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Island life – classification, speciation and cryptic species of *Pycnandra* (Sapotaceae) in New Caledonia

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Pycnandra (Sapotaceae), the largest endemic genus in New Caledonia, comprises 66 species classified in six subgenera. We tested phylogenetic relationships and a proposed infrageneric classification by sampling 60 species for sequences of nuclear ribosomal DNA (ETS, ITS, *RPB2*) and plastid DNA (*trnH–psbA*) and nine morphological characters. Data were analysed with Bayesian inference, parsimony jackknifing and lineage through time. We recovered a phylogenetic tree supporting the recognition of six proposed subgenera (*Achradotypus*, *Leptostylis*, *Pycnandra*, *Sebertia*, *Trouettia* and *Wagapensia*). Because a subgeneric classification is used, the nomenclature will be stable when the members are transferred to *Pycnandra*. Morphological traits were optimized in the BEAST analysis, adding evidence to earlier work that morphology has limited value for successfully diagnosing groups in Sapotaceae. We confirm a previously suspected case of cryptic species that exhibit the same morphological features and require the same abiotic conditions, but are distantly related in the phylogenetic tree. We detected two possible new cases of cryptic sibling species that might warrant recognition. A slowdown in speciation rate in several genera has been suggested as evidence that New Caledonia was once submerged after rifting from Australia. Plotting lineages through time reveals two important intervals at 7.5–8.6 Ma and present to 1.5 Ma, when net molecular diversification within the genus was zero. This indicates that the genus presently has reached a dynamic equilibrium, providing additional evidence that New Caledonia is an old Darwinian island, being submerged during the Eocene and colonized after re-emergence *c*. 37 Ma. *Botanical Journal of the Linnean Society*, 2015, **179**, 57–77.

ADDITIONAL KEYWORDS: anagenesis – Chrysophylloideae – morphology – phylogeny.

INTRODUCTION

The archipelago of New Caledonia, a renowned hotspot for biodiversity (Myers *et al*., 2000; Lowry *et al*., 2004), is located *c*. 1500 km east of Queensland, Australia, in the south-western Pacific Ocean. It occupies an area of 19 060 km^2, with Grande Terre being the largest island covering some 16 595 km^2 (Neall & Trewick, 2008). Most of New Caledonia (with the exception of the geologically recent Loyalty Islands) is of continental origin, having rifted away from Australia 65–80 Mya, reaching its present position some 50 Mya, at which time it was entirely submerged (McLoughlin, 2001; Hall, 2002; Neall & Trewick, 2008). Before its re-emerged *c*. 37 Mya (Grandcolas *et al*., 2008), the basement of New Caledonia was overthrusted by lithospheric ultramafic rocks rich in nickel and cobalt

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(Cluzel, Aitchison & Picard, 2001; Cluzel *et al*., 2012), which gave rise to the mineral-rich substrates that are extensively exploited today, primarily for nickel. Most mining is done by scraping off mountain tops, where the best quality ore is concentrated, a process that removes the entire vegetation. This represents an acute threat to the biodiversity of the island, especially given the limited area that is under full protection (Jaffré, Bouchet & Veillon, 1998; Jaffré, 2005; Pascal *et al*., 2008).

The known vascular flora of New Caledonia comprises 3371 species, of which 74.7% are endemic (Morat *et al*., 2012). Sapotaceae are the third largest family with *c*. 135 species and *Pycnandra* Benth. is the largest endemic genus in the archipelago with 66 species (some of which remain to be described). Species currently placed in *Pycnandra* were previously assigned to seven genera by Aubréville (1967) and three by Pennington (1991), but both classifications have been shown to be unnatural as they do not reflect phylogenetic relationships and more recent studies have had difficulty delimiting genera that are both monophyletic and morphologically coherent (Bartish *et al*., 2005; Swenson, Bartish & Munzinger, 2007a; Swenson *et al*., 2008a). Based on unpublished nuclear ribosomal (nr) DNA sequence data, Swenson & Munzinger (2009) adopted a broader circumscription of *Pycnandra* including all 66 currently known species and they provided an interim key to six subgenera using nearly a dozen morphological characters that exhibited limited homoplasy. Subsequently, revisions using a morphological species concept were published of subgenera *Pycnandra*, *Achradotypus* (Baill.) Swenson & Munzinger, *Trouettia* (Pierre ex Baill.) Swenson & Munzinger and *Sebertia* (Pierre ex Engl.) Swenson & Munzinger (Swenson & Munzinger, 2009, 2010a, b, c) and treatments of subgenera *Leptostylis* ined and *Wagapensia* ined are submitted elsewhere for publication. The most complete phylogenetic studies conducted to date have analysed 38 and 44 species, respectively, using combined data for plastid and nrDNA (Swenson *et al*., 2008a) or just nrDNA sequences (Swenson, Nylinder & Munzinger, 2013), with moderate success resolving deep nodes and reasonable success resolving terminal nodes. Phylogenetic relationships among the subgenera, the placement of *c*. 20 species and the diagnostic power of the morphological characters, however, remain to be tested.

Cryptic species have become an issue in recent years as identified, for example, in earthworms (James *et al*., 2010), birds (Alström *et al*., 2011) and geckos (Nielsen *et al*., 2011). Cryptic species are recognized when the members of two or more distinct lineages are morphologically indistinguishable and can be detected only by other features such as differences in behaviour (differences in songs or mating calls in animals), host/parasite relationships (such as in figs and their associated fig wasps) or in molecular sequence data (Bickford *et al*., 2007). Some authors stipulate that cryptic species should be recently diverged, separable only by molecular data, occur in sympatry or be reproductively isolated (Stebbins, 1950), features we do not regard as essential for being termed cryptic species. Detecting the presence of cryptic species has implications for classification, conservation and biogeography. In New Caledonia, only two cases of cryptic flowering plant species have been revealed, in *Spiraeanthemum* A.Gray (Cunoniaceae; Pillon *et al*., 2009) and *Diospyros* L. (Ebenaceae; Turner *et al*., 2013a). However, based on unpublished molecular data, Swenson & Munzinger (2010b) indicated that cryptic species might be present in *Pycnandra*. The two shrubby taxa now placed in *Pycnandra* but originally described as *Chrysophyllum lissophyllum* Pierre ex Baill. (Fig. 1A) and *C. lissophyllum* f. *obscurinervum* Vink (Fig. 1B) are morphologically highly similar but genetically dissimilar. The second of these taxa was originally recognized on the basis of obscure leaf vein characters (Vink, 1958), but was subsequently treated as a synonym of the former by Aubréville (1967) and was more recently recognized as the distinct species *P. obscurinerva* (Vink) Swenson & Munzinger (Swenson & Munzinger, 2010b). The morphology of these two entities is in fact so similar that the most practical way to distinguish them is by their geographical distributions: *P. lissophylla* occurs on the large ultramafic plain of southern Grande Terre whereas *P. obscurinerva* grows on the ultramafic mountains along the north-western coast of the island (Swenson & Munzinger, 2010b, fig. 15B). This case of possible cryptic species remains, however, to be tested in a phylogenetic framework.

Several other systematic problems have been identified in *Pycnandra* that likewise deserve attention. For instance, a molecular analysis including four accessions of *P. fastuosa* Vink indicated that the species might not be monophyletic (Swenson *et al*., 2008a). *Pycnandra fastuosa*, as currently circumscribed, forms canopy trees up to 35 m tall and is distributed from the southern tip of Grande Terre to the Koniambo massif in the north-west, always occurring on ultramafic substrate (Swenson & Munzinger, 2010b). Examination of herbarium material coupled with field observations suggests that this species could comprise two distinct taxa that differ on the basis of the density of secondary veins and the colour of the lower leaf blade. The majority of specimens have rather close secondary venation and a brownish shade on the lower leaf surface (Fig. 1C), whereas the remainder have a more open venation with a copper-shaded blade (Fig. 1D). For practical reasons, we refer

Figure 1. Selected images of members of the New Caledonian endemic genus *Pycnandra* (Sapotaceae). A, *P. lissophylla*. B, *P. obscurinerva*. C, *P. fastuosa*, the closed-veined type. D, *P. fastuosa*, the open-veined type. E, *P.* Veillon8117. F, *Leptostylis goroensis*. G, *P. kaalaensis*. H, *P. gordoniifolia*. I, *P. blanchonii*. Photos: A, F, I by Jérôme Munzinger; B, C, D, G, H by Ulf Swenson; E by Gildas Gâteblé.

to these as the 'close-veined' and the 'open-veined' types. There is not, however, a clear-cut difference between these two types and intermediate specimens can be found. Possible differences in floral morphology cannot yet be assessed as flowers are poorly known in the closed-veined type. Moreover, the two types are sympatric in the southern part of the distribution of the species, although the closed-veined type is restricted to the extreme south of the main island (its northern location is Rivière Bleue reserve) and below 550 m, whereas the open-veined type is found from Forêt Nord in the far south to Koniambo in the north-west, and up to 1500 m. Hence, it is not clear whether *P. fastuosa* represents another example of cryptic species, incipient species, introgression or just morphological variation in a single species.

Pycnandra is almost entirely restricted to Grande Terre, with two species also present in the Belep Islands to the north of Grande Terre. However, in December 2013, material clearly belonging to the genus was collected by Jean-François Butaud for the first time on the low-lying calcareous island Ouvéa (Loyalty Islands) to the east of Grande Terre. The phylogenetic relationships of this material are unknown and it may represent a novel species.

