 2013, 2019). This sister relationship was calibrated with an exponential decay and an offset of 23.2 Ma (mean 0.55; upper 97.5% credibility interval, 25.2 Ma).

Phylogenetic inference and dating. — Phylogenetic relationships and dates of splits were simultaneously estimated with Bayesian inference (Rannala & Yang, 1996; Yang & Rannala, 1997) in BEAST v.1.10.4 (Drummond & al., 2012; Suchard & al., 2018). Each locus was treated as a unique partition and tested for the best-fit substitution model using jModelTest2 (Darriba & al., 2012), assigning an HKY substitution model for each locus (Hasegawa & al., 1985). Binary (indel) information was treated under a simple model without gamma. The aligned matrices were prepared in BEAUti v.1.10.4 (part of the BEAST package) as an output file for BEAST. We modelled the distribution of mutation rates across the topologies using an uncorrelated relaxed molecular clock with a gamma distribution of rates shared for all three loci, and a separate, strict clock rate for the binary data. A Birth-Death tree prior (Gernhard, 2008) was used to accommodate for lineage births and extinctions across the trees.

BEAST was run 10 times, each for 50 million generations while sampling from the posterior every 50,000 generations. After removal of a portion of each run as burn-in, the chains were checked for convergence and stable states in Tracer v.1.7 (Rambaut & al., 2018). Samples were combined in LogCombiner v.1.10.4, and trees were summarized onto a maximum clade credibility (MCC) tree in TreeAnnotator v.1.10.4 (part of the BEAST package). We used FigTree v.1.4.3 (Rambaut, 2013) to visualize the MCC tree. Clade support is reported as a posterior probability (PP), where PP ≥ 0.95 is considered as strong support, PP 0.85–0.94 as moderate support, and PP ≤ 0.84 is regarded as weak support or indication of relationship.

■ RESULTS

The MCC tree obtained from the Bayesian analysis of Australasian Chrysophylloideae concurs with previous analyses of the group (Swenson & al., 2013, 2014, 2019, 2020). *Pleioluma* is a rather isolated genus with strong support (Fig. 2). *Pichonia* and *Sersalisia* are closely allied and strongly supported. The monotypic genus *Sahulia* is sister to the clade of *Amorphospermum*, *Niemeyera*, *Pycnandra*, and *Planchonella*. The phylogenetic positions of *Magodendron* and *Van-royena* are uncertain in the backbone of the phylogeny (node 10; PP 0.36), here suggesting that *Magodendron* (node 3; PP 0.52) is sister to the pair of *Pichonia* and *Sersalisia*. *Gayella valparadisaea* finds no strongly supported relationship, but is not nested in any of the strongly supported genera, and recovered with weak support (PP 0.72) as the sister taxon to the monotypic Australian genus *Van-royena*. The complete xml-file and the MCC tree can be downloaded from the journal's web site as supplementary data (suppl. Appendices S1 and S2).

Estimated divergence times of splits and crown groups in Australasian Chrysophylloideae, compared with estimates by Swenson & al. (2014), are reported in Table 1. *Gayella* is estimated to have split from *Van-royena* at 40.0 Ma (50.5–25.3 Ma) (Fig. 2, node 2).

■ DISCUSSION

Systematic position of *Gayella* and comparison with *Van-royena*. — The phylogenetic analysis using a very exhaustive taxon sample of Australasian Sapotaceae clearly supports the view of Pierre (1890) that the Chilean species *Gayella valparadisaea* has a very isolated position in the family. *Gayella* is embedded in the monophyletic clade of Australasian Chrysophylloideae, but not nested within any other recognized genus, and instead most likely sister to *Van-royena*. Pennington (1991: 229) noted that "It is more difficult to justify separation of *Pichonia* from *Pouteria* section *Gayella*, […] *P. splendens* (confined to northern Chile) is morphologically closest to *Pichonia* species, […]." Indeed, Pennington saw the connection across the Pacific Ocean, but the purpose of his reasoning was to find arguments to maintain *Pichonia*, rather than uniting it with *Pouteria*. In any case, Pennington's (1990) action to include *Gayella* in *Pouteria* as the Neotropical *P.* sect. *Gayella* is here shown to be incorrect with *Gayella* nested among the Australasian genera of Chrysophylloideae.

Gayella differs markedly from *Van-royena* in several characters (Table 2), such as leaves 3-whorled, opposite or alternate even on the same plant (versus consistently alternate), corolla rotate and (5–)6-lobed (versus tubular and 5-lobed), and radicle exserted below the cotyledon commissure (Fig. 3E), a rather rare feature (versus included in the cotyledons). For this reason, we strongly prefer the option to keep these two monotypic genera, rather than uniting them under *Gayella*, which is the name with priority.

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***Gayella* compared with other genera. —** Pierre (1890) considered *Gayella* to have a distinct flower and seed morphology as well as several unique anatomical characters that separate it from *Lucuma*, a South American genus (Swenson & al., 2023). We believe that *Gayella* is better compared with its closest relatives, those from Australasia, rather than with taxa from the same continent that are not closely related. Flowers of *Gayella* possess staminodes, a feature absent in *Amorphospermum*, *Niemeyera*, and *Pycnandra* (Swenson & al., 2013), three genera not further discussed. Seeds are also important to examine with either foliaceous cotyledons, an exserted radicle below the cotyledon commissure, and endosperm, or plano-convex cotyledons, an included radicle, and absence of endosperm. *Pleioluma* with 40 species distributed in New Caledonia to Southeast Asia (Swenson & al., 2018; Jessup, 2019) and *Planchonella* with 110 species found from the Seychelles to Hawaii (Swenson & al., 2018, 2019, 2020; Jessup, 2019) are two well-supported genera with foliaceous cotyledons and endosperm, and are therefore not further discussed. This leaves us to compare *Gayella* with another four genera: *Magodendron* (2 species, New Guinea; Vink, 1995), *Pichonia* (13 species, New Caledonia to Maluku; Swenson &

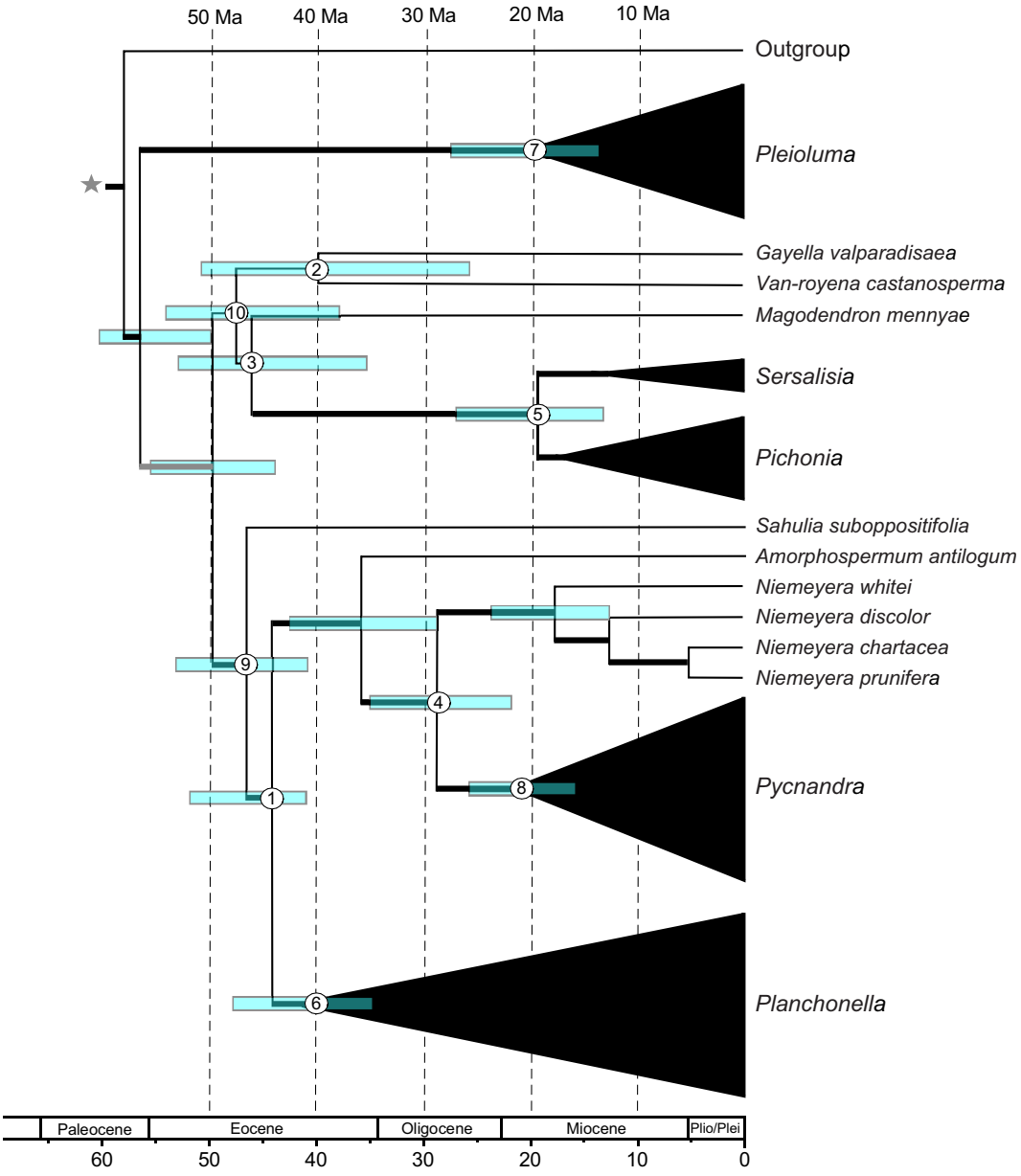


Fig. 2. Maximum clade credibility tree and divergence-time estimates (Table 1) obtained from BEAST analyses of nrDNA (ETS, ITS, *RPB2*) of Australasian Chrysophylloideae (Sapotaceae), a tree rooted on *Aubregrinia* from Africa and *Ecclinusa* from South America. *Gayella valparadisaea*, the only native Sapotaceae species in Chile, is indicated with weak support (PP 0.72) as being sister to the Australian genus *Van-royena*. Strong clade support is shown with thick black branches (PP ≥ 0.95), moderate support with thick grey branches (PP 0.85–0.94 [one branch]), and thin branches indicate weak support. Star indicates the calibration point of 58 Ma (mean 0.8; upper 97.5% credibility interval, 61 Ma).

