Molecular Systematics of the New Caledonian Cryptocaryeae (Lauraceae)

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Abstract

New Caledonia is an archipelago located in the southwest pacific. It has a tropical climate influenced by the surrounding sea and is recognised as a “biodiversity hotspot”. The flora of New Caledonia is poorly understood especially in regards to Lauraceae which has not undergone taxonomic revision since Kostermans 1974 taxonomic treatment.

The aim of this study was to test the taxonomic delimitations of the Lauraceae sub-family Cryptocaryeae in New Caledonia. This study tested whether the New Caledonian *Beilschmiedia, Cryptocarya* and *Endiandra* are monophyletic. Were these genera the result of one or more colonization events? This study tested if the *Cryptocarya* group forms two clades as suggested by Rowher et al. (2014) and van der Merwe et al. (2016).

The phylogenetic analyses were conducted using ITS and Bayesian inference, 58 new complete ITS sequences were generated. Majority of the sequences generated were New Caledonian specimens, overall the topology of the tree was well supported.

New Caledonian *Beilschmiedia* and *Endiandra* are monophyletic, whereas, the New Caledonian *Cryptocarya* are not monophyletic. New Caledonian *Beilschmiedia* and *Endiandra* are most likely the result of a single colonization event for each genus and subsequent radiation. New Caledonian *Cryptocarya* are most likely the result of multiple colonization events. The relationship between the clades of *Beilschmiedia* and *Endiandra* are unresolved. *Cryptocarya* forms two strongly support clades supporting the findings of Rohwer et al. (2014) and van der Merwe et al. (2016).

Between *Beilschmiedia, Cryptocarya* and *Endiandra*, there are at least six putative new species and five genetically diverse species. These samples need to undergo taxonomic revision and potential reidentification. The biogeographical relationship between New Caledonian Cryptocaryeae and the rest of the Cryptocaryeae sampled is unresolved and requires further data collection and study.

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To the student who continues this research, good luck. I wish you all the best. I hope you have as successful time as I did.

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Chapter One

Literature Review

1.1 New Caledonia

The archipelago of New Caledonia is located in the southwest Pacific. It is approximately 1200 km east of Queensland Australia and 1700 km north of New Zealand (Buerki et al. 2012). It is recognised as a biodiversity "hotspot" (Meyrs et al. 2000), which is defined as an area with high concentrations of endemic species that are undergoing significant habitat loss. The current flora is estimated to contain over 3000 native vascular plant species (Morat et al. 2012; Munzinger et al. 2016). Species-level endemism is estimated to be between 76-80% (Jaffré 1993; Morat et al. 2012; Munzinger et al. 2016) whilst generic-level endemism is around 14%. Three families are endemic to New Caledonia they are Amborellaceae, Oncothecaceae and Phellinaceae (Morat et al. 2012; Munzinger et al. 2016). This high level of endemism is believed to be an artefact of multiple colonisation events after New Caledonia resurfaced during the Oligocene period (Grandcolas et al. 2008; Morat et al. 2012; Munzinger et al. 2016).

New Caledonia was partially formed from a continental fragment that broke away from Gondwana during the formation of the Tasman Sea ca. 83Ma (Grandcolas et al. 2008). New Caledonia is connected to New Zealand by a long, thin piece of continental crust along the Norfolk ridge (McLoughlin 2001; Grandcolas et al. 2008). This section of Gondwana, though mainly submerged, is the continent of Zealandia (Mortimer et al. 2016). New Caledonia is considered to be a relatively young landmass as it is only around 37 Mya (Grandcolas et al. 2008). During the Palaeozoic to Cenozoic (McLoughlin 2001), New Caledonia was submerged during the Palaeocene, where it stayed submerged for 20 Mya, emerging again during the Oligocene (Grandcolas et al. 2008; Keppel 2009). The remerging during the Oligocene and subsequent tectonic activity, has since formed New Caledonia into the archipelago that is present today (McLoughlin 2001; Grandcolas et al. 2008; Grandcolas 2016).

New Caledonia has land mass of 16,890km². The main island, Grande Terre is 500km long and 50km wide with an elevation greater then 1600m along its mountain range (Grandcolas et al. 2008). The submersion during the Palaeozoic and Cenozoic caused layers of oceanic sedimentation, fine-grained black chert and other ultramafic rocks to be formed (Grandcolas et al. 2008; Pillion et al. 2010). Other rock layers such as the ophilitic nappe were formed during tectonic activity which caused oceanic crust to be layered over the continental crust (Grandcolas et al. 2016). These layers have then gone on, to produce metalliferous and ultramafic soils across Grand Terre (Grandcolas et al. 2008; Pillon at al. 2010).

Île des Pins is the closest geographically to Grand Terre. It is located 50km south of Grand Terre (Geneva et al. 2013). It is approximately 150km² and surrounded by small satellite islands. These islets are made of raised fossil coral heads with a maximum elevation of 10m. The fossil corral heads formed around 118,000 and were raised during the Pleistocene. Île des Pins and Grand Terre have been connected in the past when sea levels were lower. Presently however, they are separated by a series of shallow straights, reefs lagoons and passes (Geneva et al. 2013).

The Loyalty Islands are a string of uplifted coral reefs, which run roughly parallel to the eastern side of Grand Terre (Daza et al. 2015). The Loyalty Islands are separated from Grand Terre by the Loyalty basin, which is 110km wide and 2,000m at its deepest. All of the islands are relatively low lying with Maré being the highest point in the chain at 138m. The chain starts in the northwest with Ovéa (160km²), moving southwards towards Lifou, which is the largest island in the chain at 1,150km². The next in the chain is Tiga (10km²), which is followed by a series of small islands before Maré (650km²). The last in the chain Ile Walpole (2km²), which is located approximately 160km southeast of the main chain (Daza et al. 2015). The vegetation on the Loyalty islands is highly depauperate compared to

Grand Terre, the main cause of this being, due to the islands only forming recently in terms of a geological timeframe (Jaffré 1993). There are less than 400 plant species, which mainly consist of coastal strand vegetation, which is similar to mainland and inland humid forests (Jaffré 1993; Daza et al. 2015).

New Caledonia has a tropical climate that is influenced by the surrounding ocean (Fig 1.1) (Jaffré 1993). The dominant vegetation types in New Caledonia are the wet evergreen forests, and the anthropogenic savannahs in the lowlands. There are also highly fragmented sclerophyll forests and maquis, which have been strongly impacted by anthropological activities (Grandcolas et al. 2008; Heywood & Davis 1995).

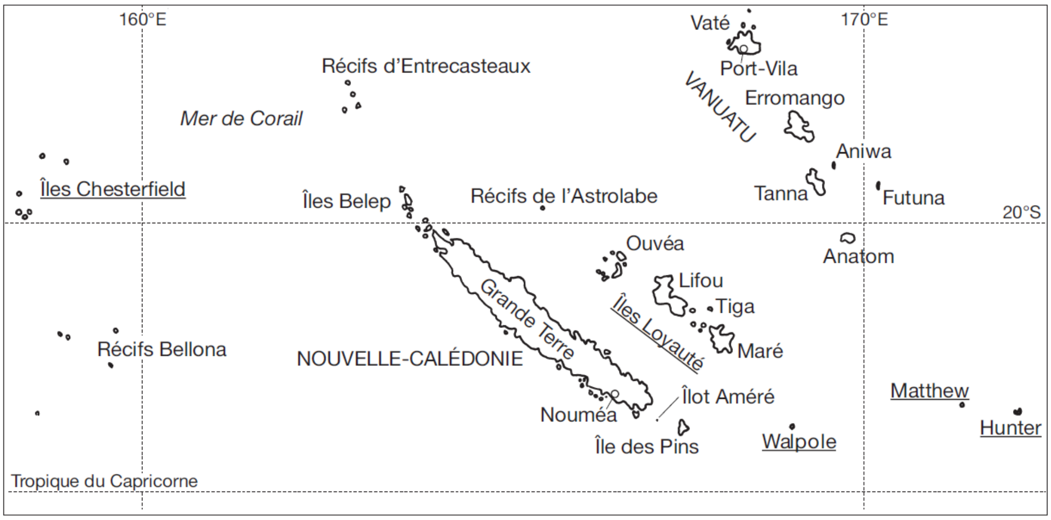

Figure 1.1: New Caledonia and surrounding archipelagos including Vanuatu and Wallis and Futuna. Sourced from Morat et al. (2012)

The tropical rainforest in New Caledonia is found growing on multiple substrates including basalt, limestone, clays and ultramafic soils. The ultramafic soils are high in magnesium and other heavy metals such as nickel and manganese, whilst being deficient in potassium and phosphorus (Morat et al. 1986). These inhospitable soil conditions are believed to be a contributing factor, along with New Caledonia's isolation during its geological history, to the abundance of endemic and relic species that New Caledonia is known for (Morat et al. 1986; Murienne et al. 2005). Growing on these ultramafic substrates is the iconic maquis that covers approximately 30% of the land area of Grande Terre (Heywood & Davis 1995).

The high level of endemism and speciation of the New Caledonian flora has meant that the impact from anthropogenic activities is greater than in areas of low endemism and species diversity. Anthropogenic activities include nickel mining, forest logging, forest burning, and being out competed by introduced animal and invasive plant species (Grandcolas et al. 2008). There are few invasive plant species due to the majority of introduced plants inability to adapt to the ultramafic soils, which are common in New Caledonia (Morat 1993). However, feral deer, goats, pigs and rats have had a significant negative impact on the New Caledonian flora (Grandcolas et al. 2008). The anthropogenic activity that has had the biggest impact to the native flora of New Caledonia is fire (Jaffré et al. 1998).

Jaffré et al. (1998) found that only 2.7% of New Caledonia’s land area was conserved in 25 sites. However, 83% of the known endangered species lived outside of these areas (Jaffré at el. 1998). The focus now is on preventing fires as well as rehabilitating areas that have been degraded by mining back into areas of high biodiversity. As of 2009, New Caledonia had increased its protected areas to 3.4% of its total land area (Morat et al. 2012; Munzinger et al. 2016).

There are 126 plant families found in New Caledonia (Morat et al. 2012; Munzinger et al. 2016). The Lauraceae is the 14^{h} equal largest angiosperm family in New Caledonia. Six genera are found in New Caledonia, *Adenodaphne* Nees, *Beilschmiedia* Nees, *Cryptocarya* R. Br., *Cassytha* L., *Endiandra* R. Br., and *Litsea* Lam. (Morat et al. 2012; Munzinger et al. 2016). *Cryptocarya* and *Beilschmiedia* are the most species rich genera within Lauraceae (Morat et al. 2012; Rohwer et al. 2014; Munzinger et al. 2016). Of these six genera three are found in the sub-family Cryptocaryeae, *Beilschmiedia, Cryptocarya* and *Endiandra*), with the remaining three genera within the subfamily Laureae (van der Werff and Richter 1996).

1.2 Systematics of Lauraceae

The Lauraceae Jussieu is a magnoliid angiosperm family with fossil records dating back to the late cretaceous period (Rohwer 1993). The family Lauraceae is a member of the order Laurales, which is comprised of seven families and approximately 85 genera (Renner and Chanderbali 2000). Within Lauraceae there are approximately 50 genera with 2500-3500 species (Rohwer 1993).

Within the literature there are two main schools of thought as to 1) how Lauraceae and its genera interact with other families, within the Laurales, and 2) how the genera themselves interact with each other. In 1957 Kostermans hypothesised that there were five sub-families within Lauraceae. These sub-families were based on flower and fruit characteristics (van der Werff and Richter 1996). However, van der Werff and Richter (1996) hypothesised that there are three sub-families within Lauraceae, Laureae van der Werff & Richter, Perseeae Nees, and Cryptocaryeae Nees. Stevens (2001 onwards) has adopted the hypothesis that Lauraceae forms a clade with Hernandiaceae and Monimiaceae.

Rohwer (1993) described the Lauraceae as being mostly evergreen trees or shrubs. The leaves are alternate to opposite or whorled. The leaf shape is simple, entire and often coriaceous. The inflorescences are mostly axillary, and thyrsopaniculate or pseudo-umbellate. The flowers are small, usually green, yellow or white and rarely red. The flowers are actinomorphic, bisexual or unisexual, and usually trimerous. The fruits are a one-seeded berry, covered entirely or only at the base by a fleshy to woody cupule (Fig.1.2).

Figure 1.2: *Cryptocarya leptospermoides* Kosterm (P00537973) collected in 1969 by H. S. MacKee (Mackee 21334) New Caledonia. Sourced from National Museum of Natural History, Paris.

The Lauraceae is currently one of the largest and most widespread families of woody plants in the subtropical and tropical regions (Fig.1.3) (Carpenter et al. 2010). The main centres for diversity are the Indomalayan and, Central and South American regions. The habitat with the most diversity is lowland rainforests (Rohwer 1993), though their range can extend from lowland to montane forests (Arifiani 2010). Lauraceae can also be found on oceanic islands such as Fiji, Hawaii, New Caledonia, New Zealand, Papua New Guinea and Vanuatu (Morat et al. 2012; Munzinger et al. 2016). New Zealand is the southern limit for Lauraceae with two species of *Beilschmiedia* and one species of *Litsea* (Breitwieser et al. 2010).