The geological and biogeographical history of New Caledonia has long interested systematists, ecologists and evolutionary biologists. Grandcolas *et al*. (2008) drew attention to the idea that New Caledonia might best be regarded as an oceanic island rather than a continental fragment, as has long been held, pointing to geological evidence that strongly suggests a long-term submersion during the Palaeocene and Eocene prior to re-emergence *c*. 37 Mya (Paris, 1981; Cluzel *et al*., 2001, 2012; Hall, 2002; Pelletier, 2006). If this interpretation is correct, then the New Caledonian biota in its entirety must have originated from elements that reached the island by dispersal, not through vicariance, which has long been regarded as the case (e.g. Raven & Axelrod, 1972; Heads, 2008, 2010). Phylogenetic studies that have included divergence time estimates, reviewed by Pillon (2012) and Cruaud *et al*. (2012), have consistently indicated dispersal to the archipelago after 37 Mya, a scenario also supported by work on Sapotaceae (Swenson, Nylinder & Munzinger, 2014). Apart from dating analyses, it is also possible to test whether an area has been saturated with species over a long period (consistent with vicariance resulting from persistent dry land) or became available for colonization at a particular point in time (consistent with emergence and subsequent dispersal) by comparing speciation and extinction rates across time in the framework of the 'museum' and 'recolonization' models (Gaston & Blackburn, 1996; Espeland & Murienne, 2011). The museum model predicts constant speciation and an equal rate of extinction that should lead to zero change in the number of species over time whereas the colonization model, which is density-dependent, predicts a reduction in the rate of diversification over time as niches become full. Espeland & Murienne (2011) found strong evidence for a slowdown in diversification in eight out of the nine phylogenetic analyses they examined, one of which was *Pycnandra* (referred to as *Niemeyera* F.Muell. at the time), although only 47 of 66 currently recognized *Pycnandra* spp. were included in their analysis.

The primary goal of the present study is to estimate the phylogeny of *Pycnandra*, to test the subgeneric circumscription proposed by Swenson & Munzinger (2009) and to test the diagnostic value of the morphological characters they used to distinguish the subgenera. For this, we have assembled an almost complete taxon sample (62 out of 68 known taxa) and obtained sequence data for nrDNA (ETS, ITS, *RPB2*) and plastid DNA (*trnH–psbA*) markers, which we have analysed with parsimony jackknifing and Bayesian inference. A secondary goal is to explore the possible presence of cryptic species in certain cases where species delimitation has proven problematic in our earlier work (Swenson *et al*., 2008a; Swenson & Munzinger, 2009, 2010a, b, c). This has been done by including multiple accessions of these problematic taxa, resulting in a total sample of 97 accessions, including one sample each of five outgroup taxa.

MATERIAL AND METHODS

Nomenclature and taxon sampling

We follow the infrageneric classification of *Pycnandra* proposed by Swenson & Munzinger (2009) with subsequent revisions (Swenson & Munzinger, 2010a, b, c). Names in the genera *Chrysophyllum* L. and *Leptostylis* Benth. that refer to species embedded in *Pycnandra* (Swenson *et al*., 2013) but that have not yet been transferred there can be found either in the checklist of Sapotaceae (Govaerts, Frodin & Pennington, 2001) or the online *World Checklist of Selected Plant Families* at the Royal Botanic Gardens, Kew (http://apps.kew.org/wcsp/home.do).

We sampled 62 of the 68 known taxa of *Pycnandra*, including 51 of the 54 currently described species, two subspecies and nine new, as yet undescribed species. When the collector and collection number of a specimen are indicated, for example, *Pycnandra* Munzinger3385 and *Pycnandra* Veillon8117, they indicate an undescribed species represented by two or more accessions. The only taxa missing from our sample are those currently known as *Leptostylis longiflora* Benth. and *L. micrantha* Beauvis (both believed to be extinct) and *P. paniensis* Aubrév. and three new

species for which fresh material is not yet available. Six accessions of *P. fastuosa*, three of the closed-veined type and three of the open-veined type, were also selected. Including samples of taxa represented by multiple accessions, a total of 97 terminals were used in this study (Appendix). *Amorphospermum* F.Muell. and *Niemeyera* F.Muell., comprising one and four taxa, respectively, have been shown to be the closest relatives of *Pycnandra* (Swenson *et al*., 2007a, 2013) and were used as outgroups.

Molecular data

Plant material for DNA extraction was collected either as silica gel-dried leaf samples from living plants or fragments removed from herbarium specimens. The information content provided by various molecular markers used for phylogenetic studies of Sapotaceae was reviewed by Swenson *et al*. (2013), who concluded that the nrDNA loci ETS and ITS (ITS1, ITS2, 5.8S and parts of 18S and 26S), the nuclear gene *RPB2* (Oxelman & Bremer, 2000), and, if combined with plastid DNA, the spacer *trnH–psbA*, contain the richest source of phylogenetically informative data. We selected these four markers, which yielded 42, 42, 49 and 46 new sequences of ETS, ITS, *RPB2* and *trnH–psbA*, respectively, by following the DNA protocols for primers, extraction, amplification and sequencing described by Swenson *et al*. (2008a, 2013), Bartish *et al*. (2005), Swenson *et al*. (2013) and Hamilton (1999), respectively. Purified products were sequenced using an ABI3130xl Automated DNA Sequencer (Applied Biosystems).

Both ITS and ETS may occur in multiple copies in a genome, which can indicate the hybrid origin of a taxon (Poczai & Hyvönen, 2010). Among Sapotaceae, multiple copies of ETS have been detected in some species of *Planchonella* Pierre (Swenson, Munzinger & Bartish, 2007b) and a few species of *Pycnandra* (Swenson *et al*., 2008a), but only as autapomorphic substitutions, which are not of any phylogenetically informative value. We nevertheless carefully checked each of the sequences used in the present study for double peaks in the proofreading procedure to detect whether multiple copies might be present.

New sequences were added to data matrices resulting from earlier studies (Swenson *et al*., 2008a, 2013) and were aligned by hand. Visual alignment was easy and informative gaps for each locus were manually scored as binary (presence/absence) characters in a separate partition (Simmons & Ochoterena, 2000). Each gene partition was tested separately for the best-fit substitution model using jModelTest (Posada, 2008) under the Bayesian information criterion (BIC) (Schwartz, 1978; Posada & Buckley, 2004) to minimize the number of substitution rate parameters. Binary data (gaps) were assigned a simple substitution model allowing unconstrained reversible gains/losses.

Phylogenetic analyses

Phylogenetic relationships were estimated with Bayesian inference (Rannala & Yang, 1996; Yang & Rannala, 1997) and parsimony jackknifing (Farris *et al*., 1996). We performed separate and concatenated analyses of plastid DNA and nrDNA. The aligned matrix was prepared in BEAUti v1.8.1 (part of the BEAST package) as an output file for Bayesian inference in BEAST v1.8.1 (Drummond *et al*., 2012). Each locus was treated as a unique partition with all nucleotide data being assigned a linked lognormal clock model whereas the binary data were assigned a simple strict clock as no prior assumption regarding rate distributions could be made for the evolution of these characters. Substitution models were set by manual modification of the rate parameters. We used the BEAST package to estimate tree topology but not divergence times 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 tree prior was set to a birth–death process (Gernhard, 2008). The Monte Carlo Markov chains (MCMCs) were set to run five times, each for 30 million generations, to ensure independent convergence on all parameters (effective sample size values > 200), sampling trees every 15 000 generations. Convergence and chain mixing were reviewed in Tracer v1.5 (Rambaut & Drummond, 2009). A proportion of the samples in each run was discarded as burn-in, and the posterior set of trees was summarized as a Maximum Clade Credibility (MCC) tree in TreeAnnotator v1.8.1 (Drummond *et al*., 2012). The resulting tree was then viewed in FigTree v1.4.1 (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 0.8–0.94 to indicate weak to moderate support and of 0.95 or more to be strong indicators of node support, whereas JK values of 50–74% are regarded as weak, 75–89% moderate and 90–100% strong support. Nodes that receive support values less than JK = 50% and

PP = 0.8 are collapsed in the phylogeny with two exceptions representing two deep splits in the phylogeny that are considered to provide informative indications of relationships.

Morphological data

Morphology is highly homoplastic in Sapotaceae and unique synapomorphies are very rare or absent, so character combinations must be used to circumscribe most groups (Swenson & Anderberg, 2005; Swenson *et al*., 2007a, 2008a, 2013; Swenson, Richardson & Bartish, 2008b; Gautier *et al*., 2013). For example, in this assemblage of New Caledonian taxa, an isomerous versus anisomerous flower and the number of stamens opposite each corolla lobe, two features traditionally used as cardinal characters, have been shown to be of little taxonomic use (Swenson *et al*., 2008a). Swenson & Munzinger (2009, 2010a, b, c) used a suite of nearly a dozen characters for *Pycnandra*, which we have adopted here as traits in the BEAST analysis. These traits are mapped as discrete units, as implemented in BEAST (Lemey *et al*., 2009), which integrates over the uncertainty of the trait model as well as the tree topology. Character changes are reported when PP values exceed 50%. Morphological terms follow Harris & Harris (1997).

Character 1. Leaves are usually alternate in *Pycnandra* (Fig. 1), but opposite and decussate leaves are diagnostic for the species traditionally placed in *Leptostylis* (Fig. 1F). One species currently referred to as *Chrysophyllum wagapense* Guillaumin has alternate to sub-opposite leaves with very short internodes, resulting in a 'subverticillate' leaf arrangement.

Character 2. Malpighiaceous trichomes are usually present in Sapotaceae, forming an indument on various organs. The lower surface of leaves is pubescent, glabrescent or glabrous, a rather stable character in many taxa. Some species have a silvery pellicle formed by stalkless trichomes that are tightly appressed to the surface.

Character 3. Tertiary veins generally form four patterns: reticulate, reticulate and parallel, reticulate and oblique, or oblique. A reticulate pattern is characterized by irregular and oblique tertiaries that cross between and anastomose with adjacent secondaries at an angle of approximately 90°. Apart from these two rather distinct patterns, reticulate veins are combined with some parallel or oblique tertiaries.

Character 4. In Sapotaceae, one or more bracts usually subtend each flower. In *Pycnandra*, there are usually several bracts, often borne along the pedicel, and sometimes they increase in size towards the flower, becoming difficult to distinguish from the sepals.

Character 5. The calyx of most members of *Pycnandra* usually has five (or more) sepals, but four sepals are diagnostic for those traditionally placed in *Leptostylis* (Pennington, 1991).