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Munzinger, 2012), *Sahulia* (monotypic, New Guinea; Swenson & Kearey, 2020), and *Sersalisia* (5 species in Australia to Malesia; Jessup, 2019) (Table 2).

Leaves of Sapotaceae are simple, entire (with three exceptions) and usually alternate or sometimes opposite, but leaves in *Gayella* are in whorls of three, opposite, or alternate, often on the same plant or even the same branch (Fig. 1). Leaves are opposite in *Sahulia* and sometimes in *Pichonia*, but otherwise alternate. Leaves are usually flat in Sapotaceae, but *Gayella* has revolute leaf margins, very similar to the Hawaiian endemic *Planchonella spathulata* (Hillebr.) Pierre. This is most likely an adaptation to prevent transpiration in dry habitats (Havran & al., 2021). Indeed, *Gayella* is restricted to dry ravines and gullies near the coast and is dependent on the mist from the Pacific Ocean (Hechenleitner & al., 2005).

Tertiary and higher leaf venation has been demonstrated to often be consistent within clades and therefore useful in delimitation of genera (Swenson & al., 2013, 2023; Faria & al., 2017). Leaf venation consists of a midvein with a various number of secondaries forming a brochidodromous or eucamptodromous venation, patterns that may transform from one to another in the same leaf. Between the secondaries, or perpendicular to the midvein, are tertiaries forming different patterns. At higher magnification, a fine areolate pattern is sometimes present, here characteristic for *Magodendron*, *Pichonia*, and *Sersalisia*. *Gayella* also has an areolate venation, but it is found between the secondaries (not the tertiaries) and is often hard to observe. It is best seen on the lower side but obscured by presence of indumentum.

The Sapotaceae corolla is sympetalous with a corolla tube and free corolla lobes. Depending on the ratio between the length of the tube and the lobes, as well as the length of the sepals, the corolla is campanulate, cup-shaped, dome-shaped, rotate, or tubular. Among the compared genera, *Gayella* is the only taxon with a rotate flower, i.e., having a short calyx, a short corolla tube, and a rotate, wide open corolla with spreading lobes to form an almost flat structure (Fig. 1B,E). The other genera have either a cup-shaped or tubular corolla (Table 2). *Pradosia* Liais, a Neotropical genus with 23 species, is well-known for its rotate flowers, but differs from *Gayella* in the lack of staminodes (Terra-Araujo & al., 2015, 2016). *Gayella* also differs from the other genera in its anisomerous flower with five sepals and generally six (sometimes five) corolla lobes instead of having 5-merous flowers (*Sahulia*, *Sersalisia*) or up to eight corolla lobes (*Magodendron*, *Pichonia*).

Staminodes are present in the lobe sinuses of all six genera. They are usually entire, glabrous, and frequently flask-shaped to lanceolate. However, *Magodendron* and *Gayella* have lacerate to dentate staminodes, best developed in the former (Vink, 1995), but certainly present and variable in the latter (Fig. 3A–D).

The fruit of Sapotaceae is usually considered to be a berry even if the pulp in many species is scarce, but sometimes it is a dry, dehiscent capsule (Sapotoideae; Pennington, 1991) or drupaceous (*Pradosia*; Terra-Araujo & al., 2013). In *Gayella*, the mature fruit is yellow-orange-red, resembling small plums (Fig. 1C), poor in pulp and 1-seeded (Fig. 1F). The seed has a rather large ventral seed scar, clearly distinct from the pale brown testa (Fig. 3F–H). Pierre (1890) stated that these fruit characters made *Gayella* a distinct genus, but in contrast, we find fruit morphology in this genus to be rather typical for Sapotaceae. However, the combination of plano-convex cotyledons, absence of endosperm, and *exserted radicle* (Fig. 3E) is an unusual combination in subfamily Chrysophylloideae, otherwise only known in *Magodendron* and the Neotropical genera *Elaeoluma* Baill. (5 spp.), *Englerella* Pierre (monotypic), and *Pradosia* (23 spp.).

Harley (1991) made an extensive study of Sapotaceae pollen for 48 of 53 genera as defined by Pennington (1991). She classified them into 12 types and numerous subtypes, in addition to several anomalous pollen types. Six out of eight species placed by Pennington in *Pouteria* sect. *Gayella* were studied, and four types and five subtypes of pollen were found. *Gayella valparadisaea* (as *Pouteria splendens*) was

Table 1. Comparison of Bayesian posterior divergence-time estimates of nodes (in Fig. 2; alphabetic order) in Australasian Chrysophylloideae (Sapotaceae) between the present and previous study (Swenson & al., 2014).

Node and number	Present analysis	Swenson & al. (2014)
1. *Amorphospermum–Pycnandra/Planchonella*	44.2 Ma (50.5–38.5 Ma)	43.5 Ma (50.3–32.0 Ma)
2. *Gayella/Van-royena*	40.0 Ma (50.5–25.3 Ma)	not estimated
3. *Magodendron*	45.9 Ma (53.8–35.2 Ma)	47.0 Ma (55.6–38.6 Ma)
4. *Niemeyera/Pycnandra*	28.4 Ma (35.1–22.0 Ma)	29.8 Ma (38.0–22.3 Ma)
5. *Pichonia/Sersalisia*	19.8 Ma (27.4–13.9 Ma)	20.4 Ma (27.6–14.6 Ma)
6. *Planchonella* (crown node)	42.3 Ma (48.3–36.7 Ma)	41.2 Ma (48.6–35.0 Ma)
7. *Pleioluma* (crown node)	20,4 Ma (28.0–14.2 Ma)	17.5 Ma (23.7–12.0 Ma)
8. *Pycnandra* (crown node)	21.0 Ma (26.3–16.1 Ma)	16.2 Ma (21.1–12.1 Ma)
9. *Sahulia*	46.8 Ma (53.8–40.8 Ma)	not estimated
10. *Van-royena* + *Gayella/Magodendron*	47.7 Ma (54.5–38.2 Ma)	43.7 Ma (52.9–33.9 Ma)

represented by two specimens having rather different pollen types (3B and 6C), types that are not found in any other member of the Australasian clade (Table 2).

Pierre (1890) stated that *Gayella* was distinct due to its anatomy, for example the elliptic stomata are restricted to the lower leaf surface, protected by indumentum. Modern anatomical studies of Sapotaceae are scarce, apart from a series of 38 papers by Kukachka between 1978 and 1982 (Miller & Mori, 1984), and studies in the monotypic genus *Diploon* Cronquist (Lima & al., 2019) and in *Pouteria andarahiensis* T.D.Penn. (Carvalho & Carneiro, 2021). Kukachka (1981) denied a close relationship of *Gayella* and *Pouteria*, and instead proposed an affiliation with *Pradosia*, which here and elsewhere is rejected (Swenson & al., 2023).

In summary, morphology of *Gayella* stands out in comparison with its relatives in Australasia. It is the only taxon with 3-whorled, opposite, or alternate leaves, often on the same plant, areolate venation instead of tertiaries, rotate flowers, often with six corolla lobes, and odd pollen types (3B and 6C). In addition, *Gayella* shares with *Magodendron* lacerate (to dentate) staminodes and plano-convex cotyledons with an exserted radicle, features that seem to indicate a close relationship, but the molecular signal points instead to *Van-royena*.

Biogeography of *Gayella*. — *Gayella* originated via a split within Sapotaceae in the late Eocene at 40.0 Ma (50.5–25.3 Ma), in a continent corresponding to modern Australia and New Guinea (Hall, 2002). The sole descendent of this lineage is currently restricted to the central Chilean coast and it is an intriguing question whether this disjunction is a result of vicariance or long-distance dispersal. Molecular dating of Chrysophylloideae suggested that the subfamily may have been established in Australasia by range expansion from South America via Antarctica at 60–65 Ma (Bartish & al., 2011) and radiated further in Australasia at about 52.5 Ma (59.3–45.7 Ma), an age close to the current estimate of 56.2 Ma (60.2–49.9 Ma). However, following the reasoning by Crisp & al. (2011), both events are too old to be considered vicariance since the divergence pre-dates the development of the geological barrier with, respectively, 25–35 Ma in the deepest node and up to 15 Ma in the second. It is instead possible that the presence of *Gayella* in South America originated by vicariance since the lineage split overlaps the geological splits of southern Gondwana. Australia split from Antarctica about 35 Ma and Antarctica split from South America about 30–35 Ma (McLoughlin, 2001). Hence, these ages are consistent with the estimated split between *Gayella* and *Van-royena* at 40.0 Ma (50.5–25.3 Ma) (Table 1).

Climatic events played a crucial role for the vegetational development along the Antarctic coast in the Eocene. Antarctica hosted a near-tropical vegetation in the early Eocene, but in the middle of the epoch, global cooling caused tropical elements to be replaced by temperate forests with genera such as *Nothofagus* Blume (Contreras & al., 2013). According to Hinojosa (2005) and Hinojosa & al. (2006), a subtropical Gondwanic palaeoflora would have predominated in what is today southern South America from the beginning of the Eocene. From the end of the Eocene to the beginning of the Miocene, under a cooler and less humid climate, a mixed palaeoflora would have developed. A notable feature of this flora was the increase of elements of current Austral-Antarctic distribution. From the lower to the upper Miocene, under a relatively warmer and wetter climate with a tendency to summer

Table 2. Morphological features of *Gayella* and closely related genera of Australasian Chrysophylloideae (Sapotaceae).

