CONTRIBUTIONS TO THE CENOZOIC MACROFOSSIL RECORD OF THE MYRTACEAE IN SOUTH EASTERN AUSTRALIA

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Dedicated to my mum,
***Jennifer Lois Tarran** (12.7.1956 – 27.9.2017),*
Who just wanted me to hurry up and finish my thesis.

"There's a crack in everything,
that's how the light gets in."

TABLE OF CONTENTS

GENERAL INTRODUCTION

LITERATURE REVIEW

A CRITICAL REVIEW OF THE CENOZOIC VEGETATIVE AND REPRODUCTIVE MACROFOSSIL RECORD OF THE MYRTACEAE: A VIEW FROM THE SOUTHERN HEMISPHERE

OLDEST RECORD OF *METROSIDEROS* (MYRTACEAE): FOSSIL FLOWERS, FRUITS AND LEAVES FROM AUSTRALIA

TWO FOSSIL SPECIES OF *METROSIDEROS* (MYRTACEAE) FROM THE OLIGO-MIOCENE GOLDEN FLEECE LOCALITY IN TASMANIA, AUSTRALIA

IDENTIFYING FOSSIL MYRTACEAE LEAVES: THE FIRST DESCRIBED FOSSILS OF *SYZYGIUM* FROM AUSTRALIA.

GENERAL DISCUSSION AND CONCLUSIONS

LIST OF FIGURES

CHAPTER 3

CHAPTER 4

CHAPTER 5

LIST OF TABLES

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

Thesis Abstract

The Myrtaceae are a large and diverse Angiosperm family, containing iconic groups of plants such as the Eucalypts, Lily Pillys, Melaleucas, Ti-Trees, Guavas, Feijoas and Bottlebrushes. The Myrtaceae are a key family in the vegetation of the Southern Hemisphere, and in Australia are often a dominant component of virtually all terrestrial ecosystems, from rainforest to sclerophyll heath. Despite the importance of the family, their macrofossil record is historically poorly studied. In this thesis, the macrofossil record of the Myrtaceae is reviewed, and it is found that the majority of published records of Myrtaceae fossils are poorly identified or equivocal. In the subsequent chapters, macrofossils of myrtaceous affinity from several Cenozoic sites in South Eastern Australia are identified, taking advantage of recent advances in molecular phylogenetic studies of the family, as well as recent fundamental botanical work, to identify fossils in a rigorous phylogenetic framework. Fossils of the capsular-fruited genus *Metrosideros,* one of the most widely distributed woody, flowering plant genera in the Pacific, are described in Chapters 3 and 4 from Eocene to Oligo-Miocene deposits in Tasmania, including Hasties, Little Rapid River, and the newly discovered Golden Fleece locality. These fossils provide the first evidence of this capsular-fruited genus in Australia, and demonstrate that its absence from the continent is the result of extinction, rather than failure of dispersal. In Chapter 5, fossil leaves of the fleshy-fruited genus *Syzygium* are described from Miocene sediments of Kiandra, New South Wales, which may provide the first confident identification of non-Eucalypt fossil Myrtaceae leaves using cuticle micromorphological characters. The fossils described in this thesis are among the best described Myrtaceae macrofossils from anywhere in the world, and pose significant advances in the understanding of the fossil record of these key genera within the family, as well a providing a framework upon which the identification of future Myrtaceae macrofossils might be based.

Thesis declaration

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint-award of this degree.

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My paternal family, my Dad Marko, my Pappou, Alex, and my late grandmother Norma, always encouraged my love for learning and for science, and helped to kindle for me what has become an inexhaustible love affair with the natural world. My most sincere thanks go to my Pappou, who has financially supported me throughout the entirety of my schooling and university life. Many of the opportunities I have taken would not have been possible without this help and encouragement, and for this they have my love and gratitude.

My mum, Jenny, got very sick throughout the course of my PhD, but was surrounded by love and no shortage of people who cared for her. In particular her sister Ruth who would drop everything at a moment's notice when things got hard, and her dear friends Sally, Tony, Dianne and Shane, who looked after Mum as things got harder. When she died, these friends, as well as the extended Tarran family were all right there to help. I would not have been able to continue my PhD if it was not for these people, and they have my love and admiration.

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Chapter 1:

General Introduction

On the fossil record and biogeography of the Myrtaceae

"Among the various families that are represented in numerous fossil floras, none has excited greater interest among students of recent floras and geographical distribution than the family Myrtaceae." - E. W. Berry, 1915

The Myrtaceae are the eighth largest flowering plant family in the world, comprising approximately 5,900 species in 145 genera, with a predominantly Southern Hemisphere distribution (Grattapaglia et al., 2012; The Plant List, 2013). The family has traditionally been divided into subfamilies along the lines of fruit type, the dry or capsular fruited Leptospermoideae and the fleshy-fruited Myrtoideae (Briggs and Johnson, 1979), though it is now known that these are not natural groupings. The family is most recently understood to comprise 17 tribes in two subfamilies, the Psiloxyloideae and Myrtoideae. The Psiloxyloideae is comprised of two monotypic tribes, Heteropyxideae and Psiloxyleae, which are restricted to South Eastern Africa and the Islands of Mauritius and Réunion respectively, and are basal to the core Myrtoideae, which comprises the remaining 15 tribes, now understood to contain both fleshy and dry-fruited genera (Wilson, 2011).

Approximately half of the species in the family occur in the speciose, fleshy-fruited tribes Syzygieae (with centres of diversity in Australia and Tropical Asia), and Myrteae (with its centre of diversity in South America). Genera of these fleshy-fruited tribes are typically broadleaved, grow in rainforests, and have edible fruits with seeds dispersed by animals. The evolution of fleshy fruits and animal dispersal has lead to a wide geographic distribution and rapid diversification and speciation within both of these large tribes (Biffin et al., 2010). The remaining half of the species occur in the predominantly capsular-fruited tribes, the most diverse of which are the Melaleuceae, Chamelaucieae, Leptospermeae and Eucalypteae, and have their centre of diversity in Australia. These tribes, particularly the Eucalypteae, have come to dominate Australian fire-dependant habitats (Crisp et al., 2011), and the majority of species are either adapted to survive or re-seed after fire, and in the case of many eucalypts, actively promote fire (Hill et al., 2017). Only one tribe within the Myrtoideae does not have representatives occurring naturally in Australia, the capsular-fruited Metrosidereae which, due to highly vagile seeds, has representatives throughout the Pacific, in South America, Africa, New Zealand, New Guinea, Hawaii, and many other Pacific Islands, and its absence from the Australian continent has been considered a biogeographic puzzle in the Myrtaceae (Basinger et al., 2007).

Even more than a century ago, before a phylogenetic understanding of the family was possible, and before the general acceptance of plate tectonics and continental drift, writers like Andrews (1913) and Berry (1915), understood that the evolution and biogeographic distribution of extant Myrtaceae required special explanation. Andrews (1913) believed that the fossil record suggested an origin of the family somewhere in the tropics during the Cretaceous, which then dispersed throughout the world achieving a more of less cosmopolitan distribution during equable climates of the Tertiary. He also considered that fleshy fruits were the ancestral condition for the family, and that dry/capsular fruits evolved from these forms in response to the development of arid conditions in Australia toward the close of the Tertiary. Berry (1915) considered that the fossil record and modern distribution of the family supported a North American origin, and a cosmopolitan Tertiary distribution. Berry reported that about 150 fossil records of Myrtaceae (mostly of leaves) had already been found by 1915, and that nearly half of these were from the Cretaceous, with most of these occurring in the Northern Hemisphere. A third of these fossils were of *Eucalyptus,* and these were also largely reported from the Northern Hemisphere.

A century on, in the light of the scientific revolutions in molecular phylogenetics and the theories of continental drift and plate tectonics, we know that nearly the opposite of all of this is true. The Myrtaceae likely had a Gondwanic origin (Thornhill et al., 2015), and the ancestral forms of Myrtaceae were dry-fruited, with fleshy-fruited forms arising from dry-fruited ancestors not once, but convergently evolving multiple times in separate capsular-fruited tribes (Biffin et al., 2010; Wilson 2011). Fossil records of *Eucalyptus* from the Northern Hemisphere have been repeatedly reinvestigated, and repeatedly refuted

(Deane, 1900; Rozefelds, 1996; Hill et al., 2017), and the fossil record of more than 150 described fossil forms of Myrtaceae reported by Berry (1915), most of which were historically placed in living genera based on leaf impressions, are of dubious value when submitted to modern scrutiny. In more recent history, the fossil record was considered to be “meagre and unpromising” by Briggs and Johnson (1979), and described little better more three decades later as “relatively scanty” by Wilson (2011).

A number of factors have contributed to the paucity of good fossil evidence for the evolution and paleobiogeography of the Myrtaceae. As will be illustrated in the following literature review [Chapter 2], a large number of myrtaceous fossils have been reported in the paleobotanical literature over the last century from Tertiary deposits throughout the world. Fossils have often been placed in extant genera, but little confidence in many of these identifications is justifiable under close scrutiny. Most of the Myrtaceae macrofossils that have been reported in the literature are fossil leaves, with comparatively few fossil reproductive structures having been reported. The majority of the fossil leaves in the published literature are impression or compression material, and as such identification is based upon gross leaf architecture. Little evidence has been demonstrated to date that secure phylogenetic placement is possible in many cases on the basis of leaf architectural characters alone, even identifications to family level in many cases are doubtful. Adding to the difficulty of identifying myrtaceous fossil remains, comparative work of fossils with extant taxa made more challenging by the very large size of the family when compared with other angiosperm families with well worked macrofossil records, such as the Nothofagaceae, Proteaceae and Casuarinaceae (Hill, 1994). This difficulty has been compounded by the fact that for most of the history of fossil Myrtaceae identification, relationships within this large and speciose family have been poorly understood.

The advent of phylogenetic analysis revolutionised our understanding of relationships within the Myrtaceae, with the first phylogenies produced by Briggs and Johnson (1979), and Johnson and Briggs (1984) serving as the first comprehensive phylogenetic treatment of the family, and were constructed with meticulously collected and scored morphological characters. Then the advent of molecular phylogenetic techniques revolutionised our understanding once more, taking into account both morphological characters as well as the wealth of characters made available with molecular data, and the family wide molecular phylogenies produced by Wilson et al. (2001; 2005) for the first time provided a robust, relatively stable set of phylogenetic relationships for the family, and have solidified our understanding of the taxonomy and relationships among the major groups. The taxonomy of the family is by no means fully resolved; revisions still frequently occur and there is a great deal of diversity still to be described, but the basic contours of the taxonomy and systematics of the family are, for the first time, well understood (Wilson, 2011). As molecular data becomes cheaper and easier to produce, and phylogenetic analyses have become increasingly sophisticated, even greater resolution of the infrafamilial relationships has become possible, and robust phylogenies and molecular studies have been produced for many of the key groups and genera in the family (Grattapaglia et al., 2012).

Even working with fragmentary reproductive or vegetative macrofossils, with a limited range of morphological characters, the now relatively stable and confident taxonomy and phylogeny of the family means that it is possible to test the phylogenetic value of a limited number of characters against robust understandings of the relationships within the family. In this light, the work of identifying Myrtaceae macrofossils can take place with fresh confidence not possible to earlier researchers and systematic research into the macrofossil record of the Myrtaceae can begin in earnest.

Thesis Overview

In this thesis I review the vegetative and reproductive macrofossil record of the Myrtaceae, and then identify several fossil species of Myrtaceae from organically preserved fruits, flowers and leaves found from several Cenozoic deposits in South Eastern Australia. I take advantage of the now well understood phylogenetic relationships within the Myrtaceae, and take advantage of fundamental botanical work with the family which has been published over the last few decades, allowing me to make identifications of macrofossils at much higher taxonomic resolution and with a much greater degree of confidence in fossil identifications than has generally been possible previously for paleobotanical work on fossil Myrtaceae.

CHAPTER 2 – (Literature Review) – A critical review of the Cenozoic vegetative and reproductive macrofossil record of the Myrtaceae.

This chapter reviews the literature reporting Cenozoic reproductive and vegetative macrofossil records of the Myrtaceae in the last century, providing a background and understanding of the field. It is apparent that much of the published myrtaceous macrofossil record can be regarded as equivocal. Only a handful of Myrtaceae macrofossils have ever been identified confidently to living genera, and of these, very few have been fossil leaves. This review contextualises the fossil identifications carried out in chapters 3, 4 and 5 of this thesis, and hopefully serves as a useful consolidation of the currently understood state of the macrofossil record of the family.

CHAPTER 3 – Oldest record of *Metrosideros* (Myrtaceae): Fossil flowers, fruits, and leaves from Australia.

The capsular-fruited Metrosidereae are one of the most widely dispersed groups of woody flowering plants throughout the Pacific region, with representatives in Africa, South America, New Zealand, Hawaii and numerous other Pacific Islands. It is the only tribe of the subfamily Myrtoideae with no naturally occurring representatives in Australia. In this chapter, fossil fruits, flowers and leaves are described from the Oligocene aged Little Rapid River deposit, from Tasmania, along with leaves that are reinvestigated from the Eocene aged Hasties deposit, which had previously been misidentified. The fossils are described as *Metrosideros leunigii,* and share affinities with the subgenus *Metrosideros,* extant species of which are the most widely dispersed around the Pacific today. They represent the oldest described fossil record of the genus, as well as the first record of the genus in Australia. I put forward a hypothesis that these fossils may suggest an Australian origin for the genus.

CHAPTER 4 – Two fossil species of *Metrosideros* (Myrtaceae) from the Oligo-Miocene Golden Fleece locality in Tasmania, Australia.

In this chapter, further fossils of *Metrosideros* are described from the newly discovered Golden Fleece locality in Tasmania, and palynological biostratigraphic work published in this study provides a confident Oligo-Miocene age for these sediments. The fossils are the first macrofossils to be described from the new locality, and two new fossil taxa of *Metrosideros* are described, *M. dawsonii* and *M. wrightii,* with apparent affinities to species in the formerly recognized subgenus *Mearnsia.* Unlike subgenus *Metrosideros,* species in the formerly recognized subgenus *Mearsnia,* the remaining species in the genus, are much less widely dispersed around the Pacific, and occur on largely Gondwanic landmasses; New Zealand, New Caledonia, Papua New Guinea as well as the Philippines and the Solomon Islands. I suggest that these fossils provide even stronger evidence of an Australian origin for the genus.

CHAPTER 5 – Identifying fossil Myrtaceae leaves: The first described fossils of *Syzygium* from Australia.

In the history of work on the fossil record of the Myrtaceae, a great number of fossil leaves have been reported, illustrated and described over the last century, as established in Chapter 2. However, the majority of fossil leaf identifications occur without corroborating evidence from fossil reproductive material, or organic preservation of cuticle so that cuticular micromorphological characters might be utilised for identification. As such, the identification of many of the fossil Myrtaceae leaves in the literature relies upon gross leaf architecture and venation, which are demonstrably inadequate for confident identification of fossil Myrtaceae leaves, even to family level in many cases. In this chapter, organically preserved fossil leaves of *Syzygium* from the Miocene of Kiandra, New South Wales, are identified. The fossils are identified using a small but phylogenetically informative set of cuticle micromorphological characters, compared against a large dataset of extant Myrtaceae leaves compiled from vouchered herbarium specimens as well as gathered from the literature. This is the first time that fossil Myrtaceae leaves have been convincingly described from cuticle micromorphological detail to a living genus.

CHAPTER 6 – General discussion and conclusions

In this chapter I consolidate my major findings, and summarise the conclusions and implications of the research in the previous chapters, and finally suggest directions for future research in the fossil record of the Myrtaceae, particularly in resolving some of the biogeographic questions remaining for the capsular fruited Metrosidereae, and suggestions for high priority work into the fossil record of the Myrtaceae in the future.

Chapter 2:

Literature Review

A critical review of the Cenozoic vegetative and reproductive macrofossil record of the Myrtaceae: A view from the Southern Hemisphere

INTRODUCTION

Our understanding of the evolutionary and phylogenetic relationships within the Myrtaceae has been revolutionised by molecular phylogenetic analyses in the past two decades (Wilson et al., 2001; Wilson et al., 2005; Biffin et al., 2007; Lucas et al. 2007; Biffin et al., 2010; Wilson, 2011; Vasconcelos et al. 2017), but interpreting the origin and paleobiogeography of the family, and the calibration of phylogenies and molecular clock models, still must by necessity rely heavily on the macrofossil and microfossil record (Thornhill and Macphail, 2012; Thornhill et al., 2012b; Thornhill et al., 2015). As such, a critical and comprehensive review of these fossil records is necessary. While recent work by Thornhill et al. (2012) has comprehensively reviewed the paleobiogeographic and phylogenetic value of the microfossil (pollen) record of the Myrtaceae, no such review of the macrofossil record of the Myrtaceae exists. The pollen record is important for calibration of molecular models, phylogenies and reconstruction of paleobiogeography, but it is apparent that in many cases fossil pollen is rarely identified at high taxonomic resolution. As has been discussed by Sauquet et al. (2011), the identification of fossil pollen is generally based upon gross morphological similarity, and is not often supported by synapomorphies. Macrofossils and mesofossils of fruits, flowers and leaves however can be identified based on analytical, phylogenetic placement, and thus provide much higher taxonomic resolution. This is clear in the case of the Myrtaceae, where pollen do not often possess enough diagnostic characters to confidently propose infrageneric, generic or tribal relationships (Thornhill et al., 2012a). Similarly, Myrtaceae wood anatomy is largely uninformative at high taxonomic resolution (van Vliet and Baas 1985; Wilson, 2011), and as such fossil woods have rarely been confidently referred to living genera. These facts highlight the importance of, and need for, critical study of the reproductive and vegetative macrofossil record of the Myrtaceae.

Short but non-comprehensive checklists and reviews of key fossils in the Myrtaceae macrofossil record do exist as part of the introduction to fossil work conducted by Basinger et al. (2007), and in the introduction to Wilson's (2011) guide to the genera within the family, but a systematic review of the macrofossil record of the Myrtaceae is lacking. Several reviews of the fossil record of the eucalypts have been published; a review of many early Australian fossil eucalypts was published by Maiden (1922), and a brief review is published in a history of selected Australian taxa by Hill (1994), as well as a critical review of the fossil record of the eucalypts published by Rozefelds (1996), and most recently a review of the eucalypt fossil record was published by Hill et al. (2017), with an aim to help understand the evolution and paleobiogeography of the genus. However, none of these reviews are comprehensive of the published fossil record for the whole family.

The following review is an attempt to take a systematic, critical approach to a large number of the Myrtaceae reproductive and vegetative macrofossils that have been reported in the literature in the last century.

METHODS AND CRITERIA FOR INCLUDING AND ASSESSING FOSSILS

For the purposes of this review, the published fossil record of the Myrtaceae is broken up in to categories based on the geographic region where the fossils have been found, and the categories are **(1)** Australia, **(2)** New Zealand, **(3)** South America, **(4)** Antarctica, and while the focus of this review is in the Southern Hemisphere, the vegetative and reproductive fossil record of India, as an old Gondwanic landmass with a long history in the Southern Hemisphere, is reviewed in table **(5)**. Some key fossils from the Northern Hemisphere are included in the discussion in table **(6),** but the fossil record from Africa is not included here in a table due to a paucity of macrofossils having been described from the continent.

The regional tables are then broken up into hierarchical sub-categories notionally sorting from the most high-resolution taxonomic treatment and information, to the least. Fossils of (or, with associated) reproductive material are often more diagnostic than fossils of just vegetative material, and fossils that have been formally described into living genera and then form genera are considered more diagnostic than fossils that are undescribed. As such, the fossils in each table follow these categories where applicable; **(a)** described (living genera): reproductive structures, **(b)** described (form genera): reproductive structures, **(c)** described (living genera): leaves, **(d)** described (form genera): leaves, **(e)** undescribed: reproductive structures, and **(f)** undescribed: leaves. These subcategories are omitted from the tables where not applicable, for example there are no fossils described and attributed to living genera in Antarctica and so the next applicable category, undescribed reproductive structures, is the top category. Where taxa are formally described, and treated as a single taxon or referred to an extant or fossil genus, they are counted as a single record in the table. Where several taxa may occur, but they are undescribed, they are included in one record in the table.

In each table, the fossils are listed in reverse chronological order of publication, with most recently published fossils appearing at the top of the list. This is because the quality of the research on more recently published fossils is often better than in older publications. The proposed taxonomic affinity of each fossil is reviewed, which is briefly summarised in each table. Species authors occur only in the tables, unless it is necessary to include them in the text to avoid confusion. The fossils are then discussed, and justifications for the review of taxonomic affinity are discussed after each table. Fossils that do not have enough characters to justify identification as Myrtaceae are considered 'uncertain'. Fossils that have only have enough characters to be considered as *possible* Myrtaceae, or possibly belonging to a given tribe or genus, are prefaced with a '?', i.e. '?Myrtaceae', '?Myrteae', '?*Syzygium'*. For fossil species that have been formally described, the species authorship is listed in the table and only in the text where necessary.

My approach is to be especially critical with leaf fossils. As Hickey and Wolfe (1975) note; pinnate, brochidodromous venation and intramarginal veins occur in at least some representatives of most families within the Myrtales. Vickulin (1999) correctly points out that even outside the Myrtales, representatives in other, more distantly related families may show the development of intramarginal veins, such as the Apocynaceae, Moraceae, Clusiaceae, Sapotaceae and Anacardiaceae. As such, fossil leaves of some species in other families could conceivably be mistaken for Myrtaceae in impression or compression fossil material. As Manchester et al. (1998) note, there is often a wide variety of leaf architectural patterns observable even in a given genus, and it is therefore dangerous to assign fossil leaves to living genera of Myrtaceae in the absence of some other corroborating evidence. Fossil leaves identified as Myrtaceae or placed into living genera, without organic preservation to determine the presence of lid-cells (sensu Lange 1980), or of some other well described and illustrated diagnostic feature (such as reproductive structures, or the diagnostic falcate leaf shape of some members of the *Eucalypteae,* i.e. Pole 1993), and/or in the absence of demonstrated comparative work, are generally considered of uncertain taxonomic affinity or only possibly Myrtaceae.

This review is not exhaustive but is hopefully demonstrative of much of the work carried out on the Myrtaceae in the last century. Only fossil records published in the last 100 years are included, and even then we have not included work by some early researchers, such as E.W. Berry, who placed numerous fossil leaves into extant genera of Myrtaceae from the Americas, though much of this fossil record must now be regarded as uncertain or equivocal (see discussion). Fossil species or form genera published in early research has been included if still in use by modern researchers. In this case, the modern records of these species or genera are included. The reasons for omitting fossils older than this have been discussed in the Australian context by Hill (1988, 1994). Much of the work by early workers such as Ettingshausen, Deane and Johnston in Australia, or Dusén, Engelhardt and Berry in South America and Unger, who published Tertiary fossil Myrtaceae from New Zealand, as well as from many early reports from Europe, is poor by modern standards. Fossil leaves, often only with a single preserved leaf without organic preservation, were often placed into new species of living genera by these authors, with very little comparative work demonstrated, and are usually poorly illustrated and dated.

RESULTS

TABLE 1: REPORTED FOSSIL RECORDS OF MYRTACEAE FROM AUSTRALIA

FOSSIL	*TAXONOMIC AFFINIY*	*AGE*	*LOCATION*	*KEY REFERENCE*
		AUSTRALIA		
		(a) Described (living Genera): Reproductive structures		
Metrosideros dawsonii Tarran, P.G.Wilson et R.S.Hill	*Metrosideros*, aff. subg. *Mearnsia*	Oligo-Miocene	Golden Fleece, Tasmania	Tarran et al., 2017
Metrosideros wrightii Tarran, P.G.Wilson et R.S.Hill	*Metrosideros,* aff. subg. *Mearnsia*	" "	" "	Tarran et al., 2017
Metrosideros leunigii Tarran, P.G.Wilson et R.S.Hill	*Metrosideros*, aff. subg. *Metrosideros*	Early-Oligocene	Little Rapid River, Tasmania	Tarran et al., 2016
Eucalyptus bugaldiensis Holmes et Holmes	*Eucalyptus*	Middle-Miocene	Chalk Mountain, New South Wales	Holmes et al., 1983
		(b) Described (form genera): Reproductive structures		
Tristaniandra alleyi P.G.Wilson et Basinger	tribe Kanieae, similarities with *Tristaniopsis*	Middle-Eocene	Golden Grove, South Australia	Basinger et al., 2007
		(c) Described (living Genera): Leaves		
Syzygium christophelii Tarran, R.Paull et R.S.Hill	*Syzygium, aff. subg. Acmena*	Early-Miocene	Kiandra, New South Wales	Tarran et al. 2018, in review, Chapter 5 this thesis
Rhodomyrtus australis R.S.Hill et Merrifield	?Myrtaceae, ?*aff. Rhodomyrtus*	Tertiary, possible Middle-Late Eocene	West Dale Flora, Western Australia	Hill and Merrifield, 1993
Eucalyptus kitsonii H.Deane	*Eucalyptus*	Late Oligocene-Early Miocene	Berwick Quarry Flora, Victoria	Pole et al., 1993
Tristania angustifolia (?) H.Deane	Uncertain	Tertiary, possible Early Oligocene	West of Lake Torrens, Central South Australia	Chapman, 1937
Tristania praeconferta (?) F.Chapm.	Uncertain	" "	" "	" "
Eucalyptus diemenii Ettingsh.	Uncertain	" "	" "	" "
Eucalyptus houtmannii Ettingsh.	Uncertain	" "	" "	" "
Eucalyptus kitsonii H.Deane	Uncertain	" "	" "	" "
Eucalyptus mitchellii Ettingsh.	Uncertain	" "	" "	" "
Eucalyptus kitsonii H.Deane	Uncertain	Tertiary, probable Late Oligocene	Darlimurla, Gippsland	Paterson, 1935
Eucalyptus cf. kitsonii H.Deane	Possible eucalypt?	Tertiary, probable Late Oligocene	Narracan, South Gippsland	Chapman, 1926
		(d) Described (form genera): Leaves		
Myrtaceaephyllum pleistocenicum G.J.Jordan	Myrtaceae	Early Pleistocene	Regatta Point, Western Tasmania	Jordan, 1997
Myrtaciphyllum striatum R.S.Hill et Merrifield	Myrtaceae	Tertiary, possible Middle-Late Eocene	West Dale Flora, South-West Western Australia	Hill and Merrifield, 1993
M. sinuatum R.S.Hill et Merrifield	" "	" "	" "	" "
M. brochidromum, R.S.Hill et Merrifield	" "	" "	" "	" "
M. westdaliense R.S.Hill et Merrifield	" "	" "	" "	" "
M. annulatum R.S.Hill et Merrifield	" "	" "	" "	" "
Myrtaciphyllum eremaensis Christophel, Scriven et	Myrtaceae	Middle Eocene	Nelly Creek, Central South Australia	Christophel et al., 1992

D.R.Greenwood				
Myrtaciphyllum douglasii Christophel et S.D. Lys	Myrtaceae	Upper Eocene	Anglesea, Victoria	Christophel and Lys, 1986
Myrtaciphyllum undulatum Christophel et S.D.Lys	" "	" "	" "	" "
Tristanites angustifolia H.Deane	Uncertain	Tertiary, probable Late Oligocene	Narracan, South Gippsland	Paterson, 1935
Tristanites angustifolia H.Deane	Uncertain	Tertiary, probable Late Oligocene	Narracan, South Gippsland	Chapman, 1926
(e) Undescribed: Reproductive structures				
Lightning Ridge Fruits and Leaves	Myrtaceae, *aff.* Eucalypteae and Melaleuceae	Cenozoic, possibly latest Oligocene to mid-late-Miocene	Lightning Ridge, New South Wales	Carpenter et al., 2011
Redbank Plains fruits	*Eucalyptus*	Paleocene-Eocene, though could be younger	Redbank Plains Formation, south-eastern Queensland	Rozefelds, 1996
Nelly Creek 'leptospermoid' fruits	Capsular fruited Myrtaceae, possible eucalypt group?	Middle-Eocene	Nelly Creek, Central South Australia	Christophel et al., 1992
Stuart Creek fruits	Myrtaceae aff. Eucalypteae or Melaleuceae	Probably, Miocene-Pliocene, could be older	Stuart Creek, central South Australia	Ambrose et al., 1979
Island Lagoon Fruits and leaves	Myrtaceae aff. Eucalypteae, Leptospermeae, Melaleuceae	Tertiary	Island Lagoon, near Woomera, central South Australia	Lange, 1978
(f) Undescribed: Leaves				
Dispersed Myrtaceae Cuticles	Myrtaceae	Middle Eocene	Lefroy and Cowan paleodrainages, Kambalda-Norseman region, Western Australia	Carpenter and Pole, 1995
Agonis sp.	Myrtaceae, *aff. Agonis*	Tertiary, possible Middle-Late Eocene	West Dale Flora, Western Australia	Hill and Merrifield, 1993
***Myrtaciphyllum* sp. 1**	?Myrtaceae	" "	" "	" "
Maslin Bay Myrtaceae	Myrtaceae	Middle Eocene	Maslin Bay, South Australia	Scriven, 1993
cf. *Xanthomyrtus* leaf	Myrtaceae	Eocene	Hasties, north eastern Tasmania	Pole, 1992
Myrtaceae leaf	?Myrtaceae	Oligocene	Cethana, north east Tasmania	Carpenter, 1991
***Eucalyptus* leaves?**	?Myrtaceae	Middle-Eocene	Eyre Formation, Central South Australia	Greenwood 1991
***Myrtaciphyllum* sp.**	?Myrtaceae	Middle Eocene	Golden Grove, South Australia	Christophel and Greenwood, 1987
aff. Myrtaceae macrofossils, dispersed cuticle & mummified leaves: 12 taxa	Myrtaceae	Oligo-Miocene	Yallourn and Morwell seams of Latrobe Valley coals, Victoria	Blackburn, 1985
Myrtaceae leaf	Myrtaceae	Oligocene	Pioneer, north east Tasmania	Hill and Macphail, 1983
Myrtaceae leaves	Myrtaceae	Early Miocene	Kiandra, New South Wales	Selkirk, 1969

1) Critical review of Australian fossil records of Myrtaceae

(a) Described (living genera): reproductive structures

Two fossil taxa are described by Tarran et al. (2017, Chapter 4 of thesis) from organically preserved reproductive structures from the Oligo-Miocene Golden Fleece locality in northeast Tasmania. The fossil of *Metrosideros dawsonii* is a 3-locular capsule, with valves exserted beyond the hypanthial rim, and 5 prominent veins running up the hypanthium terminating in the sepals. Sepals deltoid, inserted upon prominent hypanthial rim. The fossils of *Metrosideros wrightii* are also 3-locular capsules, distinguished from *M. dawsonii* by having thinner exserted valves which extend just beyond the rim of the fruit. Sepals reduced. In both cases, the 5 veins slightly visible running up the hypanthium terminating in the sepals are interpreted as a synapomorphy for *Metrosideros* (*sensu* Wilson 2011).

The first and oldest record of *Metrosideros* in Australia are reported by Tarran et al. (2016, Chapter 3 of thesis) who describe organically preserved fossil fruits, flowers and associated leaves from the Early Oligocene Little Rapid River deposit in northwestern Tasmania, the leaves of which have been previously compared with identical fossil leaves illustrated from the Middle-Late Eocene Hasties deposit (~40 Ma) in northeastern Tasmania by Pole (1992, see section 2F). Fruits are 3-locular capsules with valves exserted well beyond the hypanthial rim. On the fossil flower petal, style and stamen base scars are visible. Fossils are compared with a range of extant capsular-fruited Myrtaceae and several synapomorphies for *Metrosideros* are demonstrated, with affinities to the subgenus *Metrosideros.*

Holmes (1983) described *Eucalyptus bugaldiensis* from fossil reproductive structures preserved in Middle Miocene diatomite from Chalk Mountain, New South Wales. Fossils are hemispherical, ribbed fruits with broad rims and exserted valves. Fruits are an infructesence of umbellasters attached to peduncles. These fruits very convincingly represent *Eucalyptus*, and are found in association (though without organic connection) with two different forms of fossil eucalypt leaves. Although these leaves lack organic preservation, they appear to represent genuine eucalypt fossils, with suggested affinities of one form similar to *Corymbia* or *Angophora*, and the other to species of *Eucalyptus.* These fossils have been considered convincing in reviews of the eucalypt fossil record by by Rozefelds (1996) and Hill et al. (2016),

(b) Described (form genera): reproductive structures

The only reproductive structures in Australia that have been assigned to a form genus are published by Basinger et al. (2007), who describe *Tristaniandra alleyi* from the middle Eocene of Golden Grove, South Australia. These fossils are highly flattened and deformed organically preserved fruits and flowers, but key diagnostic characters have been preserved. Possible lid-cells were demonstrated on the cuticle of one of the fossil fruit specimens and tricoplate, *Myrtaceidites*-type pollen was found adhered to the surface of a sepal. The flower is pentamerous, perigynous and has sepals, petals and stamens inserted on the rim of the hypanthium. Stamens are in a single whorl, but fused into five bundles. The fruit is 3-locular, with an exserted ovary. These characters not only strongly support placement in the Myrtaceae, but the fused staminal bundles are characteristic of several species in the tribe Kanieae *sensu* Wilson (2011), and similarities are drawn with the extant genus *Tristaniopsis,* though the staminal bundles are digitate in the case of the fossils, where extant *Tristaniopsis* staminal bundles are arranged in brush-like stamina fascicles.

(C) Described (living genera): leaves

Very few Myrtaceae leaf fossils from Australia have been placed convincingly into living genera.

Tarran et al. (2018, in review, Chapter 5 this thesis) describe fossils of *Syzygium christophelii* from mummified remains from the Miocene of Kiandra, New South Wales. These fossils have organic preservation, and so cuticular characters are preserved. The authors utilised a set of simple, but phylogenetically informative characters, assessed against a data-set of cuticles of 233 extant taxa from vouchered herbarium samples and cuticle data collected from the literature. These fossils were found to lack trichome bases or any evidence of indumentum, a strong syzygyoid character first foreshadowed by Briggs and Johnson (1979), as well as cyclo-staurocytic stomata, which in isolation as the sole stomatal type, appear only to be found in the *Syzygium* subgenus *Acmena*, and in some species of subgenus *Perikion*, as found by Soh and Parnell (2011) in a large scale study of *Syzygium* leaf micromorphological characters.

Hill and Merrifield (1993) described a number of myrtaceous macrofossils from the West Dale flora of South-West Western Australia. These fossils are not precisely dated, but inferred to be possibly middle-late Eocene in age*.* *Rhodomyrtus australis* is assigned to the extant genus *Rhodomyrtus* on the basis of characteristic paired, basal secondary veins, similar to those seen in the genera *Rhodomyrtus* and *Rhodamnia,* an absence of any characters that might suggest placement of fossils in another family where such venation might be observed in some genera, particularly the Lauraceae, and then a general agreement of leaf architecture, cuticle and stomatal arrangement and morphology with living species of *Rhodomyrtus* examined. Lid-cells are not observed on the fossil leaf surface, which would usually confirm assignment to Myrtaceae. These fossils do share gross similarity with leaves of extant *Rhodomyrtus,* as is demonstrated in comparison with leaves of the extant *R. elegans* (Blume) A.J. Scott*.* However in the recent molecular phylogeny of the Myrteae, Vasconcelos et al. (2017) the fossils of *Rhodomyrtus australis, "*were not considered" for dating the phylogeny "due to the lack of morphological characters that can assign them confidently into Myrteae."

Pole et al. (1993) reviewed fossils attributed to *Eucalyptus* by Deane (1902), who described 7 species of *Eucalyptus* from the Berwick Quarry flora, including two that had previously been described by Ettingshausen (1888). Pole et al. (1993) found that that several of these putative species, *E. howittii, E. woollsii, E. muelleri, E. hermanii* are virtually indistinguishable from *E. kitsonii,* and regarded that they should be considered synonyms. However, Pole et al. (1993) did not propose an emended species diagnosis, as the fossil material is too fragmentary, and only based on leaf material. These fossils are considered to possess enough characters for confident placement in *Eucalyptus*.

The rest of the fossil Myrtaceae described to living genera from leaf material in Australia are much less confidently placed, as illustrated by some examples here, but this list is not exhaustive. Chapman (1937) described six fossil species of Myrtaceae from Tertiary silcrete material, with a suggested Oligocene age, from a site West of Lake Torrens, in Central South Australia. Five of these species had been previously described by earlier work of Deane and Ettingshausen. Chapman (1937) placed two species into the living genus *Tristania,* but this appears to have been a mistake, as one species is said to be placed into a fossil species erected by Deane (1902), *Tristania angustifolia,* though Deane (1902) never placed any fossils into the living genus *Tristania*, only the form genus *Tristanites* to encompass a species with the same species epithet. Chapman also describes fossils of *Tristania praeconferta*. The descriptions of these taxa are brief and rely solely on gross architectural features. Illustrations of these taxa do not show the specimens in enough detail to make out diagnostic characters. No comparative work with extant taxa is demonstrated, though these fossils are compared most favourably with species which have subsequently been re-circumscribed, *Tristaniopsis laurina* (Sm.) Peter G.Wilson & J.T.Waterh. and *Lophostemon confertus* (R.Br.) Peter G.Wilson & J.T.Waterh. respectively. We regard these fossils as of uncertain taxonomic affinity.

Chapman (1937) also described several species of *Eucalyptus,* placing them in fossil species erected by Deane and Ettingshausen, *E. diemenii*, *E. houtmannii***,** *E. kitsonii***,** and *E. mitchellii*. The descriptions are brief and rely solely on gross architectural features. Illustrations of these taxa do not show the specimens in enough detail to make out diagnostic characters, except for overall leaf shape. The illustrations of *E. diemenii, E. houtmannii* and *E. kitsonii,* have a vaguely eucalypt like shape. However, based on the quality of the plates and the brevity of the description, we regard these fossils as of uncertain taxonomic affinity; though possibly they do represent members of the eucalypt group.

Paterson (1935) reported three fossil taxa of Myrtaceae from Tertiary sediments with a suggested Oligocene age at Narracan, South Gippsland, Victoria, placing the taxa in fossil species *Tristanites angustifolia* as well as another taxon cf. *Tristanites muelleri*, and one fossil species also originally described from Tertiary sediments at Darlimurtla, Gippsland, *Eucalyptus kitsonii*. The only one of these taxa that is illustrated is cf. *Tristanites muelleri,* and no diagnostic features are visible in this illustration. The descriptions of all of these taxa are very brief and general, and based only on gross architectural features. Without further investigation, these fossils must be considered equivocal, and of uncertain taxonomic affinity.

Patterson (1935) notes that a small number of leaves from Tertiary sediments somewhere in Narracan were described nine years earlier by Chapman (1926), as fossil taxa of Myrtaceae, though it is not clear if these are the same sediments that Paterson's (1935) material was collected from. Chapman (1926) places these fossils into two taxa previously erected by Deane (1902), *Tristanites angustifolia*, and *Eucalyptus* cf. *kitsonii.* The descriptions of the fossils are very brief, and diagnosis is based on gross architectural features. Both taxa are illustrated. The leaf shape of the specimen of *Eucalyptus* cf. *kitsonii* is falcate, and the description of a clear intramarginal vein in combination with this is very suggestive of the eucalypt group, and as such we regard these fossils as possible eucalypt group members. The illustration of *Tristanites angustifolia* from this deposit is unclear and these fossils are regarded here as equivocal.

(d) Described (form genera): leaves

Jordan (1997) described one myrtaceous taxon, *Myrtaceaephyllum pleistocenicum* from the Pleistocene of Regatta Point, Western Tasmania. These fossils were to be placed in the form genus *Myrtaciphyllum* Christophel and Lys (1986), but the spelling of the form genus in the species diagnosis has been misspelled as *Myrtac**eae**phyllum.* The fossil possess an intramarginal vein, oil glands and lid cells proving a confident myrtaceous diagnosis. These fossils provide evidence of a relatively recent extinction of a rainforest species of Myrtaceae from Tasmania, with affinities suggested to two species of *Austromyrtus* (Nied.) Burret*,* although it is worth noting, as pointed out in Tarran et al. (2016, Chapter 3 of thesis), that neither of the two species that were favourably compared with *Myrtaceaephyllum pleistocenicum* remain in the genus *Austromyrtus,* with one having now been referred to the genus *Gossia* (Lucas et al., 2007), and the other to *Lenwebbia,* a genus not closely related to any other Australian Myrteae (Snow et al., 2003). Whatever the relation of this fossil taxon, it seems it is a rainforest Myrtaceae with no modern equivalents in Tasmania.

Hill and Merrifield (1993) also described five species of *Myrtaciphyllum* from the West Dale flora in southwest Western Australia. The five named species of *Myrtaciphyllum* are *M. striatum, M. sinuatum, M. brochidromum, M. westdaliense* and *M. annulatum*, and a sixth is described from a single leaf as *Myrtaciphyllum sp. 1.* These are largely described from fragmentary or few remains, and so the diagnoses for each taxon is brief. Although these fossils are impression material, enough impressional detail is preserved to observe epidermal structures that suggest placement in *Myrtaciphyllum.* All five taxa are broadleaved and hypostomatic, and possess pinnate, brochidodromous venation and an intramarginal vein. There are enough characters to justify the placement of these fossils into so many separate species, however lid-cells are only described on one of the five species, *M. sinuatum.* A sixth species, *M. sp 1* does appear different enough to be a separate species, but preservation is deemed too poor for description of a new fossil species. These six taxa remain the greatest number of Myrtaceous taxa described from a single deposit to date in Australia.

Another species of *Myrtaciphyllum*, *M. eremaensis* is described from Middle Eocene dated sediments at Nelly Creek in Central South Australia by Christophel et al. (1992). These leaves appear similar the *Myrtaciphyllum* leaves reported by Christophel and Lys (1986), being hypostomatic, with brochidodromous venation, and dense, high angled secondary venation. Lid cells *sensu* Lange (1980) and rare trichomes are present on the cuticle surface. These fossils were also found in association, although without direct organic connection, with small capsular 'leptospermoid' fruits (see next section). Similarities are proposed with both capsular fruited (*Lophostemon)* and fleshy-fruited (*Syzygium)* genera, although it is worth noting that most species of *Lophostemon* lack an intramarginal vein, and most species of *Syzygium* are entirely glabrous (Briggs and Jonson 1979; Tarran et al., 2018 under review, Chapter 5 this thesis). I regard these leaves as certain Myrtaceae, but generic relationships are uncertain. This fossil taxon may represent an extinct lineage.