Character 6. The corolla of Sapotaceae is actinomorphic and partly sympetalous, comprising a tube and free corolla lobes. In *Pycnandra*, the corolla is quite homogeneous and is usually cup-shaped, but the number of corolla lobes varies, even between sister taxa, which introduces noise in phylogenetic analysis (Swenson *et al*., 2008a). One potentially informative character, however, is whether the corolla is pubescent or glabrous. Regardless of the density of indument, which may vary from the presence of a few trichomes to tomentulose, it has always been scored simply as 'pubescent'.

Character 7. Another pertinent character used in the interim subgeneric key to the subgenera of *Pycnandra* is whether the corolla lobes are recurved (Fig. 1F) or spreading (Fig. 1H). Recurved corolla lobes are typical for subgenus *Pycnandra* and spreading corolla lobes are present in subgenera *Achradotypus* and *Trouettia*, but it is less clear how this character is expressed elsewhere in the genus.

Character 8. Ovaries in Sapotaceae are either pubescent or glabrous, a character strongly correlated with the generic boundaries foreseen by Swenson *et al*. (2008a). As with the corolla, the presence of indument, even if only represented by a minute ring of trichomes around the ovary base, has been scored as 'pubescent'.

Character 9. Classifying the form of fruits is difficult and at least in part subjective because it may vary depending on whether a fruit is immature or mature, the ovules it contains are unfertilized or fertilized, or whether insects have infested it. Moreover, characterization of fruits must often be done based on herbarium specimens that are poorly preserved and/or are fragmentary, bearing a limited number of fruits. Notwithstanding these difficulties, we have applied the forms ellipsoid, obovoid, cylindrical, ovoid and globose to the best of our ability, decisions in many cases based on field observations in addition to examined herbarium material.

Diversification analysis

To estimate and visualize relative speciation rates in *Pycnandra*, the mode of speciation (i.e. the relationship between speciation and extinction) was estimated using the laser package in R (Rabotsky, 2006; R Core Team, 2014). The topology was tested against seven speciation scenarios (Pure birth, Birth/Death, Logistic density dependency, Exponential density dependency, Variable speciation vs. constant extinction, Constant speciation vs. variable extinction, and Variable speciation vs. variable extinction) using the lowest Akaike

information criterion (AIC) score as selection criterion. We plotted the cumulative accumulation of lineages for the genus as well as for each of its subgenera separately, using Lineage Through Time (LTT) plots in R (Nee *et al*., 1995) based on the posterior MCC tree from the Bayesian analysis. As LTT plots are sensitive to sampling density, species represented by multiple accessions were reduced to a single sample. Also, as the Bayesian tree topology lacks a time calibration, the ages of the lineages are represented by relative values between present time (0) and the arbitrarily set age of the root (100), which corresponds to the split between *Pycnandra* and *Niemeyera* estimated at 29.8 (22.3–38.0) Mya (Swenson *et al*., 2014).

RESULTS

Data

The complete molecular matrix contains 3186 characters, of which 3150 are from aligned nuclear sequences and 36 from four partitions of coded gaps (Table 1). ETS is represented by 444 nucleotides of which 79 (19.1%) are parsimony informative, ITS of 891 nucleotides of which 138 (15.5%) are informative, *RPB2* of 1218 nucleotides of which 50 (4.1%) are informative, and *trnH–psbA* of 597 nucleotides with only 10 (1.7%) informative sites. Comparing the nucleotide information content in the *Pycnandra* matrix with that for the entire group of Australasian Chrysophylloideae (Swenson *et al*., 2013) shows a decrease in information content ranging from 56 to 68%, depending on the marker. Moreover, *trnH–psbA* contributes only ten informative sites in the *Pycnandra* matrix, which is few given that it is the most useful plastid DNA marker in Sapotaceae as a whole. The model test resulted in the selection of K80+G for ETS and ITS, and HKY+G for *RPB2* and *trnH–psbA*.

Tree topology

Bayesian analysis and parsimony jackknifing of the molecular dataset recovered similar tree topologies. After collapsing nodes with support below the defined thresholds (PP = 0.8 and JK = 50%), the main differences in topology are that the Bayesian inference tree shows better resolution at deep nodes than the parsimony tree (Fig. 2). Eleven of the nodes supported in the Bayesian tree lack jackknife support, and the converse applies to four nodes. Two deep nodes for which support was less than the adopted threshold values are reported here only as an indication of relationships of main clades. The poor resolution of the earliest diversification events found in the tree presented here is consistent with the results of previous studies (Swenson *et al*., 2007a, 2008b, 2013). Analyses of the plastid DNA dataset alone, to discover incongruence, yielded only a comb with significant support (PP 0.96) for two accessions of *Pycnandra obscurinerva* (data not shown).

The species are recovered in five well-supported clades that correspond to the groups recognized in the classification proposed by Swenson & Munzinger (2009). A clade of four species analysed here for the first time, namely *Pycnandra confusa* Swenson & Munzinger, *P. heteromera* (Vink) Swenson & Munzinger, *P. intermedia* (Baill.) Swenson & Munzinger and *P. lissophylla* (Pierre ex Baill.) Swenson & Munzinger, are recovered as sister to subgenus *Sebertia*, which Swenson & Munzinger (2010c) circumscribed with only two species (Fig. 2).

Chrysophyllum wagapense, suggested to represent *Pycnandra* subgenus *Wagapensia* (Swenson & Munzinger, 2009), is strongly supported as sister to subgenus *Leptostylis*, a group that currently is under review for publication elsewhere. Together, these two groups are sister (PP 0.80) to the well-supported (PP 1.0) subgenus *Achradotypus*. Subgenera *Pycnandra* and *Trouettia* are both recovered with strong Bayesian support (PP 1.0), although their sister relationship is not well supported (PP 0.75).

With respect to possible cryptic species, two, *Pycnandra lissophylla* (two accessions) and *P. obscurinerva* (four accessions), are placed in subgenera *Sebertia* and *Trouettia*, respectively, in which the

Table 1. Characteristics of molecular sequences in each of the data partitions

	Number of characters					
Data	Genome	Aligned	Constant	Uninformative	Potentially informative	Gaps
ETS	nrDNA	444	280	85	79 (19.1%)	8
ITS	nrDNA	891	657	96	138 (15.5%)	21
RPB2	nDNA	1218	1055	113	50 (4.1%)	3
trnH–psbA	plastid DNA	597	545	42	10 (1.7%)	4
Total	totDNA	3150	2536	336	278 (8.8%)	36

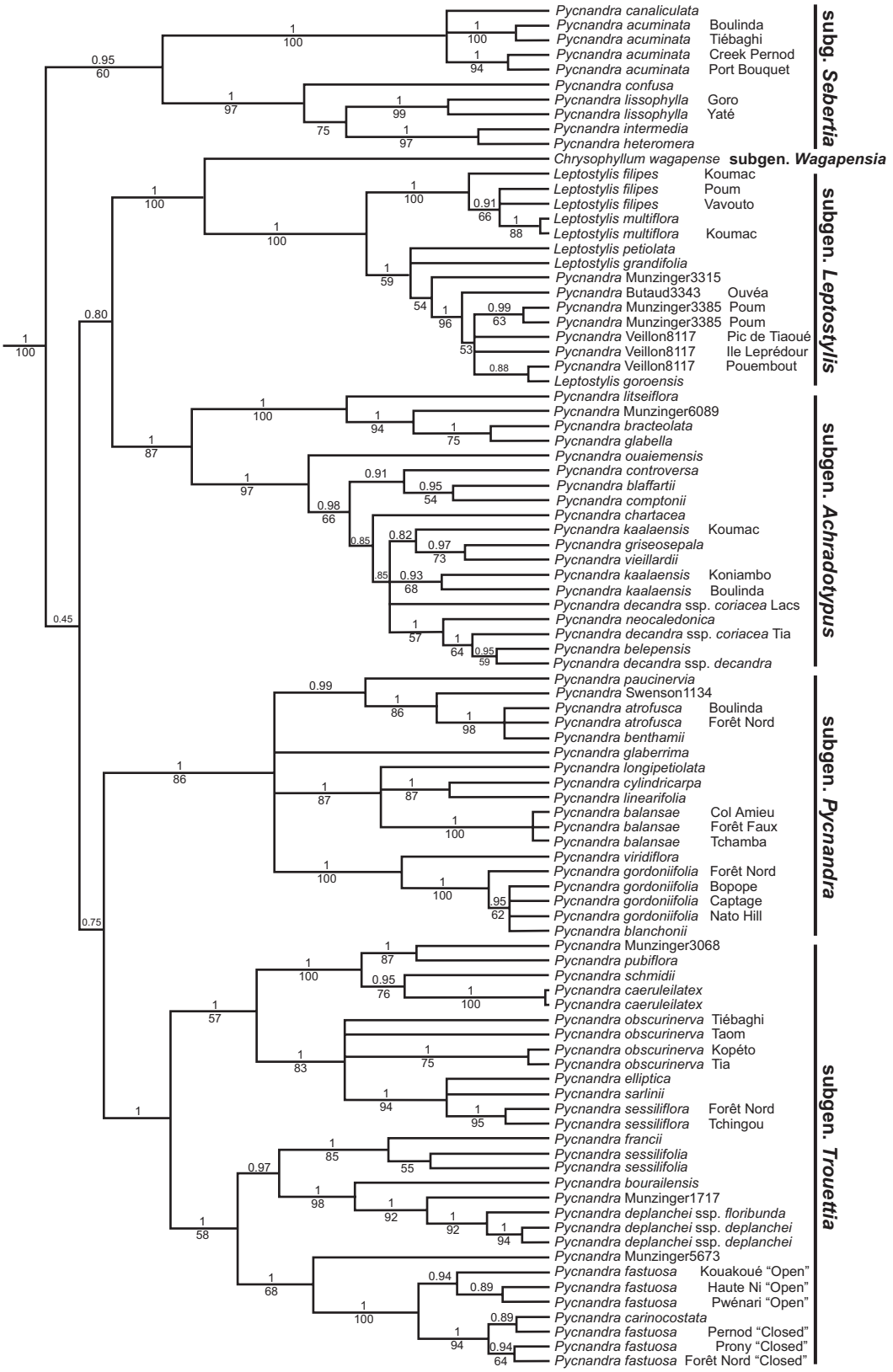

Figure 2. See caption on next page.

