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Towards a natural classification of Sapotaceae subfamily Chrysophylloideae in Oceania and Southeast Asia based on nuclear sequence data

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Abstract Generic limits within subfamily Chrysophylloideae (Sapotaceae) from Oceania and Southeast Asia are reconciled based on a molecular phylogeny. We analysed sequences of nuclear ribosomal DNA (ETS, ITS) and the nuclear gene RPB2 with BEAST and parsimony jackknifing, using a sample of 168 terminals. Eight morphological characters were traced on a condensed majority-rule consensus tree to identify diagnostic character combinations for the genera. Accepted genera with character support are *Magodendron*, *Pichonia*, *Planchonella*, *Pycnandra*, *Sersalisia*, and *Van-royena*, while *Beccariella* and *Niemeyera* require amendment. *Beccariella*, a widely distributed group, is an illegitimate later homonym and we propose that the genus *Pleioluma* is resurrected in its place. The Australian genus *Niemeyera* is paraphyletic, but it is rendered monophyletic by reinstating *Amorphospermum* for *N. antiloga*. *Beauvisagea*, *Blabeia*, *Fontbrunea*, and *Krausella* are all segregates of *Planchonella* and rejected, while *Wokoia* is a later synonym of *Pichonia*. *Planchonella baillonii*, an endemic species of New Caledonia, is the sole member of an old lineage and firmly placed as the sister to a clade comprising the other congeners. *Planchonella sandwicensis*, a Hawaiian species, previously proposed to be a distinct genus, is a member of *Planchonella*. In the Pacific, *P. tahitensis* (including *P. grayana*) is a polymorphic species, widely distributed and adapted to a wide range of habitats. We provide a generic key (excluding *Xantolis*), diagnostic character combinations for all genera, and the necessary taxonomic combinations for *Pichonia*, *Planchonella*, *Pleioluma*, and *Sersalisia* to render each genus monophyletic.

Keywords *Amorphospermum*; Australasia; Ericales; morphology; Pacific Ocean; phylogeny; *Pleioluma*; Sapotaceae

Supplementary Material Aligned data matrix is available as Supplementary Data of the online version of this article (<http://www.ingentaconnect.com/content/iapt/tax>).

INTRODUCTION

Sapotaceae are an important component of the rainforests around the world. Its members are readily identified based on the presence of white latex, malpighiaceae trichomes, simple and entire leaves, and flowers in fascicles. Natural groups in the family have been difficult to circumscribe because of morphological homoplasy. Various systems of classification recognizing anything from 53 to 122 genera have been proposed (Lam, 1939; Aubréville, 1964; Baehni, 1965; Pennington, 1991). Recent phylogenetic analyses using molecular data, often combined with morphological characters (Anderberg & Swenson, 2003; Smedmark & al., 2006), have identified three major lineages, which now are formally recognized as subfamilies Chrysophylloideae, Sapotoideae, and Sarcospermatoidae (Swenson & Anderberg, 2005). Chrysophylloideae are most diverse in South America and Australasia, Sapotoideae in Africa and Asia, while Sarcospermatoidae are restricted to Asia. Many systematic and biogeographic problems remain unsolved within each subfamily, and this paper focuses on systematic issues in the Chrysophylloideae of Oceania and Southeast Asia.

All members of Chrysophylloideae in Australasia form a monophyletic group (Swenson & Anderberg, 2005; Bartish & al., 2005; Swenson & al., 2008b), and molecular dating suggests emergence in the area by the Early Eocene, some 52 million years ago (Ma), with subsequent radiation, range expansion and multiple dispersals to New Caledonia (Bartish & al., 2011). Phylogenetic analyses of the Australasian members (Bartish & al., 2005; Triono & al., 2007; Swenson & al., 2007a) suggest that at least seven lineages can be delineated as genera, which prompted Swenson & al. (2007a) to recognize *Magodendron* Vink, *Niemeyera* F. Muell. and *Pichonia* Pierre, and to resurrect the *Pouteria* Aubl. segregates *Beccariella* Pierre, *Planchonella* Pierre, *Sersalisia* R. Br. and *Van-royena* Aubrév. (Fig. 1). However, the phylogenetic study by Swenson & al. (2007a) revealed several problems: (i) a large polytomy prevented them from conclusive hypotheses about intergeneric relationships, (ii) *Van-royena* either grouped with the Australian species *Niemeyera antiloga* (F. Muell.) T.D. Penn. or collapsed into a polytomy, and (iii) generic limits remained unclear within an Australian – New Caledonian clade, the *Niemeyera* complex.

Generic limits in the *Niemeyera* complex have been assessed by phylogenetic analyses using nuclear (ETS, ITS) and chloroplast (*trnH-psbA*, *trnS-G*) sequence data, as well as morphology (Swenson & al., 2008a). The complex included seven genera in the classification by Aubréville (1964, 1967), a number that was decreased to three by Pennington (1991). Both authors recognized *Leptostylis* Benth., a genus distinguished by opposite (rather than alternate) leaves and four sepals (not five or more). There are two strongly supported clades in the complex, one confined to Australia and another to New Caledonia, the latter with several subclades but with weak internal node support. Two morphological characters traditionally used for generic recognition in the *Niemeyera* complex are the anisomerous flower and the number of stamens inserted opposite each corolla lobe. Both characters are highly homoplastic and are not diagnostic even for small subclades (Swenson & al., 2008a). A generic framework based on a monophyletic criterion was proposed that allowed recognition of anywhere from one to five genera, a framework differing from the concept used by Aubréville or Pennington. Nonetheless, based on unpublished molecular data and the discovery of several new species, Swenson & Munzinger (2009) found that a narrow generic concept was untenable and accepted *Niemeyera* for the species in Australia and *Pycnandra* Benth. for the lineage confined to New Caledonia. The New Caledonian subclades were relegated to subgeneric rank. However, it is still unclear if *Leptostylis* can be recognized at generic level or if it is better subsumed in *Pycnandra*.

Beccariella and *Planchonella* are usually rainforest trees or shrubs in maquis vegetation. They are widely distributed in Oceania and Southeast Asia and have convoluted taxonomic histories (Swenson and Morat, 2008; Swenson and Tehler, 2009). As currently circumscribed, *Beccariella* includes some 20 species and *Planchonella* about 60 species (Swenson & al., 2007a, 2007b). Some outdated revisions are available for Malesia, but at that time the species were distributed among *Planchonella* (99 spp.; van Royen, 1957), *Krausella* H.J. Lam (4 spp.; Herrmann-Erlee & Lam, 1957), and *Pouteria* (28 spp.; Herrmann-Erlee & van Royen, 1957). Groups were so

poorly delimited that the revision of *Pouteria* treated taxa that now are firmly placed in *Beccariella*, *Pichonia*, *Planchonella*, *Pycnandra*, and *Sersalisia* (Swenson & al. 2007a; Swenson & Munzinger, 2010a). *Pouteria* is a genus restricted to South America (Swenson & al., 2008b). There are no unique synapomorphies for either *Beccariella* or *Planchonella*, but they are distinguished based on character combinations. Common characters of both genera include flowers with a corolla with staminodes, styles with stigmatic areas visible using a hand lens, seeds with foliaceous cotyledons, a radicle that extends below the cotyledon commissure, and an endosperm. Species of *Beccariella* are identified by areolate leaf venation (tertiaries or quaternaries), stamens inserted in the middle or near the base of the corolla tube, a fruit with usually one (or two) seed(s), and a linear and shorter seed scar that often is 50–75% of the length of the seed. Species of *Planchonella* are recognized by the lack of areolate leaf venation, stamens that are inserted just below the tube orifice (with a few exceptions), a fruit having up to five seeds, and a long seed scar that often is linear and covers 90–100% of the seed length. However, in contention with this, a search (accessed March 2013) in the online World Checklist at the Royal Botanical Garden, Kew (<http://apps.kew.org/wcsp/home.do>) for taxa in these genera (and native to Southeast Asia and Oceania), revealed 17 species of *Beccariella*, 107 of *Planchonella*, and 28 of *Pouteria*, which we believe reflects an unnatural classification.

Planchonella is the largest and most widely distributed genus of Chrysophylloideae in Oceania and Southeast Asia. It has a circum-Pacific distribution extending from southern China, Thailand, south to Australia and New Zealand, into the Pacific to include French Polynesia, Hawaii and back to Taiwan. New Caledonia is recognized as an important hotspot of biodiversity (Myers & al., 2000; Lowry & al., 2004) and includes almost 40 species of *Planchonella* (Munzinger & Swenson, 2009). Species of this genus exhibit intriguing traits, such as a gynomonocious sexual system (Méndez & Munzinger, 2010), as well as being successful colonizers of the Pacific islands (Bartish & al., 2005). One New Caledonian endemic species, *P. baillonii* (Zahlbr.) Dubard, is the sole member of a lineage that is sister to the entire genus (Swenson & al., 2007a; Triono & al., 2007). This sister position was maintained in a phylogenetic analysis using nine cpDNA and nrDNA loci (Swenson & al., 2008b), but the study only included seven species of *Planchonella*. It is pertinent to address the phylogenetic position of *P. baillonii* in a broader context because New Caledonia seems to have been submerged after rifting from Australia and therefore unavailable for colonization before 37 Ma (Grandcolas & al., 2008), but see Heads (2008) for an alternative view.

Apart from the species in New Caledonia, few studies have addressed problems concerning the *Planchonella* species occurring in the Pacific. Here we will address phylogenetic relationships among taxa found in Hawaii and French Polynesia. *Planchonella sandwicensis* (A. Gray) Pierre grows on all main islands of Hawaii. It is an extremely variable species that has inspired some scholars to recognize up to six different species (see Wagner & al., 1990). There are two widely different hypotheses on its relationships. Swenson & al. (2007a, 2007b) found a close relationship to taxa in Fiji. In contrast, Triono & al. (2007) found it as the sister species to subfamily Chrysophylloideae, i.e., a possible member of Sapotoideae or Sarcospermatoideae. If the former is correct, the species is most probably derived from a common ancestor within the Pacific region, which colonized Hawaii from islands in the west, but if the latter is true, then the evolutionary lineage ought to be very old and its origin is more difficult to explain, since the closest relatives are presently found in continental Southeast Asia. However, the generated sequences by Triono & al. (2007) were never submitted to GenBank (<http://www.ncbi.nlm.nih.gov/> last accessed March 2013), making them inaccessible for further testing.

Two Pacific species of *Planchonella*, *P. grayana* H. St. John and *P. tahitensis* (Nadeaud) Pierre ex Dubard (Fig. 1J), are at odds with all other species of the genus by having stamens inserted near the base of the corolla tube, rather than below the tube orifice as is diagnostic for the genus (Swenson & al., 2007b). *Planchonella grayana* occurs from Vanuatu in the west to Tuamotu (French Polynesia) in the east, while *P. tahitensis* is restricted to the Society Islands. Distinct morphological forms have also been described from Tahiti (Fosberg, 1992) or are possibly novel species, for instance from Raiatea (Society Islands). The phylogenetic positions of

these species are of interest due to their odd floral morphology, taxonomic status, and conservation status. The native flora of the Society Islands, including *P. tahitensis* (Taputuari & Tchung, 2003; Pouteau & al., 2012), is under threat from the invasive alien *Miconia calvescens* DC. (Melastomataceae; Meyer & Florence, 1996).

The present study aims to estimate phylogenetic relationships within Chrysophylloideae in Oceania and Southeast Asia, excluding the distantly related Asian *Xantolis* ?? (Anderberg & Swenson, 2003; Swenson & Anderberg, 2005), by using an extended taxon sample and nrDNA sequence data (ETS, ITS, RPB2), analysed using Bayesian inference and parsimony jackknifing. Our primary goals are to: (i) resolve the backbone polytomy; (ii) test the generic concept proposed by Swenson & al. (2007a); (iii) investigate the relationships of *Van-royena* and *Niemeyera antiloga*; (iv) optimize diagnostic morphological characters on the phylogeny; (v) solve the specific questions pertinent to *Planchonella* in French Polynesia, *P. baillonii* in New Caledonia, and *P. sandwicensis* in Hawaii; and (vi) make nomenclatural changes as far as possible to obtain monophyletic genera.

MATERIALS AND METHODS

Nomenclature and taxon sampling. — We follow the subfamily classification of Swenson & Anderberg (2005). The checklist of Sapotaceae (Govaerts & al., 2001) follows Pennington's (1991) generic classification and includes a full list of published names, but accepted names are continuously updated online at the World Checklist of Selected Plant Families, Royal Botanical Garden, Kew (<http://apps.kew.org/wcsp/home.do>). This online resource follows the amended classification proposed by Swenson & al. (2007a), which we herein follow and aim to test.

A total of 168 terminals were selected for this study, including all type species of the genera recognized to date except for *Leptostylis longiflora* Benth. (probably conspecific with *L. filipes* Benth.) and *Magodendron* (Appendix 1) as well as the generi-types of two *Pouteria* segregates: *Blabeia* Baehni (represented by *Planchonella endlicheri* (Montrouz.) Guillaumin) and *Fontbrunea* Pierre (represented by *Pouteria malaccensis* (C.B. Clarke) Baehni). We also included two species of *Krausella*, one of *Beauvisagea* Pierre, represented by *Pouteria maclayana* (F. Muell.) Baehni (Govaerts & al., 2001), two unplaced species of *Chrysophyllum* L., and finally three species of *Leptostylis* (Aubréville, 1967). The remaining terminals are names to be found online at the World Checklist resource (accessed March 2013). A few taxa, however, are either novel or impossible to determine and are therefore indicated by quotation marks. The systematic problem of *Planchonella sandwicensis* is addressed using three accessions, two from Oahu and one from Kauai. The problem of French Polynesian *Planchonella* is approached with seven accessions collected in Wallis and Futuna (a French territory northeast of Fiji) and from several archipelagos of French Polynesia (Austral, Society, and Tuamotu Islands). Our sample includes all accepted species of *Beccariella* and *Niemeyera*, 80% of *Pichonia* and *Sersalisia*, 72% of *Pycnandra*, and 57% of *Planchonella*. In addition, nine accessions of *Pouteria* are included that are predicted to belong to one or the other clade.

When an outgroup is selected it ought to be as closely related as possible, but not necessarily the sister group to the ingroup, and it need not necessarily include more than one taxon (Nixon & Carpenter, 1993). *Xantolis* and the Australasian clade represent Chrysophylloideae in Southeast Asia and Oceania; the latter has been demonstrated monophyletic in all recent cladistic analyses using morphology and/or molecular evidence (Bartish & al., 2005, 2011; Swenson & Anderberg; Swenson & al., 2007a, 2008b). *Xantolis* is sister to the entire subfamily and strongly diverged from the Australasian taxa, and therefore not an appropriate outgroup. Genera that form the sister clade to the Australasian taxa are all from South America, a clade that possibly includes the African genus *Aubreginia* Heine. We therefore selected two species of *Ecclinusa*, a genus suggested to be one of the closest relatives to the Australasian taxa (Swenson & al., 2008b; Bartish & al., 2011). If any of the

additional taxa included here were not to be member of this clade, they are expected to fall between the outgroup and the Australasian clade, not within it.

Molecular data. — Selection of molecular markers to provide a sufficient number of informative characters needs consideration. Different cpDNA regions vary in their relative utility to resolve relationships within angiosperm families (Shaw & al., 2005, 2007). Broad studies of Sapotaceae have used several coding and noncoding cpDNA and nrDNA regions with varying success. Of the cpDNA regions used for phylogenetic estimates (*atpβ-rbcL*, *ndhF*, *petN-psbM*, *psbM-trnD*, *psbB-psbH*, *rpl20-rps12*, *trnC-petN*, *trnH-psbA*, *trnL-trnF*, and *trnS-trnG*) the average number of informative substitutions is close to 3%, where *trnS-trnG* has 1% (Swenson & al. 2008a) and *trnH-psbA* has 6% informative sites (Swenson & al., 2008b). In contrast, the nrDNA loci ITS and ETS have proven to be much more useful with some 23–54% informative characters (Bartish & al., 2005; Swenson & al., 2008b), which is why they were selected for this study.

Plant material for DNA extraction was collected either as silica gel dried leaf material or fragments removed from herbarium specimens. New sequences of ITS1 and ITS2 were obtained from 61 accessions, following the protocol for DNA extraction, amplification, and sequencing described by Bartish & al. (2005), and added to 106 previously published sequences. All primers are listed in Table 1. ETS sequences of 122 accessions were obtained by using two primers, 18S-ETS (Baldwin and Markos, 1998) and Sap-1 (Swenson & al., 2008a), following the touchdown PCR protocol: 95°C for 5 min, followed by 4 cycles of 95°C for 30 s, 57°C for 30 s, 72°C for 1 min 15 s, 4 cycles of 95°C for 30 s, 55°C for 30 s, 72°C for 1 min 15 s, and 32 cycles of 95°C for 30 s, 53°C for 30 s, 72°C 1 min 15 s followed by 72°C for 8 min. Both ITS and ETS may occur in multiple copies in a genome, which can indicate hybrid origin of a taxon (Poczai and Hyvönen, 2010). We carefully checked the sequences for double peaks in the proof reading procedure for the presence of multiple copies. Multiple copies of ETS were detected in eight *Planchonella* species, all from a clade confined to New Caledonia, i.e. Clade D3b identified by Swenson & al. (2007b). We decided to exclude these and reduced the clade to three species (*P. glauca*, *P. lauracea*, and *P. "Ile Yande"*) in order to minimize problems related to concerted evolution or lineage sorting (Álvarez & Wendel, 2003).

We sought to include an additional nuclear marker and selected RPB2, which has proven to be useful for phylogenetic estimates on high as well as low systematic level (Oxelmann & Bremer, 2000; Oxelman & al., 2004; Eggens & al., 2007). The RPB2 region for 161 accessions was amplified using the primers P6F and P7R (Denton & al., 1998), and several herein designed primers to obtain sequences around poly-T-regions, followed by the same PCR protocol described above. Purified products were sequenced using an ABI3130xl Automated DNA Sequencer (Applied Biosystems, Foster City, California, USA).

Alignment, gap coding, and model testing. — Alignments were performed on each separate sequenced locus in MAFFT v.6.818b (Katoh & al., 2005) using the L-INS-i predefined parameter settings. Resulting matrices were imported into MESQUITE (Maddison & Maddison, 2011) and minor manual adjustments were made to the alignments. Following the method of Simmons and Ochoterena (2000), gaps for each locus were manually scored as binary characters (present/absent) in separate partitions, disregarding uninformative deletions or inserts. Each gene partition was tested for the best-fit substitution model using jModelTest (Posada, 2008) under the Bayesian information criterion (BIC) (Schwartz 1978; Posada & Buckley, 2004) in order to minimize the number of substitution rate parameters. Binary data (gaps) were assigned a simple substitution model allowing unconstrained reversible gains/losses of characters.