The form genus *Myrtaciphyllum* was originally erected by Christophel and Lys (1986) to encompass two myrtaceous taxa from the upper Eocene Anglesea locality in Victoria, *M. undulatum* and *M. douglasii*. It is important in the history of foliar fossil identification in the Myrtaceae, for while numerous other fossil form or organ genera had been proposed in Australia such as *Myrtonium* and *Callistemonophyllum* (Ettingshausen, 1888) or *Tristanites* (Deane, 1902), this was the first form genus to take into account both leaf architectural features, as well as cuticular micromorphology, emphasizing the importance of lid-cells *sensu* Lange (1980). The leaves are hypostomatic, venation is brochidodromous, with secondary veins joining to form distinct intramarginal veins. as a diagnostic myrtaceous character. The combination of good architectural and micromorphological characters confirm these cuticles as Myrtaceae. Lid cells however are only described on the cuticles of *M. undulatum,* which also possesses trichomes. No lid cells are described on *M. douglasii,* and the cuticle is glabrous.

As discussed by Tarran et al. (2018, under review, Chapter 5 this thesis), in describing these species, Christophel and Lys (1986) performed a 'Numerical Taxonomic Analysis' in which 19 characters were selected, and fossil taxa were compared against 65 leaves of 11 Myrtaceous taxa, from 5 genera; *Syzygium, Caryophyllus, Acmena, Carpolepis* and *Lophostemon*. This represents the most comprehensive comparative work done up to this time in identifying fossil Myrtaceae leaves. However, two of these genera, *Caryophyllus* and *Acmena* have subsequently been included in *Syzygium* (Craven et al., 2006; Craven and Biffin, 2010a). Therefore, according to the most recent understanding of relationships within the Myrtaceae, only 3 genera were actually used for comparison. No convincing suggestions of generic relationships are made.

(e) Undescribed: reproductive structures

Some of the most impressive Myrtaceae macrofossils in Australia, many of them eucalypt-like, have not been formally described.

Carpenter et al. (2011) described a silicified flora from Lightning Ridge, New South Wales. These sediments are imprecisely dated, but they are suggested to have a late Oligocene to mid-late Miocene age, and are certainly Cenozoic. A number of silicified leaf forms are present, with at least one falcate leaf, possibly suggesting eucalptoid affinity. A number of silicified reproductive structures also exist, with two specemins, which are interpreted as clusters of woody fruits*.* Another larger reproductive structure with a five-parted inferior ovary is also described. None of these fossils however are placed in living genera. Affinities are suggested to Melaleuceae and Eucalypteae.

Rozefelds (1996) reports “One of the potentially oldest records” of eucalypt group fossils in Australia from the Redbank Plains formation in southeastern Queensland. This material was discovered in 1990, and is considered to be Paleocene or Eocene in age although a younger age is also possible. “At least six, possibly seven, fruits are preserved as impressions and partial impressions in a fine-grained, red-brown mudstone. The fruits are not in organic connection but appear to have been originally grouped into a probable umbellaster.” Hill et al. (2017) also consider that these fossils may represent the stratigraphically oldest *Eucalyptus* fossils in Australia, but the lack of a confirmed age on these sediments reduces their value.

Christophel et al. (1992) illustrate “leptospermoid” fruits from the Eocene locality of Nelly Creek in Central South Australia. These fruits are small, pedicelate and capsular with the capsule of the fruit perhaps just slightly raised beyond the hypanthium. There is no evidence of insertion of sepals on the hypanthial rim. Unfortunately, this material has subsequently been lost, and the material may never be re-investigated unless other material is found or the site is re-collected.

Ambrose et al. (1979) describe a range of eucalypt-like fossils preserved from the Stuart Creek silcretes in central South Australia. The fossils in this paper are only very briefly illustrated and described, but at least two distinct taxa with agglomerate infructesences consisting of several woody, fused gumnut fruits, as well as several larger solitary fruits. The fruits are suggested to represent *Eucalyptus,* although without characters to suggest otherwise these fruits may also represent forms of Melaleuceae or Leptospermeae. These silcretes are compared with the Island Lagoon silcretes, about 100km south of the Stuart Creek silcretes, described by Lange (1978), who illustrates a range of silicified casts of Myrtaceae fruits that are preserved at this deposit, consistent with *Eucalyptus, Leptospermum, Melaleuca, Callistemon, Calothamnus* and *Angophora* (*Callistemon* and *Calothamnus* have subsequently synonymized with *Melaleuca* by some authors (Craven et al., 2014), though this is still controversial.) Unfortunately, while it is understood that these represent Cenozoic floras, no way of confidently dating the central South Australian silcrete floras has yet been discovered. While the value of these inland silcrete fossils is greatly diminished by the lack of a confident age on the material, these fossils still provide excellent paleobiogeographic data, and are evidence of the existence of a xeromorphic vegetation with an assemblage of eucalypts and other capsular fruited Myrtaceae, in a rich mixture not found today in the region. The *Calothamnus*-like fruits are particularly interesting, bearing distinctive smooth, round, swollen sepals, characteristic of the genus. Today *Calothamnus* is restricted in native range to southwest Western Australia, and if these represent that group, the presence in this fossil flora indicate a formerly much broader range into central Southern Australia.

(f) Undescribed: leaves

A number of formally undescribed Myrtaceae leaves, and dispersed cuticles of Myrtaceae, have also been published from Australia. Carpenter and Pole (1995) described three parataxa of Myrtaceae from Middle Eocene sediments recovered in core sample material drilled from the Lefroy and Cowan paleodrainages in the Kambalda-Norseman region of Western Australia. These are identified as myrtaceous due to the presence of characteristic lid-cells observable. One of the taxa is found to be hypostomatic, though probably all of the taxa were. Nearest living relatives of other fossil taxa at this site indicate mesothermal-microthermal, non-seasonal rainforest. No generic or infrafamilial affinities are suggested for the myrtaceous taxa.

Hill and Merrifield (1993), also from the West Dale flora*,* report formally undescribed leaves of *Agonis cf. flexuosa* (Willd.) Sweet. These fossils are illustrated, but not treated to a formal description and only briefly described in the discussion. They are referred to this genus on the basis of gross overall architectural features, being hypostomatic with similar venation, and similarity of cuticle detail namely a random stomatal arrangement and the presence of large ‘probable’ glandular structures, although cuticle detail is only preserved poorly. The fossil leaves are compared with cleared leaves of extant *A. flexuosa,* and the two taxa do share a great similarity, however not enough characters exist for confident diagnosis.

At the Eocene Maslin Bay locality in South Australia, Scriven (1993) suggests 8 taxa with affinities to Myrtaceae, while 4 more are suggested with potential affinities to Myrtaceae. Affinities to extant genera are not suggested. Leaves range from notophyllous to mesophyllous. Cuticular features are often preserved, and oil-glands are preserved on many of the cuticles of these fossils, suggesting a confident myrtaceous diagnosis. Myrtaceae were once thought to comprise an insignificant part of the Maslin Bay flora, but Scriven’s (1993) doctoral studies found that out of 177 leaf taxa, some 8-12 myrtaceous taxa were present.

Pole (1992) illustrated myrtaceous leaves from the Eocene Hasties locality, as part of a broad paleofloristic analysis, tentatively identified them cf. *Xanthomyrtus*. Intramarginal veins and lid-cells support a myrtaceous diagnosis, but as Tarran et al. (2016, Chapter 3 this thesis) note, this identification was based on a single potentially diagnostic character of "stomatal clumping", with very little other evidence to support identification beyond family level. Pole (1992) compared these leaves with the myrtaceous leaf illustrated by Hill and Macphail (1983) from the Oligocene Pioneer flora, as well as being considered to be identical to as yet unpublished leaf fossils from the Oligocene flora at Little Rapid River. These leaves were revisited by Tarran et al. (2016), and found to possess no characters to verify affinities with *Xanthomyrtus,* but instead to share micromorphological characters with capsular fruited genera, notably *Kania* and *Metrosideros,* conistent with the capsular fruits and flowers of *Metrosideros leunigii* from Little Rapid River [See section 1A]. Carpenter (1991) illustrates Myrtaceae like-leaves with intramarginal veins and drip tips from the paleoflora at Cethana, which look very similar to those found from Hasties, Little Rapid River and Pioneer, although no cuticle was preserved and so cannot be confidently assigned.

Greenwood (1991) reported *Eucalyptus* leaves from the Middle Eocene of the Eyre Formation of central South Australia, in a conference abstract. These fossils however have yet to be subsequently described, or illustrated anywhere in the published literature. Hill (1994) was sceptical of these fossils, noting that earlier work by Greenwood et al. (1990) on the same flora mentioned only leaves assigned to '*Eucalyptophyllum*', about which it was "not possible to determine the affinities of this leaf type." These fossils are again mentioned as *Eucalyptus*-like leaves from the Poole Creek palaeochannel of the Lake Eyre formation by (Greenwood, 1996), but still not described or illustrated. The fossils as reported by Greenwood (1991) were claimed to be the oldest record at the time for *Eucalyptus.* It is interesting to note, that even without description or illustration, these fossils were used to date the Eucalyptoid node of the Myrtaceae in a Myrtales-wide phylogeny by Sytsma et al. (2004).

Christophel and Greenwood (1987) illustrate another taxon, refered to as *Myrtaciphyllum* sp., from the Middle Eocene Golden Grove locality in South Australia. One leaf is illustrated, and pinnate brochidodromous venation and an intramarginal vein are clearly visible, however lid cells are not described or illustrated. It is stated that a preliminary investigation finds that they do not belong to the same *Myrtaciphyllum* species described by Christophel and Lys (1986). These specimens are still to be formally described.

Blackburn (1985) described a series of myrtaceous taxa from mummified leaves, leaf fragments and dispersed cuticle from the Oligo-Miocene Morewell and Yallourn coal seams in Victoria. In total, 12 taxa are described. These are mostly informally described as having affinities to extant genera, such as aff. *Acmena*, aff. *Austromyrtus*, aff. *Calytrix*, aff. *Eugenia* sp. 1, aff. *Eugenia* sp. 2, aff. *Eugenia* sp. 3, aff. *Metrosideros*, aff. *Tristania* sp. 1, aff. *Tristania* sp. 2. One taxon is called *Baeckea,* since the cuticles are thought to resemble those of extant *Baeckea* very closely. Another two taxa are not assigned any affinities, and are named ‘Taxon 45’ and ‘Taxon 46’. Oil gland lid cells are found on almost all taxa, supporting myrtaceous diagnosis, but comparative work for most taxa is not demonstrated and is minimal in most cases. As such, for now, the generic affinities of the taxa are regarded as uncertain. None of these taxa can be regarded as having been formally described, and reinvestigation of them should be considered a high priority.

Selkirk (1969) described a number of mummified myrtaceous leaves from the Miocene of Kiandra, New South Wales. One taxon has previously been compared to the now radically re-circumscribed subfamily Myrtoideae (Wilson et al., 2005), including the same genus (*Xanthomyrtus*) that Pole (1992) referred Myrtaceae fossils from the Hasties vegetation to, as discussed earlier, as well as compared to *Eugenia*, *Acmena (Syzygium), Austromyrtus* and *Backhousia* (Selkirk, 1969; Owen, 1988). Cuticular preservation is good, and oil glands are present on the cuticle surface, confirming the myrtaceous diagnosis. Selkirk only briefly treated these Myrtaceae leaves, as his study focus was identification of fossil epiphyllous fungi and bryophytes. These fossils remain unidentified, but have been subsequently re-examined (Tarran, unpub. data) and share a number of characters with the leaves the Eocene Hasties vegetation and Oligocene Little Rapid River deposits (Tarran et al., 2016). Selkirk (1969) also noted that there might be a second myrtaceous species at this locality, which is re-visited and treated by Tarran et al. (2018, under review, Chapter 5 of thesis) [See section 1C].

TABLE 2: REPORTED FOSSIL RECORDS OF MYRTACEAE FROM NEW ZEALAND

FOSSIL	*TAXONOMIC AFFINIY*	*AGE*	*LOCATION*	*KEY REFERENCE*
NEW ZEALAND				
(a) Described (living Genera): Reproductive structures				
Leptospermum pliocenicum W.R.B.Oliv.	Uncertain.	Late Pliocene	Waipaoa series, Poverty Bay District, North Island	Oliver, 1928
(b) Described (living Genera): Leaves				
Metrosideros laeta W.R.B.Oliv.	Uncertain	Tertiary, Miocene to Pliocene. Undetermined.	Kaikorai Valley, Otago, South Island	Oliver, 1936
Metrosideros pliocenica W.R.B.Oliv.	" "	" "	" "	" "
(c) Undescribed: reproductive structures				
***Metrosideros* fruits**	*Metrosideros,* aff. subg. *Mearnsia*	Early to Middle Miocene	Manuherikia Group, Central Otago, South Island	Pole et al., 2008
"Myrtaceae sp. A"	*?Myrtaceae*	Early-Middle Eocene	Taratu Formation, Otago, South Island	Pole, 1994
"Myrtaceae sp. B" aff. *Eucalyptus* sp.	?eucalypt group	" "	" "	" "
***Eucalyptus* fossils**	*Eucalyptus*	Early to Middle Miocene	Manuherikia Group, Central Otago, South Island	Pole, 1993
(d) Undescribed: Leaves				
4 x cf. Myrtaceae leaf species	Myrtaceae	Middle to Late Miocene	Double Hill, Otago, South Island	Reichgelt et al., 2014
***Metrosideros*-like and *Syzygium*-like leaves**	Myrtaceae	Late Eocene	Pikopiko Fossil Forest, western Southland	Lee et al., 2012
Dispersed Cuticles - aff. *Syzygium*, aff. *Metrosideros* + *Others*	Myrtaceae, probable *Syzygium* and possible *Metrosideros*	Early Miocene	Manuherikia Group and Gore Lignite Measures, South Island	Pole et al., 2008
Dispersed Cuticles - aff. *Metrosideros*	Uncertain	Pliocene	Arapito gravels, Karamea	Pole, 2007
Myrtaceae Leaf	?Myrtaceae	Early Miocene	Foulden Hills Diatomite, South Island	Pole, 1996
aff, *Rhodomyrtus/Rhodamnia* sp.	?Myrtaceae, ?Aff. *Rhodomyrtus/Rhodamnia*	Early-Middle Eocene	Taratu Formation, Otago, South Island	Pole, 1994
***Metrosideros* sp. & undetermined Myrtaceae leaves**	*?Metrosideros*	Early to Middle Miocene	Manuherikia Group, Central Otago, South Island	Pole, 1993

2) Critical review of New Zealand fossil records of Myrtaceae

(a) Described (living genera): reproductive structures

Despite a reasonable representation of Myrtaceae in the fossil record of in New Zealand, the only fossils of Myrtaceae formally described to a living genus from reproductive structures so far reported are of *Leptospermum*, from the Late Pliocene of New Zealand described by Oliver (1928). *Leptospermum pliocenicum* is described, but not illustrated, from a specimen reported as containing several capsules with no preserved leaves. The capsules are described small, broader than high, with projecting points representing calyx segments with preserved short, persistent styles. The fossils are favourably compared with capsules of extant *Leptospermum ericoides,* now *Kunzea ericoides* (A. Rich.) J. Thompson (1983). Without an illustration of the fossil however, these can only be considered as uncertain. Re-assessment and illustration of this material would be necessary to confirm this diagnosis, which may prove important, as this would represent the only described fossil record of either genus.

(b) Described (living genera): leaves

Only two fossil species of Myrtaceae have been formally described from leaf material in New Zealand. Oliver (1936) described two fossil species of *Metrosideros, M. laeta* and *M. pliocenica,* from Tertiary sediments with a suggested possible Miocene to Pliocene age, in the Kaikorai Vally, Otago. Both of these taxa are described from single leaf impressions, and identification is based on gross venation characters, relying on the intramarginal vein. *M. laeta* is compared favourably with leaves of extant *M. robusta* A. Cunn., and *M. pliocenica* is compared favourably with *M. diffusa* (G. Forst.) Sm. Both specimens are illustrated with a single line diagram. Descriptions of these fossils are brief, and comparative work is poor. These fossils are regarded as of uncertain taxonomic affinity.

(c) Undescribed: reproductive structures

Interestingly, the bulk of myrtaceous fossils reported from New Zealand are not formally described, although a number of these undescribed fossils can still be confidently assigned to living genera. Most recently, Pole (2008) described fossil capsular fruits from the Early to Middle Miocene sediments of the Manuherikia group, Central Otago, with the five prominent veins in the hypanthium, which terminate in the sepals. This character is now being regarded as a synapomorphy for the genus *Metrosideros* (See Wilson, 2011; Tarran et al., 2017), although these fossils remain undescribed. Pole et al. (2008) considered that these fruits, with strongly developed veins and small size, were most similar to extant New Caledonian species of the formerly recognized subgenus *Mearnsia.* These fossils are also found in association with a number of myrtaceous cuticle parataxa described by Pole et al., with at least one of these cuticle parataxa having suggested affinities to *Metrosideros.* These fruits certainly represent *Metrosideros*, and were favourably compared with fossils of *Metrosideros dawsonii* by Tarran et al. (2017, Chapter 4 this thesis) [See section 1A] an extinct species of *Metrosideros* from Oligo-Miocene sediments in Tasmania, Australia, which too were found to share affinities with species of the formerly recognized subgenus *Mearnsia.* Tarran et al. suggest that *M. dawsonii* is more similar to these fossil fruits than to any other observed living genera, and that they may both represent a related lineage extinct from both landmasses.

Earlier, Pole (1994) described two myrtaceous taxa from reproductive structures from the Early-Middle Eocene Taratu Formation in North East Otago. “Myrtaceae sp. A” described from two specimens, is a branched paniculate inflorescence with sessile clusters of copular or obconical capsules. This inflorescence is compared favourably with *Allosyncarpia* and *Eucalyptopsis,* and perhaps some similarities with species of *Syzygium* or *Heteropyxis.* There are not enough characters here for a confident diagnosis, though these are interpreted to represent a possible extinct lineage of Myrtaceae from New Zealand. Pole (1994) also described eucalypt-like fruits, called “Myrtaceae sp. B” by the author, represented by two specimens. One of these specimens is an umbel of at least seven or eight barrel-shaped capsules attached by tapering pedicels to a longer peduncle, found in association (although not in organic connection) with narrow, elliptic leaves described with a sometimes falcate shape and brochidodromous-acrododromous venation with an intramarginal vein. Hill et al. (2017) only regarded these fossils as possible *Eucalyptus* macrofossils, and similar to the macrofossils of *Eucalyptus* from South America. Although preservation is poor, Hill et al. (2017) considered that these fossils should not be excluded as possible, very early evidence of this taxon, and that the presence of *Eucalyptus* in the Eocene of New Zealand is not impossible.

Pole (1993) also described the first possible *Eucalyptus* fruits and leaves from New Zealand, from the Early to Middle Miocene Manuherikia Group sediments in Central Otago. Pole (1993) writes that this material has been considered by Johnson and Hill (pers. comm.) to be consistent with *Symphyomyrtus* or possibly an extinct, early offshoot of this group. The fruits are found in association with fossil leaves, which have a falcate leaf shape characteristic of members of the eucalypt group. However, there is a lack of diagnostic characters or synapomorphies in this material, including an operculum, to confidently refer this material to subgenus *Symphyomyrtus.* Rozefelds (1996) did not consider that there were enough characters even for referral to the eucalypt group more generally. Hill et al. (2017) acknowledged that these fossils required more rigorous assessment, but that superficial resemblance to *Eucalyptus* was very strong and the observable characters were good. These authors assumed the fossils to be a reliable record of the eucalypt group for the purposes of a review of the eucalypt fossil record.

(d) Undescribed: leaves

A number of undescribed myrtaceous leaf fossils have been reported from New Zealand, some of which are informative and important, although most are not confidently compared with living genera. Most recently, Reichgelt et al. (2014) described a number of taxa from impressions with no preservation of cuticle, from the Middle to Late Miocene Double Hill formation in Otago. These taxa referred to as cf. Myrtaceae sp. *A, B, C & D,* and are referred to Myrtaceae on the basis of brochidodromous-acrododromous venation and intramarginal veins, as well as the presence of oil-gland impressions on some of the fossils. These fossils are considered to probably represent species of *Syzygium* or *Metrosideros,* but limited comparisons with extant taxa are demonstrated.

Lee et al. (2012) reports that fossil leaves with close affinities to the genera *Metrosideros* and *Syzygium* occur in the Late Eocene Pikopiko paleoflora in the Western Southland*.* Only the *Metrosideros*-like leaf is figured. Impressions of oil glands are figured on the surface of one of these fossils, but none of these leaves or taxa have yet been described in detail. These fossils may represent a metrosideroid taxon, but with present characters are regarded here simply as Myrtaceae.

Pole et al. (2008) also described seven parataxa of Myrtaceae from dispersed cuticle pieces from the Early Miocene of the Manuherikia group, Central Otago. Linnaean affinities for two taxa are suggested as *Syzygium,* and one *Metrosideros.* For another, a possible *Syzygium* or *Metrosideros* affinity is suggested, and for the remaining three taxa no affinities are suggested. A confident myrtaceous diagnosis is based on the presence of lid-cells. For the two taxa with suggested affinities to *Syzygium,* one is suggested on the basis of a number of characters, with the diagnostic character being anomocytic and 'networked' stomatal complexes, and the only extant species of New Zealand *Syzygium, S. maire* is suggested as being the most similar in overall cuticle micromorphology.

The other with suggested affinities to *Syzygium* is also discussed and compared to fossils of *Syzygium* from the Miocene of Kiandra, NSW (See section 2C) by Tarran et al. (2018, under review, Chapter 5 this thesis), and is distinguished by Pole (2008) as having tangentially oriented subsidiary cells around cyclocytic stomata. These subsidiary cells are typically straight-edged and "give a 'pin-wheel' appearance" to the stomatal complexes. All of the suggested nearest living relatives suggested belong to the now recognized subgenus *Acmena sensu* Craven and Biffin (2010), and cuticles with just these stomata are reported by

Soh and Parnell (2011), who refer to these stomata as 'cyclostaurocytic', in the subgenus *Acmena.* This evidence supports Pole's (2008) taxonomic placement, and suggests that further investigation and perhaps formal description of this taxon may be warranted. The final taxon with affinities to *Metrosideros* is distinguished on the basis of "small, somewhat aligned stomata, and strongly buttressed epidermal cells". This taxon is favourably compared with extant *M. diffusa.* The remaining myrtaceous taxa areidentified here due to the presence of lid-cells, but no generic affinities are suggested.

Pole (2007) described a myrtaceous taxon with affinities to *Metrosideros* from dispersed cuticle recovered from the Pliocene aged Arapito gravels, Karamea. However, this identification is made from a single piece of dispersed cuticle, without lid-cells. As such, this fossil must be considered equivocal, and the taxonomic affinities uncertain.

Pole (1996) described a myrtaceous leaf from the Early Miocene Foulden Hills diatomite. The specimen is a single entire margined, elliptical leaf, with brochidodromous/acrododromous venation with an intramarginal or "longitudinal" vein. However, there is no cuticle present for observation of lid-cells or other characters, which might allow for infra-familial placement.

Pole (1994) described myrtaceous leaves with affinities to either *Rhodomyrtus* or *Rhodamnia* from the Early-Middle Miocene Taratu formation, Otago. This diagnosis is based upon similar first order venation patterns that are found in the genera *Rhodomyrtus* and *Rhodamnia,* with two first order lateral veins that are paired or slightly staggered, which form longitudinal veins. These leaves are compared with illustrations of some extant *Rhodamnia* and *Rhodomyrtus* species, and while these fossils do agree in gross morphology with the extant species illustrated, there are not enough characters here for confident assignment to either of these genera, or to the Myrteae more generally.

Pole (1993) also described a number of unidentified myrtaceous leaves from the Early-Middle Miocene of the Manuherikia group. One of these fossil leaf taxa is compared most favourably with *Metrosideros,* and this identification is based on the presence of longitudinal veins which are supra-basal, flanked basally by external loops or a pair of laterals. This character differentiates this taxon from any of the other Myrtaceae fossil taxa described from this deposit, and is observed to occur in many species of New Zealand *Metrosideros,* although no survey of other extant Myrtaceae for this character is demonstrated. This character may be useful in future for identifying other fossil *Metrosideros* leaves, though this would require a survey of other extant Myrtaceae to ascertain if this character is diagnostically useful, or a potential synapomorphy. Another myrtaceous taxon is referred to as Myrtaceae gen. et sp. indet., different from the other myrtaceous taxa at Manuherikia in that it has several veins diverging from the midrib at the base of the lamina, including the 'longitudinal veins' or intramarginal veins. A number of other myrtaceous leaves were recovered from the deposit, which are morphologically distinct, but the material is too limited or fragmentary to make an extended description or diagnosis.

TABLE 3: REPORTED FOSSIL RECORDS OF MYRTACEAE FROM SOUTH AMERICA

FOSSIL	***TAXONOMIC AFFINIY***	***AGE***	***LOCATION***	***KEY REFERENCES***
SOUTH AMERICA				
(a) Described (living genera): reproductive structures				
Eucalyptus* organ taxa (hypothesised single taxon):** ***Eucalyptus lynchieae Gandolfo et Hermsen ***Eucalyptus caldericola*** Hermsen, Gandolfo et Zamaloa ***Eucalyptus frengueliana*** Gandolfo et Zamaloa	*Eucalyptus*	Early Eocene	Laguna del hunco, Chubut Province, Argentina	Hermsen et al., 2012; Gandolfo et al., 2011; Wilf et al., 2003.
Eucalyptus patagonica Frenguelli	Uncertain	Miocene	Neuquén, Argentina	Frenguelli, 1953
(b) Described (living genera): Leaves				
***Eugenia* sp.**	Uncertain	Middle Eocene	Río Turbio formation, Santa Cruz Province, Argentina	Panti, 2014
***Myrcia* sp.**	" "	" "	" "	" "
***Myrcianthes* sp.**	" "	" "	" "	" "
cf. *Eucalyptus* sp.	Possible eucalypt?	" "	" "	" "
cf. *Campomanesia* sp.	" "	" "	" "	" "
Myrcia deltoidea Engelh.	Uncertain	Early Eocene	Quinamavida paleoflora, Chile	Troncoso, 1992
***Myrcia* sp.**	Uncertain	" "	" "	Troncoso, 1992
Aff. *Agonis* sp.	?Myrtaceae	Miocene	Navidad formation, Chile	Troncoso, 1991
Aff. *Callistemon* sp.	Uncertain	" "	" "	" "
***Amomyrtus* sp.**	?Myrtaceae	" "	" "	" "
8 x *Aulomyrcia* sp.	" "	" "	" "	" "
4 x *Myrceugenia* sp.	" "	" "	" "	" "
***Myrcia* sp.**	" "	" "	" "	" "
(c) Described Macrofossils (form genera): Leaves				
Myrtiphyllum bagualense Dusén	Uncertain	Late Oligocene	Río Leona Formation, Argentinian Patagonia	Césari et al., 2015
***Myrtiphyllum* sp.**	" "	" "	" "	" "
Myrciophyllum paranaesianum Anzótegui & Aceñolaza	Uncertain	Middle-Upper Miocene	Paraná formation, Entre Ríos, Argentina	Anzótegui and Aceñolaza, 2008
***Myrciophyllum* sp. 1**	Uncertain	Middle Miocene	San José Formation, Catamarca Province, Argentina	Anzótegui and Herbst, 2004
***Myrciophyllum* sp. 3**	Uncertain	" "	" "	" "
Myrciophyllum tucumanensis	Uncertain	Middle Miocene	San José Formation, Tucuman Province, Argentina	Anzótegui, 2002
***Myrciophyllum* sp. 1**	Uncertain	" "	" "	" "
***Myrciophyllum* sp. 2**	Uncertain	" "	" "	" "
cfz. *Myrtiphyllum* sp.	Uncertain	Early Eocene	Quinamavida paleoflora, Chile	Troncoso, 1992

3) Critical review of South American fossil records of Myrtaceae

a) Described (living genera): reproductive structures

Hermsen et al. (2012) described three fossil species of *Eucalyptus* from fruits, flowers and leaves, from the Early Eocene of the Leguna del Hunco flora, in Chubut Province Argentina. It is important to acknowledge that, while described as separate fossil species, these are considered as organ taxa. In a phylogenetic analysis of the fossils, Gandolfo et al. (2011) note that while the different organ types are not found in organic connection, they are found repeatedly in the same stratigraphic levels, and quarry sites, in single slabs. From the co-occurrence of these organs, it is inferred that many of these organs were produced by the same plant species. Two of these organ-species are described from reproductive structures, *E. lynchieae* and *E. caldericola*. *E. lynchieae* is represented by fossils with pedicellate flower buds with a globose-ovoid shape, with a hemispherical to obconic hypanthium. There is an obvious calycine scar between the hypanthium, and the corrolline operculum. These fossils are easily distinguished from the second organ taxon *E. caldericola,* with cupular, pedicellate 5 to 6-locular dehiscent capsules, with the valves level with the disk when closed. The fruits are attached in umbellasters of three, five or seven. These fossil reproductive structures are found in association with fossil leaves described as *E. frengueliana,* from long falcate leaves with alternate phyllotaxy, and camptodromous venation with an intramarginal vein. These fossils unequivocally represent *Eucalyptus,* and the phylogenetic analysis finds that they have strong affinities with subgenus *Symphyomyrtus.* They represent the only fossils of *Eucalyptus* reliably identified outside of Australia and New Zealand.

The possibility of *Eucalyptus* occurring in South America had previously been raised by Frenguelli (1953), who described *Eucalyptus patagonica* from a single specimen of what appears to be three short, capsular, pedicellate fruits. These fossils have been examined by Hermsen et al., (2012), and found not to possess enough characters for confident placement into *Eucalyptus,* and have been regarded with scepticism or caution in a number of reviews of the fossil records of *Eucalyptus* (Rozefelds, 1996; Gandolfo et al., 2011; Hill et al., 2017), and are regarded here as uncertain.

b) Described (living genera): leaves

Other than the *Eucalyptus* leaves mentioned above, none of the fossil Myrtaceae ascribed to living genera from leaf material reviewed from South America are found to have enough characters to support a confident diagnosis to a living genus, as such we have only reviewed some of the most recent examples here. The most recently described fossil Myrtaceae leaves placed into living genera in South America are reported by Panti (2014), who described 12 taxa in total from the Middle Eocene of the Río Turbio formation, Santa Cruz Province, Argentina. The taxa are all referred to extant genera *Eugenia, Myrcia, Psidium, Myrcianthes* and possible *Eucalyptus* and *Campomanesia.* No organic preservation exists at this site, and so the diagnoses are based upon gross architectural features and venation. Some of these fossils may represent real records of Myrtaceae and Myrteae, but at the present level of description, comparative work and illustration regard these fossils as equivocal. Vasconcelos et al. (2017) review the reported fossil Myrteae for use in dating their phylogeny of the Myrteae and conclude that “None of these fossil leaves were considered due to the lack of morphological characters that can assign them confidently into Myrteae”, despite nearly all of them being named to living Myrteae genera.

Troncoso (1992) ascribed two fossil species of Myrtaceae to living genera based on leaf impressions from the Early Eocene Quinamavida paleoflora, Chile. He placed one into the previously erected fossil species *Myrcia deltoidea* Engelh., and described the other as *Myrcia* sp. The description of the *M. deltoidea* is brief, and then most favourably compared to another fossil of *Myrciaria acuminata* Engelh. The fossils of *Myrcia* sp. are designated as such based on gross architectural features of pinnate venation, with secondary veins joined together with an intramarginal vein. Fossil material is not compared with any extant taxa, but is compared most favourably with fossil species previously described by earlier researchers like Engelhardt (1981), Berry (1938) and Dusén (1899). Without further investigation, these fossils are regarded as equivocal, and of uncertain taxonomic affinity.

Earlier, Troncoso (1991) described 16 separate myrtaceous taxa from impression material recovered from the Miocene aged Navidad Formation of Central Chile. Among these were two taxa with nearest living relatives from Australia, designated *aff. Agonis* sp. and *aff. Callistemon* sp. The remaining 14 species are placed into living genera of the tribe Myrteae; The author describes one species of *Amomyrtus* sp., 8 taxa are assigned to *Aulomyrcia* sp. (which is now a section within the genus *Myrcia* (Lucas et al., 2011)), 4 taxa are assigned to *Myrceugenia,* and another to *Myrcia* sp. Lamellar/laminar glands are reported on the surface of *aff. Agonis* sp. and *aff. Callistemon* sp., which may be taken to refer to impressions of oil-glands. On the presented evidence there are no characters to justify placement in either of these extant genera. Impressions of laminar glands are also reported on the surfaces of the species of *Aulomyrcia* sp., and some of the species of *Myrceugenia* sp*.* Overall diagnosis of these taxa is based on gross architectural features and venation. Illustrations of these taxa show very little diagnostic detail. Some of these fossils may well represent Myrtaceae, but are here regarded as equivocal, and taxonomic affinities are uncertain. Further investigation of these fossils is warranted, as this is the highest number of species of Myrtaceae fossils reported anywhere in the world, but at the present level of description and illustration they cannot be regarded with confidence.

c) Described (form genera): leaves

There is a long history of describing fossil Myrtaceae to form genera in South America. Most recently, Césari et al. (2015) described two myrtaceous taxa from the Late Oligocene aged Río Leona Formation in Argentinian Patagonia, placing them all in the form genus *Myrtiphyllum* erected by Dusén (1899), to describe entire-margined, coriaceous fossil leaves with a ‘*randnerv*’ (intramarginal vein).

These leaves were compared favourably by Dusén to leaves of extant *Eugenia,* but could not be identified to this genus. Some of the original material described by Dusén (1899) was revisited by Berry (1928), who included it in a description of a fossil species in an extant genus, *Myrcia nitens,* that had been described by Engelhardt (1891), from the Tertiary of Argentina. Césari et al. (2015) correctly observed that Berry (1928) did not have enough evidence to place the Argentinian fossils into a living genus. Accordingly, they chose to continue to operate with Dusén's form genus and published descriptions of two species of *Myrtiphyllum.* One is placed in to the fossil species *Myrtiphyllum bagualense* Dusén, and the other designated *Myrtiphyllum* sp. These fossils are designated to the form genus on the basis of gross architectural features and leaf venation, and comparison with extant taxa is minimal. The fossils described by Césari et al (2015) may represent Myrtaceae, but there are not enough characters demonstrated here for confident placement. They are regarded here as equivocal.

Anzótegui and Aceñolaza (2008) described a myrtaceous fossil taxon from the Middle-Upper Miocene of the Paraná formation, in Entre Ríos, Argentina. The authors place it in the form genus *Myrciophyllum* Engelhardt emended by Anzótegui (2002), a form genus provisionally erected by Engelhardt (1891), who, when describing species of fossil Myrtaceae from the Tertiary of Chile, proposed the form genus *Myrciophyllum,* for leaves that were *Myrcia*-like but where preservation was considered too poor for diagnosis to a living genus. *Myrciophyllum paranaesianum* is described from impression material, and the diagnosis is based upon gross architectural features and venation, and is compared most favourably with extant species of *Psidium* and *Paramyrciaria* from the present-day regional flora. The fossil is also favourably compared with the fossil taxon *Myrciophyllum* sp. 3 of Anzótegui and Herbst (2004). The fossil taxon is illustrated, and venation detail is visible. These fossils may represent a genuine fossil record of Myrtaceae, but at present must be regarded as equivocal on the basis of the presented comparative work, and taxonomic affinity is regarded as uncertain.

Earlier, Anzótegui and Herbst (2004) had described another two myrtaceous taxa from impression material, placing them into the form genus *Myrciophyllum* Engelhardt emend Anzótegui (2002), from the Middle Miocene of the San José Formation outcropping in Catamarca province, Argentina. These fossils are designated to the species *Myrciophyllum* sp*.* 1, and *Myrciophyllum* sp. 3. These fossils were assigned to these species on the basis of gross architectural features, and are compared most favourably with extant taxa from the regional flora; *Myrcianthes cisplatensis* (Cambess.) Berg, and *Paramyrciaria delticulata* (DC.) Kausel respectively. *Myrciophyllum* sp. 3 was compared favourably with fossil taxa *Myrcia angustifolia* Hünicken (Hünicken 1995), which has not been reviewed here due to difficulty obtaining a copy of the publication, as well as *M. chubutensis* Berry and *M reticulato-venosa* Engelhardt. The fossil taxa are illustrated, but little detail can be observed, and no illustrations of comparative material are made. These fossils may represent Myrtaceae, but upon the basis of current comparative work and characters, they are regarded as equivocal and their taxonomic affinities uncertain.

Anzótegui (2002) described three myrtaceous taxa from the Middle-Miocene San José Formation, outcropping in the Tucumán province of Argentina. She emended the original diagnosis of *Myrciophyllum* from Engelhardt's (1891), to encompass impressions of leaves with brochidodromous to acrododromous venation with intramarginal veins, and intersecondary and tertiary veins in a branching pattern. She places the three taxa in this genus, designating them *Myrciophyllum tucumanensis* Anzótegui, *Myrciophyllum* sp. 1 and *Mycriophyllum* sp. 2. The description of these taxa is brief, and based entirely on gross leaf architecture and venation pattern. The illustrations of the fossils support these descriptions, but no comparative extant taxa are illustrated. As such, these leaves do not meet the criteria for confident placement in the Myrtaceae, and are regarded as in need of confirmation.

TABLE 4: REPORTED FOSSIL RECORDS OF MYRTACEAE FROM ANTARCTICA

FOSSIL	*TAXONOMIC AFFINIY*	*AGE*	*LOCATION*	*KEY REFERENCE*
ANTARCTICA				
(a) Described (form genera): Leaves				
Myrciophyllum santacruzensis (Berry) Zastawniak	Uncertain	Late Cretaceous	King George Island, Antarctic Peninsula	Zastawniak, 1994
?Myrtiphyllum bangalense Dusén	Uncertain	Early-Middle Eocene	Fossil Hill flora, Fildes Peninsula, King George Island	Li, 1994
?*Myrtiphyllum* leaves	Uncertain	Early Tertiary	Fildes Peninsula, King George Island	Czajkowski and Rosler, 1986
(b) Undescribed: Reproductive structures				
Myrtaceae-Like Flowers	?Myrtaceae	Late Santonian	Antarctic Peninsula	Eklund, 2003
(c) Undescribed: Leaves				
Cretaceous Myrtaceae leaf	Uncertain	Santonian-early Campanian, Cretaceous	Santa Marta formation, James Ross Island	Hayes, 1999
Myrtaceae-Like leaves	Uncertain	Middle-Eocene	La Meseta Formation, Seymour Island, Antarctic Peninsula	Gandolfo et al., 1998
Myrtaceae-type leaf Impressions	Uncertain	Early-Eocene to Latest-Paleocene	Dufayel Island Group, King George Island	Birkenmajer and Zastawniak, 1986; 1989

4) Critical review of Antarctic fossil records of Myrtaceae

(a) Described (Form Genera): Leaves

Zastawniak (1994) published a fossil species of Myrtaceae, *Myrciophyllum santacruzensis*, from fossil leaf impressions from the Late Cretaceous of the Antarctic Peninsula. These fossils lack organic preservation of cuticular characters that might confirm these as myrtaceous, and as such the only characters that distinguish these leaves as potentially belonging to the Myrtaceae are the pinnate, brochidodromous venation with a distinct intramarginal vein. The name *Myrciophyllum* was used by Zastawniak (1994), who considered that assigning other fossils to the living genus *Myrcia* was untenable, correctly observing that many of the diagnostic characters used by various authors are present in other genera of the Myrtaceae. Zastawniak (1994) therefore transferred the fossil species *Myrcia santacruzensis*, described by Berry (1937a), to *Myrciophyllum santacruzensis* and suggested that other fossils from the Cretaceous of West Antarctica could be referrable to the same form genus. Anzótegui (2002) correctly noted that Zastawniak had published the name *Myrciophyllum* as a new genus, without reference to Engelhardt (1891) and concluded that the name *Myrciophyllum* Zastawniak was a homonym and illegitimate, and the new combination invalid. However, Anzótegui (2002) was in error as Engelhardt's generic name was explicitly provisional ("Provisorische Gattung") and thus invalid according to Article 36.1 of the ICN. Since Zastawniak's name was validly published, Anzótegui's new species *Myrciophyllum tucumanensis* was also validly published, despite her nomenclatural error and her view that the two generic concepts were quite different. Anzótegui also differentiated her concept of *Myrciophyllum* from that of another form genus, *Myrtoidea* (Passalia et al., 2001) from the Cretaceous of Argentina, which had similarly been erected for fossil Myrtales leaves using venation characters from impression fossils. Regardless, the fossils are poorly figured in the paper, and are regarded as of uncertain affinity.

Fossils of another potential myrtaceous form genus are reported by Li (1994), who described myrtaceous fossils from leaf impressions from the Early-Middle Eocene of the Fossil Hill flora of the Fildes Peninsula of King George Island on the Antarctic Peninsula, which are tentatively placed in a previously erected fossil species ?*Myrtiphyllum bagnalense*, however this species epithet is a misspelling of the original ***bagualense*** erected by Dusén (1899, see section 3C). A question mark denotes lack of confidence in this identification. These fossils are only briefly described from gross architectural features, and are poorly figured. These are considered to be of uncertain taxonomic affinity.

More fossils of ?*Myrtiphyllum* sp. have also previously been illustrated by Czajowski and Rosler (1986) from the early Tertiary of the Fildes Peninsula of King George Island. However these fossils are only illustrated and are not described in the text. These are considered as of uncertain taxonomic affinity.

(b) Undescribed: reproductive structures

The only myrtaceous fossil reproductive structures reported from the Late Cretaceous of Antarctica are organically preserved, charcoalified structures published by Eklund (2003), which have been preserved in a marine setting, interpreted as being the mouth of an estuary or deltaic channel. The taxon is represented by three very small specimens. The fossil reproductive structures are interpreted as cup shaped, and potentially calyptrate, leading the authors compare the fossils to modern *Eucalyptus,* though they then state that since the operculum in *Eucalyptus* is derived from the fusion of the tetramerous calyx or corolla, it seems unlikely that it is homologous with the cap like structure of the fossil flowers. Basinger et al. (2007) reviewed the fossils, and noted that the structure at the top of the apex of the fruit appears to represent a tripartite stigmatic area, and therefore cannot be interpreted as a eucalypt-like calyptra. Eklund (2003) claims that it is possible that these fossils may represent an extinct ancestral lineage in the Myrtaceae. If these fossils do genuinely represent Myrtaceae, these represent one of the oldest macrofossils of the family, but the evidence here is not clear.

(c) Undescribed: leaves

A number of undescribed fossil leaves of Myrtaceae have been reported from Antarctic paleofloras. Hayes (1999) described myrtaceous leaves from the Upper Cretaceous of the Santa Marta formation from James Ross Island on the Antarctic Peninsula. Several leaf fragments are illustrated, but are reported as rare in the deposit. The taxon is distinguished by brochidodromous venation, with regularly spaced secondary veins, and a prominent intramarginal vein. The author compares this most favourably with a leaf of *Metrosideros robusta* A. Cunn., but it is improbable that this represents the same taxon or genus. Given so few characters for assignment to family level, and the Cretaceous age of these fossils, the taxonomic affinity of these fossils is uncertain.