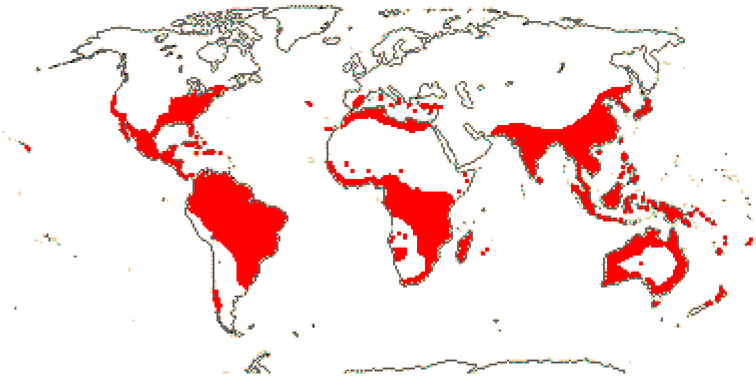

Figure 1.3: The global distribution of Lauraceae. Sourced from Stevens (2001 onwards).

The Lauraceae family is strongly supported as monophyletic at the familial level (Little et al. 2009). However, it is not well defined systematically at the genus and species levels (Chanderbali et al. 2001), despite floristically being among one of the most important tropical woody families (Li et al. 2007). Some genera within the family appear to be polyphyletic, based on molecular phylogenetic analyses (Chanderbali et al. 2001, Little et al. 2009), including *Beilschmiedia, Potameia* Kosterm. and *Yasunia* van der Werff (Rohwer and Rudolph 2005). Major clades such as *Cryptocarya, Beilschmiedia* and *Endiandra* have been identified using molecular markers. However, when morphological characters are added to the phylogenetic analyses these clades are no longer supported as some characters are not synapomorphies (Chanderbali et al. 2001).

Morphological data reveals considerable evidence of diversity within a family and between genera (Rohwer et al. 2014). The suite of diagnostic characters (i.e. flower and fruit characteristics) for each genus appear in various combinations. These are useful when attempting to differentiate between genera. One of the most informative morphological characters used to differentiate between genera is fruit type (Rohwer et al. 1991). Common sequences of traits also tend to correspond with larger genera. Whereas the rarer combinations of traits, which are either treated as small genera of their own or treated as oddities within a larger genus (Rohwer et al. 1991). Morphological data complements genetic analyses and is often used in phylogenetic analyses.

Kostermans (1974) produced the last taxonomic treatment of the New Caledonian Lauraceae, which indicates a significant gap in our knowledge of the Lauraceae in the Australasian region. Rohwer (2000) suggested that there is a close relationship between *Beilschmiedia, Cryptocarya* and *Endiandra*. Carpenter et al. (2010) has suggested that *Cryptocarya* is sister to the majority of the other genera within the Lauraceae. However, whilst *Cryptocarya* is monophyletic based on molecular analyses, it is too diverse morphologically to be easily defined (Rohwer 2000).

The most defining characteristic between the genera of the sub-family Cryptocaryeae are the flowers and fruits. The leaves vary too much within each species to be a useful diagnostic tool, when identifying individual species, let alone at the genera level (van der Werff 2008). The sub-family Cryptocaryeae was originally circumscribed by van der Werff and Richter (1996) based on paniculate and/or cymose inflorescences. The lateral flowers of the cyme are not quite opposite and can appear individually along an inflorescence axis. The genera within the sub-family Cryptocaryeae all have a tree or shrub growth habit (Table 1.1). Majority of the genera have alternate leaves except for *Beilschmiedia* and *Triadodaphne* Kosterm. All of the genera have inflorescences that differ between the genera along with their fruit. The sub-family Cryptocaryeae can be found in Africa to Central America to Southern Asia and though out the Pacific.

Cryptocarya is the largest genus in the sub-family Cryptocaryeae (van der Werff and Richter 1996; Rohwer et al. 2014) with around 250-350 species, which are found throughout the pantropics (Rohwer et al. 2014). The leaves are usually alternate and penninerved, although occasionally they can be opposite and/or triplinerved (Rohwer 1993). *Cryptocarya* inflorescences appear in triplets and the flowers are bisexual. The flower tepals are either deciduous or persist as small remnants. There are usually nine fertile? stamens and the filaments are normally shorter than the anthers. The fruit, a one-seeded berry, develops on an open tubular receptacle (Rohwer 1993).

Table 1.1: Comparison between the genera of the subfamily Cryptocaryeae.

Genera	Description	Distribution	Species count	Citations
Beilschmiedia	Trees (8-40m tall) and shrubs. Leaves opposite to sub-opposite. Inflorescences are axillary, paniculate, solitary and bracteate. Flowers are bisexual and hermaphroditic. They are also trinumerous and small. Drupes are ellipsoid to ovoid and usually black or purple-black when mature. All *Beilschmiedia* drupes lack cupules.	Africa, tropical America, tropical Asia, Eastern Australia, islands of Melanesia and New Zealand	ca. 250 species	Wallich 1831; Knowles and Beveridge 1982; Wright 1984; Nishida 1999; Gangopadhyay 2008
Cryptocarya	Tree (up to 30m tall) and shrubs. Leaves are alternate, obovate to obovate-elliptic. Inflorescences are linear and 3.5 – 9cm in length. Inflorescences are either axillary or terminally and solitarily positioned. Flowers are small, bisexual and trinumerous. Fruit drupe-like and completely enveloped by fleshy or hard perianth tube.	Pantropical (South America, South Africa, Madagascar, Asia, Australia and Oceania)	ca. 200-250 species	Baker 1905; van der Werff 2008; Moraes and van der Werff 2010; Rohwer et al. 2014; de Kok 2016

Genera	Description	Distribution	Species count	Citations
Endiandra	Trees. Leaves alternate, spiral and pinnately-veined. Inflorescences paniculate and axillary. Flowers are small and bisexual. Fruits berries, ellipsoid, cupule absent.	Southern China, Taiwan, Malesia and Australia to Fiji.	ca. 100 species	Wallich 1831; von Mueller 1892; Arifiani 2001; Arifiani 2010
Potameia	Leaves are alternate, simple, entire, oblong-lanceolate. Flowers, which are tetramers and very small are grouped in large numbers of supra-axillary inflorescences. The flowers produce a drupe fruit and a single fleshy embryo. The endosperm is absent.	Madagascar, India to Southeast Asia.	ca. 25 species	Baillon 1870; Gangopadhyay 2008; Rohwer et al. 2014
Triadodaphne	Trees. Leaves spirally arranged and elliptic. Inflorescences on axillary branchlets. Flowers small 2-2.5mm diameter, stamens sessile. Fruits are unknown.	Borneo, New Guinea and Solomon Islands	ca. 3 species	Kostermans 1993

1.3 Phylogenetic Analyses of Lauraceae

The Pacific Ocean covers close to half the world's surface. Within it over 20,000 islands are scattered over millions of kilometres of open water (Cantley et al. 2014). This has resulted in extreme isolation for the majority of these island's biota, which has resulted in high levels of endemism throughout the Pacific (Meyrs et al. 2000). This extreme isolation has meant that for many islands their biodiversity is poorly understood. A method that is currently being employed to better our understanding of these species is molecular phylogenetic analyses.

The nuclear ribosomal internal transcribed region (ITS) region is especially useful for plant species-level analyses (Baldwin et al. 1995). Gemmill et al. (2002) used ITS to test the monophyly of Hawaiian *Pittosporum* species and to reconstruct relationships among Pacific species of *Pittosporum*. Due to majority of the variation in the ITS region being at the single nucleotide level (Baldwin et al. 1995), ITS can also be amplified and sequenced relatively easily in herbarium specimens, which is useful for rare or hard to access species (Baldwin et al. 1995).

There are multiple studies of island taxa that have used ITS to create their phylogenetic trees. Some of the Islands, which have had taxa studied using ITS include New Caledonia (Gemmill et al. 2002), New Zealand (Nelson et al. 2013), Juan Fernandez Islands (Ruiz et al. 2000), Japan (Ito et al.2014), Jeju Island (Ito et al. 2014) and the Hawaiian Islands (Cantley et al. 2014).

In New Caledonia, multiple families and genera have been studied using ITS, two of these are *Diospyros* (Ebanaceae; Turner et al. 2016) and *Halfordia* (Rutaceae; Bayly et al. 2016). Turner et al. (2015) found that *Diospyros* had established on New Caledonia through four separate colonisation events (Tuner et al. 2015). It also showed that whilst New Caledonian *Diospyros* are morphologically and ecologically diverse they show very little genetic divergence among species? (Turner et al. 2015). Bayly and coworkers (2016) studied *Halfordia,* which is found in New

Guinea, New Britain, New Caledonia, Vanuatu and eastern Australia). New Caledonian *Halfordia* is morphologically distinct. Their study suggested that *Halfordia* most likely established in New Caledonia after a single dispersal event from northern Australia (Bayly et al. 2016).

Five chloroplast markers that are commonly used in plant phylogenetic studies at the lower taxonomic levels are *mat*K, *trn*K, *trn*L-*trn*F, *rpl*16 and *psb*A-*trn*H (Li et al. 2004; Liu et al. 2013; Rohwer et al. 2014). Multiple studies have been performed using these multiple markers in conjunction with ITS on Lauraceae. ITS has the highest percentage of informative sites for Lauraceae with 11-37%, the other markers have less than 10% (Li et al. 2004; Li et al. 2007; Liu et al. 2013; Rohwer et al. 2014). Whilst ITS is the most variable of the markers, it is not able to resolve relationships among distantly related species, which is why it is usually used in conjunction with a chloroplast marker (Li et al. 2004; Rohwer et al. 2014). The chloroplast marker, which has the most informative sites for Lauraceae is *trn*L-*trn*F with 5.75% (Liu et al. 2013) and the marker with the least number of informative sites was *rbl16* with 0.78% (Liu et al. 2013).

1.4 Methods of Phylogenetic analyses

The two most currently used methods of phylogenetic analyses for Lauraceae are, Maximum likelihood and Bayesian inference (Rohwer and Rudolph 2005). Maximum likelihood creates trees based on decisions, which adequately explain the data (Schmidt and Haesler 2009). Maximum-likelihood analyses makes the assumption, that the sequences used have evolved according to the phylogenetic tree. This means that multiple Maximum likelihood analyses are required to be performed in order to ensure that the trees produced are accurate.

Bayesian inference creates trees, which are based on the mathematical formalisation of a probability decision process (Ronquist et al. 2009). Bayesian inference generates a single clade credibility tree, with posterior probabilities simultaneously (Drummond and Rambaut 2007). Genetic sequences are used to obtain the posterior probability distribution. If the posterior probabilities analyses have been performed correctly there is nothing controversial about them and they can be used to analyse any area of interest (Ronquist et al. 2009). However, prior distributions can override parameter values (Drummond and Rambaut 2007). This can be an advantage when palaeontological data is available.

Phylogenetic analyses using Bayesian inference has been used for the Lauraceae previously (Rohwer and Rudolph 2005). It is not as sensitive as parsimony analysis to taxon sampling (Schmidt and Haesler 2009). This means that it gives a more consistent result, across analyses based on different sets of taxa (Drummond and Rambaut 2007). It has also been found that Maximum likelihood analyses, whilst similar to Bayesian inference were less resolved (Rohwer et al. 2014).

1.5 Research Aims

Lauraceae as a family is monophyletic. However, there are still large gaps in our knowledge. It is unclear how many of the currently recognised genera are monophyletic and what the relationships between theses genera are. Resolving some of these phylogenetic questions, will help with more reliable interpretations, of how certain characters evolved, as well as giving us a useful insight into the biogeographical history of Lauraceae (Rohwer 2000).

There is a clear lack of research on New Caledonian Lauraceae, with the last comprehensive taxonomic treatment being carried out by Kostermans in 1974. My research tests Kostermans's classification of the genera *Beilschmiedia*, *Endiandra* and *Cryptocarya* using a modern molecular systematics approach. The genetic markers ITS will be used, as they produce, the highest number of informative sites for Lauraceae. This will allow for the monophyly of the genera to be tested along with their biogeographical history.

This research will provide the foundation for future investigation into the sub-family Cryptocaryeae in New Caledonia. In future research, more species will be included as well as samples per species. An additional marker (*trn*L-*trn*F) will also be used to help the resolution of the phylogenetic analyses. It will also generate the data required to undertake future conservation assessments and risk of extinction for the IUCN.

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Chapter Two

Molecular Systematics of New Caledonian Cryptocaryeae (Lauraceae)

This chapter has been written for submission to Australian Systematic Botany with authors S. N. Carter, J. Munzinger, S. J. Meyer and C. E. C. Gemmill. As such information within this manuscript may be repeated from other sections.

Author contributions: J.M. and C.E.C.G conceived the study; J.M. collected the field samples; S.N.C and S.J.M. collected the data; S.N.C led the writing with support from CECG. All the authors discussed results and commented on the text.