Phylogenetic analyses. — Phylogenetic relationships were estimated with Bayesian inference (Rannala & Yang, 1996; Yang & Rannala, 1997) and parsimony jackknifing (Farris & al., 1996). The aligned matrix was prepared in BEAUti 1.6.2 (part of the BEAST package) as an output file for Bayesian inference in BEAST 1.6.2

(Drummond & Rambaut, 2007). Each locus was treated as a unique partition. Substitution models were set by manual modification of the rate parameters. This study used the BEAST package to primarily derive a tree topology, not divergence time estimates under a molecular clock assumption. The molecular clock was therefore unconstrained and the root was fixed by using a normal prior with an arbitrary mean (100) and a narrow standard deviation (0.1). The Monte Carlo Markov chains (MCMC) were set to run five times, each for 100 million generations, to assure independent convergence on all parameters (ESS values >200), sampling trees every 25,000 generations. Convergence and chain mixing were reviewed in Tracer v1.5 (Rambaut & Drummond, 2009). A proportion of the samples in each run were discarded as burn-in, and the posterior set of trees was summarized in TreeAnnotator 1.6.2 (Drummond & Rambaut, 2007). The resulting tree was then visualized in FigTree v1.3.1 (Rambaut, 2009).

Jackknife analysis, implemented in PAUP* 4.0 (Swofford, 2002), was also performed on the dataset to retrieve parsimony support values. The settings were as follows: 1000 jackknife replicates with a single random addition sequence, TBR branch swapping, collapsing branches of zero length, steepest descent not in effect, and saving a maximum of 1000 trees in each replicate. The excluded fraction of characters in each replicate was set to 37%.

Posterior probability (PP) and parsimony jackknife values (JK) below 0.8 and 50%, respectively, are not reported. We consider PP values of 0.95 or more to be strong indicators of node support, whereas JK values of 50–74% are weak, 75–89% moderate, and 90–100% are considered strong. Nodes that receive less than JK 50% and below PP 0.8 posterior support are collapsed in the phylogeny with one exception (the plausible position of *Van-royena*).

Morphological data. — Morphology is highly homoplastic in Sapotaceae and unique generic synapomorphies are absent or very rare. Swenson & al. (2007a) proposed that character state combinations ought to be used for generic recognition. The morphological data used here have been gathered from earlier studies (Swenson & Anderberg, 2005; Swenson & al., 2007a, 2007b, 2008a, 2008b), revisions (van Royen, 1957; Herrmann-Erlee & Lam, 1957; Herrmann-Erlee & van Royen, 1957) and herbarium material deposited at L, MO, NOU, P, PAP, and S (abbreviations follow Holmgren & al., 1990). The morphological terminology follows Harris & Harris (1997). We used MacClade 4.0 (Maddison & Maddison, 2000) to optimize the characters on the maximum clade credibility tree (MCC) obtained from the BEAST analysis. We then condensed the phylogeny, opting for genera to be in proportion to the number of the species, and traced eight characters of which seven have been identified as useful for diagnostic purposes (Swenson & al., 2007a). One character, pubescence on sepals, is used here for the first time. The condensed tree is designed to comprehensibly visualize the characters.

Character 1. — Tertiary leaf venation has been used for diagnostic purposes with variable success (van Royen, 1957; Pennington, 1991; Triono & al., 2007). A fine areolate venation, formed when higher orders of veins anastomose and form a closed reticulate pattern, easily observed with a hand lens (Swenson & Munzinger, 2009), is diagnostic for *Beccariella*, *Pichonia*, and *Sersalisia* (Swenson & al., 2007a).

Character 2. — Malpighiaceae trichomes are usually present as an indument on sepals on inner, outer, or both surfaces, but can also be secondarily lost. Revisional work has demonstrated that the distribution of trichomes can indicate relationships. For example, sepals of *Planchonella* and *Pycnandra* are usually pubescent outside but glabrous inside (Swenson & al., 2007b; Swenson & Munzinger, 2009), while members of *Pichonia* usually have an indument on both sides of the sepals (Swenson & Munzinger, 2012). Thus, presence or absence of trichomes on the inner surface may be congruent with clades.

Character 3. — The corolla of Sapotaceae is actinomorphic and partly sympetalous, comprising a tube and free corolla lobes. Depending on the ratio between the length of the corolla tube and the lobes, and the corolla length versus the calyx length, the corolla can be cup-shaped, urn-shaped, narrowly campanulate, or tubular. This character is in fact a combination of different features and could be reductively coded for phylogenetic analyses, but it is also homoplastic (Swenson & Anderberg, 2005; Swenson & al., 2007a, 2008b). There is no doubt that flower types are frequently difficult to characterize, but we wanted to investigate their potential diagnostic value as a character. The calyx of a cup-shaped flower is usually less than 50% of the length of the corolla, the corolla tube is shorter than the lobes, and the lobes are spreading (Fig. 1A, D). The corolla of an urn-shaped flower usually has a tube and corolla lobes of equal length (or slightly shorter lobes), and the calyx often extends above the corolla tube orifice (Fig. 1 I–J). A campanulate flower is similar to an urn-shaped and/or a tubular flower, but the corolla exerts slightly above the sepals and forms a small bell (Fig. 1L). Tubular flowers have a visible corolla tube, longer than the sepals and clearly longer than the corolla lobes (Fig. 1F–H).

Character 4. — Stamens in Sapotaceae are inserted at different levels in the corolla tube. This character was important for Aubréville (1964) and less so for Pennington (1991), but has been found to be diagnostic for monophyletic groups (Swenson & al., 2007a). Hence, stamens are inserted in the tube orifice (*Niemeyera*, *Pichonia*, and *Pycnandra*), just below the tube orifice (*Planchonella*), in the middle of the tube or near the corolla base (*Beccariella*).

Character 5. — One entire style is always present in Sapotaceae, which may, however, differ at the apex. It has either visible, small, round stigmatic areas readily identified with a hand lens (Fig. 1F), a character suggested diagnostic for *Beccariella*, *Planchonella*, *Sersalisia*, and *Van-royena* (Swenson & al., 2007a). In contrast, if no stigmatic areas are visible (Fig. 1A), the style apex is termed simple as in *Niemeyera*, *Pichonia*, and *Pycnandra* (Pennington, 1991; Swenson & Anderberg, 2005).

Character 6–8. — A number of fruit characters show strong congruence and can be amalgamated to three features: (i) cotyledons foliaceous, having a radicle extending below the cotyledon commissure, endosperm present; (ii) plano-convex cotyledons without a visible radicle, endosperm absent; and (iii) plano-convex cotyledons with an exerted radicle, endosperm absent.

RESULTS

Data. — The complete matrix contains 2563 characters, of which 2486 are from aligned nuclear sequences and 77 are from three partitions of coded gaps (Table 2). ETS is represented by 403 nucleotides of which 198 (49.1%) are parsimony informative, ITS of 914 nucleotides of which 320 (35%) are parsimony informative, and RPB2 of 1169 nucleotides of which 151 (12.9%) are parsimony informative.

The model test resulted in the selection of TrN+ Γ for both ETS and ITS, and TPM1+ Γ for RPB2. Initial analyses revealed nested parameter ranges for ITS and ETS, and the two loci were therefore set to share the substitution model in order to decrease the total number of parameters.

Tree topology. — Bayesian analysis and parsimony jackknifing of the molecular dataset recovered similar tree topologies. Taxa not formerly analysed in any phylogenetic context are all recovered with maximum support within the previously identified Australasian clade. After collapsing nodes with support below the defined thresholds (0.8 PP and 50% JK), the tree topologies are close to identical (Fig. 2). Polytomies are mainly restricted to terminal positions in each genus. One deep node receives only moderate JK support (83%) and no

Bayesian support. Similar to previous results, the placements of the Australian *Van-royena* and the New Guinean *Magodendron* are still uncertain, and no other taxon is identified as closely related to these genera which, in addition, have rather unusual diagnostic character combinations (Swenson & Anderberg, 2005; Swenson & al., 2007a).

All species included in our analyses were dispersed across six distinct clades with strong Bayesian support and frequently with moderate or strong jackknife support. Each of these clades include one generic type (from top to bottom in Figure 2): *Beccariella sebertii* (Panther) Pierre, *Sersalisia sericea* (Aiton) R. Br., *Pichonia balansana* Pierre, *Niemeyera prunifera* (F. Muell.) F. Muell., *Pycnandra benthamii* Baill., and *Planchonella obovata* (R. Br.) Pierre. Embedded in these six clades are species of *Chrysophyllum*, *Krausella*, *Leptostylis*, *Pouteria*, and *Planchonella* (in *Beccariella*) and the genera can only be rendered monophyletic following taxonomic transfers. However, *Niemeyera* is not monophyletic in its present circumscription since *N. antiloga* is rendered sister to the two clades corresponding to *Niemeyera* and *Pycnandra*. Both genera are strongly supported, but subclades relegated to subgeneric rank in the latter genus (Swenson & Munzinger, 2009) are all recovered in a polytomy. All species of *Leptostylis* and the unplaced *Chrysophyllum wagapense* Guillaumin form a clade that is sister, with weak support, to subgenus *Sebertia* (Pierre ex Engl.) Swenson & Munzinger (Swenson & Munzinger, 2010a).

Planchonella is largely monophyletic with the exception of four species that are recovered in *Beccariella* with strong support. Again, *P. baillonii* is sister to the entire genus. The unplaced *Chrysophyllum bakhuizenii* P. Royen, the *Pouteria* segregate *Krausella*, and some species currently placed in *Pouteria*, are all embedded in *Planchonella*. Overall, the clades identified by Swenson & al. (2007b; Clades D1, D2, and D3), are all strongly supported in this phylogeny and mutual clade relationships find good support. Two widely distributed species in Southeast Asia, *Pouteria maclayana* and *P. malaccensis*, are sisters to Clades D1 and D2. All three accessions of *P. sandwicensis* from Hawaii group together within *Planchonella*, a group with close affinity to taxa from Fiji. All accessions of *P. grayana* and *P. tahitensis*, from Alofi and Futuna in the west to Tuamotu in the east, are found monophyletic with maximum support, but mutual molecular differences are small and accessions are not reconciled to species or distribution. One clade circumscribes three accessions of *P. linggensis* (Burck) Pierre, one of *P. chartacea* (F. Muell. ex Benth.) H.J. Lam (Australia), and one of *P. solida* P. Royen (New Guinea), in which *P. linggensis* is polyphyletic.

Optimization of morphology. — Figure 3 shows the eight morphological characters optimized on the majority-rule consensus tree obtained from the BEAST analysis of nuclear sequences of Chrysophylloideae in Oceania and Southeast Asia. They show all high congruence with the generic concept proposed by Swenson & al. (2007a), but some characters still show a degree of homoplasy. This will be discussed below.

DISCUSSION

Overall resolution. — Our phylogenetic analyses based on nuclear sequence data yielded improved resolution and a better understanding of phylogenetic relationships within Chrysophylloideae (Bartish & al., 2005; Swenson & al., 2007a, 2007b, 2008a; Triono & al., 2007). Exact affinities of *Magodendron* and *Van-royena* remain unclear and both genera, in principle, fall back to an unresolved polytomy. Nevertheless, our current analyses find no close relationship between *Van-royena* and *Niemeyera antiloga*, since the latter is strongly supported as the sister to *Pycnandra* and a narrowly defined *Niemeyera* (Fig. 2). The proposal that *Chrysophyllum* and *Pouteria* are not present in Australasia (Swenson & al., 2007a, 2008b; Swenson & Munzinger, 2009) finds strong phylogenetic support, because the included taxa are deeply embedded in different Australasian groups. Instead, for this region, the genera *Beccariella*, *Magodendron*, *Niemeyera*, *Pichonia*, *Planchonella*, *Pycnandra*, *Sersalisia*, and *Van-royena* are reconfirmed, and no other important lineage of the

subfamily is identified. Hence, members currently placed in *Chrysophyllum* or *Pouteria* need to be transferred. *Leptostylis* need to be relegated to subgeneric level within *Pycnandra*, and a revision is under preparation. However, two systematic problems remain to be solved: the polyphyly of *Niemeyera* and the unresolved nomenclatural problem concerning the name *Beccariella* (Swenson & Tehler, 2009; Brummitt, 2011b).

The overall well resolved phylogeny brings to light interesting biogeographic perspectives, such as whether New Caledonia hosts a relict biota or was submerged about 37 Ma and later emergent (Grandcolas & al., 2008); and whether the Fijian flora is derived from immigrants from Asia, Australia, and/or New Caledonia (Keppel & al., 2009) or evolved in situ (Heads, 2006). A detailed biogeographic study of this Australasian-Pacific group will be addressed elsewhere.

Useful morphological characters. — Morphology has repeatedly been demonstrated to be homoplastic in Sapotaceae. Examples of traditionally used characters believed useful but shown to be homoplastic include the number of petals, the number of stamens opposite each corolla lobe, and the ratio between the length of the corolla tube and the corolla lobes (Swenson & al., 2007a, 2008a, 2008b). Presence of staminodes in Sapotaceae is a plesiomorphic feature, which has been reduced several times in Chrysophylloideae (Swenson & Anderberg, 2005; Swenson & al., 2008b) and Sapotoideae (Smedmark & al., 2006), but can be diagnostic for less inclusive groups. Staminodes are present in most Chrysophylloideae in the studied group, but have been reduced once, in the clade *Niemeyera* – *Pycnandra*. Hence, absence of staminodes is diagnostic for this clade. Another useful character to distinguish between genera is where the flowers are born. All genera, except *Magodendron* and *Pycnandra*, generally have axillary flowers, whereas the former is cauliflorous and the latter is usually ramiflorous. Apart from morphology, geographic distribution is a very strong indicator of clade affinity, except in the widespread genera *Beccariella*, *Planchonella*, and *Sersalisia*. In the discussion below of the eight morphological characters used here, taxon names are ordered as they appear in Fig. 3 (not alphabetically).

Areolate venation is present in all species of *Beccariella*, *Sersalisia*, *Pichonia*, and *Magodendron*, including all species of *Planchonella* and *Pouteria* that are recovered in these clades (Fig. 3A). In contrast, members of *Van-royena*, *Niemeyera*, *Pycnandra* and *Planchonella* always lack areolate venation, and instead have visible tertiary leaf venation, in agreement with the findings of Triono & al. (2007).

The sepals of most Chrysophylloideae taxa are pubescent on the outer surface, except when the indument is secondarily lost, but presence or absence of indument on the inner surface seems to contain strong phylogenetic information (Fig. 3B). In *Beccariella* and *Van-royena*, trichomes are always present on the sepals' inner surface, often covering the entire area and forming a tomentose or even woolly indument. Sepal indument is homoplastic in *Sersalisia* and *Pichonia*, and the sepals of *P. balansana*, *P. deplanchei* (Baill.) Swenson & Munzinger, and *P. lecomtei* (Guillaumin) T.D. Penn. are glabrous inside. However, if an indument is present on the inner surface, the trichomes are usually concentrated in the upper part of the sepals (Swenson & Munzinger, 2012). Sepals of all other genera are glabrous inside, except in some species scattered in the *Planchonella* phylogeny (*P. australis* (R. Br.) Pierre, *P. chartacea*, and *P. cyclopaensis* P. Royen), in which the density of indument varies, often even between sepals in the same flower.

Classification of floral types is partly subjective and sometimes difficult according to the definition above. Nevertheless, the corolla can be termed narrowly campanulate in *Beccariella*, *Van-royena*, and some *Sersalisia* (Fig. 3C). A cup-shaped corolla with spreading lobes is characteristic for *Pichonia*, *Magodendron*, *Niemeyera*, and *Pycnandra*, and in the two latter the corolla lobes are frequently revolute (Fig. 1A, D). The type of corolla in *Planchonella* is generally urn-shaped, where the calyx is more or less as long as, or slightly longer than, the corolla tube (Fig. 1I–J). Urn-shaped flowers never have spreading or revolute corolla lobes comparable to the cup-shaped flower. Exceptions to the urn-shaped flower in *Planchonella* are found in *P. baillonii*, *P. ericiflora* Munzinger & Swenson and *P. myrsinoides* (Benth.) S.T. Blake ex Francis, species that are scattered across the genus and have tubular flowers with a well-exposed corolla tube (Fig. 1G–H).

Stamens are inserted opposite the corolla lobes in Sapotaceae, and it has been controversial whether the insertion point within the corolla tube carries any phylogenetic information. Both Aubréville (1967) and van Royen (1957) used the character, as opposed to Pennington (1991) who could not find significant correlation between the insertion point of stamens and other characters, perhaps because his circumscription of *Pouteria* was an unnatural amalgamation of different lineages, which obscured character correlations. However, the phylogenetic study by Swenson & al. (2007a) found strong correlation between stamen insertion and monophyletic groups. Our analysis agrees with these previous findings, but, again, there are exceptions (Fig. 3D). All species of *Beccariella* (and *Van-royena*) have stamens inserted either in the middle or near the base of the tube. Swenson & al. (2007a) reported that the species from Australia have stamens inserted near the base whereas those from New Caledonia have the stamens inserted in the middle of the corolla tube. In fact, this statement needs amendment, since there are species of *Beccariella* in Australia, New Caledonia, and New Guinea that have stamens inserted either near the base *or* in the middle of the corolla tube. However, it is still valid that no species of *Beccariella* have stamens inserted in or just below the tube orifice, character states that are restricted to the other genera under study. Stamen insertion in *Van-royena* has been reported as basal (Herrmann-Erlee & Lam, 1957; Aubréville, 1963; Swenson & al., 2007a), but the point of insertion is at or just above the middle of the corolla tube, while the filament is attached to the tube and run down to the base. In *Sersalisia* and *Pycnandra* the character varies, and exceptions in *Pycnandra* are *P. atrofusca* Swenson & Munzinger, *P. benthamii*, *P. carinocostata* Vink, *P. fastuosa* (Baill.) Vink and *P. kaalaensis* Aubrév., species that represent three subgenera and have stamens inserted just below the tube orifice. *Leptostylis filipes*, which will be transferred to *Pycnandra*, has tubular flowers and stamens inserted in the middle of the corolla tube. *Pichonia*, *Magodendron*, and *Niemeyera* have stamens inserted in the tube orifice. Finally, all except for some species of *Planchonella* have stamens inserted just below the tube orifice. Stamens in *P. aneityensis* (Guillaumin) H.J. Lam ex P. Royen are inserted in the middle of the corolla tube, and in *P. grayana* and *P. tahitensis* the stamens are inserted at the corolla base, a unique position within the genus. These three taxa are all found in the same clade of Pacific species.

Styles with several stigmatic areas at the apex, easy to identify with a hand lens, was suggested as an important character to differentiate *Beccariella*, *Van-royena*, *Sersalisia*, *Magodendron*, and *Planchonella* from the simple style without such clearly visible stigmatic areas in *Pichonia*, *Niemeyera*, and *Pycnandra* (Swenson & al., 2007a). We found no deviation from this pattern in the sampled species and suggest that this character does contain strong phylogenetic signal, useful in character combination for circumscribing groups, as well as in the field (Fig. 3E).