Character	*Gayella*	*Magodendron*	*Pichonia*	*Sahulia*	*Sersalisia*	*Van-royena*
Leaf arrangement	3-whorled/opposite/alternate	alternate	alternate/opposite	opposite	alternate	alternate
Tertiary leaf venation	areolate, obscure	oblique, laxly reticulate	laxly reticulate	horizontal/reticulate	reticulate/areolate	reticulate
Higher leaf venation	absent	areolate	areolate	non-areolate	areolate	non-areolate
Corolla shape	rotate	cup-shaped	cup-shaped	tubular	tubular	tubular
Corolla lobes	(5–)6	5(–8)	5–8	5	5	5
Stamens inserted in	corolla tube orifice	corolla tube orifice	corolla tube orifice	middle of tube	corolla tube orifice	middle of tube
Staminodes	lacerate/dentate	lacerate	flask-shaped	lanceolate	lanceolate	oblong, terete at base
Fruit	1-seeded	1(–3)-seeded	1-seeded	1(–2)-seeded	1–5-seeded	1–2-seeded
Cotyledons	plano-convex	plano-convex	plano-convex	foliaceous	plano-convex	plano-convex
Radicle below commissure	exserted	exserted	included	exserted	included	included
Endosperm	absent	absent	absent	present	absent	absent
Pollen type	3B/6C	8A	5A, 5C	?	7B, 7E, 7G	?

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drought, central Chile would have had a Neogene subtropical palaeoflora. The south-central coastal mountain range, where *Gayella* presently occurs, was presumably little affected by the pre-Pleistocene and Quaternary glaciations and served as a refuge for the forests during this period. As summarized by Hinojosa & al. (2006): "Apparently, the western margin of the continent at mid latitudes remained fairly stable through these great convulsions, allowing for the conservation of ancient floristic assemblages." The fossil record of *Sapotaceoidaepollenites rotundus* W.K.Harris in the Miocene Navidad Formation (Barreda & al., 2011), indicates that Sapotaceae has been present in central Chile at least since this time. As *S. rotundus* was first described from early Tertiary sediments of southern Australia (Harris, 1972), the record is compatible with an Austral-Antarctic origin of this member of Sapotaceae that may be an ancestor of *G. valparadisaea*. Furthermore, the fossil pollen (Harris, 1972: figs. 17, 18; Barreda & al., 2011: fig. 3A) is very similar to extant pollen of *G. valparadisaea* (Harley, 1991: fig. 25E,F). The final uplift of the Andes during the end of the Miocene and Pliocene (Garzione & al., 2008), would have isolated the subtropical forests of central Chile from other such forests in South America. Maybe, *G. valparadisaea* today persists in the last habitable pockets available for this species.

Long-distance dispersal is another possible explanation, and the presence of Sapotaceae in many Pacific islands is explained by repeated dispersals (Smedmark & Anderberg, 2007; Bartish & al., 2011; Swenson & al., 2014, 2019). The longest Sapotaceae leap known in the Pacific is by *Planchonella* from an area near Fiji 20.5 Ma (15.6–25.8 Ma) to an establishment in the Hawaiian-Emperor seamount (Swenson & al., 2019). The most widespread species in the Pacific is *P. tahitensis* (Nadeaud) Pierre ex Dubard, which occurs from Fiji in the west to Ile Anaa (17°23′15″S; 145°34′58″W), Tuamotus, in the east (French Polynesia). *Gayella* may have colonized South America via long-distance dispersal but, in that case, it will never be known if it took place by a single or several events. However, as pointed out by Crisp & al. (2011) for long-distance dispersal in general, a single long leap is "likely to be more probable than are multiple, shorter steps". Dry land

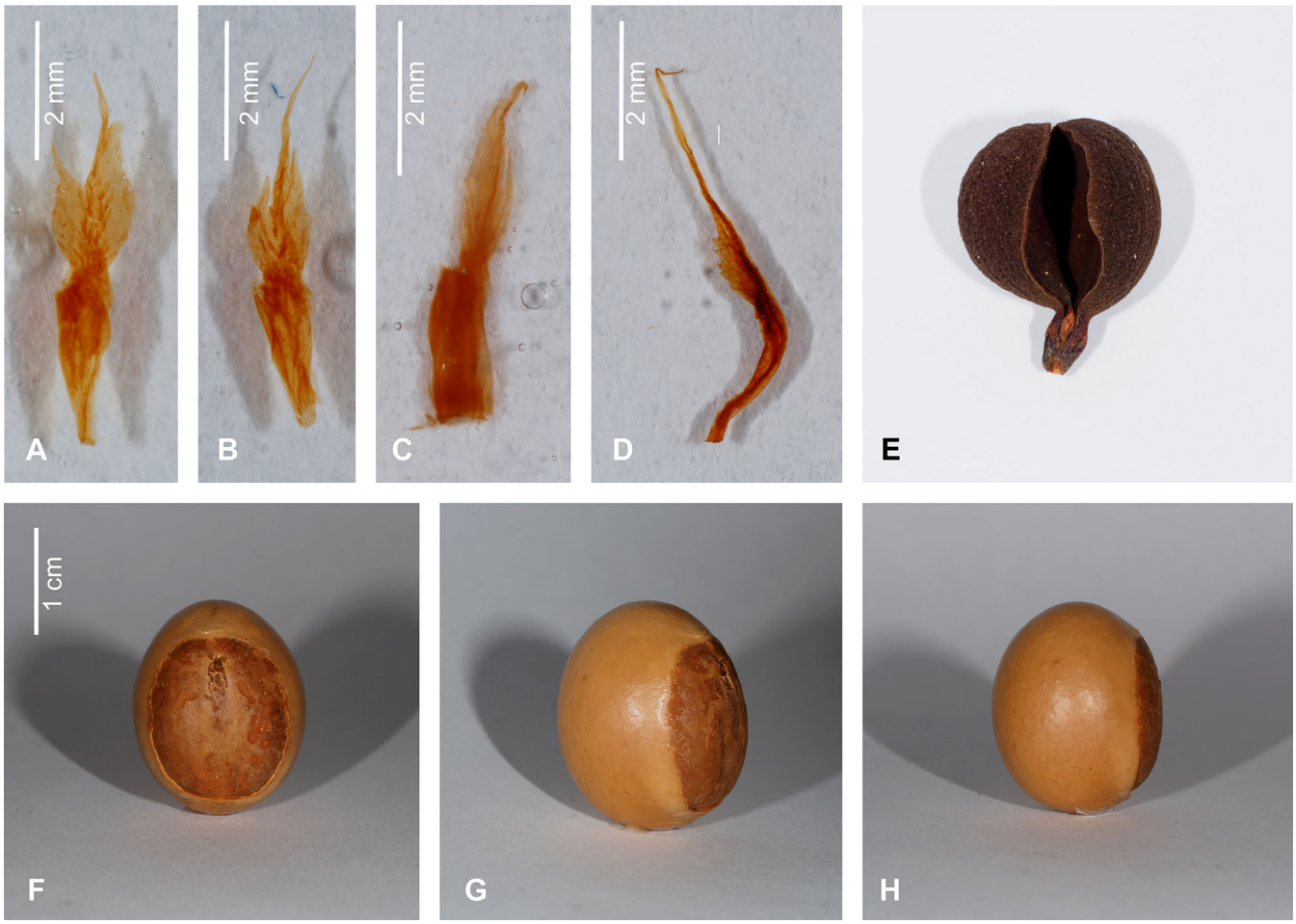


Fig. 3. Morphological details of *Gayella valparadisaea* (Sapotaceae). **A–D**, Staminodes (A–B, *Lammers & al. 6369*; C, *Dillon & Teillier 4950*; D, *Schegele 536*); **E**, Plano-convex cotyledons with an exserted radicle (*Montero 8149*); **F–H**, Seed and seed scar, seen from the scar (left), obliquely (middle), and side (right) (*Dillon & Teillier 4950*) (all material from CONC). — Photos: Ulf Swenson.

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was scarce in the southwest Pacific in the Paleogene, but the development of the Melanesian arc system of Solomon-Vanuatu-Fiji-Tonga began around 40–45 Ma (Hall, 2002; Crawford & al., 2003; Schellart & al., 2006) and might have played a role in intermediate dispersal. The area east of the Melanesian arc system consists of a massive water body. West of continental South America lies the Nazca Plate, which is covered by deep waters between 4000 and 6000 m (Bello-González & al., 2018). The Nazca Plate and oceanic crust west thereof hosts several hotspot-generated volcanic islands, seamounts, and plateaus, such as the Tuamotu Plateau, Easter Seamount Chain, and Juan Fernandez Ridge, all of which provided temporary land during various time windows since the Paleogene before submergence and subduction (Bello-González & al., 2018).

In conclusion, the hypothesis that the presence of *Gayella* in South America is a result of vicariance is consistent with the timing of the geological splits of southern Gondwana, as well as with evidence from fossil pollen. Still, establishment after long-distance dispersal is an alternative explanation that remains possible, although perhaps less likely.

■ REINSTATEMENT AND TAXONOMY

Gayella Pierre, Not. Bot.: 26. 1890 – Type: *Gayella valparadisaea* (Molina) Pierre (≡ *Lucuma valparadisaea* Molina).