Gandolfo et al. (1998) illustrate a Myrtaceae-like leaf from the Middle-Eocene of the La Meseta Formation of Seymour Island on the Antarctic Peninsula. Specimens determined as belonging to the Myrtaceae are reported here, but are not described in great detail. It is difficult to make out much detail on the fossils presented. As such it is difficult to make much comment on these fossils. We regard these fossils as of uncertain taxonomic affinity.

Birkenmajer and Zastawniak (1986) illustrate two specimens of Myrtaceae-like leaves from Early Eocene to Latest Paleocene sediments from the Dufayel Island Group, King George Island. These are illustrated with simple line drawings. The only distinguishing characters are pinnate, brochidodromous venation and an intramarginal vein, which runs close to the margin of the leaf. These specimens are poorly figured, and regarded here as of uncertain affinity.

TABLE 5: REPORTED FOSSIL RECORDS OF MYRTACEAE FROM INDIA

FOSSIL	*TAXONOMIC AFFINIY*	*AGE*	*LOCATION*	*KEY REFERENCE*
		INDIA		
		a) Described (form genera): Reproductive structures		
Callistemonites indicus Bande, R.C.Mehrotra et U.Prakash	Not Myrtaceae	Late Cretaceous-Early Paleocene	Deccan Intertrappean Beds, Madhya Pradesh	Bande et al., 1986
		b) Described (living genera): Leaves		
Syzygium kasauliense Guleria et R.Srivast.	?Myrtaceae	Early Miocene	Kasauli Sediments, Himachal Pradesh	Arya et al., 2001
S. nangalbibrense R.C.Mehrotra	?Myrtaceae	Upper Paleocene	Tura formation, Meghalaya, India	Mehrotra, 2000
S. miocedentalis M.Prasad, J.S.Antal, P.P.Tripathi et V.K.Pandey	?Myrtaceae	Middle Miocene	Siwalik sediments, Nepal	Prasad et al., 1999
S. palaeocumini M.Prasad et N.Awasthi	Uncertain	Middle Miocene	Siwalik sediments, West Bengal	Antal and Prasad, 1997
S. palaeocumini M.Prasad et N.Awasthi	Uncertain	Upper Miocene	Siwalik sediments, Nepal	Prasad and Awasthi, 1996
S. palaeobracteatum N.Awasthi et R.N.Lakhanpal	Uncertain	Possible Neogene?	Bhikhnathoree, Bihar	Awasthi and Lakhanpal, 1990
S. kachchhense R.N.Lakhanpal et Guleria	Uncertain	Lower Eocene	Kachchh, Gujarat	Lakhanpal and Guleria, 1981

5) Critical review of Indian fossil records of Myrtaceae

a) Described (form genera): Reproductive structures

The only fossil reproductive structures from India found in the course of this review of the literature are described by Bande et al. (1986), from the Latest Cretaceous to Early Paleocene Deccan Intertrappean beds of Madhya Pradesh, the form genus *Callistemonites,* and the organ taxon *C. indicus* from cast material. The specimen resembles a spike-like inflorescence made up of ovoid, small fruits enclosed by a persistent cup-shaped perianth. The authors compared these specimens with a number of *Callistemon* (now synonymized to *Melaleuca* (Craven et al., 2014)) and *Melaleuca* species*.* The outward appearance of the fossil specimens is similar to the illustrated infructescences of extant *Melaleuca leucadendra* (L.) L., and *Callistemon lanceolatus* (Sm.) Sweet. There are very few characters observable other than those described by the authors, any characters that would help to confirm the assignment, such as internal fruit characters like the presence of a loculicidally dehiscent capsule below the level of the hypanthium, are not discussed. Subsequently, the taxonomy of *C. indicus* has been questioned and revised, being found to bear a greater resemblance to seeds of a ZIngiberaceous fruit, and have been transferred to the fossil species *Musa cardiosperma* Jain (Bande et al. 1993). The fossils are therefore regarded as not representing Myrtaceae.

However, the fossils are found in association with a range of myrtaceous woods identified by Bande et al. (1986), with several placed in living genera like *Eucalyptus* and *Tristania,* as well as a form genus *Callistemonoxylon.* While some of these woods have been reviewed by other authors, especially the purported fossil *Eucalyptus,* and have been rejected (i.e. Rozefelds 1996, Hill et al. 2017), a recent reinvestigation of these fossil woods by Wheeler et al. (2017) found that while generic placement of these wood fossils was not supported, that they are myrtaceous and share characteristics with the subfamily Myrtoideae. If accepted, these fossils, which range from uppermost Masstrichtian to lower Paleocene in age, represent the oldest macrofossil evidence of the Myrtaceae.

b) Described (living genera): Leaves

A number of myrtaceous fossil leaves from India have been assigned to the living genus *Syzygium* by various authors.

Most recently, Arya et al. (2001) described myrtaceous leaves from early Miocene sediments in Himachal Pradesh, northern India. The authors describe *Syzygium kasauliense* from a well preserved leaf impression with a long lamina, tapering to an acuminate ‘drip tip’. Venation is pinnate, brochidodromous with closely spaced secondary veins and an intramarginal vein. Comparative work is minimal, but leaves are compared most favourably with leaves of *S. jambos* (L.) Alston and *S. heyneana,* now synonymized to *S. salicifolium* (Wight) J. Graham. The gross morphological and architectural features observable are similar to the illustrated extant leaf of *Syzygium* but there are not enough characters demonstrated here for confident assignment to a living genus, and without further supporting evidence are regarded here as only possibly Myrtaceae.

Mehrotra (2000) described *Syzygium nangwalbibrense* from myrtaceous fossil leaf impressions from the Upper Paleocene of the Tura formation*,* in Meghalaya. These fossils are narrow, elliptic, entire margined, with venation described as eucamptodromous with secondary veins joining to become an intramarginal vein. The fossil leaves are not compared directly with any extant taxa, and compared favourably only with other fossil species of *Syzygium* earlier described from India. While they do bear a strong myrtaceous resemblance, and may be regarded as possible Myrtaceae, these characters are not enough for confident placement into a living genus.

Prasad et al. (1999) described *Syzygium miocedentale* from a single leaf impression from the Middle-Miocene lower Siwalik sediments of Nepal. The fossils are narrow, elliptic, entire margined leaves with venation described as pinnate eucamptodromous with secondary veins, which join together to form an intramarginal vein, and are compared most favourably with *S. occidentale* (Bourd.) Gandhi, an endemic species to India. The fossil leaves do bear a myrtaceous resemblance, but are not clearly illustrated. These fossils are regarded here as possible Myrtaceae, but there are not enough characters to support confident placement into a living genus.

Antal and Prasad (1997) described fossils of *S. palaeocumini* from the Middle-Miocene aged middle-lower Siwalik sediments where they outcrop in West Bengal. The taxon is described from a single impression specimen, with a wide, elliptic, entire margined leaf, with eucaptodromous venation and secondary veins that join together to form an intramarginal vein. These fossils were compared most favourably with leaves described earlier, from the Late Miocene of the upper Siwalik Sediments in Nepal, by Prasad and Awasthi (1996) who described the first record of *S. palaeocumini*. The fossils are described from impression material, as narrow, elliptic entire margined leaves with pinnate, eucamptodromous venation with a large number of pairs of secondary veins, which join to form an intramarginal vein. Comparative work is minimal, but the leaves are compared most favourably with *S. cumini* (L.) Skeels. In both cases, the fossils bear some resemblance to extant Myrtaceae leaves, but are poorly illustrated. There are not enough characters here for confident assignment to a living genus, and these fossils are regarded here as of uncertain taxonomic affinity.

Awasthi and Lakhanpal (1990) described *S. palaeobracteatum* from a single leaf impression recovered from sediments with a 'possible' Neogene age from the Bhikhnathoree flora, Bihar. The specimen is described as wide elliptic, entire margined with pinnate hyphodromous venation (only a single, faint and straight midvein), with other details not preserved. No extant species of *Syzygium* have hyphodromous venation. Comparative work is not demonstrated, and from the described characters and illustration of the fossil, there are not enough characters here for confident placement into the living genus, nor to the family Myrtaceae. These fossils are regarded here as uncertain.

Lakhanpal and Guleria (1981) described the first reported fossil record of *Syzygium* from India, with *S. kachchhense* from the Lower Eocene of Kachchh, Western India. The fossil taxon is described from two incomplete leaf impressions, as a entire margined, ovate-elliptic leaf with pinnate, brochidodromous venation, with secondary veins joining together to form an intramarginal vein. The fossils are illustrated, and do bear some gross resemblance to extant Myrtaceae leaves, and are regarded here as possible Myrtaceae, but there are not enough characters to confidently assign these to a living genus.

TABLE 6: KEY FOSSILS OF MYRTACEAE REPORTED FROM NORTHERN HEMISPHERE

FOSSIL	*TAXONOMIC AFFINIY*	*AGE*	*LOCATION*	*KEY REFERENCE*
NORTH AMERICA				
(a) Described (form genera): reproductive structures				
Syzygiodes americana (Lesq.) Manchester, Dilcher et S.L.Wing	?Myrtaceae,	Lower to Middle Eocene	Green River Formation, Colorado	Manchester et al., 1998
Paleomyrtinaea princetonensis Pigg, Stockey et S.L.Maxwell	Tribe Myrteae, Myrtaceae	Middle Eocene	Princeton Chert, British Columbia, Canada	Pigg et al., 1993
(b) Undescribed: reproductive structures				
***Psidium*-like Myrtaceae fruits**	Myrtaceae, ?Myrteae	Paleocene	Sentinel Butte Formation, North Dakota	Crane et al., 1990
EURASIA				
(a) Described (form genera): ***Reproductive structures***				
Palaeorhodomyrtus subangulata (Bowerb.) E.Reid et M.Chandler	Uncertain	Early Eocene	London Clay Formation, England	Reid and Chandler, 1933; DeVore et al., 2006.
(c) Described (form genera): Leaves				
Rhodomyrtophyllum reticulosum **(**Rossm.) Knobloch & Z.Kvayek	Uncertain	Eocene	Many sites throughout Europe, see discussion*	Knobloch et al., 1996; Glinka and Walther, 2003
Rhodomyrtophyllum pasekovicum Vickulin	Uncertain	Late Eocene-Early Oligocene	Pasekovo, Russia	Vickulin, 1999; Vickulin, 2002
Rhodomyrtophyllum sinuatum (Bandulska) Walther	Uncertain	Eocene	Many sites throughout central Europe, see discussion*	Rüffle and Jähnichen, 1976; Mai and Walther, 1985.

5) Critical review of Key Northern Hemisphere fossils of Myrtaceae

a) Described (form genera): Reproductive structures

Two important North American fossils of Myrtaceae with reproductive material have been placed in form genera.

Manchester et al. (1998) described *Syzygioides americana*, from the Lower to Middle Eocene of the Green River formation, Colorado. The specimens described are of compressed twigs with attached leaves and panicles of fruits and flowers. The leaves are described as having pinnate, eucamptodromous venation and a prominent intramarginal vein. The inflorescence is made up of axillary, dichotomously branched panicles with pedicellate fruits. Flowers are perigynous to epigynous with possible stamen filaments arising from the hypanthial rim, and a persistent style with a capitate stigma. The fruits are ellipsoidal, with 5 'closely apressed' tepals, and a persistent style, with persistent capitate stigma. The foliage had been described before in the absence of reproductive material, first by Lesquerex (1872, 1878), as *Eucalyptus? americana,* and then later assigned by MacGinitie (1969) to *Eugenia americana* (Lesquereux) MacGinitie, and the most recent identification was only possible due to the discovery of attached reproductive material. These fossils present an important cautionary tale about describing fossil Myrtaceae leaves to living genera from only gross leaf architectural features. This combination of vegetative and reproductive characters does not closely resemble any known extant genus, and have been reviewed by Basinger et al. (2007) and Wilson (2011), and considered to represent an extinct lineage of Myrtaceae of unknown affinity. It is worth noting that later, Manchester (2001) described a myrtaceous infloresence from the late Eocene of the Florissant Beds of Colorado, a panicle of three flowers with numerous stamens, which also resembles the flowers found attatched with *Syzygioides americana.*

Pigg et al. (1993) described *Paleomyrtinaea princetonensis* from permineralised fossil reproductive structures from the Middle Eocene Princeton Chert, in British Colombia, Canada. Five fruit specimens in total are recovered, as well as over 1000 isolated seeds. Fruits are berries, estimated to contain over 100 seeds each. Fruits appear unilocular, but extensions from the fruit wall in one specimen are interpreted as septa, and fruits are estimated to be five-locular. Placentation is parietal, and numerous seeds are campylotropous, with a curved embryo cavity. The fruit wall is three layered, and includes a pulpy endocarp. The fruits and seeds are compared most favourably with genera *Mosiera* and *Psidium*, in the tribe Myrteae. These fossils have been reviewed by Basinger et al. (2007), and considered to appear to represent tribe Myrteae, and Wilson (2011) considered that these could confidently be placed in the tribe Myrteae. These fossils have been a popular choice for calibrating molecular phylogenies of fleshy fruited Myrtaceae, with Vasconcelos et al. (2017) most recently using the fossil to calibrate the *Myrtus* and the 'Main Neotropical Lineage' clade of the Myrteae in their phylogeny.

Reid and Chandler (1933) described fossil fruits of myrtaceous affinity from the Early Eocene of the London Clay formation, England, naming them *Palaeorhodomyrtus subangulata* The fossils were then revisited by Collinson (1983), who also considered that they might be Myrtaceae. Most recently, these fossils were reinvestigated by DeVore et al. (2006) using high-resolution X-ray tomography, and suggest that the higher resolution allowed by this technique confirms placement in the Myrtaceae. These fossils were subsequently reviewed by Basinger et al. (2007), who regarded the fossils with scepticism, noting that the presence of a persistent five-partite calyx that strongly encloses the fruit and does not agree with any known myrtaceous fruit. On this basis, the fossils must be considered as of uncertain affinity.

b) Undescribed: Reproductive structures

Crane et al. (1990) describe fossil fruits and seeds from the Paleocene of the Sentinel Butte formation of Almont, North Dakota. The fruits consist of compressed and globular with a thin and poorly preserved fruit wall, surrounding seed bearing tissue filled with numerous small seeds. Seeds are reniform, and slightly laterally flattened. These fruits are considered to closely resemble those of *Psidium guineense* Sw., and other species within the genus *Psidium,* and the authors claim that these fossils are securely placed in the Myrtaceae, subfamily Myrtoideae, but that determination of a more precise taxonomic position will require better anatomical comparison with a large number of extant *Psidium* species. These fossils are reviewed by Basinger et al. (2007) and are considered to appear to represent fruits of Myrteae. They are not however reviewed by Wilson (2011). Pigg et al. (1993) later studied specimens of these fossil fruits and seeds, and considered them to represent the fossil genus *Paleomyrtinaea,* but could not be confidently placed in the species *P. princetonensis* due to their older age and a lack of key comparative characters.

c) Described (form genera): Leaves

Rhodomyrtophyllum is perhaps the most widely published fossil form genus of Myrtaceae, with a long taxonomic history, confined to the European literature. Its origins trace back to the first attempt at identifying fossil myrtaceous leaves with organic preservation, using leaf architecture **as well as** cuticle from the London Clays of England, by Bandulska (1931), who described three species of fossil Myrtaceae, placing them in living genera, with two fossil taxa from deposits dating to the Eocene of Bournemouth, England (*Rhodomyrtus sinuata* and *Tristania bournensis*) and one from a Pliocene site in Tuscany, Italy (*Tristania toscana*). Many of the (very few) extant taxa used for comparison, none of which were cross-referenced to herbarium vouchers, have been subsequently assigned to other genera, making these identifications doubtful. However, *Rhodomyrtus sinuata* (Bandulska) Bandulska, which had already been combined and synonymized with a fossil taxon, *Dicotylophyllum sinuatum* earlier described by Bandulska (1923) was then revisited by Rüffle and Jänichen (1976), who synonymized it with a number of other fossil forms from central European paleofloras. Rüffle and Jänichen also erected the new form genus *Rhodomyrtophyllum* for leaves that looked like *Rhodomyrtus*, but did not possess enough characters for confident placement to the genus. *Rhodomyrtus sinuata* (Bandulska) Bandulska was then transferred to the fossil form genus *Rhodomyrtophyllum* Rüffle and Jänichen, by Mai and Walther (1985), who in describing leaves from 24 Upper Eocene and two Middle Eocene sites of the Weißelster Basin point out uncertainties in the demarcation of the species established by Rüffle and Jänichen (1976), and synonymize all species reported by Rüffle and Jänichen to *Rhodomyrtophyllum sinuatum* (Bandulska) Walther, except for two species, *R. tristaniodes* and *R. angustum.*

Knobloch et al. (1996) then synonymized *Rhodomyrtophyllum sinuatum* (Bandulska) Walther with a number of other fossil forms, including *Phyllites reticulosus* Rossmaessler (1840) and, according to the rules of priority, changed the name to *Rhodomyrtophyllum reticulosum* (Rossm.) Knobloch & Z. Kvaček, with fresh evidence from the Late Eocene flora of the Staré Sedlo Formation in

Bohemia. These leaves all still lack intramarginal veins, and Knobloch et al. (1996) themselves note that "*Mesophylldrüsen*", the mesophyllary glands, which are described as very characteristic of Myrtaceae, and characterized by differently shaped epidermis cells, have never been detected in this fossil species. They acknowledge that the complicated stomatal apparatus also speaks against the association with the Myrtaceae, which they state usually have simple paracytic-cyclocytic or anomocytic stomata.

Glinka and Walther (2003) synonymized the remaining species of *Rhodomyrtophyllum* sensu Rüffle and Jänichen (1976), with *Rhodomyrtophyllum reticulosum* (Rossm.) Knobloch & Z. Kvaček, analysing a dataset of nearly 500 leaves from the Weißelster Basin in central Germany. Contradicting this, Knobloch et al. (1996), describe mesophyllary glands, as important cuticular characters of *Rhodomyrtophyllum reticulosum,* but the 'glands' illustrated by Glinka and Walther (2003), on both the fossils and extant species of Myrtaceae do not satisfactorily correspond morphologically with lid-cells *sensu* Lange (1980) depicted by other authors, and actually appear to represent damaged cuticle, or cork-warts.

Vickulin (1999) described *R. pasekovicum* from Late Eocene/Early Oligocene sediments in Pasekovo, Russia, and Glinka and Walther (2003) argue that there were enough different characters here to support a continued position for this taxon as a different species to *Rhodomyrtophyllum reticulosum* (Rossm.) Knobloch & Z. Kvaček. Diagnosis by Vickulin (1999) takes into account both architectural and cuticle micromorphological characters, but none of the cuticular micromorphological characters employed in the diagnosis are demonstrated as convincing synapomorphies for Myrtaceae. For instance, Vickulin (1999) does not describe or define lid-cells or oil-glands (*sensu* Lange 1980), which are defining micromorphological characters of the Myrtaceae, but includes "giant stomata with distinct cuticular striations" as a defining character, despite giant stomata with such striations being found on cuticles across many angiosperm families (Wilkinson, 1980).

As far as can be understood, through all of this nomenclatural change, the assignment of these fossils to Myrtaceae is based on the initial assignment of *Rhodomyrtus sinuata* Bandulska (1931) to the Myrtaceae, which is simply assumed to be correct, and is not justified on the basis of the characters described and illustrated by Bandulska (1931). None of the more modern authors, such as Vickulin (1999) or Glinka and Walther (2003) who have subsequently described species of *Rhodomyrtophyllum*, despite demonstrating at least some comparative work with extant taxa, have illustrated convincing characters or synapomorphies for Myrtaceae. Yet it is worth noting that *Rhodomyrtophyllum* species have come to be considered to be a characteristic taxon of the central European Eocene, are reported widely across the Tertiary of Europe, and are utilised in a number of paleoenvironmental studies (Walther, 1994; Desa et al., 2010; Grein et al., 2010; Velitzelos et al., 2014).

On the available evidence, none of these *Rhodomyrtophyllum* fossils can be regarded as confidently assigned to the Myrtaceae. For the purposes of this review they are considered as possible Myrtaceae, and are deemed deserving of additional investigation.

DISCUSSION

This review finds that only a handful of Myrtaceae vegetative and reproductive macrofossils reported from across the globe have been identified securely with diagnostic characters. All of the fossils that have been formally described into extant genera are from the Southern Hemisphere, including six fossils described from Australia; three fossil specimens of *Metrosideros, M. leunigii, M. dawsonii* and *M. wrightii,* and one species of *Syzygium, S. christophelii* that are described in this thesis (Chapters 3,4,5) and two fossil species of *Euclyptus, E. bugadliensis* and *E. kitsonii* [See Table 1]. The only other fossil Myrtaceae confidently described to a living genus are the fossil *Eucalyptus* species from South America, *E. frengueliana, E. lynchieae* and *E. caldericola,* described from the Eocene of Argentina, though these have been considered to potentially represent a single taxon in the phylogenetic analysis by Gandolfo et al. (2011). Two fossil form genera have also been proposed which allow for secure phylogenetic placement to at least tribal level, both for fossil reproductive structures, *Tristaniandra alleyi* [Table 1], with affinities to the tribe Kanieae from the Eocene of South Australia, and *Paleomyrtinaea princetonensis* [Table 6] from the Eocene of North America, with affinities to the tribe Myrteae.

A number of important, relatively well dated, yet formally undescribed fossils of Myrtaceae have also been reported in the literature, from Australia, New Zealand and North America are also sufficiently well illustrated and discussed to be confident of probable generic or tribal identifications; notably, the "Redbank Plains' *Eucalyptus* fruits which provide the potentially oldest record of the genus in Australia [Table 1], a number of fossil reproductive structures from New Zealand with characters that suggest placement in *Metrosideros* and *Eucalyptus* [Table 2], and the *Psidium*-like fruits described by Crane et al. (1990), subsequently considered to belong to the fossil genus *Palaeomyrtinaea* by Pigg et al. (1993) from the Paleocene of North America [Table 6]. It is worth noting, that most of these confident taxonomic identifications to date are based on fossil reproductive material.

The majority of fossil Myrtaceae leaves that have been described in extant genera in the literature are assigned on the basis of gross leaf architecture and venation, and do not meet our criteria for confident placement. Most of these from the global literature reviewed here are considered either uncertain or only possible Myrtaceae. A large subset of fossil leaves previously attributed to living genera have been omitted from this review in the interests of length and time, some from the century before last, and some from the previous century, especially those identified from throughout the Tertiary of the America's by Berry (1918; 1922b, a; 1928; 1937b, a; 1938). The majority of these fossils were placed into extant neotropical genera, such as *Psidium* and *Myrcia,* but again are done so on the basis of gross leaf morphology, with poor comparative work and minimal illustration. Further re-investigation of these fossils may find that some of these identifications are warranted, but they are considered of uncertain taxonomic affinity here.

A number of form genera for fossil leaves of Myrtaceae have also been proposed where formal identification was attempted, but leaves could not be confidently placed in living genera. The value of fossils placed into these form genera, in most cases, is minimal. It is interesting to note the difference between the fossil record of Australia and New Zealand compared with the rest of the world, where it appears that in Europe and South America that there is a much greater tradition of modern researchers adhering to names erected in older paleobotanical work. Species diagnoses for fossil organ genera, such as *Myrtiphyllum* Dusén (1899), and *Myrciophyllum* Engelhardt (1891), are still being published by modern authors. Elsewhere in the Southern Hemisphere, the earliest published Myrtaceae fossil form genus appears to be by Unger (1864), who described *Myrtifolium* from Tertiary sediments in New Zealand, and in Australia, where Ettingshausen (1888) described a large number of fossil taxa from the Tertiary of Australia, including two form genera, *Myrtonium* for leaves that were Myrtaceae-like, and *Callistemonophyllum* for leaves that were *Callistemon*-like (hence Myrtaceae). He placed several species in these form genera as well as assigning several fossil leaves to the extant myrtaceous genus *Eucalyptus.* Deane (1902) described yet another form genus, *Tristanites,* for leaves that were *Tristania* like. None of these early form genera or fossil identifications have found favour with modern researchers in Australia and New Zealand, and have largely been neglected in more recent research regarding the identification of myrtaceous foliar remains.

Paleobiogeography and support for a Gondwanic Origin— Despite so few fossils having been confidently described to generic or even tribal levels, the macrofossil record when examined in its entirety supports the hypothesis of a Gondwanic origin for the family. Most recent phylogenetic models suggest a Late Cretaceous origin of the family (Thornhill et al. 2015), although the exact location of this event in Gondwana is still uncertain. Modelling by Berger et al. (2016) interprets an origin of the Myrtaceae in Africa in line with the oldest known microfossils, and a subsequent long distance dispersal and establishment (LDDE) event to Australia. However, recent review of Myrtaceae wood macrofossils with affinities to the subfamily Myrtoideae from India by Wheeler et al. (2017) suggest that these represent the oldest known macrofossils of the family, and may support an East Gondwanan origin. Only further fossil evidence will increase certainty around this issue.

To accept a Gondwanic origin for the family, one first has to explain the distribution of Myrtaceae in the Northern Hemisphere. Thornhill et al. (2015) suggest that if a Gondwanic origin of the family is accepted, the Laurasian Myrtaceae must have originated from a northward long distance dispersal event, and that the simplest explanation for the distribution of *Myrtus* in Eurasia is a single long distance dispersal event during the Eocene. The most recent phylogeny by Vasconcelos et al. (2017) suggests that the Central and northern South American neotropical lineage of Myrteae are sister to *Myrtus,* and so virtually all of the sister taxa to *Myrtus* are concentrated here, suggesting a likley origin of the group. However, Thornhill et al. (2015) also suggest that the Myrtaceae may have had a broader Northern Hemisphere distribution in the past, citing the North American fossil evidence of *Paleomyrtinaea princetonensis* (Pigg et al., 1993) and *Syzygioides americana* (Manchester et al., 1998)*,* as well as microfossil evidence of *Myrtaceidites solidus* from the Early Tertiary of Canada (Jarzen, 1982; Sweet, 1986). Thornhill and Macphail (2012) note that "no *Myrtaceidites solidus* grains have been found associated with *Paleomyrtinaea princetonensis* or *Syzygioides americana* specimens" and that therefore any possible link between the North American macro- and microfossil record remains unclear. Nevertheless, the macrofossil record supports both hypotheses when also taking into account the Paleocene and Eocene *Psidium*-like fruits of *Palaeomyrtinaea* described by Crane et al. (1990) and by Pigg et al. (1993).

The reported fossil records of Myrtaceae leaves from the western Laurasian landmasses are less clear. The only carpological fossil material from Europe much less clearly represents Myrtaceae, with the only convincing identified fossil, *Palaeorhodomyrtus subangulata,* first described from the London Clay by Reid and Chandler (1933), having been revisited by DeVore et al. (2006), and being treated with scepticism by Basinger et al. (2007) as not having affinities with any known myrtaceous fruits. A long published record of *Rhodomyrtophyllum* species, assigned to the family Myrtaceae by a number of authors, exists from central Europe and Russia from Paleogene deposits. This review finds that the evidence that these fossil leaves represent Myrtaceae is not entirely compelling, and greater comparative work needs to be demonstrated with extant taxa before these fossils can be considered convincing records. Nevertheless, these fossils represent a plausible hypothesis that Myrtaceae were widespread in Europe during the Tertiary, and if they are Myrtaceae, their presence in Europe is clearly not inexplicable. Supporting the hypothesis that fleshy-fruited Myrtaceae had dispersed to the western Laurasian landmasses during the Paleogene, are some of the most convincing fossil myrtaceous wood specimens with affinities to the tribe Myrteae from the Eocene of China, suggesting that fleshy-fruited Myrtaceae arrived during a similar timeframe to those in North America (Oskolski et al., 2013).

The dispersal of Myrtaceae to the Northern Hemisphere almost certainly occurred as a result of long distance dispersal, facilitated by flying birds or possibly mammals (Thornhill et al., 2015), and this may have occurred by the Paleocene, or possibly earlier, as the fossils of Crane et al. (1990) suggest. The convincing record of fleshy fruited Myrtaceae from several parts of the Northern Hemisphere, along with the absence of any convincing fossils of capsular-fruited genera (which in most cases have much more limited ability for dispersal) from the Northern Hemisphere supports the Gondwanic origin hypothesis, especially in the light of an understanding that fleshy fruited Myrtaceae evolved from dry/capsular fruited ancestors (Biffin et al., 2010).

Conclusions—This review finds that the majority of Myrtaceae vegetative and reproductive macrofossils published in the last century are equivocal. Only a handful of fossils have been convincingly shown to have affinities with extant tribes or genera, and even fewer have been placed convincingly via formal description into living genera to date. Most of the fossils that have been confidently placed into living genera are fossils of (or with) reproductive structures, while fossil leaves generally do not meet our criteria for confident identification. This review demonstrates that the macrofossil record supports a Gondwanic origin for the family, in line with previous biogeographic models and evidence from the microfossil record. The fossil record suggests that fleshy-fruited Myrtaceae began radiating into the Northern Hemisphere by as early as the Paleocene, and perhaps even earlier. Much more work is needed to achieve confident identifications of Myrtaceae macrofossils, particularly of fossil leaves, to interpret the complex paleobiogeography of the family.

Chapter 3:

Oldest record of *Metrosideros* (Myrtaceae): Fossil flowers, fruits and leaves from Australia

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Contribution to the Paper	Peter is an expert on the taxonomy of this group, and assisted with characterisation of the morphological characters of fossils and of extant material, as well as providing feedback on taxonomic and nomenclatural issues encountered throughout manuscript preparation. Peter edited the manuscript, and assisted with discussion and analysis of the results.		
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Contribution to the Paper	Bob originally collected much of the fossil material worked on in this paper, and as curated collections of other fossil material used in this paper not collected by himself. Bob provided feedback on the manuscript at all stages of preparation, and assisted in the discussion and interpretation of results.		
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ABSTRACT

PREMISE OF THE STUDY: Myrtaceous fossil capsular fruits and flowers from the northwest of Tasmania, in the Early Oligocene-aged Little Rapid River (LRR) deposit, are described. The reproductive organs are found in association with Myrtaceous leaves previously thought to belong to a fleshy-fruited genus, *Xanthomyrtus* at both LRR, and an Eocene Tasmanian site at Hasties, which are reassessed with fresh morphological evidence.

METHODS: Standard Light Microscopy (LM) and Scanning Electron Microscopy (SEM) were used to investigate cuticular characters and an auto-montage camera system was used to take high-resolution images of fossil and extant fruits. Fossils are identified using a nearest living relative (NLR) approach.

KEY RESULTS: The fossil fruits and flowers share a number of characters with genera of capsular-fruited Myrtaceae, in particular sharing several synapomorphies with species of *Metrosideros* subg. *Metrosideros* (tribe: Metrosidereae). The fossil is here described, and named *Metrosideros leunigii,* sp. nov.

CONCLUSIONS: This research establishes the presence of *Metrosideros* (aff. subg. *Metrosideros*) in the Eocene-Oligocene (~40-30 mya) of Tasmania, Australia. This is the first fossil record of *Metrosideros* in Australia, as well as the oldest conclusive fossil record, and may provide evidence for an Australian origin of the genus. It is also yet another example of extinction in the Tertiary of a group of plants on the Australian mainland that is only found today on nearby Pacific landmasses.

INTRODUCTION

One of the great remaining biogeographical puzzles for Southern Hemisphere phytogeographers concerns the capsular-fruited tribe Metrosidereae, of the family Myrtaceae (Basinger et al., 2007). The genus *Metrosideros* is one of the most widespread plant genera in the Pacific. Dawson (1984) regarded *Metrosideros* as containing two recognizable subgenera. The subgenus *Metrosideros* (~26 spp.) is the most widely spread, growing from the sub-Antarctic islands of New Zealand to Bonin Islands near Japan and to Hawaii (Fig. 1A). Subgenus *Mearnsia* (~24 spp.) in contrast, is more restricted in its distribution, occurring on the Gondwanic landmasses of New Zealand, New Caledonia, New Guinea, as well as the Solomons and the Philippines. The puzzle is that despite the genus being one of the most widespread in the Pacific, it is absent from the Australian mainland, and despite a clear propensity of at least subg. *Metrosideros* toward long-distance dispersal (Wilson, 1996; Wright et al., 2000, 2001). Though it is interesting to note that *Metrosideros* is technically present in Australia, as a political unit, but not a geologic or biogeographic one, since Lord Howe Island, a political territory of Australia, has two endemic species of *Metrosideros*.

The most recent circumscription of the genus by Pillon et al. (2015) has posited an expanded genus that includes the two other genera commonly recognized within the Metrosidereae, the monotypic South American *Tepualia* and the New Caledonian *Carpolepis,* which would make the genus even more widely spread. This research also challenges the monophyly of subgenus *Mearnsia,* as anticipated by Wilson (1996). Pillon et al. (2015) acknowledge that the deep relationships within the tribe Metrosidereae remain poorly resolved, and it will require more research to establish these phylogenetic relationships. For the purposes of our study, we have continued to operate with the narrow circumscription of *Metrosideros* with two subgenera, based largely upon carpological and floral morphological characteristics, which is adequate for the purposes of this fossil identification (Dawson, 1984).

Wilson (1996) suggested that New Zealand is the landmass where the two subgenera of *Metrosideros* first diverged, and was the site of initial radiation of subg. *Metrosideros.* Wright et al. (2000) considered that a long fossil record, coupled with the absence of any *Metrosideros* fossils on other Gondwanic landmasses, is evidence to support a New Zealand origin, in conjunction with their molecular data which suggest multiple radiation events with New Zealand at the epicenter, and *M. umbellata* Cav. as basal to three major clades within the subgenus. Lee et al. (2012) also consider that the molecular data of Wright et al. (2000, 2001) support a postulated New Zealand origin. However, this evidence for a New Zealand origin of the genus is largely equivocal, since none of these studies exhaustively sampled *Metrosideros*, or the species of *Carpolepis* and *Tepualia.* The study by Pillon et al. (2015) is the only study to have sampled all three genera, but the resolution is still too low to infer a geographical origin of the genus.

The 'long fossil record' discussed by Wright et al. (2000) was primarily based on pollen fossils, before the discovery of the stratigraphically oldest, unequivocal *Metrosideros* macrofossils, capsular fruits from the Miocene-aged Manuherikia deposit in New Zealand by Pole et al. (2008), which represent subgenus *Mearnsia*. *Metrosideros*-like leaves and pollen have also recently been reported from Eocene sediments at Pikopiko in southern New Zealand, though the fossil leaves are not diagnosed (Lee et al., 2012). The value of the fossil pollen record must be questioned in light of a recent palynological survey of the Myrtaceae by Thornhill et al. (2012a) who suggest that "...in comparison with other Tribes of Myrtaceae, Metrosideros pollen are not dissimilar to Melaleuceae, Syzygieae, Eucalypteae and Xanthostemoneae."

Metrosideros fossils have never been described from Australia. Pole (1992) described mummified Myrtaceae leaves from the Late Eocene Hasties flora in Tasmania, and tentatively compared them to those of the fleshy-fruited genus *Xanthomyrtus* (tribe Tristanieae). Pole regarded these fossils as identical to a similar leaf fossil described from Oligocene sediments at Pioneer by Hill and Macphail (1983). This identification was extended to unpublished leaf fossils of the same taxon discovered from Early Oligocene sediments at Little Rapid River (Fig. 1B).

The description of the Hasties fossils by Pole (1992) was brief, and was part of a very broad, paleofloristic analysis. The fossil comparison was based on a comparative cuticular morphological analysis, using the single character of 'stomatal clumping'. Pole stated that without broader cuticular analysis of Myrtaceae, "the Hasties fossils are merely compared to *Xanthomyrtus*" (Pole, 1992). The fossil discovery has been reported in subsequent literature, for example, Carpenter et al. (1994) write, in their account of the Cenozoic vegetation of Tasmania, that *"...Leaves comparable to* Xanthomyrtus" occur. Wilson (2011) writes that the "leaf fossil attributed to *Xanthomyrtus*, from the Eocene of northeastern Tasmania, does seem to show strong similarities to leaves of extant taxa from New Caledonia and Malesia." It is interesting to note that after *Metrosideros*, *Xanthomyrtus* is one of the most widely distributed genera of Myrtaceae in the Pacific, though with a closer to Gondwanic distribution, similar to that of *Metrosideros* subg. *Mearnsia,* but with a distribution more heavily skewed toward New Guinea (Wilson, 1996).

Since Pole's (1992) treatment of the Hasties flora, similar *Xanthomyrtus*-like taxa have been proposed at other Cenozoic, southeastern Australian sites such as Cethana, Tasmania (Hill and Scriven, 1997), and Kiandra, New South Wales (NSW) (Macphail et al., 1994). Fossils attributed to cf*. Xanthomyrtus* were one of only four angiosperm taxa found in multiple Oligocene-Miocene sites in Tasmania, Cethana, LRR and Hasties, in a Nearest Living Relative (NLR) paleoclimate analysis (Hill and Scriven, 1997). Whether these specimens represent an identical taxon, or closely related taxa is uncertain, though they clearly represent a group that was once widespread in southeastern Australia.

In this paper, we re-examine the *Xanthomyrtus*-like leaf fossils first described by Pole (1992) along with the fossil leaves and newly discovered, *Metrosideros* capsular fruits and flowers from Little Rapid River (LRR), bringing Pole's (1992) tentative diagnosis of *Xanthomyrtus* into question. Investigation of the foliar fossils tentatively identified from LRR and Hasties reveal previously undescribed details of the cuticular morphology, which strongly suggest a capsular-fruited, rather than fleshy-fruited, NLR. While no organic connection among the fossil leaves, fruits, and flowers exists, the possibility that both the leaves and fruits belong to the same taxon is discussed, and the possibility that all of these fossils in fact represent the regionally extinct *Metrosideros* must be considered.

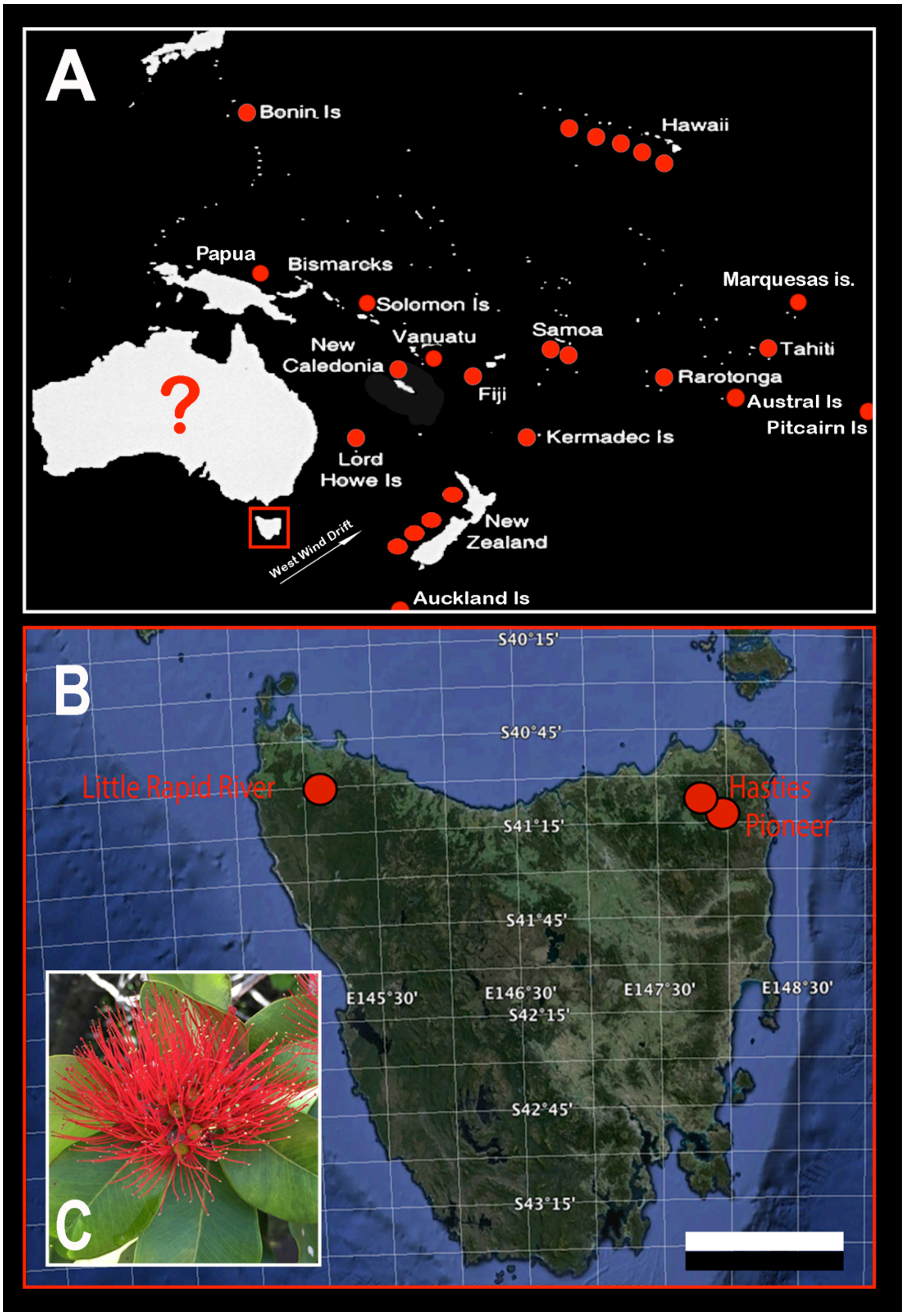

FIGURE 1: A) Distribution of *Metrosideros* subg. *Metrosideros* in the Pacific based on maps from Wright et al. (2000, 2001) with a question mark in Australia indicating its absence from the Australian mainland. **B)** Map of fossil sites in Tasmania. Little Rapid River (LRR) in the north-west is Early Oligocene in age; the Hasties deposit in the north-east, is a Middle-Late Eocene deposit; Pioneer, where a single leaf was found, is late Oligocene/Early Miocene. [Scale bar approx.100 kilometres.] Map data: Google, DigitalGlobe 7.1.2.2041. **C)** Flowers of *Metrosideros robusta* from New Zealand, courtesy of John G. Conran.

FOSSIL SITES AND AGES

Little Rapid River— The fossil-bearing deposits are assigned palynologically to the *Proteacidites tuberculatus* zone, providing strong evidence for an Early Oligocene age (~30 mya) for the fossil-bearing sediments (Macphail et al., 1994). The site is located in northwestern Tasmania, 35 km south of Smithton, c. 90 m above sea level. The fossiliferous sediments consist of two main horizons of fine sand and silt (referred to henceforth as LRR1 and LRR2 respectively) separated by a thin band of lignite. It is likely that the deposits were laid down in a lacustrine environment, which underwent some changes in depositional regime between the two main horizons (Wells and Hill, 1989). The fossil assemblage represents a diverse rainforest community that grew in an environment of high, even rainfall and moderate temperatures. There is a particularly high diversity of *Nothofagus* species, including *Nothofagus* subgenus *Brassospora* at these deposits, and many angiosperm, fern, and conifer macrofossil taxa have also been recovered from the sediments (Hill and Scriven, 1997).