The distribution of foliaceous or plano-convex cotyledons, absence or presence of an exserted radicle, and absence or presence of an endosperm, are clearly correlated among members of the study group, and are reported in a single figure (Fig. 3F). Three combinations of the characters are known: (i) seeds of *Beccariella* and *Planchonella* have foliaceous cotyledons, an exserted radicle and an endosperm, (ii) *Magodendron* has plano-convex cotyledons, an exserted radicle and non-endospermous seeds, and (iii) all other genera have seeds with plano-convex cotyledons, an included radicle and no endosperm. The character combination for *Magodendron* is rare in Chrysophylloideae, only found in *Chromolucuma* Ducke and *Pradosia* Liais (Swenson & Anderberg, 2005), and in some species of *Pouteria* (South America) and *Synsepalum* (A.DC.) Daniell (Africa) sensu Pennington (1991).

In summary, despite a high degree of morphological homoplasy in Chrysophylloideae, the characters here overlaid in the condensed phylogeny show high or full congruence with the identified groups. We believe that we have now arrived at a stage where unique character combinations can be used to identify natural groups within Chrysophylloideae present in Oceania and Southeast Asia.

Resurrection of *Amorphospermum*. — *Niemeyera* and *Amorphospermum* F. Muell. were originally described with one species each, *N. prunifera* and *A. antilogum* F. Muell. (Mueller, 1870), hence, these species are the two generi-types. The genera were described as close relatives, *Niemeyera* being distinguished by its berry-like fruit and thin seed coat (testa) in contrast to *Amorphospermum* with its drupe-like fruit and thick seed coat. Both genera were later united with *Chrysophyllum* (Vink, 1958), but Aubréville (1964) resurrected them in his system of classification, accepting two species in each genus. By contrast, Pennington (1991) accepted *Niemeyera* but not *Amorphospermum*, and considered the seed coat differences to be merely of specific importance. In fact, *Niemeyera* sensu Pennington was an unnatural assemblage of Australian species (now in *Niemeyera*) and seven taxa from New Caledonia (now *Pycnandra*; Swenson & Munzinger, 2009, 2010a, 2010c).

Niemeyera antiloga, a species confined to the rainforest of Queensland, was unsatisfactorily accommodated in *Niemeyera*, because phylogenetic analyses of nuclear sequences grouped it with *Van-royena*, in conflict with combined morphological and molecular data, which grouped it with other species of *Niemeyera* (Swenson & al., 2007a). The current phylogenetic study lends strong support to *N. antiloga* being the sister species of *Niemeyera* plus *Pycnandra*. Our study demonstrates that the circle is now closed and we are back to the generic notion Mueller (1870) suggested over 140 years ago. Therefore, we propose that *Amorphospermum* is resurrected, presently as a monotypic genus. Apart from seed coat differences, *Amorphospermum* is readily distinguished based on leaf characters. The texture is never translucent, the upper surface is glossy green while the lower is paler with a persistent indument, and the tertiary venation is parallel (Fig. 1B). Species of *Niemeyera* have leaves of similar colour on both surfaces, are usually glabrescent below, and have horizontal or oblique tertiary leaf venation (Fig. 1A). Other floral and fruiting characters of *Amorphospermum* and *Niemeyera* share many similarities.

Resurrection of *Pleioluma* (Baill.) Baehni. — *Beccariella* is strongly supported as an independent lineage with maximum Bayesian and jackknife support. This relationship is fully congruent with earlier findings (Bartish & al., 2005; Swenson & al., 2007a), and Clade C of Triono & al. (2007). The position within the Australasian Chrysophylloideae is unambiguous but its sister relationship receives only moderate jackknife support. The clade, however, is readily identified with a character combination of (i) leaves with areolate venation, (ii) sepals that are pubescent on both surfaces, (iii) presence of staminodes, (iv) stamens inserted in the middle of the corolla tube or near the base, (v) style with stigmatic areas, and (vi) seeds with foliaceous cotyledons, exerted radicle, and endosperm (Fig. 3). The genus currently contains about 20 species and another seven species (*Planchonella firma* (Miq.) Dubard, *P. lamprophylla* (K. Krause) H.J. Lam, *P. ledermanii* (K. Krause) H.J. Lam, *P. moluccana* (Burck) H.J. Lam, *Pouteria gillsonii* Vink, *P. richardii* (F. Muell.) Baehni and *P. wandae* Vink) are here recovered in this clade and need to be transferred to it, but the name *Beccariella* is a later homonym and cannot be used (Swenson & Tehler, 2009; Brummitt, 2011b).

When Pierre (1890) described *Beccariella* in Sapotaceae he was probably unaware of the fact that the name was already occupied for a fungal genus from Borneo. Hence, *Beccariella* became a later homonym and illegitimate already at publication. Subsequent classification systems like Herrmann-Erlee & Lam (1957), van Royen (1957), Baehni (1965), and Pennington (1991) have not used *Beccariella* or identified the assemblage as a natural group. In contrast, Aubréville (1962) resurrected the genus and designated *B. sebertii* (included in this study) as the generic type, and since then the name has been used in New Caledonia (Aubréville, 1964, 1967), but not in Australia or New Guinea. Swenson & Tehler (2009) addressed this nomenclatural problem and suggested conserving *Beccariella* Pierre (Sapotaceae) against the rarely used name *Beccariella* Ces. (Podoscyphaceae), a proposal the Nomenclatural Committee for Vascular Plants was unable to agree upon (Brummitt, 2011b). Thus, species belonging to *Beccariella* (or that clade) are currently left in limbo and need to be accommodated under a valid name.

Several of the proposed Sapotaceae genera (*Albertisiella* Pierre ex Aubrév., *Bureavella* Pierre, *Iteiluma* Baill., *Peuceuma* Baill., and *Pyriluma* Aubrév.) in Australasia are polyphyletic or embedded in *Planchonella* (Swenson & al., 2007a, 2007b). Some generic names are still in synonymy with *Pouteria* (Pennington, 1991; Govaerts & al., 2001) and could be used instead of *Beccariella* if the generic type is demonstrated to be a member of this clade. However, three generi-types are here recovered in *Planchonella* and cannot be used: *Beauvisagea* that is united with *Pouteria maclayana* (Govaerts & al., 2001), *Fontbrunea* represented by *Pouteria malaccensis*, and *Blabeia* represented by *Planchonella endlicheri* (Fig. 2). Three generic names remain to be explored: *Krausella*, *Pleioluma*, and *Wokoia* Baehni.

The genus *Krausella* was described by Lam (1932) and believed to include four to six species from New Guinea, but much of the studied material was incomplete or even sterile (Herrmann-Erlee & Lam, 1957). The generic type *K. polyneura* (K. Krause) H.J. Lam is currently classified as *Pouteria multinervis* T.D. Penn. (see Pennington, 1991: 202). After receiving permission from Kew Gardens, we removed a leaf fragment from the type collection of *K. polyneura* and amplified most of ITS and ETS (unsuccessful with RPB2), as well as all three markers for *K. patentinervia* (K. Krause) Erlee. These two species are embedded within *Planchonella*, sister to *P. torricellensis* (K. Schum.) H.J. Lam (Fig. 2). In fact, the sequences of *K. polyneura* and *K. patentinervia* are identical. We are confident that both species are members of *Planchonella* and not *Beccariella* (or any other genus) since, in addition, the leaf venation is not areolate, the sepals are glabrous inside, staminodes are present, stamens are inserted below the tube orifice, and the styles possess stigmatic areas. Thus, *Krausella* is here united with *Planchonella*.

Pouteria rhopalocarpa P. Royen was described from New Guinea, but its status as a new genus was in doubt because of a 3-merous flower, staminodes, and a peculiar fruit (van Royen, 1959). In any event, Baehni (1964) described *Wokoia* and suggested a close relationship to the Malagasy genus *Tsebona* Capuron, a member of tribe Omphalocarpeae sensu Pennington (1991), which is polyphyletic and subsumed in Chrysophylloideae (Swenson & Anderberg, 2005). However, from the morphological description (van Royen, 1959; Vink, 2002) and the generic framework here proposed, this species is clearly a member of *Pichonia*. The leaf venation is areolate, sepals are glabrous on the inside at the base but tomentose on the upper part, flowers have staminodes, anthers are inserted in the tube orifice, styles are simple without clear stigmatic areas, and the seeds have plano-convex cotyledons, an included radicle and lack endosperm. We therefore unite *Wokoia* with *Pichonia*, which has nomenclatural priority.

The remaining option to accommodate the species of *Beccariella* is the genus *Pleioluma* (Baehni, 1965). *Pleioluma*, first described as a section of *Sersalisia* (Baillon, 1891) and later transferred to a section of *Sideroxylon* L. (Engler in Engler & Prantl, 1897), was based on *Sideroxylon crebrifolium* (Baill.) Engl. and has never been used in any classification. In fact, Baehni (1965) simultaneously transferred this species to *Pouteria* (p. 59) and in the same publication (p. 150) accepted it at generic level as *Pleioluma* with uncertain relationship. Regardless of this confusion (his publication appeared after he had deceased), we demonstrate that *Sideroxylon* (*Beccariella*) *crebrifolium* is deeply nested in the clade called *Beccariella* and we suggest, in accordance with Article 11.3 of the International Code of Botanical Nomenclature (McNeill & al., 2006), that *Pleioluma* is used for this genus since it is the earliest legitimate name available. Indeed, it is an appropriate name since ‘pleio-’ is of Greek origin and means ‘more’, whereas ‘luma’ (of unclear origin) means ‘cavity’, and could likely refer to the areolate leaf venation.

Problems in *Planchonella*. — *Planchonella* is strongly supported as a monophyletic group. The genus can be characterized by non-areolate leaf venation, sepals that are generally tomentulose on the outer surface but glabrous inside, flowers with staminodes and stamens inserted just below the tube orifice, a style with stigmatic areas, and seeds that have foliaceous cotyledons, an exerted radicle and an endosperm. Exceptions to this character combination are few. Swenson & al. (2007b) accepted 60 species in *Planchonella* and another six taxa

are here recovered within the genus. Based on the above diagnostic character combination and available herbarium material, it is safe to transfer several species that have not been available for molecular analysis (see below). Hence, *Planchonella* contains approximately 110 known species, of which some are still to be described, especially from New Caledonia.

Planchonella baillonii with its tubular, rather than urn-shaped, flowers is again found as sister to the rest of the genus with strong to moderate support (PP 1; JK 88). We believe the species represents an old evolutionary lineage, the sole extant member confined to New Caledonia. *Planchonella baillonii* is also the type species of *Iteiluma*, a name rejected in favour of *Planchonella* (Swenson & Morat, 2008; Brummitt, 2011a), but considering its phylogenetic position it is possible to recognize a monotypic genus. However, we reject this solution since *P. baillonii* possesses the entire set of characters diagnostic for *Planchonella*.

Chrysophyllum bakhuiizenii was described from New Guinea by van Royen (in Vink, 1958) as a close relative of *C. gordoniiifolium* S. Moore (now in *Pycnandra*) from New Caledonia, because of similar morphology and alleged lack of staminodes. However, examination of one bud of the original material reveals presence of staminodes and the remaining morphology falls within the concept of *Planchonella*. In addition our analyses clearly recover it within the genus.

Planchonella sandwicensis is distributed across all main islands of Hawaii forming the north-eastern outpost of the generic distribution in the Pacific. Triono & al. (2007) used two accessions that were recovered as sisters, and found sister to the entire subfamily Chrysophylloideae, casting doubt on whether this species is a member of *Planchonella* or even the subfamily. They further proposed that *P. sandwicensis* should be separated and recognized on generic level. Our analysis of three accessions from Kauai and Oahu found maximum support of monophyly and the species is retained inside *Planchonella*, with close affinity to taxa from Fiji, i.e. *P. smithii* (P. Royen) A.C. Sm. and *P. umbonata* (P. Royen) A.C. Sm. This result is consistent with earlier findings using nrDNA and morphology (Swenson & al., 2007a, 2007b). The only reasonable explanation for Triono & al. (2007) reporting a relationship outside the subfamily is that they possibly sequenced material of *Sideroxylon polynesianum* (Hillebr.) Smedmark & Anderb., a species that is somewhat similar in leaf venation, but belongs to Sapotoideae, not Chrysophylloideae (Smedmark & al., 2006; Smedmark & Anderberg, 2007).

Scattered over the Pacific islands is a polymorphic complex of *Planchonella* that has puzzled earlier botanists. Lam (1942) accepted two varieties of *Planchonella costata* (Endl.) Pierre, a classification that van Royen (1957) amended and extended to include another two varieties. Smith (1981) in his flora of Fiji accounted for nine species of *Planchonella*, in which he treated all former varieties as separate species (*P. grayana*, *P. smithii*, *P. umbonata*) and relegated *P. costata* to be restricted to New Zealand and Norfolk Island. The present sample includes six accessions from Fiji (*P. membranacea* H.J. Lam, *P. smithii*, *P. umbonata*, *P. vitiensis* Gillespie, *P. "Munzinger 6490"*, and *P. "Munzinger 6514"*), as well as *P. costata* from New Zealand and seven accessions of *P. grayana* and *P. tahitensis* gathered from Futuna in the west to French Polynesia in the east (but not from Fiji). All of these taxa, except for *P. grayana* and *P. tahitensis*, are scattered throughout the *Planchonella* phylogeny and their closest relatives are usually from another area. Hence, Smith's (1981) species concept is easy to reconcile with the molecular phylogeny.

The two species *Planchonella grayana* and *P. tahitensis* have caused confusion as to whether one, two, or several taxa should be recognized (Grant & al., 1974; Smith, 1981; J.-F. Butaud, pers. comm.). In Fiji, *P. grayana* occurs from the coast to about 400 m altitude and usually forms trees 6–14 m tall, but can be stunted to no more than one meter tall if growing on exposed sites (Smith, 1981). In French Polynesia, *P. tahitensis* occurs as a small tree or up to 20 m tall, from sea level to 700 m altitude in Raiatea and Tahiti, on calcareous or various volcanic soils, often in mesic to wet forests (Butaud & al., 2011; Pouteau & al., 2012). All seven accessions analysed here are recovered in a single, strongly supported clade, with some support for internal resolution, and all have a unique triple-T-insertion in the ITS sequence (positions 788–790). The clades, however, are incongruent with species or area (archipelago) of origin. No qualitative morphological characters differ between

the suspected taxa. Both differ from all congeners in that the stamens are inserted near the base of the corolla tube (not below the tube orifice). The small greenish (Fig. 1J) or somewhat whitish flowers are bisexual or female, which possibly renders the species gynomonocious, a sexual system found in *Planchonella* (Méndez & Munzinger, 2010). Variable characters are restricted to the size of the foliage and the fruit. For example, leaves of the sample from Futuna are elliptic and large (16–25 x 7–10 cm) in comparison to narrowly elliptic and small (7–11 x 2–3 cm) in the closely related sample from Tahiti (*P. grayana* var. *florencei* Fosberg). Hence, we are confident that this is one variable, widely distributed species, adapted to different soils, humidity and altitudes, but we do not exclude the possibility that a subspecies concept could be applicable. In any event, the correct name to be used is *P. tahitensis*.

Planchonella linggensis is a widely distributed species in Malesia and many islands in the Pacific. It grows in fairly different habitats, such as low altitudinal forests on calcareous soil in Alofi (Wallis and Futuna) and moist rainforests at about 800 m altitude on ultramafic substrate in New Guinea. Previous phylogenetic analyses have rendered this species paraphyletic, possibly conspecific with *P. chartacea*, and it has been suggested to form a complex of similar species with unclear species limits (Swenson & al., 2007a, 2007b). Here, we included three accessions of *P. linggensis*, one each from Futuna, New Guinea and Vanuatu. All accessions group together with maximum support but are intermingled with *P. chartacea* and *P. solida* (Fig. 2, Clade D2). A cursory inspection of the accessions used reveals morphological similarities but also differences, such as presence or absence of indument on different organs. A molecular study of a wider sample from different areas, soil types and altitudes, together with a close examination of the morphology, ought to reveal species limits within this clade.

Unplaced taxa. — Our present findings make significant progress towards an understanding of the natural groups within subfamily Chrysophylloideae in Oceania and Southeast Asia, but there are several unplaced taxa that are still unavailable for molecular analysis and are of special interest. We acknowledge that some of these problems may remain unresolved because the plants are known from few old collections, often treated with poison such as mercuric chloride. Because of large-scale deforestation, the relationships among these taxa may never be known. Here, we mention three examples.

Boerlagella spectabilis (Miq.) H.J. Lam, the generic type of the family Boerlagellaceae (Lam, 1925), is still an enigmatic taxon. It was originally described from only one leaf and its vein characters, accompanied by a discussion of the axillary, 5-celled fruit with one seed that has an exerted radicle. This is fragmented information, but Dubard (1912), as well as Pennington (1991), associated the species with *Planchonella* (or *Pouteria* section *Oligothea*). Despite the incomplete material, these characters are in full agreement with the character combination of *Planchonella*. Our careful inspection of the available leaf and fruit (type material) reveals the absence of areolate venation and an overall venation pattern that is similar to *P. torricellensis*, a species we predict it is closely related to.

One species from New Guinea, currently classified as *Planchonella kaernbachiana* (Engl.) H.J. Lam, has a character combination that is a mixture between *Pichonia* (sepals pubescent inside, stamens in the tube orifice and simple style) and *Planchonella* (non-areolate venation, foliaceous cotyledons and an endosperm). It is unclear if this taxon is simply another example of the homoplasy typical in Sapotaceae, a taxon of mixed collections, or if it represents yet another evolutionary lineage in the area.

Pouteria celebica Erlee from Sulawesi (Celebes), collected in rainforest at 800 m altitude, is known only from incomplete type material (floral buds). The overall morphology is very similar to the frequently cultivated Neotropical *P. multiflora* (A.DC.) Eyma. However, the latter has four sepals (Pennington, 1990) rather than five as in *P. celebica* (Herrmann-Erlee & van Royen, 1957). Future research will tell if this species represents an early introduction or an extreme case of parallel evolution.

Towards a natural classification. — The present analyses reconcile earlier findings (Bartish & al., 2005; Swenson & Anderberg, 2005; Swenson & al., 2007a) and strengthen the conclusion that there are nine lineages of Chrysophylloideae in Oceania and Southeast Asia (ten with *Xantolis*) that warrant formal recognition. Below, we provide a generic key using fertile and leaf material. In addition, each recognized genus is enumerated with its synonyms, diagnostic character combination, number of recognized species, distribution, and necessary combinations that render each genus monophyletic. Homotypic and heterotypic synonyms are cited for genera, but only the basionym and homotypic synonyms are cited for species in order to save space. Type citations follow the text on the label, or the original description if the type material has not been viewed (n.v.). For more complete nomenclature, see Govaerts & al. (2001) and the World Checklist at the Royal Botanical Garden (<http://apps.kew.org/wcsp/home.do>). On going floristic work in Australia appear in *Flora of Australia*, but the volume of Sapotaceae is currently unpublished (L. Jessup, pers. comm.). Typifications of Australian species, if needed, will appear in this flora. Typification of *Pleioluma* species occurring in New Caledonia will appear in an upcoming revision we aim to publish in a near future. A summary of the proposed classification, including new combinations, is shown in Fig. 4.