Description. – Hermaphroditic, evergreen, small tree or shrub; white latex exuding sparsely. *Leaves* simple, entire, 3-whorled, opposite or alternate, coriaceous; margin usually revolute; secondary venation brochidodromous, of 12–15 pairs, weak, almost perpendicular to the midvein, sometimes branching; tertiaries forming an obscure areolate venation. *Flowers* in axillary fascicles, bisexual, often anisomerous. *Sepals* 5 in a single whorl, free, quincuncial, tomentulose outside, glabrous inside. *Corolla* rotate with 6 (or 5) corolla lobes, glabrous, smooth (not papillate); corolla lobes often revolute, giving the flower a star-like appearance; margin somewhat fimbriate. *Stamens* 1 opposite each corolla lobe, inserted in corolla tube orifice, glabrous, as long as the corolla, well exposed in open flowers. *Staminodes* (5–)6(–7), lanceolate, aristate; margin lacerate to dentate. *Gynoecium* tomentose with 4 or 5 loculi; style exserted, glabrous, simple. *Fruit* a berry, yellow-orange-red, with a thin layer of pulp, 1-seeded, globose to broadly ellipsoid, crowned by a 2–4 mm long remnant style; seed of the same form as the fruit; cotyledons plano-convex with a radicle extending below cotyledon commissure; endosperm absent.

Gayella valparadisaea (Molina) Pierre, Not. Bot.: 27. 1890 ≡ *Lucuma valparadisaea* Molina, Sag. Stor. Nat. Chili: 187, 352. 1782 – Neotype (designated by Thulin & al. in Gayana, Bot. 78: 166. 2021): Chile, Región V, Prov. Valparaíso, Laguna Verde, 33°05′19″S, 71°39′33″W, 75 m alt., 10 Nov 2004, *O. Fernandez C. s.n.* (CONC No. 162240!; isoneotype: JBN No. 1058!).

= *Lucuma splendens* A.DC., Prodr. 8: 171. 1844 ≡ *Pouteria splendens* (A.DC.) Kuntze, Revis. Gen. Pl. 3(2): 195. 1898 ≡ *Gayella splendens* (A.DC.) Aubrév. in Adansonia, n.s., 1: 180. 1962 – Lectotype (designated by Pennington in Fl. Neotrop. Monogr. 52: 520. 1990): Chile, Valparaíso, Jan 1830, [fl.], *Bertero 1115* (G-DC barcode G00139756!; isolectotypes: G barcode G00439564!, P barcode P0064 8073!, S No. 20-26477!, US barcode 00930753!).

– "*Vitellaria valparadisaea*" Dubard in Ann. Mus. Colon. Marseille, sér. 2, 10: 18. 1912, pro syn.

Note. – *Lucuma splendens* was typified by Pennington (1990), who designated *Bertero 1115* in G-DC as lectotype, with duplicates in F, NY, P, TUB, and US. According to Pennington, the lectotype material was collected in "Jan 1829", but the sheet in G-DC has the date "Jan 1830". Since then, material of *Bertero 1115* has been located also in BM, BR, G, M, MPU, S, U and UPS, and the material all together seems to correspond to at least three collections. Apart from the lectotype and isolectotypes cited above, the material is dated "1829" without month (BM barcode BM000952618!, F barcode V0072066F!, G barcode G00439563!, M barcode M-1974352!, P barcode P00648074!, UPS No. V-557447), "1830" without month (P barcode P00648072!), "August 1830" (GH barcode 00075650!), undated (BR barcode 000001349 2502!, NY barcode 00273520!, U barcode U 0006699!), and undated without collection number (MPU barcode MPU01 9056!). Specimens other than "Jan 1830" are here considered as syntypes.

Description. – Plant 2–3(–6) m tall, with fawn indumentum on young branches, petiole, midvein, pedicels and sepals, turning greyish with age. *Leaves* broadly elliptic to obovate, 3.5–9.0 × 1.5–6.0 cm, glabrous above, usually greyish tomentulose below; apex acute, obtuse, rounded or emarginate; base rounded to somewhat cuneate; petiole 5–8 mm long. *Flowers* 5–10 in each fascicle; pedicel 4–7 mm long. *Sepals* 3.0–4.0 mm long, ovate; apex acute to rounded. *Corolla* greenish with white centre, 6–7 mm long, 10–11 mm wide when fully open, corolla tube shorter than lobes. *Stamens* glabrous, geniculate in bud; filaments white; anther 2.0 mm, ovate, calcarate up to 50% of its length, first white, turning fawn. *Staminodes* white, glabrous. *Gynoecium* flask-shaped; style 6–8 mm long, greenish with a pinkish apex. *Fruit* 20–30 × 18–25 mm; seed scar 35% of the circumference and 80%–90% of seed length; testa dull, light brown, thin, 0.2–0.3 mm thick (Figs. 1, 3).

Phenology. – The species is flowering from July to January and fruiting from November to March. The fruits are slowly ripening, sometimes over an entire year (Hechenleitner & al., 2005).

Distribution and habitat. – *Gayella valparadisaea* is a rare plant restricted to the provinces of Choapa (Coquimbo Region) and San Antonio (Valparaíso Region) of central Chile (Fig. 4). It grows in rocky slopes, ravines and gullies, usually below 100 m altitude and within reach of sea mist, but with two subpopulations up to 400 m (Hechenleitner & al., 2005). The coastal part of central Chile to which *G. valparadisaea* is confined has a Mediterranean-type climate with winter rainfall

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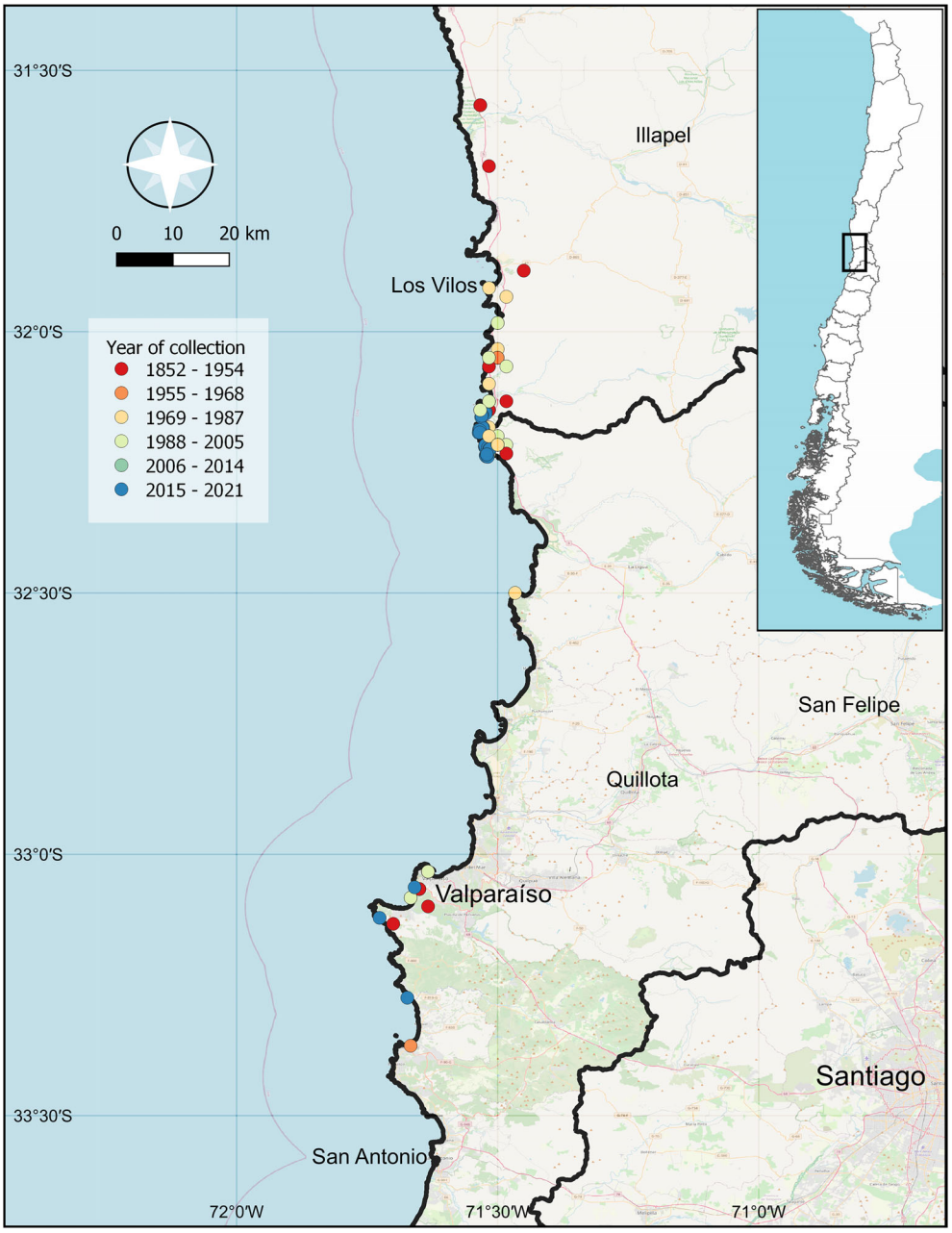


Fig. 4. Distribution of *Gayella valparadisaea* (Sapotaceae) in central Chile. Year of collections are colour coded from 1852 to 2021 to capture distribution across time.

and summer drought (Armesto & al., 2007). Its area of distribution falls within the "Chilean winter rainfall-Valdivian forests", one of 34 global biodiversity hotspots (Arroyo & al., 2004).

Etymology. – The species is named after Valparaíso in central Chile, from where it was reported in the protologue (Molina, 1782).

Conservation. – *Gayella valparadisaea* is listed as Endangered (EN) by Ministerio del Medio Ambiente (especies.mma.gob.cl), but does not occur inside any protected area. Threats against the species include urban development, road construction, collection of firewood, fires, and grazing of cattle. We urge the Chilean authorities to increase the efforts towards protection of this very special plant.