The 40 foliar fossils and 7 fruit fossils from the LRR1 deposit were stored in ethanol and given collection codes (see Table 1 , Fig. 1C, D).

Hasties— The Hasties sediments have been placed within the *Nothofagidites asperus* zone, providing a Middle-Late Eocene age (~40 mya) (Bigwood and Hill, 1985). The fossil deposit is located in northeastern Tasmania (Pole, 1992), with the plant remains occurring in a carbonaceous/slightly lignitic unit, within several meters of quartzose gravel.

Fossils were collected and stored in the University of Adelaide David Blackburn Palaeobotany collection. Twenty-five foliar fossils and fragments from the Hasties collection were mounted in phenol-glycerine jelly on glass slides, with several prepared cuticles stained with safranin O, prepared by Pole for his (1992) account of the flora (see Table 1, Fig. 1A, B).

The fossil leaves from the two deposits occur as mummified cuticular envelopes, preserving cuticular tissue and details of cuticular structure of the leaves.

Occasionally architectural features of venation are preserved.

Pioneer— While no material from the Oligocene aged Pioneer deposit was directly studied in this research, Pole (1992) compared the Hasties cf. *Xanthomyrtus* fossil leaf with a single leaf found at the Pioneer deposit considered to be identical.

MATERIALS & METHODS

Extant capsular fruits and flowers were observed, and collected for comparison, from vouchers in the National Herbarium of New South Wales, the State Herbarium of South Australia, and the University of Adelaide Herbarium (accession numbers in Appendix 1). Leaf cuticles were prepared from 175 species of extant Myrtaceae from across the tribal (16/16 tribes) and generic diversity (52/ 130 genera) following the phylogenies constructed by Thornhill et al. (2012b) and Biffin et al. (2010).

Cuticle slides were prepared from the extant and fossil leaves and mounted on glass slides for standard light microscopy and mounted on aluminum stubs for analysis under the Philips XL30 FEG field emission scanning electron microscope (FEI, Eindhoven, Netherlands). Fossil and extant leaf cuticles were cleared in a 20% aqueous solution of chromium trioxide (CrO_3) for several days until internal leaf tissue or detritus had been loosened and macerated. Any adhering internal tissue was removed with fine paintbrushes under a dissecting microscope. Cuticles were stained with a saturated solution of Sudan Black in ethanol.

Fossil fruits were mounted on aluminum stubs and photo-graphed using SEM, as well as under an Auto-montage Visionary Digital BK+ imaging system with a Canon EOS 7D 18 megapixel camera. Images were produced using PMax image stacking in Zerene Stacker, PMax software (Zerene Systems LLC, Richland, Washington, USA).

Both the leaf cuticle and fruit images from SEM and Automontage photography were cropped, resized, and adjusted for contrast and brightness in Adobe

Photoshop CS6 (Adobe Systems, San Jose, California, USA).

Fossil taxa are described using a Nearest Living Relative (NLR) approach. General taxonomy of the Myrtaceae follows Wilson (2011). Specific *Metrosideros* taxonomy follows Dawson (1970a, 1976, 1984).

TABLE 1: Fossil specimens and reference codes for all fossil material in present study. Fossil specimens are stored in the David Blackburn Paleobotany Collection, University of Adelaide.

Fossil Deposit	**Fossil Leaf Specimens**	**Fossil Fruit & Flower Specimens**
Hasties (Eocene)	**SB**-090, 093, 095, 096, 097, 098, 099,100,101,102,103,104,105,106,107,109,111, 112,115,139,140,141,142,143,145 (*25 Total*)	**None**
Little Rapid River (Oligocene)	**LRR2-** 1223, 1224, 1225,1231,1232,1233,1234,1235,1236,1237,1238,1239,1240,1241,1242,1244,1245,1251,1252,1253,1254,1255,1262,1263,1264,1265 **LRR1-** 006,012,110,111,191,425,426,428,429,898,899, 900,913,1924 (*40 total*)	**FRUITS-LRR1** 712, 1204, 1211,1350,13921393, 2212 (*7 total*) **FLOWERS-LRR1**-4089, 4156 (2 total)

DESCRIPTION

Floral and fruit morphology— The fossil fruits are capsular, three-locular, with the free part of the capsule strongly exserted from the hypanthium, making up 1/2 to 2/3 of the length of the fruit, which is loculicidally dehiscent when mature (Figs. 2, 3). These characters in combination are diagnostically Myrtaceous, and are indicative of genera within the tribes *Kanieae* and *Metrosidereae* (Wilson, 2011). The capsules range from 2 to 3 mm in length, and are approximately 2 mm wide, although width is a slight overestimate due to flattening of the fossils during fossilization. One of the fossil flowers appears slightly smaller at around 1.5 to 2 mm in length, but this difference in size is attributed to the fossil flower having retained its three-dimensional shape while all of the others have been flattened during fossilization Fig. 2. As seen in Fig. 2, the fossil flowers are mostly missing sepals (Fig. 2A, B), but these sepals would have numbered five. On one specimen, LRR1-4089, (Fig. 2A, D), elliptical petal (P) scars are visible between sepals.

Also visible on specimen LRR1-4089 are scars of staminal bases. These stamen scars number <15 on the hypanthial rim, which is prominent and appears as a swollen 'lip' around the capsule (compare with Fig. 2E, F, partially mature fruits/flowers of two species of *Metrosideros* subg. *Metrosideros, M. kermadacensis* W.R.B.Oliv. and *M. robusta* A.Cunn, respectively). The stamens appear not to be fused, rather occurring in a single whorl inserted on the inner surface of the prominent hypanthial rim, above the sepals (compare with extant senescing flower of *Metrosideros kermadacensis* (Fig. 2E) & *M. robusta* (Fig. 2F)). It is important to note the differences between the species of *Kanieae* and *Metrosideros* represented in Figs. 3 and 4, with the presence of the prominent hypanthial rim in *Metrosideros*, and the relative position of the sepals to the rim, as highlighted in Fig. 4.

The prominent hypanthial rim persists into the mature fruit stage (Figs. 2C, 3), though stamen/petal/style scars are only observable on the immature fruit/flower (Fig. 2D). In all specimens with adequate preservation (LRR1-4089, 4156, 712, 1204), sepals are rounded to deltoid, and in the mature fruits appear strongly re- flexed back against the hypanthium, although not as much on the partially ripened flower. A shallow pit on the apex of the capsule of the fossil flower (Fig. 2A, D) and the nondehisced fruit (Fig. 3H) indicates the point of insertion of the style.

Description of leaf and cuticle morphology— The leaves from Hasties and Little Rapid River were considered to be identical by Pole (1992) and are also here considered identical. They are isobilateral, with prominent drip tips. The leaves are hypostomatic, despite those from Hasties being diagnosed as amphistomatic by Pole (1992). Venation is pinnate, and all fossils with sufficient preservation possess a prominent intramarginal vein (Fig. 5). Leaves range from 1-3 cm in length. Lid cells/oil glands are visible on both the abaxial and adaxial cuticle of all leaves under LM and SEM (Fig. 6A-D). The fossil leaves can be confidently assigned to the Myrtaceae due to the presence of the intramarginal veins and oil glands/lid cells. While not all Myrtaceae possess these characters, they are considered synapomorphies for Myrtaceae, and in combination are conclusive evidence for placement in the Myrtaceae (Lange, 1980; Christophel and Lys, 1986).

The 'stomatal clumping' of the Hasties and LRR fossils and *Xanthomyrtus montivaga* A.J.Scott, the taxon they were compared favorably with by Pole (1992), is distinctly different. In *X. montivaga* the stomata are tightly clumped and there is a clear demarcation between stomatiferous and nonstomatiferous areas (Fig. 6E). However, in the fossil taxa (Fig. 6D) there is more space between adjacent stomata, and the degree of tightness of clumping is obviously lower. Also, the stomatal length of *X. montivaga* and the other *Xanthomyrtus sp.* assessed is consistently half that of the fossil taxon, ~5 μm compared with ~10 μm (Fig. 7).

Conspicuous water stomata are present on the surface of the fossil leaves. These water stomata are surrounded by radially arranged striations of various size and length (Fig. 8A, B). This is a conspicuous character, which does not occur in all tribes of Myrtaceae, and appears to occur predominantly in rainforest species (Denton, 2004). Conspicuous water stomata, striate or otherwise, are completely absent on the cuticles of *Xanthomyrtus montivaga,* and the other *Xanthomyrtus* species examined (Figs. 6, 7).

Distinct peristomatal rings surround each individual stomate in the fossil taxon, a character shared with only a few other species of Myrtaceae, and not *Xanthomyrtus montivaga* (Fig. 7). This is an exceedingly uncommon character on the cuticles of Myrtaceae, though similar structures could have evolved convergently in several unrelated lineages. Figure 7C, D shows an individual stomate, and a group of stomata on the cuticles of a LRR leaf and Hasties leaf respectively. The peristomatal ring is present in both. These are compared with individual stomata of *Kania eugenioides* Schltr. (Kanieae) and *Metrosideros robusta* (Metrosidereae), which both clearly possess peristomatal rims (Fig. 7). The chief difference is the degree of cuticular ornamentation, with the papillose cuticular texture of the fossils being much more similar to that of *K. eugenioides* than that of *M. robusta.* However, cuticular ornamentation of *M. robusta* is better seen in Fig. 8D. The fossil taxon, *K. eugenioides*, and *M. robusta* all possess a much greater degree of cuticular ornamentation than *X. montivaga.* Figure 8A also shows the cuticle of one of the Hasties leaves with fossilized fungal hyphae on the surface, appearing to be redirected around stomata by the margin of the peristomatal ring. The potential paleoenvironmental significance of these features will be expanded upon in the discussion.

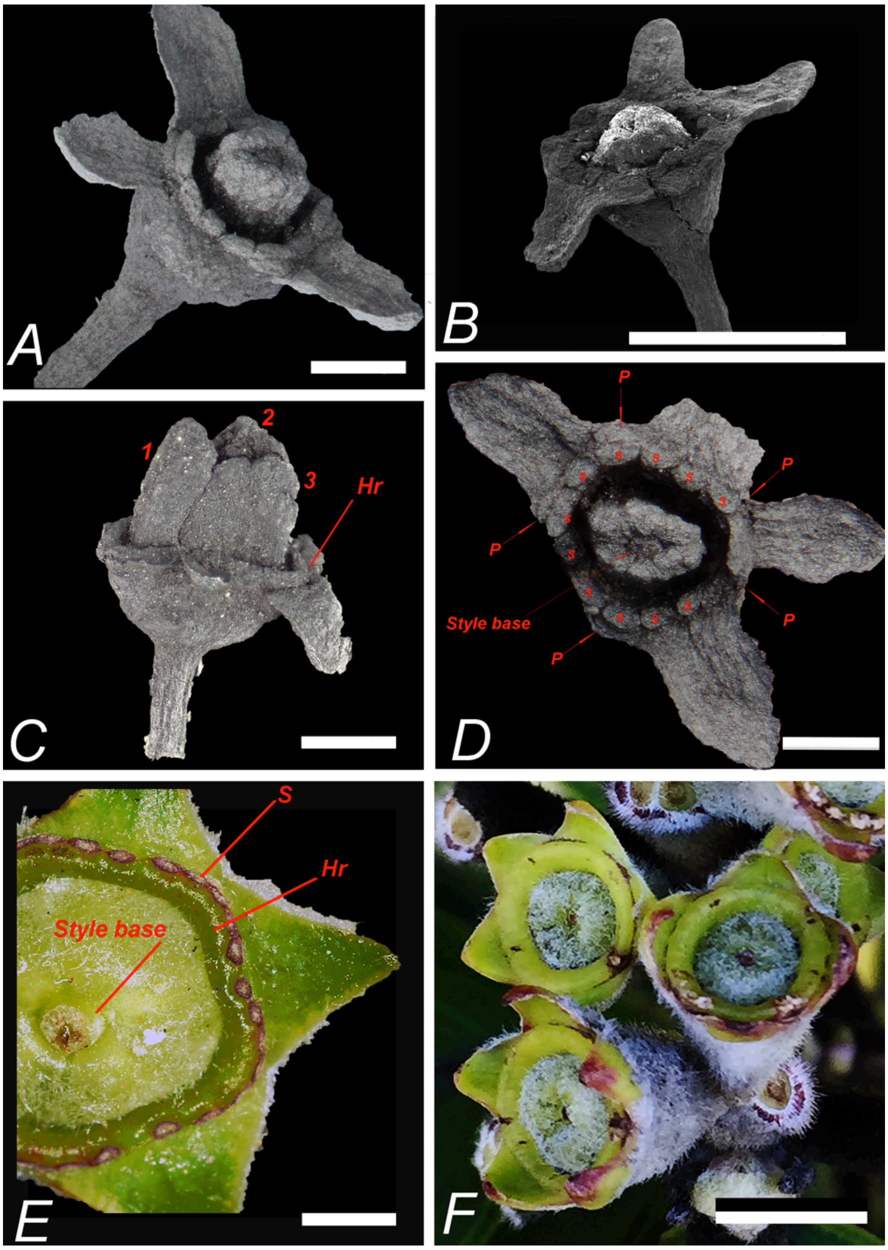

FIGURE 2: Fossil flowers from LRR compared with some modern *Metrosideros* flowers. **A)** LRR1-4089, [scale bar 1mm.] **B)** LRR1-4156, [Sscale bar 2mm.] **C)**, *LRR1-712*, Note the 3 locules (denoted 1,2,3) and the hypanthial rim (Hr) [Scale bar 1mm.] **D)** Top down view of LRR1-4089, with annotations denoting stamen scars (S) set about the hypanthial rim, petal (P) and style base scars. [Scale bar 1mm] **E)** Extant partially mature fruit of *Metrosideros kermadacensis,* showing the abscised style base, the stamen scars (S) and swollen hypanthial rim (Hr) [Scale bar 1mm] **F)** *Metrosideros robusta* post-flowering, partially mature fruits, note the prominent/swollen hypanthial rim and the insertion of the sepals just below this [Scale bar 3mm]. Photographs **E&F** taken by John G. Conran.

FIGURE 3: Representative capsular fruits of extant and fossil taxa at different stages of development. **A)** *Tristaniopsis capitulata* (Kanieae), mature fruit, completed dehiscence**. B)** *Tristaniopsis laurina* (kanieae) mature fruit, just beginning dehiscence. **C)** *Tristanopsis collina* (Kanieae) nearly mature fruit, pre-dehiscence **D)** *Kania eugenioides* (Kanieae) nearly mature fruit, pre-dehiscence. **E)** *Metrosideros bartlettii* (Metrosidereae) fully mature, complete dehiscence **F)** *Metrosideros robusta*, mature, dehisced fruit, **G,H & I)** Fossil fruits, LRR1-712, 1204, 1211 respectively. [Scale bar 1mm x 1mm]

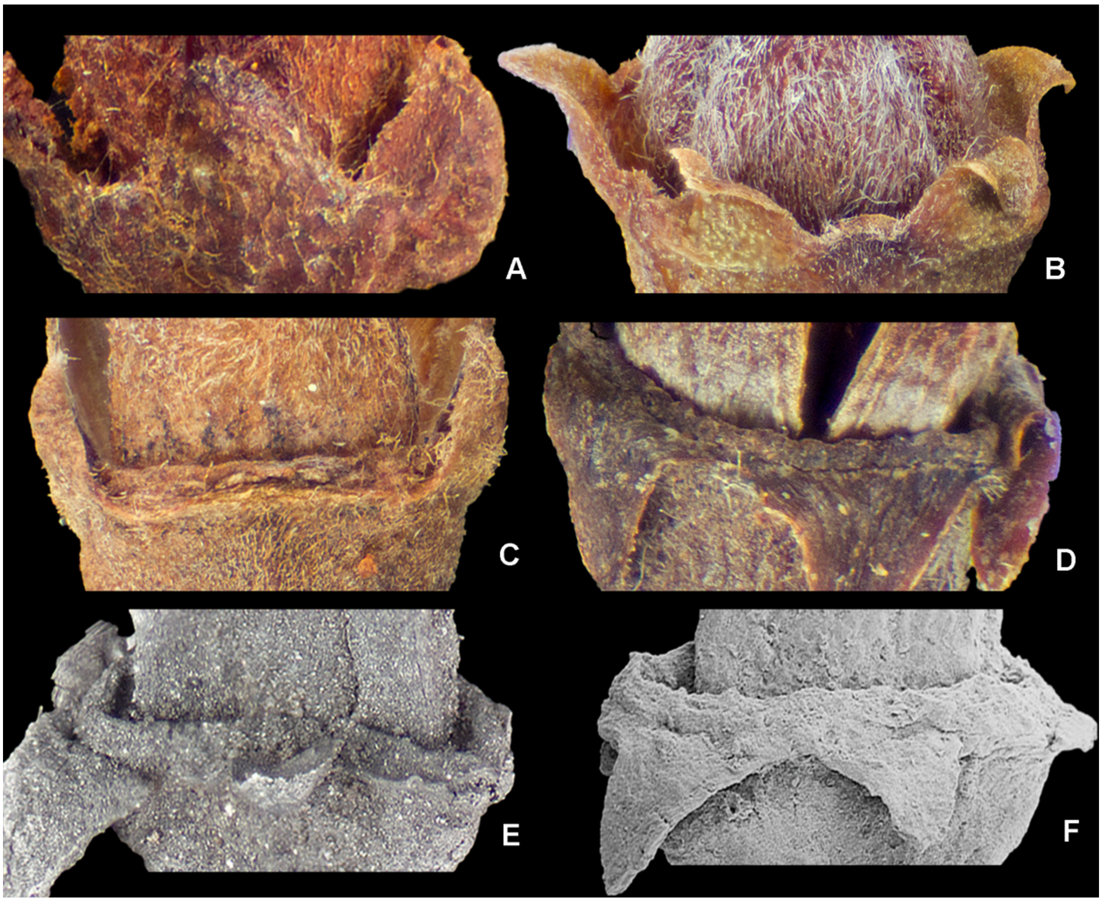

FIGURE 4: Close up view of the hypanthial rim of the mature fossil and extant fruits. **A)** *Kania eugenioides*, **B)** *Tristaniopsis collina*, **C)** *Metrosideros robusta*, **D)** *Metrosideros bartlettii*, **E)** LRR1-712 **F)** LRR1-1204. Note that the representatives of the Kanieae do not possess the prominent hypanthial rim. Also note the relative position of the sepals to the hypanthial rim between the *Metrosideros* species (C&D) and the genera within Tribe Kanieae (A&B) [See scale bar Fig. 3, 1mm x 1mm].

SYSTEMATICS

Fossil fruits and flowers—

Order: Myrtales

Family: Myrtaceae

Tribe: Metrosidereae

Genus: *Metrosideros*

Subgenus: aff. *Metrosideros*

Species: *Metrosideros leunigii*, sp. nov. Myall Tarran, Peter G. Wilson and Robert S. Hill.

Etymology—Specific epithet is in honor of Australian cartoonist, Michael Leunig.

Diagnosis—Flowers 5-merous. Sepals rounded to deltoid, sometimes unequal. Stamens not grouped, free, forming a single whorl numbering up to c. 15, inserted on the prominent hypanthial rim, which appears as a raised 'lip' around the capsule. Ovary 3-locular with the style inserted in a shallow pit on the summit. Fruit a small, loculicidal capsule, strongly exserted from the fruiting hypanthium when mature. Sepals persistent and strongly deflexed in the mature fruit.

Holotype—LRR1-4089 (Fig. 2A, D), housed in the David Blackburn Palaeobotany Collection at the University of Adelaide.

Paratypes—LRR1-4156, LRR1-0712

Type locality—Little Rapid River, Tasmania, Australia (41′09' S, 145′14' E).

DISCUSSION

Justification of assignment to the genus: Fruits and flowers— *Metrosideros leunigii* sp. nov. can be assigned to the Myrtaceae with confidence, having 5-merous flowers, with a tricarpellate ovary and a three-locular, loculicidal capsule that is strongly exserted from the hypanthium, making up one-half to two-thirds of the length of the fruit (Basinger et al., 2007; Wilson, 2011).

Most of the fossil fruits have been significantly flattened during fossilization. Only one flower is not significantly flattened (Fig. 2A, D). As such, many taxonomically important floral and fruit characteristics cannot be deter- mined, such as differences in anther connective, placenta position, and in the attachment of the ovules (Wilson, 1982). X-ray tomography of the fossil fruits revealed no internal characteristics of diagnostic value. Even without internal characters, the fossil organs bear external characters of potential diagnostic value. However, several synapomorphies support placement within *Metrosideros,* and strongly suggest affinities with subg. *Metrosideros.* These synapomorphies are:

(1) Strongly exserted capsule—According to Wilson (2011), fruits with a high degree of capsule exsertion from the hypanthium, only occur in a handful of genera within the Myrtaceae, all within two tribes. It is a character of some genera in the tribe Kanieae, and is present in at least some species of all of the genera within the tribe Metrosidereae. The capsule of *Carpolepis* is exserted, but not strongly so (Dawson, 1984). Within *Metrosideros,* many (though not all) of the species in the *Metrosideros* subgenus possess capsules strongly exserted from the hypanthium, while all fruits of the *Mearnsia* subgenus, have capsules included within the hypanthium (Wilson, 1996) except for *Metrosideros perforata* (J.R.Forst. & G.Forst.) Druce*,* which does have exserted capsules but not strongly. This difference in fruit morphology is broadly indicative of the different modes of fruit dehiscence observed between the groups. In the *Mearnsia* subgenus, most commonly seeds are released through irregular openings in the thinner parts of the fruiting hypanthium between the thickened veins (Dawson, 1970b). In the case of the *Metrosideros* subgenus, however, only

the capsule is split during dehiscence and seed release occurs through the free part of the capsule (Wilson, 1996). In the case of the fossil taxon *M. leunigii,* the fruits all have intact hypanthia, and in those that could represent dehisced fruits (Fig. 3G, I) the valves of the capsule appear to be disconnected from each other, and the hypanthium is still intact, suggesting seed release through the free part of the capsule.

(2) Stamen scars in a single whorl—

What appear to be stamen base scars are visible (Fig. 2D) and appear to occur in a single whorl, nonfused or clustered, inserted on the hypanthial rim, These characters differentiate the fossil taxon from many members of the tribe Kanieae, such as *Tristaniopsis* or *Sphaerantia*, or the *Tristaniandra* fossil genus described from the Eocene of South Australia (Basinger et al., 2007).

While many genera within the tribe Kanieae show staminal bundles/fusing, no member of the Metrosidereae shows this character (Basinger et al., 2007). This is strong, though not conclusive, evidence for their placement in Metrosidereae as opposed to Kanieae, for many of the genera within Kanieae have stamens "*frequently in* [fused] *bundles*", though this is not the case for some genera such as *Kania* and *Lysicarpus,* which show a degree of clustering but no fusion (Wilson, 2011). This evidence demonstrates that *Metrosideros leunigii* cannot be assigned to any of these genera.

(3) Hypanthial rim—In the treatment of the groups that would later become the two subgenera of *Metrosideros*, Dawson (1970a, b; 1976) notes an important character that stamens are "*in a single whorl, set behind the rim formed distally from the hypanthial lining*," and in some cases, in the *Mearnsia* group, "arising directly from it." In the literature surrounding the taxonomy of capsular Myrtaceae, single whorls of stamens are also found in some *Xanthostemon* species (Dawson, 1972a) and *Baeckea* sensu lato [species now in *Sannantha*] (Dawson, 1978) but both of these groups have very different fruits. A single whorl of stamens, on a prominent hypanthial rim, in conjunction with the strongly exserted capsule is a combination of characters unique to the tribe Metrosidereae.

(4) Insertion of the style base in the ovary—A further important character strongly suggestive of *Metrosidereae* is the insertion of the style base *in* the apex of the ovary in a distinct shallow pit. Within the *Kanieae,* the style is almost always terminal on (i.e., at the tip of) the ovary, only rarely inserted in a shallow pit, whereas for the tribe *Metrosidereae,* the style is always inserted *in* the apex of the ovary (Wilson, 2011).

(5) Strongly deflexed sepals on mature fruit—The external insertion of strongly deflexed sepals, underneath the distal hypanthial rim, is a recorded diagnostic character for only one species, *Metrosideros bartlettii* J.W.Dawson (Dawson, 1985). However, this has also been observed at least once in the closely related *M. robusta* (unpublished data). The great superficial similarity of *M. leunigii* to *M. bartlettii*, the closest relatives of which are *M. robusta* and *M. excelsa* Sol. ex Gaertn. (Drummond et al., 2000), is noteworthy.

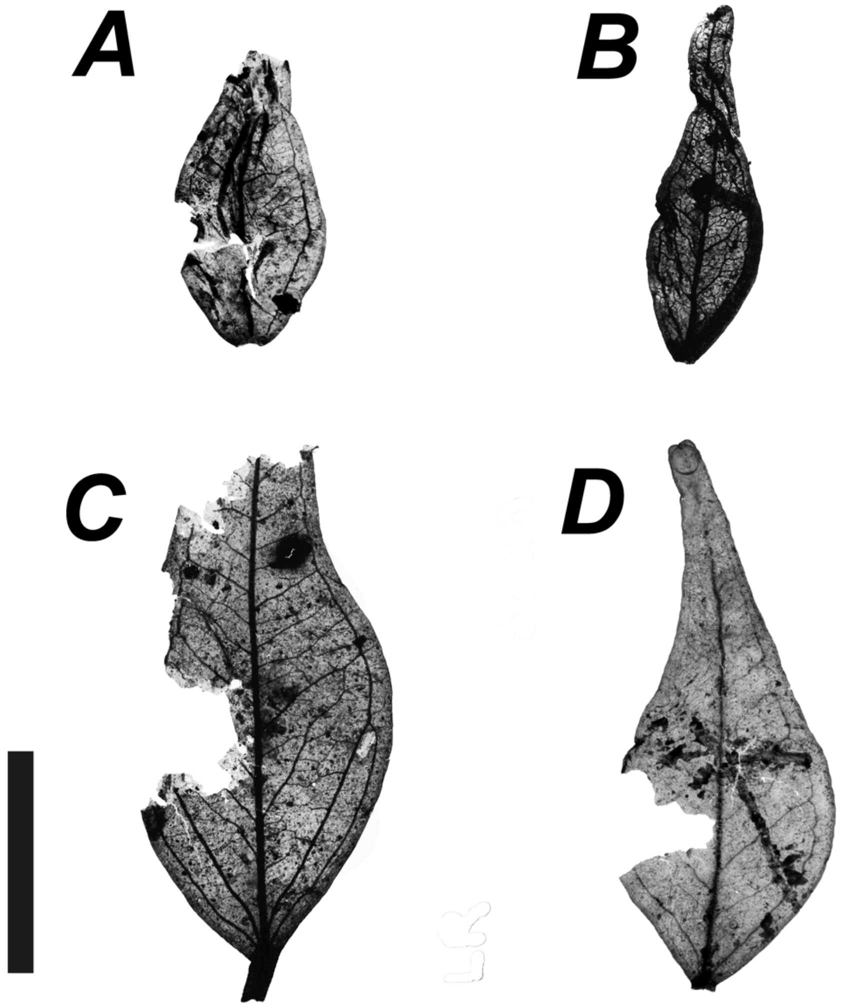

FIGURE 5: Mummified leaves: **A)** SB139, **B)** SB143, **C)** LRR1-006, **D)** LRR2-1261. Note that the average size of the Hasties fossils (Represented by A-B) is slightly smaller than those from Little Rapid River. The preservation of the LRR leaves is also better, allowing for preservation of detail of venation. Note that the 'drip tip' on specimens B & D, which must be inferred on samples A & C. [Scale bar 1cm]

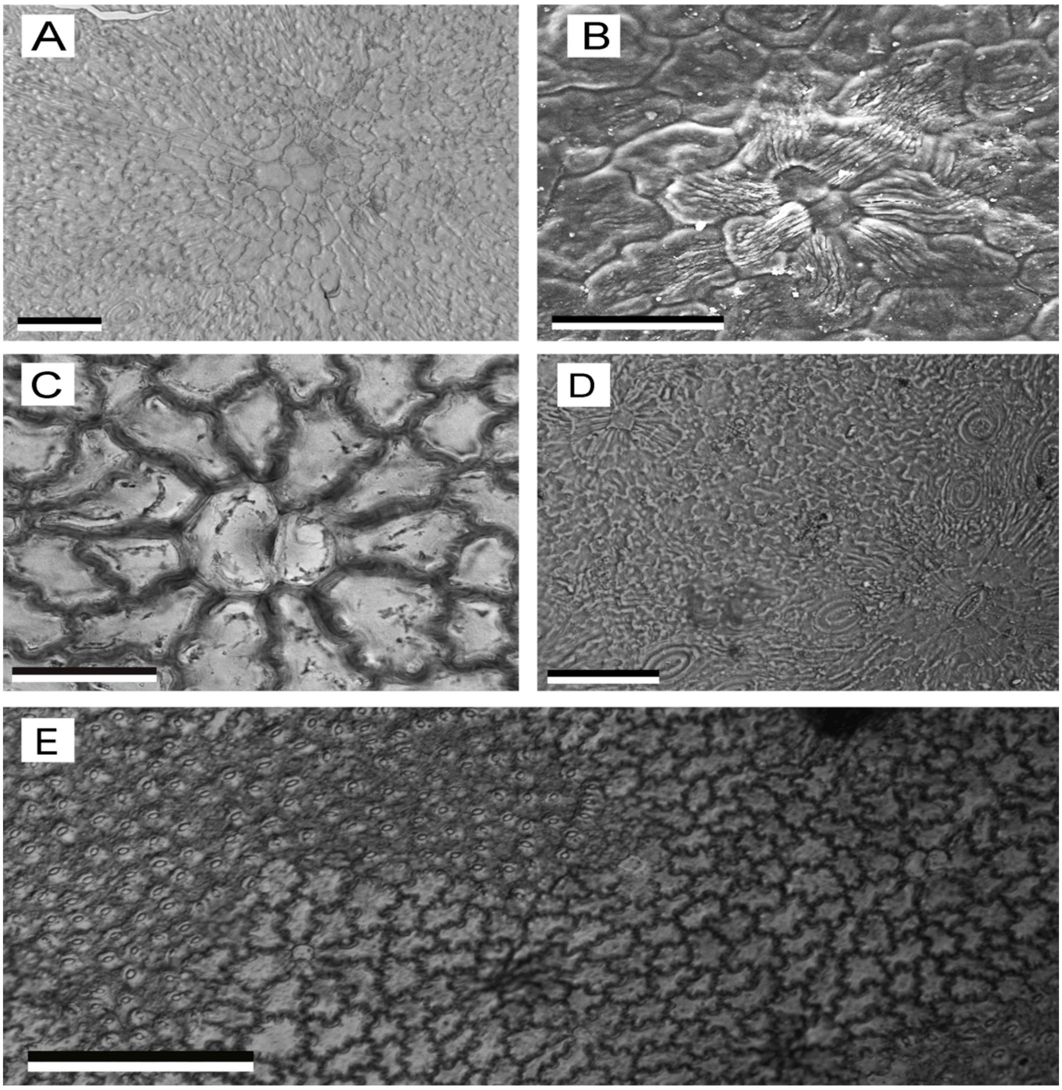

FIGURE 6: Comparing elements of cuticular micromorphology: **A)** Abaxial cuticle of LRR2-1236 3-celled lid-cell/oil-gland. Note faint radial striations in all direction from the lid cells. [Scale bar 50µm] **B)** SEM micrograph of adaxial 2-celled lid cells on one of the Hasties leaf macrofossils. Note the radial striations leading outwards from the lid cells. [Scale bar 50µm] **C)** 2-celled lid-cell/oil gland on the cuticle of *Xanthomyrtus montivaga*, note the lack of striations. [Scale bar 50µm] **D)** Cuticle of LRR2-1224 showing a single celled lid-cell (top left) and a striate water stomate (Bottom right, compare with Fig. 8) note the non stomatiferous area around the oil gland, and the distance between the stomata. Also note the 'rings' visible around each stomate (compare with Fig. 7). Note the striations around both the oil gland and the water stomate. [Scale bar 50µm] **E)** Abaxial cuticle of *Xanthomyrtus montivaga* showing stomatal clump (left) and non-stomatiferous area of the cuticle (right), compare stomatiferous areas with Fig. 6D, particularly the lack of distance between stomata, lack of striate water stomata, and lack of peristomatal rings. [Scale bar 200µm]

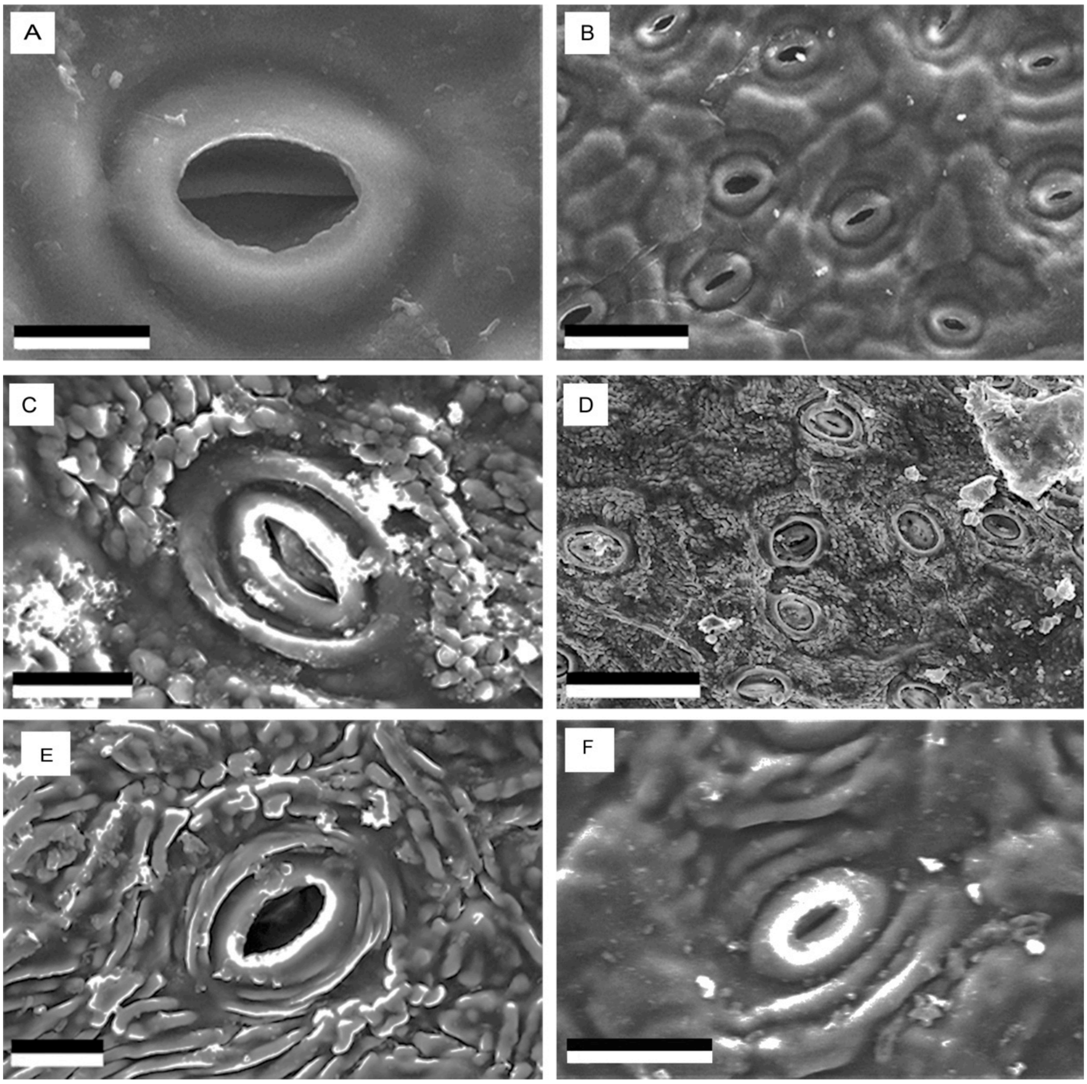

FIGURE 7: Scanning electron micrographs of extant and fossil taxa*. **A)*** Stomate of *Xanthomyrtus montivaga* [Scale bar 5µm] **B)** Stomata and cuticular surface *of Xanthomyrtus montivaga,* [Scale bar 20µm] **C)** Stomate of LRR2-1236 [Scale bar 10µm] **D)** Stomata and cuticular surface Hasties SB-091 [Scale bar 50µm] **E)** Stomate of *Kania eugenioides* single stomate, note the granular/papilose cuticular texture and the cuticular 'ring' around the stomatal pore which is lowest at the ends of the stomata [Scale bar 10µm] ***F*)** Stomate of *Metrosideros robusta,* note the cuticular rim and slightly papilose cuticular texture [Scale bar 10µm]

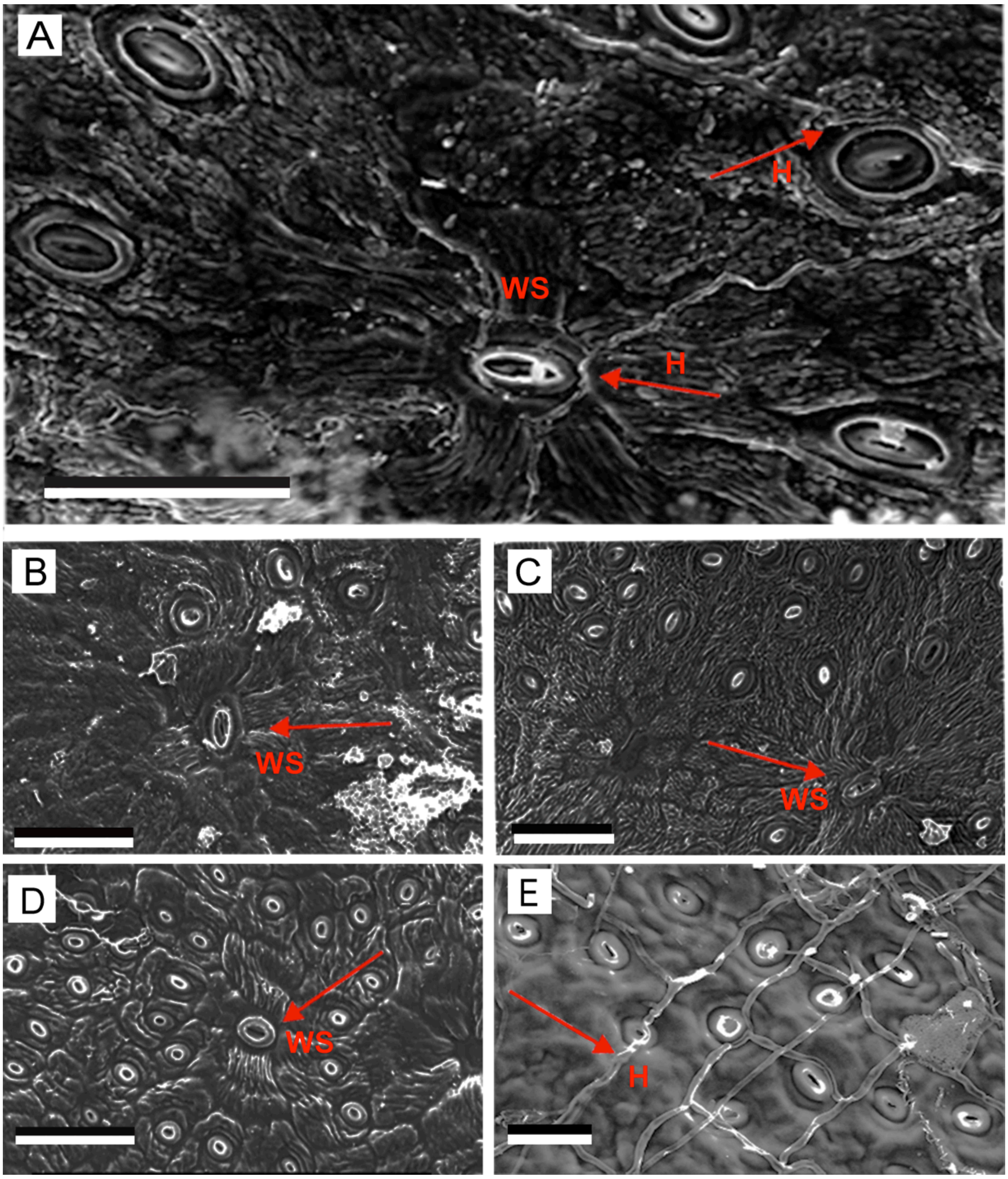

FIGURE 8: Water stomata, on the cuticles of the fossil and extant taxa. **A)** Hasties Myrtaceae fossil SB-091, note the central water stomate with radially arranged cuticular striations. Note the granular/papilose cuticular texture, the peristomatal rings, and several fossilized fungal hyphae (H) being redirected around stomates. [Scale bar 50μm] **B)** LRR2 1224, note the central water stomate with similar radiating striae [Scale bar 50μm]. **C)** *Kania eugenioides*, note the striate water stomate near the bottom right of the image. [Scale bar 50μm]. **D)** *Metrosideros robusta,* cuticle may still be called papillose but less so, and peristomatal rings less pronounced than in the fossils and *Kania eugenioides* [Scale bar 50μm]. **E)** Extant *Xanthomyrtus montivaga*, covered in fungal hyphae. Note the lack of conspicuous water stomata, striate or otherwise, the lack of cuticular texturing, and the absence of peristomatal cuticular ridges [Scale bar 20μm].

Discussion on the foliar cuticular morphology— Pole (1992) tentatively identified the Myrtaceous leaf fossils from Little Rapid River as being *Xanthomyrtus,* as an extension of the identification of identical leaves at the Eocene Hasties site. This diagnosis was based on a single character, "Stomatal clumping" which was considered of potential diagnostic value. Other than this character, which is not simple to define, there is very little reason to support the tentative identification to *Xanthomyrtus*.

Here, a suite of characters were defined from the fossil cuticles which may be of diagnostic value: (1) peristomatal rings; (2) distinctive granulate-papillose cuticular texture; (3) striate water stomata and lid cells; and (4) varying degrees of stomatal clumping.