Figure 2. Maximum clade credibility tree and jackknife tree obtained, respectively, from the BEAST and the parsimony analyses of nrDNA and plastid DNA sequences of *Pycnandra* (Sapotaceae) from New Caledonia. To the right are locations of multiple accessions and the subgeneric classification proposed by Swenson & Munzinger (2009). Posterior probabilities (PP; above) and parsimony jackknifing (JK; below) are given along the branches. Nodes with support less than PP 0.8 and JK 50% are collapsed, except for two early splits. The outgroups, *Amorphospermum* and *Niemeyera*, have been pruned from the figure.

former is monophyletic and the latter forms a polytomy with four other species. All six accessions of *P. fastuosa* and *P. carinocostata* Vink form a clade with maximum support. Accessions of this group are placed in two subclades, with moderate to strong support (PP 0.94–1.0), which include the closed- and open-veined types, respectively. However, *P. carinocostata* is embedded in the closed-veined type. The accession from Ouvéa, Loyalty Islands (Butaud 3343), is sister, with weak parsimony support (JK 53%), to one described and two undescribed species, one of which, *P.* Veillon8117, is not rendered monophyletic. Similar situations of paraphyly or non-monophyly are revealed for *Leptostylis filipes* Benth., *P. kaalaensis* Aubrév., *P. decandra* (Montrouz.) Vink and *P. gordoniifolia* (S.Moore) Swenson & Munzinger.

Optimization of morphology

Figures 3 and 4 report eight morphological characters as traits on the MCC tree obtained from the BEAST analysis. All of these characters except leaf arrangement and the number of sepals (character 5, data not shown) exhibit at least some degree of homoplasy, as discussed below.

Diversification through time

The best-fit speciation model (ΔAIC>10) for *Pycnandra* was a logistic density-dependent function with constant speciation rate coupled to an increasing extinction rate. The LTT plots for *Pycnandra* and each of its subgenera indicate three potential relative time intervals during which the net speciation rate has been zero (Fig. 5). This decrease in speciation rate is most apparent at the two later time intervals (intervals II and III).

DISCUSSION

Classification of *Pycnandra*

Diagnostic characters for *Pycnandra* include non-areolate higher leaf venation, sepals glabrous inside, stamens usually inserted in the corolla tube orifice, no staminodes, a simple style, a fruit with a single seed, included radicle and pink plano-convex cotyledons with no endosperm (Swenson *et al*., 2013). The phylogenetic analysis of *Pycnandra* presented here based on samples of all but six of the currently recognized species (including nine that remain to be described) groups the species in six well to strongly supported clades (Fig. 2). Sampling, resolution and branch support are improved compared with the previous phylogenetic estimate (Swenson *et al*., 2008a), and the clades themselves, here assigned to subgenera, are generally the same. Consideration must therefore be given to whether these clades are better recognized as genera *sensu* Swenson *et al*. (2008a) or subgenera *sensu* Swenson & Munzinger (2009). Beginning with the deep nodes, support is weak or negligible so relationships of the main clades remain uncertain. Turning to the surveyed morphological characters, we conclude that all but two features (leaf arrangement and number of sepals) are homoplasious and cannot in any combination clearly diagnose meaningful genera (Figs 3, 4). Opposite leaves (Fig. 3A) combined with four sepals (data not shown) are diagnostic for *Leptostylis*, which is embedded in the larger clade. Moreover, the discovery of *P. viridiflora* Swenson & Munzinger and the examination of its characters, which prompted Swenson & Munzinger (2009) to propose recognizing a single, broad genus (*Pycnandra s.l.*) in which subgenera are recognized, disqualifies the glabrous ovary as a synapomorphy for *Pycnandra s.s.* (Fig. 4C). Similar patterns of homoplasy are evident for the other characters, and we therefore concur with Swenson & Munzinger (2009) that it is preferable to circumscribe *Pycnandra* broadly and to recognize subgenera in order to reflect phylogenetic information in the group. This approach upholds the principle of monophyly, facilitates identification of the genus and maximizes nomenclatural stability (Backlund & Bremer, 1998), necessitating eight new combinations rather than 32 if the alternative approach were used. Below we explore how the optimized characters converge with the tree topology and how well they align with the proposed subgenera.

Subgenus *Sebertia* was distinguished by the presence of small, 2- to 3-mm-wide, white, open flowers, a fruit with a scale-like epidermis and the absence of a remnant style on the fruit apex (Swenson & Munzinger, 2010c). The analyses presented here place four additional species (*P. confusa*, *P. heteromera*, *P. intermedia* and *P. lissophylla*), originally included tentatively in subgenus *Trouettia*, as sister to the clade that includes the two species originally assigned

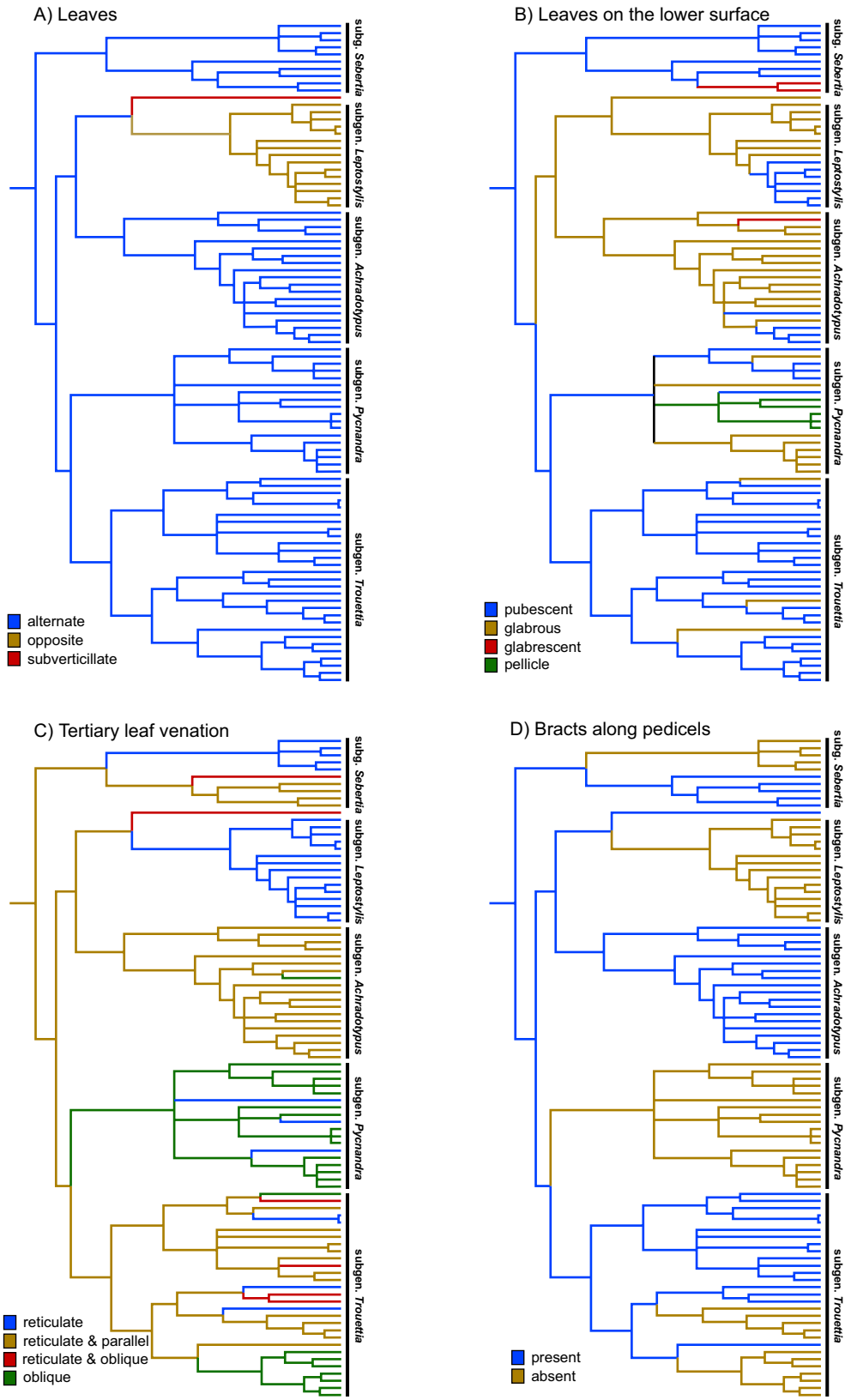

Figure 3. Four morphological characters visualized on the maximum clade credibility tree obtained in the BEAST analysis of molecular data of *Pycnandra* (Sapotaceae). The distribution of sepal number (not shown) is similar to A, where subgenus *Leptostylis* has four sepals (brown) and all other taxa have five or more sepals (blue or red).