■ AUTHOR CONTRIBUTIONS

US conceived the study, aligned the matrices, studied the morphology, produced the figures (except the distribution map), and wrote the bulk of the text, assisted by MT and BL. SN and US analyzed the data. AM dealt with various issues in Chile. — US, https://orcid.org/0000-0003-1064-9404; SN, https://orcid.org/0000-0001-5199-7128; AM, https://orcid.org/0000-0001-9740-4455; MT, https://orcid.org/0000-0001-5970-8343; BL, https://orcid.org/0000-0002-3281-2973

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Baxter, who allowed us to use their field images, Felipe Hinojosa for information on southern South American palaeofloras, Patricio Novoa and Gaston Carvallo for providing distribution data, and Diego Alarcón, who prepared the distribution map. Directors and staff of the herbaria CONC, EIF, S, and SGO are acknowledged. No external funds supported this project.

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Appendix 1. Voucher specimens of material included in molecular phylogenetic analysis to place *Gayella* in the subfamily Chrysophylloideae (Sapotaceae). The classification follows Swenson & al. (2013). Sequences that failed to amplify are abbreviated "NS".

Taxon name, origin, collector(s) and number (herbaria), ETS accession, ITS accession, *RPB2* accession.

ROOT. ***Aubregrinia taiensis*** (Aubrév. & Pellegr.) Heine, Ghana, *A.A. Enti 6871* (P), MN796269, DQ377520, MN796278. ***Ecclinusa guianensis*** Eyma, Brazil, *Ducke Reserve 05-906* (K), HE860152, DQ246677, HE995661. ***Ecclinusa ramiflora*** Mart., Suriname, *H.S. Irwing & al. 55081* (S), HE860153, DQ246678, HE995602. **INGROUP.** ***Amorphospermum antilogum*** F.Muell., Australia, *I.V. Bartish & L. Jessup 4* (BRI, S), HE860156, DQ154055, HE995662. ***Gayella valparadisaea*** (Molina) Pierre, Chile, *F. Luebert & H.H. Hilger 3128* (BONN, S), MW924277, MW843557, MZ340486. ***Magodendron mennyae*** Vink, Papua New Guinea, *W. Takeuchi, D. Ama & B. Siga 16570* (S), HE860155, AY552114, HE995685. ***Niemeyera chartacea*** (F.M.Bailey) C.T.White, Australia, *I.V. Bartish & L. Jessup 5* (BRI, S), HE860157, DQ154057, HE995606. ***Niemeyera discolor*** Jessup, Australia, *A. Ford 2429* (QRS, S), EU661389, EF025089, HE995607. ***Niemeyera prunifera*** (F.Muell.) F.Muell., Australia, *L. Jessup 5238* (S), HE860158, DQ154058, HE995608. ***Niemeyera whitei*** (Aubrév.) Jessup, Australia, *A.G. Floyd s.n.* (S), EU661388, AY552137, HE995609. ***Pichonia balansae*** (Baehni) Swenson & Munzinger, New Caledonia, *J. Munzinger 975* (MO, NOU, P), HE860159, AY552102, HE995720. ***Pichonia balansana*** Pierre, New Caledonia, *J.-M. Veillon 799* (NOU, P), HE860160, AY552109, HE995610. ***Pichonia daenikeri*** (Aubrév.) Swenson, Bartish & Munzinger, New Caledonia, *T. Jaffré & F. Rigault 3038* (NOU, P), HE860161, AY552108, HE995690. ***Pichonia deplanchei*** (Baill.) Swenson & Munzinger, New Caledonia, *J.-M. Veillon 377* (NOU, P), HE860162, AY552103, HE995699. ***Pichonia dubia*** (Pierre ex Guillaumin) Swenson & Munzinger, New Caledonia, *U. Swenson, J. Munzinger & L. Barrabé 918* (NOU, P, S), HE860164, HE860080, HE995722. ***Pichonia grandiflora*** Swenson & Munzinger, New Caledonia, *U. Swenson & J. Munzinger 930* (NOU, P, S), HE860165, HE860081, HE995611. ***Pichonia lecomtei*** (Guillaumin) T.D.Penn., New Caledonia, *J. Munzinger 2170* (MO, NOU, P, S), HE860166, DQ154061, HE995723. ***Pichonia munzingeri*** Gâteblé & Swenson, New Caledonia, *G. Gâteblé 1011* (G, MO, MPU, NOU, P, S), MN796272, MN796263, MN796280. ***Pichonia occidentalis*** (H.J.Lam) Aubrév., Papua New Guinea, *W. Takeuchi & D. Ama 22233* (L, LAE, MEL, MO, S), HE860167, HE860082, HE995750. ***Planchonella amieuana*** (Guillaumin) Aubrév., New Caledonia, *V. Dumontet, C. Zongo & P. Maituku 510* (NOU, P, S), HE860168, EF025090, HE995612. ***Planchonella aneityensis*** (Guillaumin) H.J.Lam ex P.Royen, Vanuatu, Espiritu Santo, *J. Munzinger, P. Lowry & M. Tuiwawa 3665* (NOU, P, S), HE860169, HE860083, HE995724. ***Planchonella annamensis*** Pierre ex Dubard, Thailand, *D.J. Middleton & al. 3762* (L), MH193998, MH194061, MH194110. ***Planchonella anteridifera*** (Lane-Poole) H.J.Lam, Papua New Guinea, *W. Takeuchi & D. Ama 17902* (LAE, S), HE860170, EF025109, HE995751. ***Planchonella arnhemica*** (F.Muell. ex Benth.) P.Royen, Australia, *R.K. Harwood 1170* (S), HE860171, AY552107, HE995663. ***Planchonella asterocarpon*** (P.Royen) Swenson, Bartish & Munzinger, Australia, *I.V. Bartish & A. Ford 25* (BRI, S), HE860172, DQ154078, HE995664. ***Planchonella australis*** (R.Br.) Pierre, Australia, *A.G. Floyd s.n.* (S), HE860173, AY552148, HE995613. ***Planchonella baillonii*** (Zahlbr.) Dubard, New Caledonia, Dumbéa, *H.S. MacKee 9914* (P), MH194000, AY552141, MH194111. ***Planchonella brevipes*** A.C.Sm., Fiji, Viti Levu, *J. Munzinger 6514* (NOU, SUVA), HE860212, HE860107, HE995737. ***Planchonella calcarea*** (Hosok.) P.Royen, Caroline Islands, Palau, *Costion 3352* (PTBG), MH194002, MH194064, MH194113. ***Planchonella cauliflora*** Munzinger & Swenson, New Caledonia, *J. Munzinger & al. 3495* (MO, NOU, P, S), HE860175, HE860085, HE995666. ***Planchonella chartacea*** (F.Muell. ex Benth.) H.J.Lam, Australia, Queensland, *I.V. Bartish & L. Jessup 1* (BRI, S), HE860176, HE862231, HE995665. ***Planchonella cinerea*** (Pancher ex Baill.) P.Royen, New Caledonia, *J.