A few of the capsular-fruited genera examined were found to possess all of these characters, and bear the closest resemblance to the fossil taxon, in particular two species of *Kania*, *K. eugenioides* and *K. urdanetensis* (Elmer) Peter G. Wilson, and the monotypic genus *Barongia lophandra* Peter G.Wilson & B.Hyland, a highly restricted plant from far-northern Queensland. Some of these characters were also observed in some *Metrosideros* species, particularly *M. robusta* (Figs. 7, 8). Furthermore, similar though not identical peristomatal rings, striate water stomata, and papillose cuticular texture were seen on the cuticles of specimens of *Lophostemon lactifluus* (F.Muell.) Peter G.Wilson & J.T.Waterh., in the much more distantly related tribe *Lophostemoneae*, which suggests that these or similar characters may arise convergently. Further study of the cuticular features of the Myrtaceae is necessary before the taxonomic value of these external foliar cuticle characters can be used to confidently diagnose foliar Myrtaceous fossils.

However, this review of cuticular characters demonstrates significant morphological differences between the fossil taxa, and the proposed NLR of *Xanthomyrtus montivaga* in Pole's (1992) account of the Hasties paleoflora. *X. montivaga* lacks all of the distinctive external cuticular features of the fossils, except for a high degree of 'stomatal clumping', but even that is of a different nature (Fig. 6). The stomatal clumping displayed by *Xanthomyrtus* is much more marked than that of the fossil taxon, and ‘stomatiferous’ vs. nonstomatiferous areas are strongly defined, with little room for epidermal cells in the stomatiferous areas, when compared with the fossil leaves. Furthermore, *X. montivaga* leaves lack water stomata, striate or otherwise, papillose cuticular texturing, and peristomatal rings, and these characters are conspicuously present in several genera of closely related capsular-fruited Myrtaceae.

As well as being potentially valuable diagnostically, cuticle characters are also potentially valuable as palaeoclimate indicators. For instance, peristomatal rings may play a similar role to the ‘Florin rings’ described by Mohammadian et al. (2009) on the cuticles of extant *Agathis* (Araucariaceae), as a physical stomatal defense from hyphal infection. These Florin rings were found to influence the growth of hyphae on fungus inoculated leaves by directing them away from the stomatal pore. The cuticular rims in *Metrosideros leunigii* (Fig. 8A) appear to have diverted the growth of fungal hyphae. This is the first known instance, to our knowledge, of this being observed in the fossil record. Parasitic fungal invasion of stomata has been shown to be detrimental, as the fungi extract nutrients from the plant tissues they invade impacting plant growth and health, and furthermore may physically block stomata, reducing and preventing gas exchange (Manter et al., 2000).

Another feature of paleoenvironmental significance is the highly textured and papillose cuticular surfaces. In modern plants, such surfaces are known to increase hydrophobicity of the cuticle surface (Lee and Michielsen, 2006), reducing the surface contact of water droplets with the leaf, facilitating the shedding of water and the removal of pathogens and detritus from the surface of the leaf. This is known as the “Lotus effect” (Barthlott and Neinhuis, 1997; Neinhuis and Barthlott, 1997).

The peristomatal rings and hydrophobic cuticles of the fossils might indicate that these plants evolved in conditions where extreme wetness and humidity become selective pressures. In combination, the drip tip and the hydrophobic cuticle are potentially effective structures for removal of excess water from the surface of the leaf. In highly wet conditions these structures may also be advantageous, as leaf wetness is critical for development of foliar fungal pathogens, and foliar adaptations that reduce leaf water retention may reduce incidence of disease (Bradley et al., 2003). Furthermore, even physical blockage of stomatal pores by water on the surface of leaves is detrimental to efficient gas exchange, with CO_2 diffusing 10,000 times slower through water than it does through air (Brewer and Smith, 1997).

Cuticular papillae have often been interpreted as a xeromorphic feature, to increase the boundary layer resistance of the leaf, hence decreasing transpiration (Haworth and McElwain, 2008). However, Hill (1998) posits that the environmental adaptivity of cuticular papillae in the Proteaceae is uncertain, stating that the feature could either be interpreted as a xeromorphic adaptation or as a mesomorphic adaptation to help shed water from the surface of the leaf. In these fossil Myrtaceae leaves, in combination with the suite of other mesomorphic characters, these papillae are interpreted as unequivocally mesomorphic.

Lastly, the fossil leaves have water stomata, which are enlarged stomata with a hypothesized role in facilitating leaf guttation (Sitholey and Pandey, 1971). These are more common, and occur more frequently on the leaves of rainforest species of Myrtaceae (Denton, 2004), but occur in many species. In the fossil taxon, and several of the nearest living relatives, the water stomata are surrounded by radially arranged cuticular striations. While no physiological research has investigated whether there is any specialized purpose or function of water stomata, cuticular striations have been interpreted as indicators of everwet environments in the fossil record of the Proteaceae (Hill, 1998). Their presence around water stomata may help to facilitate guttation. The cuticular features treated above as potentially valuable diagnostically, are also potentially useful for interpreting paleoclimate.

Very few cuticles of the Myrtaceous species examined were found to possess many of these features, and even fewer were found to possess all of them. The few that did were *Lophostemon lactifluus* (tribe Lophostemoneae), *Barongia lophandra* which are respectively found today in humid tropics at low latitudes in far-north Northern Territory, northern Queensland, and *Kania eugenioides* (tribe Kanieae) found in mossy forests at various altitudes in Papua New Guinea.

However, no leaves of the observed modern *Metrosideros* species possessed leaves with the same degree of mesomorphic adaptation, and three hypotheses are proposed here to explain this:

(1) It is a possible given that all of these external cuticle characters are likely to be environmentally adaptive, and that they evolved convergently. The conditions in the Eocene-Oligocene of southeastern Australia were very wet and humid, and high densities of epiphyllous fungi that occur on leaf fossils from deposits around this time attest to this;

. (2) Perhaps these characters are taxonomically informative, and (assuming that the leaves and fruits come from the same taxon) in combination with the fossil fruits and flowers, *Metrosideros leunigii* is representative of an ancestral form closer to the divergence of the capsular fruited tribes *Kanieae* and *Metrosidereae*;

. (3) However, it is possible that the genus *Kania* actually belongs in the tribe Metrosidereae. Unpublished molecular analysis may place *Kania* as sister to the Metrosidereae rather than the other taxa referred to Kanieae (Wilson, unpublished data).

Paleobiogeography— This new fossil species is the second description of capsular Myrtaceous fruits and flowers from Cenozoic southeastern Australia, following the discovery and description of capsular fruits and flowers, *Tristaniandra* (tribe Kanieae) in Eocene sediments at Golden Grove, South Australia (Basinger et al., 2007). The fossil fruits and flowers recovered from those sediments have been compared with fruits of *Tristaniopsis*, which in Australia only occurs along the southeastern coast (Basinger et al*.,* 2007). No Myrtaceous leaf fossils have been described from the Golden Grove deposit to date.

The only extant, endemic Myrtaceae in Tasmania are in the genera *Kunzea*, *Leptospermum* (tribe Leptospermeae), *Baeckea*, *Calytrix*, *Euryomyrtus*, *Thyryptomene* (tribe Chamelaucieae), *Eucalyptus* (tribe Eucalypteae), and *Melaleuca* (tribe Melaleuceae) (Curtis, 1956). There is a large range of leaf morphology represented in these genera, but none of the extant species in Tasmania could be said to possess mesomorphic or hydromorphic leaf morphology. The capsular-fruited *Metrosidereae* and *Kanieae* are entirely absent from Tasmania, and the *Metrosidereae* are absent from the Australian continent altogether. Other 'rainforest' Myrtaceae may have held on in Tasmania until as recently as the Pleistocene, with one taxon being described by Jordan (1997) as having affinities with *Austromyrtus* (tribe Myrteae) from Regatta Point. Interestingly the species they were compared with are no longer in the genus *Austromyrtus,* with one now referred to the genus *Gossia* (Lucas et al., 2007), and the other to *Lenwebbia,* which is a genus not closely related to any other Australian Myrteae (Snow et al., 2003)

To find *Metrosideros* in southeastern Australia during the Cenozoic is unexpected, but within the context of the many other genera and species described from Cenozoic deposits in southeastern Australia it is not surprising. Many species that are common in the Australian paleobotanical record are now extinct regionally, and only grow on the nearby landmasses of New Zealand, Papua New Guinea, New Caledonia, and some other Pacific islands. Examples include *Dacrycarpus* (Podocarpaceae), *Nothofagus* (subg. *Brassospora*, Nothofagaceae), *Weinmannia* (Cunoniaceae), *Libocedrus* (Cupressaceae), and *Gymnostoma* (Casuarinaceae) (Hill, 2004). Today *Metrosideros* is found in vegetation types throughout the Pacific growing in sympatry with some, or even all of these taxa (such as on New Caledonia, for example), and all of these taxa (except *Weinmannia*) are found in the LRR fossil locality with *M. leunigii*. The discovery of *Metrosideros* in these sediments adds to the weight of evidence indicating not only the disappearance of specific genera from the Australian mainland, but also of entire vegetation types, in response to dramatic Tertiary climate change (Hill, 2004).

These fossils have significant implications for the current understanding of the biogeography of *Metrosideros*. Wilson (1996) suggested that New Zealand was the landmass where the two subgenera of *Metrosideros* first diverged, and Wright et al. (2000) considered that absence of any *Metrosideros* fossils on other Gondwanic landmasses, was good evidence to support this. The presence of *M. leunigii* in the Eocene-Oligocene of Tasmania may indicate however, an Australian origin for *Metrosideros.*

CONCLUSIONS

These fossils establish the presence of *Metrosideros,* with affinities to the *Metrosideros* subgenus in the Eocene-Oligocene of Tasmania. Until now, the oldest definitive *Metrosideros* fossils are from the Miocene of New Zealand, where they are still a prominent element in the rainforest vegetation (Pole et al., 2008), and those fossils appear to represent subgenus *Mearnsia*. It is surprising that, given the apparent propensity of *Metrosideros* subgenus *Metrosideros* toward long-distance dispersal, making it one of the most widely distributed flowering plant genera in the Pacific, that it is absent from the Australian mainland today. This fossil find demonstrates that their absence from Australia is a result of extinction, rather than nondispersal, and may indicate an Australian origin for the genus.

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Chapter 4:

Two fossil species of *Metrosideros* (Myrtaceae) from the Oligo-Miocene Golden Fleece locality in Tasmania, Australia

Myall Tarran, Peter G. Wilson, Michael K. Macphail, Greg J. Jordan, and Robert S. Hill **American Journal of Botany**, 104: 891–904.

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Principal Author

Name of Principal Author (Candidate)	Myall Tarran		
Contribution to the Paper	Lead author, identification of fossil material, collection and preparation of extant plant material for analysis and comparison with fossil material. Performing microscopy and photography, analysing and interpreting results, writing discussion.		
Overall percentage (%)	70%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature	[redacted]	Date	3·7·18

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);
ii. permission is granted for the candidate in include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Peter G. Wilson		
Contribution to the Paper	Peter is an expert on the taxonomy of this group, and provided helpful comments on the manuscript and several stages of production, especially around taxonomic and nomenclatural issues encountered. Peter assisted with editing of the manuscript, and discussion and interpretation of the results.		
Signature	[redacted]	Date	26 Feb 2018

Name of Co-Author	Michael K. Macphail		
Contribution to the Paper	Michael performed all of the palynological methods of this paper, identifying and photographic fossil pollen and spores, and interpreting those to arrive at paleoenvironmental and stratigraphic conclusions. Michael also provided helpful comments on the manuscript at various stages of preparation, and contributed to the analysis and discussion of the results.		
Signature	[redacted]	Date	22-2-2018

Please cut and paste additional co-author panels here as required.

Name of Co-Author	Greg J. Jordan		
Contribution to the Paper	Greg collected the fossil material worked on in this paper, and curated a collection of this fossil material at UTAS. Greg also provided helpful comments on the manuscript at various points of preparation, and contributed to the discussion and interpretation of the results.		
Signature		Date	21/2/2018

Name of Co-Author	Robert S. Hill		
Contribution to the Paper	Bob supervised the preparation of the manuscript at all stages, providing comments and technical support through lab work, edited the manuscript, and contributed to the discussion and interpretation of the results.		
Signature		Date	3/7/18

ABSTRACT

PREMISE OF THE STUDY: The capsular-fruited genus *Metrosideros* (Myrtaceae) is one of the most widely distributed flowering plant genera in the Pacific but is extinct in Australia today. The center of geographic origin for the genus and the reason for and timing of its extinction in Australia remain uncertain. We identify fossil *Metrosideros* fruits from the newly discovered Golden Fleece fossil flora in the Oligo-Miocene of Tasmania, Australia, shedding further light on these problems.

METHODS: Standard paleopalynological techniques were used to date the fossil-bearing sediments. Scanning electron microscopy and an auto-montage camera system were used to take high-resolution images of fossil and extant fruits taken from herbarium specimens. Fossils are identified using a nearest living relative approach.

KEY RESULTS: The fossil-bearing sediments are palynostratigraphically dated as being *Proteacidites tuberculatus* Zone Equivalent (ca. 33–16 Ma) in age and provide a confident Oligo-Miocene age for the macrofossils. Two new fossil species of *Metrosideros* are described and are here named *Metrosideros dawsonii* sp. nov. and *Metrosideros wrightii* sp. nov.

CONCLUSIONS: These newly described fossil species of *Metrosideros* provide a second record of the genus in the Cenozoic of Australia, placing them in the late Early Oligocene to late Early Miocene. It is now apparent not only that *Metrosideros* was present in Australia, where the genus is now extinct, but that at least several *Metrosideros* species were present during the Cenozoic. These fossils further strengthen the case for an Australian origin of the genus.

KEY WORDS capsular fruit; Cenozoic; fossil; fossil record; Golden Fleece; Metrosideros; Miocene; Myrtaceae; Oligocene; Oligo-Miocene; Tasmania

INTRODUCTION

Recently described fossils of *Metrosideros*, with affinities to subgenus *Metrosideros* from the Late Eocene to Early Oligocene of Australia, have helped us understand one of the great biogeographic puzzles of the capsular-fruited Metrosidereae, namely the absence of this tribe from Australia despite a widespread distribution around the Pacific (Fig. 1), and a clear adaptation for long-distance dispersal in at least subgenus *Metrosideros* (Tarran et al., 2016). These fossils contribute to an interpretation of the current absenceof the Metrosidereae from Australia as being a result of extinction, rather than an absence of dispersal from some other landmass, such as New Zealand.

While these fossils contribute to our understanding of the paleobiogeography of the group, other pertinent questions still remain surrounding (1) the geographic origin of the genus, (2) the deep infrageneric relationships within *Metrosideros*, and (3) the poorly resolved relationships with the other closely related tribes Backhousieae, Kanieae, Myrteae, Syzygieae, and Tristanieae (Pillon et al., 2015). Further fossil records of this group may help reveal key insights into these problems.

The delimitation of genera in the tribe Metrosidereae (*sensu* Wilson et al., 2005) has been the subject of much debate, with the number of genera recognized varying from four (e.g., Wilson et al., 2005) to only one (Pillon et al., 2015). *Metrosideros* itself has often been divided into two subgenera, *Metrosideros* and *Mearnsia*, on the basis of vegetative and inflorescence characters (e.g., Dawson, 1992). However, published analyses have shown that while the subgenus *Metrosideros* is monophyletic, the subgenus *Mearnsia* is polyphyletic (Wright et al., 2000a; Papadopulos et al., 2011; Pillon et al., 2015). In terms of understanding the paleobiogeography of the genus, the two morphology-based subgeneric groupings may still hold some value, since it is the subgenus *Metrosideros* that has dispersed so widely around the Pacific. Although the formerly recognized subgenus *Mearnsia* (which encompassed most of the remaining species in the genus) may no longer be taxonomically valid, the species within it are less widely distributed around the Pacific (Wilson, 1996), occurring only on the Gondwanic landmasses of New Zealand, New Caledonia, and New Guinea as well as the Solomon Islands and the Philippines (Fig. 1A, with one outlier in South Africa, to be discussed later). As such, it might be considered that they are not as well adapted for long-distance dispersal as some species in subgenus *Metrosideros*. Discovery of fossils of subgenus *Mearnsia* in Australia, in conjunction with the subgenus *Metrosideros* fossils previously described by Tarran et al. (2016), might then be considered further evidence of an Australian origin for the genus.

A new record of *Metrosideros* fruits is reported here from carpological remains in late-Early Oligocene to late-Early Miocene (hereafter “Oligo-Miocene”) sediments from the fossil-bearing Golden Fleece Rivulet strata in northeastern Tasmania (Fig. 1B, C). These are the first macrofossils published from the Golden Fleece Rivulet.

Metrosideros-type pollen has not been recorded from the fossil-bearing sediments; however, fossil Myrtaceae pollens (with nearest living relatives in parentheses) are present in low abundance: *Myrtaceidites eucalyptoides* (*Eucalyptus* sensu lato), *M. parvusmesonesus* (Myrtaceae), and *M. verrucosus* (*Rhodamnia*-type). The most recent palynological survey of the extant Myrtaceae by Thornhill et al. (2012a) suggests that, compared with other tribes of Myrtaceae, *Metrosideros* pollen is not dissimilar to pollen of Melaleuceae, Syzygieae, Eucalypteae, and Xanthostemoneae, and so at least two of these pollen types could plausibly also represent *Metrosideros*. The equivocal affinity of fossil Myrtaceae pollen highlights the importance of macrofossil evidence in interpreting the paleobiogeography of this family.

Here, two new fossil species of *Metrosideros* are described from the Oligo-Miocene of Tasmania, Australia, and compared with fruits of Metrosidereae from around the Pacific, as well as with other strikingly similar Miocene fossil fruits from New Zealand that were reported by Pole et al. (2008) but not formally described as new fossil species.

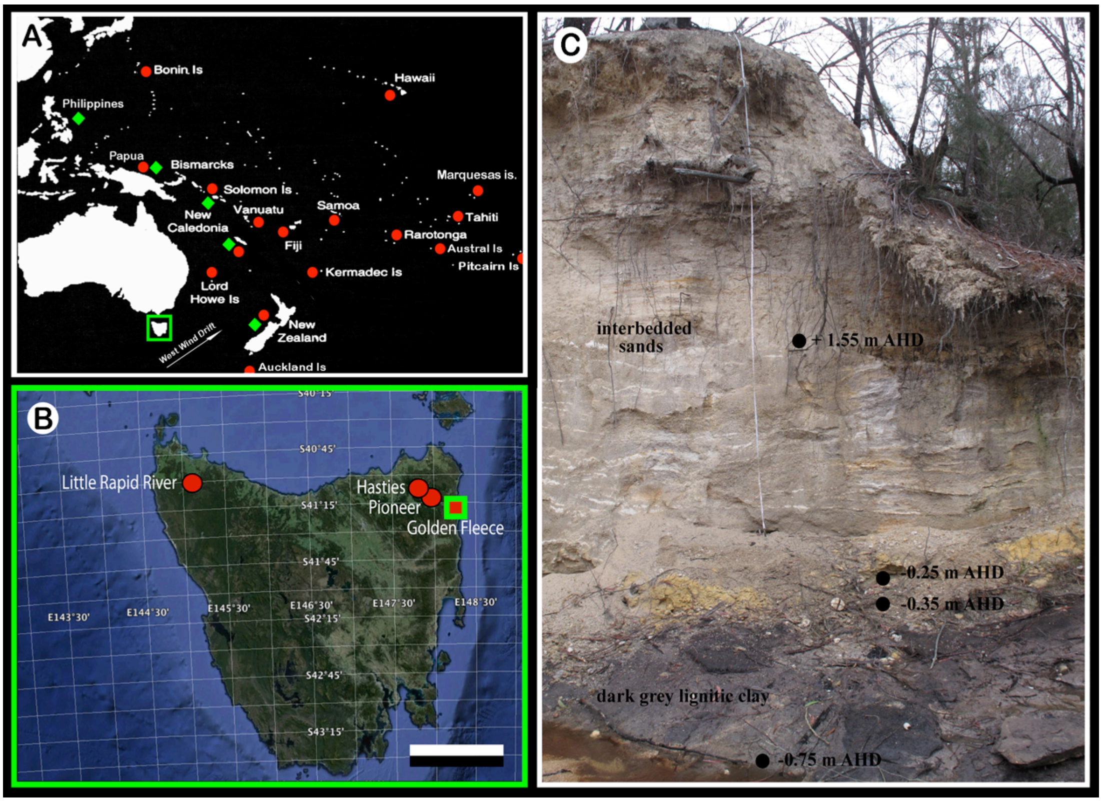

FIGURE 1: (A) Distribution of *Metrosideros* subgenus *Metrosideros* (red circles) and subgenus *Mearnsia* (green diamonds) in the Pacific, based on maps from Wright et al. (2000b, 2003) with a question mark in Australia indicating their absence from the Australian mainland. Note that this map doesn't include the distribution of the South African *Metrosideros angustifolia* of subg. *Mearnsia*, or the South American *Tepualia stipularis*, which has been placed in *Metrosideros* by the most recent circumscription of the genus by Pillon et al. (2015) extending the range of distribution of the genus. (B) Map of fossil sites in Tasmania. The Golden Fleece Rivulet is located in the far northeast. The Early Oligocene Little Rapid River site, where the fruits and flowers of *M. leunigii* were discovered, is in the northwest; leaves were found at the Middle-Late Eocene Hasties site in the northeast; and a single leaf was found at the late Oligocene/Early Miocene Pioneer site. Scale bar = ~100 km. Map data: Google, DigitalGlobe 7.1.2.2041. (C) Photograph of the fossil-bearing outcrop at the Golden Fleece Rivulet, showing the interbedded sands of Pliocene/Pleistocene age overlying the dark gray lignitic clays. The four points at +1.55 m, −0.25 m, −0.35 m, and −0.75 m indicate the horizons from which sediment samples were taken for palynostratigraphic analysis and age control. The fossils occur within the dark gray lignitic clays between the −0.35 m and −0.75 m sample points.

MATERIALS AND METHODS

Fossil sites and setting— The *Metrosideros* fossil fruits are preserved in a thin, lignitic clay that outcrops at water level on the northern bank of the Golden Fleece Rivulet (41°18′06″S, 148°10′03″; 50 m elevation) ~5 km west of St Helens on the northeast coast of Tasmania. The stream is located within a former course (Thureau's Deep Lead) of the Georges River (Georges River Palaeovalley) incised into Silurian-Early Devonian marine sediments (upper Mathinna Supergroup) and Devonian granitic rocks. The fossiliferous outcrop is partly buried under sands and silts from talus dumped into the rivulet during tin-mining operations in the nineteenth century.

Lithostratigraphy— Sediments exposed in the ~4.75 m high cliff forming the stream bank comprise an upper section of friable, fine to coarse, ripple-bedded sands and cross-bedded yellow silts unconformably overlying gray silty clays, which become darker in color and clay-rich down section (Fig. 1C). A thin interval of laminated lignites appears to separate the two units at one point in the outcrop.

Topography and vegetation—Topographic relief in the St Helens district is subdued, with elevations exceeding 100–250 m above sea level only in the headwaters of the rivulet and in hills to the south of the township. Much of the present-day forest vegetation is post mining re-growth, but remnant stands are of low–medium open forest types, especially *Eucalyptus sieberi* dry sclerophyll forest and woodland, occurring on more fertile sites.

Age control— Samples from the sediments taken at four intervals up the cliff (−0.70 m, −0.35 m, −0.25 m, and +1.55 m on the Australian Height Datum [AHD]) were dated using time distribution data from the Gippsland and Murray basins in southeast Australia and in northwest Tasmania (Macphail and Hill, 1994; Macphail, 1999; Partridge, 1999, 2006; Fig. 1C and Table 1). The data confirm that two (possibly three) sedimentary units are present in the cliff section, although all have been contaminated with modern exotic pollen (e.g., *Pinus*).

The *Metrosideros* macrofossils were recovered from the dark gray lignitic clays between −0.35 and −0.75 m AHD (Fig. 1C); they are dated as Early Oligocene to Early Miocene *Proteacidites tuberculatus* Zone Equivalent (ca. 33–16 Ma) using the combined microfossil evidence from both samples. Key age-diagnostic taxa are *Cyatheacidites annulatus* (*Lophosoria*; Fig. 2D) and *Mutisiapollis* cf. *patersonii* (*Mutisia*), which first occur in the Early Oligocene Lower *Proteacidites tuberculatus* Zone in the Gippsland Basin and north-west Tasmania, respectively; and *Dryptopollenites retequetrus* (extinct angiosperm) and *Proteacidites rectomarginis* (extinct Proteaceae; Fig. 2F), which last occur in the Upper *Proteacidites tuberculatus* Zone in the Gippsland Basin and northwest Tasmania, respectively. This age range can be narrowed to ca. 31.5–19 Ma if the absence of other age-diagnostic taxa such as *Granodiporites nebulous* (which last occurs in the Lower *P. tuberculatus* Zone) and *Acaciapollenites myriosporites* (which first occurs in the Upper *P. tuberculatus* Zone) is regarded as reliable evidence.

Immediately overlying the fossil-bearing sediments is a light gray, sandy silt at −0.25 m AHD, which does not preserve macrofossils. It is unclear whether the sample comes from a thin but discrete silt overlying the lignitic clays unit or the basal unit in the overlying sands. Assuming that the 19 specimens of *Nothofagidites emarcidus-heterus* (*Nothofagus* subgenus *Brassospora*; Fig. 2J) are in situ, the very sparse microflora is no more recent than the Late Pliocene, but the maximum age cannot be determined due to the very low yield.

The topmost unit in the cliff section consists of sands and silts, which preserve fossil pollen and spores but not macrofossils. A sample at +1.55 m AHD yielded a mixed-age microflora with fossil species that first occur in southeastern Australian in the Early Pliocene (5.3 Ma) and become extinct in the Early Pleistocene (1.8 Ma; e.g., *Myrtaceidites* cf. *lipsis*, *Eucalyptus spathulata*-type; Fig. 2B) and species that first occur in the Early Pleistocene (<2.59 Ma; e.g., *Leucopogon*-type [*Leucopogon*] and *Thymelaepollis* sp. [*Pimelea*]; Fig. 2C). This unit is likely to represent aggradation in the Golden Fleece Rivulet of talus derived from tin mining in the area.

The combined evidence provides a confident Oligo-Miocene age for *Metrosideros* macrofossils preserved in the dark gray lignitic clays between −0.35 m and −0.75 m AHD, which is clearly delineated from the overlying sediments, and securely dates any further macrofossils to be described from this site.

Depositional environment and paleovegetation— The microflora recovered from the macrofossil-bearing organic clays is dominated by fungal spores (165–310%, with percentages calculated in relation to the pollen sum; see Materials and Methods) and tree pollen taxa, notably *Nothofagidites emarcidus-heterus* (59–65%; Fig. 2J) and *Podocarpidites* (*Podocarpus-Prumnopitys*), while wetland herbs such as *Cyperaceaepollis* (Cyperaceae) and freshwater algal cysts are virtually absent. The relative abundance of these taxa compared to the low relative abundance of spores of shade-intolerant tree-ferns such as *Matonisporites ornamentalis* (Fig. 2H) and *Cyathidites* spp. (Cyatheaceae, e.g., Fig. 2D) is best interpreted as evidence that the organic clay accumulated in a depression within the closed canopy of Podocarpaceae-*Nothofagus* rainforest.

Compared to other Oligo-Miocene sites on granite in northeast Tasmania (e.g., Pioneer; Hill and Macphail, 1983), subcanopy angiosperms with thermophilous nearest living relatives are very rare, such as *Sapotaceoidaepollenites rotundus* (Sapotaceae), or else completely absent as in the case of *Bluffopollis scabratus* (Strasburgeriaceae), *Cupanieidites orthoteichus* (Cupanieae), and *Quintiniapollis psilatispora* (*Quintinia*). One exception is *Myrtaceidites verrucosus* (*Rhodamnia*-type), but the overall impression is of a temperate rainforest community growing under relatively cool (lower mesotherm) conditions.

Paleopalynology— Standard laboratory treatments were used for the recovery of palynomorphs for palynological dating from the dated samples. This process involves removal of inorganic mineral material by the initial dissolution of the rock in hydrochloric and hydrofluoric acids, followed by heavy-liquid (density) separation of the particulate organic matter from any remaining undissolved mineral matter using zinc bromide solution. From the organic residue recovered in the float, separate unfiltered and >10 µm filtered kerogen slides were prepared for each productive sample. The remaining residues were then oxidized using *Schultz* solution, followed by an equivalent short treatment in hot ammonia solution, and the final oxidized-residue additional slides were prepared filtered at >10 µm.

For all samples, 250 identifiable pollen and spores (or more) were counted as the pollen sum, and then miospores of individual taxa were calculated as a percentage of the total pollen and spore count, excluding fungal spores. Values of <1% of the pollen sum were denoted by '+' in the pollen count, and any remaining rare taxa were recorded outside the pollen count and denoted by 'x' (Table 2).

TABLE 1: Pollen and spore sample data from the exposed cliff face at the Golden Fleece Rivulet.

SAMPLE	**DEPTH**	**SAMPLE**	**LITHOLOGY**	**YIELD**	
				Organic yield	**Spore-pollen**
GFC2	+1.55 m	outcrop	charcoal-rich silt	high	medium
GFC4	–0.25 m	outcrop	light grey silt	low	very low
DATUM (top of organic silty clay)					
GFC3	–0.35	outcrop	dark grey organic silty clay	very high	abundant
GFC1	–0.75	outcrop	dark grey organic clay	very high	abundant
Water level at time of sampling (–0.75 m)					

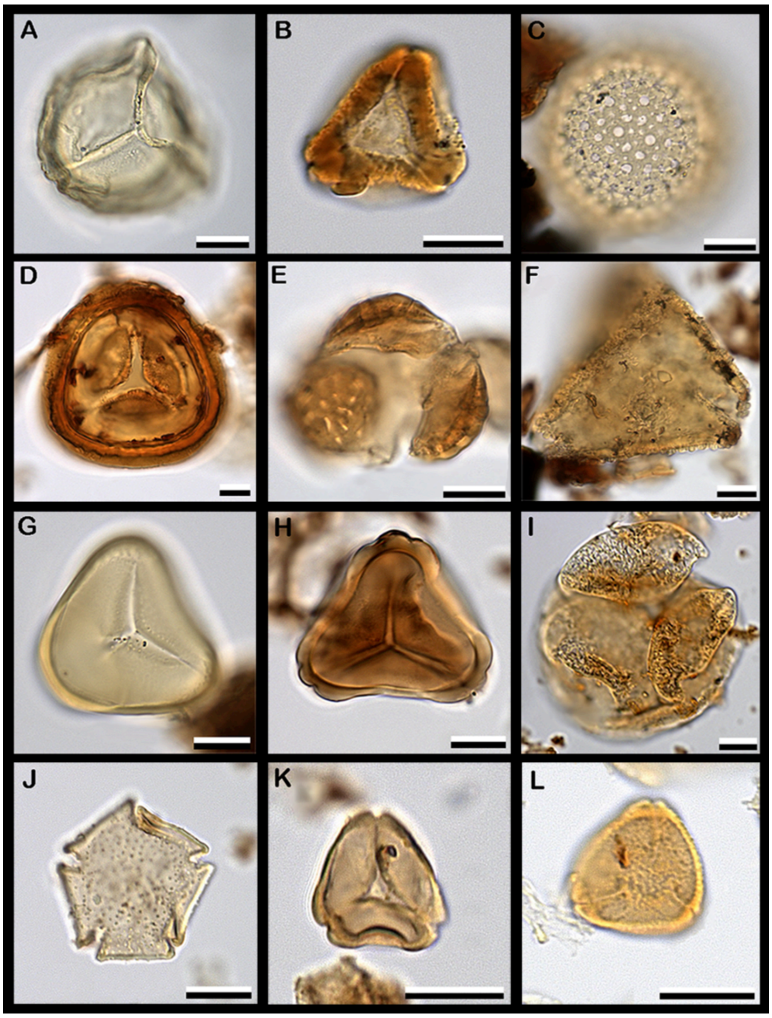

FIGURE 2: Selected taxa used for biostratigraphic age constraint of the fossil-bearing sediments, with nearest living relative in parentheses: (A) *Densoisporites implexus* (*Selaginella uliginosa*); spore in high (proximal) optical view, +1.55 m AHD. (B) *Myrtaceidites* cf. *lipsis* (*Eucalyptus spathulata*-type); pollen in median optical view, +1.55 m AHD. (C) *Thymelaepollis* sp. (*Pimelea* sp.); pollen in high optical view, +1.55 m AHD. (D) *Cyatheacidites annulatus* (*Lophosoria*); spore in median optical view showing diagnostic three contact pads on proximal surface, −0.75 m AHD. (E) *Dryadopollis retequetrus* (extinct angiosperm); pollen in oblique lower optical view showing coarsely reticulum in mesocolpial areas, −0.35 m AHD. (F) *Proteacidites rectomarginis* (extinct Proteaceae); corroded pollen in median optical view showing parallel groves in exine around the apertures, −0.75 m AHD. (G) *Cyathidites australis* (*Cyathea*); spore in high optical view, – 0.25 m AHD. (H) *Matonisporites ornamentalis* (*Dicksonia*); spore in median optical view, −0.75 m AHD. (I) *Dacrycarpites australiensis* (*Dacrycarpus*); pollen (proximal surface uppermost) showing three large sacci, −0.35 m AHD. (J) *Nothofagidites emarcidus-heterus* (*Nothofagus* subgenus *Brassospora*); pollen in median optical view, −0.35 m AHD. (K) *Myrtaceidites parvus-mesonesus* (Myrtaceae); pollen in median optical view, −0.35 m AHD. (L) *Myrtaceidites verrucosus* (*Rhodamnia*-type); pollen in high optical view showing diagnostic verrucate ornamentation, −0.75 m AHD.

TABLE 2: Stratigraphic distribution and relative abundance data. Values for samples yielding over 250 identifiable pollen and spores are calculated as a percentage of the total pollen and spore count excluding fungal spores. '+' indicates values less than 1%. Raw counts are given in parentheses for samples yielding <250 pollen and spores. ‘x’ indicates rare species recorded outside the pollen count.

Fossil Equivalent	**Nearest Living Equivalent**	**Golden Fleece Rivulet (m AHD)**			
		1.55	**-0.25**	**-0.35**	**-0.75**
Exotic taxa					
Pinus	*Pinus*	+	+	+	x
Asteraceae (Liguliflorae)	Cichorieae	+			
Polygonum aviculare-type	Polygonum aviculare	x			
Algae					
Circulisporis parvus	Zygnemataceae	+			x
Amorphous &unassigned types	unknown		(abund)		
Fungi					
Pesavis	-			x	x
Spores and hyphae	-	34%	-12	165%	310%
Mosses and liverworts					
Baculatisporites disconformis	Hymenophyllaceae			x	+
Baculatisporites cf *scabridus*	Hepaticae?				x
Baculatisporites sp.	Hepaticae	x	-3	2%	4%
Cingulatisporites bifurcatus	*Phaeoceros* (Anthocerotae)	x			
Cingutriletes/Stereisporites australis	Sphagnaceae			x	x
Densoisporites implexus	*Selaginella uliginosa*	x			
Herkosporites elliottii	*Lycopodium deuterodensum*			x	
Latrobosporites marginis	*Lycopodiella lateralis*	x			
Pilularia-type	Marsileaceae	x			
Rudolphisporis rudolphi	*Anthoceros* (Anthocerotae)	x			x
Ferns & fern allies					
Baculatisporites disconformis	Hymenophyllaceae			+	+

Cyatheacidites annulatus	*Lophosoria*			+	x
Cyathidites australis/paleospora	*Cyathea*	1%	-4	+	+
Cyathidites cf. *splendens*	Cyatheaceae?			x	x
Cyathidites cf. *subtilis*	*Cyathea*		x		
Gleicheniidites spp.	Gleicheniaceae	x			
Hypolepis australis	*Hypolepis*	1%			
Ischyosporites cf. *lachlanensis*	unknown			x	+
Laevigatosporites ovatus/major	includes Blechnaceae	3%		1%	x
Matonisporites ornamentalis	*Dicksonia antarctica*	56%	-5	2%	2%
cf. *Matonisporites ornamentalis*	immature *Dicksonia* spores?	15%	x	x	x
Peromonolites baculatus ms	Blechnaceae?			1%	x
Peromonolites densus	Blechnaceae?			x	x
Peromonolites vellosus	Blechnaceae?			x	x
Polypodiisporites histiopteroides	*Histiopteris*	3%			
Polypodiisporites spp.	includes *Microsorium*	4%			
Retitriletes austroclavatidites	*Lycopodium*			x	x
Rugulatisporites mallatus	*Calochlaena*	x			x
Rugulatisporites trophus	*Calochlaena*	x			
Trilites tuberculiformis	Dicksoniaceae			x	+
Verrucosisporites cristatus	unknown			x	x
Verrucosisporites kopukuensis	unknown			x	
unassigned spores	(numerous families)	3%		2%	+
Gymnosperms					
Araucariacites australis	*Araucaria*		-1	+	+
Cupressacites	Cupressaceae-Taxodiaceae				
Dacrycarpites australiensis	*Dacrycarpus*			x	x
Dacrydiumites florinii	*Dacrydium*			+	+
Dilwynites granulatus	*Agathis/Wollemia*			+	
Microcachryidites antarcticus	*Microcachrys*				x
Microalatidites palaeogenicus	*Phyllocladus*	x		+	1%

Phyllocladidites mawsonii	*Lagarostrobos franklinii*		-1	1%	2%
Podocarpidites spp.	*Podocarpus*	x	-3	14%	9%
Podosporites erugatus	*Pherosphaera*				x
Podosporites parvus/microsaccatus	extinct Podocarpaceae			+	+
Angiosperms					
Acaciapollenites myriosporites	*Acacia*	x	-1		
Banksieaeidites cf. *elongatus*	*Banksia*	x			cf.
Chenopodipollis chenopodiaceoides	Chenopodiaceae	+			
Cunoniaceae	Cunoniaceae				x
Cyperaceaepollis spp/	Cyperaceae	x			+
Dodonaea viscosa-type	*Dodonaea viscosa*-type			cf.	
Dryadopollis retequetrus	extinct clade?			x	
Ericipites spp.	Epacridaceae	9%		+	x
Graminidites	Poaceae	x	-1		
Gyropollis psilatus	Gyrostemonaceae	x			
Haloragacidites haloragoides	*Haloragis/Gonocarpus*	+			
Haloragacidites harrisii	Casuarinaceae	8%	-45	+	+
Leucopogon-type	*Leucopogon*	x			
Liliacidites bainii	Arecaceae/Liliaceae			x	
Liliacidites spp.	Arecaceae/Liliaceae			x	+
# *Malvacipollis subtilis*	*Austrobuxus*			x	+
Milfordia hypolaenoides	Restionaceae	+			
Monotocidites galeatus	*Monotoca*	x			
Mutisiapollis cf. *patersonii*	*Mutisia*				x
Myrtaceidites eucalyptoides	*Eucalyptus* sensu lato			x	
Myrtaceidites parvus-mesonesus	Myrtaceae			+	x
Myrtaceidites aff. *leptospermoides*	*Melaleuca*-type		-1		
cf. *Myrtaceidites lipsis*	*Eucalyptus spathulata*?	x			
Myrtaceidites verrucosus	*Rhodamnia*-type				x
Nothofagidites asperus	*Nothofagus (Lophozonia)*			2%	2%
Nothofagidites brachyspinulosus	*N.* (*Fuscospora*) spp.		-4	6%	6%

Nothofagidites falcatus	*N.* (*Brassospora*) sp.			+	+
Nothofagidites emarcidus-heterus	*N.* (*Brassospora*) spp.	+	-19	59%	65%
Nothofagidites flemingii	*N.* (*Nothofagus*) spp.			x	
Periporopollenites demarcatus	Trimeniaceae			+	
Poluspissusites ramus	Goodeniaceae				cf.
Polyporina granulata	*Stellaria*	x			
Proteacidites obscurus	cf. *Agastachys*			x	x
Proteacidites pseudomoides	extinct? clade Proteaceae			x	x
Proteacidites scaboratus	extinct? clade Proteaceae			x	x
Proteacidites rectomarginis	extinct clade Proteaceae				x
Proteacidites spp.	Proteaceae	x		+	+
Rhoipites ampereaformis	*Amperea*	4%			
Rhoipites sp.	numerous taxa	x			x
Sapotaceoidaepollenites rotundus	Sapotaceae				x
Tetracolporites cf. *palynius*	extinct? clade				x
Thymelaepollis sp.	*Pimelea*	x		x	x
Tricolpites reticulatus	Gunneraceae			x	x
Tricolpites/Tricolporites	numerous taxa	x		+	1%
Tricolporopollenites chnosus	extinct clade Proteaceae?			x	x
Tubulifloridites antipoda/simplis	Asteraceae	x			
POLLEN SUM		**295**	**-85**	**388**	**382**
REWORKED TAXA					
Jurassic-Cretaceous (*Annulispora folliculosa*)					x
Jurassic (*Nevesisporites reduncuts*)					x
Permian *(Plicatipollenites sp)*				x	
Devonian? spore		x			

Macrofossil preparation and identification— Fossil fruits were mounted on aluminum stubs for scanning electron microscopy and coated in carbon. In total, there are 11 fossil fruits, given the specimen codes GF001–GF011. These fossils are stored in the David T. Blackburn Palaeobotany collection, at the University of Adelaide.

Extant *Metrosidero*s fruits were collected and observed for comparison, from vouchers in the National Herbarium of New South Wales, and the Australian National Herbarium in Canberra (for accession numbers, see Appendix 2).

Fossil fruits were first observed under a Philips XL30 FEG field emission scanning electron microscope (FEI, Eindhoven, The Netherlands), and then fossil and extant fruits were photographed under an Auto-Montage Visionary Digital BK+ imaging system with a Canon EOS 7D 18 megapixel camera. Images were produced using PMax image stacking in Zerene Stacker PMax software (Zerene Systems, Richland, Washington, USA) and cropped and resized in Adobe Photoshop CS6 21 (Adobe Systems, San Jose, California, USA).

The fossil taxa are identified using a nearest-living-relative approach. General taxonomy of the Myrtaceae follows Wilson (2011). Specific *Metrosideros* taxonomy follows Dawson (1970a, 1970b, 1976, 1984).

DESCRIPTION

There is a great deal of morphological variation among the fossil fruits presented; all are are 2–3 mm in length and 1.5–2.5 mm in width (Fig. 3). The fruits have all been significantly flattened during fossilization, and so these measurements may be a slight overestimate of their true size. All of the fossil fruits appear to be three- locular capsules, with at least some free part of the capsule exserted from the hypanthium. However, we conclude that there are two different taxa represented by these fruits.