2.1 Introduction

New Caledonia is the northern most emergent island system on the mainly submerged (ca. 94% submerged) continent Zealandia. The narrowest point between Zealandia and Australia is the Cato Trough, which is 25km across and 3600m deep (Mortimer et al. 2016). Zealandia connects New Caledonia to New Zealand by a thin piece of continental crust along the Norfolk ridge (Fig 2.1) (McLoughlin 2001; Mortimer et al. 2016). New Caledonia along with the rest of Zealandia was submerged during the Palaeocene, until it re-emerged 20 Mya later during the Oligocene (Grandcolas et al. 2008; Keppel 2009). Whilst Zealandia is continental in origin there is evidence to support that it was not a past terrestrial geographical unit and is simply a complex series of rock formations, where several ephemeral islands are scattered (Grandcolas 2016). The submersion caused layers of oceanic sediment, fine grained chert, ophiolitic nappe and other ultramafic rocks to form (Pillion et al. 2010; Grandcolas 2016). Some of these layers have formed slowly during the submersion of Zealandia whereas other layers such as ophiolitic nappe were lain over New Caledonia during strong tectonic events (Grandcolas 2016). These layers of sediment and rock have helped form the ultramafic soils that New Caledonia is known for (Pillon et al. 2010; Grandcolas 2016).

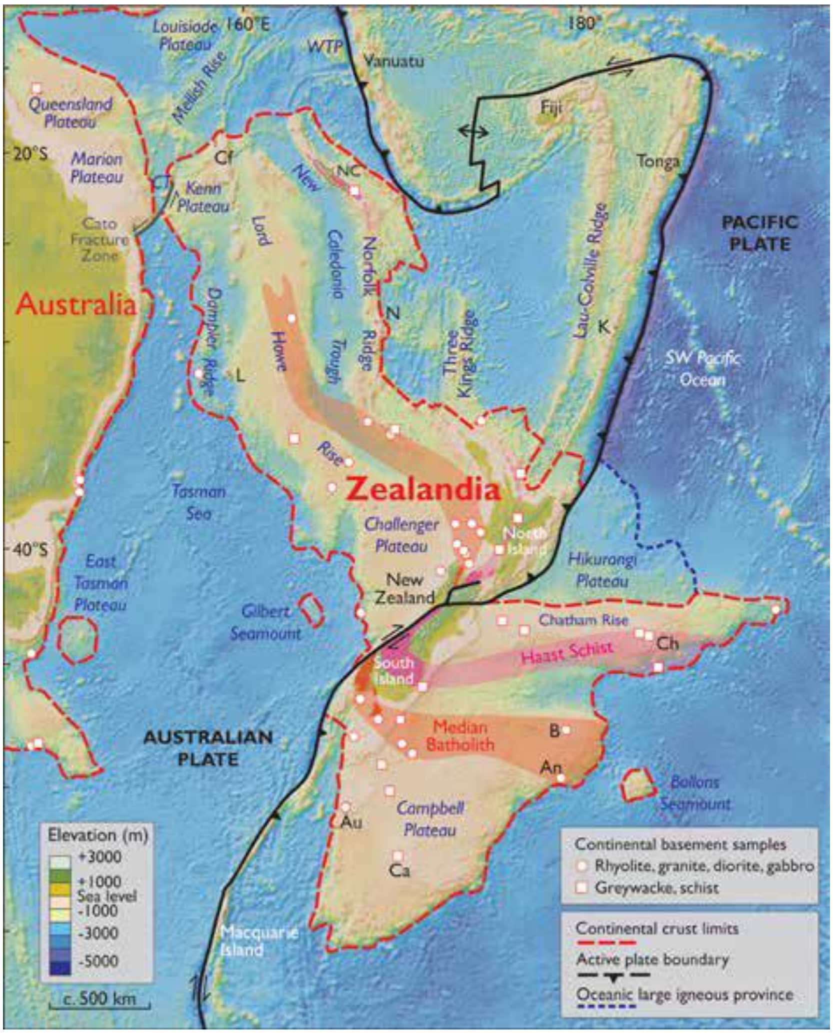

Figure 2.1: The continent of Zealandia with depth, rock type and locations mapped. New Caledonia is located in the north east of Zealandia. Sourced from Mortimer et al. (2016)

New Caledonia is an archipelago located in the southwest Pacific. It is approximately 1700km north of New Zealand and 1200km east of Queensland Australia (Buerki et al. 2012). New Caledonia has a land mass of 16,890km² (Fig 2.2). Grande Terre, the main island, is 500km long and 50km wide with an elevation over 1600m along its mountain range (Grandcolas et al. 2008). Île des Pins is approximately 150km² with small satellite islets and is located 50km south of Grand Terre (Geneva et al. 2013). The Loyalty Islands are located across the 110km wide Loyalty basin running parallel to the eastern side of Grand Terre (Daza et al. 2015). These islands were formed from coral heads around 118,000 years and uplifted during the Pleistocene. Lifou is the largest island in this chain at 1,150km^2 and Maré is the highest point in the chain at 136m.

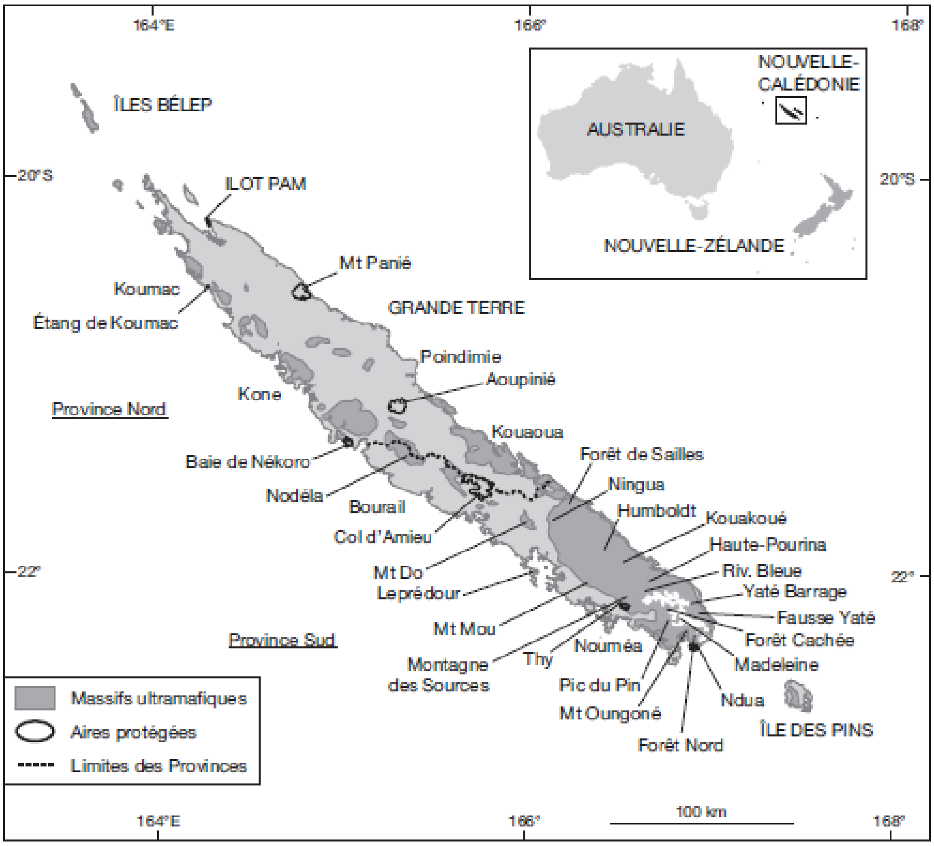

Figure 2.2: Location of the communes and protected areas. Location of New Caledonia in relation to Australia and New Zealand. Sourced from Morat et al. (2012)

Due to its location, New Caledonia has a tropical climate, which is influenced by the surrounding ocean (Jaffré 1993). It is recognised as a biodiversity “hotspot” with over 3000 native vascular plant species (Meyrs et al. 2000; Morat et al. 2012). An area is classed as a biodiversity “hotspot” when there are high concentrations of endemic species that are undergoing significant habitat loss (Meyrs et al. 2000). The level of vascular plant species endemism is estimated to be between 76-80% (Jaffré 1993; Morat et al. 2012, Munzinger et al., 2016). The high level of endemism is believed to be an artefact of multiple colonisation events after New Caledonia resurfaced during the Oligocene (Grandcolas et al. 2008).

There are four major types of vegetation in New Caledonia, humid rainforests, anthropogenic savannahs, sclerophyll forests and the maquis. The last two vegetation types have become highly fragmented due to anthropological activities such as nickel mining, forest logging and forest burning (Heywood & Davis 1995; Morat et al. 2012; Munzinger et al. 2016). These forests are also affected by introduced animals such as feral deer (*Cervus timorensis*), goats (*Capra aegagrus hircus*), pigs (*Sus scrofa*) and rats (*Rattus* sp.). Invasive plant species also out complete native species, however, this happens rarely due to the ultramafic soils, which the majority, of plant species cannot readily adapt to (Grandcolas et al. 2008; Morat et al. 2012; Munzinger et al. 2016).

The rainforests are the most wide-spread vegetation type in New Caledonia. It is divided into three main categories, low and middle altitude forests, high altitude forests (above 1000m) and limestone forests (Jaffré 1993). The rainforest are found across a range of geological substrates and are found most readily in places of high rainfall. The rainforests cover 3350km^2 on Grand Terre and 550km^2 on the Loyalty islands which equates to 22% of New Caledonia’s terrestrial area. The rainforest also has an endemism rate of 80% for vascular plant species (Jaffré 1993; Morat 1993).

The anthropogenic savannahs have formed in areas of rainforest and sclerophyll forest that have been destroyed, the main cause of destruction being fire (Jaffré 1993). It covers approximately 6000km^2 and contains around 120 species, few of which are endemic (Jaffré 1993).

Sclerophyll forests are found on ultramafic substrates in the driest regions of New Caledonia (Jaffré 1993). It currently only exists in various states of degradation on the west coast of Grand Terre. It contains around 400 vascular species in an area ca. 400-500km^2. It has an endemism rate of 34% for vascular plant species (Jaffré 1993). The species found within the sclerophyll forests tend to be semi-deciduous trees with a maximum height of 12m and woody evergreen sclerophyllous trees (Morat 1993). Usually there is a patchy layer of herbaceous *Cyperaceae* and *Gramineae* within the forests.

The maquis covers 4500km^2 (26% of Grand Terre) and contains 1064 vascular plant species, 955 of these are endemic. The maquis has the highest rate of endemism between the four forest types found in New Caledonia at 90% (Jaffré 1993). The maquis is usually associated with specific edaphic conditions which are created by ultramafic substrates and are only found on Grand Terre (Jaffré 1993; Morat 1993). Morat (1993) described the maquis as being primitive in nature. This was hypothesised to be due to the ultramafic soils that the maquis is adapted too.

The flora of New Caledonia is poorly understood. It is approximated that only 65% of the currently described species have been revised since 1967 (Morat et al. 2012; Munzinger et al. 2016). New Caledonia contains 126 families three of which are endemic. There are approximately 3371 species in New Caledonia including 3099 for dicotyledons alone. The endemism rate for dicotyledons at the species level is 85.6%. The flora however, is disharmonic as some groups are missing or underrepresented whilst others are more highly represented than expected (Morat et al. 2012; Munzinger et al. 2016). This phenomenon however, is common is island flora (Meyrs et al. 2000). Only 3.4% of the New Caledonia’s total surface area is protected. The areas that are conserved are mainly comprised of secondary vegetation and provide a limited role in conserving the native flora. The conservation efforts also include rehabilitation of old mining sites (Jaffré et al. 1998; Morat et al. 2012; Munzinger et al. 2016).

The Lauraceae Jussieu is a magnoliid angiosperm family with fossil records dating back to the late cretaceous. The family Lauraceae is one of seven families, which make up the order Laurales. Within Lauraceae there are approximately 50 genera with 2500-3500 species (Rohwer 1993). Lauraceae is one of the largest and most wide spread families of woody plants throughout the subtropical and tropical regions (Carpenter et al. 2010) and is the 14th equal largest angiosperm family in New Caledonia (Morat et al. 2012; Munzinger et al. 2016).

In 1996 van der Werff and Richter hypothesised that there were three sub-families within the Lauraceae. The three sub-families are Laureae, which was distinguished by majority of its genera having racemose inflorescence, the Perseeae Nees with paniculate-cymose inflorescence, and the Cryptocaryeae Nees with paniculate inflorescence. The sub-family Cryptocaryeae contains the genera *Beilschmiedia* Nees*,* *Cryptocarya* R. Br., *Endiandra R. Br., Potameia* Kosterm. and *Triadodaphne* Kosterm (van der Werff and Richter 1996).

The Cryptocaryeae are represented in New Caledonia *Beilschmiedia* (2 species), *Cryptocarya*. (22 species), and *Endiandra* (6 species) (Morat et al. 2012; Rohwer et al. 2014; Munzinger et al. 2016). Witihin New Caledonia, 98% of the Lauraceae species are endemic (Morat et al. 2012; Munzinger et al. 2016). Within these three genera all of the New Caledonian, species of Cryptocaryeae are endemics.