-M. Veillon 7878* (P), MH194004, AY552144, MH194115. ***Planchonella clemensii*** (Lecomte) P.Royen, Hainan, *F.C. How 73783* (S), HE860177, HE860086, HE995692. ***Planchonella contermina*** Pierre ex Dubard, New Caledonia, *J. Munzinger & V. Dumontet 2285* (NOU, P, S), MH194005, DQ154065, MH194116. ***Planchonella costata*** (Endl.) Pierre, Australia, Norfolk Island, *R.D. Hoogland 11355* (CANB), MW924257, MW843537, NS. ***Planchonella costata*** (Endl.) Pierre, New Zealand (cultivated in Edinburgh), *Robertson 9* (E), HE860178, MH194065, HE995726. ***Planchonella cotinifolia*** (A.DC.) Dubard, Australia, Queensland, *L. Jessup 5280* (BRI), MH194006, MH194066, MH194117. ***Planchonella crassinervia*** Dubard, New Caledonia, *J. Munzinger 2275* (NOU, P, S), HE860180, DQ154067, HE995667. ***Planchonella dothioensis*** (Aubrév.) Swenson, Bartish & Munzinger, New Caledonia, *J. Munzinger 995* (MO, NOU, P, S), HE860183, AY552138, HE995668. ***Planchonella duclitan*** (Blanco) Bakh.f., Philippines, Camiguin Island, *R. Fuentes & L. Fernando 37140* (L), HE860184, HE860089, NS. ***Planchonella duclitan*** (Blanco) Bakh.f., Philippines, Mindoro, *C.E. Risdale, M.J.E. Coode & E. Reynoso 1188* (L), MH194007, MH194067, NS. ***Planchonella eerwah*** (F.M.Bailey) P.Royen, Australia, *A.G. Floyd s.n.* (S), EU661400, AY552147, HE995669. ***Planchonella endlicheri*** (Montrouz.) Guillaumin, New Caledonia, *J. Munzinger, P. Lowry & D. Létocart 2038* (NOU, S), HE860185, DQ154068, HE995614. ***Planchonella ericiflora*** Munzinger & Swenson, New Caledonia, *J. Munzinger & al. 4197* (MO, NOU, P, S), HE860186, HE860090, HE995660. ***Planchonella euphlebia*** (F.Muell.) Francis, Australia, *I.V. Bartish & A. Ford 18* (BRI, MO, S), HE860187, DQ154069, HE995727. ***Planchonella forbesii*** (S.Moore) H.J.Lam, West New Guinea, *K. Armstrong 317* (E, S), HE860154, HE860078, HE995686. ***Planchonella garberi*** Christoph., Samoa (cultivated in McBryde Garden, Kauai), *U. Swenson & al. 1606* (CAU, S), MH194009, MH194069, MH194119. ***Planchonella garcinioides*** (K.Krause) Swenson, Papua New Guinea, *W. Takeuchi, A. Towati & D. Ama 17286* (LAE, S), HE860226, EF025104, HE995675. ***Planchonella glauca*** Swenson & Munzinger, New Caledonia, *U. Swenson, G. McPherson & A. Mouly 625* (S), HE860189, AY552104, HE995728. ***Planchonella grandifolia*** (Wall.) Pierre, Thailand, *J.F. Maxwell 91-362* (L), MH194010, MH194070, NS. ***Planchonella kaalaensis*** Aubrév., New Caledonia, *U. Swenson & J. Munzinger 706* (S), HE860196, HE860097, HE995694. ***Planchonella koumaciensis*** Aubrév., New Caledonia, *J. Munzinger 2665* (NOU), HE860197, EF025095, HE995682. ***Planchonella kuebiniensis*** Aubrév., New Caledonia, *J. Munzinger & D. Létocart 2057* (S), HE860198, DQ154070, HE995670. ***Planchonella laetevirens*** (Baill.) Pierre ex Dubard, New Caledonia, *J. Munzinger, M. Pignal & P. Lowry 2001* (NOU, P, S), HE860199, DQ154071, HE995618. ***Planchonella latihila*** Munzinger & Swenson, New Caledonia, *J. Munzinger & G. Dagostini 2394* (NOU, P, S), MH194011, EF025097, MH194120. ***Planchonella lauracea*** (Baill.) Dubard, New Caledonia, *G. McPherson & J. Munzinger 18070* (MO, S), HE860201, AY552145, HE995731. ***Planchonella leptostylidifolia*** Guillaumin, New Caledonia, Vallée de Tontouta, *G. Dagostini 850* (NOU, P, S), MH194012, DQ154072, MH194121. ***Planchonella lifuana*** (Baill.) Pierre ex Dubard, New Caledonia, Loyalty Islands, Lifou, *J. Munzinger 3317* (NOU, P, S), MH194013, EF025098, MH194122. ***Planchonella linggensis*** (Burck) Pierre, New Caledonia, *unknown collector* (P00208707), MH194014, AY552140, MH194123. ***Planchonella luteocostata*** Munzinger & Swenson, New Caledonia, *J. Munzinger, T. Jaffré & F. Roumagnac 2375* (NOU, S), EU661401, EF025099, HE995755. ***Planchonella maclayana*** (F.Muell.) Swenson, Papua New Guinea, *Regaldo & Katik 1102* (L), HE860239, HE860118, HE995698. ***Planchonella maingayi*** (C.B.Clarke) P.Royen, Malaysia (cult. in Singapore Botanical Garden), *P. Wilkie & A.T. Gwee 507* (E), HE860205, HE860102, HE995620. ***Planchonella malaccensis*** (C.B.Clarke) Swenson, Malaysia (cult. in Singapore Botanical Garden), *U. Swenson & al. 1017* (S, SING), HE860240, HE860119, HE995679. ***Planchonella mandjeliana*** Munzinger & Swenson, New Caledonia, *J. Munzinger & Y. Pillon 2861* (NOU, P, S), HE860206, EF025100, HE995680. ***Planchonella membranacea*** H.J.Lam, Fiji, Viti Levu, *A.C. Smith 4609* (S), HE860207, DQ154074, HE995621. ***Planchonella micronesica*** (Kaneh.) Kaneh. ex. H.J.Lam, Caroline Islands, Kosrae, *Wood 13609* (PTBG, S), MH194017, MH194126, MH194073. ***Planchonella microphylla*** Pierre ex Dubard, New Caledonia, *J. Munzinger & G. Dagostini 2163* (NOU, P, S), MH194018, DQ154075, MH194127. ***Planchonella mindanaensis*** H.J.Lam, Philippines, *M.S. Clemens 1015* (PNH), HE860208, HE860103, HE995622. ***Planchonella minutiflora*** Munzinger & Swenson, New Caledonia, *H.S. MacKee 16639* (NOU, P, S), HE860209, HE860104, HE995734. ***Planchonella*** **Munzinger 6490**, Fiji, Vanua Levu, *J. Munzinger 6490* (NOU, SUVA), HE860211, HE860106, HE995736. ***Planchonella myrsinifolia*** subsp. ***howeana*** (F.Muell.) Jessup, Australia, Lord Howe Island, *Le Cussan 1210* (BRI), HE860194, EF025094, HE995681. ***Planchonella myrsinifolia*** (F.Muell.) Swenson subsp. ***myrsinifolia***, Bartish & Munzinger, Australia, *I.V. Bartish & L. Jessup 11* (BRI, S), HE860179, DQ154066, HE995701. ***Planchonella myrsinodendron*** (F.Muell.) Swenson, Bartish & Munzinger, Australia, *I.V. Bartish & L. Jessup 2* (BRI, S), MH194019, DQ154077, MH194128. ***Planchonella obovata*** (R.Br.) Pierre, Australia, *B. Gray 5180* (L), MH194021, MH194074, MH194129. ***Planchonella orkor*** (Vink) Swenson, West New Guinea, *A.M. Polak 1365* (L), HE860181, HE860087, HE995693. ***Planchonella petaloides*** (Pierre) Dubard, Papua New Guinea, *J. Munzinger & al. 6979* (LAE, MPU, S), MH194059, MH194108, MH194167. ***Planchonella*** **Pillon 150**, New Caledonia, *Y. Pillon, L. Barrabé & F. Rigault 150* (NOU, P, S), HE860215, HE860108, HE995696. ***Planchonella pinifolia*** (Baill.) Dubard, New Caledonia, *H.S. MacKee 13886* (L, P), MH194027, AY552111, MH194136. ***Planchonella pohlmaniana*** (F.Muell.) Pierre ex Dubard, Australia, *I.V. Bartish*