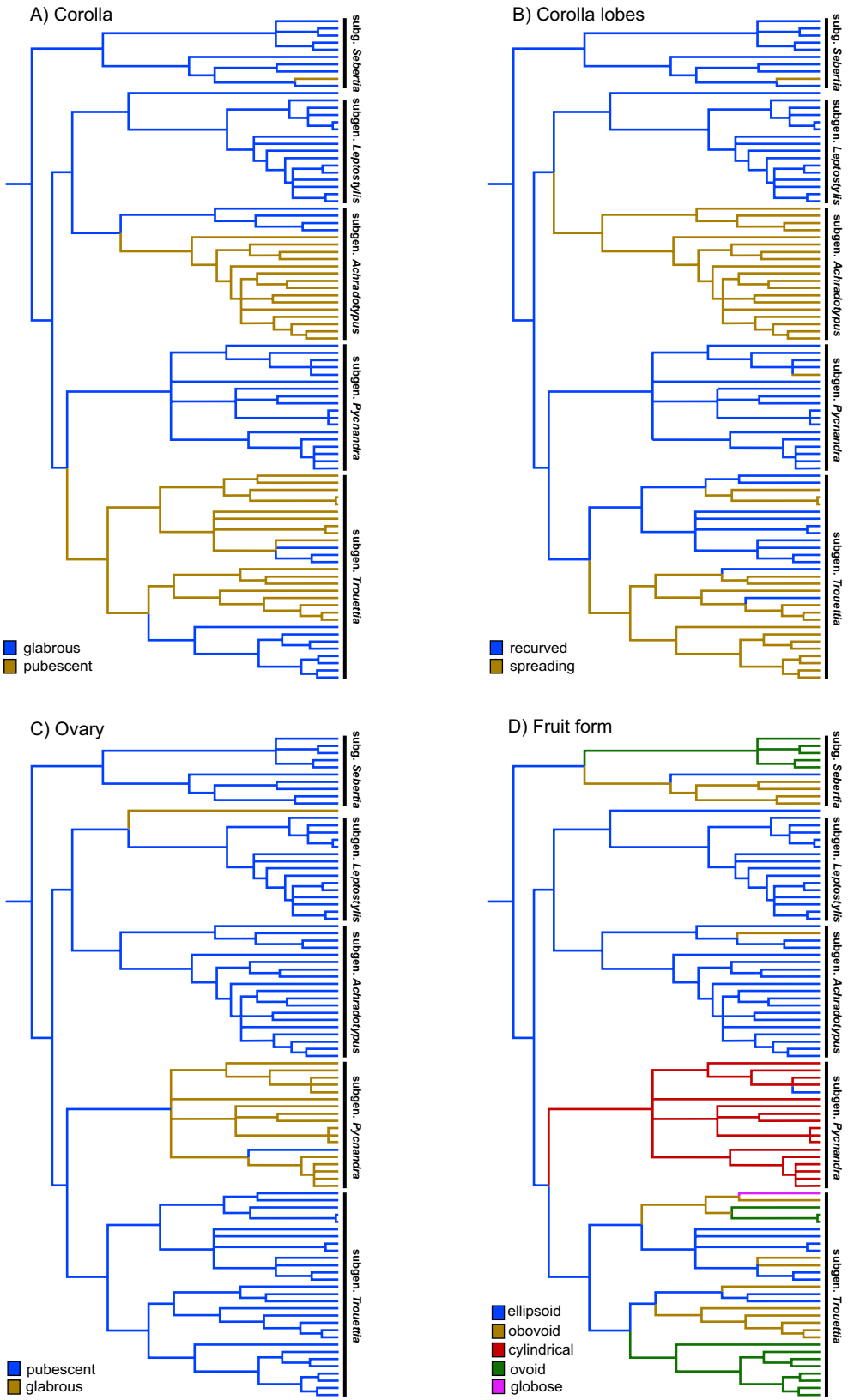

Figure 4. Four morphological characters visualized on the maximum clade credibility tree obtained in the BEAST analysis of molecular data of *Pycnandra* (Sapotaceae).

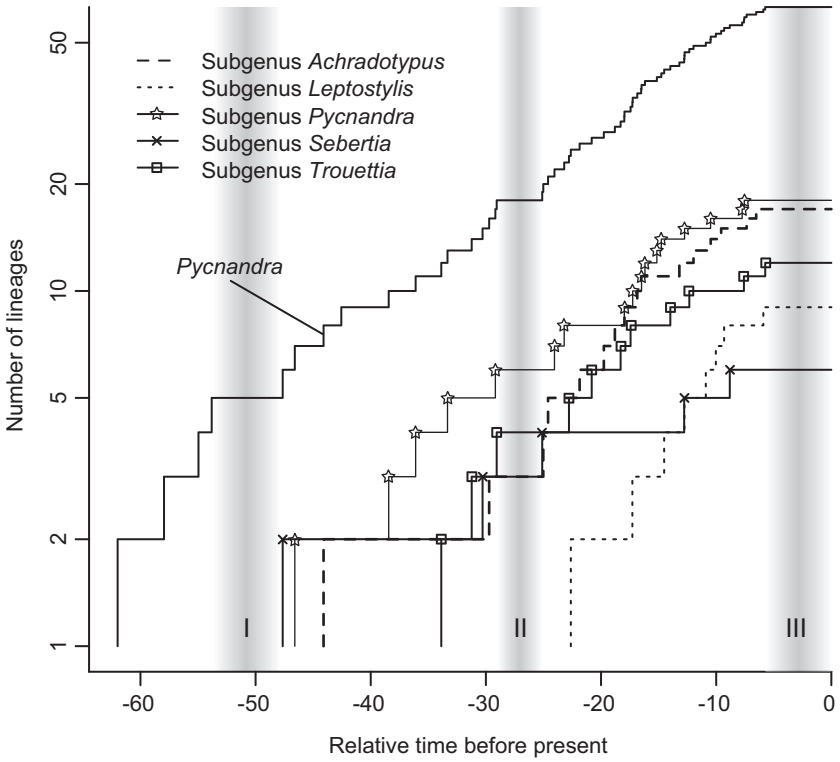

Figure 5. Lineage through time (LTT) plots of *Pycnandra* (Sapotaceae) and its subgenera in New Caledonia, showing that speciation rate drastically decreases to zero in three intervals (I, II and III) relative to present time.

to subgenus *Sebertia*. These four species, however, have a somewhat larger corolla (3–6 mm wide), lack scales on the fruits and have a minute remnant style. Among the other characters examined, only leaf arrangement, number of sepals and the presence of indument on the ovary are shared among all members of this clade, but these characters are also present in subgenera *Achradotypus* and *Trouettia*. It is thus difficult to characterize subgenus *Sebertia*, and although the four new additions could be treated as a seventh subgenus, we refrain from doing so because this new group would have a combination of characters similar to subgenera *Achradotypus* and *Trouettia*.

Our results indicate that the proposed subgenus *Wagapensia*, comprising a single species (*Chrysophyllum wagapense*), merits recognition as a monotypic taxon. It is easily distinguished from all congeners by its sub-verticillate leaves (Fig. 3A), shoots that are borne beneath the apical clusters of leaves and a trilocular ovary. The last two characters are autapomorphies, and as such are uninformative for assessing phylogenetic relationships and were therefore not optimized in the BEAST analysis. Subgenus *Wagapensia* shares a glabrous ovary with most members of subgenus *Pycnandra* (Fig. 4C), but is easily distinguished by its leaf and shoot arrangement.

Subgenus *Leptostylis* is distinguished by the presence of opposite and decussate leaves (Figs 1F, 3A), four sepals (not shown) and an ovary with four locules. All other members of the genus have alternate leaves (sub-verticillate in subgenus *Wagapensia*) and flowers with five or more sepals. Subgenus *Leptostylis* is thus readily identified on the basis of these characters, but because the clade is embedded in the broad *Pycnandra* clade, it cannot be recognized as a distinct genus if the other groups are maintained as subgenera in *Pycnandra*.

Presence or absence of indument on the lower leaf surface (Fig. 3B) and of bracts along the pedicel (Fig. 3D) were suggested to be useful by Swenson & Munzinger (2009) to distinguish between subgenera *Achradotypus* and *Trouettia*. These two characters, however, prove to be less informative when a larger taxon sample is used. All except two species of subgenus *Achradotypus* (*P. belepensis* Swenson & Munzinger and *P. decandra*) have glabrous leaves, but this feature is also found in three undescribed species recovered in subgenus *Trouettia* (*P.* Munzinger1717, *P.* Munzinger3068 and *P.* Munzinger5673). Likewise, bracts along the pedicel are found in all members of subgenus *Achradotypus* and the majority of species in subgenus *Trouettia*. In general, however, subgenus *Achradotypus* usually has one to three bracts borne

KEY TO THE SUBGENERA OF *PYCNANDRA*

1. Leaves opposite; sepals four; ovaries with four locules……*P.* subgenus *Leptostylis*
1. Leaves alternate or ± verticillate; sepals five or more; ovaries with three, five or more locules……2
2. Leaves ± verticillate; leafy shoots borne beneath clusters of leaves; ovaries with three locules……
……*P.* subgenus *Wagapensia*
2. Leaves alternate; leafy shoots not as described above; ovaries with five or more locules……3
3. Ovaries glabrous (except in *P. viridiflora*); fruits cylindrical (except *P. benthamii*)……*P.* subgenus *Pycnandra*
3. Ovaries pubescent, at least around the base; fruits not cylindrical……4
4. Lower leaf surface glabrous (except in *P. belepensis* and *P. decandra*)……*P.* subgenus *Achradotypus*
4. Lower leaf surface pubescent (except in three as yet undescribed species)……5
5. Corolla usually pubescent (except in *P. carinocostata*, *P. fastuosa*, *P. sarlinii* and *P. sessiliflora*)……
……*P.* subgenus *Trouettia*
5. Corolla glabrous (except in *P. intermedia*)……*P.* subgenus *Sebertia*

along the pedicel, in contrast to subgenus *Trouettia* with sessile or shortly pedicellate flowers, such that the bracts are imbricate and closely spaced, making it difficult to distinguish them from the sepals. This is true for *P. caeruleilatex* Swenson & Munzinger, *P. elliptica* Swenson & Munzinger, *P. sarlinii* (Aubrév.) Swenson & Munzinger and *P. sessiliflora* Swenson & Munzinger, but not for the others. If a specimen has a corolla bearing some trichomes or indument, it probably belongs to either subgenus *Achradotypus* or *Trouettia*, except for *P. intermedia* in subgenus *Sebertia* (Fig. 4A). Apart from this, we have found no better diagnostic character for these two subgenera, despite the strong molecular support for each of them and the fact that they do not comprise sister groups in the genus.