Key to the genera of Chrysophylloideae in Southeast Asia and Oceania (excluding *Xantolis*)

- 1. Staminodes absent 2
- 1. Staminodes present 4
- 2. Flowers usually along the branches; cotyledons red (or pinkish); New Caledonia *Pycnandra*
- 2. Flowers axillary; cotyledons white; Australia 3
- 3. Leaves below pubescent, not translucent; leaf venation brochidodromous *Amorphospermum*
- 3. Leaves below glabrous or glabrescent (except for veins), ± translucent; leaf venation eucamptodromous *Niemeyera*
- 4. Tertiary or quaternary leaf venation areolate 5
- 4. Tertiary or quaternary leaf venation never areolate 8
- 5. Flowers born on trunk *Magodendron*
- 5. Flowers axillary 6
- 6. Stamens inserted in lower half of corolla tube; foliaceous cotyledons *Pleioluma*
- 6. Stamens inserted in or just below corolla tube orifice; cotyledons plano-convex 7
- 7. Flowers cup-shaped; style simple *Pichonia*
- 7. Flowers narrowly campanulate or tubular; style with several stigmatic areas *Sersalisia*
- 8. Stamens inserted just below corolla tube orifice; foliaceous cotyledons *Planchonella*
- 8. Stamens inserted near middle of corolla tube; plano-convex cotyledons *Van-royena*

Amorphospermum F. Muell., Fragm. 7: 112 (1870). — Type: *Amorphospermum antilogum* F. Muell., Fragm. 7: 113 (1870). ≡ *Lucuma amorphosperma* F.M. Bailey, Queensl. Fl. 3: 955 (1900), nom. illegit. ≡ *Sersalisia antiloga* (F. Muell.) Domin, Biblioth. Bot. 89: 508 (1928). ≡ *Chrysophyllum antilogum* (F. Muell.) Vink, Blumea 9: 65 (1958). ≡ *Niemeyera antiloga* (F. Muell.) T.D. Penn., Gen. Sapotac.: 235 (1991). Lectotype designated by Vink (1958): Australie, Queensland, *Thozet s.n.*, 1870 (MEL n.v.), isolectotype (P!).

Diagnostic character combination. — Leaves pubescent below, not translucent; tertiary leaf venation parallel, higher venation non-areolate; sepals glabrous inside; flowers axillary, cup-shaped; stamens inserted in corolla tube orifice; staminodes absent; style simple; cotyledons plano-convex, white; radicle included in cotyledons; endosperm absent.

A single species in forests of eastern Australia, from New South Wales to Papua New Guinea. There seems to exist another, as yet undescribed species (L. Jessup, pers. comm.).

Magodendron Vink, Nova Guinea, n.s., 8: 124 (1957). — Type: *Magodendron venefici* (C.T. White & W.D. Francis) Vink, Nova Guinea, n.s., 8: 125 (1957). ≡ *Achradotypus venefici* C.T. White & W.D. Francis, Proc. Roy. Soc. Queensland 38: 254 (1927).

Diagnostic character combination. — Leaf venation areolate; sepals glabrous inside; flowers born on trunk, cup-shaped; stamens inserted in corolla tube orifice; staminodes present, irregularly incised; style with stigmatic areas; cotyledons plano-convex with a radicle extending below cotyledon commissure; endosperm absent.

Two species confined to New Guinea (Vink, 1995).

Niemeyera F. Muell., Fragm. 7: 114 (1870), *nom. cons.* — Type: *Niemeyera prunifera* (F. Muell.) F. Muell., ≡ *Chrysophyllum pruniferum* F. Muell.

Diagnostic character combination. — Leaves glabrous or glabrescent below, usually translucent; tertiary leaf venation oblique, non-areolate; sepals glabrous inside; flowers axillary, cup-shaped; stamens inserted in corolla tube orifice; staminodes absent; style simple; cotyledons plano-convex, white; radicle included in cotyledons; endosperm absent.

Three described species and one undescribed species (L. Jessup, pers.comm.), all confined to Australia. No modern treatment is available, but will appear in Flora of Australia.

Pichonia Pierre, Not. Bot. Sapot.: 22 (1890). — Type: *Pichonia balansana* Pierre.

≡ *Epiluma* Baill., Hist. Pl. 11: 287 (1891). — Type: *Epiluma pyriformis* Baill.

= *Rhamnoluma* Baill., Hist. Pl. 11: 287 (1891). — Type: *Rhamnoluma novocaledonica* (Engl.) Baill. ≡ *Lucuma novocaledonica* Engl.

= *Wokoia* Baehni, Arch. Sci. 17: 78 (1964). — Type: *Wokoia rhopalocarpa* (P. Royen) Baehni ≡ *Pouteria rhopalocarpa* P. Royen

= *Arnanthus* Baehni, Arch. Sci. 17: 78 (1964). — Type: *Arnanthus balansae* Baehni ≡ *Chrysophyllum balansae* Baill., *nom. illeg.*

Diagnostic character combination. — Tertiary leaf venation laxly reticulate, higher venation areolate; sepals usually pubescent inside in upper part or sometimes glabrous; flowers usually axillary, cup-shaped; stamens inserted in corolla tube orifice; staminodes present, generally entire; style simple; cotyledons plano-convex, radicle included in cotyledons; endosperm absent.

Twelve known species, of which seven are endemic to New Caledonia (Swenson & Munzinger, 2012) and five to New Guinea, one reaching as far east as the Solomon Islands.

Pichonia hochreutineri (H.J. Lam) Swenson, **comb. nov.** ≡ *Planchonella hochreutineri* H.J. Lam, Boissiera 7: 92 (1943). ≡ *Pouteria hochreutineri* (H.J. Lam) H.J. Lam, Blumea 5: 337 (1943). Holotype: New Guinea, Boridi, c. 1400 ft alt., 9.IX.1935, C. E. Carr 13023 (L!), isotypes (BM!, K!, SING!).

Distribution: New Guinea.

Pichonia rhopalocarpa (P. Royen) Swenson, **comb. nov.** ≡ *Pouteria rhopalocarpa* P. Royen, Nova Guinea, n.s., 10: 134 (1959). ≡ *Wokoia rhopalocarpa* (P. Royen) Baehni, Arch. Sci 17 (1): 78 (1964). Holotype: West New Guinea, Manokwari District, Oransbari, alt. 50 m, 11.X.1955, R. P. Mangold 51 (L!), isotype (MAN n.v.).

Distribution: New Guinea.

- Planchonella*** Pierre, Not. Bot. Sapot.: 34 (1890), *nom. cons.* — Type: *Planchonella obovata* (R. Br.) Pierre ≡ *Sersalisia obovata* R. Br.
- = *Iteiluma* Baill., Bull. Mens. Soc. Linn. Paris 2: 892 (1890), *nom. rej.* — Type: *Iteiluma baillonii* (Zahlbr.) Baill. ≡ *Lucuma baillonii* Zahlbr. ≡ *Poissonella* Pierre, Not. Bot. Sapot.: 29 (1890).
- = *Peucecluma* Baill., Bull. Mens. Soc. Linn. Paris 2: 895 (1890), *nom. rej.* — Type: *Peucecluma pinifolia* Baill.
- = *Beauvisagea* Pierre, Not. Bot. Sapot.: 15 (1890). — Type: *Beauvisagea pomifera* Zippel ex Baill.
- = *Bureavella* Pierre, Not. Bot. Sapot.: 16 (1890). — Type: *Bureavella maclayana* (F. Muell.) Pierre. ≡ *Bassia maclayana* F. Muell.
- = *Fontbrunea* Pierre, Not. Bot. Sapot.: 31 (1890). — Type: *Fontbrunea malaccensis* (C.B. Clarke) Pierre ≡ *Sideroxylon malaccense* C.B. Clarke
- = *Krausella* H.J. Lam, Nova Guinea 14: 566 (1932). — Type: *Krausella polyneura* (K. Krause) H.J. Lam ≡ *Sideroxylon polyneurum* K. Krause
- = *Albertisiella* Pierre ex Aubrév., Adansonia, n.s., 4: 42 (1964). — Type: *Albertisiella novoguineensis* (Vink) Aubrév. ≡ *Chrysophyllum novoguineense* Vink
- = *Blabeia* Baehni, Arch. Sci. 17 (1): 77 (1964). — Type: *Blabeia endlicheri* (Montrouz.) Baehni ≡ *Sapota endlicheri* Montrouz.
- = *Pyriluma* Aubrév., Fl. Nouv.-Caléd. 1: 83 (1967). — Type: *Pyriluma sphaerocarpa* (Baill.) Aubrév. ≡ *Sideroxylon sphaerocarpa* Baill. in Bull. Mens. Soc. Linn. Paris 2: 891. 1890.

Diagnostic character combination. — Tertiary leaf venation usually reticulate or oblique, higher venation non-areolate; sepals glabrous inside or rarely pubescent to varying degree; flowers usually axillary, urn-shaped or rarely tubular; stamens inserted just below corolla tube orifice, rarely in middle of tube or near base; staminodes present, usually entire; style with stigmatic areas; cotyledons foliaceous with a radicle extending below cotyledon commissure; endosperm present.

Planchonella is the largest genus of Chrysophylloideae in the Old World with approximately 110 known species. Several species in New Caledonia and the west Pacific Islands remain to be described (or resurrected). *Planchonella* is distributed from Thailand and southern China in the north, through Malesia, Australia, New Caledonia, and on to the Pacific Islands, reaching French Polynesia and Hawaii. The highest diversity is in New Caledonia (c. 40 spp.), followed by New Guinea (c. 30 spp.), and Australia (12 spp.). No modern revision is available, but see Aubréville (1967) for New Caledonia and Swenson & al. (2007b) for an amended generic description.

Note. — *Planchonella* is conserved against *Iteiluma* and *Peucecluma* (Swenson & Morat, 2008; Brummitt, 2011a). However, Pierre (1890) described *Planchonella*, *Beauvisagea*, *Bureavella*, and *Fontbrunea* in the same publication, i.e., four competing names with equal priority. Swenson & al. (2007a) found *Bureavella* to be embedded in *Planchonella* and chose the latter over the former. Since no choice has been made between *Planchonella*, *Beauvisagea*, and *Fontbrunea*, we choose, in accordance with Article 11.5 of the International Code of Botanical Nomenclature (McNeill & al., 2006), *Planchonella* over *Beauvisagea* and *Fontbrunea*, as the latter two have never (or very rarely) been used, and therefore the choice requires fewer new combinations, retaining nomenclatural stability.

- Planchonella forbesii*** (S. Moore) H.J. Lam, Bull. Jard. Bot. Buitenzorg, III, 7: 217 (1925). ≡ *Sideroxylon forbesii* S. Moore, J. Bot. 61 (Suppl.): 30 [June] (1923). ≡ *Pouteria forbesii* (S. Moore) Baehni, Candollea 9: 408 (1942). ≡ *Krausella forbesii* (S. Moore) H.J. Lam, Boissiera 7: 92 (1943). — Holotype: New Guinea, Sogeri Region, Mt. Wori-Wori, alt. 5000 ft, 1885-6, *H. O. Forbes 756* (MEL n.v.), isotypes (E!, FI n.v, L!, K!).
- = *Sideroxylon patentinervium* K. Krause, Bot. Jahrb. Syst. 58: 474 [November] (1923). ≡ *Krausella patentinervia* (K. Krause) Erlee, Blumea 8: 448 (1957). — Lectotype designated by Herrmann-Erlee &

Lam (1957): Kaiser-Wilhelmsland [New Guinea], Kani Geberges, 1000 m alt., 31 October 1907, *R. Schlechter 16746* (P!).

Note. — We used an accession determined as *Krausella patentinervia*. A careful examination of the types and additional material reveals that the leaf characters used by Herrman-Erlee and Lam (1957) to distinguish the above species are overlapping and the two are better conceived as conspecific, but different from the generic type *K. polyneura*. The name *Sideroxylon forbesii* was published a few months before *S. patentinervium* and has priority. We mention this here in order to avoid an unnecessary combination. Distribution: New Guinea.

Planchonella garcinioides (K. Krause) Swenson, **comb. nov.** ≡ *Sideroxylon garcinioides* K. Krause, Bot. Jahrb. Syst. 58: 477 (1923). ≡ *Lucuma garcinioides* (K. Krause) H.J. Lam, Nova Guinea 14: 568 (1932). ≡ *Pouteria garcinioides* (K. Krause) Baehni, Candollea 9: 338 (1942). — Lectotype designated by Vink (2002): New Guinea, Sepik-Gebiet, im alluvial wald am Sepik, beim Larger Malu, alt. 20-40 m, I.1913, *Ledermann 10728* (L!) (holotype in B, destroyed).

= *Planchonella solida* P. Royen, Blumea 8: 404, 433 (1957). — Holotype: New Guinea, Yalu, near Lae, 5.III.1950, *D. Fryar 3344* (SING!), isotype (L!, LAE n.v.).

Note. — Herrmann-Erlee and van Royen (1957), in their revision of *Pouteria*, repeated the original Latin description of *Pouteria garcinioides* since no material was available and the type in Berlin was destroyed during World War II. Simultaneously, van Royen (1957) described *Planchonella solida*, but Wim Vink (Leiden) united these two species in an unpublished record. We have used an accession of *P. solida*, but this species should be united with *Sideroxylon garcinioides*, a name that has priority but needs to be combined with *Planchonella*. Distribution: New Guinea.

Planchonella lamii P. Royen, Blumea 8: 398, 432 (1957). — Holotype: Amboina, near Sirimau, 450 m alt., 11.II.1930, *NIFS bb 14283* (L!).

= *Chrysophyllum bakhuiizenii* P. Royen, Blumea 9: 74 (1958). — Holotype: New Guinea, Alola, alt. 2000 m, *C. E. Carr 14159* (L!), isotype (BM n.v.).

Distribution: Maluku Islands, New Guinea.

Note. — We sequenced an accession determined as *Chrysophyllum bakhuiizenii*, but an examination of the available material of this species and *Planchonella lamii* shows that they are conspecific and should be united.

Planchonella maclayana (F. Muell.) Swenson, **comb. nov.** ≡ *Bassia maclayana* F. Muell., Vict. Chem. & Druggist 7 (April): 93 (1885). ≡ *Illipe maclayana* (F. Muell.) F. Muell., Descr. Notes Papuan Pl. 2 (6): 12 (1885). ≡ *Bureavella maclayana* (F. Muell.) Pierre, Not. Bot. Sapot.: 16 (1890). ≡ *Lucuma maclayana* (F. Muell.) H.J. Lam, Bull. Jard. Bot. Buitenzorg, III, 7: 22 (1925). ≡ *Pouteria maclayana* (F. Muell.) Baehni, Candollea 9: 307 (1942). — Type: New Guinea, Miklouho-Maclay (MEL!, P!).

Distribution: Widespread in Malesia, Solomon Islands.

Planchonella macrantha (Merr.) Swenson, **comb. nov.** ≡ *Sideroxylon macranthum* Merr., Publ. Bur. Sci. Gov. Lab. 35: 56 (1905 publ. 1906). ≡ *Lucuma macrantha* (Merr.) H.J. Lam, Bull. Jard. Bot. Buitenzorg, III, 7: 225 (1925). ≡ *Pouteria macrantha* (Merr.) Baehni, Candollea 9: 328 (1942). ≡ *Bureavella macrantha* (Merr.) Aubrév., Adansonia, n.s., 3: 331 (1963). — Holotype: Philippines, Luzon, Province Bataan, Lamo River, Mt. Mariveles, March 1905, *T. E. Borden 21736* (= Forestry Bureau 2741) (PNH, destroyed), isotypes (BO!, K!, SING!, US!).

Distribution: Philippines to Maluku.

Planchonella malaccensis (C.B. Clarke) Swenson, **comb. nov.** \equiv *Sideroxylon malaccense* C.B. Clarke in J.D. Hooker, Fl. Brit. India 3: 537 (1882). \equiv *Fontbrunea malaccensis* (C.B. Clarke) Pierre, Not. Bot. Sapot.: 31 (1890). \equiv *Lucuma malaccensis* (C.B. Clarke) Dubard, Ann. Mus. Colon. Marseille, sér. 2, 10: 19 (1912). \equiv *Pouteria malaccensis* (C.B. Clarke) Baehni, Candollea 9: 302 (1942). \equiv *Xantolis malaccensis* (C.B. Clarke) Baehni, Boissiera 11: 23 (1965). — Holotype: Malaya, 1871, *A. C. Maingay 994* (SING!), isotypes (K!, L!, P!).

Widely distributed: Thailand, Malay Peninsula, Sumatra, Sulawesi, Borneo and New Guinea.

Planchonella menait (Vink) Swenson, **comb. nov.** \equiv *Pouteria menait* Vink, Blumea 47: 131 (2002). —

Holotype: Papua New Guinea, East Sepik Province, Hunstein Range (Mt. Samsai), at the site "Camp 3" on slopes above the main streamcourse, 450 m alt., 04°29'S, 142°41'E, 19.VII.1990, *W. Takeuchi 6276* (L!), isotype (L!).

Distribution: New Guinea.

Planchonella orkor (Vink) Swenson, **comb. nov.** \equiv *Pouteria orkor* Vink, Blumea 47: 134 (2002). — Holotype:

New Guinea, Saidor Subdistrict, Naho-Rawa, Budemu, 4150 ft alt., 24.X.1964, *C. D. Sayers NGF 21329* (L!), isotypes (BM!, LAE n.v.).

Distribution: New Guinea.

Planchonella paucinervia (Erlee) Swenson, **comb. nov.** \equiv *Pouteria paucinervia* Erlee, Blumea 8: 503 (1957).

— Holotype: Indonesia, Sumatra, Riouw District, Indragiri, Moeata Pedjanki, 11.IV.1939, *P. Buwalda 6503* (L!), isotypes (A n.v., BO n.v., PNH!, SING!).

Distribution: Malay Peninsula, Sumatra.

Planchonella polyneura (K. Krause) Swenson, **comb. nov.** \equiv *Sideroxylon polyneurum* K. Krause, Bot. Jahrb.

Syst. 58: 475 (1923). \equiv *Krausella polyneura* (K. Krause) H.J. Lam, Nova Guinea 14: 567 (1932). \equiv *Pouteria multinervis* T.D. Penn., Gen. Sapotac.: 202 (1991). — Lectotype selected by Herrmann-Erlee & Lam (1957): Deutsch-Neuguinea, Sepikgebiet, *Ledermann 9054* (K!), isolectotype (SING!).

Distribution: New Guinea.