Kostermans (1974) conducted the last comprehensive taxonomic revision of the New Caledonian Lauraceae. The original western scientific collections, taxonomic cataloguing and descriptions of the New Caledonian flora began with Captain Cook’s visit in 1774, with the collections of Forsters (Guillaumin 1967). The first species of New Caledonian *Beilschmiedia* were described in the late 1800s by Pancher and Sebert. Sclechter added four species of *Cryptocarya* and two species of *Endiandra* in 1906. The first taxonomic treatment of New Caledonain Lauraceae was completed by Guillaumin in 1925 (Guillaumin 1925). This treatment included 10 species of *Cryptocarya* and five species of *Endiandra*. Guillaumin (1925) did not recognise any species of *Beilschmiedia*, the species that are currently classfied as *Beilschmiedia* were placed in either *Cryptocarya* or *Endiandra*. Kostermans (1974) taxonomic revision identified a total of 44 species of Lauraceae in New Caledonia including the genera *Adenodaphne* and *Litsea* all of which are endemic. In Kostermans revision he resurrected *Beilschmiedia* as well as adding one new *Beilschmiedia* (2 species) species and added one species of *Endiandra* (6 species). For *Cryptocarya* (19 species) he added 11 species and identified several potentially new species but did not describe them due to insufficient material (Kostermans 1974).

Cryptocarya is the largest of the Lauraceae genera with ca. 200-250 species throughout the Pantropics (de Kok 2016). *Beilschmiedia* has ca. 250 species (Nishida 1999) ranging across Africa, tropical America, tropical Asia, Eastern Australia, islands of Melanesia and New Zealand (Nishida 2008). *Endiandra* has ca. 100 species throughout Southern China, Taiwan, Malesia and Australia to Fiji (Arifiani 2001). The distinguishing feature between these genera is fruit type. *Beilschmiedia* has drupes that lack cupules (Knowles and Beveridge 1982). *Cryptocarya* fruits are drupe-like and either partially or completely covered enveloped by a fleshy or hard perianth tube (de Kok 2016). *Endiandra* has ellipsoid berries without a cupule (von Meuller 1892).

Molecular phylogenetic analyses (Rohwer 2000; Chanderbali et al. 2001; Rohwer et al 2014) using ITS suggest that *Beilschmiedia*, *Cryptocarya* and *Endiandra* are sister taxa. Rohwer et al. (2014) suggested that *Beilschmiedia* is paraphyletic unless *Sinopora* Li, Xia & Li, *Yasunia* van der Werff & Nishida and *Potameia* are merged with *Beilschmeidia*. It is unknown whether Endiandra is nested within the Beilschmiedia group as it is weakly supported as being a sister taxa with ITS analysis. These authors further suggested that *Cryptocarya* is monophyletic if *Ravensara* Kosterm is included, and that New Caledonian *Cryptocarya* are the result of multiple colonization events. van der Merwe et al. (2016) has suggested that *Cryptocarya* has two well-supported clades within the genus. Fruits within *Cryptocarya* vary in shape from globose to transversely ellipsoid and leaf venation, pinnate vs. pluerinerve, may be important within *Cryptocarya*. *Endiandra* is monophyletic if *Triadodaphne* is included, and that Endiandra in New Caledonia is a result of a single colonisation event (Rohwer et al. 2014).

The aim of this study is to test the taxonomic delimitations of the New Caledonian Cryptocaryeae. This study will test whether the New Caledonian *Beilschmiedia, Cryptocarya* and *Endiandra* are monophyletic. Are these genera the result of one or more colonization events? This study will test if the *Cryptocarya* group forms two clades as suggested by Rowher et al. (2014) and van der Merwe et al. (2016).

2.2 Methods

Samples of plant material and sequences were obtained from sources listed in Table 2.1, and further details are given in the Appendix. Many of the samples sequenced for this study were collected by Munzinger, as a result of extensive field work. Majority of the samples used were freshly collected and dried in silica. Specimens from herbaria samples came from NOU and WAIK herbariums.

Extraction of total genomic DNA was conducted using 50-100 mg of dried leaf tissue using an Isolate II Plant DNA kit (Bioline) following the manufacturer’s instructions, with a 3 hour lysis period. The internal transcribed spacer (ITS) region of 18S – 26S nuclear ribosomal DNA was used in this study because ITS has the highest percentage of informative sites for Lauraceae (11-37% (Li et al. 2004; Li et al. 2007; Liu et al. 2013; Rohwer et al. 2014)) and has proven useful in numerous other studies of island plants (Gemmill et al., 2002; Bayly et al. 2016; Turner et al. 2016). The other markers that are commonly used (*mat*K, *trn*K, *trn*L-*trn*F, *rpl*16 and *psb*A-*trn*H) have less than 10% informative sites for Lauraceae (Li et al. 2004; Li et al. 2007; Liu et al. 2013; Rohwer et al. 2014). In this study we strategically chose to maximize the number of samples sequenced for a single a marker, rather than sequence fewer samples for more than one marker; we are in the process of sequencing all of these samples for *trn*L-*trn*F at present as a result of recent additional funding from the Australasian Systematic Botany Society Hansjörg Eichler Scientific Research Fund.

Table 2.1: New Lauraceae samples sequenced for the internal transcribed spacer region (ITS). For the New Caledonian samples commune was given. For the New Caledonian Cryptocarya soil type, fruit type and leaf venation were given. UM means ultrmafic soils and NUM means non-ultramafic soil.

Name	Authority	Collector No#	Country	Commune	Soil Type	Friut	Leaves
Beilschmiedia neocaledonica	Kosterm.	McPherson 19086	New Caledonia	Mt. Colnett	NUM		
Beilschmiedia oreophila	Schltr.	Dagostini 1444	New Caledonia	Yaté	UM		
Beilschmiedia oreophila	Schltr.	Munzinger 2474	New Caledonia	Haute Ni	UM		
Beilschmiedia tarairi	(A.Cunn.) Kirk	McIntosh s.n.	New Zealand				
Beilschmieda sp.	Nees	Munzinger 7246	New Caledonia	Aoupinié	NUM		
Beilschmiedia sp.	Nees	Munzinger 5762	New Caledonia	Pont des Japonais	UM		
Beilschmiedia sp.	Nees	Munzinger 5816	New Caledonia	Mandjélia	NUM		
Beilschmiedia sp.	Nees	Munzinger 5878	New Caledonia	Tchamba	NUM		
Beilschmiedia sp. (Munzinger 6408)	Nees	Munzinger 6097	New Caledonia	Panié.	NUM		
Cryptocarya adpressa	Munzinger & McPherson	Munzinger 4849	New Caledonia	Plateau de Dogny	NUM	Globose	Pinnate
Cryptocarya aristata	Kosterm.	Munzinger 5866	New Caledonia	Tchamba	NUM	Transverse Ellipsoid	Pinnate
Cryptocarya aristata	Kosterm.	Munzinger 7668	New Caledonia	Bwa Bwi	NUM	Transverse Ellipsoid	Pinnate
Cryptocarya barrabeae	Munzinger & McPherson	Munzinger 5841	New Caledonia	Mandjélia	NUM		Pinnate
Cryptocarya barrabeae	Munzinger & McPherson	Munzinger 5854	New Caledonia	Ponandou	NUM		Pinnate
Cryptocarya chrysea	Munzinger & McPherson	Munzinger 7657	New Caledonia	Bwa Bwi	NUM	Globose	Pinnate

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Name	Authority	Collector No#	Country	Commune	Soil Type	Friut	Leaves
Cryptocarya constricta		Munzinger 7367	Fiji				
Cryptocarya densiflora	Blume	Munzinger 6975	Papua New Guinea				
Cryptocarya elliptica	Schltr.	Munzinger 5852	New Caledonia	Ponandou	NUM	Globose	Pinnate
Cryptocarya elliptica	Schltr.	Munzinger 5870	New Caledonia	Tchamba	NUM	Globose	Pinnate
Cryptocarya gracilis	Schltr.	McPherson 19129	New Caledonia	Mont Colnett	NUM		
Cryptocarya gracilis	Schltr.	Munzinger 5808	New Caledonia	Mandjélia	UM & NUM	Globose	Pinnate
Cryptocarya guillauminii	Kosterm.	Munzinger 7630	New Caledonia	Bwa Bwi	UM	Globose or Transverse Ellipsoid	Plurinerve
Cryptocarya leptospermoides	Kosterm.	Munzinger 7285	New Caledonia	Tiébaghi	UM & NUM	Globose	Pinnnate
Cryptocarya lifuensis	Guillaumin	Munzinger 6064	New Caledonia	Ile des Pins	NUM	Transverse Ellipsoid	Pinnate
Cryptocarya lifuensis	Guillaumin	Munzinger 6725	New Caledonia	Koumac	NUM	Transverse Ellipsoid	Pinnate
Cryptocarya longifolia	Kosterm.	Munzinger 5754	New Caledonia	Ile Art	UM	Transverse Ellipsoid	Pinnate
Cryptocarya longifolia	Kosterm.	Munzinger 5837	New Caledonia	Mandjélia	UM	Transverse Ellipsoid	Pinnate
Cryptocarya longifolia	Kosterm.	Munzinger 7215	New Caledonia	Aoupinié	UM	Transverse Ellipsoid	Pinnate
Cryptocarya longifolia	Kosterm.	Munzinger 7283	New Caledonia	Tiébaghi	UM	Transverse Ellipsoid	Pinnate
Cryptocarya odorata	Guillaumin	Munzinger 4933	New Caledonia	Tontouta	UM	Globose	Pinnate
Cryptocarya odorata	Guillaumin	Munzinger 5159	New Caledonia	Goapin	NUM	Globose	Pinnate
Cryptocarya oubatchensis	Schltr.	Munzinger 7078	New Caledonia	Tchingou	UM	Turbinate	Pinnate

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Name	Authority	Collector No#	Country	Commune	Soil Type	Friut	Leaves
Cryptocarya phyllostemon	Kosterm.	Barrabé 409	New Caledonia	Forêt de Bon Secours	UM	Turbinate	Pinnate
Cryptocarya phyllostemon	Kosterm.	Munzinger 7730	New Caledonia	Bwa Bwi	UM	Turbinate	Pinnate
Cryptocarya pluricostata	Kosterm.	Munzinger 7780	New Caledonia	Auberge des Koghis	UM & NUM	Turbinate	Pinnate
Cryptocarya tannaensis Guillaumin	R.Br.	Munzinger 7504	Vanuatu				
Cryptocarya tannaensis Guillaumin	R.Br.	Munzinger 7506	Vanuatu				
Cryptocarya tranversa	Kosterm.	Munzinger 7079	New Caledonia	Tchingou	UM	Globose	Plurinerve
Cryptocarya turbinate	Gillespie	Munzinger 6502	Fiji				
Cryptocarya turbinate	Gillespie	Munzinger 7359	Fiji				
Cryptocarya velutinosa	Kosterm.	Munzinger 5868	New Caledonia	Tchamba	NUM	Globose	Pinnate
Cryptocarya "aff. aristata" (Munzinger 5874)	R.Br.	Munzinger 5882	New Caledonia	Tchamba	NUM		
Cryptocarya sp.	R.Br.	Lowry 7345	Fiji				
Cryptocarya sp.	R.Br.	Munzinger 5722	New Caledonia	Ile Art	UM		
Cryptocarya sp.	R.Br.	Munzinger 5752	New Caledonia	Ile Art	UM		
Cryptocarya sp.	R.Br.	Munzinger 6510	Fiji				
Cryptocarya sp. "aff. aristata" (Munzinger 5874)	R.Br.	Munzinger 6534	New Caledonia	Tchamba	NUM		
Cryptocarya sp. (McPherson 4408)	R.Br.	Munzinger 7784	New Caledonia	Auberge des Koghis	NUM		
Cryptocarya sp. (Munzinger 5178)	R.Br.	Munzinger 5178	New Caledonia	Aoupinié	NUM		

Continued on next page …

Name	Authority	Collector No#	Country	Commune	Soil Type	Friut	Leaves
Cryptocarya sp. aff. gracilis (Brinon 1104)	R.Br.	Grignon 323	New Caledonia	Thy	UM/NUM		
Endiandra baillonii	(Pancher & Sebert) Guillaumin	Munzinger 5987	New Caledonia	Kuébini	UM		
Endiandra sebertii	Guillaumin	Munzinger 5825	New Caledonia	Mandjélia	NUM		
Endiandra sebertii	Guillaumin	Munzinger 7125	New Caledonia	Yaté	UM		
Endiandra euadenia	Kosterm.	Munzinger 6985	Papua New Guinea				
Endiandra sp.	R.Br.	Munzinger 7082	New Caledonia	Tchingou	UM		
Endiandra sp.	R.Br.	Munzinger 7652	New Caledonia	Bwa Bwi	UM		
Endiandra sp. "Mandjélia" (JM5839)		Munzinger 5833	New Caledonia	Mandjéia			
Endiandra sp. Humboldt [McP3119-JM5719]	(Pancher & Sebert) Guillaumin	Munzinger 5719	New Caledonia	Humboldt	UM		

The ITS region consists of the spacers ITS1 and ITS2 along with the subunit 5.8S (Baldwin 1995). For the genera *Beilschmiedia* and *Endiandra* the universal eukaryote primer ITS-4 (5'-TCCTCCGCTTATTGATATGC-3') and the reverse primer ITS-5 HP (5'-GGAAGGAGAAGTCGTAACAAGG-3') (White et al. 1990) were used to amplify this region. PCR was conducted using a total reaction volume of 20 µL which consisted of 12.6 µL MiliQ water, 1.25X MyTaq™ Red Reaction Buffer (Bioline), 0.25 µM of each primer, 0.1% bovine serum albumin (BSA), 0.05U of MyTaq™ Polymerase (Bioline), and 1.0 µL unquantified total genomic DNA. Reactions were run on an Eppendorf Mastercycler® pro thermal cycler with an initial denaturation of 94˚C for 5 min, followed by 36 cycles of 94˚C for 30 s, 54˚C for 30s and 72˚C for 1 min, with a final extension of 72˚C for 10 min. For *Cryptocarya* the primers used to amplify the ITS region were ITS18F (5'-CRATCACTCTTTTGACTTTGG-3') and the reverse primer ITSHR (5'-CGGTTCGCTCGCCGTTACTA-3') (Rohwer et al. 2014). PCR was as above but with an initial denaturation of 3 min and annealing at 56.8˚C for 2 min.