Two features characterize the majority of members in subgenus *Pycnandra*: a glabrous ovary (Fig. 4C) and a cylindrical fruit (Fig. 4D). However, two species deviate from this character combination. The generic type, *P. benthamii* Baill., is the only member of the subgenus with an ellipsoid fruit, and it also has rather large, up to 25-mm-wide, red flowers (vs. 5- to 7-mm-wide, white flowers elsewhere in the subgenus) with spreading instead of recurved corolla lobes (Fig. 4B). *Pycnandra viridiflora* is strongly embedded in subgenus *Pycnandra*, despite having a rather atypical combination of characters. It is the only member with greenish flowers and indument on the ovary. The fruit is predicted to be cylindrical, but to date it remains unknown. Species with leaves bearing a silvery pellicle on the lower surface can easily be recognized and belong to subgenus *Pycnandra* (Fig. 3B).

In summary, we propose that the species of *Pycnandra* are best classified in six subgenera as circumscribed here, because these infrageneric groups are consistent with and well supported by the results from phylogenetic estimates. Relationships among some of the subgenera, however, remain uncertain. Subgenera *Leptostylis*, *Pycnandra* and *Wagapensia* are each readily distinguished on the basis of one or more characters (with the exception of *P. viridiflora*) and species of subgenus *Achradotypus* are usually recognizable. Members of subgenera *Sebertia* and *Trouettia* are, however, difficult to place based on morphology. With this in mind, we provide a provisional key to the subgenera of *Pycnandra*.

CRYPTIC SPECIES

The results of our phylogenetic analyses show that *P. lissophylla* and *P. obscurinerva* belong to separate subgenera (*Sebertia* and *Trouettia*, respectively), confirming that they represent separate species despite their strong morphological similarity (Swenson & Munzinger, 2010b). The potentially most reliable character we have been able to find to distinguish between them is fruit form, which is obovoid in *P. lissophylla* and ellipsoid or fusiform in *P. obscurinerva* (Fig. 4D). Due to the potential risk of misidentification, this finding has important implications for conservation. *Pycnandra lissophylla* is a rather common shrub in the large southern ultramafic plain of Grande Terre, with populations in the Fausse Yaté and Yaté Barrage protected areas, and has been assigned a preliminary IUCN risk of extinction status of Least Concern. In contrast, *P. obscurinerva* is restricted to the unprotected mountain massifs along the north-west coast, many of which are being impacted by mining and fire, resulting in a preliminary IUCN status of Vulnerable.

The six accessions of *P. fastuosa* used in our study are placed in a maximally supported clade that also includes the single accession of *P. carinocostata*. In this clade, two well-supported subclades are found, one corresponding to three accessions of *P. fastuosa* with open-veined leaves and the other to three accessions of this same species with closed-veined leaves, among which the sample of *P. carinocostata* is nested. These findings suggest the possibility that *P. fastuosa*, as currently circumscribed, may represent two sepa-

rate entities. They also reveal a potential problem regarding the position of *P. carinocostata*, which is readily distinguished by its small, oblong and brochidodromous-veined leaves and the presence of pedicellate flowers not borne on burls, whereas *P. fastuosa* has rather large, ovate or elliptical, eucamptodromous-veined leaves and sessile flowers borne on burls (see figures in Swenson & Munzinger, 2010b). Both of these species are trees and occupy humid forests on ultramafic substrate, and their distributions are more or less the same on Grande Terre. There seems little doubt that the closed-veined type of *P. fastuosa* and *P. carinocostata* share a common ancestor, but the fact that the former do not form a clade is perplexing. This may be a case of incomplete lineage sorting, plastid capture or anagenetic speciation, but the currently available information is not sufficient to determine whether any of these possible explanations is correct. Regardless, it seems likely that the open- and closed-veined types of *P. fastuosa* could be considered a cryptic sibling sister species pair *sensu* Bickford *et al*. (2007), i.e. two species that are each other's closest relative but have not diverged sufficiently to be easily distinguishable from one another. As mentioned above, the differences in venation patterns and altitudinal range triggered our suspicion that they might represent two separate entities and prompted us to include three accessions of each type in our study. Leaves of the type material *P. fastuosa* correspond to the closed-veined type, and we therefore suggest that the open-veined type may merit recognition as a new species, although adequate flowering and fruiting material is not yet available for a full comparison and formal description.

Incipient speciation

By exploring the number of lineages through time in New Caledonian plants and animals, Espeland & Murienne (2011) found a decrease in speciation rate over time in eight out of nine groups, supporting the view that the island was once fully submerged and that colonization by dispersal took place when it subsequently re-emerged, corresponding to the notion of an old Darwinian island (Grandcolas *et al*., 2008). Additional studies, including Pillon's (2012) review based on 12 plant lineages and subsequent studies based on dated phylogenetic trees in *Ficus* L. section *Oreosycea* (Miq.) Corner (Moraceae) and their *Dolichoris* pollinators (Hymenoptera, Agaonidae) (Cruaud *et al*., 2012), *Diospyros* L. (Ebenaceae, Turner *et al*., 2013b) and Psychotrieae (Rubiaceae, Barrabé *et al*., 2014), also concluded that the presence of each of these groups in New Caledonia dates back to < 35 Mya. Our phylogenetic analysis using 91% of *Pycnandra* spp. based on nuclear and plastid DNA data shows the same pattern and indicates that the diversification rate came to an almost complete halt during three time intervals (Fig. 5). Considering that the split between *Pycnandra* and *Niemeyera* occurred *c*. 29.8 Mya (Swenson *et al*., 2014) and that this event was arbitrarily set to a value of 100 for the present study, these three intervals of arrested diversification correspond to 15.8–14.3, 8.6–7.5, and 1.5 Mya to present. The first of these events suggests no diversification at the time of establishment in New Caledonia and the subsequent events indicate slowdowns once diversification had begun. A slowdown in molecular divergence does not, however, necessarily mean that morphological evolution also ceased. For example, several morphologically distinct species evolved during the most recent of the three periods. Although it may not be possible to determine whether the evolution of species in *Pycnandra* is due to concerted evolution, incomplete lineage sorting, hybridization, recent cladogenesis, anagenesis or some combination thereof (Stuessy, Crawford & Marticorena, 1990; Álvarez & Wendel, 2003; Stuessy *et al*., 2006), we nevertheless explore three cases below: (i) *Pycnandra* Veillon8117 and *L. goroensis* Aubrév.; (ii) *P. kaalaensis*; and (iii) *P. gordoniifolia* and *P. blanchonii* (Aubrév.) Swenson & Munzinger.

Pycnandra Veillon8117, a well-delimited, undescribed species belonging to subgenus *Leptostylis*, grows in dry forests of coastal western Grande Terre, where it occurs exclusively on black clays and calcareous substrates. The three accessions included in our analysis do not form a monophyletic group, but rather are part of a polytomy, in which one accession from Pouembout forms a weakly supported clade (PP 0.88) with the sole accession of *P. goroensis*, a locally endemic species known only from extreme south-eastern Grande Terre, where it grows on rocky slopes near the sea on ultramafic substrates. These two species are clearly distinct: *P*. Veillon8117 is a small tree with oblanceolate leaves and flowers that are pinkish and *c*. 3 mm wide, whereas *P. goroensis* is a shrub with obovate leaves and flowers that are pure white and 9–12 mm wide (Fig. 1E, F). The placement of *P. goroensis* may represent incomplete lineage sorting, an example of anagenetic speciation or a stochastic artefact. However, hybridization or introgression is unlikely, because these species are separated by > 100 km that includes several mountain ranges and they occur on different soil types.

Pycnandra kaalaensis is a member of subgenus *Achradotypus* and is widely distributed in maquis vegetation along the north-western coast of Grande Terre, from the Boulinda massif northward to the hills west of Poum (Fig. 1G). In their revision of the subgenus, Swenson & Munzinger (2010a) noted that the size of the leaves and petioles varies in this species, suggesting that it might indicate the presence of several

lineages. In an attempt to explore this possibility, we included three accessions of *P. kaalaensis* in the present study, one from Koumac in the north, one from Koniambo near the centre of the range of the species and one from Boulinda in the south. Resolution and support for relationships in the part of the phylogenetic tree that includes this species are weak, but there is some indication that the accession from Koumac may not be conspecific with those from more southern populations. On the other hand, the accessions from Koumac and Boulinda have leaves with similar morphologies, in particular short petioles and oblanceolate lamina, but they do not group together. In contrast, the accession from Koniambo, in the middle of the range, has elliptic leaves with 3- to 4-cm-long petioles, and it groups with the other morphological type from Boulinda. This suggests a possible case of incipient speciation, incomplete lineage sorting or hybridization.

Pycnandra gordoniifolia and *P. blanchonii* belong to subgenus *Pycnandra* and form a clade with maximum support, sister to *P. viridiflora*. The first of these species is morphologically homogeneous, comprising white flowered trees up to 12 m tall that occur in humid, mesophyll and gallery forests on substrate derived from various rock types such as schist, greywacke and serpentinite (Swenson & Munzinger, 2009). In contrast, *P. blanchonii* forms red flowered shrubs, restricted to maquis vegetation on ultramafic substrates (in particular serpentinite), and is easily distinguished from *P. gordoniifolia* (Fig. 1H, I). These two species (except the accession from Forêt Nord) have identical molecular sequences in our study. On the other hand, *P. blanchonii* has been confused with *P. kaalaensis* of subgenus *Achradotypus* discussed above, a shrubby species with pink or red flowers growing in maquis, suggesting convergence in these two lineages associated with adaptation to similar abiotic factors. It is therefore tempting to speculate that *P. blanchonii* originated from *P. gordoniifolia* through anagenesis and species radiation.