Taxon 1 —Specimen E possesses the most obvious characters. The capsule of the fruit is exserted beyond the hypanthial rim, making up nearly a third of the length of the fruit. The fruit is pentamerous, with the sepals inserted on a prominent hypanthial rim, which appears as a swollen "lip" around the capsule. Five persistent veins are visible running up and down the hypanthium, terminating in each of the five sepals (Fig. 4A, B). The presence of only "five major veins" is a synapomorphy for the tribe Metrosidereae (Wilson, 1996, 2011), a feature visible in many of the extant fruits used for comparison (Fig. 5). For further comparison, this synapomorphy can also be seen in the mummified, Miocene-aged *Metrosideros* fruits described by Pole et al. (2008) (Fig. 4C, D), although these veins are more strongly developed, and the valves less strongly defined, as the fruit does not appear to have reached maturity and dehiscence. In Figure 4B the external side of the middle valve (valve 2) can be clearly seen.

While there is some cracking and breakage of the lower half of specimen E, the valve is intact, and there is a clear groove running up the middle of the valve, which terminates in a shallow groove in the top of the valve. This indicates the point of style insertion, in a shallow pit on the summit of the ovary.

Taxon 2— The second taxon (Fig. 3A–D, F) possesses sepals that are apparent on some specimens but highly reduced or residual when compared with the first taxon. The fruits are pentasepalous, and the veins in the hypanthium, terminating in the sepals, are less prominent on these fruits (Fig. 3A, B) than in Taxon 1. The specimens shown in Figure 3A and 3F, with reduced width and size, may represent fruits of this taxon that are less mature.

The specimens shown in Figure 3B, C, D (and to a lesser degree F) are "urn-shaped" fruits, with a slight restriction just below the hypanthial rim, with very reduced yet persistent sepals. In some of these fruits (such as Fig. 6A, B), faint veins can be seen running along the hypanthium and terminating in the sepals, though not as pronounced as in Figure 3 E. The hypanthial rim is prominent and appears as a swollen "lip," particularly in the more mature fruits (Fig. 3B, C, D).

The most unusual character on all of the fruits, and worthy of note, is the thin and attenuated valves of the capsule, which is threeparted (Fig. 3A, C, D), ruling out any potential that this structure may represent a persistent style base. In the case of the specimens in Figure 3A and 3F, these valves are very strongly exserted.

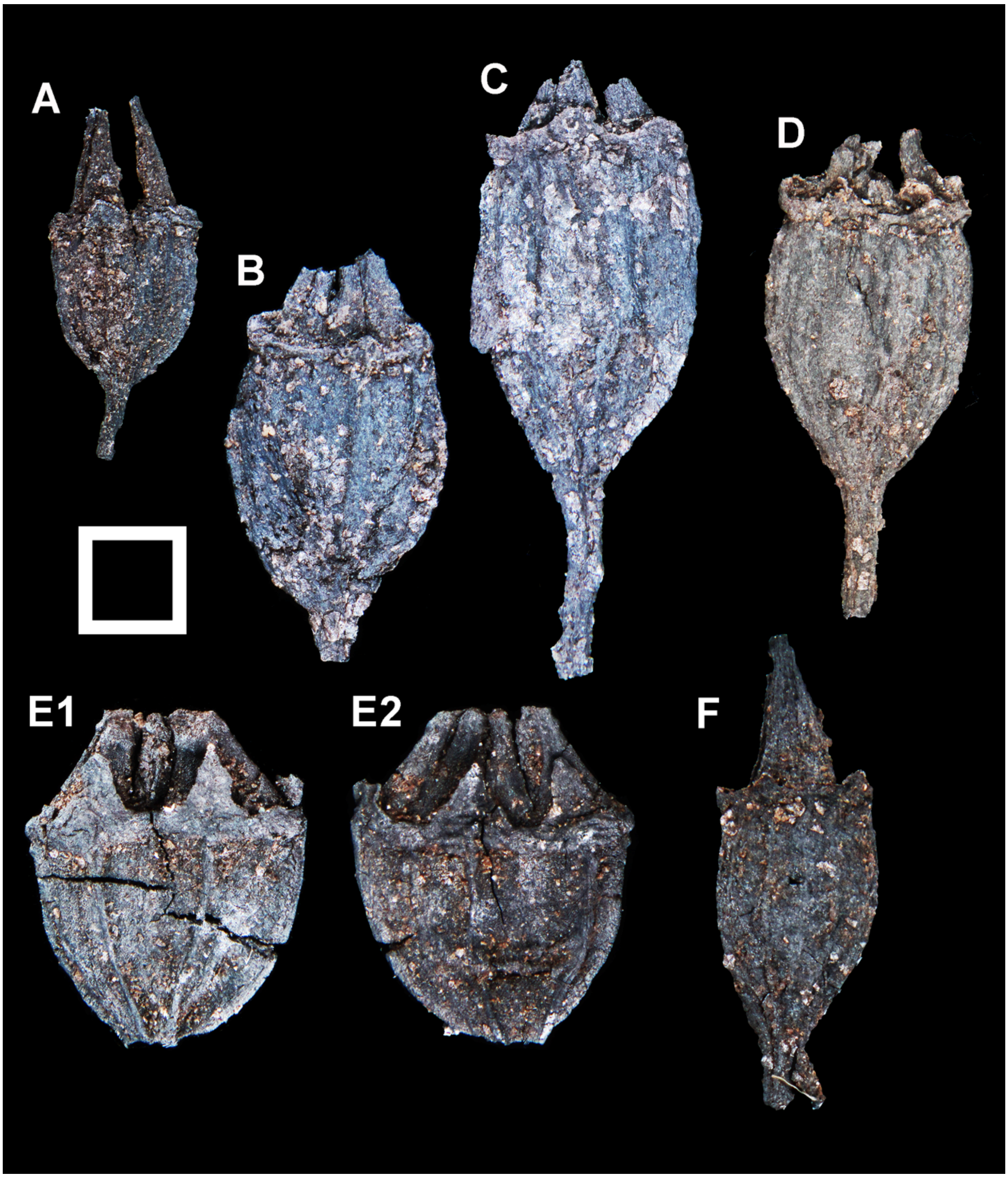

FIGURE 3: Fossils, named by their collection codes, recovered from the Golden Fleece Rivulet: (A) GF006, (B) GF002, (C) GF004, (D) GF001, (E1, E2) GF005 (both sides of the fruit), (F) GF009. Scale bar = 1 × 1 mm.

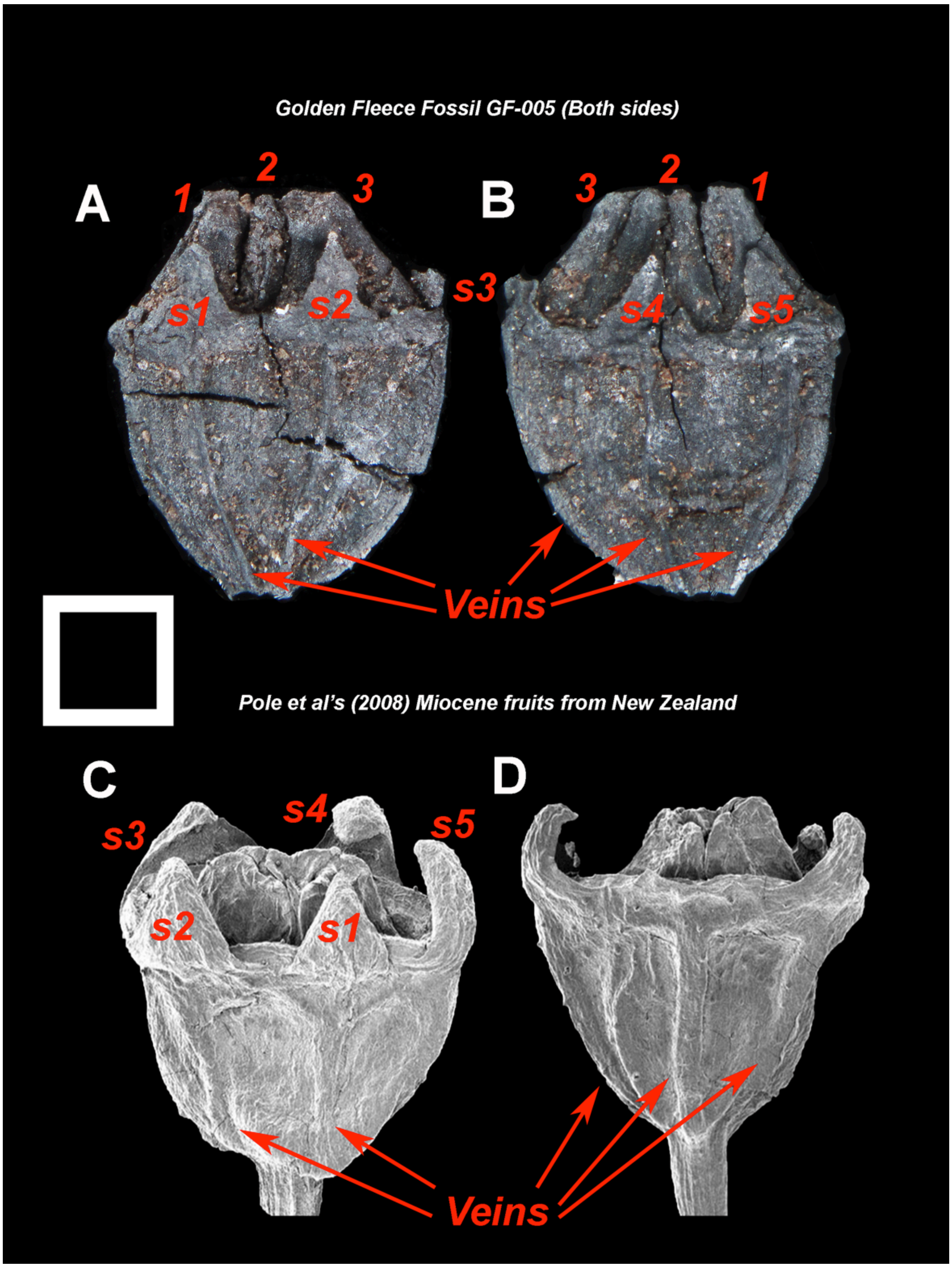

FIGURE 4: Anatomy of Taxon 1, *Metrosideros dawsonii* sp. nov., in comparison with fossils found from the Miocene of New Zealand by Pole et al. (2008). (A, B) Both sides of fruit GF005. Valves are denoted 1, 2, 3 and are shown from both sides of the fruit. Sepals are denoted S1, S2, S3, etc. Note how the five veins run up the hypanthium and terminate in the sepals. (C, D) Fossil *Metrosideros* fruits from the Miocene of New Zealand depicted by Pole et al.'s (2008) specimens S-1274 and S-1270. Note the same number of sepals and same number of veins. The fruit does not appear to be as mature as GF-005, and valves are not easily distinguishable. Scale bar = 1 × 1 mm.

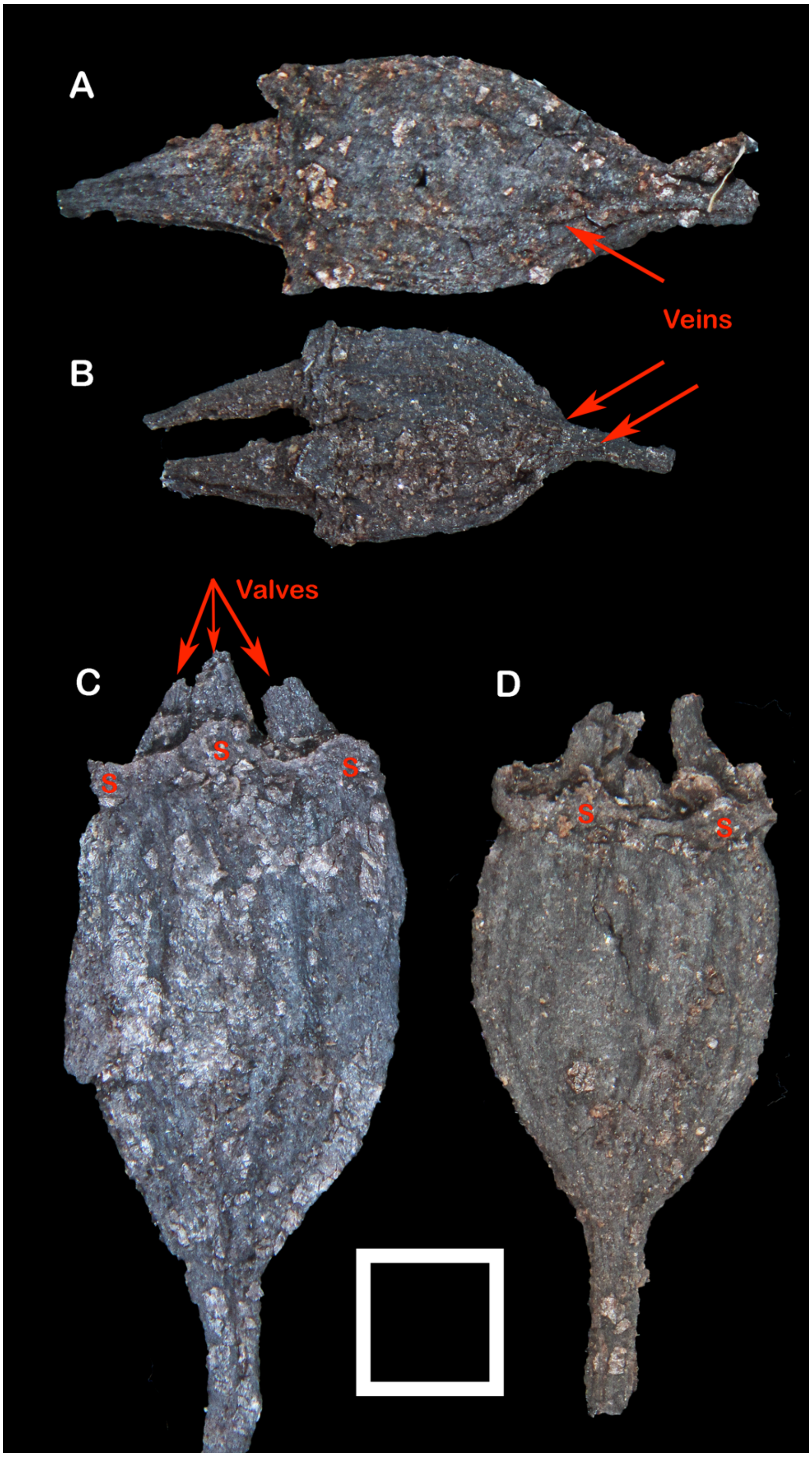

FIGURE 5: A collection of *Metrosideros* fossils in comparison with extant taxa: (A) *Metrosideros wrightii* sp. nov.; (B) *M. dawsonii* sp. nov.; (C) Pole et al.'s (2008) *Metrosideros* fossils from the Miocene of New Zealand; (D) *M. leunigii*, the Little Rapid River fossils described in Tarran et al. (2016); (E) *M. angustifolia*; (F) *Tepualia stipularis*; (G) *M. bartlettii*; (H) *M. robusta*; (I) *M. cherrieri*; (J1, J2) *M. punctata*, two fruits at different stages of decomposition, highlighting the prominent five major veins; (K) *M. sclerocarpa*; (L) *M. operculata*. Scale bar = 1 × 1 mm.

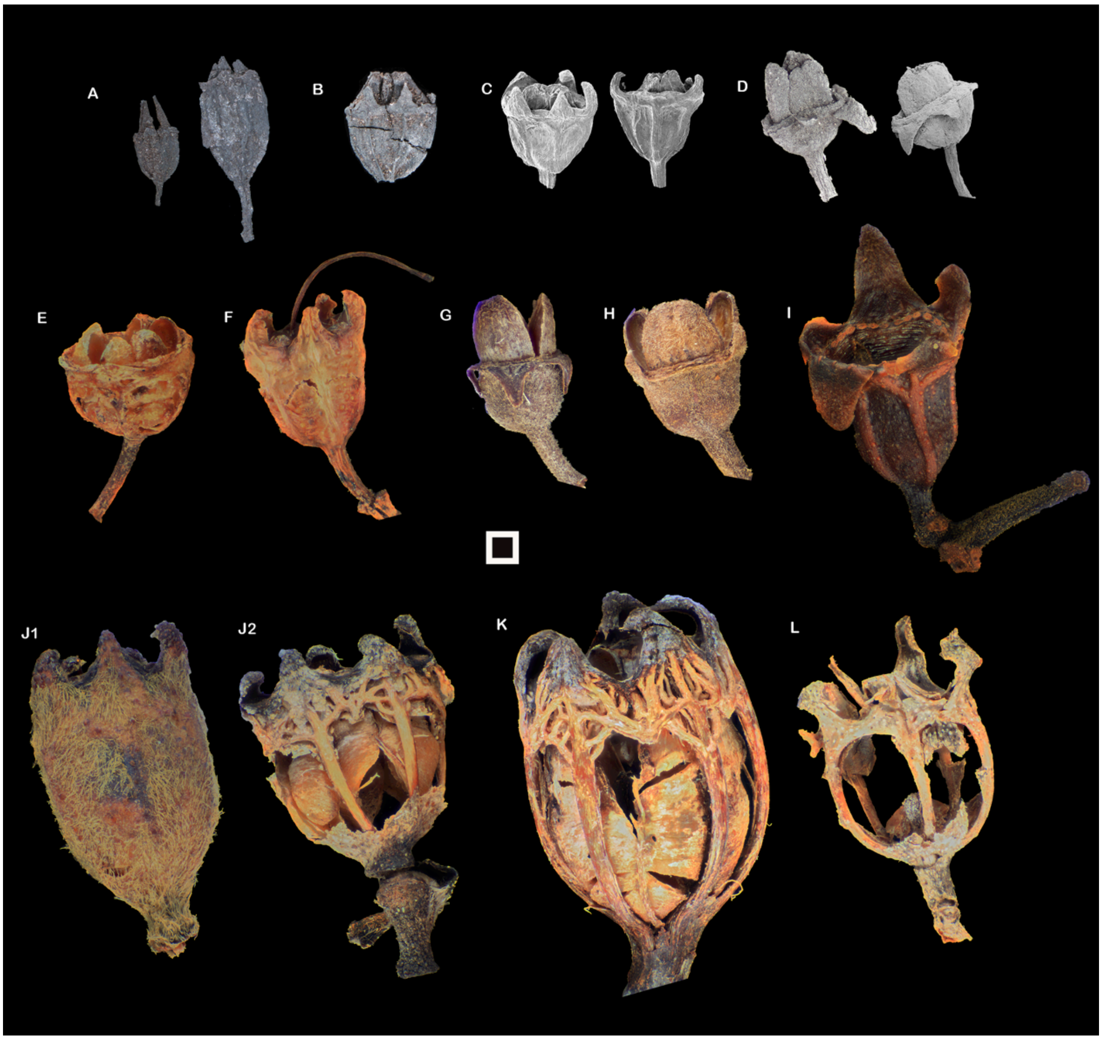

FIGURE 6: Anatomy of Taxon 2, *Metrosideros wrightii* sp. nov.: (A) GF006, (B) GF009, (C) GF004, (D) GF001. Note that the veins denoted by arrows in specimens A and B are faint, but recognizable. Valves are demonstrated on specimen C, and the reduced sepals (S) are denoted on specimens C and D. Scale bar = 1 × 1 mm.

SYSTEMATICS

TAXON 1 —

Order: Myrtales

Family: Myrtaceae

Tribe: Metrosidereae

Genus: *Metrosideros*

Species: *Metrosideros dawsonii* sp. nov.

Etymology: Named for John W. Dawson, in recognition of his work illustrating and classifying the extant Pacific capsular-fruited Myrtaceae. Diagnosis: Fruit a small, loculicidal capsule, strongly exserted from the fruiting hypanthium when mature. Ovary 3-locular, loculicidally dehiscent capsule with style inserted in a shallow pit on the summit. Flower 5-merous. Sepals deltoid, inserted on the prominent hypanthial rim, which appears as a swollen “lip” around the capsule. Five main, persistent hypanthial veins, terminating in the sepals.

Holotype: GF-005

TAXON 2 —

Order: Myrtales

Family: Myrtaceae

Tribe: Metrosidereae

Genus: *Metrosideros*

Species: *Metrosideros wrightii* sp. nov.

Etymology: Specific epithet for Shane Wright, in recognition of all of the work he has done contributing to understanding the biogeography and evolution of *Metrosideros*.

Diagnosis: Fruit a small, loculicidally dehiscent capsule, slightly exserted from the fruiting hypanthium when mature. Ovary 3-locular. Flower 5-merous. Locules of the capsule attenuated. Sepals persistent, highly reduced, inserted on the prominent hypanthial rim, which appears as a swollen “lip” around the capsule. Five main, persistent hypanthial veins, terminating in the sepals.

Holotype: GF-004

Paratype: GF-001.

DISCUSSION

Justification for assignment to genus— Several synapomorphies on the fossil fruits, particularly in combination, can be used to confidently diagnose these fossils as belonging to the Myrtaceae, and then to the genus *Metrosideros*:

(1) Loculicidally dehiscent, tricarpellate ovary— Both taxa, *Metrosideros dawsonii* and *Metrosideros wrightii*, can be confidently assigned to the Myrtaceae due to the presence of a diagnostic set of characters. The ovary is tricarpellate, and partially exserted beyond the hypanthial rim upon maturity of the fruit, which is a dry, loculicidally dehiscent capsule. The fruit in all cases is pentasepalous, which indicates pentamery. These characters are highly consistent with assignment to the Myrtaceae and are particularly suggestive of the tribes Kanieae and Metrosidereae (Basinger et al., 2007; Tarran et al., 2016).

(2) Five main veins in the hypanthium— The most important character for identification of both fossil taxa is the presence of five main veins in the hypanthium, terminating in the sepals. This is a synapomorphy for the tribe Metrosidereae as defined by Wilson (2011). It is not the case that the fruits of all Metrosidereae *only* have five veins, but there are five major vascular traces. Remnants of the tops and bottoms of intermediate, non-major veins can be seen between the main veins in some extant *Metrosideros* postdehiscence (Fig. 5J2, K). The character of five, persistent and highly conspicuous, externally visible veins running along the hypanthium is a feature commonly seen in the genus *Tepualia* (Dawson, 1972c) and in the (formerly) broadly defined *Metrosideros* subgenus *Mearnsia* (Dawson, 1970b, 1972b) (Fig. 5). It is now unlikely that what has been called subgenus *Mearnsia* is a monophyletic group (Pillon et al., 2015), so we cannot suggest subgeneric affinities, other than to comment that they do not have any characters that suggest placement in subgenus *Metrosideros*, as we could with *M. leunigii* (Tarran et al., 2016).

The character of five main veins occurs in all Metrosidereae (Wilson, 2011), though they are not always “strongly developed” and, hence, visible on the fruit externally, such as in many of the extant taxa within the broadly defined subgenus *Metrosideros* as such, this was not a character used for identifying *M.*

leunigii from Oligocene sediments at Little Rapid River in Tasmania (Tarran et al., 2016). The character of five prominent veins visible in the hypanthium is largely consistent with the formerly recognized subgenus *Mearnsia*, or at least it is inconsistent with most of the species in the subgenus *Metrosideros*, which often have more weakly developed veins (see Fig. 5D, G, H) that are not always visible without skeletonizing or sectioning the fruit. The character was a critical one for Wilson (1993) in demonstrating that the phylogenetic placement of *M. queenslandica* (the only species on the Australian mainland referred to *Metrosideros* at the time) was incorrect. From this reassessment, the species was referred to the tribe Tristanieae and renamed *Thaleropia queenslandica.*

Even in the species with more strongly developed veins, largely in the formerly recognized subgenus *Mearnsia*, the veins are not always highly visible on the surface of the hypanthium. For example, in *Metrosideros punctata* J. W. Dawson (Fig. 5J1, J2) this character is clearly visible only in the later stages of fruit maturity, where the thinner parts of the hypanthium break down between the five thickened major veins.

(3) Hypanthial rim— A further character that Tarran et al. (2016) used to identify *M. leunigii* from other closely related capsular-fruited Myrtaceae in the tribe Kanieae was the prominent hypanthial rim, which appears as a swollen lip. This character was observed in many *Metrosideros* species, but lacking in many species from the tribe Kanieae. It was observed that in the treatment of the groups that would later become the two subgenera of *Metrosideros*, Dawson (1970a, b, 1976) notes that the stamens are "in a single whorl, set behind the rim formed distally from the hypanthial lining," and in some cases, in the *Mearnsia* group, "arising directly from it." Dawson considered this an important character. While stamen scars are not visible on any of the Golden Fleece *Metrosideros* fossils, unlike in *M. leunigii*, the swollen hypanthial rim is a strong indicator of Metrosideroid affinity.

(4) Insertion of style base in the ovary— Additionally, *Metrosideros dawsonii* has a shallow groove running down the middle of the valve, denoting the boundary of the carpel, which terminates in a v-shaped groove at the top of the valve. This

is seen in many modern representatives of *Metrosideros* and evidences the point of style insertion in a shallow pit in the summit of the ovary where the v-shaped grooves at the top of each valve meet. This is particularly visible on the valves of *M. angustifolia* (L.) Sm. pictured in Figure 5E. This character was one of the final characters used by Tarran et al. (2016) to describe *M. leunigii*, as it can help distinguish Metrosidereae fruits from those of the Kanieae, because the latter often have the style terminal on the ovary summit, rather than being inserted in a shallow pit.

Worthy of note is the large degree of superficial resemblance between *M. dawsonii* and the oldest (Miocene) fossil *Metrosideros* fruits from New Zealand illustrated by Pole et al. (2008), which were never formally described. The similarity between these fossils is greater than that between either of the described fossils and any extant taxon. Pole et al. (2008) makes a comparison of their Miocene fossils with the New Caledonian species *M. operculata* and *M. patens*, both belonging to the formerly recognized subgenus *Mearnsia*. Interestingly, the two characters of (1) the five persistent, visible, hypanthial veins terminating in the sepals and (2) the locules of the ovary being exserted well beyond the hypanthial rim do not occur in combination in either of the extant species that Pole et al. (2008) illustrate and compare with those fossil fruits. We observe here that these two characters are not found in combination in any modern representatives of *Metrosideros* in New Zealand and are not observed in any extant species of the formerly recognized subgenus *Mearnsia*.

Subtle character differences—such as the difference in thickness of the five hypanthial veins, and the difference in size of sepals, between *M. dawsonii* and the undescribed fruits illustrated by Pole et al. (2008)—make us reluctant to formally assign those specimens to the same fossil species, especially without personally examining the fruits used by Pole et al. (2008). Nevertheless, the similarities are striking, and we suggest that the *Metrosideros* fruits and *M. dawsonii* undescribed by Pole et al. (2008) potentially represent a closely related lineage that is now extinct from both Australia and New Zealand.

Metrosideros wrightii is even more unusual, with its long acuminate valves. This character has not been observed in any modern Metrosidereae. The closest example of such acuminate valves is in some species in the genus *Eucalyptus*, such as *E. socialis* F.Muell. ex Miq. However, in the case of *E. socialis* the acuminate valves are derived from a persistent style base, rather than a conical capsule summit.

Paleobiogeography— This is the second record of fossil *Metrosideros* species from the Cenozoic of southeastern Australia, and both taxa described here represent different species than those described from the Early Oligocene sediments at Little Rapid River (Tarran et al., 2016). The fossil record of the capsular-fruited Myrtaceae has been called "largely equivocal" (Basinger et al., 2007), but the fossil record of *Metrosideros* in southeastern Australia, along with Basinger's record of Kanieae in South Australia, is beginning to highlight that the Myrtaceous component of the Cenozoic southeastern Australian vegetation differed markedly from the present-day flora. Clearly, these closely related capsular-fruited groups, the Kanieae and Metrosidereae, were once much more widespread in Australia than they are today, with the Metrosidereae now entirely extinct in Australia, and the Australian distribution of Kanieae now mostly restricted to the eastern margins of Australia (particularly the genera *Baronigia*, *Sphaerantia*, *Ristantia*, *Mitrantia*, and *Tristaniopsis*) or else to the tropics of Papua New Guinea and surrounding landmasses in the Indonesian archipelago (*Kania*, *Basisperma*, *Tristaniopsis*) or New Caledonia (*Tristaniopsis*, *Cloezia*) (Basinger et al., 2007; Wilson, 2011).

Wilson (1996) proposed that New Zealand was the landmass where the two subgenera of *Metrosideros* first diverged, and Wright et al. (2000b) hypothesized that a lack of a fossil record on other Gondwanic landmasses, plus a "long fossil record" in New Zealand, pointed toward a New Zealand origin for the genus. Contrary to this, Tarran et al. (2016) proposed an Australian origin. The fossils reported here, in conjunction with those described previously, establish that *Metrosideros* was not only present in Australia, but there was some diversity of species, and these may have persisted in the vegetation from the Eocene-Oligocene, to at least the Oligo-Miocene.

Making any inferences of infra-generic paleobiogeography is difficult because the relationships within *Metrosideros* at this taxonomic level are poorly resolved (Pillon et al., 2015). It now seems that while the subgeneric classification of subgenus *Metrosideros* represents a monophyletic lineage, subgenus *Mearnsia* is not a monophyletic group, and there could not have been a single divergence event between the subgenera *Metrosideros* and *Mearnsia*.

The fossils described in the present study are of a similar age to those described by Pole et al. (2008) and are strikingly similar in superficial appearance. While subgenus *Mearnsia* species do occur in New Zealand, none exist with such strongly defined persistent hypanthial veins. Pole et al. (2008) note that these fruits do not bear close resemblance to any of the extant New Zealand genera of either subgenus *Metrosideros* or subgenus *Mearnsia*, and they suggest that the fossils most closely resembled species of subgenus *Mearnsia* from New Caledonia and Papua New Guinea.

While it is apparent that the traditional subgeneric groupings may not hold up to phylogenetic scrutiny, they may still hold some value for paleobiogeographic interpretation, since it is only the subgenus *Metrosideros* that is widely distributed around the Pacific, probably due to their lightweight and highly vagile seeds (Corn, 1972; Drake, 1992; Wilson, 1996). Therefore, it is feasible that any given fossils of subgenus *Metrosideros* in Australia might represent taxa that arrived via long-distance dispersal rather than vicariance; and, as such, it is not possible to say with certainty that the fossils of *M. leunigii* described by Tarran et al. (2016) support an Australian origin of the genus. On the other hand, what was called subgenus *Mearnsia* (now just the remaining species in the genus) is more re- stricted in its distribution than subgenus *Metrosideros*, occurring only on the Gondwanic landmasses of New Zealand, New Caledonia, and New Guinea as well as the Solomon Islands and the Philippines. As such, the fossil species *M. dawsonii* and *M. wrightii*, which do not recognizably belong to the subgenus *Metrosideros* — and may share affinities with members of the formerly recognized *Mearnisa* group — are more likely to represent long-standing vicariant populations.

The superficial resemblance of *M. dawsonii* and, even more, of Pole et al.'s (2008) undescribed fruits to *Tepualia stipularis* — or *M. stipularis* if the most recent circumscription by Pillon et al. (2015) is accepted — is also worthy of comment (see Fig. 5F). Analyses by Wilson (1996) and Thornhill et al. (2015) show that *Tepualia* is sister to much of the Metrosideroid diversity. Prior to this most recent circumscription of the genus, Thornhill et al. (2015) speculated that the disjunction between the occurrence of *Tepualia* in South America and *Metrosideros* in the rest of the Pacific, from New Zealand to New Caledonia, Hawaii, and South Africa, might have arisen in a number of ways: through (1) extinction of *Metrosideros* in South America, (2) extinction of *Tepualia* in New Zealand, (3) a long-distance dispersal event of *Metrosideros* from New Zealand to Africa, or (4) the extinction of a more widespread ancestor leaving its relicts in South America and Africa. The long fossil record of *Metrosideros* now found in Australia may be considered evidence for this final option.

Finally, it is interesting to consider why *Metrosideros* became extinct in Australia. It is likely that this extinction occurred during the time of extreme rainforest contraction in the Neogene and early Quaternary, as Australian climates became drier and fires became more widespread and frequent (Hill, 2004; Byrne et al., 2011). Extant *Metrosideros* species now largely occur on islands that, prior to human arrival, had relatively few fires but also often had no mammalian browsers. The hypothesis that aridification was a direct driver of the extinction of *Metrosideros* from Australia is relatively weak, because the species extend to relatively dry climates today. More likely is that fire was important, and it is also possible that evolution of large mammalian browsers may have contributed to the loss of *Metrosideros* from Australia. In New Zealand, the preferential browsing of *Metrosideros* spp. by invasive possums is a significant conservation concern and, in some cases, has led to significant dieback of forests (Batcheler, 1983). These hypotheses for extinction in Australia can be tested with more detailed analysis of the improving fossil record of the tribe, especially taking phylogeny and functional traits into account.

CONCLUSIONS

The discovery of *M. dawsonii* sp. nov. and *M. wrightii* sp. nov. establishes the presence of two species of *Metrosideros* in the Oligo-Miocene of Tasmania, without clear affinities to the more widely spread subgenus *Metrosideros*. Although *Metrosideros* is no longer present in Australia today, this new fossil evidence, combined with the fossils described in Tarran et al. (2016), demonstrate that not only was *Metrosideros* once present in Australia during the Cenozoic, but a diversity of *Metrosideros* species persisted at least from the Eocene-Oligocene of southeastern Australia into the Oligo-Miocene. This further strengthens the hypothesis, previously put forward by Tarran et al. (2016), of an Australian origin of the genus, and further adds to the mystery of its extinction on the continent.

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CHAPTER 5:

Identifying fossil Myrtaceae leaves: the first described fossils of *Syzygium* from Australia.

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Overall percentage (%)	70%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	3.7.18

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Peter G. Wilson		
Contribution to the Paper	Peter is an expert in the taxonomy of this group, and assisted with characterisation of morphological characters of the fossils, and their taxonomic interpretation, as well as providing advice around nomenclatural issues, and providing comments on the manuscript at various stages of development.		
Signature		Date	26 Feb 2018

Name of Co-Author	Ed Biffin		
Contribution to the Paper	Ed is an expert in the taxonomy of this group, and provided helpful feedback on the manuscript around taxonomic issues, as well as providing helpful discussion and interpretation of the results.		
Signature		Date	26/2/18

Name of Co-Author	Rosemary Paull		
Contribution to the Paper	Rosemary performed much of the initial collection, curation and preparation of the fossil material studied in this paper, and provided helpful comments and feedback on the manuscript.		
Signature	[redacted]	Date	21-2-18

Name of Co-Author	Robert S. Hill		
Contribution to the Paper	Bob supervised the preparation of this manuscript from early stages, and provided feedback throughout manuscript preparation, Bob provided technical advice through the lab work of this research, and offered helpful interpretation and discussion of results, and edited the manuscript.		
Signature	[redacted]	Date	3/7/18

ABSTRACT

PREMISE OF THE STUDY: Despite having leaves that are easy to identify to family level, very few studies have convincingly identified fossil Myrtaceae leaves to living genera. In this study, we used a broadly comparative approach with a large dataset of extant taxa to confidently assign the mummified remains of myrtaceous leaves from early Miocene sediments at Kiandra (New South Wales, Australia) to a living genus.

METHODS: Fossils were identified using a nearest living relative (NLR) approach, against a database of 232 extant broadleaf, rainforest Myrtaceae species. Leaf cuticles were prepared from 106 species, sourced from herbarium specimens as well as some living individuals, and a further 127 records were assembled from the literature. A set of simple but phylogenetically informative cuticular characters were observed, described and recorded under both scanning electron microscopy and standard light microscopy.

KEY RESULTS: A new fossil species of *Syzygium* Gaertn. is described from mummified remains found in early Miocene (21.5-21.7Ma) sediments. The fossil taxon is here named *Syzygium christophelii* sp. nov*,* in honor of the late Australian paleobotanist, David Christophel.

CONCLUSIONS: These fossils represent some of the most confidently described Myrtaceae leaf fossils published to date, and are the first and oldest described fossil record of *Syzygium* from Australia*.* While several fossil parataxa have been illustrated from New Zealand, and several fossil species of *Syzygium* have previously been proposed in the literature, many of these fossils lack characters for a confident diagnosis.

INTRODUCTION

INTRODUCTION

The Myrtaceae, despite their prominence in the modern day Southern Hemisphere vegetation, have an underworked macrofossil record when compared to other important Southern Hemisphere angiosperm families such as the Nothofagaceae and the Proteaceae. This is particularly true of leaf fossils, even though many extant taxa have leaves that are relatively easy to identify to family level. The fossil record of the Myrtaceae has been reviewed and summarised as ‘meagre and unpromising’ by Briggs and Johnson (1979), and little better in recent history as ‘scanty’ (Wilson, 2011). In a checklist and review of recent literature reporting confidently described fossil Myrtaceae, Basinger et al. (2007) show that of 63 publications reporting fossil Myrtaceae, 44 report fossil leaves, while only 19 report fossil fruits, flowers or wood. However, research into the identification of Myrtaceae leaf macrofossils has rarely been systematic or yielded promising or definitive infra-familial diagnoses. As a result, many Myrtaceae leaf fossils described in the literature to date are of limited use to systematists or biogeographers who seek confidently identified fossils to calibrate molecular studies, or to interpret paleobiogeographic patterns.

Most fossil Myrtaceae leaves reported in the literature are described from impression and compression material with little-to-no preservation of leaf cuticle material, and therefore rely solely on gross architectural features for diagnosis. Following the leaf architectural nomenclature of Hickey (1973), the primary character for identification to family-level is a pinnate venation, which can be eucamptodromous, brochidodromous, or acrodromous. The most common of these in the Myrtaceae is the brochidodromous venation type, where secondary veins arch up before reaching the leaf margin, and the loops culminate in a pronounced intramarginal vein. More than any other character, intramarginal veins have been used to infer myrtaceous affinity of fossil leaves. However, it is important to note that all of these venation types occur in other closely related families, and intramarginal veins occur in at least some representatives of most families within the Myrtales (Hickey & Wolfe 1975). Vickulin (1999) considers that diagnosis of fossil Myrtaceae leaves based exclusively on macromorphological characters is unsatisfactory, and notes that even outside the Myrtales, representatives in other more distantly related families, such as the Apocynaceae, Moraceae, Clusiaceae, Sapotaceae and Anacardiaceae, may show the development of intramarginal veins. So, some fossil leaves that belong to unrelated families, could conceivably be mistaken for Myrtaceae in impression or compression fossil material when taking only these characters into account. Manchester et al. (1998) note that, even if placement in Myrtaceae is correct, there may be a wide range of leaf architectural patterns observable within a given extant genus, and that it is dangerous to assign myrtaceous leaf material to modern genera in the absence of corroborative evidence from fossil reproductive structures. Occasionally, in the absence of associated reproductive structures, Myrtaceae leaves have been shown to have enough diagnostic characters to be confidently compared with living genera, but this is essentially limited to Eucalypt leaves, with their characteristic falcate shape (e.g. Pole's (1993) *Eucalyptus* fossil leaves from New Zealand). In South America, some of the most unequivocal myrtaceous fossils are of *Eucalyptus* leaves, although these are also found in association with well-preserved fruits and flowers, as illustrated by Gandolfo et al. (2011), and described by Hermsen et al. (2012), and it was the reproductive structures that allowed the most confident identification, and the assignment of sub-generic affinities.

In the absence of evidence from reproductive structures, cuticle micro-morphological characters have been convincingly utilised in identification of fossil leaves for a number of angiosperm families. In the Southern Hemisphere the most notable examples of this are with the Nothofagaceae and Proteaceae, as well as some important conifer families, but this has yet to be satisfactorily demonstrated with fossil Myrtaceae leaves. Lid-cells *sensu* Lange (1980) appear to be common epidermal features over oil-glands, which are considered one of the fundamental features of the family, and they are present in virtually all genera (Wilson, 2011). Lid-cells, when cuticle preservation exists, in combination with the macro-morphological characters, allow much more confident referral of foliar remains to Myrtaceae. This character allowed Christophel and Lys (1986) to make a significant advance in identification of myrtaceous foliar remains, taking into account leaf architectural features as well as cuticle micro-morphological details. They erected the form genus *Myrtaciphyllum*, and described two fossil taxa, *M. douglasii* and *M. undulatum,* from the Eocene Anglesea locality in Victoria, Australia, although lid-cells were only reported on the cuticles of *M. undulatum*. Since then, authors reporting Southern Hemisphere fossils of Myrtaceae have used lid-cells as a hallmark cuticle character and synapomorphy. For instance, in Scriven's (1993) treatment of the Eocene Maslin Bay flora, potential Myrtaceae leaves lacking lid-cells were not diagnosed to that family. The presence of lid-cells has also been used for confident taxonomic placement of fragmentary leaves and dispersed cuticles (e.g Carpenter and Pole, 1995; Pole, 2007; Pole et al., 2008). In the absence of other sufficiently convincing evidence, the presence of lid-cells should be considered important for confident diagnosis of myrtaceous foliar remains.

Hill and Merrifield (1993) regarded most attempts in the literature to describe Myrtaceae fossils prior to the work of Christophel and Lys (1986) to have been based on very poor comparisons with extant taxa. However, even though *Myrtaciphyllum* does provide a much more confident myrtaceous designation, fossils assigned to this genus still prove of little value to systematists or biogeographers seeking resolution past family level. Christophel and Lys (1986), when describing their two species of *Myrtaciphyllum*, compared the fossils with a number of extant taxa. They performed a 'Numerical Taxonomic Analysis' in which 19 characters were selected, and fossils were compared with 65 leaves of 11 myrtaceous taxa, from 5 genera: *Syzygium, Caryophyllus, Acmena, Carpolepis* and *Lophostemon*. Two of these genera, *Caryophyllus* and *Acmena* have subsequently been considered synonyms of *Syzygium* (Craven et al., 2006; Craven and Biffin, 2010a) and so, according to most recent understanding of relationships within the Myrtaceae, only 3 genera (from 3 tribes) were actually used for comparison, and no confident identification past family level could be made. Building on the work of Christophel and Lys (1986) and Christophel et al. (1992), a number of other fossils have been placed into the form genus *Myrtaciphyllum,* but no studies have come close to confident generic identification of non-eucalypt myrtaceous foliar remains.

Since the pioneering work by Christophel and Lys (1986), the publication of rigorous and now relatively stable molecular phylogenies with clearly understood and delineated infra-familial relationships (e.g. Wilson et al., 2001; Wilson et al., 2005; Biffin et al., 2007; Biffin et al., 2010; Wilson, 2011) have revolutionised our understanding of relationships within the Myrtaceae. As a result, it is now possible to test conclusions of relatedness based upon fossil and extant cuticle morphology in a robust phylogenetic framework. Further to this, a modest amount of research has been published exploring the taxonomic and phylogenetic significance of leaf architectural and cuticle micro-morphological characters in extant Myrtaceae. The most rigorous of the modern studies have used cuticle micro-morphological as well as internal leaf, stem and petiole characters (e.g. Retamales and Scharaschkin 2015; Soh and Parnell 2011). However, when identifying mummified angiosperm leaf remains, cuticle micro-morphology and gross leaf architecture usually provide the only characters that are regularly well preserved.