Planchonella pullenii (Vink) Swenson, **comb. nov.** \equiv *Pouteria pullenii* Vink, Blumea 47: 98 (2002). —

Holotype: New Guinea, Milne Bay District, Baniara Subdistrict, south of Opanabu village, 149°43'E, 10°01'S, 600-700 m alt., 16.VII.1969, *A. Kanis 1243* (L!), isotypes (A n.v., BRI n.v., CANB n.v., CHR n.v., K n.v., LAE n.v.).

Distribution: New Guinea.

Planchonella ridsdalei (Vink) Swenson, **comb. nov.** \equiv *Pouteria ridsdalei* Vink, Blumea 47: 136 (2002). —

Holotype: Philippines, Mindoro, Mt. Halcon area near Paitan, Dulangan Range, 13°12'N, 121°12'E, 8.V.1986, *C. E. Ridsdale 1695* (L!), isotype (K!).

Distribution: Philippines.

Planchonella stellibacca (J.F. Maxwell) Swenson, **comb. nov.** \equiv *Pouteria stellibacca* J.F. Maxwell, Nat. Hist.

Bull Siam Soc. 50: 90 (2002). — Holotype: Thailand, Nakhon Nayok Province, Muang District, Khao Yai National Park, 14°24.5'N, 101°23'E, Klong Sai area, 760 m alt., 8.III.2001, *P. Charoenchai 1024* (CMU n.v.), isotypes (A n.v., BHF n.v., CAS n.v., L!).

Distribution: Borneo, Thailand.

Planchonella villamilii (Merr.) Swenson, **comb. nov.** ≡ *Sideroxylon villamilii* Merr., Philipp. J. Sci., C 10: 59 (1915). ≡ *Pouteria villamilii* (Merr.) Baehni, Candollea 9: 318 (1942). ≡ *Bureavella villamilii* (Merr.) Aubrév., Adansonia, n.s., 3: 331 (1963). — Holotype: Philippines, Luzon, Province of Laguna, VI.1913, A. Villamil, Forest Bureau 19762 (PNH, not found), isotype (US!).
Distribution: Philippines.

Planchonella whitmorei (Vink) Swenson, **comb. nov.** ≡ *Pouteria whitmorei* Vink, Blumea 47: 142 (2002).
Holotype: Solomon Islands, south Vella Lavella Island, Oula River area, 14.VIII.1968, C. Kotali & al. BSIP 11182 (L!).
Distribution: Solomon Islands.

Pleioluma (Baill.) Baehni, Boissiera 11: 150 (1965). ≡ *Sersalisia* section *Pleioluma* Baill., Hist. Pl. 11: 280 (Sept.-Oct. 1891). — Type: *Pleioluma crebrifolia* (Baill.) Swenson & Munzinger ≡ *Lucuma crebrifolia* Baill. = *Beccariella* Pierre, Not. Bot. Sapot.: 30 (1890), *nom. illeg., non Beccariella* Ces. in Atti. Reale Accad. Sci. Fis. 8: 9 (1879). — Type: *Beccariella sebertii* (Pancher) Pierre ≡ *Chrysophyllum sebertii* Pancher

Diagnostic character combination. — Leaf venation areolate; sepals pubescent inside; flowers usually axillary, narrowly campanulate; stamens inserted in middle or at base of corolla tube; staminodes present, usually entire; style with stigmatic areas; cotyledons foliaceous with a radicle extending below cotyledon commissure; endosperm present.

About 30 species are here attributed to *Pleioluma*, but several species are to be described from New Caledonia and New Guinea. The highest diversity is in New Guinea (14 spp.) and New Caledonia (13 spp.), extending to Malesia and Southeast Asia. The only available treatment, then under *Beccariella*, is in the flora of New Caledonia by Aubréville (1967).

Pleioluma azou (P. Royen) Swenson & Munzinger, **comb. nov.** ≡ *Planchonella azou* P. Royen, Blumea 8: 308, 428 (1957). ≡ *Beccariella azou* (P. Royen) Aubrév., Adansonia, n.s., 2: 193 (1962). — Holotype: Nouvelle-Calédonie, Port Boisé, zone maritime, X.1903, *Cribs 1424* (P!), isotype (L!).
Distribution: New Caledonia.

Pleioluma balansana (Pierre ex Baill.) Swenson & Munzinger, **comb. nov.** ≡ *Sideroxylon balansanum* Pierre ex Baill., Bull. Mens. Soc. Linn. Paris 2: 889 (1890). ≡ *Planchonella balansana* (Pierre ex Baill.) Pierre ex Dubard, Ann. Mus. Colon. Marseille, sér. 2, 10: 46 (1912). ≡ *Pouteria balansana* (Pierre ex Baill.) Baehni, Candollea 9: 317 (1942). ≡ *Beccariella balansana* (Pierre ex Baill.) Aubrév., Adansonia, n.s., 2: 193 (1962). — Lectotype designated by van Royen (1957): Nouvelle Calédonie, 11.IV.1869, *Balansa 1327a* (P!).

Distribution: New Caledonia. *Beccariella brevipedicellata* sensu Aubréville (1967), a later described taxon, is possibly conspecific with *P. balansana* but is not put into synonymy here; instead we await future results.

Pleioluma baueri (Montrouz.) Swenson & Munzinger, **comb. nov.** ≡ *Sapota baueri* Montrouz., Mem. Acad. Roy. Sci. Lyon, Sect. Sci. 10: 229 (1860). ≡ *Planchonella baueri* (Montrouz.) Dubard, Ann. Mus. Colon. Marseille, sér. 2, 10: 53 (1912). ≡ *Pouteria baueri* (Montrouz.) Baehni, Candollea 9: 329 (1942). *Beccariella baueri* (Montrouz.) Aubrév., Adansonia, n.s., 2: 193 (1962). — Holotype: Nouvelle-Calédonie, Ile Art, *Montrouzier 133* (P), isotype (G).
Distribution: New Caledonia.

Pleioluma brownlessiana (F. Muell.) Swenson & Munzinger, **comb. nov.** ≡ *Achras brownlessiana* F. Muell., *Fragm.* 7: 111 (1870). ≡ *Sideroxylon brownlessianum* (F. Muell.) F. Muell., *Fragm.* 8: 111 (1873). ≡ *Sersalisia brownlessiana* (F. Muell.) Domin, *Biblioth. Bot.* 89: 508 (1928). ≡ *Pouteria brownlessiana* (F. Muell.) Baehni, *Candollea* 9: 318 (1942). ≡ *Planchonella brownlessiana* (F. Muell.) P. Royen, *Blumea* 8: 343 (1957). ≡ *Beccariella brownlessiana* (F. Muell.) Swenson, Bartish & Munzinger, *Cladistics* 23: 221 (2007). — Type: Australia, Queensland, Rockingham Bay, *Dallachy s.n.* (MEL!).
Distribution: Australia.

Pleioluma crebrifolia (Baill.) Swenson & Munzinger, **comb. nov.** ≡ *Lucuma crebrifolia* Baill., *Bull. Mens. Soc. Linn. Paris* 2: 897 (1891). ≡ *Sideroxylon crebrifolium* (Baill.) Engl. in H.G.A. Engler & K.A.E. Prantl, *Nat. Pflanzenfam., Nachtr.* 1: 277 (1897). ≡ *Planchonella crebrifolia* (Baill.) Pierre ex Dubard, *Ann. Mus. Colon. Marseille, sér. 2, 10*: 53 (1912). ≡ *Beccariella crebrifolia* (Baill.) Aubrév., *Adansonia, n.s.*, 2: 193 (1962). ≡ *Pouteria crebrifolia* (Baill.) Baehni, *Boissiera* 11: 59 (1965). — Lectotype designated here: Nouvelle Calédonie, Collines éruptives entre Canala et Couaoua, IV.1871, *Balansa 3154* (P00282377!), isoelectotypes (P00282375!, P00282376!, P00282378!).
Distribution: New Caledonia.

Note. — Baillon (1891a) described *Lucuma crebrifolia* based on three collections, viz. *Vieillard 191*, *Vieillard 2906*, and *Balansa 3154*, all deposited in the Paris Herbarium (P). Later that year, Baillon (1891b) described section *Pleioluma* of the genus *Sersalisia*, referring to his earlier work, but did not assign any type collection. *Lucuma crebrifolia* remained untypified until Aubréville (1967) stated, in his flora of New Caledonia, "Holotype: *Balansa 3154* (P)". However, there are four specimens of this collection in Paris, none bearing any sign of being seen by Aubréville. Hence, and in accordance with Article 9.2 of the International Code of Botanical Nomenclature (McNeill & al., 2006), one well-preserved and fertile specimen of *Balansa 3154* is here designated as lectotype.

Pleioluma densinervia (K. Krause) Swenson, **comb. nov.** ≡ *Sideroxylon densinervium* K. Krause, *Bot. Jahrb. Syst.* 58: 476 (1923). ≡ *Planchonella densinervia* (K. Krause) H.J. Lam, *Nova Guinea* 14: 562 (1932). ≡ *Pouteria densinervia* (K. Krause) Baehni, *Candollea* 9: 342 (1942). — Lectotype selected by van Royen (1957): Neuguinea, Sepikgebiet, 1912/13, *Ledermann 12698* (L!), isoelectotypes (BM!, K!).
Distribution: New Guinea.

Pleioluma dies-reginae (P. Royen) Swenson, **comb. nov.** ≡ *Planchonella dies-reginae* P. Royen, *Blumea* 8: 352, 431 (1957). ≡ *Pouteria dies-reginae* (P. Royen) Vink, *Blumea* 47: 103 (2002). — Holotype: New Guinea, 4 km SW of Bernhard Camp, Idenburg River, III.1939, *L. J. Brass & C. Versteegh 13150* (L!), isotype (A n.v.).
Distribution: New Guinea.

Pleioluma firma (Miq.) Swenson, **comb. nov.** ≡ *Chrysophyllum firmum* Miq., *Fl. Ned. Ind., Eerste Bijv.*: 579 (1861). ≡ *Sideroxylon firmum* (Miq.) Pierre ex Burck, *Ann. Jard. Bot. Buitenzorg* 5: 17 (1885). ≡ *Beccariella firma* (Miq.) Pierre, *Not. Bot.*: 30 (1890). ≡ *Planchonella firma* (Miq.) Dubard, *Ann. Mus. Colon. Marseille, sér. 2, 10*: 59 (1912). ≡ *Pouteria firma* (Miq.) Baehni, *Candollea* 9: 284 (1942). — Type: *Teysmann s.n.* (BO n.v.).
Distribution: Widespread, from Thailand via Malesia to Solomon Islands.

Pleioluma foxworthyi (Elmer) Swenson, **comb. nov.** ≡ *Sideroxylon foxworthyi* Elmer, Leaflet Philipp. Bot. 5: 1836 (1913). ≡ *Planchonella foxworthyi* (Elmer) H.J. Lam, Proc. Pacific Sci. Congr. 6 (4): 678 (1940). — Type: Philippine Islands, Island of Palawan, Puerto Princesa, Mt. Pulgar, III.1911, *Elmer 12824* (E!, FI n.v., G!, L!, NSW n.v., P!, PNH [destroyed], US!, Z!).
Distribution: Philippines.

Pleioluma gillisonii (Vink) Swenson, **comb. nov.** ≡ *Pouteria gillisonii* Vink, Blumea 47: 104 (2002). — Holotype: Papua New Guinea, Morobe Province, Morobe Subprovince, Waiu Bay, 7°30'S, 147°15'E, 300 m alt., 14.VIII.1968, *Gillison & Kairo NGF 25627* (L!), isotypes (A n.v., BRI n.v., CANB n.v., CHR n.v., LAE n.v.).
Distribution: New Guinea.

Pleioluma krausei (H.J. Lam) Swenson, **comb. nov.** ≡ *Sideroxylon spathulatum* K. Krause, Bot. Jahrb. Syst. 58: 474 (1923), *nom. illeg., non* Hillebr., Fl. Hawaiian Isl.: 277 (1888). ≡ *Planchonella krausei* H.J. Lam, Nova Guinea 14: 561 (1932). ≡ *Pouteria krausei* (H.J. Lam) Baehni, Candollea 9: 322 (1942). — Lectotype designated by van Royen (1957): Nieuw Guinea, Kaiser Wilhelmsland, Gomadjiji, c. 450 m alt., 23.VIII.1909, *R. Schlechter 19915* (L!), isolectotype (BR!, P!).
Distribution: New Guinea.

Pleioluma lamprophylla (K. Krause) Swenson, **comb. nov.** ≡ *Sideroxylon lamprophyllum* K. Krause, Bot. Jahrb. Syst. 58: 481 (1923). ≡ *Planchonella lamprophylla* (K. Krause) H.J. Lam, Nova Guinea 14: 564 (1932). ≡ *Pouteria lamprophylla* (K. Krause) Baehni, Candollea 9: 333 (1942). — Lectotype designated by van Royen (1957): Neu-Guinea, Sepik-Gebeit, 1912-1913, *Ledermann 10318* (L!), isolectotype (K!).
Distribution: New Guinea.

Pleioluma lanatifolia (P. Royen) Swenson, **comb. nov.** ≡ *Planchonella lanatifolia* P. Royen, Blumea 8: 306, 428 (1957). ≡ *Pouteria lanatifolia* (P. Royen) Vink, Blumea 47: 107 (2002). — Holotype: Dutch New Guinea, Angi, Arfak Mts., 2200 m alt., 9.IV.1940, *R. Kanehira & S. Hatusima 13891* (A!).
Distribution: New Guinea.

Pleioluma lasiantha (Baill.) Swenson & Munzinger, **comb. nov.** ≡ *Sideroxylon lasianthum* Baill., Bull. Mens. Soc. Linn. Paris 2: 887 (1890). ≡ *Planchonella lasiantha* (Baill.) Dubard, Ann. Mus. Colon. Marseille, sér. 2, 10: 58 (1912). ≡ *Pouteria lasiantha* (Baill.) Baehni, Candollea 9: 324 (1942). ≡ *Beccariella lasiantha* (Baill.) Aubrév., Fl. Nouv.-Caléd. 1: 114 (1967). — Holotype: Nouvelle-Calédonie, Mont Mi, 25.III.1869, *Balansa 1322* (P!), isotype (L!).
Distribution: New Caledonia.

Pleioluma laurifolia (A. Rich.) Swenson, **comb. nov.** ≡ *Sersalisia laurifolia* A. Rich. in J.S.C. Dumont d'Urville, Voy. Astrolabe 2: 84 (1834). ≡ *Achras laurifolia* (A. Rich.) F. Muell ex Benth., Fl. Austral. 4: 282 (1868). ≡ *Sideroxylon laurifolium* (A. Rich.) Engl., Bot. Jahrb. Syst. 12: 517 (1890), *nom. illeg.* ≡ *Planchonella laurifolia* (A. Rich.) Pierre, Not. Bot.: 36 (1890). ≡ *Beccariella laurifolia* (A. Rich.) Aubrév., Adansonia, n.s., 2: 193 (1962). ≡ *Sideroxylon richardii* F. Muell., Syst. Census Austral. Pl.: 92 (1882). ≡ *Pouteria richardii* (F. Muell.) Baehni, Candollea 9: 287 (1942). — Type: Voyage de l'Astrolabe 6 (E!, P!).
Distribution: Australia.

Pleioluma ledermannii (K. Krause) Swenson, **comb. nov.** ≡ *Sideroxylon ledermannii* K. Krause, Bot. Jahrb. Syst. 58: 475 (1923). ≡ *Planchonella ledermannii* (K. Krause) H.J. Lam, Nova Guinea 14: 561 (1932). ≡ *Pouteria ledermannii* (K. Krause) Baehni, Candollea 9: 341 (1942). — Neotype: designated by van Royen (1957) (original type, Lederman 12248 in B, destroyed): Neu-Guinea, Kaiser Wilhelmsland, Sepik Region, *Ledermann 6956* (K!), isotype (E!).

Distribution: New Guinea.

Pleioluma longipetiolata (Aubrév.) Swenson & Munzinger, **comb. nov.** — *Beccariella longipetiolata* Aubrév., Fl. Nouv.-Caléd. 1: 121 (1967). — Holotype: Nouvelle-Calédonie, Prony, XI.1914, *I. Franc 1885* (P!), isotype (P!).

Distribution: New Caledonia.

Pleioluma lucens (P. Royen) Swenson & Munzinger, **comb. nov.** ≡ *Planchonella lucens* P. Royen, Blumea 8: 429 (1957). ≡ *Pouteria royenii* Baehni, Boissiera 11: 55 (1965). ≡ *Beccariella lucens* (P. Royen) Aubrév., Adansonia, n.s., 2: 193 (1962). Holotype: Nouvelle-Calédonie, 19.X.1909, *Mr. & Mrs. Le Rat 763* (P!), isotype (L!).

Distribution: New Caledonia.

Pleioluma macrocarpa (P. Royen) Swenson, **comb. nov.** ≡ *Planchonella macrocarpa* P. Royen, Blumea 8: 320, 429 (1957). ≡ *Pouteria pearsoniorum* Jessup, Austrobaileya 6: 163 (2001). ≡ *Beccariella macrocarpa* (P. Royen) Swenson, Bartish & Munzinger, Cladistics 23: 221 (2007). — Holotype: Australia, Queensland, Cook District, Kaban, *Pearson Brothers s.n.* (BRI!), isotype (BRI!).

Distribution: Australia.

Pleioluma macropoda (H.J. Lam) Swenson, **comb. nov.** ≡ *Planchonella macropoda* H.J. Lam, Nova Guinea 14: 563 (1932). ≡ *Pouteria macropoda* (H.J. Lam) Baehni, Candollea 9: 410 (1942). Neotype designated by van Royen (1957): New Guinea, Alola, 6000 ft alt., 5.XII.1935, *C. E. Carr 13631* (L!), isotypes (BM!, K!, SING!).

Distributed: Sulawesi to New Guinea.

Pleioluma moluccana (Burck) Swenson, **comb. nov.** ≡ *Sideroxylon moluccanum* Burck, Ann. Jard. Bot. Buitenzorg 5: 19 (1885). ≡ *Beccariella moluccana* (Burck) Pierre, Not. Bot. Sapot.: 30 (1890). ≡ *Planchonella moluccana* (Burck) H.J. Lam, Bull. Jard. Bot. Buitenzorg, III, 7: 200 (1925). ≡ *Pouteria moluccana* (Burck) Baehni, Candollea 9: 327 (1942). — Lectotype: Archipel. Ind., *Teysmann 7819* (BO), isolectotype (L).

Distribution: Widespread, from Java to New Guinea.

Pleioluma monticola (K. Krause) Swenson, **comb. nov.** ≡ *Sideroxylon monticulum* K. Krause, Bot. Jahrb. Syst. 58: 481 (1923). ≡ *Planchonella monticola* (K. Krause) H.J. Lam, Nova Guinea 14: 561 (1932). ≡ *Pouteria monticola* (K. Krause) H. J. Lam, Blumea 5: 337 (1943). — Neotype designated by van Royen (1957): New Guinea, Uniri River, 2200 m alt., 18.I.1936, *C. E. Carr 15189* (L!), isotypes (BM!, SING!).