Gel electrophoresis was used to verify amplification, with 3 µL of PCR product loaded into a 1% 0.5X TBE agarose gel containing 0.005% amount of RedSafe™ Nucleic Acid Staining Solution (iNtRON Biotechnology, Inc.) and run for 30 min at 45 V. A 100bp DNA ladder (Invitrogen) was used as a size standard. Using an AlphaImager™ (Innotech) the gel was visualised under UV light and photographed. Products that produced a single strong band around 700bp were then purified for sequencing via a standard ExoSap or ExoProStar protocol. The reaction mixture of 10U of Exo, 2U of SAP, and 5 µL of PCR product was prepared and incubated at 37˚C for 15min followed by 80˚C for 15 min using an Eppendorf Mastercycler® pro thermal cycler.

Sequencing was conducted at the University of Waikato DNA Sequencing Facility using a BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems®) using an Applied Biosystems 3130xl Genetic

Analyzer. Sequences were edited and initial alignments performed using Sequencher version 5.3 (Gene Codes http://www.genecodes.com). Sequences were verified using the NCBI database BLASTn search alogarithm (Altschul et al. 1990). The multiple sequence alignment was optimized using MUSCLE (Edgar 2004) as implemented within SEAVIEW version 4.5.4 (Galtier et al. 1996; Gouy et al. 2010).

Bayesian phylogenetic analyses were conducted using the BEAST2 2.4.5 suite of software programs (Bouckaert et al., 2014). BEAUTi was used to generate the .xml file for input into BEAST2. We used bModelTest (Bouckaert 2015) to average across all nucleotide models, a relaxed log-normal clock (Drummond et al 2006) to allow rates to vary among lineages, and the birth-death model (Heath et al., 2014) to account for extinctions. We used broad priors and specified a beta distribution for nucleotide frequencies uniform distribution for BMT_gammashape, and gamma distributions for birth rate, relative death and ucldStdev. Preliminary analyses using a chain length of 50 million produced convergence of chains and high ESS values in Tracer (Rambaut et al. 2014). Final analyses used a chain length of 10 million generations, saving every 1000 trees. We ran this analysis 5 times with a different starting seed to optimize searching tree space. The log and tree files from each of the analyses were combined in LogCombiner with a 10% burn-in. Convergence and ESS values were assessed using Tracer (Rambaut et al. 2014). Tree Annotator was used to summarize the tree files and the maximum clade credibility tree was visualized using FigTree (Rambaut 2016).

2.3 Results

The sequences were of a high quality and bidirectional reads were obtained for all 171 samples. The truncated optimised multiple sequence alignment was 821 base pairs with individual sequences ranging from 551 to 651 base pairs. The mean pairwise identity was 85.5% with 16.5% of the sites being identical across all sequences. Base frequencies were for C:G 33.7% and A:T 16.4%.

Overall the topology of the tree is well supported (Fig 2.3). For the outgroup taxa *Aspidostemon* is strongly supported as sister to *Dagrenodendron* (PP 1) and *Potoxylon* is strongly supported (PP 1) as sister to *Eusideroxylon*. The relationship to *Hypodaphnis* is unresolved. Together the ingroup taxa form a strongly supported clade (PP 1). Within the ingroup there are two main clades, Clade B is composed of *Beilschmiedia, Sinopora, Syndiclis, Yasunia, and Potameia* (PP .99), which is sister to *Endiandra* and *Triadodaphne* (PP 1). Clade C is composed of *Cryptocarya* and *Ravensara* (PP 1). Hence neither *Beilschmiedia* nor *Cryptocarya* are monophyletic as currently circumscribed.

Within Clade B, three large clades are strongly supported. B1 is composed of *Beilschmiedia, Sinopora, Syndiclis, Yasunia* and *Potameia* (PP .99; Fig 2.4) with specimens representing all of the geographic regions except New Caledonia. This clade has many smaller clades that are strongly to weakly supported. Strongly supported clades include a relatively large clade composed of Chinese and South American samples (PP .96). This clade includes 14 Chinese *Beilschmiedia* species, three indeterminate Vietnamese specimens and two South American *Beilschmiedia* species. All four Chinese *B. yunnanensis* samples form a clade (PP1). Chinese *Sindiclis* and *Sinopora* form a strongly supported clade (PP1) and in turn are sister (PP .98) to two South American *Bielschmiedia* species (PP 1). The two New Zealand *Beilschmiedia* species, *B. tawa* (PP1) and *B. taraire (PP 1)*, do not form a clade, while *B. tarairi* is sister to two Australian species. Two other moderately-supported clades include samples from South America (PP .7) that include two *Yasunia* species, and Africa and Madagascar (PP.67) that include a species of *Potameia*.

Clade B2 (PP 1) is composed solely of New Caledonian *Beilschmiedia* specimens. Within this clade *B. oreophila* form a clade with an

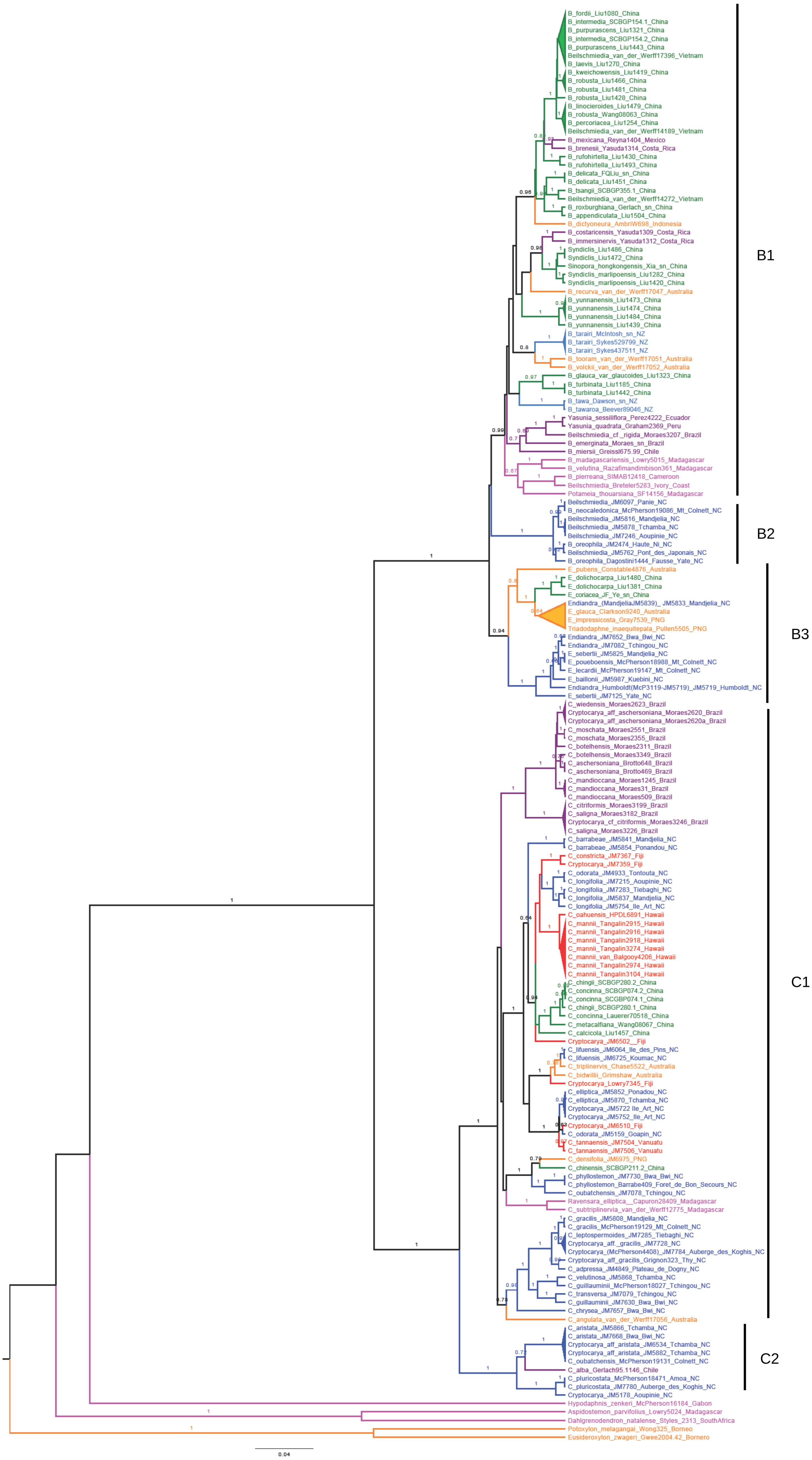

Figure 2.3: This tree shows the phylogenetic relationship of the subfamily Cryptocaryeae and outgroups. The ITS sequence matrix was analysed using Bayesian Inference. Posterior probabilities >0.6 are given on the tree branches. Geographic areas are colour-coded. Asia, green; South America, purple; Pacific, red; Australasia and Indonesia, orange; Africa and Madagascar, pink; New Zealand, pale blue; New Caledonia, dark blue.

indeterminate specimen (PP .62) and *B. neocaledonica* forms a clade with four indeterminate specimens from a range of localities.

Clade B3 (PP .94) contains the four species and indeterminate specimens of *Endiandra* from New Caledonia (PP1), that are sister, to a clade of species from Australia, Papua New Guinea and China, as well as *Triadodaphne* (PP .94) from Papua New Guinea.

Figure 2.4: *Beilschmiedia, Sinopora, Syndiclis, Endindra, Potameia* and *Triadodaphne* clade (B1, B2 and B3). The ITS sequence matrix was analysed using Bayesian Inference. Posterior probabilities >0.6 are given on the tree branches. Geographic areas are colour-coded. Asia, green; South America, purple; Australasia and Indonesia,

orange; Africa and Madagascar, pink; New Zealand, pale blue; New Caledonia, dark blue.

Within the *Cryptocarya* clade there are two strongly supported clades (PP1; Fig 2.5), Clade C1 and Clade C2. C1 (PP 1) is composed of three species and three undetermined specimens from New Caledonia, along with C. alba from Chile. Two *C pluricostata* samples are strongly supported as sister taxa (PP 1) and in turn form a clade with an indeterminate specimen (PP 1). The remaining six samples form a moderately supported clade (PP .72) with the Chilean *C. angulata* sister to a strongly supported clade (PP1) comprised of two *C. aristata*, one *C. oubatchensis* and two indeterminate *Cryptocarya* samples all from New Caledonia.

C2 is a large geographically diverse clade comprised of numerous subclades. A clade of all South American species included in this study is strongly supported (PP1). A large and diverse clade (PP 1) includes species from New Caledonia, the Pacific and Asia. Strongly supported relationships of New Caledonian taxa within this clade include two *C barrabae* samples (PP 1), *C ordorata* and *C longifolia,* and, *C elliptica* and two indeterminate specimens from New Caledonia (PP. 97). Additionally, taxa from Fiji, Hawaii and Vanuatu form clades. *Cryptocarya phyllostemon* and *C oubtatchencis* form a strongly supported clade (PP 1) and in turn are sister to a clade of Chinese and Papua New Guinea species. The *Cryptocarya* and *Ravensara* species from Madagascar are strongly supported as sister (PP 1). A large clade of New Caledonian *Cryptocarya* is strongly supported (PP .96) and includes seven species as well as some indeterminate specimens. Within this clade *C. chrysea* is sister to the rest of the clade. Whilst in turn *C velutinosa*, *C. guillauminii* and *C. transversa* are sister to the rest of the clade, including three indeterminate species.

Figure 2.5: *Cryptocarya* and *Ravensara* clade (C1 and C2). The ITS sequence matrix was analysed using Bayesian Inference. Posterior probabilities >0.6 are given on the tree branches. Geographic areas are colour-coded. Asia, green; South America, purple; Pacific, red; Australasia and Indonesia, orange; Africa and Madagascar, pink; New Zealand, pale blue; New Caledonia, dark blue.

2.4 Discussion

This study generated 58 new complete ITS sequences, the majority of which were from New Caledonian specimens. This included both of the currently recognised New Caledonian *Beilschmiedia* species, along with five indeterminate *Beilschmiedia* specimens. For *Endiandra* three of the six currently recognised New Caledonian species, along with four indeterminate specimens. Of the 22 currently recognised New Caledonian

Cryptocarya species, 16 were sequenced along with nine indeterminate *Cryptocarya* specimens.