The present study is an attempt to identify and describe myrtaceous leaf fossils, using a simple, but systematic stomatographic and cuticular morphological analysis, which can be easily extended in future. Fossil identification is informed by phylogenetic relationships, as understood from modern molecular phylogenies, using a large comparative dataset of extant leaves and cuticles collected from the literature and referenced herbarium specimens. In total, we investigate the cuticle micromorphology of 232 extant broadleaved myrtaceous taxa for stomatal characteristics and the presence/absence of foliar trichomes for comparison with fossil material. The fossils described in the present study are from the early Miocene of Kiandra, New South Wales (NSW), where a large number of mummified leaves referable to the Myrtaceae have been recovered, representing two distinct parataxa. Originally reported by Selkirk (1969) who was studying fossil epiphyllous fungi, the first of these taxa was tentatively compared to several genera in the now radically re-circumscribed subfamily Myrtoideae (Wilson et al., 2005) including *Xanthomyrtus*, *Eugenia*, *Acmena (Syzygium), Austromyrtus* and *Backhousia* (Selkirk, 1969). These fossils were confirmed as myrtaceous by Christophel and Lys (1986), and were alluded to most recently by Macphail et al. (1994). However, Selkirk (1969) also noted that there might be a second myrtaceous species at this locality, hitherto unreported and undiagnosed. Re-investigation of the Kiandra fossil material finds that Selkirk was correct, and this is the subject of the present study, which focuses on the unreported myrtaceous taxon. Given the poorly studied nature of the myrtaceous fossil record, a site with more than one potential fossil taxon is deserving of special attention.

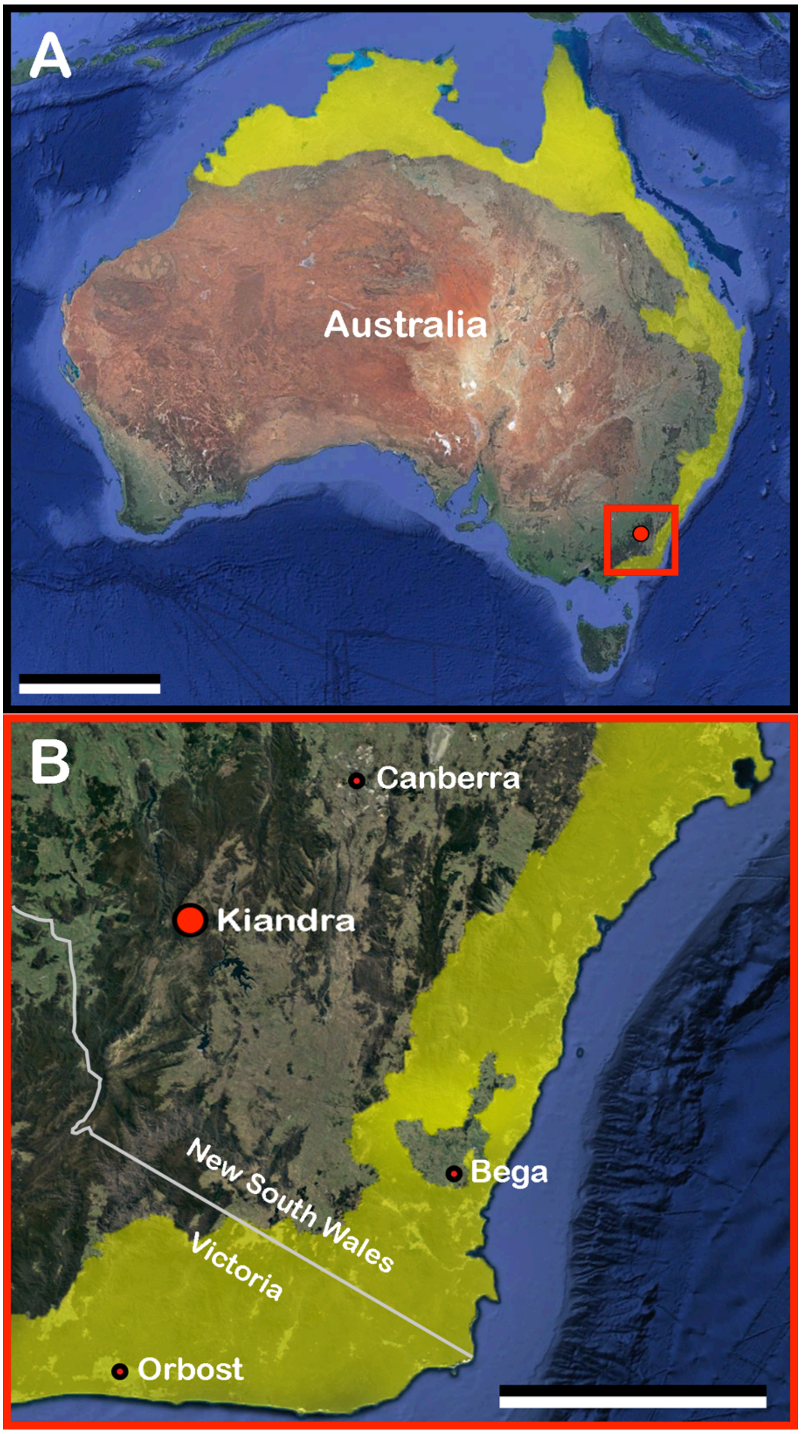

FIGURE 1: A) Map of Australia showing the approximate distribution and range of the genus *Syzygium* Gaertn. on the continent, highlighted in yellow along the northern and eastern coast, and the location of the study site highlighted by the red box which shows the study site of Kiandra. Scale bar = approx. 1000km **B)** A map of New South Wales and northern Victoria, showing the border between the two states, the approximate distribution of the genus *Syzygium* in this region highlighted in yellow, and the location of the study site at Kiandra further inland. Scale bar = 100km. Note that the study site occurs inland, nearly 100km away from the nearest extant occurrences of the genus *Syzygium.* Map data: Google, DigitalGlobe 7.1.2.2041

MATERIALS AND METHODS

Fossil site and age— The macrofossils in the present study were collected from the Homeward Bound diggings, New Chum Hill (35°52′S, 148°29′E), an old gold mining site in Eastern Highlands of New South Wales at 1400m asl. The mine site is 1km north of the abandoned mining town of Kiandra (Fig. 1), for which the fossil locality has been named. A deeply dissected and largely treeless plateau, varying in height from 1375-1600m asl. surrounds the town site. In 1859–1860 gold-seeking activities at New Chum Hill exposed fossiliferous sediments from a single formation in three pits: Homeward Bound diggings, Cornishman's diggings and Pattinson's diggings (see Owen, 1988). Gill and Sharp (1957) interpreted the New Chum Hill sediments as representing three sedimentary cycles, collectively about 32 m thick. Each of the three cycles begins with rapidly deposited, poorly sorted coarse sands that grade upwards to still-water, fine, laminated sands, silts, and carbonaceous, highly fossiliferous clays. The latter were deposited under reducing conditions. All three sedimentary cycles terminate in a lignite phase with irregular surfaces, suggesting short periods of intercycle erosion. The carbonaceous lake sediments exhibit no evidence of bioturbation indicating that each sedimentary cycle experienced periods of stagnation. There is no significant difference in age between the floras recovered from each of the diggings, or between the lignite cycles. The sediments are biostratigraphically dated by correlation of key spore and pollen taxa within the middle subdivision of the *Proteacidites tuberculatus* Zone of the Gippsland Basin, suggesting an early Miocene age (Owen, 1988), which is consistent with radiometric (K-Ar) age estimates of basalts overlying the uppermost lignite cycle of 21.5 Ma (±0.6 Ma) to 21.7 Ma (±0.4 Ma). These K-Ar dates have been considered fairly accurate, falling within a 4 million-year age range (22-18Ma) of a total of 9 ages derived from basalts in the surrounding Snowy Province (Wellman and McDougall, 1974; Owen, 1988). Even allowing for possible errors associated with older K-Ar dates, this indicates a probable minimum Aquitanian (early Miocene) age for the fossil assemblage.

The macro- and micro-fossil floras indicate moist, closed forest vegetation with higher temperatures and precipitation than at the present (Owen, 1988), consistent with the warmer and wetter global climate of the early Moicene (Zachos et al., 2001; Zachos et al., 2008). However, very little else has been published about the deposit. Owen (1988) described the palynoflora in great detail, but the only angiosperm macrofossils described from the deposit so far are of *Nothofagus kiandrensis,* a rare macrofossil record of subgenus *Brassospora*, which is prominent throughout southern Australia in the pollen record for much of the Cenozoic (Hill 1987; Paull and Hill, 2003). Today, the vegetation at Kiandra is primarily alpine eucalypt woodland to alpine heath, and experiences regular winter snow cover.

Fossil preparation and identification—A large collection of mummified leaves from the Kiandra locality is stored in the David T. Blackburn Palaeobotany Collection at the University of Adelaide, on glass slides mounted in phenol-glycerin jelly. 13 specimens in total have been given collection numbers, and have all been examined in this study: K-216, 272, 344, 447, 448, 546, 625, 634, 648, 688, 694, 707 and 710 (See Fig. 2). Many of these specimens were collected and prepared by Charman (1993) and Paull (2002). A number of other fossil leaves of this taxon may exist in material collected from this locality, but these have not yet been given collection codes.

Leaves of extant Myrtaceae were collected for comparison, from vouchers in several herbaria, at the National Herbarium of New South Wales, the State Herbarium of South Australia, and the University of Adelaide Herbarium, and fresh leaves of some taxa were collected from the Adelaide Botanic Gardens (accession numbers and collection codes in Appendix 1). Leaf cuticles were prepared from 105 species of extant broadleaf, rainforest Myrtaceae, and data from a further 127 species of living broadleaf, rainforest Myrtaceae were sourced from the literature, for a total of 232 species. Most of these data were sourced from Soh and Parnell's (2011) study of leaf and cuticle morphology across the sub-generic diversity of *Syzygium.* We also included cuticle and stomatal descriptions from a number of other studies (Khatijah et al. 1992, Retamales et al. 2014, Retamales & Scharaschkin 2015 and Haron & Moore 1995) where A) information was available on cuticle and stomatal morphology, and B) information about the presence or absence of foliar trichomes on cuticles was also recorded.

For the extant taxa sampled, species were selected from 10 of the 16 tribes in the family, from 38 genera following the phylogenies constructed by Wilson et al., (2005), Biffin et al., (2010), and Thornhill et al., (2012b). Only broadleaf, rainforest Myrtaceae taxa were selected, as these taxa are more likely to be nearest living relatives (NLR's) to fossils found in the rainforest fossil assemblage. Cuticle pieces were prepared from the extant and fossil leaves and mounted on glass slides for standard light microscopy. Cuticles were cleared in a 20% aqueous solution of chromium trioxide (CrO_3) for several days until internal leaf tissue or detritus had been loosened and macerated. Any adhering internal tissue was removed with fine paintbrushes under a dissecting microscope. Cuticles were stained with a saturated solution of Sudan Black in ethanol, or a 5% solution of Crystal Violet. LM Images were cropped, resized, and adjusted for contrast and brightness in Adobe Photoshop CS6 (Adobe Systems, San Jose, California, USA). General cuticle and stomatal terminology follows Wilkinson (1980), which was originally published in Metcalfe and Chalk (1979), as well as the stomatal terminology of Soh and Parnell (2011). For the purposes of this study, we have opted to work with a simple topographic approach, rather than an ontogenetic classification.

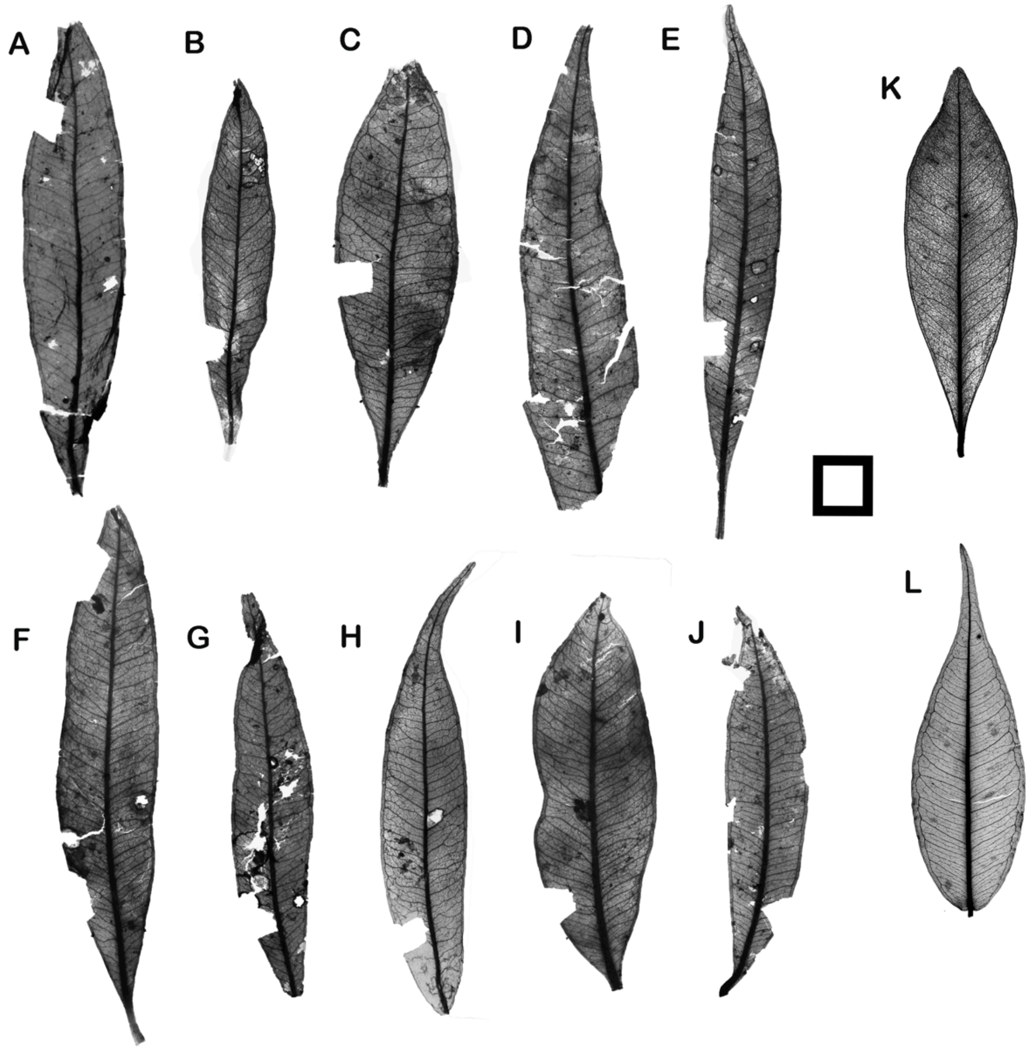

FIGURE 2: ***Syzygium christophelii* sp. nov. A)** Holotype K707 **B)** K216 **C)** K329 **D)** K444 **E)** K522 **F)** K545 **G)** K625 **H)** K688 **I)** K694 **J)** K710. Note the brochidodromous venation of all samples, the prominent intramarginal vein in all specimens as well as the prominent drip tip preserved in some of the specimens. **(K-L)** Two leaves of extant *Syzygium* species for comparison, *S. smithii* (Poir.) Nied. and *S. apodophyllum* (F.Muell.) B.Hyland respectively, taken from Christophel and Hyland's (1993) Leaf Atlas of Australian Tropical Rainforest Leaves. Scale box (center) = 1 cm x 1cm.

Defining stomatal terminology**—**Soh and Parnell (2011) describe four stomatal complex types on the cuticles of 81 species of *Syzygium* taken from herbarium collections. These are: i) paracytic, ii) anisocytic, iii) anomocytic, and iv) cyclostaurocytic. We follow their stomatal descriptions, abbreviated here, as follows:

1) Paracytic: the guard cells are flanked by two subsidiary cells, either extending over the poles of guard cells or not, and of equal or unequal size (Fig. 3A,B).
2) Anisocytic: the guard cells are surrounded by three cells that are not radially arranged. The subsidiary cells are mostly unequal in size, and one of the three is smaller than the other two cells (Fig. 3C,D).
3) Anomocytic: the cells surrounding the guard cells do not form any recognizable and consistent pattern, and they are not differentiated from other epidermal cells.
4) Cyclostaurocytic: four or more subsidiary cells surrounding the guard cells in single or double layers, more or less radially arranged and ring-like. The radial diameter of the subsidiary cells can be larger than their tangential width or smaller, giving rise to narrow or thick ring-like formations respectively. (Fig. 3E,F)

For the purposes of fossil identification, methodological consistency, and to avoid difficulties in defining different stomatal classifications, we have only indicated the presence or absence of these stomatal types as defined by Soh and Parnell (2011) in Table 1. The most common stomatal types in the Myrtaceae are anomocytic, paracytic and anisocytic. Occasionally other stomatal types are observed which may fit better into categories of staurocytic or cyclocytic following the terminology of Wilkinson (1980), but these types are rare in the surveyed literature and in our own survey of cuticles of extant Myrtaceae, and they have usually been found in conjunction with one of the four main stomatal types. In only one species in our survey were we unable to satisfactorily apply any of the four main stomatal classificatory types: *Ristantia pachysperma* (F.Muell. & F.M.Bailey) Peter G.Wilson & J.T.Waterh. This species appears to have more traditionally defined cyclocytic stomata, which are still radially arranged around the stomata, but lack the narrow and consistent ring-like appearance as defined by Soh and Parnell (2011) for cyclostaurocytic stomata. Where this species appears in Table 1, there are no stomatal types scored because, although stomata are present, they do not fit into any of the four stomatal types defined above. Giant or water stomata are not included in the stomatal count for any of the species, as they are usually actinocytic across all species in which they occur in any given family (Metcalfe and Chalk, 1979; Wilkinson, 1980).

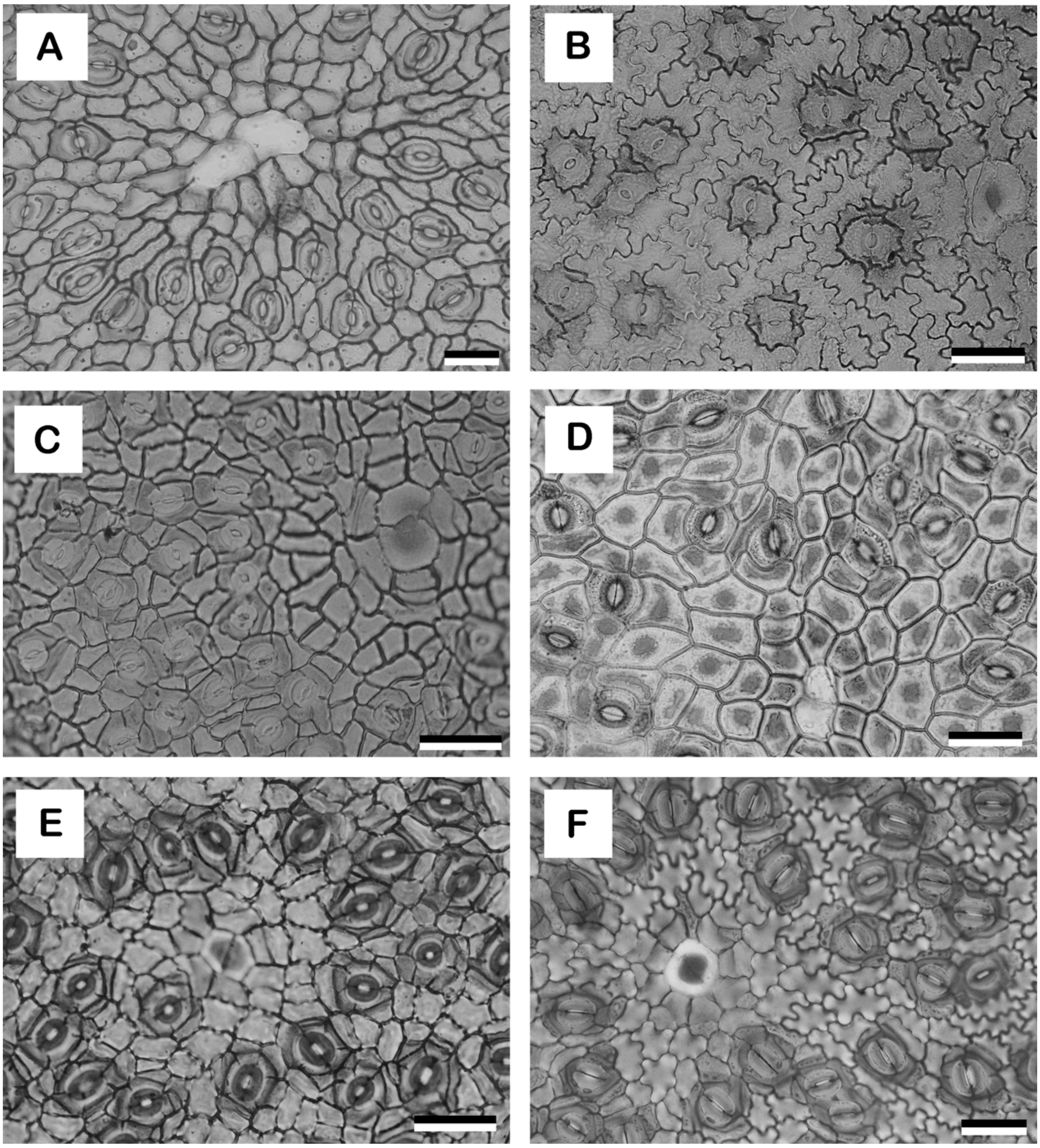

FIGURE 3: Different stomatal morphologies across subgenera in *Syzygium* Gaertn. A) Paracytic stomata in *Syzygium branderhorstii* Lauterb. (subgenus *Syzygium*), with large double-lid-cell in center. Scale bar = 20 µm **B)** Paracytic stomata in *Syzygium paniculatum* Gaertn. (subgenus *Syzygium*), with highly sinuous epidermal cells and a double-lid-cell on the right. Scale bar = 40 µm **C)** Anisocytic and cyclostaurocytic stomata in *Syzygium claviflorum* (Roxb.) Wall. Ex A.M.Cowan & Cowan (subgenus *Perikion*) with large double-lid-cell in center-right. Scale bar = 40 µm. **D)** Paracytic, anisocytic and occasionally staurocytic stomata in *Syzygium suborbiculare* (Benth.) T.G.Hartley & L.M.Perry (subgenus *Syzygium*) with double-lid-cell at the bottom-center. **E)** Cyclostaurocytic stomata on the cuticle of *Syzygium hemilamprum* (F.Muell.) Craven & Biffin (subgenus *Acmena*) Scale bar = 50 µm **F)** Cyclostaurocytic stomata in *Syzygium smithii* (Poir.) Nied. (subgenus *Acmena*), note the ring-like arrangement of subsidiary cells with straighter edges than the surrounding epidermal cells. Scale bar = 40 µm.

RESULTS

Trends in cuticle micromorphology within extant Myrtaceae— Table 1 shows that broad trends in stomatal subsidiary cell arrangement are observable in many genera, and across some tribes. For the very large genus *Syzygium*, mostly reported here from the dataset compiled by Soh and Parnell (2011), there appears to be large agreement in the stomatal subsidiary cell arrangements between species within the same subgenera, which supports the infrageneric subgroupings. Within subgenus *Syzygium* all species possess paracytic stomata, and may or may not have anisocytic stomata. Species surveyed from subgenus *Acmena* all possess only the cyclostaurocytic stomatal type, and this is the only subgenus to have such a consistent stomatal morphology. Species in subgenus *Sequestratum* have occasional anomocytic stomata, while the species in subgenus *Perikion* share a much less consistent stomatal morphology, while some species also possess what Soh and Parnell (2011) described as cyclostaurocytic stomata.

Within the tribe Myrteae, there is high consistency in stomatal morphology intra-generically. A greater sample size of *Eugenia* species would be necessary to make any useful observation about trends of stomatal morphology in this genus since the existing literature on the stomatal and cuticular morphology is confusing, and this very large genus has been poorly sampled. After *Syzygium, Eugenia* is the next largest genus in the Myrtaceae, with over 1000 species, and Mazine et al. (2016) recognize 9 sections within the genus. It is possible that sampling across these newly defined groupings within the genus would reveal useful cuticular characters to differentiate these groups.

Anomocytic stomata appear to be the most common type in the closely related capsular fruited tribe Metrosidereae, as well as Kanieae and Tristanieae, though greater sampling of all species and genera within these tribes is still needed to confirm this.

These data suggest that a complete lack of trichomes or hair bases is extremely uncommon in the rainforest Myrtaceae, and is highly characteristic of the tribe Syzygieae*.* One species of Eucalypteae in this survey, *Allosyncarpia ternata* also lacked trichomes. Greater sampling of the tribe Eucalypteae would have revealed many species to be essentially glabrous, or lacking “standard” myrtaceous hairs (Briggs and Johnson, 1979), as well as in the related tribe Melaleuceae (unpublished data), but in rainforest Myrtaceae complete lack of indumentum is a strong Syzygioid character.

TABLE 1: ***Cuticle Surfaces of Extant Myrtaceae -*** Selected cuticle morphological characters scored across the diversity of the rainforest Myrtaceae with a total of 232 taxa, some first described in this study, as well as others gathered from the literature. Stomatal complex type, and the simple presence or absence of trichomes are scored; (+) indicates presence of character, (-) indicates absence of character, (±) indicate that the character may be uncommon, or else may or may not be present, (?) indicates that the character was somehow obscured, usually only in the cases of extremely hairy species where stomata were not visible under indumentum, (++) is only used for the character of trichomes where the cuticle was considered to be extremely hairy.[1]Cuticle data from Soh and Parnell (2011), [2]from Khatijah et al. (1992), [3]from Retamales & Scharaschkin (2015), [4]from Haron & Moore (1995), [5] from Retamales et al. (2014)

GENUS	SPECIES	STOMATAL COMPLEX				TRICHOMES
		Anomocytic	Paracytic	Anisocytic	Cyclostaurocytic	(+/-)
		TRIBE: SYZYGEAE				
Syzygium						
Subg. *Syzygium*	[1]*S. angakae*	-	+	-	-	-
	[2]*S anisosepalum*	-	+	?	-	-
	S. angophoroides	-	+	-	-	-
	S. alatoramulum	-	+	-	-	-
	[1]*S. aqueum*	-	+	±	-	-
	[1]*S. aromaticum*	-	+	±	-	-
	S. attopeuense	-	+	±	-	-
	[1]*S. balsameum*	-	+	±	-	-
	[1]*S. borneense*	-	+	±	-	-
	[1]*S. bullockii*	-	+	±	-	-

[1]*S. campanulatum*	-	+	-	-	-
[2]*S. chloranthum*	-	+	?	-	-
S. cumini	-	+	+	-	-
[2]*S. curtisii*	-	+	?	-	-
[1]*S. diospyrifolium*	-	+	-	-	-
[2]*S. duthieanum*	-	+	?	-	-
[2]*S. dyerianum*	-	+	?	-	-
S. erythrodoxum	-	+	-	-	-
S. eucalyptoides	-	+	+	-	-
[1]*S. fastigiatum*	-	+	-	-	-
S. fibrosum	-	+	-	-	-
[1]*S. formosum*	-	+	-	-	-
S. fratris	-	+	±	-	-
[1]*S. grande*	-	+	-	-	-
[2]*S. griffithii*	-	+	?	-	-
[1]*S. hancei*	-	+	±	-	-
[1]*S. harmandii*	-	+	-	-	-
[2]*S. helferi*	-	+	?	-	-
[1]*S. hemisphericum*	-	+	±	-	-
[1]*S. imitans*	-	+	-	-	-
[2]*S. inophyllum var. bernardi*	-	+	?	-	-
[1]*S. jambos*	-	+	±	-	-
[1]*S. khaoyensis*	-	+	-	-	-
[2]*S. leptostemon*	-	+	?	-	-
[1]*S. levinei*	-	+	±	-	-
[1]*S. lineatum*	-	+	-	-	-
S. longipes	-	+	-	-	-
[1]*S. malaccense*	-	+	±	-	-
[1]*S. megacarpum*	-	+	-	-	-
S. minutuliflorum	-	+	+	+	-
S. nervosum	-	+	-	-	-
[1]*S. nigrans*	-	+	-	-	-
[1]*S. oblatum*	-	+	±	-	-
[1]*S. pachysarcum*	-	+	±	-	-
S. paniculatum	-	+	-	-	-
[2]*S. papillosum*	-	+	?	-	-
[1]*S. phengklaii*	-	+	-	-	-
[1]*S. pierrei*	-	+	±	-	-
[1]*S. polyanthum*	-	+	-	-	-
S. porphyrocarpum	-	+	-	-	*+
[1]*S. praecox*	-	+	±	-	-
[2]*S. pseudosubtilis*	-	+	?	-	-
S. puberulum	-	+	-	-	-
[2]*S. pycnanthum*	-	+	?	-	-
[1]*S. ripicola*	-	+	±	-	-
[1]*S. sclerophyllum*	-	+	±	-	-

	[1]*S. siamense*	-	+	±	-	-
	[1]*S. sterrophyllum*	-	+	-	-	-
	S. suborbiculare	-	+	+	-	-
	[2]*S. subdecussatum*	-	+	?	-	-
	[2]*S. symingtonianum*	-	+	?	-	-
	[1]*S. syzygioides*	-	+	-	-	-
	[1]*S. tetragonum*	-	+	-	-	-
	[1]*S. thorelii*	-	+	±	-	-
	[1]*S. tonkinense*	-	+	-	-	-
	[1]*S. vestitum*	-	+	-	-	*+
	S. xerampelium	-	+	-	-	-
	[1]*S. zimmmermannii*	-	+	±	-	-
Subg. *Acmena*						
	[1]*S. (Piliocalyx) francii*	-	-	-	+	-
	[1]*S. acuminatissimum*	-	-	-	+	-
	[1]*S. divaricatum*	-	-	-	+	-
	[5]*S. floribundum*	-	-	-	+	-
	[1]*S. graveolens*	-	-	-	+	-
	[1]*S. gustavioides*	-	-	-	+	-
	[1]*S. hedraiophyllum*	-	-	-	+	-
	S. hemilamprum	-	-	-	+	-
	[1]*S. mackinnonianum*	-	-	-	+	-
	[1]*S. mulgraveanum*	-	-	-	+	-
	S. smithii	-	-	-	+	-
	[1]*S. unipunctatum*	-	-	-	+	-
Subg. *Sequestratum*						
	[1]*S. aksornae*	±	-	+	-	-
	[1]*S. araiocladum*	±	-	+	-	-
	[1]*S. bankense*	±	-	+	-	-
	[1]*S. bicolor*	±	-	+	-	-
	[1]*S. cryptophlebium*	±	-	+	-	-
	[1]*S. francisii*	±	-	+	-	-
	[1]*S. antisepticum*	±	-	+	-	-
	[1]*S. jasminifolium*	±	-	+	-	-
	[1]*S. kinabaluense*	±	-	+	-	-
	[1]*S. luehmannii*	±	-	+	-	-
	[1]*S. multibracteolatum*	±	-	+	-	-
	[1]*S. nummularium*	±	-	+	-	-
	[1]*S. odoratum*	±	-	+	-	-
	[1]*S. polycladum*	±	-	+	-	-
	[1]*S. stapfianum*	±	-	+	-	-
	[1]*S. tenuirame*	±	-	+	-	-
	[1]*S. tephrodes*	±	-	+	-	-
	[1]*S. tetrapterum*	±	-	+	-	-

	[1]*S. tsoongii*	±	-	+	-	-
	[1]*S. wilsonii*	±	-	+	-	-
Subg. *Perikion*	[1]*S. abortivum*	-	-	±	+	-
	[1]*S. apodophyllum*	-	+	+	-	-
	[1]*S. attenuatum*	-	-	+	+	-
	[1]*S. boisianum*	-	-	+	±	-
	[1]*S. canicortex*	-	-	-	+	-
	[1]*S. championii*	-	-	+	+	-
	S. claviflorum	-	-	+	+	-
	[1]*S. coryanthum*	-	+	+	-	-
	[1]*S. multipetalum*	-	-	-	+	-
	S. pringlei	-	-	+	+	-
Subg. *Wesa*	*S. wesa*	-	-	+	-	-
Subg. *Anetholea*	*S. anisatum*	+	-	-	-	-
TRIBE: BACKHOUSEAE						
Backhousia	*B. angustifolia*	-	+	-	-	+
	B. citriodora	-	+	-	-	+
	B. enata	-	+	-	-	+
	B. hughesii	-	+	±	-	+
	B. kingii	-	+	±	-	+
	B. leptopetala	-	+	±	-	+
	B. myrtifolia	-	+	-	-	+
	B. oligantha	-	+	-	-	+
	B. sciadaphora	-	+	-	-	+
TRIBE: LINDSAYOMYRTEAE						
Lindsayomyrtus	*L. racemoides*	-	+	-	-	+
TRIBE: MYRTEAE						
Amomyrtus	[3]*A. luma*	+	-	-	-	+
	[3]*A. meli*	+	-	-	-	+
Blepharocalyx	[3]*B. cruckshanksii*	+	-	-	-	-
Decaspermum	*D. urvillei*	-	+	-	-	+
	D. prunoides	-	+	±	-	+
Legrandia	[3]*L. concinna*	+	-	-	-	+
Lenwebia	*L. lasioclada*	-	+	±	-	+
	L. prominens	-	+	±	-	+
Luma	[3]*L. apiculata*	-	+	-	-	+

	[3]*L. chequen*	-	+	-	-	+
Myrceugenia	[3]*M. chysocarpa*	+	-	-	-	+
	[3]*M. colchaguensis*	+	-	-	-	+
	[3]*M. correifolia*	+	-	-	-	+
	[3]*M. exsucca*	+	-	-	-	+
	[3]*M. lanceolata*	+	-	-	-	+
	[3]*M. leptospermoides*	+	-	-	-	+
	[3]*M. obtusa*	+	-	-	-	+
	[3]*M. ovata*	+	-	-	-	+
	[3]*M. ovata var. nannophylla*	+	-	-	-	+
	[3]*M. parvifolia*	+	-	-	-	+
	[3]*M. pinifolia*	+	-	-	-	+
	[3]*M. planipes*	+	-	-	-	+
	[3]*M. rufa*	+	-	-	-	+
Myrcianthes	[3]*M. coquimbensis*	-	+	-	-	+
Myrteola	[3]*M. nummularia*	-	+	-	-	+
Nothomyrcia	[3]*N. fernandeziana*	+	-	-	-	+
Gossia	*G. alaternoides*	-	+	+	-	+
	G. versteeghii	+	+	+	-	+
Rhodomyrtus	*R. sericea*	?	?	?	?	++
	R. pervagata	-	+	±	-	+
Lithomyrtus	*L. grandifolia*	?	?	?	?	++
	L. hypoleuca	?	?	?	?	++
	L. kakaduensis	?	?	?	?	++
Archirhodomyrtus	*A. beckleri*	+	-	-	-	+
Rhodamnia	*R. pauciovulata*	?	?	?	?	++
	R. rubescens	-	-	+	-	++
Ugni	[3]*U. candollei*	±	-	+	-	+
	[3]*U. molinae*	+	-	-	-	+
	[3]*U. selkirkii*	+	-	-	-	+
Uromyrtus	*U. archboldiana*	-	+	+	-	+
	U. lamingtonensis	-	+	+	-	+
	U. metrosideros	-	+	+	-	+
	U. tenella	-	+	+	-	+

Eugenia	[4]*E. axillaris*	-	+	-	-	+
	E. biflora	-	+	+		+
	E. capensis	-	+	+	-	+
	[4]*E. choapamensis*	-	+	-	-	+
	[4]*E. doubledayi*	-	+	-	-	+
	[4]*E. hirta*	-	+	-	-	+
	[4]*E. prasina*	-	+	-	-	+
	[4]*E. punicifolia*	-	+	-	-	+
	E. reinwardtiana	-	-	+	-	+
	E. stricta	-	+	-	-	+
	[4]*E. uniflora*	-	+	-	-	+
Myrtella	*M. beccarii*	-	+	-	-	+
				TRIBE: KANIEAE		
Barongia	*B. lophandra*	-	-	+	-	+
Lysicarpus	*L. angustifolius*	+	-	-	-	+
Kania	*K. eugenioides*	+	-	-	-	+
	K. hirsutula	+	-	-	-	+
	K. nettotensis	+	-	-	-	+
	K. platyphylla	+	-	-	-	+
Mitrantia	*M. bilocularis*	-	-	+	-	+
Ristantia	*R. pachysperma*	-	-	-	-	+
Tristaniopsis	*T. calobuxus*	+	-	-	-	+
	T. capitulata	+	-	-	-	+
	T. collina	+	-	-	-	+
	T. exiliflora	+	-	-	-	+
	T. glauca	+	-	-	-	+
	T. guillainii	+	-	-	-	+
	T. laurina	+	-	-	-	+
	T. mcphersonii	+	-	-	-	+
	T. reticulata	+	-	-	-	+
				TRIBE: METROSIDEREAE		
Metrosideros	*M. albiflora*	+	-	-	-	+
	M. bartlettii	+	-	-	-	+
	M. brevistylis	+	-	-	-	+
	M. (Carpolepis) elegans	+	-	-	-	+
	M. excelsa	+	-	-	-	+
	M. (Carpolepis) tardiflora	+	-	-	-	+
	M. (Tepualia) stipularis	+	-	-	-	"?" +

	M. macropus	+	-	-	-	+
	M. patens	+	-	-	-	+
	M. cherrieri	+	-	-	-	+
	M. salomonensis	+	-	-	-	+
	M. microphylla	+	-	-	-	+
	M. operculata	+	-	-	-	+
	M. fulgens	-	+	+	-	+
	M. oreomyrtus	+	-	-	-	+
	M. parkinsonii	+	-	-	-	+
	M. paniensis	+	-	-	-	+
	M. robusta	+	-	-	-	+
	M. ramiflora	-	+	-	-	+
	M. perforata	+	-	-	-	+
	M. longipetiolata	+	-	-	-	+
TRIBE: TRSTANIEAE						
Cloezia	*C. artensis*	+	-	-	-	+
	C. aquarum	+	-	-	-	+
Xanthomyrtus	*X. flavida*	+	-	-	-	+
	X. montivaga	+	-	-	-	+
TRIBE: LOPHOSTEMONEAE						
Lophostemon	*L. confertus*	+	-	-	-	+
	L. grandiflorus	+	-	-	-	+
	L. lactifluus	+	-	-	-	+
	L. suaveolens	+	-	-	-	+
TRIBE: XANTHOSTEMONEAE						
Xanthostemon	*X. formosus*	-	+	-	-	+
	X. umbrosus	-	+	-	-	+
	X. verticillatus	-	+	-	-	+
	X. whitei	-	+	-	-	+
TRIBE: EUCALYPTEAE						
Allosyncarpia	*A. ternata*	-	+	-	-	-

SYSTEMATICS

Order: Myrtales
Family: Myrtaceae Juss.
Tribe: Syzygieae Peter G.Wilson
Genus: *Syzygium* Gaertn.
Species: *Syzygium christophelii sp. nov.* Tarran, R.Paull et R.S.Hill

SPECIFIC DIAGNOSIS: Leaves petiolate; lamina size category microphyll to notophyll. Lamina dorsiventral, ovate to lanceolate; margins entire; apex acute to acuminate, sometimes tapering to a drip tip; base acute. Venation pinnate, brochidodromous with well-defined intramarginal vein. Leaf hypostomatic; stomata cyclostaurocytic with subsidiary cells in a single layer, radially arranged in a narrow ring, with straighter edges than surrounding epidermal cells. Epidermal lid-cells showing double-lid cell arrangement. Anticlinal cell walls of abaxial and adaxial surfaces sinuous; lacking hair-base scars.

ETYMOLOGY: Named in honour of the late David Christophel (1947-2018), for his significant contributions to Australian paleobotany, and particularly for his pioneering work identifying fossil Myrtaceae leaves.

HOLOTYPE: K707, housed in the David T. Blackburn Palaeobotany Collection at the University of Adelaide (Fig. 2A).

PARATYPES: K216, 272, 344, 447, 448, 546, 625, 634, 648, 688, 694, 707, 710, housed in the David T. Blackburn Palaeobotany Collection at the University of Adelaide.

TYPE LOCALITY: New Chum Hill, Kiandra, New South Wales, 35°52′S, 148°29′E; Aquitanian (early Miocene).

Description—Leaves ovate to lanceolate, dorsiventral and characterised by a long lamina, with the leaf apex sometimes extending into a prominent drip-tip

(Fig. 2A-J). The Holotype K707, is 1.7cm at its widest point, and is 7.6cm long, although missing its tip (Fig. 2A). The longest specimens range up to about 8.6cm. What appear to be smaller or juvenile leaf forms also occur (Fig. 2B), but these are indistinguishable based on cuticle morphology. The venation of the leaf can also be defined as pinnate and brochidodromous, with secondary veins ending in a prominent intramarginal vein running parallel to the leaf margins meeting in a closed "loop" at the leaf apex. The leaf margin is entire, and the leaf base is acute to acuminate.

The leaves are hypostomatic, with epidermal cells on both the adaxial and abaxial surfaces possessing highly sinuous anticlinal cell walls (Figs. 4A,B; 2CD). The adaxial and abaxial cuticles are completely glabrous, lacking any indication of indumentum in the form of obvious hair-base scars anywhere on the cuticle (Fig. 4A,B). However, there are some highly conspicuous morphological features on the surface of almost all of these fossils, not to be confused with hair bases, which are consistent with definitions of various kinds of "cork-warts" formed via some form of insect/fungal damage or necrosis (Fig. 5A,B).

The stomatal complexes always have four or more subsidiary cells surrounding the guard cells. These are more or less radially arranged and ring-like, mostly in single layers (Fig. 6A-D). Thus, stomatal morphology is consistent with the cyclostaurocytic stomatal type proposed by Soh and Parnell (2011), where the radial diameter of the subsidiary cells can be larger than their tangential width or smaller, giving rise to rings of subsidiary cells that can be either narrow or thick, with straighter edges than the surrounding cells. The size of subsidiary cells varies from equal to more or less unequal. The subsidiary cells stain more darkly than the surrounding epidermal cells (Fig. 6C,D). Stomata are cyclostaurocytic except around the enlarged water stomata, which are usually actinocytic (Wilkinson, 1980), consistent with the Myrtaceae and most angiosperm families.