Distribution: New Guinea.

Pleioluma novocaledonica (Dubard) Swenson & Munzinger, **comb. nov.** ≡ *Planchonella novocaledonica* Dubard, Notul. Syst. (Paris) 2: 84 (1911). ≡ *Sideroxylon novocaledonicum* (Dubard) Baehni, Candollea 9: 428 (1942), *nom. illeg.* ≡ *Beccariella novocaledonica* (Dubard) Aubrév., Adansonia, n.s., 2: 193 (1962). ≡

Pouteria egassia Baehni, Boissiera 11: 60 (1965). — Holotype: Nouvelle-Calédonie, *Petit 130* (P!), isotypes (G!, L!).

Distribution: New Caledonia.

Pleioluma papyracea (P. Royen) Swenson, **comb. nov.** ≡ *Planchonella papyracea* P. Royen, Blumea 8: 431 (1957). ≡ *Beccariella papyracea* (P. Royen) Aubrév., Adansonia, n.s., 3: 335 (1963). ≡ *Pouteria papyracea* (P. Royen) Baehni, Boissiera 11: 59 (1965). — Holotype: Australia, Queensland, Cook District, c. 30 km NE of Atherton, *Krauss 102* (BRI n.v.).

Distribution: Australia.

Pleioluma queenslandica (P. Royen) Swenson, **comb. nov.** ≡ *Planchonella queenslandica* P. Royen, Blumea 8: 341, 430 (1957). ≡ *Beccariella queenslandica* (P. Royen) Aubrév., Adansonia, n.s., 3: 335 (1963). ≡ *Pouteria queenslandica* (P. Royen) Jessup, Austrobaileya 6: 161 (2001). — Holotype: Australia, Queensland, Eungella Mts, 31.III.1937, *H. H. Haines 136Q* (K!).

Distribution: Australia.

Pleioluma rigidifolia (K. Krause) Swenson, **comb. nov.** ≡ *Sideroxylon rigidifolium* K. Krause, Bot. Jahrb. Syst. 58: 474 (1923). ≡ *Planchonella rigidifolia* (K. Krause) H.J. Lam, Nova Guinea 14: 560 (1932). ≡ *Pouteria rigidifolia* (K. Krause) Baehni, Candollea 9: 319 (1942). — Lectotype designated here: New Guinea, Torricelli Mts., 800 m alt., 22.IX.1909, *R. Schlechter 20322* (P00648143), isolectotype (P00648141) (holotype in B destroyed).

Distribution: New Guinea.

Pleioluma rubicunda (Pierre ex Baill.) Swenson & Munzinger, **comb. nov.** ≡ *Lucuma rubicunda* Pierre ex Baill., Bull. Mens. Soc. Linn. Paris 2: 883 (1890). ≡ *Beccariella rubicunda* (Pierre ex Baill.) Pierre, Not. Bot. Sapot.: 30 (1890). ≡ *Planchonella rubicunda* (Pierre ex Baill.) Dubard in Guillaumin, Ann. Mus. Colon. Marseille, sér. 2, 9: 287 (1911). ≡ *Pouteria rubicunda* (Pierre ex Baill.) Baehni, Candollea 9: 31 (1942). — Holotype: Nouvelle Calédonie, forêt situées au sud de Canala, vers 900 m alt., 20.XI.1869, *Balansa 1825* (P00282282!), isotypes (P00282281!, P00282283!).

Distribution: New Caledonia.

Pleioluma sebertii (Pancher) Swenson & Munzinger, **comb. nov.** ≡ *Chrysophyllum sebertii* Pancher in J. A. I. Pancher & H. Sebert, Not. Bois Nouv. Caléd.: 194 (1874). ≡ *Beccariella sebertii* (Pancher) Pierre, Not. Bot. 1: 30 (1890). ≡ *Planchonella sebertii* (Pancher) Dubard, Ann. Mus. Colon. Marseille, sér. 2, 10: 58 (1912). ≡ *Pouteria sebertii* (Pancher) Baehni, Candollea 9: 297 (1942). — Type: Nouvelle Calédonie, *Sébert & Fournier 49* (P!).

Distribution: New Caledonia.

Pleioluma singuliflora (C.T. White & W.D. Francis) Swenson, **comb. nov.** ≡ *Sideroxylon singuliflorum* C.T. White & W.D. Francis, Proc. Roy. Soc. Queensland 37: 161 (1926[1925]). ≡ *Pouteria singuliflora* (C.T. White & W.D. Francis) Baehni, Candollea 9: 316 (1942). ≡ *Planchonella singuliflora* (C.T. White & W.D. Francis) P. Royen, Blumea 8: 345 (1957). ≡ *Beccariella singuliflora* (C.T. White & W.D. Francis) Swenson, Bartish & Munzinger, Cladistics 23: 221 (2007). — Syntypes: Australia, Bellenden Ker, near summit of Central Peak, North Queensland, south of Cairns, I.1923, *C. T. White s.n.* (BRI!, K!).

Distribution: Australia.

Pleioluma vieillardii (Baill.) Swenson & Munzinger, **comb. nov.** ≡ *Sideroxylon vieillardii* Baill., Bull. Mens. Soc. Linn. Paris 2: 886 (1890). ≡ *Planchonella vieillardii* (Baill.) Dubard, Ann. Mus. Colon. Marseille, sér. 2, 10: 58 (1912). ≡ *Pouteria vieillardii* (Baill.) Baehni, Candollea 9: 414 (1942). ≡ *Beccariella vieillardii* (Baill.) Swenson, Bartish & Munzinger, Cladistics 23: 221 (2007). — Holotype: Nouvelle Calédonie, Gatope, 1861–67, *Vieillard 2889* (P!), isotypes (K!, L!).
Distribution: New Caledonia.

Pleioluma wandae (Vink) Swenson, **comb. nov.** ≡ *Pouteria wandae* Vink, Blumea 47: 118 (2002). —
Holotype: Indonesia, Irian Jaya, surroundings of Ayawasi, 01°14'S, 132°12'E, c. 450 m alt., 16.I.1996, *W. Ave 4163* (L!), isotypes (BO n.v., CANB n.v., MAN n.v.).
Distribution: New Guinea.

Pleioluma xerocarpa (F. Muell. ex Benth.) Swenson, **comb. nov.** ≡ *Achras xerocarpa* F. Muell. ex Benth., Fl. Austral. 4: 281 (1868). ≡ *Sideroxylon xerocarpum* (F. Muell. ex Benth.) Benth. & Hook f. ex F. Muell., Syst. Census Austral. Pl. 1: 91 (1882). ≡ *Planchonella xylocarpa* (F. Muell. ex Benth.) H.J. Lam, Bull. Jard. Bot. Buitenzorg, III, 7: 218 (1925). ≡ *Sersalisia xerocarpa* (F. Muell. ex Benth.) Domin, Biblioth. Bot. 89: 508 (1928). ≡ *Pouteria xerocarpa* (F. Muell. ex Benth.) Baehni, Boissiera 11: 58 (1965). ≡ *Beccariella xerocarpa* (F. Muell. ex Benth.) Aubrév., Adansonia, n.s., 3: 335 (1963). — Syntypes: Australia, Rockingham Bay, *Dallachy s.n.* (BRI!, K!, L!, MEL!, P!).
Distribution: Australia.

Pycnandra Benth., in G. Bentham and J.D. Hooker, Gen. Pl. 2: 658 (1876). — Type: *Pycnandra benthamii* Baill.
= *Leptostylis* Benth., in G. Bentham and J.D. Hooker, Gen. Pl. 2: 659 (1876). — Lectotype: *Leptostylis longiflora* Benth., designated by Vink in Nova Guinea, n.s., 8: 87 (1957).
= *Achradotypos* Baill., Bull. Mens. Soc. Linn. Paris 2: 881 (1890). — Type: *Achradotypos vieillardii* Baill.
= *Trouettia* Pierre ex Baill., Bull. Mens. Soc. Linn. Paris 2: 945 [3 Jun.] (1891). — Type: *Trouettia leptoclada* Pierre ex Baill.
= *Chorioluma* Baill., Hist. Pl. 11: 287 [Sep.-Oct.] (1891). — Type: *Chorioluma coriacea* (Baill.) Baill. ≡ *Sideroxylon coriaceum* Baill.
= *Ochrothallus* Pierre ex Baill., Hist. Pl. 11: 298 [Sep.-Oct.] (1891). — Type: *Ochrothallus sessilifolius* (Pancher & Sebert) Pierre ex Baill. ≡ *Chrysophyllum sessilifolium* Pancher & Sebert
= *Sebertia* Pierre ex Engl., Nat. Pflanzenfam., Nachtr. 4 (1): 280 (1897). — Type: *Sebertia acuminata* (Baill.) Engl. ≡ *Sersalisia acuminata* Baill.
= *Tropalanthe* S. Moore, J. Linn Soc., Bot. 45: 354 (1921). — Type: *Tropalanthe comptonii* S. Moore
= *Corbassona* Aubrév., Fl. Nouv.-Caléd. 1: 72 (1967). — Type: *Corbassona deplanchei* (Baill.) Aubrév. ≡ *Chrysophyllum deplanchei* Baill.

Diagnostic character combination. — Higher leaf venation non-areolate; sepals glabrous inside; flowers usually born along branches, cup-shaped (rarely tubular); stamens usually inserted in corolla tube orifice (rarely below); staminodes absent; style simple; cotyledons plano-convex, red or rarely pinkish, radicle included in cotyledons; endosperm absent.

Some 55 recognized species with another ten waiting to be described, all restricted to New Caledonia. Current classification accepts four subgenera (Swenson & Munzinger, 2009, 2010a, 2010b, 2010c), and *Pycnandra* subgenus *Leptostylis* is under revision. Most species are restricted to either ultramafic or none-ultramafic substrates, and a few to calcareous soils, which means many species are threatened to the point of extinction due to habitat destruction from mining, logging and deliberately set fires.

Sersalisia R. Br., Prodr. Fl. Nov. Holl.: 529 (1810). — Type *Sersalisia sericea* (Aiton) R. Br. ≡ *Sideroxylon sericeum* Aiton

Diagnostic character combination. — Higher leaf venation areolate; sepals pubescent or glabrous inside; flowers axillary, narrowly campanulate or tubular; stamens inserted in or just below corolla tube orifice; staminodes present, entire; style with stigmatic areas; cotyledons plano-convex, radicle included in cotyledons; endosperm absent.

Four to six species, depending on the future status of some undescribed taxa and the relationships of the Australian species *Pouteria unmackiana* (F.M. Bailey) Erlee, which is still not analysed but probably belongs to this genus. One widely distributed species, *S. luzoniensis*.

Sersalisia luzoniensis (Merr.) Swenson, **comb. nov.** ≡ *Sideroxylon luzoniense* Merr., Philipp. J. Sci. 1 (Suppl.): 222 (1906). ≡ *Lucuma luzoniensis* (Merr.) H.J. Lam, Bull. Jard. Bot. Buitenzorg, III, 7: 227 (1925). ≡ *Pouteria luzoniensis* (Merr.) Baehni, Candollea 9: 365 (1942). ≡ *Fontbrunea luzoniensis* (Merr.) Aubrév., Adansonia, n.s., 3: 333 (1963). — Original type material in PNH is destroyed. Lectotype designated here: Philippines, Luzon, Province of Rizal, I.1906, *Foxworthy 127* (K!), isolectotype (US!).

Distribution: Widespread, from the Philippine Islands in the north, Borneo, Sulawesi, and New Guinea in the south.

Van-royena Aubrév., Adansonia, n.s., 3: 329 (1963). — Type: *Van-royena castanosperma* (C.T. White) Aubrév. ≡ *Chrysophyllum castanospermum* C.T. White.

Diagnostic character combination. — Tertiary leaf venation parallel and reticulate, non-areolate; sepals pubescent inside; flowers axillary, narrowly campanulate; stamens inserted near middle (or just above) of the corolla tube; staminodes present, entire; style with stigmatic areas; cotyledons plano-convex, radicle included in cotyledons; endosperm absent.

A single species restricted to northeast Australia, poorly monographed, but van Royen (1957) provided a treatment with an acceptable illustration.

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Figure legends

Fig. 1. Field images of members of subfamily Chrysophylloideae (Sapotaceae) growing in Oceania. **A**, *Niemeyera chartacea*; **B**, *Niemeyera antiloga*; **C**, *Van-royena castanosperma*; **D**, *Pycnandra belepensis*; **E**, *Pichonia deplanchei*; **F**, *Sersalisia sericea*; **G**, *Planchonella baillonii*; **H**, *Planchonella ericiflora*; **I**, *Planchonella minutiflora*; **J**, *Planchonella tahitensis*; **K**, *Planchonella rufocostata*; **L**, *Beccariella* spec. nov. Photos: A, C, F by Hugh Nicholson (Australia); B by Glenn Leiper (Australia); D, I by Ulf Swenson (Sweden); E by Jean-Louis Ruiz (New Caledonia); G, H, K, L by Jérôme Munzinger (France); J by Jean-François Butaud (Tahiti).

Fig. 2. Maximum clade credibility tree obtained from the BEAST analysis of nuclear sequences of Chrysophylloideae (Sapotaceae) from Oceania and Southeast Asia. Currently accepted names are colour-coded according to the legend. Posterior probabilities (PP; above) and parsimony jackknifing (JK; below) are found along the branches. Nodes with support below PP 0.8 and JK 50 are collapsed, except for the estimated relationship of *Van-royena*. Three subclades (D1–D3) within *Planchonella*, identified by Swenson & al. (2007b), are marked with arrows. The outgroup *Ecclinusa* is pruned from the figure.

Fig. 3. Eight morphological characters of diagnostic value mapped on a condensed generic phylogeny of Chrysophylloideae (Sapotaceae) present in Oceania and Southeast Asia. Three seed characters are mapped in **F**. Black lines represent an equivocal state. Embedded triangles or lines in different colours represent taxa with homoplasious characters (see text).

Fig. 4. Summary of proposed classification and necessary combinations of Oceanian and Southeast Asian Chrysophylloideae (Sapotaceae) based on BEAST and jackknife analyses of nrDNA sequences. Accepted genera are (A) *Pleioluma*, (B) *Sersalisia*, (C) *Pichonia*, (D) *Niemeyera*, (E) *Pycnandra*, (F) *Planchonella*, and the small genera *Amorphospermum*, *Magodendron* and *Van-royena*. Type species of genera are indicated in bold. Undescribed species and those not transferred here appear in citation marks.

Table 1. List of primers used

DNA region	Primer	Sequence 5'-3'	Reference
ETS	18S-ETS	ACT TAC ACA TGC ATG GCT TAA TCT	Baldwin & Markos (1998)
ETS	Sap-1	CGT ACT TGA GCG TGT TGG TGT	Swenson & al. (2008a)
ITS	18SF	GAA CCT TAT CGT TTA GAG GAA GG	Rydin & al. (2004)
ITS	26RN	CCG CCA GAT TTT CAC GCT GGG C	Rydin & al. (2004)
RPB2	P6F	TGG GGA ATG ATG TGT CCT GC	Denton & al. (1998)
RPB2	P7R	CCC ATG GCT TGC TTC CCC AT	Denton & al. (1998)
RPB2	270F-Sap	CCT AGT GTT ACC TTT TAC CCT GAT TG	This study*
RPB2	570F-Sap	CAT GGC ATT CAA CTA CTG AAG AGT TG	This study*
RPB2	540R-Sap	CAA CTC TTC AGT AGT TGA ATG CCA TG	This study*
RPB2	435F-Sap	TAA TAT GTC AGC TTG TGG TGG AGA G	This study*
RPB2	435R-Sap	CTC TCC ACC ACA AGC TGA CAT ATT A	This study*
RPB2	800F-Sap	GCA TCT CTG TCC TCT TGA TTA CTT GAA TG	This study*
RPB2	800R-Sap	CAT TCA AGT AAT CAA GAG GAC AGA GAT GC	This study*
RPB2	1020F-Sap	GCT ACT TTG AAG CAC TTG CTA GAA TCT	This study*
RPB2	1020R-Sap	AGA TTC TAG CAA GTG CTT CAA AGT AGC	This study*

*Primers designed by Bodil Cronholm, Swedish Museum of Natural History.

Table 2. Characteristics of nuclear sequences in each of the data partitions (excluding the outgroup)

Data	<u>Number of characters</u>				
	Aligned	Constant	Uninformative	Informative	Gaps
ETS	403	114	91	198 (49.1%)	22
ITS	914	418	176	320 (35.0%)	42
RPB2	1169	483	535	151 (12.9%)	13
Total	2486	1015	802	668 (26.9%)	77

Appendix 1. Voucher information in the following order: Taxon name with authority, country, collector(s), collector number, (herbarium abbreviation), and GenBank accessions (ETS, ITS, RPB2). Informal or unpublished names are given in quotation marks and sequences published here have the prefix HE or HF.