Where to look for cryptic species in New Caledonia

There is no doubt that the evolution of the New Caledonian biota is complex and it is interesting to consider where one might search for additional possible examples of cryptic species. Pillon *et al*. (2009) identified polyphyly in two species of *Spiraeanthemum* A. Gray (Cunoniaceae), which they interpreted as cryptic species with one element growing on ultramafic substrate and the other on non-ultramafic substrate. Given that about 25% of the forest species in New Caledonia are found on both types of substrates (Ibanez *et al*., 2014), we suggest that they may contain additional cases of cryptic species. However, the example of cryptic species represented by *P. lissophylla* and *P. obscurinerva* is rather different in that these two entities occur in similar habitat on ultramafic soil but appear to be geographically and genetically separated between the large ultramafic plain in the south and the ultramafic mountains along the north-west coast. This suggests that a disjunct distribution between geographically separated areas of ultramafic substrate may present a barrier to gene flow and thus lead to the evolution of cryptic species. In yet another example, the open- and closed-veined types of *P. fastuosa*, which we have also identified as a case of cryptic sibling species, co-occur on the same substrate type and exhibit a slight differentiation in elevational range (the open-veined type occurs also at higher elevations), suggesting that abiotic factors may be important for speciation even though the lineages are sympatric. In terms of reproductive biology, virtually nothing is known about Sapotaceae except for three species of *Planchonella* in New Caledonia (Méndez & Munzinger, 2010) and one species of *Micropholis* (Griseb.) Pierre in South America (Terra-Araujo *et al*., 2012). Taken together, these examples point toward a diversity of situations that could have led to the evolution of cryptic species in New Caledonia such as differences in substrate type and disjunctions between areas with the same type of substrate, all of which may have contributed to this process. It may be that a significant portion of the plant diversity of New Caledonia has long been hidden and remains to be discovered.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Aligned data matrix.

APPENDIX

Voucher information in the following order: taxon name with authority, country or island of New Caledonia (sometimes with locality), collector(s), collector number, (herbarium abbreviation), and European Nucleotide Archive/GenBank accessions (ETS, ITS, RPB2, *trnH–psbA*). Species not yet described are indicated by collector and number. The 174 sequences published here have the prefix LN.

Taxon	Area (locality)	Voucher	ETS	ITS	*RPB2*	*trnH–psbA*
Amorphospermum antilogum F.Muell.	Australia	*Bartish & Jessup 4* (S)	HE860156	DQ154055	HE995662	DQ344119
Chrysophyllum wagapense Guillaumin	Grande Terre	*Munzinger et. al. 5634* (NOU, P, S)	HE860151	HE860077	HE995601	LN809210
Leptostylis filipes Benth.	Grande Terre, Koumac	*Webster & Hildreth 14665* (P)	EU661382	AY552135	HE995603	DQ344113
Leptostylis filipes Benth.	Grande Terre, Poum	*Munzinger et al. 4695* (NOU, P, S)	LN809080	LN809121	LN809162	LN809211
Leptostylis filipes Benth.	Grande Terre, Vavouto	*Munzinger et al. 2365* (NOU, P, S)	LN809081	LN809122	LN809163	LN809212
Leptostylis goroensis Aubrév.	Grande Terre	*Munzinger 2288* (NOU, P, S)	EU661383	DQ154052	HE995604	EU661501
Leptostylis grandifolia Vink	Grande Terre	*Munzinger & Oddi 2121* (MO, NOU, P, S)	EU661384	DQ154053	HE995605	EU661502
Leptostylis multiflora Vink	Grande Terre, Koumac	*Munzinger 6692* (NOU)	LN809082	LN809123	LN809164	LN809213
Leptostylis multiflora Vink	Grande Terre, Koumac	*Munzinger 6744* (NOU)	LN809083	LN809124	LN809165	LN809214
Leptostylis petiolata Vink	Grande Terre	*Swenson & Munzinger 714* (NOU, S)	EU661385	LN809125	LN809166	LN809215
Niemeyera chartacea (F.M.Bailey) C.T.White	Australia	*Bartish & Jessup 5* (S)	HE860157	DQ154057	HE995606	EU661506
Niemeyera Ford2429	Australia	*Andrew Ford 2429* (S)	EU661389	EF025089	HE995607	EU661508
Niemeyera prunifera (F.Muell.) F.Muell.	Australia	*Jessup 5238* (S)	HE860158	DQ154058	HE995608	DQ344120
Niemeyera whitei (Aubrév.) L.W.Jessup	Australia	*Floyd s.n.* (S)	EU661388	AY552137	HE995609	EU661507
Pycnandra acuminata (Baill.) Swenson & Munzinger	Grande Terre, Boulinda	*Swenson & Munzinger 1114* (NOU, S)	LN809084	LN809126	LN809167	LN809216
Pycnandra acuminata (Baill.) Swenson & Munzinger	Grande Terre, Creek Pernod	*Munzinger et al. 5761* (NOU, S)	LN809085	LN809127	LN809168	LN809217
Pycnandra acuminata (Baill.) Swenson & Munzinger	Grande Terre, Port Bouquet	*Munzinger 1006* (MO, NOU, P)	EU661430	AY552124	HE995631	EU661544

Appendix *Continued*

Taxon	Area (locality)	Voucher	ETS	ITS	*RPB2*	*trnH–psbA*
Pycnandra acuminata (Baill.) Swenson & Munzinger	Grande Terre, Tiébaghi	*Swenson et al. 924* (NOU, P, S)	LN809086	LN809128	LN809169	LN809218
Pycnandra atrofusca Swenson & Munzinger	Grande Terre, Boulinda	*Munzinger al. 4968* (NOU, P, S)	LN809087	LN809129	LN809170	LN809219
Pycnandra atrofusca Swenson & Munzinger	Grande Terre, Forêt Nord	*Munzinger et al. 2618* (NOU, P, S)	EU661419	EU661443	HE995632	EU661533
Pycnandra balansae (Baill.) Swenson & Munzinger	Grande Terre, Col Amieu	*Barrabé et al. 275* (NOU, P, S)	LN809088	LN809130	LN809171	LN809220
Pycnandra balansae (Baill.) Swenson & Munzinger	Grande Terre, Forêt Faux	*MacKee 37668* (NOU)	LN809089	LN809131	LN809172	LN809221
Pycnandra balansae (Baill.) Swenson & Munzinger	Grande Terre, Tchamba	*Munzinger et al. 1451* (MO, NOU, P, S)	EU661387	AY552123	HE995754	EU661505
Pycnandra belepensis Swenson & Munzinger	Art Island	*Swenson*, *Munzinger & Barrabé 913* (S)	HE860243	HE860123	HE995687	LN809222
Pycnandra benthamii Baill.	Grande Terre	*Munzinger et al. 2228* (NOU, P, S)	EU661404	EU661436	HE995633	EU661519
Pycnandra blaffartii Swenson & Munzinger	Grande Terre	*Swenson et al. 597* (NOU, S)	EU661423	AY552127	HE995634	EU661537
Pycnandra blanchonii (Aubrév.) Swenson & Munzinger	Grande Terre	*Munzinger et al. 2576* (NOU, S)	EU661390	DQ154059	HE995635	EU661509
Pycnandra bourailensis Swenson & Munzinger	Grande Terre	*Munzinger et al. 2963* (K, MO, NOU, S)	EU661428	EU661450	LN809173	EU661542
Pycnandra bracteolata Swenson & Munzinger	Grande Terre	*Munzinger*, *Pillon & Butin 2885* (NOU, S)	EU661421	EU661445	HE995636	EU661535
Pycnandra caeruleilatex Swenson & Munzinger	Grande Terre, Forêt Nord	*Munzinger et al. 2622* (MO, NOU, P, S)	EU661426	EU661448	HE995637	EU661540
Pycnandra caeruleilatex Swenson & Munzinger	Grande Terre, Kuébini	*Munzinger & Beauvallet 6001* (NOU, S)	LN809090	LN809132	LN809174	LN809224
Pycnandra canaliculata Swenson & Munzinger	Grande Terre	*Munzinger et al. 2067* (MO, NOU, P, S)	EU661431	DQ154092	HE995638	EU661545
Pycnandra carinocostata Vink	Grande Terre	*McPherson & Munzinger 18091* (NOU, S)	EU661405	AY552132	HE995639	EU661520
Pycnandra chartacea Vink	Grande Terre	*Munzinger & Swenson 3059* (NOU, P, S)	EU661406	EU661437	LN809175	EU661521
Pycnandra comptonii (S.Moore) Vink	Grande Terre	*Lowry et al. 5780A* (MO, NOU, S)	EU661407	AY552131	HE995640	DQ344145
Pycnandra confusa Swenson & Munzinger	Grande Terre	*Munzinger & Beauvallet 5629* (NOU, S)	LN809091	LN809133	—	LN809225
Pycnandra controversa (Guillaumin) Vink	Grande Terre	*Lowry et al. 5787* (MO, NOU, P, S)	EU661408	AY552126	HE995641	EU661522
Pycnandra cylindricarpa Swenson & Munzinger	Grande Terre	*Swenson et al. 615* (NOU, S)	EU661429	AY552110	HE995757	EU661543
Pycnandra decandra (Montrouz.) Vink	Art Island	*Swenson*, *Munzinger & Barrabé 920* (S)	HE860244	HE860124	HE995688	LN809226
Pycnandra decandra ssp. *coriacea* (Baill.) Swenson & Munzinger	Rivière des Lacs	*Munzinger et al. 2031* (MO, NOU, P, S)	EU661409	DQ154091	LN809176	EU661523
ssp. *coriacea* (Baill.) Swenson & Munzinger	Tia	*Swenson et al. 700b* (NOU, S)	EU661413	EU661439	LN809177	EU661527
Pycnandra deplanchei (Baill.) Swenson & Munzinger	Grande Terre, Port Bouquet	*Munzinger 978* (MO, NOU, P, S)	EU661380	AY552120	HE995642	EU661499
Pycnandra deplanchei (Baill.) Swenson & Munzinger	Grande Terre, Mt. Kokoréta	*Cochereau s.n.* (NOU)	EU661380	AY552119	LN809178	EU661499
ssp. *floribunda* (S.Moore) Swenson & Munzinger	Grande Terre	*Munzinger 2199* (NOU, P, S)	LN809092	DQ154050	LN809179	LN809227
Pycnandra elliptica Swenson & Munzinger	Grande Terre	*Munzinger 5631* (NOU, S)	LN809093	LN809134	LN809180	LN809228
Pycnandra fastuosa (Baill.) Vink	Grande Terre, Forêt Nord	*Munzinger & Swenson 2993* (NOU, S)	EU661394	EU661434	HE995643	EU661512
Pycnandra fastuosa (Baill.) Vink	Grande Terre, Haute Ni	*Munzinger et al. 2027* (NOU, P, S)	EU661412	EU661438	—	EU661526
Pycnandra fastuosa (Baill.) Vink	Grande Terre, Kouakoué	*Munzinger et al*. 1694 (MO, NOU, P, S)	EU661411	AY552121	—	EU661525
Pycnandra fastuosa (Baill.) Vink	Grande Terre, Pernod	*Munzinger et al. 5763* (NOU, S)	LN809095	LN809136	—	LN809230
Pycnandra fastuosa (Baill.) Vink	Grande Terre, Prony	*Munzinger 6004* (NOU)	LN809094	LN809135	LN809181	LN809229