Sequence variation in ITS provided sufficient resolution to differentiate between the major genera in this study (Fig. 2.4), as well as provide resolution among species. However, relationships among some of the clades were not resolved preventing biogeographic inference in some regions of the tree.

For the outgroup taxa *A. parvifolius* from Madagascar and *D. natalense* from South Africa are strongly support as sister taxa. *Potoxylon melagangai* and *Eusideroxylon zwageri,* both from Borneo, are also strongly support as sister taxa. The relationship between the Borneo taxa, the South American taxa and *H. zenkeri* is unresolved, supporting the findings of Rowher et al. (2016).

Clade B, the "*Beilschmiedia* Group", contains three strongly supported clades (B1, B2 and B3); the relationships among these three clades remain unresolved. The *Beilschmiedia* specimens are not supported as monophyletic and form two strongly supported clades. The first clade (B1) contains *Beilschmiedia, Sinopora, Syndiclis, Yasunia* and *Potameia*. There are three strongly supported clades of Asian *Beilschmiedia*. The Chinese species form strongly supported clades with species from different geographical regions such as South America and Australasia suggesting that the centre of diversity for *Beilschmiedia* is unresolved. The largest of these clades contains 16 Chinese species, three indeterminate Vietnamese specimens and two South American species *B. mexicana* and *B. brenesii*. The four samples of Chinese *B. yunnanensis* form a strongly supported clade, whose relationship is unresolved in relation to the other clades. *Beilschmiedia glauca* and *B. turbinata* from China form a strongly supported clade. However, the relationship of this clade with the rest of *Beilschmiedia* is also unresolved. There is also a strongly supported clade of *Sinopora hongkongensis* and *Syndiclis* (four samples) both from china, which is strongly supported as sister to *B. costaricensis* and *B. immersinervis* from Costa Rica. The nesting of *Sinopora, Yasunia* and

Potameia within *Beilschmiedia* supports the previous findings by Rowher et al. (2014).

Three South American *Beilschmiedia,* representing Brazil and Chile form a moderately supported clade with two species of *Yasunia* from Ecuador and Peru. Species from Australia, Indonesia and Papua New Guinea are distributed across this clade. This is most likely due to multiple colonisation events. The two New Zealand *Beilschmiedia* species do not form a monophyletic group, supporting Rowher et al. (2014) findings, and suggest two separate dispersal events onto New Zealand. *Beilschmiedia tarairi* is sister to Australian *B. tooram* and *B. volckii,* while the position of *B. tawa* (syn. *B. tawaroa*) remains unresolved.

For the Beilschmiedia clade (B1), it is evident that it has evolved from a series of complex biogeographic patterns. Only the Beilschmiedia species from Madagascar and Africa form a single clade. As in previous studies the biogeographic and dispersal patterns remain obscured (Liu et al. 2013; Rowher et al. 2014). The nesting of *Syndiclis* within the *Beilschmiedia* clade does not support the findings of Liu et al. (2013). In order for *Beilschmiedia* to be monophyletic, taxonomic revision of the genera *Sinopora, Syndiclis, Yasunia* and *Potameia* needs to be considered. One option would be to transfer these small genera into *Beilschmiedia*. An alternative that would retain these genera is that *Sinopora* and two South American *Beilschmiedia*, *B. costaricensis* and *B. immersinervis* are merged with *Syndiclis*, and the African *Beilschmiedia* are merged with *Potameia*. This option is useful for conservation purposes as it is easier to conserve a small genus than a large one.

The second clade (B2) is composed solely of New Caledonian *Beilschmiedia* specimens. The single clade formed by the New Caledonian *Beilschmiedia* suggests a single colonisation event and small radiation within New Caledonia. There are two *Beilschmiedia* species currently recognised in New Caledonia (Morat et al. 2012; Munzinger et al. 2016), though the phylogeny suggests that there may be at least one currently unidentified species within the clade comprised of the three unidentified samples that are sister to *B neocaledonica.* Within this clade is *B. neocaledonica*, two samples of *B. oreophila* and five indeterminate specimens. *Beilschmiedia oreophila* occurs in two separate places within the clade. The two samples of *B. oreophila* have a pairwise sequence identity of 99.2% suggesting that *B. oreophila* is genetically diverse and may need taxonomic revision as they are most likely two separate species. The relationship between the New Caledonian *Beilschmiedia* and the rest of the *Beilschmiedia* group is unresolved. The unresolved relationship of this clade suggests that *Beilschmiedia* may be absent from the New Caledonian flora and placing these samples within a new genus may be warranted.

The third clade (B3) contains *Endiandra* and *T. inaequitepala*. This clade is distinct from the *Beilschmiedia* clades with a pairwise difference of 4.5%. The New Caledonian *Endiandra* form a monophyletic clade that is sister to the rest of the *Endiandra* samples included. The single clade formed by the New Caledonian *Endiandra* suggests a single colonisation event and radiation within New Caledonia. *Endiandra sebertii* is found in two separate places within the New Caledonian clade. The two samples have a pairwise sequence identity of 94.3% suggesting that this species is genetically diverse and may need taxonomic revision as they are most likely two separate species. The second clade consists of samples of *Endiandra* from China, Australia and Papua New Guinea and one *T. inaequitepala* sample from Papua New Guinea. *Endiandra pubens* from Australia is sister to the rest of the species in this clade. The two Chinese species are sister to the weakly supported clade of Australasian *Endiandra* and Papua New Guinean *T. inaequitepala*. The dispersal patterns for these *Endiandra* species are unresolved. *Triadodaphne inaequitepala* is nested within *Endiandra* supporting the findings of Rowher et al. (2014) and suggests that *T. inaequitepala* needs to be merged with *Endiandra*. The relationship between B1, B2 and B3 are not resolved. It is possible that Endiandra is nested within B1. With more data, and a second genetic marker there is a higher chance that these relationships may be better resolved (Rowher at al. 2014)

There are two strongly supported clades within the *Cryptocarya* group supporting the findings of Rowher et al. (2014) and van der Merwe et al. (2016). Clade C1 is comprised of three New Caledonian *Cryptocarya* species, three indeterminate New Caledonian specimens and one *Cryptocarya* species from Chile. This finding is similar to the findings of Rowher et al. (2014) which suggested that *C. alba* from Chile was nested in a clade of *Cryptocarya* from New Caledonia. The two specimens of *Cryptocarya pluriscosta* form a strongly supported clade and are sister to an indeterminate New Caledonian specimen JM 5178, taxonomic work is required to ascertain whether this specimen is a new species or conspecific to *C. pluricosta*. This clade is in turn sister to Chilean *C. alba* which is sister to a clade composed of *C. aristata, C. oubatchensis* and two specimens resembling *C. aristata* from New Caledonia. Whilst this clade contains *C. alba* from Costa Rica it suggests that there was only a single colonisation event and radiation for these *Cryptocarya* in New Caledonia.

Clade C2 is large and geographically diverse with numerous subclades. There is no clear pattern of dispersal within this clade due to lack of support for the topology among the clades. New Caledonian taxa are found in six strongly supported clades, suggesting at least two colonisation events for New Caledonian *Cryptocarya* within this clade. Within one of the strongly supported subclades there are four strongly supported New Caledonian clades. This clade also includes samples from the Pacific and Asia, though the relationships between the clades are unresolved. Taxa from Fiji, Hawaii and Vanuatu form strongly supported clades. Two New Caledonian *Cryptocarya* (*C. odorata* JM4933 and *C. longifolia*) form a small strongly supported sister clade to *C. chinensis* from China and *C. densiflora* from Papua New Guinea. *Cryptocarya triplinervis* and *R. elliptica* from Madagascar are strongly support as sister taxa.

Three of the New Caledonian *Cryptocarya* species have specimens, that come out in multiple places on the tree. This suggests that these species determinations may need to be reviewed. These species are *C.*

oubatchensis (pairwise sequence identity 89.2%), *C. gullauminii* (94.1%) and *C. odorata* (97.1%). The pairwise identity values suggests that these species are genetically diverse and may need taxonomic revision. The nesting of *Ravensara* within *Cryptocarya* supports previous research by Rowher et al. (2014). It also suggests that *Ravensara* should be merged with the genus *Cryptocarya*.

For the New Caledonian *Cryptocarya* between clade C1 and C2 there is no correlation between the substrate, fruit shape or leaf venation. However, for some of the species which appear in multiple places throughout the tree, there is a difference in the substrate they are found on. van der Merwe et al. (2016) found that it was difficult to assign synapomorphies for internal clades due to the diverse morphology within the genus. A problem, which all of the genera within Cryptocaryeae, seem to share (Rohwer et al. 2000; Chanderbali et al. 2001).

The lack of regional monophyly within the *Beilschmiedia* and *Cryptocarya* groups, suggests that the species forming these groups have dispersed and radiated across the subtropical and tropical regions through complex biogeographical patterns (Liu et al. 2013; Rowher et al. 2014; van der Merwe et al. 2016).

My study is comparable with other studies on plant taxa such as *Podonephelium* (Sapindaceae), *Halfodia* (Rutaceae) and *Diospyros* (Ebanaceae) in New Caledonia. The markers used in these studies for *Halfodia* were ITS and ETS for the nrDNA markers and *rbc*L and *trn*L-*trn*F for the chloroplast markers (Bayly et al. 2016) and for *Diospyros* the whole plastid genome and nrDNA were used (Turner et al. 2016). All of the studies found that there was a lack of genetic and morphological divergence, which inhibited their ability to resolve relationships between New Caledonian clades and their geographical origin (Munzinger et al. 2013; Bayly et al. 2016; Turner et al. 2016). Munzinger et al. (2013) and Bayly et al. (2016) found that there was only a single colonisation event for *Podonephilium* and *Halfodia* into New Caledonia. Whereas the Turner et al. (2016) found that there had been multiple colonisation events for *Diospyros* into New Caledonia.

New Caledonia is a sink for Cryptocarya which is evident in the multiple colonisation events of this genus. The New Caledonian *Beilschmiedia* form a strongly supported monophyletic clade that may need to be reclassified. There is at least one putative new species in *Beilschmiedia* and at least two putative new in *Endiandra.,* and two new species in *Cryptocarya* has at least three putative new species. There is evidence to support that substrate might be important for species delimitations within New Caledonia. New Caledonia has a complex biogeographical heritage in the case of the sub-family Cryptocaryeae that is only just beginning to be understood.

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Chapter Three

Conclusions and Future Directions

New Caledonian Cryptocaryeae are a product of a complex biogeographical history. The aim of this study was to test the taxonomic delimitations of the New Caledonian Cryptocaryeae. This study tested whether the New Caledonian *Beilschmiedia*, *Cryptocarya* and *Endiandra* are monophyletic. Were they the result of one or more colonization events? This study tested if the *Cryptocarya* group forms two clades as suggested by Rowher et al. (2014) and van der Merwe et al. (2016).

This study generated 58 new complete ITS sequences, majority of which were New Caledonian specimens. This data also gave the first insight into New Caledonian Cryptocaryeae since Kostermans taxonomic revision in 1974.

New Caledonian *Beilschmiedia* and New Caledonian *Endiandra* are monophyletic (Fig 2.3). This is indicative of a single colonization event and radiation for these genera into New Caledonia. The New Caledonian *Cryptocarya* are not monophyletic and form two distinct clades. The first clade (C1) is dominated by *Cryptocarya* from New Caledonia suggesting a single colonization event and radiation. However, in the second clade (C2) *Cryptocarya* species form multiple clades, indicating multiple colonization events into New Caledonia.

The New Caledonian *Beilschmiedia* form a strongly supported clade (Fig 2.3), whose relationship to the other clades is unresolved. The phylogeny provided evidence to suggest that there is at least one putative new species of New Caledonian *Beilschmiedia* and one genetically diverse species (*B. oreophila*) that requires taxonomic revision of their current delimitations. Among New Caledonian *Endiandra* there is at least two putative new species and one genetically diverse species (*E. sebertii*) that require taxonomic revision of their current delimitations. The New Caledonian *Cryptocarya* have at least three putative new species and three genetically diverse species (*C. oubatchensis, C. guillauminii* and *C. odorata*) that require taxonomic revision of their current delimitations.

The biogeographical relationship between the New Caledonian Cryptocaryeae and the rest of the Cryptocaryeae samples included in this study are unresolved. This is because the tree in this study only samples 79 species for *Beilschmiedia*, *Cryptocarya* and *Endiandra* out of a potential 600 species. Further research needs to be conducted.

This study tested whether the New Caledonian *Beilschmiedia*, *Cryptocarya* and *Endiandra* are monophyletic and found that the New Caledonian *Beilschmiedia* and *Endiandra* are monophyletic. However, New Caledonian *Cryptocarya* are not monophyletic. New Caledonian *Beilschmiedia* and *Endiandra* are most likely the result of a single colonization event. Whereas New Caledonian *Cryptocarya* are most likely the result of multiple colonization events. This study also tested if the *Cryptocarya* group forms two clades as suggested by Rowher et al. (2014) and van der Merwe et al. (2016). This study found that there were two strongly supported *Cryptocarya* clades.