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Appendix 1. Continued.

& A. Ford 22 (BRI, S), HE860216, DQ154079, HE995672. ***Planchonella polyneura*** (K.Krause) Swenson, Papua New Guinea, *J. Munzinger & al. 7010* (LAE, MPU, S), MH194028, MH194081, MH194137. ***Planchonella pomifera*** (Pierre) Dubard, West New Guinea, *McDonald & Ismail 3750* (L), MN796275, MN796266, MN796283. ***Planchonella povilana*** Swenson & Munzinger, New Caledonia, *U. Swenson & J. Munzinger 732* (BRI, NOU, P, S), MH194029, EF025102, MH194138. ***Planchonella pronyensis*** Guillaumin, New Caledonia, *J. Munzinger 2051* (NOU), HE860217, DQ154080, HE995623. ***Planchonella pullenii*** (Vink) Swenson, Papua New Guinea, *W. Takeuchi, Jisaka, A. Towati & D. Ama 21157* (LAE, S), NS, HE860120, HE995630. ***Planchonella reticulata*** (Baill.) Pierre ex Dubard, New Caledonia, *J. Munzinger, Pignal & P. Lowry 2004* (MO, NOU, P, S), MH194030, MH194082, MH194139. ***Planchonella rheophytopsis*** P.Royen, New Caledonia, *G. Dagostini 818* (NOU), MH194031, DQ154082, MH194140. ***Planchonella roseoloba*** Munzinger & Swenson, New Caledonia, *J. Munzinger 2311* (NOU, P, S), HE860218, DQ154090, HE995673. ***Planchonella rufocostata*** Munzinger & Swenson, New Caledonia, *J. Munzinger, J.-N. Labat & J.-P. Butin 2583* (NOU, S), HE860219, DQ154089, HE995684. ***Planchonella saligna*** S.Moore, New Caledonia, *J. Munzinger, D. Létocart & G. Gâteblé 2218* (NOU, P, S), HE860220, DQ154083, HE995624. ***Planchonella sandwicensis*** (A.Gray) Pierre, Hawaii, Oahu, Makaha, *K. Togikawa 1* (S), MH194047, MH194098, MH194156. ***Planchonella serpentinicola*** Swenson & Munzinger, New Caledonia, *U. Swenson & J. Munzinger 715* (S), HE860195, EF025091, MH194158. ***Planchonella skottsbergii*** Guillaumin, New Caledonia, *J. Munzinger, G. Gâteblé & R. Amice 2391* (NOU, P, S), HE860224, DQ154085, HE995674. ***Planchonella smithii*** (P.Royen) A.C.Sm., Fiji, Vanua Levu, *J. Munzinger 6495* (NOU, S, SUVA), HE860225, HE860111, HE995743. ***Planchonella spathulata*** (Hillebr.) Pierre, Hawaii, Big Island, Puuanahulu, *U. Swenson & V. Ulfsson 1617* (BISH, CAU, S), MH194032, MH194083, MH194141. ***Planchonella spectabilis*** (Miq.) Dubard, Indonesia, Sumatra, *Teysmann s.n.* (L), MN796271, MN796262, MN796279. ***Planchonella sphaerocarpa*** (Baill.) Dubard, New Caledonia, *F. Tronchet, J. Munzinger & A. Oddi 389* (MO, P), EU661403, AY552139, HE995625. ***Planchonella stellibacca*** (J.F.Maxwell) Swenson, Thailand, *A. Boonkongchart & S. Chongko 146* (L), HE860241, HE860121, HE995700. ***Planchonella tahitensis*** (Nadeaud) Pierre ex Dubard, French Polynesia, Tahiti, *J.Y. Meyer & R. Taputuarai 3051* (PAP), HE860228, EF025105, HE995744. ***Planchonella*** **Takeuchi 7166**, Papua New Guinea, *W. Takeuchi 7166* (L), MH194053, MH194103, MH194163. ***Planchonella*** **Takeuchi 25495**, Papua New Guinea, *W. Takeuchi, D. Ama & Gambia 25495* (LAE, S), HE860182, HE860088, HE995752. ***Planchonella thiensis*** Aubrév., New Caledonia, *J. Munzinger, G. Dagostini, F. Rigault & D. Kurpisz 2625* (S), HE860229, EF025106, HE995676. ***Planchonella thyrsoidea*** C.T.White, Papua New Guinea, *T.J.S. Whitfeld PA-2E-0072* (LAE, MIN, S), HE860230, HE860112, HE995745. ***Planchonella torricellensis*** (K.Schum.) H.J.Lam, Wallis and Futuna, Futuna, *J. Munzinger 5284* (NOU), HE860232, HE860114, HE995747. ***Planchonella ulfii*** Munzinger, New Caledonia, *J. Munzinger 6150* (NOU), HE860210, HE860105, HE995735. ***Planchonella umbonata*** (P.Royen) A.C.Sm., Fiji, Taveuni, *A.C. Smith 8298* (K), HE860233, DQ154086, HE995627. ***Planchonella velutina*** (Elmer) H.J.Lam, Philippines, Luzon, *J.S. Burley 97* (L), MH194057, MH194107, NS. ***Planchonella vitiensis*** Gillespie, Fiji, Ovalau, *A.C. Smith 7700* (S), HE860234, DQ154088, HE995628. ***Planchonella wakere*** (Pancher & Sebert) Pierre, New Caledonia, *J. Munzinger 1069* (MO, P, S), MH194058, AY552149, MH194166. ***Planchonella xylocarpa*** (C.T.White) Swenson, Bartish & Munzinger, Papua New Guinea, *W. Takeuchi, A. Towati & D. Ama 17284* (CANB, MO, P, S), HE860236, EF025107, HE995677. ***Pleioluma acutifolia*** Swenson & Munzinger, New Caledonia, *J. Munzinger & al. 5759* (NOU, P, S), HE860126, HE860065, HE995703. ***Pleioluma balansana*** (Pierre ex Baill.) Swenson & Munzinger, New Caledonia, Poya, *J. Munzinger & al. 4196* (MO, NOU, P, S), HE860127, HE860066, HE995704. ***Pleioluma baueri*** (Montrouz.) Swenson & Munzinger, New Caledonia, Yaté, *J. Munzinger 340* (NOU, P, S), HE860128, AY552113, HE995705. ***Pleioluma belepensis*** Swenson & Munzinger, New Caledonia, Art Island, *U. Swenson & al. 917* (MO, NOU, P, S), HE860129, HE860067, HE995706. ***Pleioluma brownlessiana*** (F.Muell.) Swenson & Munzinger, Australia, *I.V. Bartish & A. Ford 17* (BRI, MO, NOU, P, S), HE860131, DQ154063, HE995708. ***Pleioluma crebrifolia*** (Baill.) Swenson & Munzinger, New Caledonia, Kuebuni, *J. Munzinger & al. 2036* (NOU, P, S), HE860132, DQ154042, HE995597. ***Pleioluma densinervia*** (K.Krause) Swenson, West New Guinea, *A.M. Polak 1372* (L), MF572840, MF572878, MF572906. ***Pleioluma dioica*** Swenson & Munzinger, New Caledonia, Mandjélia, *U. Swenson & J. Munzinger 722* (NOU, P, S), MF572867, MF572905, NS. ***Pleioluma ferruginea*** Jessup, Australia, Queensland, *A. Ford & J. Holmes 2452* (BRI, S), MN796274, MN796265, MN796282. ***Pleioluma gillisonii*** (Vink) Swenson, Papua New Guinea, *W. Takeuchi & D. Ama 19050B* (LAE, S), HE860237, HE860116, HE995748. ***Pleioluma lamprophylla*** (K.Krause) Swenson, Papua New Guinea, *W. Takeuchi*, *D. Ama & Gambia 25573* (G, LAE, MO, P, S), HE860200, HE860098, HE995619. ***Pleioluma lasiantha*** (Baill.) Swenson & Munzinger, New Caledonia, Yaté, *J. Munzinger 2308* (NOU, P, S), HE860133, DQ154044, HE995598. ***Pleioluma laurifolia*** (A.Rich.) Swenson, Australia, *D.J. Dixon & G.J. Leach 1032* (BRI, DNA, S), HE860134, HE860069, HE995749. ***Pleioluma ledermannii*** (K.Krause) Swenson, Papua New Guinea, *W. Takeuchi & al. 17700* (LAE, S), HE860202, HE860099, HE995732. ***Pleioluma longipetiolata*** (Aubrév.) Swenson & Munzinger, New Caledonia, Ouaïème, *J. Munzinger & al. 2911* (NOU, P, S), HE860136, HE860070, HE995710. ***Pleioluma lucens*** (P.Royen) Swenson & Munzinger, New Caledonia, Yaté, *J. Munzinger & D. Létocart 2310* (NOU, P, S), HE860137, HE860071, HE995711. ***Pleioluma macrocarpa*** (P.Royen) Swenson, Australia, *I.V. Bartish & A. Ford 24* (S), HE860138, DQ154073, HE995712. ***Pleioluma macropoda*** (H.J.Lam) Swenson, Papua New Guinea, *J. Munzinger & al. 6862* (LAE, MPU, S), MF572856, MF572894, MF572911. ***Pleioluma moluccana*** (Burck) Swenson, Papua New Guinea, *W. Takeuchi, D. Ama & Gambia 25550* (S), HE860139, HE860072, HE995671. ***Pleioluma monticola*** (K.Krause) Swenson, Papua New Guinea, *van Valkenburg 451* (L), MF572857, MF572895, MF572912. ***Pleioluma novocaledonica*** (Dubard) Swenson & Munzinger, New Caledonia, Yaté, *J. Munzinger 2304* (MO, NOU, S), HE860141, HE860074, HE995714. ***Pleioluma papyracea*** (P.Royen) Swenson, Australia, *I.V. Bartish & A. Ford 20* (S), HE860142, DQ154046, HE995715. ***Pleioluma queenslandica*** (P.Royen) Swenson, Australia, *I.V. Bartish & L. Jessup 8* (S), HE860143, DQ154043, HE995659. ***Pleioluma rubicunda*** (Pierre ex Baill.) Swenson & Munzinger, New Caledonia, Mount Colnett, *U. Swenson & al. 596* (NOU, P, S), HE860144, AY552160, HE995716. ***Pleioluma sebertii*** (Pancher) Swenson & Munzinger, New Caledonia, *J. Munzinger & al. 1975* (MO, NOU, P, S), HE860145, DQ154047, HE995717. ***Pleioluma singuliflora*** (C.T.White & W.D.Francis) Swenson, Australia, *A. Ford & Metcalfe 4547* (QRS, S), HE860146, DQ246699, HE995718. ***Pleioluma tchingouensis*** Swenson & Munzinger, New Caledonia, *J. Munzinger, J.-N. Labat & J.P. Butin 2581* (NOU, P, S), HE860140, HE860073, HE995713. ***Pleioluma vieillardii*** (Baill.) Swenson & Munzinger, New Caledonia, *J. Munzinger 2282* (NOU, P, S), HE860148, DQ154087, HE995719. ***Pycnandra acuminata*** (Baill.) Swenson & Munzinger, Grande Terre, Port Bouquet, *J. Munzinger 1006* (MO, NOU, P), EU661430, AY552124, HE995631. ***Pycnandra amplexicaulis*** Munzinger & Swenson, Grande Terre, Plum, *J. Munzinger* (leg. *Lagrange*) *3315* (NOU), LN809113, LN809154, NS. ***Pycnandra atrofusca*** Swenson & Munzinger, Grande Terre, Boulinda, *J. Munzinger & al. 4968* (NOU, P, S), LN809087, LN809129, LN809170. ***Pycnandra balansae*** (Baill.) Swenson & Munzinger, Grande Terre, Tchamba, *J. Munzinger & al. 1451* (MO, NOU, P, S), EU661387, AY552123, HE995754. ***Pycnandra belepensis*** Swenson & Munzinger, Art Island, *Swenson, J. Munzinger & Barrabé 913* (S), HE860243, HE860123, HE995687. ***Pycnandra benthamii*** Baill., Grande Terre, Tchamba, *J. Munzinger & al. 2228* (NOU, P, S), EU661404, EU661436, HE995633. ***Pycnandra blaffartii*** Swenson & Munzinger, Grande Terre, Mt Colnett, *U. Swenson & al. 597* (NOU, S), EU661423, AY552127, HE995634. ***Pycnandra blanchonii*** (Aubrév.) Swenson & Munzinger, Grande Terre, Gatope, *J. Munzinger & al. 2576* (NOU, S), EU661390, DQ154059, HE995635. ***Pycnandra bourailensis*** Swenson & Munzinger, Grande Terre, Bourail, *J. Munzinger & al. 2963* (K, MO, NOU, S), EU661428, EU661450, LN809173. ***Pycnandra bracteolata*** Swenson & Munzinger, Grande Terre, Roche Ouaïème, *J. Munzinger, Y. Pillon & J.P. Butin 2885* (NOU, S), EU661421, EU661445, HE995636. ***Pycnandra caeruleilatex*** Swenson & Munzinger, Grande Terre, Forêt Nord, *J. Munzinger & al. 2622* (MO, NOU, P, S), EU661426, EU661448, HE995637. ***Pycnandra canaliculata*** Swenson & Munzinger, Grand Terre, Les Electriques, *J. Munzinger & al. 2067* (MO, NOU, P, S), EU661431, DQ154092, HE995638. ***Pycnandra carinocostata*** Vink, Grande Terre, Tchingou, *G. McPherson & J. Munzinger 18091* (NOU, S), EU661405, AY552132, HE995639. ***Pycnandra chartacea*** Vink, Grande Terre, Port Boisé, *J. Munzinger & U. Swenson 3059* (NOU, P, S), EU661406, EU661437, LN809175. ***Pycnandra comptonii*** (S.Moore) Vink, Grande Terre, Ignambi, *P.P. Lowry & al. 5780A* (MO, NOU, S), EU661407, AY552131, HE995640. ***Pycnandra comptonioides*** Swenson & Munzinger, Grande Terre, Ponandou, *J. Munzinger & al. 3068* (IND, NOU, P, S), LN809112, LN809153, LN809201. ***Pycnandra confusa*** Swenson & Munzinger, Grande Terre, *J. Munzinger & Beauvallet 5629* (NOU, S), LN809091, LN809133, NS. ***Pycnandra controversa*** (Guillaumin) Vink, Grande Terre, Ignambi, *P.P. Lowry & al. 5787* (MO, NOU, P, S), EU661408, AY552126, HE995641. ***Pycnandra cylindricarpa*** Swenson & Munzinger, Grande Terre, Mt Colnett, *U. Swenson & al. 615* (NOU, S), EU661429, AY552110, HE995757. ***Pycnandra decandra*** (Montrouz.)