Beccariella "acutifolia" Swenson & Munzinger, New Caledonia, *Munzinger & al. 5759* (NOU, P, S), HE860126, HE860065, HE995703. *Beccariella balansana* (Pierre) Aubrév., New Caledonia, *Munzinger & al. 4196* (MO, NOU, P, S), HE860127, HE860066, HE995704. *Beccariella baueri* (Montrouz.) Aubrév., New Caledonia, *Munzinger 340* (NOU, P, S), HE860128, AY552113, HE995705. *Beccariella "belepensis"* Swenson & Munzinger, New Caledonia, *Swenson & al. 917* (MO, NOU, P, S), HE860129, HE860067, HE995706. *Beccariella brevipedicellata* (P. Royen) Aubrév., New Caledonia, *Dumontet, Poullain & Zongo 658* (NOU, P, S), HE860130, HE860068, HE995707. *Beccariella brownlessiana* (F. Muell.) Swenson, Bartish & Munzinger, Australia, *Bartish & Ford 17* (BRI, S), HE860131, DQ154063, HE995708. *Beccariella crebrifolia* (Baill.) Aubrév., New Caledonia, *Munzinger, Lowry & Létocart 2036* (NOU, P, S), HE860132, DQ154042, HE995597. *Beccariella lasiantha* (Baill.) Aubrév., New Caledonia, *Munzinger 2308* (NOU, P, S), HE860133, DQ154044, HE995598. *Beccariella longipetiolata* Aubrév., New Caledonia, *Munzinger & Létocart 2264* (NOU, P, S), HE860135, DQ154045, HE995709. *Beccariella longipetiolata* Aubrév., New Caledonia, *Munzinger, Pillon & Butin 2911* (NOU, P, S), HE860136, HE860070, HE995710. *Beccariella lucens* (P. Royen) Aubrév., New Caledonia, *Munzinger & Létocart 2310* (NOU, P, S), HE860137, HE860071, HE995711. *Beccariella macrocarpa* (P. Royen) Swenson, Bartish & Munzinger, Australia, *Bartish & Ford 24* (S), HE860138, DQ154073, HE995712. *Beccariella "Munzinger2581"*, New Caledonia, *Munzinger, Labat & Butin 2581* (NOU, P, S), HE860140, HE860073, HE995713. *Beccariella novocaledonica* (Dubard) Aubrév., New Caledonia, *Munzinger 2304* (MO, NOU, S), HE860141, HE860074, HE995714. *Beccariella papyracea* (P. Royen) Aubrév., Australia, *Bartish & Ford 20* (S), HE860142, DQ154046, HE995715. *Beccariella queenslandica* (P. Royen) Aubrév., Australia, *Bartish & Jessup 8* (S), HE860143, DQ154043, HE995659. *Beccariella rubicunda* (Pierre ex Baill.) Pierre, New Caledonia, *Swenson, McPherson & Mouly 596* (NOU, P, S), HE860144, AY552160, HE995716. *Beccariella sebertii* (Pancher) Pierre, New Caledonia, *Munzinger, Pignal, Dagostini & Hopkins 1975* (S), HE860145, DQ154047, HE995717. *Beccariella singuliflora* (C.T. White & W.D. Francis) Swenson, Bartish & Munzinger, Australia, *Ford & Metcalfe 4547* (QRS, S), HE860146, DQ246699, HE995718. *Beccariella "Takeuchi25691"*, New Guinea, *Takeuchi 25691* (LAE, S), HE860147, HE860075, HE995599. *Beccariella vieillardii* (Baill.) Swenson, Bartish & Munzinger, New Caledonia, *Munzinger 2282* (S), HE860148, DQ154087, HE995719. *Beccariella xerocarpa* (F. Muell. ex Benth.) Aubrév., Australia, *Bartish & Ford 28* (BRI, S), HE860149, DQ154048, HE995683. *Chrysophyllum bakhuizenii* P. Royen, New Guinea, *Takeuchi 18997* (LAE, S), HE860150, HE860076, HE995600. *Chrysophyllum wagapense* Guillaumin, New Caledonia, *Munzinger, D. & I. Létocart 5634* (MO, NOU, P, S), HE860151, HE860077, HE995601. *Ecclinusa guianensis* Eyma, South America, Brazil, Ducke Reserve 05-906 (K), HE860152, DQ246677, HE995661. *Ecclinusa ramiflora* Mart., South America, Surinam, *Irwing & al. 55081* (S), HE860153, DQ246678, HE995602. *Krausella patentinervia* (K. Krause) Erlee, New Guinea, *Armstrong 317* (E, S), HE860154, HE860078, HE995686. *Krausella polyneura* (K. Krause) H.J. Lam, Papua New Guinea, *Ledermann 9054* (K), HF678108, HF912279, —. *Leptostylis filipes* Benth., New Caledonia, *Webster & Hildreth 14665* (P), EU661382, AY552135, HE995603. *Leptostylis goroensis* Aubrév., New Caledonia, *Munzinger 2288* (NOU, P, S), EU661383, DQ154052, HE995604. *Leptostylis grandifolia* Vink, New Caledonia, *Munzinger & Oddi 2121* (MO, NOU, P, S), EU661384, DQ154053, HE995605. *Magodendron mennyae* Vink, New Guinea, *Takeuchi, Ama & Siga 16570* (S), HE860155, AY552114, HE995685. *Niemeyera antiloga* (F. Muell.) T.D. Penn., Australia, *Bartish & Jessup 4* (S), HE860156, DQ154055, HE995662. *Niemeyera chartacea* (F.M.Bailey) C.T. White, Australia, *Bartish & Jessup 5* (S), HE860157, DQ154057, HE995606. *Niemeyera "Ford2429"*, Australia, *Andrew Ford 2429* (S), EU661389, EF025089, HE995607. *Niemeyera prunifera* (F. Muell.) F.

Muell., Australia, *Jessup* 5238 (S), HE860158, DQ154058, HE995608. *Niemeyera whitei* (Aubrév.) L.W. Jessup, Australia, *Floyd s.n.* (S), EU661388, AY552137, HE995609. *Pichonia balansae* (Baehni) Swenson & Munzinger, New Caledonia, *Munzinger* 975 (MO, NOU, P), HE860159, AY552102, HE995720. *Pichonia balansana* Pierre, New Caledonia, *Veillon* 7990 (P), HE860160, AY552109, HE995610. *Pichonia daenikeri* (Aubrév.) Swenson, Bartish & Munzinger, New Caledonia, *Jaffré & Rigault* 3038 (NOU, P), HE860161, AY552108, HE995690. *Pichonia deplanchei* (Baill.) Swenson & Munzinger, New Caledonia, *Veillon* 377 (NOU, P), HE860162, AY552103, HE995699. *Pichonia dubia* (Guillaumin) Swenson & Munzinger, New Caledonia, Grande Terre, *Munzinger & Swenson* 3065 (NOU, S), HE860163, HE860079, HE995721. *Pichonia dubia* (Guillaumin) Swenson & Munzinger, New Caledonia, Ile Art, *Swenson & al.* 918 (NOU, P, S), HE860164, HE860080, HE995722. *Pichonia grandiflora* Swenson & Munzinger, New Caledonia, *Swenson & Munzinger* 930 (NOU, P, S), HE860165, HE860081, HE995611. *Pichonia lecomtei* (Guillaumin) T.D. Penn., New Caledonia, *Munzinger & al.* 2170 (MO, NOU, P, S), HE860166, DQ154061, HE995723. *Pichonia occidentalis* (H.J. Lam) Aubrév., New Guinea, *Takeuchi & Ama* 22233 (LAE, S), HE860167, HE860082, HE995750. *Planchonella amieuana* (Guillaumin) Aubrév., New Caledonia, *Dumontet, Zongo & Maituku* 510 (NOU, P, S), HE860168, EF025090, HE995612. *Planchonella aneityensis* (Guillaumin) H.J. Lam ex P. Royen, Vanuatu, *Munzinger, Lowry & Tuiwawa* 3665 (NOU, P, S, SUVA), HE860169, HE860083, HE995724. *Planchonella anteridifera* (C.T. White & W.D. Francis ex Lane-Poole) H.J. Lam, New Guinea, *Takeuchi & Ama* 17902 (LAE, S), HE860170, EF025109, HE995750. *Planchonella arnhemica* (F. Muell. ex Benth.) P. Royen, Australia, *Harwood* 1170 (S), HE860171, AY552107, HE995663. *Planchonella asterocarpon* (P. Royen) Swenson, Bartish & Munzinger, Australia, *Bartish & Ford* 25 (BRI, S), HE860172, DQ154078, HE995664. *Planchonella australis* (R. Br.) Pierre, Australia, *Floyd s.n.* (S), HE860173, AY552148, HE995613. *Planchonella baillonii* (Zahlbr.) Dubard, New Caledonia, *Munzinger & Dagostini* 2119 (MO, NOU, P, S), HE860174, HE860084, HE995725. *Planchonella cauliflora* Munzinger & Swenson, New Caledonia, *Munzinger & al.* 3495 (K, MO, NOU, NSW, P, S), HE860175, HE860085, HE995666. *Planchonella chartacea* (F. Muell. ex Benth.) H.J. Lam, Australia, *Bartish & Jessup* 1 (BRI, S), HE860176, HE862231, HE995665. *Planchonella clemensii* (Lecomte) P. Royen, China, Hainan, *How* 73783 (S), HE860177, HE860086, HE995692. *Planchonella costata* (Endl.) Pierre, New Zealand (cultivated in USA), *Peter W. Fritsch* 1770 (CAS), —, AF396230, —. *Planchonella costata* (Endl.) Pierre, New Zealand (cultivated in Edinburgh), *Robertson* 9 (E), HE860178, —, HE995726. *Planchonella cotinifolia* (A.DC.) Dubard, Australia, *Bartish & Jessup* 11 (BRI, S), HE860179, DQ154066, HE995701. *Planchonella crassinervia* Dubard, New Caledonia, *Munzinger* 2275 (NOU, P, S), HE860180, DQ154067, HE995667. *Planchonella cycloperensis* P. Royen, New Guinea, *Polak* 1365 (L), HE860181, HE860087, HE995693. *Planchonella cycloperensis* P. Royen, New Guinea, *Takeuchi, Ama & Gambia* 25495 (LAE, S), HE860182, HE860088, HE995751. *Planchonella dothioensis* (Aubrév.) Swenson, Bartish & Munzinger, New Caledonia, *Munzinger* 995 (MO, NOU, P, S), HE860183, AY552138, HE995668. *Planchonella duclitan* (Blanco) Bakh.f., New Guinea, *Fuentes & Fernando* 37140 (L), HE860184, HE860089, —. *Planchonella eerwah* (F.M. Bailey) P. Royen, Australia, *Floyd s.n.* (S), EU661400, AY552147, HE995669. *Planchonella endlicheri* (Montrouz.) Guillaumin, New Caledonia, *Munzinger, Lowry & Létocart* 2038 (NOU, P, S), HE860185, DQ154068, HE995614. *Planchonella ericiflora* Munzinger & Swenson, New Caledonia, *Munzinger & al.* 4197 (MO, NOU, P, S), HE860186, HE860090, HE995660. *Planchonella euphlebia* (F. Muell.) Francis, Australia, *Bartish & Ford* 18 (BRI, MO, S), HE860187, DQ154069, HE995727. *Planchonella firma* (Miq.) Dubard, New Guinea, *Takeuchi, Ama & Jisaka* 21437 (LAE, S), HE860188, HE860091, HE995615. *Planchonella glauca* Swenson & Munzinger, New Caledonia, *Swenson, McPherson & Mouly* 625 (S), HE860189, AY552104, HE995728. *Planchonella grayana* H.St.John, French Polynesia, Australs, *Butaud* 192 (PAP), HE860191, HE860092, HE995616. *Planchonella grayana* var. *florencei* Fosberg, French Polynesia, Tahiti, *Florence* 3967 (BISH, PAP, S), —, HE860093, —. *Planchonella grayana* H. St.John, French Polynesia, Tuamotus, *Butaud & Lagouy* 1173 (PAP), HE860193, HE860094, HE995617. *Planchonella grayana* H.

St. John, Wallis and Futuna, Alofi, *Munzinger 5479* (NOU, P, S), HE860190, HE860095, HE995729.

Planchonella grayana H. St. John, Wallis and Futuna, Futuna, *Munzinger, Meyer & Jourdan 5282* (P, S), HE860192, HE860096, HE995730. ***Planchonella howeana*** (F. Muell.) Pierre, Lord Howe Island, *Le Cussan 1210* (BRI), HE860194, EF025094, HE995681. ***Planchonella "Ile Yande"***, New Caledonia, *Swenson & Munzinger 715* (S), HE860195, EF025091, —. ***Planchonella kaalaensis*** Aubrév., New Caledonia, *Swenson & Munzinger 706* (S), HE860196, HE860097, HE995694. ***Planchonella koumaciensis*** Aubrév., New Caledonia, *Munzinger 2665* (NOU), HE860197, EF025095, HE995682. ***Planchonella kuebiniensis*** Aubrév., New Caledonia, *Munzinger & Létocart 2057* (S), HE860198, DQ154070, HE995670. ***Planchonella laetevirens*** (Baill.) Pierre ex Dubard, New Caledonia, *Munzinger, Pignal & Lowry 2001* (MO, NOU, P, S), HE860199, DQ154071, HE995618. ***Planchonella lamprophylla*** (K. Krause) H.J. Lam, New Guinea, *Takeuchi, Ama & Gambia 25573* (LAE, S), HE860200, HE860098, HE995619. ***Planchonella lauracea*** (Baill.) Dubard, New Caledonia, *McPherson & Munzinger 18070* (MO, S), HE860201, AY552145, HE995731. ***Planchonella ledermannii*** (K. Krause) H.J. Lam, New Guinea, *Takeuchi, Towati, Jisaka & Ama 17700* (LAE, S), HE860202, HE860099, HE995732. ***Planchonella linggensis*** (Burck) Pierre, Wallis and Futuna, Futuna, *Munzinger 5330* (NOU, P, S), HE860203, HE860100, HE995733. ***Planchonella linggensis*** (Burck) Pierre, New Guinea, *Takeuchi, Jisaka, Towati & Ama 21108* (LAE, S), HE860204, HE860101, HE995695. ***Planchonella linggensis*** (Burck) Pierre, Vanuatu, *Wheatley 271* (K), —, DQ154062, —. ***Planchonella luteocostata*** Munzinger & Swenson, New Caledonia, *Munzinger, Jaffré & Roumagnac 2375* (NOU, S), EU661401, EF025099, HE995755. ***Planchonella maingayi*** (C.B. Clarke) P. Royen, Singapore, *Wilkie & Gwee 507* (E), HE860205, HE860102, HE995620. ***Planchonella mandjeliana*** Munzinger & Swenson, New Caledonia, *Munzinger & Pillon 2861* (NOU, P, S), HE860206, EF025100, HE995680. ***Planchonella membranacea*** H.J. Lam, Fiji, *Smith 4609* (S), HE860207, DQ154074, HE995621. ***Planchonella mindanaensis*** H.J. Lam, Philippines, *Clemens 1015* (PNH), HE860208, HE860103, HE995622. ***Planchonella minutiflora*** Munzinger & Swenson, New Caledonia, *MacKee 16639* (NOU, P, S), HE860209, HE860104, HE995734. ***Planchonella moluccana*** (Burck) H.J. Lam, New Guinea, *Takeuchi, Ama & Gambia 25550* (S), HE860139, HE860072, HE995671. ***Planchonella "Munzinger 6150"***, New Caledonia, *Munzinger 6150* (NOU), HE860210, HE860105, HE995735. ***Planchonella "Munzinger 6490"***, Fiji, *Munzinger 6490* (NOU, SUVA), HE860211, HE860106, HE995736. ***Planchonella "Munzinger 6514"***, Fiji, *Munzinger 6514* (NOU, SUVA), HE860212, HE860107, HE995737. ***Planchonella myrsinifolia*** (F. Muell.) Swenson, Bartish & Munzinger, Australia, *Floyd s.n.* (S), HE860213, AY552143, HE995702. ***Planchonella myrsinoides*** (Benth.) S.T. Blake ex Francis, Australia, *McDonald 3365* (QRS, S), HE860214, EF025092, HE995738. ***Planchonella obovata*** (R. Br.) Pierre, Taiwan, *Chung & Anderberg 1166* (HAST, S), EU661402, DQ154076, HE995739. ***Planchonella "Pillon 150"***, New Caledonia, *Pillon, Barrabé & Rigault 150* (NOU, P, S), HE860215, HE860108, HE995696. ***Planchonella pohlmaniana*** (F. Muell.) Pierre ex Dubard, Australia, *Bartish & Ford 22* (BRI, S), HE860216, DQ154079, HE995672. ***Planchonella pronyensis*** Guillaumin, New Caledonia, *Munzinger 2051* (NOU), HE860217, DQ154080, HE995623. ***Planchonella roseoloba*** Munzinger & Swenson, New Caledonia, *Munzinger 2311* (NOU, P, S), HE860218, DQ154090, HE995673. ***Planchonella rufocostata*** Munzinger & Swenson, New Caledonia, *Munzinger, Labat & Butin 2583* (NOU, S), HE860219, DQ154089, HE995684. ***Planchonella saligna*** S. Moore, New Caledonia, *Munzinger, Létocart & Gâteblé 2218* (NOU, P, S), HE860220, DQ154083, HE995624. ***Planchonella sandwicensis*** (A. Gray) Pierre, Hawaii, Ohau, *Koolan 119d* (GB), HE860221, DQ154084, HE995740. ***Planchonella sandwicensis*** (A. Gray) Pierre, Hawaii, Kauai, *Merello, Bess & Johnson 3227* (MO, S), HE860222, HE860109, HE995741. ***Planchonella sandwicensis*** (A. Gray) Pierre, Hawaii, Ohau, *Doug Okamoto s.n.* (S), HE860223, HE860110, HE995742. ***Planchonella skottsbergii*** Guillaumin, New Caledonia, *Munzinger, Gâteblé & Amice 2391* (NOU, P, S), HE860224, DQ154085, HE995674. ***Planchonella smithii*** (P. Royen) A.C. Sm., Fiji, *Munzinger 6495* (NOU, S, SUVA), HE860225, HE860111, HE995743. ***Planchonella solida*** P. Royen, New Guinea, *Takeuchi, Towati & Ama 17286* (LAE, S), HE860226, EF025104, HE995675. ***Planchonella sphaerocarpa*** (Baill.) Dubard,