Future research needs to focus on the obtaining ITS sequences all remaining New Caledonian Cryptocaryeae species, and given the results multiple samples of each species are required to test for cryptic species. These multiple samples need to cover morphological diversity, geographic limits and substrate types. At least one chloroplast marker also needs to be used for all of the samples that have been sequenced using ITS. This is important as it will increase the likelihood of resolving the relationships between New Caledonian samples and between New Caledonia and the samples from outside of New Caledonia.

Taxonomic revision needs to be undertaken on currently indeterminate and genetically diverse samples *B. oreophila, E. sebertii, C. oubatchensis, C. guillauminii* and *C. odorata*. The taxonomic revisions need to include morphology, geographic location and substrate type. This is important as some of these species may be in need of conservation.

Appendix

Table 3.1: Appendix containing the sample name, authority, genebank number, herbarium number, country, station where available and author of the study the sample was originally used in. All samples used in the phylogenetic analyses are in this table.

Name	Authority	Collector Number	Genebank Number	Herbarium Number	Country	Station	Author(s)
Aspidostemon parvifolius	(Scott-Elliott) van der Werff	Lowry 5024	HG315527.1		Madagascar		Rowher et al. (2014)
Beilschmiedia appendiculata	(Allen) S.K.Lee & Y.T.Wei	B. Liu 1504	KC958643.1		China		Liu et al. (2013)
Beilschmiedia brenesii	C.K.Allen	Yasuda 1314	HG315531.1		Costa Rica		Rohwer et al. (2014)
Beilschmiedia cf. rigida	Nees	Moraes 3207	HG315542.1		Brazil		Rohwer et al. (2014)
Beilschmiedia costaricensis	(Mez & Pittier) C.K.Allen	Yasuda 1309	HG315532.1		Costa Rica		Rohwer et al. (2014)
Beilschmiedia delicata	S.K.Lee & Y.T.Wei	B. Liu 1451	KC958642.1		China		Liu et al. (2013)
Beilschmiedia delicata	S.K.Lee & Y.T.Wei	F. Q. Liu s.n.	KC958641.1		China		Liu et al. (2013)
Beilschmiedia dictyoneura	Kosterm.	Ambri W698	HG315533.1		Indonesia		Rohwer et al. (2014)
Beilschmiedia emarginata	(Meisn.) Kosterm.	Moraes s.n	HG315534.1		Brazil		Rohwer et al. (2014)

Name	Authority	Collector Number	Genebank Number	Herbarium Number	Country	Station	Author(s)
Beilschmiedia fordii	Dunn	B. Liu 1080	KC958625.1		China		Liu et al. (2013)
Beilschmiedia glauca var. glaucoides	H.W.Li	B. Liu 1323	KC958638.1		China		Liu et al. (2013)
Beilschmiedia immersinervis	Nishida	Yasuda 1312	HG315535.1		Costa Rica		Rohwer et al. (2014)
Beilschmiedia intermedia	C.K.Allen	SCBGP154_1	KP092850.1		China		Liu et al. (2015)
Beilschmiedia intermedia	C.K.Allen	SCBGP154_2	KP092851.1		China		Liu et al. (2015)
Beilschmiedia kweichowensis	C.Y.Cheng	B. Liu 1419	KC958631.1		China		Liu et al. (2013)
Beilschmiedia laevis	C.K.Allen	B. Liu 1270	KC958626.1		China		Liu et al. (2013)
Beilschmiedia linocieroides	H.W.Li	B. Liu 1479	KC958627.1		China		Liu et al. (2013)
Beilschmiedia madagascariensis	(Danguy) Kosterm.	Lowry 5015	HG315536.1		Madagascar		Rohwer et al. (2014)
Beilschmiedia mexicana	(Mez) Kosterm.	Reyna 1404	HG315537.1		Mexico		Rohwer et al. (2014)
Beilschmiedia miersii	(Gay) Kosterm.	Greissl 657-99	HG315538.1		Chile		Rohwer et al. (2014)
Beilschmiedia neocaledonica	Kosterm.	McPherson 19086	HG315539.1	MO-398091	New Caledonia	Mt. Colnett, forested eastern slopes	Rohwer et al. (2014)
Beilschmiedia oreophila	Schltr.	Dagostini 1444		NOU031117	New Caledonia	Réseve botanique de la Fausse Yaté, 300-500m	This study

Name	Authority	Collector Number	Genebank Number	Herbarium Number	Country	Station	Author(s)
Beilschmiedia oreophila	Schltr.	Munzinger 2474		NOU006101	New Caledonia	Haute Ni	This study
Beilschmiedia percoriacea	C.K.Allen	B. Liu 1254	KC958628.1		China		Liu et al. (2013)
Beilschmiedia pierreana	Robyns & R.Wilczek	SIMAB 12418	HG315540.1		Cameroon		Rohwer et al. (2014)
Beilschmiedia purpurascens	H.W.Li	B. Liu 1321	KC958629.1		China		Liu et al. (2013)
Beilschmiedia purpurascens	H.W.Li	B. Liu 1443	KC958630.1		China		Liu et al. (2013)
Beilschmiedia recurva	B.Hyland	van der Werff 17047	HG315541.1		Australia		Rohwer et al. (2014)
Beilschmiedia robusta	C.K.Allen	B. Liu 1466	KC958632.1		China		Liu et al. (2013)
Beilschmiedia robusta	C.K.Allen	B. Liu 1481	KC958633.1		China		Liu et al. (2013)
Beilschmiedia robusta	C.K.Allen	Wang Z.-H. 08063	GU082363.1		China		Wang et al. (2010)
Beilschmiedia robusta	C.K.Allen	B. Liu 1428	KC958634.1		China		Liu et al. (2013)
Beilschmiedia roxburghiana	Nees	Gerlach s.n	HG315543.1		China		Rohwer et al. (2014)
Beilschmiedia rufohirtella	H.W.Li	B. Liu 1430	KC958637.1		China		KC958637.1
Beilschmiedia rufohirtella	H.W.Li	B. Liu 1493	KC958636.1		China		Liu et al. (2013)

Name	Authority	Collector Number	Genebank Number	Herbarium Number	Country	Station	Author(s)
Beilschmiedia tarairi	(A.Cunn.) Kirk	Sykes 437511	HG315548.1		New Zealand		Rohwer et al. (2014)
Beilschmiedia tarairi	(A.Cunn.) Kirk	McIntosh s.n.		WAIK 20693	New Zealand		This study
Beilschmiedia tarairi	(A.Cunn.) Kirk	Sykes 529799 A	HG315549.1		New Zealand		Rohwer et al. (2014)
Beilschmiedia tawa	(A.Cunn.) Kirk	Dawson s.n.	HG315550.1	CHR 565486A	New Zealand		Rohwer et al. (2014)
Beilschmiedia tawaroa	A.E.Wright	Beever 89046	HG315551.1	CHR 450080	New Zealand		Rohwer et al. (2014)
Beilschmiedia tooram	(Bailey) B.Hyland	van der Werff 17051	HG315552.1		Australia		Rohwer et al. (2014)
Beilschmiedia tsangii	Merr.	SCBGP355_1	KP092852.1		China		Liu et al. (2015)
Beilschmiedia turbinata	Bing Liu & Y. Yang	B. Liu 1185	KC958640.1		China		Liu et al. (2013)
Beilschmiedia turbinata	Bing Liu & Y. Yang	B. Liu 1442	KC958639.1		China		Liu et al. (2013)
Beilschmiedia velutina	(Koterm.) Kosterm.	Razafimandimbison 361	HG315553.1		Madagascar		Rohwer et al. (2014)
Beilschmiedia volckii	B.Hyland	van der Werff 17052	HG315554.1		Australia		Rohwer et al. (2014)
Beilschmiedia yunnanensi	Hu	B. Liu 1439	KC958646.1		China		Liu et al. (2013)
Beilschmiedia yunnanensis	Hu	B. Liu 1473	KC958644.1		China		Liu et al. (2013)

Name	Authority	Collector Number	Genebank Number	Herbarium Number	Country	Station	Author(s)
Beilschmiedia yunnanensis	Hu	B. Liu 1474	KC958647.1		China		Liu et al. (2013)
Beilschmiedia yunnanensis	Hu	B. Liu 1484	KC958645.1		China		Liu et al. (2013)
Beilschmieda sp.	Nees	Munzinger 7246		MPU026698	New Caledonia	Aoupinié	This study
Beilschmieda sp.	Nees	van der Werff 14189	HG315545.1		Vietnam		Rohwer et al. (2014)
Beilschmieda sp.	Nees	van der Werff 14272	HG315546.1		Vietnam		Rohwer et al. (2014)
Beilschmieda sp.	Nees	van der Werff 17396	HG315547.1		Vietnam		Rohwer et al. (2014)
Beilschmiedia sp.	Nees	Breteler 5283	HG315544.1		Ivory Coast		Rohwer et al. (2014)
Beilschmiedia sp.	Nees	Munzinger 5762		NOU051318	New Caledonia	Pont des Japonais	This study
Beilschmiedia sp.	Nees	Munzinger 5816		NOU051773	New Caledonia	Mandjélia juste sous l'antenne	This study
Beilschmiedia sp.	Nees	Munzinger 5878			New Caledonia	Tchamba	This study
Beilschmiedia sp. (Munzinger 6408)	Nees	Munzinger 6097		NOU063275	New Caledonia	Roches de la Ouaième, Panié.	This study
Cryptocarya adpressa	Munzinger & McPherson	Munzinger 4849		NOU030688	New Caledonia	Plateau de Dogny, entrée de la forêt vers la cascade	This study

Name	Authority	Collector Number	Genebank Number	Herbarium Number	Country	Station	Author(s)
Cryptocarya alba	(Molina) Looser	Gerlach 95-1146	HG315555.1		Chile		Rohwer et al. (2014)
Cryptocarya angulata	C.T.White	van der Werff 17056	HG315556.1		Australia		Rohwer et al. (2014)
Cryptocarya aristata	Kosterm.	Munzinger 5866		NOU051584	New Caledonia	Tchamba	This study
Cryptocarya aristata	Kosterm.	Munzinger 7668			New Caledonia	Bwa Bwi, contrefort sud-est	This study
Cryptocarya aschersoniana	Mez	Brotto 648	KF421007.1		Brazil		Bolson et al. (2015)
Cryptocarya aschersoniana	Mez	Brotto 649	KF421006.1		Brazil		Bolson et al. (2015)
Cryptocarya barrabeae	Munzinger & McPherson	Munzinger 5841		NOU053514	New Caledonia	Mandjélia juste sous l'antenne	This study
Cryptocarya barrabeae	Munzinger & McPherson	Munzinger 5854		NOU051356	New Caledonia	Ponandou	This study
Cryptocarya bidwillii	Meisn.	Grimshaw 2406	HG315559.1		Australia		Rohwer et al. (2014)
Cryptocarya botelhensis	P.L.R.Moraes	Moraes 2311	HG315560.1		Brazil		Rohwer et al. (2014)
Cryptocarya botelhensis	P.L.R.Moraes	Moraes 3349	HG315561.1		Brazil		Rohwer et al. (2014)
Cryptocarya calcicola	H.W.Li	B. Liu 1457	KC958656.1		China		Liu et al. (2013)
Cryptocarya chinensis	(Hance) Hemsl.	SCBGP211_2	KP092860.1		China		Liu et al. (2015)

Name	Authority	Collector Number	Genebank Number	Herbarium Number	Country	Station	Author(s)
Cryptocarya chingii	W.C.Cheng	SCBGP280_1	KP092861.1		China		Liu et al. (2015)
Cryptocarya chingii	W.C.Cheng	SCBGP280_2	KP092862.1		China		Liu et al. (2015)
Cryptocarya chrysea	Munzinger & McPherson	Munzinger 7657			New Caledonia	Bwa Bwi, contrefort sud-est, entre MAL3 et MAL4	This study
Cryptocarya citriformis	(Vell.) P.L.R.Moraes	Moraes 3199	HG315562.1		Brazil		Rohwer et al. (2014)
Cryptocarya concinna	Hance	Lauerer 70518	HG315564.1		China		Rohwer et al. (2014)
Cryptocarya concinna	Hance	SCBGP074_1	KP092863.1		China		Liu et al. (2015)
Cryptocarya concinna	Hance	SCBGP074_2	KP092864.1		China		Liu et al. (2015)
Cryptocarya constricta		Munzinger 7367			Fiji	Vanua Levu, Cakaudrove Province, Wailevu-West district, 5 km before Wailevu West district school, along Wailevu West road	This study
Cryptocarya densiflora	Blume	Munzinger 6975			Papua New Guinea	Oro Mungo, Plot 700A	This study
Cryptocarya elliptica	Schltr.	Munzinger 5852		NOU051479	New Caledonia	Ponandou, parcelle 1	This study
Cryptocarya elliptica	Schltr.	Munzinger 5870		NOU051484	New Caledonia	Tchamba	This study
Cryptocarya gracilis	Schltr.	McPherson 19129	HG315566.1	NOU004362	New Caledonia	Mont colnett	Rohwer et al. (2014)