Appendix 1. Continued.

Vink, Art Island, *U. Swenson, J. Munzinger & L. Barrabé 920* (S), HE860244, HE860124, HE995688. ***Pycnandra deplanchei*** (Baill.) Swenson & Munzinger, Grande Terre, Port Bouquet, *J. Munzinger 978* (MO, NOU, P, S), EU661380, AY552120, HE995642. ***Pycnandra elliptica*** Swenson & Munzinger, Grande Terre, Kuébini, *J. Munzinger 5631* (NOU, S), LN809093, LN809134, LN809180. ***Pycnandra fastuosa*** (Baill.) Vink, Grande Terre, Pwénari, *J. Munzinger & al. 1281* (MO, NOU, P), EU661410, AY552122, LN809182. ***Pycnandra filipes*** Benth., Grande Terre, Koumac, *G.L. Webster & R. Hildreth 14665* (P), EU661382, AY552135, HE995603. ***Pycnandra francii*** (Guillaumin & Dubard) Swenson & Munzinger, Grande Terre, Port Bouquet, *J. Munzinger 965* (MO, NOU, P), EU661391, AY552117, HE995644. ***Pycnandra glabella*** Swenson & Munzinger, Grande Terre, Goro, *J. Munzinger & al. 2615* (NOU, P, S), EU661418, EU661442, HE995645. ***Pycnandra glaberrima*** Swenson & Munzinger, Grande Terre, Tchamba, *J. Munzinger & al. 1394* (MO, NOU, P, S), EU661399, AY552133, HE995646. ***Pycnandra gordoniifolia*** (S.Moore) Swenson & Munzinger, Grande Terre, Bopope, *U. Swenson & J. Munzinger 726a* (NOU, P, S), EU661392, EU661433, HE995647. ***Pycnandra goroensis*** Aubrév., Grande Terre, Goro, *J. Munzinger 2288* (NOU, P, S), EU661383, DQ154052, HE995604. ***Pycnandra grandifolia*** Vink, Grande Terre, La Foa, *J. Munzinger & A. Oddi 2121* (MO, NOU, P, S), EU661384, DQ154053, HE995605. ***Pycnandra griseosepala*** Vink, Grande Terre, Mt Colnett, *Swenson, G. McPherson & A. Mouly 627* (MO, NOU, S), EU661414, AY552128, EU661528. ***Pycnandra heteromera*** (Vink) Swenson & Munzinger, Grande Terre, Humboldt, *J. Munzinger & al. 2798* (NOU, P, S), LN809099, LN809140, LN809186. ***Pycnandra intermedia*** (Baill.) Swenson & Munzinger, Grande Terre, Koungoualou, *J. Munzinger & G. Dagostini 2631* (NOU, P, S), LN809100, LN809141, LN809187. ***Pycnandra kaalaensis*** Aubrév., Grande Terre, Koniambo, *J. Munzinger & J.-N. Labat 2599* (NOU, S), EU661415, EU661440, HE995756. ***Pycnandra kopetoensis*** Munzinger & Swenson, Grande Terre, Mt Kopéto, *D. Fleurot 217* (S), MN796276, MN796267, MN796284. ***Pycnandra linearifolia*** Swenson & Munzinger, Grande Terre, Massif du Panié, *J. Munzinger & H. Blaffart 2786* (NOU, P, S), EU661427, EU661449, HE995753. ***Pycnandra lissophylla*** (Pierre ex Baill.) Swenson & Munzinger, Grande Terre, Goro, *J. Munzinger & al. 2103* (MO, NOU, P, S), LN809103, LN809144, LN809190. ***Pycnandra litseiflora*** (Guillaumin) Swenson & Munzinger, Grande Terre, Mt Kaala, *H.S. MacKee 16651* & Mt. Kopéto *17085* (NOU, P, S), EU661393, DQ154060, NS. ***Pycnandra longipetiolata*** Swenson & Munzinger, Grande Terre, Plateau de Tiéa, *J. Fambart-Tinel 181* (NOU), LN809105, LN809146, LN809192. ***Pycnandra margueriteae*** Munzinger & Swenson, Grande Terre, Bourail, *D. Fleurot 168* (NOU, P), MN796277, MN796268, MN796285. ***Pycnandra montana*** Swenson & Munzinger, Grande Terre, Mt Kouakoué, *J. Munzinger & al. 1717* (MO, NOU, P, S), EU661425, EU661447, LN809200. ***Pycnandra*** **Munzinger 5673**, Grande Terre, Mt Humboldt, *J. Munzinger & al. 5673* (NOU), LN809116, LN809157, LN809204. ***Pycnandra neocaledonica*** (S.Moore) Vink, Grande Terre, Col d'Amoss, *F. Tronchet & al. 426* (MO, NOU, P, S), EU661416, AY552129, HE995649. ***Pycnandra obscurinerva*** (Vink) Swenson & Munzinger, Grande Terre, Tiébaghi, *J. Munzinger 1913* (NOU), EU661432, DQ154095, LN809196. ***Pycnandra ouaiemensis*** Swenson & Munzinger, Grande Terre, Roche Ouaïème, *J. Munzinger & al. 3135* (NOU, P, S), EU661422, EU661446, HE995689. ***Pycnandra paucinervia*** Swenson & Munzinger, Grande Terre, Tchamba, *J. Munzinger & al. 1438* (NOU, P, S), EU661424, AY552159, HE995650. ***Pycnandra perplexa*** Swenson & Gâteblé, Grande Terre, Dzumac, *G. Gâteblé, Y. Isagi & Y. Suyama 1068* (MPU, NOU, P, S), MW924281, MW843560, MZ245659. ***Pycnandra petiolata*** Vink, Ile Yandé, *U. Swenson & J. Munzinger 714* (NOU, S), EU661385, LN809125, LN809166. ***Pycnandra poindimiensis*** Swenson & Munzinger, Grande Terre, Poindimié, *U. Swenson & J. Munzinger 1134* (MO, MPU, P, S), LN809118, LN809159, LN809206. ***Pycnandra pubiflora*** Swenson & Munzinger, Grande Terre, col de Mouirange, *J. Munzinger & al. 2624* (NOU, P, S), EU661420, EU661444, HE995651. ***Pycnandra sarlinii*** (Aubrév.) Swenson & Munzinger, Grande Terre, Plateau Dogny, *J. Munzinger 1860* (NOU, P, S), EU661395, EU661435, HE995652. ***Pycnandra schmidii*** (Aubrév.) Swenson & Munzinger, Grande Terre, Tchingou, *G. McPherson & J. Munzinger 18106* (NOU, S), EU661396, AY552116, HE995653. ***Pycnandra sclerophylla*** Munzinger & Swenson, Grande Terre, Pouembout, *J.-M. Veillon 8117* (NOU, P), EU661386, AY552136, LN809208. ***Pycnandra sessiliflora*** Swenson & Munzinger, Grande Terre, Forêt Nord, *J. Munzinger 2608* (NOU, S), LN809109, LN809150, LN809197. ***Pycnandra sessilifolia*** (Pancher & Sebert) Swenson & Munzinger, Grande Terre, Tchingou, *G. McPherson & J. Munzinger 18176* (MO, P), EU661397, AY552118, HE995654. ***Pycnandra versicolor*** Swenson & Munzinger, Grande Terre, Koniambo, *J. Munzinger 6089* (NOU, P, S), LN809117, LN809158, LN809205. ***Pycnandra vieillardii*** (Baill.) Vink, Grande Terre, Aoupinié, *V. Dumontet, C. Zongo & P. Maituku s.n.* (S), EU661417, EU661441, HE995655. ***Pycnandra viridiflora*** Swenson & Munzinger, Grande Terre, Poya, *J. Munzinger & al. 4195* (NOU, P, S), HE860245, HE860125, HE995656. ***Pycnandra wagapensis*** (Guillaumin) Munzinger & Swenson, Grande Terre, *J. Munzinger & al. 5634* (NOU, P, S), HE860151, HE860077, HE995601. ***Sahulia subopposititifolia*** (H.J.Lam) Swenson, Papua New Guinea, *R. Pullen 7499* (L), MN796273, MN796264, MN796281. ***Sersalisia luzoniensis*** (Merr.) Swenson, Papua New Guinea, *B.J. Conn & al. 5063* (L), HE860238, HE860117, HE995697. ***Sersalisia sericea*** (Aiton) R.Br., Australia, Northern Territory, *R.K. Harwood 1172* (S), HE860246, AY552112, HE995657. ***Sersalisia sessiliflora*** (C.T.White) Aubrév., Australia, Queensland, *I.V. Bartish & A. Ford 33* (BRI, MO, P, S), HE860247, DQ154094, HE995678. ***Van-royena castanosperma*** Aubrév., Australia, *I.V. Bartish & A. Ford 26* (BRI, MO, NOU, P, S), HE860248, DQ154096, HE995658.

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