Appendix *Continued*

Taxon	Area (locality)	Voucher	ETS	ITS	*RPB2*	*trnH–psbA*
Pycnandra fastuosa (Baill.) Vink	Grande Terre, Pwénari	*Munzinger et al. 1281* (MO, NOU, P)	EU661410	AY552122	LN809182	EU661524
Pycnandra francii (Guillaumin & Dubard) Swenson & Munzinger	Grande Terre	*Munzinger 965* (MO, NOU, P)	EU661391	AY552117	HE995644	DQ344121
Pycnandra glabella Swenson & Munzinger	Grande Terre	*Munzinger et al. 2615* (NOU, P, S)	EU661418	EU661442	HE995645	EU661532
Pycnandra glaberrima Swenson & Munzinger	Grande Terre	*Munzinger et al. 1394* (MO, NOU, P, S)	EU661399	AY552133	HE995646	EU661517
Pycnandra gordoniifolia (S.Moore) Swenson & Munzinger	Grande Terre, Bopope	*Swenson & Munzinger 726a* (NOU, P, S)	EU661392	EU661433	HE995647	EU661510
Pycnandra gordoniifolia (S.Moore) Swenson & Munzinger	Grande Terre, Captage	*Swenson & Munzinger 1130* (NOU, P, S)	LN809096	LN809137	LN809183	LN809231
Pycnandra gordoniifolia (S.Moore) Swenson & Munzinger	Grande Terre, Forêt Nord	*Munzinger & Swenson 2997* (NOU, P, S)	LN809097	LN809138	LN809184	LN809232
Pycnandra gordoniifolia (S.Moore) Swenson & Munzinger	Grande Terre, Nato Hill	*Swenson & Munzinger 1135* (NOU, P, S)	LN809098	LN809139	LN809185	LN809233
Pycnandra griseosepala Vink	Grande Terre	*Swenson, McPherson & Mouly 627* (MO, NOU, S)	EU661414	AY552128	HE995648	EU661528
Pycnandra heteromera (Vink) Swenson & Munzinger	Grande Terre	*Munzinger et al. 2798* (NOU, P, S)	LN809099	LN809140	LN809186	LN809234
Pycnandra intermedia (Baill.) Swenson & Munzinger	Grande Terre	*Munzinger & Dagostini 2631* (NOU, P, S)	LN809100	LN809141	LN809187	LN809235
Pycnandra kaalaensis Aubrév.	Grande Terre, Boulinda	*Munzinger et al. 4990* (NOU, P, S)	LN809101	LN809142	LN809188	LN809236
Pycnandra kaalaensis Aubrév.	Grande Terre, Koniambo	*Munzinger & Labat 2599* (NOU, S)	EU661415	EU661440	HE995756	EU661529
Pycnandra kaalaensis Aubrév.	Grande Terre, Koumac	*Swenson & Munzinger 928* (NOU, S)	LN809102	LN809143	LN809189	LN809237
Pycnandra linearifolia Swenson & Munzinger	Grande Terre	*Munzinger & Blaffart 2786* (NOU, P, S)	EU661427	EU661449	HE995753	EU661541
Pycnandra lissophylla (Pierre ex Baill.) Swenson & Munzinger	Grande Terre, Goro	*Munzinger et al. 2103* (MO, NOU, P, S)	LN809103	LN809144	LN809190	LN809238
Pycnandra lissophylla (Pierre ex Baill.) Swenson & Munzinger	Grande Terre, Yaté	*Munzinger & Beauvallet 6003* (NOU, S)	LN809104	LN809145	LN809191	LN809239
Pycnandra litseiflora (Guillaumin) Swenson & Munzinger	Grande Terre	*MacKee 16651* & *17085* (S)	—	DQ154060	—	EU661510
Pycnandra longipetiolata Swenson & Munzinger	Grande Terre	*Fambart-Tinel 181* (NOU)	LN809105	LN809146	LN809192	LN809240
Pycnandra neocaledonica (S.Moore) Vink	Grande Terre	*Tronchet et al. 426* (MO, NOU, P, S)	EU661416	AY552129	HE995649	EU661530
Pycnandra obscurinerva (Vink) Swenson & Munzinger	Grande Terre, Kopéto	*Swenson & Munzinger 931* (NOU, P, S)	LN809106	LN809147	LN809193	LN809247
Pycnandra obscurinerva (Vink) Swenson & Munzinger	Grande Terre, Taom	*Munzinger 3548* (NOU)	LN809107	LN809148	LN809194	LN809248
Pycnandra obscurinerva (Vink) Swenson & Munzinger	Grande Terre, Tia	*Swenson et al. 701* (BRI, MO, NOU, P, S)	LN809108	LN809149	LN809195	LN809249
Pycnandra obscurinerva (Vink) Swenson & Munzinger	Grande Terre, Tiébaghi	*Munzinger 1913* (NOU)	EU661432	DQ154095	LN809196	EU661546
Pycnandra ouaiemensis Swenson & Munzinger	Grande Terre	*Munzinger et al. 3135* (NOU, P, S)	EU661422	EU661446	HE995689	EU661536
Pycnandra paucinervia Swenson & Munzinger	Grande Terre	*Munzinger et al. 1438* (NOU, P, S)	EU661424	AY552159	HE995650	EU661538
Pycnandra pubiflora Swenson & Munzinger	Grande Terre	*Munzinger et al. 2624* (NOU, P, S)	EU661420	EU661444	HE995651	EU661534
Pycnandra sarlinii (Aubrév.) Swenson & Munzinger	Grande Terre	*Munzinger 1860* (NOU, P, S)	EU661395	EU661435	HE995652	EU661513

Appendix *Continued*

Taxon	Area (locality)	Voucher	ETS	ITS	*RPB2*	*trnH–psbA*
Pycnandra schmidii (Aubrév.) Swenson & Munzinger	Grande Terre	*McPherson & Munzinger 18106* (NOU, S)	EU661396	AY552116	HE995653	EU661514
Pycnandra sessiliflora Swenson & Munzinger	Grande Terre, Forêt Nord	*Munzinger 2608* (NOU, S)	LN809109	LN809150	LN809197	LN809250
Pycnandra sessiliflora Swenson & Munzinger	Grande Terre, Tchingou	*Munzinger & McPherson 696* (NOU, S)	EU661398	AY552161	HE995691	EU661516
Pycnandra sessilifolia (Pancher & Sebert) Swenson & Munzinger	Grande Terre, Kouakoué	*Munzinger et al. 2025* (MO, NOU, P, S)	LN809110	LN809151	LN809198	LN809251
Pycnandra sessilifolia (Pancher & Sebert) Swenson & Munzinger	Grande Terre, Tchingou	*McPherson & Munzinger 18176* (MO, P)	EU661397	AY552118	HE995654	EU661515
Pycnandra vieillardii (Baill.) Vink	Grande Terre	*Dumontet, Zongo & Maituku s.n.* (S)	EU661417	EU661441	HE995655	EU661531
Pycnandra viridiflora Swenson & Munzinger	Grande Terre	*Munzinger et al. 4195* (NOU, P, S)	HE860245	HE860125	HE995656	LN809255
Pycnandra Butaud 3343	Ouvéa	*Butaud 3343* (S)	LN809111	LN809152	LN809199	LN809223
Pycnandra Munzinger 1717	Grande Terre	*Munzinger et al. 1717* (MO, NOU, P, S)	EU661425	EU661447	LN809200	EU661539
Pycnandra Munzinger 3068	Grande Terre	*Munzinger et al. 3068* (IND, NOU, P, S)	LN809112	LN809153	LN809201	LN809242
Pycnandra Munzinger 3315	Grande Terre	*Munzinger 3315* (NOU)	LN809113	LN809154	—	LN809243
Pycnandra Munzinger 3385	Grande Terre, Poum	*Munzinger 3385* (S)	LN809115	LN809155	LN809202	LN809244
Pycnandra Munzinger 3385	Grande Terre, Poum	*Barrière 122* (NOU, P, S)	LN809114	LN809156	LN809203	—
Pycnandra Munzinger 5673	Grande Terre	*Munzinger et al. 5673* (S)	LN809116	LN809157	LN809204	LN809245
Pycnandra Munzinger 6089	Grande Terre	*Munzinger 6089* (NOU, P, S)	LN809117	LN809158	LN809205	LN809246
Pycnandra Swenson 1134	Grande Terre	*Swenson & Munzinger 1134* (NOU, P, S)	LN809118	LN809159	LN809206	LN809252
Pycnandra Veillon 8117	Grande Terre, Ile Leprédour	*Veillon 7782* (NOU, P, S)	LN809119	LN809160	LN809207	LN809254
Pycnandra Veillon 8117	Grande Terre, Pic de Tiaoué	*Fambart-Tinel 107* (NOU, S)	LN809120	LN809161	LN809209	LN809253
Pycnandra Veillon 8117	Grande Terre, Pouembout	*Veillon 8117* (NOU, P)	EU661386	AY552136	LN809208	EU661504.