Name	Authority	Collector Number	Genebank Number	Herbarium Number	Country	Station	Author(s)
Cryptocarya gracilis	Schltr.	Munzinger 5808		NOU051768	New Caledonia	Mandjélia juste sous l'antenne	This study
Cryptocarya guillauminii	Kosterm.	McPherson 18027	HG315567.1	NOU011281	New Caledonia	Massif de tchingou (850 m)	Rohwer et al. (2014)
Cryptocarya guillauminii	Kosterm.	Munzinger 7630			New Caledonia	Bwa Bwi, contrefort sud-est, autour du camp de base	This study
Cryptocarya leptospermoides	Kosterm.	Munzinger 7285		MPU028453	New Caledonia	Tiébaghi, près de l'ancien village	This study
Cryptocarya lifuensis	Guillaumin	Munzinger 6064		NOU054314	New Caledonia	Ile des Pins, camping Baie des Rouleaux	This study
Cryptocarya lifuensis	Guillaumin	Munzinger 6725		P00806960	New Caledonia	Koumac, sentier de la vierge, creek grande forêt	This study
Cryptocarya longifolia	Kosterm.	Munzinger 5754		P02033437; NOU051032	New Caledonia	Art, plateau Nord	This study
Cryptocarya longifolia	Kosterm.	Munzinger 5837		NOU051492; P01962732	New Caledonia	Mandjélia juste sous l'antenne	This study
Cryptocarya longifolia	Kosterm.	Munzinger 7215		MPU028463	New Caledonia	Aoupinié, Parcelle Pierric 2	This study
Cryptocarya longifolia	Kosterm.	Munzinger 7283		MPU028462	New Caledonia	Tiébaghi, près de l'ancien village	This study
Cryptocarya mandioccana	Meisn.	Moraes 1245	HG315570.1		Brazil		Rohwer et al. (2014)
Cryptocarya mandioccana	Meisn.	Moraes 31	HG315568.1		Brazil		Rohwer et al. (2014)
Cryptocarya mandioccana	Meisn.	Moraes 509	HG315569.1		Brazil		Rohwer et al. (2014)

Name	Authority	Collector Number	Genebank Number	Herbarium Number	Country	Station	Author(s)
Cryptocarya mannii	Hillebr.	Tangalin 2915	HG315571.1		Hawaii		Rohwer et al. (2014)
Cryptocarya mannii	Hillebr.	Tangalin 2916	HG315572.1		Hawaii		Rohwer et al. (2014)
Cryptocarya mannii	Hillebr.	Tangalin 2918	HG315573.1		Hawaii		Rohwer et al. (2014)
Cryptocarya mannii	Hillebr.	Tangalin 2974	HG315574.1		Hawaii		Rohwer et al. (2014)
Cryptocarya mannii	Hillebr.	Tangalin 3104	HG315575.1		Hawaii		Rohwer et al. (2014)
Cryptocarya mannii	Hillebr.	Tangalin 3274	HG315576.1		Hawaii		Rohwer et al. (2014)
Cryptocarya mannii	Hillebr.	van Balgooy 4206	HG315577.1		Hawaii		Rohwer et al. (2014)
Cryptocarya metcalfiana	C.K.Allen	Wang Z.-H. 08067	GU082367.1		China		Wang et al. (2010)
Cryptocarya moschata	Nees & Mart.	Moraes 2355	HG315578.1		Brazil		Rohwer et al. (2014)
Cryptocarya moschata	Nees & Mart.	Moraes 2551	HG315579.1		Brazil		Rohwer et al. (2014)
Cryptocarya oahuensis	(O.Deg.) Fosberg		HG315580.1	Hawaiian Plant DNA Library 6891	Hawaii		Rohwer et al. (2014)
Cryptocarya odorata	Guillaumin	Munzinger 4933		NOU030780	New Caledonia	Tontouta, vallée de la Ouano	This study

Name	Authority	Collector Number	Genebank Number	Herbarium Number	Country	Station	Author(s)
Cryptocarya odorata	Guillaumin	Munzinger 5159		MPU310774; NOU049137; P01952883; P01952882	New Caledonia	Goapin, bord de route	This study
Cryptocarya oubatchensis	Schltr.	McPherson 19131	HG315581.1	MO-398160	New Caledonia	Mt. Colnett, forested eastern slopes	Rohwer et al. (2014)
Cryptocarya oubatchensis	Schltr.	Munzinger 7078		P00806970; MPU026704	New Caledonia	Tchingou, face Est par l'ancienne piste minière	This study
Cryptocarya phyllostemon	Kosterm.	Barrabé 409		NOU016040	New Caledonia	Forêt de Bon Secours	This study
Cryptocarya phyllostemon	Kosterm.	Munzinger 7730			New Caledonia	Bwa Bwi, contrefort sud-est, cuvette sous le camp	This study
Cryptocarya pluricostata	Kosterm.	McPherson 18471	HG315582.1	NOU008157	New Caledonia	Amoa (120 m)	Rohwer et al. (2014)
Cryptocarya pluricostata	Kosterm.	Munzinger 7780			New Caledonia	Auberge des Koghis, juste à l'entrée de la forêt	This study
Cryptocarya saligna	Mez	Moraes 3182	HG315583.1		Brazil		Rohwer et al. (2014)
Cryptocarya saligna	Mez	Moraes 3226	HG315584.1		Brazil		Rohwer et al. (2014)
Cryptocarya subtriplinervia	(Kosterm.) van der Werff	van der Werff 12775	HG315585.1		Madagascar		Rohwer et al. (2014)
Cryptocarya tannaensis	Guillaumin	Munzinger 7504			Vanuatu	Vanuatu; Tanna; Near Green Hill, Iboa Gmen Village, Nesu Netu conservation area, near Transect 1	This study

Name	Authority	Collector Number	Genebank Number	Herbarium Number	Country	Station	Author(s)
Cryptocarya tannaensis	Guillaumin	Munzinger 7506			Vanuatu	Vanuatu; Tanna; Near Green Hill, Iboa Gmen Village, Nesu Netu conservation area, near Transect 1	This study
Cryptocarya tranversa	Kosterm.	Munzinger 7079		MPU026703	New Caledonia	Tchingou, face Est par l'ancienne piste minière	This study
Cryptocarya triplinervis	R.Br.	Chase 5522	HG315586.1		Australia		Rohwer et al. (2014)
Cryptocarya turbinata	Gillespie	Munzinger 6502		P00871519	Fiji	Naibili road from Somo-Somo to project hudrolic dawm	This study
Cryptocarya turbinata	Gillespie	Munzinger 7359		MPU115001	Fiji	Vanua Levu, Cakaudrove Province, Wailevu District, Waisali Rainforest Reserve, along the touristic trail	This study
Cryptocarya velutinosa	Kosterm.	Munzinger 5868		P06173124; NOU051585	New Caledonia	Tchamba	This study
Cryptocarya wiedensis	P.L.R.Moraes	Moraes 2623	HG315587.1		Brazil		Rohwer et al. (2014)
Cryptocarya "aff. aristata" (Munzinger 5874)	R.Br.	Munzinger 5882		P00806963	New Caledonia	Tchamba	This study
Cryptocarya aff. aschersoniana	R.Br.	Moraes 2620	HG315557.1		Brazil		Rohwer et al. (2014)
Cryptocarya aff. aschersoniana	R.Br.	Moraes 2620a	HG315558.1		Brazil		Rohwer et al. (2014)

Name	Authority	Collector Number	Genebank Number	Herbarium Number	Country	Station	Author(s)
Cryptocarya sp.	R.Br.	Lowry 7345		MO_PPL7345	Fiji	Vanua Levu, Macuata Prov., Dreketi Dist.	This study
Cryptocarya sp.	R.Br.	Munzinger 5722		P01962724; NOU051030	New Caledonia	Art, plateau Nord, entre l'aéroport et Té Waala	This study
Cryptocarya sp.	R.Br.	Munzinger 5752		NOU051035; P02033438	New Caledonia	Art, plateau Nord	This study
Cryptocarya sp.	R.Br.	Munzinger 6510		P00848716	Fiji	Viti Levu, Nadroga Navosa Province, Nadrau district, along the road between Naqelewai and Monasavu	This study
Cryptocarya sp. "aff. aristata" (Munzinger 5874)	R.Br.	Munzinger 6534		NOU063676; P00819221; P06801580	New Caledonia	Tchamba	This study
Cryptocarya sp. (McPherson 4408)	R.Br.	Munzinger 7784			New Caledonia	Auberge des Koghis, juste à l'entrée de la forêt	This study
Cryptocarya sp. (Munzinger 5178)	R.Br.	Munzinger 5178		NOU049142	New Caledonia	Aoupinié	This study
Cryptocarya sp. aff. gracilis (Brinon 1104)	R.Br.	Grignon 323		NOU050629	New Caledonia	Thy 420 m	This study
Dahlgrenodendron natalense	(Ross) van der Merwe & van Wyk	Styles 2313	HG315588.1		South Africa		Rohwer et al. (2014)

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Endiandra baillonii	(Pancher & Sebert) Guillaumin	Munzinger 5987			New Caledonia	Kuébini, près de l'ancien pont	This study
Endiandra coriacea	Merr.	J. F. Ye s.n.	KC958655.1		China		Liu et al. (2013)
Endiandra dolichocarpa	S.K.Lee & Y.T.Wei	B. Liu 1381	KC958653.1		China		Liu et al. (2013)
Endiandra dolichocarpa	S.K.Lee & Y.T.Wei	B. Liu 1480	KC958654.1		China		Liu et al. (2013)
Endiandra glauca	R.Br.	Clarkson 9240	HG315589.1		Australia		Rohwer et al. (2014)
Endiandra impressicosta	C.K.Allen	Gray 7539	HG315590.1		Papua New Guinea		Rohwer et al. (2014)
Endiandra lecardii	Guillaumin	McPherson 19147	HG315591.1		New Caledonia	Mont colnett	Rohwer et al. (2014)
Endiandra lecardii	Guillaumin	McPherson 19147	HG315591.1	MO-398131; NOU004336	New Caledonia	Mont colnett	Rohwer et al. (2014)
Endiandra poueboensis	Guillaumin	McPherson 18988	HG315592.1	MO-398124; NOU004310	New Caledonia	Mont colnett	Rohwer et al. (2014)
Endiandra pubens	Meisn.	Constable 4876	HG315593.1		Australia		Rohwer et al. (2014)
Endiandra sebertii	Guillaumin	Munzinger 5825		NOU051789	New Caledonia	Mandjélia juste sous l'antenne	This study
Endiandra sebertii	Guillaumin	Munzinger 7125			New Caledonia	Col de Yaté, juste sous le col, côté ouest	This study

Name	Authority	Collector Number	Genebank Number	Herbarium Number	Country	Station	Author(s)
Endiandra euadenia	Kosterm.	Munzinger 6985			Papua New Guinea		
Endiandra sp.	R.Br.	Munzinger 7082			New Caledonia	Tchingou, face Est par l'ancienne piste minière	This study
Endiandra sp.	R.Br.	Munzinger 7652			New Caledonia	Bwa Bwi, contrefort sud-est, COM-MAL-3	This study
Endiandra sp. "Mandjélia" (JM5839)		Munzinger 5833		NOU051480	New Caledonia	Mandjéia juste sous l'antenne	This study
Endiandra sp. Humboldt [McP3119-JM5719]	(Pancher & Sebert) Guillaumin	Munzinger 5719		NOU051038	New Caledonia	Humboldt	This study
Eusideroxylon zwageri	Teijsmann & Binnendijk	Gwee 2004-42	HG315595.1		Borneo		Rohwer et al. (2014)
Hypodaphnis zenkeri	(Engler) Stapf	McPherson 16184	HG315596.1		Gabon		Rohwer et al. (2014)
Potameia thouarsiana	(Baill.) Capuron	S.F. 14156	HG315598.1		Madagascar		Rohwer et al. (2014)
Potoxylon melagangai	(Symington) Kosterm.	Wong 325	HG315599.1		Borneo		Rohwer et al. (2014)

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Ravensara elliptica	Kosterm.	Capuron 28409	HG315600.1		Madagascar		Rohwer et al. (2014)
Sinopora hongkongensis	(Xia, Deng &Yip) Li, Xia & Li	Xia s.n	HG315601.1		China		Rohwer et al. (2014)
Syndiclis marlipoensis	H. W. Li	B. Liu 1282	KC958649.1		China		Liu et al. (2013)
Syndiclis marlipoensis	H. W. Li	B. Liu 1420	KC958650.1		China		Liu et al. (2013)
Syndiclis sp.	Hook.f.	B. Liu 1472	KC958651.1		China		Liu et al. (2013)
Syndiclis sp.	Hook.f.	B. Liu 1486	KC958652.1		China		Liu et al. (2013)
Triadodaphne inaequitepala	Kosterm.	Pullen 5505	HG315602.1		Papua New Guinea		Rohwer et al. (2014)
Yasunia quadrata	van der Werff & Nishida	Graham 2369	HG315603.1		Peru		Rohwer et al. (2014)
Yasunia sessiliflora	van der Werff & Nishida	Perez 4222	HG315604.1		Ecuador		Rohwer et al. (2014)