New Caledonia, *Tronchet, Munzinger & Oddi 389* (MO, P), EU661403, AY552139, HE995625. ***Planchonella tahitensis*** (Nadeaud) Pierre ex Dubard, French Polynesia, Raiatea, *Meyer & Taputuarai 3013* (NOU, PAP), HE860227, EF025108, HE995626. ***Planchonella tahitensis*** (Nadeaud) Pierre ex Dubard, French Polynesia, Tahiti, *Meyer & Taputuarai 3051* (PAP), HE860228, EF025105, HE995744. ***Planchonella thiensis*** Aubrév., New Caledonia, *Munzinger, Dagostini, Rigault & Kurpisz 2625* (S), HE860229, EF025106, HE995676. ***Planchonella thyrsoides*** C.T. White, New Guinea, *Whitfeld PA-2E-0072* (LAE, MIN, S), HE860230, HE860112, HE995745. ***Planchonella torricellensis*** (K. Schum.) H.J. Lam, Wallis and Futuna, Alofi, *Munzinger 5473* (NOU, S), HE860231, HE860113, HE995746. ***Planchonella torricellensis*** (K. Schum.) H.J. Lam, Wallis and Futuna, Futuna, *Munzinger 5284* (NOU), HE860232, HE860114, HE995747. ***Planchonella umbonata*** (P. Royen) A.C. Sm., Fiji, *Smith 8298* (K), HE860233, DQ154086, HE995627. ***Planchonella vitiensis*** Gillespie, Fiji, *Smith 7700* (S), HE860234, DQ154088, HE995628. ***Planchonella xylocarpa*** (C.T. White) Swenson, Bartish & Munzinger, Australia, *Bartish & Ford 31* (BRI, S), HE860235, DQ154049, HE995629. ***Planchonella xylocarpa*** (C.T. White) Swenson, Bartish & Munzinger, Papua New Guinea, *Takeuchi, Towati & Ama 17284* (LAE, S), HE860236, EF025107, HE995677. ***Pouteria "Armstrong316"***, New Guinea, *Armstrong 316* (E), —, HE860115, —. ***Pouteria gillisonii*** Vink, New Guinea, *Takeuchi & Ama 19050B* (LAE, S), HE860237, HE860116, HE995748. ***Pouteria luzoniensis*** (Merr.) Baehni, New Guinea, *Conn, Damas, Fazang, Paul & Kuria 5063* (L), HE860238, HE860117, HE995697. ***Pouteria maclayana*** (F. Muell.) Baehni, Papua New Guinea, *Regaldo & Katik 1102* (L), HE860239, HE860118, HE995698. ***Pouteria malaccensis*** (C.B. Clarke) Baehni, Singapore, *Swenson, Karim & Fadli 1017* (S, SING), HE860240, HE860119, HE995679. ***Pouteria pullenii*** Vink, New Guinea, *Takeuchi, Jisaka, Towati & Ama 21157* (LAE, S), —, HE860120, HE995630. ***Pouteria richardii*** (F. Muell.) Baehni, Australia, *Dixon & Leach 1032* (BRI, DNA, S), HE860134, HE860069, HE995749. ***Pouteria stellibacca*** J.F. Maxwell, Thailand, *Boonkongchart & Chongko 146* (L), HE860241, HE860121, HE995700. ***Pouteria wandae*** Vink, New Guinea, *Armstrong 305* (E, S), HE860242, HE860122, —. ***Pycnandra acuminata*** (Pierre ex Baill.) Swenson & Munzinger, New Caledonia, *Munzinger 1006* (MO, NOU, P), EU661430, AY552124, HE995631. ***Pycnandra atrofusca*** Swenson & Munzinger, New Caledonia, *Munzinger & al. 2618* (NOU, P, S), EU661419, EU661443, HE995632. ***Pycnandra balansae*** (Baill.) Swenson & Munzinger, New Caledonia, *Munzinger & al. 1451* (S), EU661387, AY552123, HE995754. ***Pycnandra belepensis*** Swenson & Munzinger, New Caledonia, Ile Art, *Swenson, Munzinger & Barrabé 913* (S), HE860243, HE860123, HE995687. ***Pycnandra benthamii*** Baill., New Caledonia, *Munzinger, Létocart & Gâteblé 2228* (NOU, P, S), EU661404, EU661436, HE995633. ***Pycnandra blaffartii*** Swenson & Munzinger, New Caledonia, *Swenson, McPherson & Mouly 597* (NOU, S), EU661423, AY552127, HE995634. ***Pycnandra blanchonii*** (Aubrév.) Swenson & Munzinger, New Caledonia, *Munzinger, Labat, Leveque & Mandaoué 2576* (S), EU661390, DQ154059, HE995635. ***Pycnandra bracteolata*** Swenson & Munzinger, New Caledonia, *Munzinger, Pillon & Butin 2885* (NOU, P, S), EU661421, EU661445, HE995636. ***Pycnandra caeruleilatex*** Swenson & Munzinger, New Caledonia, *Munzinger & al. 2622* (MO, NOU, P, S), EU661426, EU661448, HE995637. ***Pycnandra canaliculata*** Swenson & Munzinger, New Caledonia, *Munzinger & al. 2067* (MO, NOU, P, S), EU661431, DQ154092, HE995638. ***Pycnandra carinocostata*** Vink, New Caledonia, *McPherson & Munzinger 18091* (MO, NOU, P, S), EU661405, AY552132, HE995639. ***Pycnandra comptonii*** (S. Moore) Vink, New Caledonia, *Lowry, McPherson & Le Borgne 5780A* (MO, S), EU661407, AY552131, HE995640. ***Pycnandra controversa*** (Guillaumin) Vink, New Caledonia, *Lowry, McPherson & Le Borgne 5787* (MO, S), EU661408, AY552126, HE995641. ***Pycnandra cylindricarpa*** Swenson & Munzinger, New Caledonia, *Swenson, McPherson & Mouly 615* (MO, NOU, S), EU661429, AY552110, HE995757. ***Pycnandra decandra*** (Montrouez) Vink, New Caledonia, Ile Art, *Swenson, Munzinger & Barrabé 920* (S), HE860244, HE860124, HE995688. ***Pycnandra deplanchei*** (Baill.) Swenson & Munzinger, New Caledonia, *Munzinger 978* (MO, NOU, P, S), EU661380, AY552120, HE995642. ***Pycnandra fastuosa*** (Baill.) Vink, New Caledonia, *Munzinger & Swenson 2993* (NOU, S), EU661394, EU661434, HE995643. ***Pycnandra francii*** (Guillaumin & Dubard) Swenson & Munzinger, New

Caledonia, *Munzinger 965* (MO, NOU, P), EU661391, AY552117, HE995644. *Pycnandra glabella* Swenson & Munzinger, New Caledonia, *Munzinger & al. 2615* (NOU, P, S), EU661418, EU661442, HE995645. *Pycnandra glaberrima* Swenson & Munzinger, New Caledonia, *Munzinger & al. 1394* (MO, NOU, P, S), EU661399, AY552133, HE995646. *Pycnandra gordoniiifolia* (S.Moore) Swenson & Munzinger, New Caledonia, *Swenson & Munzinger 726a* (BRI, MO, NOU, P, S), EU661392, EU661433, HE995647. *Pycnandra griseosepala* Vink, New Caledonia, *Swenson, McPherson & Mouly 627* (MO, NOU, S), EU661414, AY552128, HE995648. *Pycnandra kaalaensis* Aubrév., New Caledonia, *Munzinger & Labat 2599* (NOU, S), EU661415, EU661440, HE995756. *Pycnandra linearifolia* Swenson & Munzinger, New Caledonia, *Munzinger & Blaffart 2786* (NOU, P, S), EU661427, EU661440, HE995753. *Pycnandra neocaledonica* (S.Moore) Vink, New Caledonia, *Tronchet, Munzinger & Oddi 426* (MO, NOU, P, S), EU661416, AY552129, HE995649. *Pycnandra ouaiemensis* Swenson & Munzinger, New Caledonia, *Munzinger, Lowry, Blaffart & Brown 3135* (NOU, S), EU661422, EU661446, HE995689. *Pycnandra paucinervia* Swenson & Munzinger, New Caledonia, *Munzinger & al. 1438* (NOU, P, S), EU661424, AY552159, HE995650. *Pycnandra pubiflora* Swenson & Munzinger, New Caledonia, *Munzinger & al. 2624* (NOU, P, S), EU661420, EU661444, HE995651. *Pycnandra sarlinii* (Aubrév.) Swenson & Munzinger, New Caledonia, *Munzinger 1860* (NOU, P, S), EU661395, EU661435, HE995652. *Pycnandra schmidii* (Aubrév.) Swenson & Munzinger, New Caledonia, *McPherson & Munzinger 18106* (MO, NOU, P, S), EU661396, AY552116, HE995653. *Pycnandra sessiliflora* Swenson & Munzinger, New Caledonia, *Munzinger & McPherson 696* (BRI, MO, NOU, P, S), EU661398, AY552161, HE995691. *Pycnandra sessilifolia* (Pancher & Sebert) Swenson & Munzinger, New Caledonia, *McPherson & Munzinger 18176* (MO, P), EU661397, AY552118, HE995654. *Pycnandra vieillardii* (Baill.) Vink, New Caledonia, *Dumontet, Zongo & Maituku s.n.* (S), EU661417, EU661441, HE995655. *Pycnandra viridiflora* Swenson & Munzinger, New Caledonia, *Munzinger, McPherson & Tuiwawa 4195* (NOU, S), HE860245, HE860125, HE995656. *Sersalisia sericea* (Aiton) R. Br., Australia, *Harwood 1172* (S), HE860246, AY552112, HE995657. *Sersalisia sessiliflora* (C.T. White) Aubrév., Australia, *Bartish & Ford 33* (BRI, MO, P, S), HE860247, DQ154094, HE995678. *Van-royena castanosperma* (C.T. White) Aubrév., Australia, *Bartish & Ford 26* (S), HE860248, DQ154096, HE995658.



Figure 1.

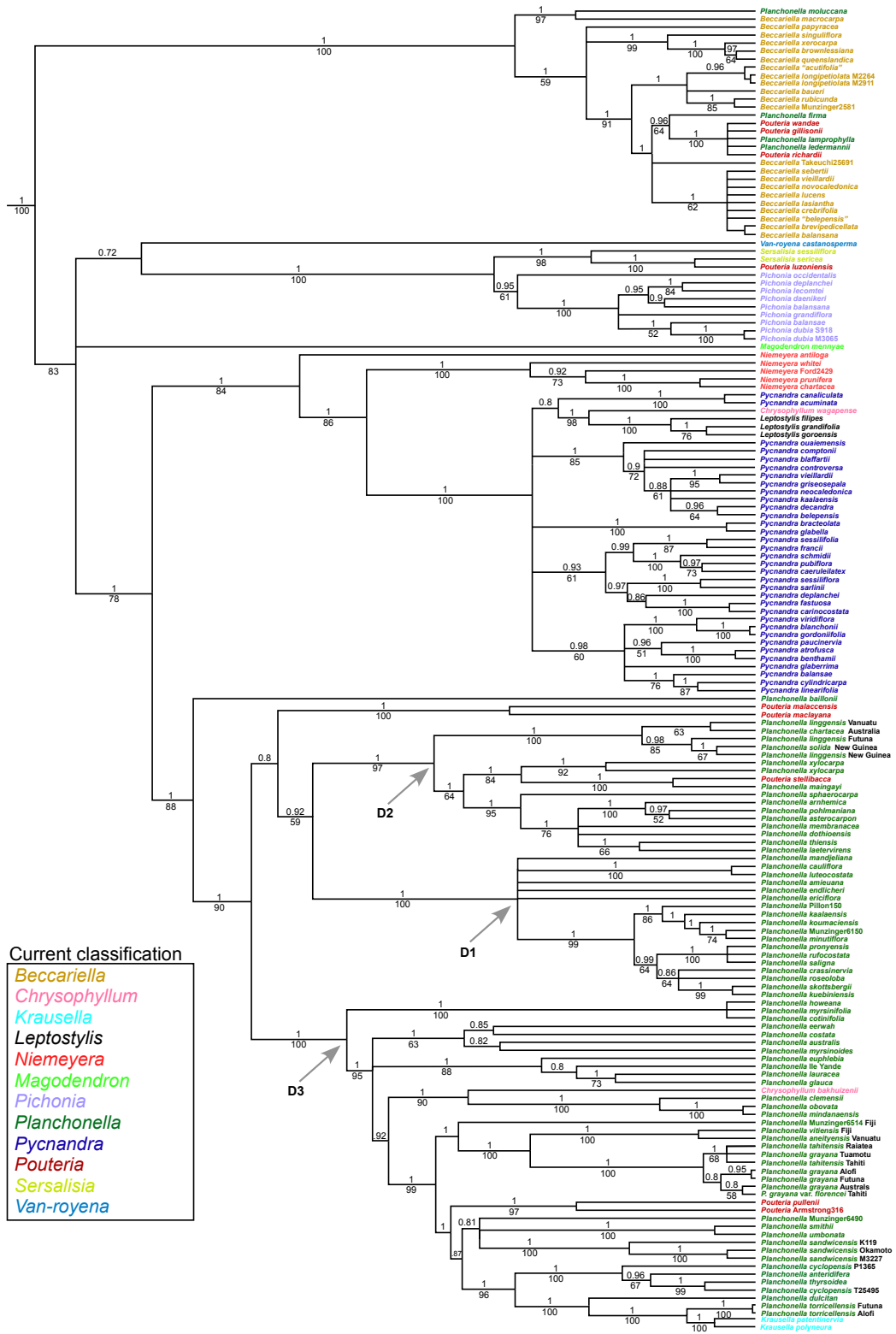


Figure 2.

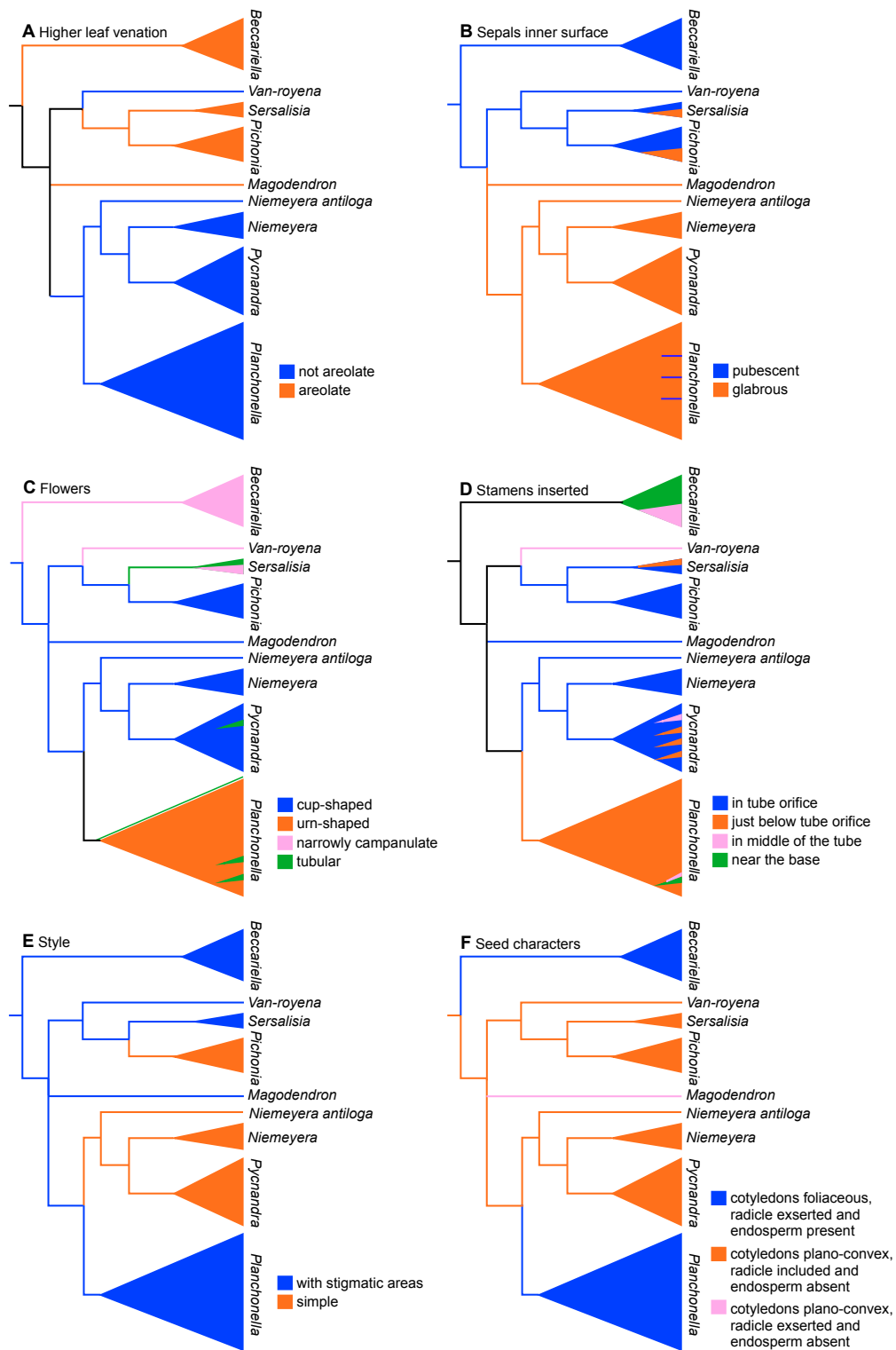


Figure 3.

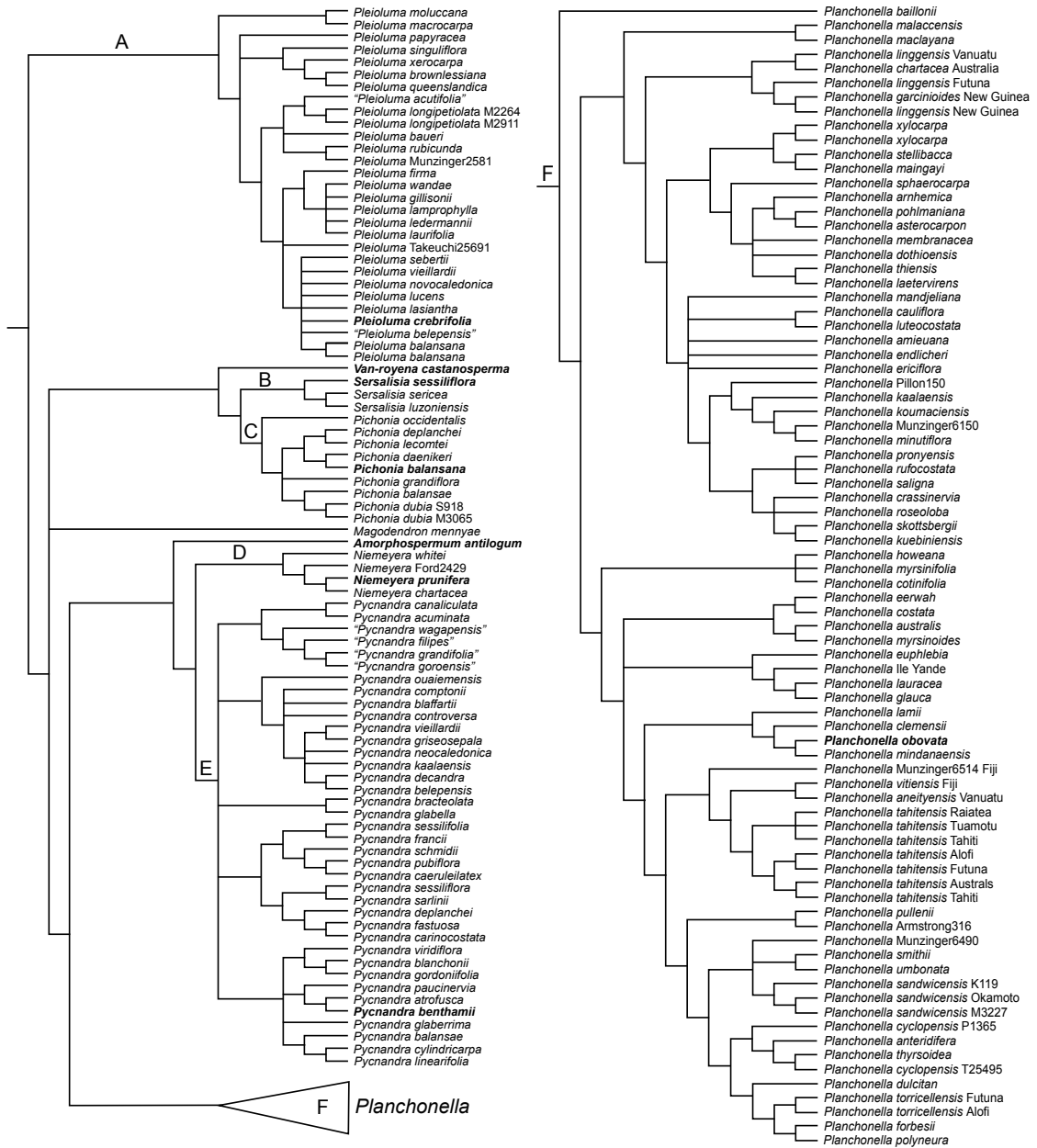


Figure 4.