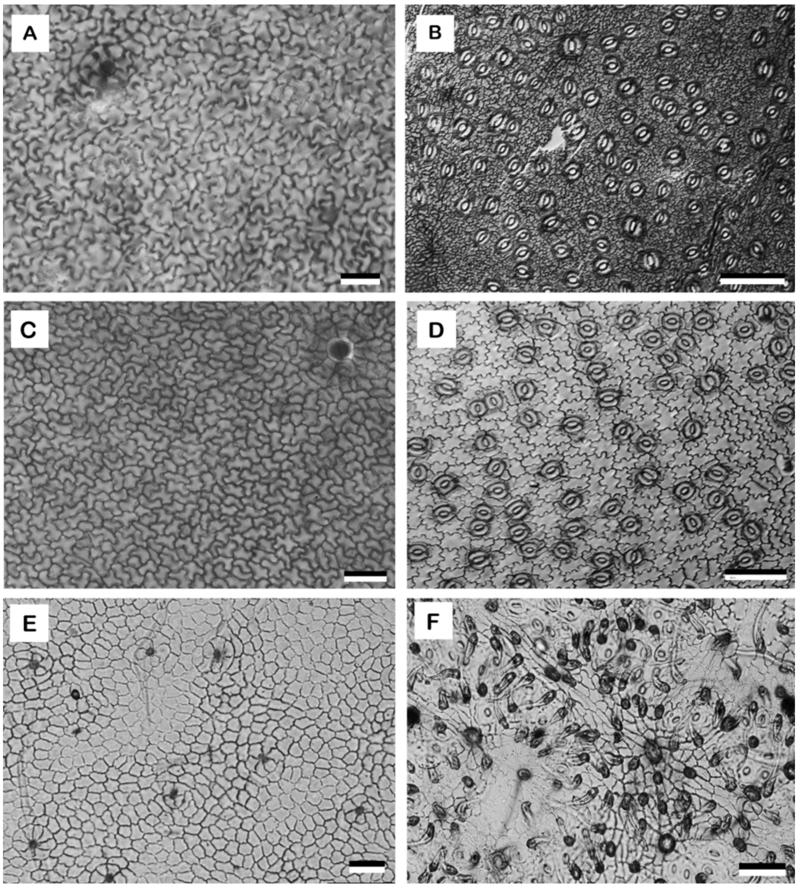

FIGURE 4: General features of fossil and extant cuticles: A) Light micrograph (LM) of adaxial cuticle from K707, holotype of *Syzygium christophelii* sp. nov. Mid-center-right is an oil gland. Lid cells are distinct from hair bases in that they have at least one, usually two or more, cells in the middle of a large ring of subsidiary cells, rather than a hair base which extends over a smaller ring of radially arranged cells which form a "star-like" pattern in their centre. Scale bar = 50 µm. **B)** LM of abaxial cuticle of *Syzygium christophelii,* specimen K757. Note random orientation of stomata, damage to cuticle and lack of recognizable hair base structures. Scale bar = 100 µm. **C)** LM of the adaxial cuticle of *Syzygium smithii* (Poir.) Nied (subgenus *Acmena*), with a lid-cell structure in the top right. Again, note the absence of recognizable hair base structures. Scale bar = 50 µm. **D)** LM of abaxial cuticle of *S. smithii* showing stomatal surface, again noting the random orientation of stomata, sinuous epidermal cell walls, and absence of recognizable hair base structures. Scale bar = 100 µm. **E)** LM of adaxial cuticle of *Eugenia reinwardtiana* (Blume) A.Cunn. ex DC. (Tribe Myrteae)*,* Australia's only endemic species of *Eugenia,* showing regular trichome bases, with distinctive 'star' like underlying epidermal cell morphology. Scale bar = 50 µm . **F)** LM of cuticle of extant species of *Backhousia citriodora* F.Muell. showing dense trichomes and stomata on the abaxial cuticle surface. Note elongated epidermal cells in non-stomatiferous area, probably indicating an underlying vein. Note also, two different sizes of hair bases, with larger ones occurring in the non-stomatiferous zones overlying the vein. Scale bar = 50 µm.

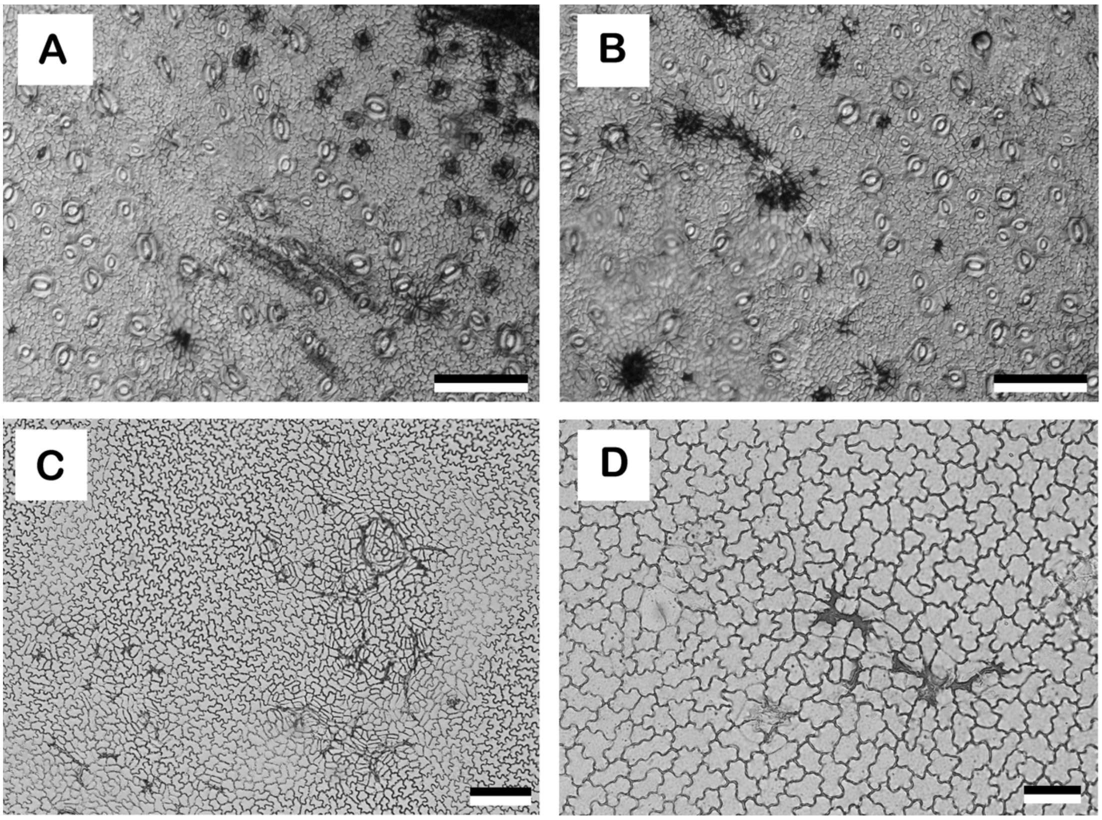

FIGURE 5: Cuticle damage in the form of cork warts A) Light micrograph (LM) of the abaxial cuticle of fossil holotype specimen K707, showing a section of extreme cuticle damage. In the top right corner of the image, a large number of stomata have been damaged by possible fungal or insect attack, and formed stomatal cork warts. Scale bar = 100 μm **B)** LM of more damage on the abaxial cuticle of K707 showing a large cork-wart in the middle-top-left, with smaller damage marks surrounding. Scale bar = 100 μm **C)** LM of adaxial cuticle of extant species *Syzygium anisatum* (Vickery) Craven & Biffin, showing large and small-scale damage, which disturbs the otherwise consistent patterns of the epidermal cell impressions on the adaxial cuticle. Scale bar = 100 μm **D)** LM of cork wart on the adaxial cuticle of extant species *Syzygium paniculatum* Gaertn., and a lid-cell to the left. These are the only structures other than epidermal cells commonly visible on the adaxial cuticles of extant *Syzygium* species. Scale bar = 50 μm.

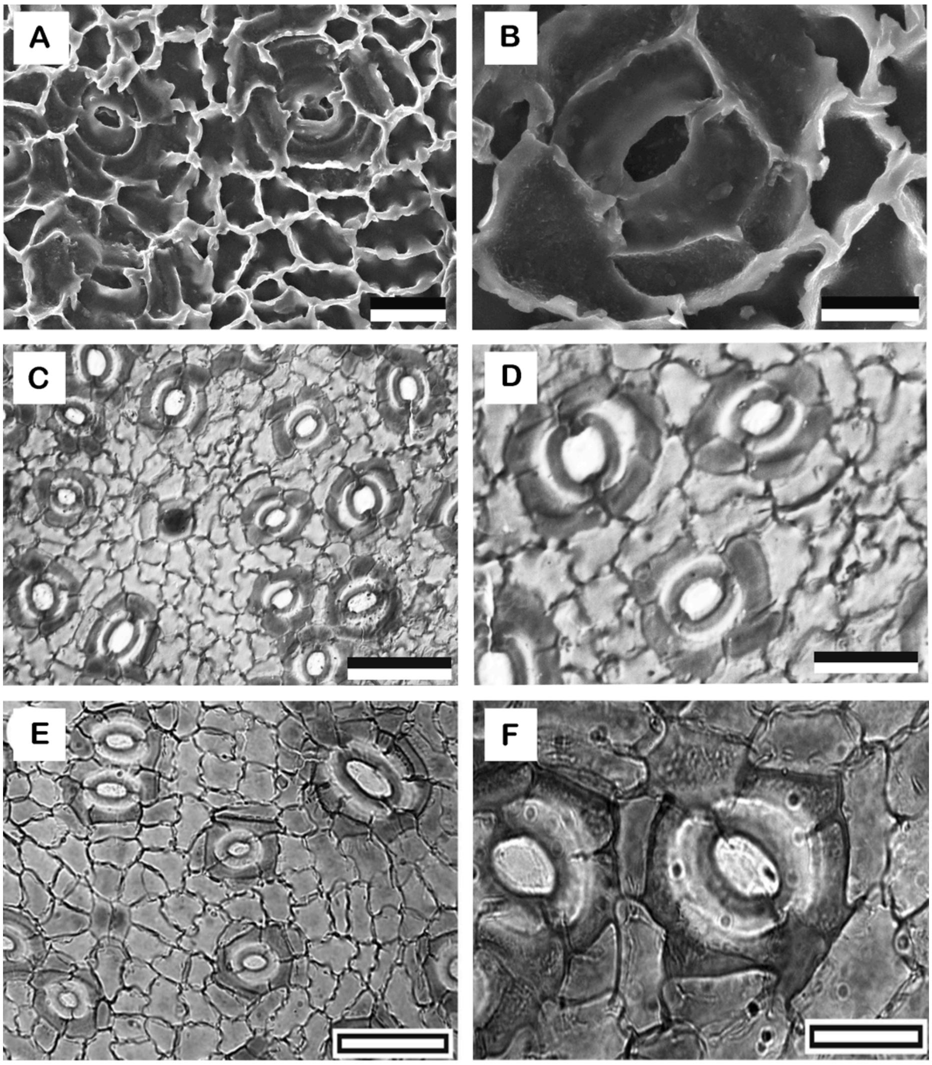

FIGURE 6: Cyclostaurocytic stomata on fossil taxa A) Scanning electron micrograph (SEM) of fossil Holotype K707 showing the underside of the abaxial cuticle and the internal impression of several stomata and epidermal cells. Scale bar = 20 µm. **B)** SEM of a single stomate showing the arrangement of four subsidiary cells around the guard cells of the stomate. Scale bar = 10 µm. **C)** Light micrograph (LM) of abaxial cuticle of K707, showing stomatal arrangement and a double-lid cell at centre left. Scale bar = **D)** LM close up view of abaxial cuticle of K707 showing subsidiary cell arrangements of three stomata, with four or more subsidiary cells in a ring around the guard cells. Scale bar = **E)** LM of parataxon 'CUT-M-DIE' taken from Pole et al's (2008) study of Miocene New Zealand fossil Myrtaceae cuticles, compared most favourably with species from *Syzygium* subgenus *Acmena,* showing what they called "tangenticytic" stomatal complexes, which we find to be synonymous with the "cyclostaurocytic" stomatal definition proposed by Soh and Parnell (2011). Original scale bar included. Scale bar = 50 µm. **F)** LM close up subsidiary cell arrangement of stomate on abaxial cuticle of parataxon 'CUT-M-DIE' taken from Pole et al's (2008) study of Miocene New Zealand fossil Myrtaceae, showing the four or more subsidiary cells in a band around the guard cells. Original scale bar included. Scale bar = 20 µm.

DISCUSSION

Justification for assignment to the genus— In terms of macromorphology and overall leaf architecture, the fossils are very similar to leaves of many species of *Syzygium.* The leaves can be confidently identified as belonging to the Myrtaceae due to the characters of brochidodromous venation with secondary veins connecting in a prominent intramarginal vein (Fig. 2), coupled with lid-cell impressions observable under light microscopy on the epidermis (Fig. 6C) (Lange, 1980; Christophel and Lys, 1986). Furthermore, two main micro-morphological characters, allow for confident placement of these fossils in the genus *Syzygium*, and with a notable affinity to subgenus *Acmena.* These characters are:

(1) Complete glabrousness/lack of indumentum— this character is uncommon in the Myrtaceae, and is diagnostic of few genera (Briggs and Johnson, 1979; Wilson, 2011). The Syzygieae are almost entirely glabrous (Schmid, 1972; Briggs and Johnson, 1979; Wilson, 2011) and characteristically lack typical 'myrtaceous' trichomes (unicellular; Briggs and Johnson, 1979). Soh and Parnell (2011) found that leaf indumentum was completely lacking in all but one of the 95 *Syzygium* species they surveyed, and the exception (*S. vestitum* Merr. & L.M.Perry) has multicellular hairs, atypical for Myrtaceae. In our own study, only one other *Syzygium* species, *S. porphyrocarpum* Greves (see Table 1), has a leaf indumentum also comprising multicellular hairs. This appears to be an uncommon, derived condition for the genus that seems to be restricted to a single subgenus, the large and variable subgenus *Syzygium.*

In contrast to this, Retamales and Scharaschkin (2015), in their survey of 26 South American species of Myrtaceae (2 tribes, Myrteae and Metrosidereae, 20 genera), recorded that glabrousness is uncommon. In their table of characters, two species are reported with no indumentum, *Blepharocalyx cruckshanksii* (Hook. & Arn.) Nied., and *Tepualia stipularis* (Hook. & Arn.) Griseb. However, in the description of *T. stipularis* they state that "*the leaves are glabrous to sparsely pubescent on midrib and margins. The hairs are simple and straight-curved.*" Our own analysis of the cuticle of *T. stipularis* indicates that rare hair bases are present on the midribs and margins of the leaf, which is consistent with other species in the capsular-fruited tribe Metrosidereae.

Further strengthening the significance of glabrousness in *Syzygium*, Haron and Moore (1996), in their study of the cuticles of 21 species of Old and New World *Eugenia,* noted that the presence of foliar trichomes is a good indicator of New World species, while Old World species were hairless. After updating nomenclature, it is apparent that all 15 of the glabrous Old World species of "*Eugenia*" studied by these authors belonged in *Syzygium,* while all New World species remained in *Eugenia.* This character, in fact, perfectly differentiates the two genera amongst the specimens studied.

It is important to acknowledge the presence of lesions caused by epidermal damage, or 'cork-wart' structures (Farooqui, 1982; Joffily and Vieira, 2010), on the cuticles of many of the fossil leaves (Fig. 5A,B). Some of these features resemble hair base scars, but lack consistency across all the surveyed fossil material. These are most favorably compared with cork-warts or epidermal damage on extant taxa (Fig. 5C,D), and we therefore dismiss the possibility of the structures being related to trichomes. It is also important to note that while leaf indumentum is not a character that always persists throughout the entirety of the lifespan of non-glabrous leaves, in plants where leaves have lost all their indumentum, hair base scars remain visible on the cuticle.

Our survey of 232 species (see Table 1) of rainforest Myrtaceae from across the Southern Hemisphere suggests that complete glabrousness is extremely uncommon in the Myrtaceae, and could be considered a very strong character for inferring Syzygioid affinity. Glabrousness (particularly the absence of uniseriate hairs, which is the most common condition in Myrtaceae) is suggested as a derived character for the tribe and genus.

(2) Cyclostaurocytic stomata— Soh and Parnell (2011) extensively surveyed the cuticles of 81 (+14 from the literature) species of *Syzygium* across the

subgenera as defined by Craven and Biffin (2010b), and we included all of these in our study (see Table 1). Their analysis found that 'cyclostaurocytic' stomata occur only in two of the subgenera: in subg. *Acmena*, in which all species possess cyclostaurocytic stomata only, and subg. *Perikion*, in which some species possess both cyclostaurocytic and anisocytic stomata, while two possess cyclostaurocytic stomata only. Our analysis of additional *Syzygium* species is consistent with the results of Soh and Parnell (2011) and we find that subgenus *Acmena* is the only subgenus to entirely lack all other stomatal types. Retamales et al. (2014) also adopted this terminology and reported, in agreement with the findings of Soh and Parnell (2011), that an additional species of *Syzygium* subgenus *Acmena*, *S. floribundum* F.Muell., also possessed the same cyclostaurocytic stomata. However, this character is not a perfect synapomorphy for the subgenus, because Soh and Parnell (2011) suggest that two species in subgenus *Perikion* also possess only cyclostaurocytic stomata.

Evidence from the published literature regarding stomatal morphology of *Syzygium* species supports this stomatal type as a strong character for subgenus *Acmena*, and also suggests that it might only occur in the genus *Syzygium.* The survey by Khatijah et al. (1992) of 25 species of Malaysian *Eugenia,* which have subsequently all been recognized as Syzygieae*,* found that all species possessed anisocytic or paracytic stomata, save one species, *E. cumingiana* Vidal*,* for which they recorded cyclocytic stomata. More recent taxonomic reassessment considers this species to be a synonym of *Syzygium acuminatissimum* (Blume) DC., a member of the subgenus *Acmena*. These cyclocytic stomata may be considered consistent with the cyclo-staurocytic stomata type defined by Soh and Parnell (2011). Not included in Table 1 due to significant overlap with taxa already sampled, are results of Kantachot et al. (2007), who investigated cuticles of Myrtaceae from Thailand, looking at 28 taxa in 12 genera (including 17 species of *Syzygium* in subgenus *Syzygium* and *Perikion*, but with no taxa from subgenus *Acmena*), found all species to possess only anisocytic, anomocytic, or paracytic stomata.

In the literature regarding stomatal morphology of other genera in the family, cyclo-staurocytic stomata or equivalent stomatal types have not been reported. Retamales & Scharaschkin (2015), in a study of South American Myrtaceae, recognized five stomatal types, including the same three types recognized by other authors: i) paracytic, ii) anisocytic and iii) anomocytic, as well as iv) actinocytic, and v) laterocytic. Laterocytic stomata were regarded as a sub-variety of paracytic stomata by Wilkinson (1980), and were only found in one of the species they surveyed, *Myrcianthes coquimbensis* (Barnéoud) Landrum and Grifo. In this case, we have identified this stomatal type as paracytic. Actinocytic and anomocytic stomata are also reported by these authors in one species, *Myrceugenia colchaguensis* (Phil.) L.E.Navas. Cyclostaurocytic stomata are not recorded in any of these non-syzygioid taxa.

Fontenelle et al. (1994) recognized five types of stomata in 11 species of Brazilian *Eugenia*. This included the same three standard stomatal types recognized by other authors: i) paracytic, ii) anisocytic and iii) anomocytic, as well as iv) cyclocytic, and v) tetracytic, types, which were less common, and, in the species where they did occur, were only recorded infrequently or were listed as “not well defined”. We did not include these results in our survey, as we have not found them to be a major stomatal type in any of the extant Myrtaceae that we have examined, nor are they prominent in any of the other literature on the stomata of extant Myrtaceae. Another form of stomatal complex was also found, anomostaurocytic, defined in a new stomatal classification proposed by van Wyk and Robbertse (1982) for stomata with 3-5 subsidiary cells, and which they conclude may also be a modification of the anomocytic type. It is interesting to note the near similarity to cyclostaurocytic stomata here, and that these are both attempts to define subsidiary cell arrangement that is variable in number, like the anomocytic type. However, none of these stomatal types are consistent with the cyclostaurocytic type.

There is also evidence to support the importance of this stomatal subsidiary cell arrangement from previous studies of fossil Myrtaceae leaves. Pole et al. (2008) illustrated leaves of a Myrtaceous parataxon from the Miocene of New Zealand that they favourably compared with cuticles of *Syzygium*. They used the term ‘tangenticytic’ to refer to the stomatal complexes with ‘4-7 irregularly shaped subsidiary cells, which give the stomatal complexes a “pin-wheel appearance” (Fig. 6E,F). Tangenticytic is a little-used ontogenetic classificatory term first proposed by Timonin (1995), which appears to be used here to describe stomata identical to those described by Soh and Parnell (2011) as cyclostaurocytic. Although neither term has been adopted widely, we have chosen to continue to use the topographic term proposed by Soh and Parnell (2011) that does not invoke ontogeny. Pole et al. (2008) go on to compare the cuticle types most favourably to three species of *Syzygium; S. hedraiophyllum* (F.Muell.) Craven & Biffin*, S. floribundum* and *S. smithii* (Poir.) Nied. While Pole et al. mention that these species of *Syzygium* are closely related. Their work pre-dated the infrageneric classification of *Syzygium* conducted by Craven and Biffin (2010) that placed all these species into subgenus *Acmena,* along with several others, so that exclusively cyclostaurocytic stomata occur in this subgenus.

Our results suggest that, in the rainforest Myrtaceae, the characters of cyclostaurocytic stomata and glabrousness are only seen in combination within *Syzygium,* particularly in subgenus *Acmena*, occasionally in subgenus *Perikion*, and perhaps in a single species of subgenus *Syzygium, S. minutuliflorum* (F.Muell.) B.Hyland (see below). These characters accordingly suggest that the fossils can be confidently diagnosed as *Syzygium*.

Palaeobiogeography and similarity to living *Syzygium* species— Due to the characteristic cyclostaurocytic stomata type, the fossils possess strong affinities to subgenus *Acmena* or some species in subgenus *Perikion.* Of the extant taxa used for comparison, we find that the cuticles and stomatal morphology of *S. christophelii* share a strong resemblance with *S. smithii* (Fig. 3F, 4A-D) in particular. In only one surveyed species in subgenus *Syzygium, S. minutuliflorum*, were stomata equivalent to the cyclostaurocytic type observed, and found in conjunction with paracytic and anisocytic stomata*.* Interestingly, *S. minutuliflorum* has often been confused with species from subgenus *Acmena*. Hyland (1983) says that this species “has been confused with *A. hemilampra* and

A. smithii", and when Mueller (1892) first described the species (as a *Eugenia*) he said, "This species stands systematically very near *E. smithii* in floral and carpic characteristics, but the leaves are of quite different shape and not shining nor dark-green above, while none of the anthers are biglobular, and all open with lateral dehiscence."

Much of subgenus *Acmena* today is less widely distributed than the rest of the members of the genus *Syzygium.* There are at least 34 species in the subgenus, with a range extending from Australia to India, China, and the Western Pacific, though almost all of the extra-Australian distribution is due to *S. acuminatissimum* (Blume) DC. The center of diversity for the subgenus is Australia, and all sections except sect. *Piliocalyx* occur on the Australian continent. The only species recorded in our dataset that is not found in Australia, is *S. francii* from New Caledonia, a species formerly assigned to the genus *Piliocalyx.* The species *S. unipunctatum* (B.Hyland) Craven & Biffin*, S. mulgraveanum* (B.Hyland) Craven & Biffin*, S. mackinnonianum* (B.Hyland) Craven & Biffin*, S. hedraiophyllum, S. graveolens* (F.M.Bailey) Craven & Biffin*, S. divaricatum* (Merr. & L.M.Pery) Craven & Biffin and *S. gustavioides* (F.M.Bailey) B.Hyland have a distribution limited to the tropics in far north Queensland, while *S. hemilamprum* has a distribution that extends through the rainforests along the northern two-thirds of Australia's east-coast, and also in the far north of the Northern Territory, and extending into Papua New Guinea. *S. smithii* is an exception to the Australian species of subgenus *Acmena* with a distribution that extends along the East Coast from far north Queensland, as far south as Wilson's Promontory in Victoria. *S. floribundum* occurs south from Mackay to the NSW mid north coast, and *S. ingens* (F.Muell. ex C.Moore) Craven & Biffin, is restricted to the Macleay-McPherson region between northern New South Wales and Queensland.

Pole et al.'s (2008) parataxon "CUT-M-DIE" (Fig 5E,F) also bears the same combination of characters used for ascribing the fossils of *S. christophelii* to genus level, being entirely glabrous and possessing cyclostaurocytic stomata, and may represent a fossil record of subgenus *Acmena* in New Zealand. This could present an important biogeographic story. In the modern day New Zealand flora, there is only one endemic species of *Syzygium*, *S. maire* (A. Cunn.) Sykes & Garn.-Jones, which belongs to the subgenus *Perikion,* but it does not possess cyclostaurocytic stomata*.* The fossils reported by Pole et al. (2008) may represent a Miocene presence of *Syzygium* subgenus *Acmena* in New Zealand, which has subsequently become extinct. This is notable for two reasons. Firstly, because this is possibly an extinction of an entire subgenus from New Zealand, which was present after the Oligocene marine transgression (Mildenhall et al., 2014) and, secondly, because subgenus *Acmena* has since been reintroduced to New Zealand, with *Syzygium smithii* having been classified as an environmental weed, joining a growing list of species from Australian genera (notably *Eucalyptus* and *Acacia*) that have fossil records in New Zealand, but have become extinct prior to human arrival (Hill et al. 2016), and that have subsequently been reintroduced, becoming very successful, naturalised weeds (Howell, 2008).

Other fossil records of *Syzygium*— The fossil reported here is not the first formally described fossil species of *Syzygium*. Several fossil species have been proposed from India: *S. kachchhense* R.N.Lakhanpal & Guleria from the Lower Eocene of Kachchh (Lakhanpal and Guleria, 1981), *Syzygium palaeobracteatum* N.Awasthi & R.N.Lakhanpal from possible Neogene sediments from the Bhikhnathoree flora (Awasthi and Lakhanpal, 1990), *S. palaeocumini* M.Prasad & N.Awasthi from Upper Miocene of the Siwalik sediments (Prasad and Awasthi, 1996), *S. miocedentale* M.Prasad, from a single leaf found in the middle Miocene lower Siwalik sediments of Nepal (Prasad et al., 1999), *S. kasauliense* Guleria & R.Srivast. from early Miocene sediments in Himachal Pradesh (Arya et al., 2001), and *S. nangalbibrense* R.C.Mehrotra from Upper Paleocene sediments of the Tura formation (Mehrotra, 2000). One fossil species, *S. chaneyi* Huzioka & Takahasi has also been reported from Eocene of Japan (Huzioka and Takahasi, 1970). However, while some of these fossils may share gross architectural and morphological features with *Syzygium*, and may even represent genuine fossil species of that genus, they are described from impression/compression foliar material, in most cases without cuticle analysis or preservation. These fossils are mostly described with poor illustrations, and poor comparative taxonomic work, lacking diagnostic characters and synapomorphies to confidently place them into a living genus, or even family in some cases. As such, these fossils must be regarded as of uncertain taxonomic affinity until more detailed investigation of these fossils can be conducted.

CONCLUSIONS

The fossils of *S. christophelii* represent the first confidently described fossil record of the genus, as well as the only confidently described non-eucalypt leaf fossil of Myrtaceae to a living genus to date. The biostratigraphic correlation to the *Proteacidites tuberculatus* Zone, and the K-Ar dates on the overlying basalts, place these fossils in the early Miocene of New South Wales, in line with molecular age estimates for the Syzygieae crown croup of c. 17-30Ma (Biffin et al. 2010, Thornhill et al. 2012b). On the available evidence, these fossils may provide a reasonable minimum age constraint for the Syzygieae crown group. These fossils are therefore potentially useful for the calibration of future dated molecular phylogenies of the genus, and of the Myrtaceae more generally. While other fossils in the Australian and global fossil record have been favourably compared to *Syzygium* or even identified as such, this is the first time that a systematic approach has been taken in conjunction with the understanding of modern molecular phylogenetic relationships, and a large database of comparative species, to provide a confident, formal diagnosis.

This fossil record occurs further inland than the natural occurrence of the genus in NSW (Fig. 1B), and at 1400m asl, the fossils of *S. christophelii* are found at a higher altitude than many Australian species in the genus are found today. While uplift in the region had not abated at the time of fossil deposition, and the altitude was probably somewhat lower at the time these fossils were growing (Paull and Hill, 2003). Extant representatives of *Syzygium* can be found today at similar or higher altitudes in rainforest vegetation in the mountains of northern New South Wales and tropical north east Queensland, such as *S. smithii* (up to 1200m asl, Fig. 2K) or *S. apodophyllum* (up to 1500m asl, Fig. 2L). These fossils contribute to the strong fossil evidence for mesothermal rainforest vegetation in the Eastern Highlands of NSW during the early Miocene, where today the vegetation is primarily alpine heath and eucalypt woodland. This is consistent with the generally warmer and wetter global climate of the early Miocene.

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Chapter 6:

General discussion and conclusions

Towards a better understanding of the fossil record of the Myrtaceae— The literature review in Chapter 2 establishes that much of the published literature surrounding Cenozoic Myrtaceae macrofossils reports poorly identified, unidentified or equivocal fossils. Only a very small number of macrofossils have been confidently identified in a phylogenetic context, and only a subset of these have been identified to living genera. In this light, it is apparent that if deep evolutionary and paleobiogeographic questions about the Myrtaceae are to be answered, greater effort needs to be made to conduct systematic study of the fossil record of the family.

As established in the introduction of this thesis, the advent of phylogenetic methods and rigorous molecular phylogenies have revolutionised our understanding of the relationships within the Myrtacaeae. It is now possible to test hypotheses of relationships of fossils to extant taxa within a rigorous phylogenetic framework, even with the potentially limited characters available when working with fragmentary plant remains, such as with fossil leaves and leaf cuticles. None of the fossils in this thesis could have been easily identified without the advances in molecular phylogenetic interpretations of the family, as well as much critical fundamental botanical work and description. The *Metrosideros* fossils described in Chapters 3 and 4 for instance, would have been much more difficult to describe in the absence of pioneering work by J.W. Dawson, who described and characterised the Pacific capsular-fruited Myrtaceae in great detail, notably the Metrosidereae (Dawson, 1968, 1970a, b, 1972a, b, c, 1976). Deep relationships within the tribe Metrosidereae are still not fully resolved but since the work of J.W. Dawson, phylogenetic analysis of the group has lead to significant advances in understanding of the infra-tribal relationships (Wilson, 1996; Pillon et al., 2015). Similarly, the fossils of *Syzygium* described in Chapter 5 could not have been described without meticulous cuticle morphology characterisation by Soh and Parnell (2011), and cuticle work undertaken by other authors, as well as the rigorous phylogenetic framework provided by the infrageneric classification of *Syzygium* proposed by Craven and Biffin (2010).

It is also the case that the biogeographic and evolutionary significance of fossil discoveries is contingent on the taxonomy and phylogeny of a group being well resolved. For instance, *Metrosideros* was considered to occur in Australia until at least 1993, when *Metrosideros queenslandica* was revised and transferred into the newly erected genus *Thaleropia,* on the basis of morphological evidence, *and* found to be related to species in the tribe Tristanieae rather than Metrosidereae (Wilson, 1993), a conclusion later borne out by molecular data (Wilson et al. 2005). *Metrosideros* went from a genus thought to occur in Australia, to one that did not occur on the continent. Had the fossils of *Metrosideros* described in Chapters 3 & 4 of this thesis been described prior to this revision, the biogeographic implications and conclusions drawn from these discoveries may have been radically different. Furthermore, Pillon et al. (2015) verified that the subgenus *Mearnsia* sensu Dawson (1976) was in fact polyphyletic, a possibility first flagged by Wilson (1996), concluding that the subgenus no longer be recognised. Had the fossils described in Chapter 4, which were compared most favourably with extant taxa belonging to the formerly recognized subgenus *Mearnsia,* been described prior to the recognition that the subgenus was not monophyletic, these fossils may have been attributed to this subgenus.

While the taxonomy of the family is not fully resolved, in the time since the first studies to attempt systematic identification of potential fossil records of Myrtaceae, our understanding of the systematics of the family has vastly improved, and a stable understanding of infra-familial relationships within the family has been achieved only relatively recently (Wilson, 2011). It is in this context, as the research in this thesis demonstrates, that systematic study of the macrofossil record of the family can now be conducted with accuracy and confidence not possible to earlier researchers, even only several decades ago.

Paleobiogeography and extinction of *Metrosideros* in Australia— The fossils of *Metrosideros* described in Chapters 3 and 4 of this thesis are significant for a number of reasons. *Metrosideros leunigii,* described in Chapter 3, is the oldest described record of this capsular-fruited genus, and the first confirmed record of the genus from Australia. The other fossil species of *Metrosideros, M. dawsonii* and *M. wrightii*, described in Chapter 4 are younger, but establish the subsequent presence of *Metrosideros*, in the Oligo-Miocene of Tasmania, from the newly discovered and previously unpublished fossil locality at Golden Fleece. Together, these fossils provide evidence that *Metrosideros* once occurred in Australia, and that a diversity of *Metrosideros* species occurred on the continent until at least the Oligo-Miocene. I hypothesised that this fossil record may be indicative of an Australian, or possibly Gondwanic, origin for the genus, yet it is worth keeping in mind that the paleobiogeographic value of these fossils may change in time, as Pillon et al. (2015) acknowledge, the deep relationships in the tribe Metrosidereae are still not fully resolved, and particularly so for the species of the formerly recognized subgenus *Mearnsia.* As the taxonomy of this group becomes better resolved, these fossils may take on fresh significance.

The discovery of these fossils in Australia, indicates that *Metrosideros,* which no longer naturally occurs on the continent, also provides conclusive evidence of the local extinction of a Tertiary rainforest element from Australia that that is still present on other nearby landmasses. Although the extinction of numerous conifer and other rainforest species present in Cenozoic fossil localities around Australia can be explained comfortably by changing climate and declining rainfall, extant *Metrosideros* species grow in a wide range of modern habitats, and so the reasons for extinction are more obscure. One hypothesis put forward in Chapter 4 is that many of the landmasses where *Metrosideros* occurs today do not have native mammalian browsers, such as the Australian brush-tailed possum (*Thrichosurus vulpecula*), which after having been introduced to New Zealand have become a significant conservation concern for *Metrosideros* species*.* Possums have been demonstrated to preferentially browse *Metrosideros* shoots and leaves, having significant destructive impacts on native

Metrosideros forests (Batcheler, 1983; Rose et al., 1992; Sweetapple et al., 2004). Other modern threats to *Metrosideros* species also suggest possible mechanisms of extinction, such the recent surge of *Metrosideros* dieback in Hawaii due to the outbreak of a fungal disease referred to as rapid `ōhi`a death (ROD), caused by *Ceratocystis* sp. fungi which was first noticed in 2010, and has caused the death of hundreds of thousands of native *Metrosideros polymorpha* trees on the archipelago, which may have devastating impacts on the local ecology if the spread continues (Mortenson et al., 2016; Barnes et al., 2018). Fears of a similar threat to the *Metrosideros* trees of New Zealand have been noted for some time, with significant concern for the health of native Myrtaceae species from the introduction of another fungal disease, Myrtle rust (Teulon et al., 2015). Since 2017, Myrtle rust has been discovered in New Zealand, and is rapidly spreading. Concerns for the conservation of indigenous *Metrosideros* species are high, and the scale of the threat at this stage is undetermined (MPINZ, 2018).

It is difficult to ascertain if factors like these contributed to the decline and extinction of *Metrosideros* in Australia, but nevertheless these provide good case studies of how *Metrosideros* could have quickly declined on the continent as the result of stressors from increased herbivory or disease.

Dating of phylogenies and molecular clock models— Another important implication of the research presented in this thesis, is that the fossils described here may be considered valuable for the calibration of future molecular phylogenetic studies. It has become increasingly important that molecular systematists have access to high quality fossils with well constrained ages, that have been identified in a phylogenetic context to be used for the calibration of evolutionary studies by providing approximate ages for nodes of phylogenetic trees (Gandolfo et al., 2008). It is the case for the majority of tribes and genera in the Myrtaceae that there are no confidently described macrofossils to provide these calibration points. Some of the more recent calibrated phylogenies of the Myrtaceae, have circumvented this problem by utilizing microfossils (pollen) for calibration of nodes of the phylogeny where there was no sufficient macrofossil evidence (Thornhill et al., 2012b; Thornhill et al., 2015). However, it is important to note that because of its morphological simplicity, fossil pollen is generally identified at low taxonomic resolution, is rarely supported by synapomorphies, and is often based on gross similarity (Sauquet et al., 2011). As such, macrofossil evidence, particularly of fruits and flowers, is generally considered to be superior for the calibration of molecular studies.

In the most recent calibrated phylogenies, the crown-age of the Metrosidereae is one of the few nodes that is dated using macrofossil evidence (Thornhill et al., 2015). The crown age of the Metrosidereae is dated using Miocene fossil fruits and leaves of *Metrosideros* reported by Pole et al. (2008). These fossils, also discussed in Chapters 2 and 4, were not formally described, but the generic identification can be considered confident. The fossils of *M. leunigii* described in Chapter 3 are older than these fossils, and constitute the oldest described macrofossils of *Metrosideros*. The fossil reproductive structures and leaves from the Little Rapid River (LRR) fossil locality are confidently dated to the early Oligocene, and thus might be used to provide and older crown-age for the group. Identical leaves to those found at LRR also occur in the late Eocene of the Hastie's paleovegetation, and with discretion might also be considered an even older suitable fossil for calibration. It is worth noting that potential fossil leaves of *Metrosideros* are also reported from the Eocene Pikopiko paleoflora in New Zealand, but these are only figured as *Metrosideros*-like, and are yet to be formally described (Lee et al., 2012).

The fossils of *Syzygium christophelii* identified in Chapter 5 provide the first confidently identified macrofossil record of the Syzygieae. As discussed in Chapter 2 and briefly in Chapter 5, most prior *Syzygium* leaf fossils are questionable, including fossil leaf taxa from India (Lakhanpal and Guleria, 1981; Awasthi and Lakhanpal, 1990; Prasad and Awasthi, 1996; Prasad et al., 1999; Mehrotra, 2000; Arya et al., 2001), and one from Japan (Huzioka and Takahasi, 1970). Only macro-morphological characters and gross leaf architecture were used to identify these taxa, and comparative work with extant taxa was very limited. As such, none of these fossils can be considered to confidently represent *Syzygium,* or even Myrtaceae in some cases, after critical interpretation. In the absence of confidently identified macrofossil evidence, the most recent calibrated phylogeny of the Myrtaceae by Thornhill et al. (2015) utilized pollen evidence to date the crown-age of the Syzygieae/Backhousieae, and this was calibrated with *Myrtaceidites eugeniioides* Cookson & Pike, first found from the Late-Eocene of Victora. Given the apparent weaknesses of microfossils as calibration points, in future dated phylogenies the fossils of *S. christophelii* should be used to provide the first confident macrofossil calibration points for dating the crown-age of at least the Syzygieae.

Implications for future research identifying fossil Myrtaceae leaves— The fossils of *Syzygium christophelii* identified in Chapter 5, represent a significant advancement in the identification of non-eucalypt fossil Myrtaceae leaves. Eucalypt leaves, with their diagnostic falcate shape, have been convincingly demonstrated in the fossil record on a number of occasions in the absence of fossil fruits in organic connection, such as those illustrated from New Zealand by Pole (1993) or fossils from Berwick Quarry first identified by Deane (1902), later revisited by Pole et al. (1993). However, the best efforts at identifying non-eucalypt fossil Myrtaceae leaves have only managed a confident identification to family level.

As the literature review in Chapter 2 establishes, very few fossil Myrtaceae leaves have been confidently identified. The earliest attempts to identify fossil Myrtaceae in studies by pioneering paleobotanists like Ettingshausen (1888), Engelhardt (1891), Dusén (1899), and Berry (Berry, 1918; 1922; 1928; 1937a, b) placed fossils in form genera, or often living genera, assuming them to be sister taxa or direct ancestors of extant taxa. In all cases, these early Myrtaceae leaf fossils were described from gross leaf architecture, with minimal to no comparative work with extant taxa that is sufficient by modern standards, and descriptions based on brief descriptions, with few illustrations. Such practice was common in paleobotany from the late 1800's until at least the 1980's, and still persists into more recent times (See Gandolfo et al., 2008 for further discussion). As such, none of these early identifications stand up to modern scrutiny. As techniques became more advanced, studies of fossil Myrtaceae leaves, such as by Bandulska (1931) who was the first to utilise cuticle micromorphological characters in a more detailed comparative framework, or later by Christophel and Lys (1986), who were the first to take a systematic approach with a larger number of extant taxa, and the first to emphasise the importance of lid-cells *sensu* Lange (1980), made headway towards confident diagnosis of myrtaceous foliar remains, but still failed to provide confident description or even comparison of fossil leaves to extant genera.

The results of the study in Chapter 5, if accepted, demonstrate for the first time a confident diagnosis of non-eucalypt fossil Myrtaceae leaves to a living genus. This study demonstrates, that with a large database of extant taxa with a robust phylogenetic framework, small numbers of characters can be assessed for phylogenetic information and hypotheses of relatedness of fossils to extant taxa can be proposed. Future studies to identify fossil Myrtaceae leaves should be based on more systematic study of potential cuticle characters, utilising characters not only observable under light microscopy, but also on both internal and external surfaces of the adaxial and abaxial cuticle, which are observable under scanning electron microscopy. This may reveal a wealth of untapped, phylogenetically informative characters, such as those described in a similarly detailed study of extant rainforest Proteaceae cuticles (Carpenter, 1994), which have been utilised in subsequent decades and formed the basis for identification of a large number of Proteaceae leaf fossils and dispersed cuticle fossils, that could not have been identified without this fundamental work e.g. (Carpenter and Jordan, 1997; Carpenter et al., 2006; Carpenter et al., 2010; Carpenter et al., 2016; Carpenter et al., 2017).

Some directions for future research— Highlighted in this thesis is the value of re-visiting previously published or reported fossil records of Myrtaceae, with fossils in both Chapters 3 and 5 being described from material that had previously been reported, but either misidentified or not described. As the literature review in Chapter 2 establishes, there is a wealth of reported Myrtaceae macrofossils in the literature, many of which may be erroneously identified or not identified correctly. In the light of better phylogenetic understandings of the relationships in the family, many fossils may be worth revisiting and being subjected to rigorous and detailed description and phylogenetic treatment. A vast number of fossil Myrtaceae leaves exist in paleobotanical collections which could now be re-investigated, and potentially identified where once identification was considered too difficult or impossible to achieve.

It may be particularly fruitful to re-investigate reports where fossil Myrtaceae leaves with organic preservation of cuticle occurs. For instance, the 12 potential taxa of Myrtaceae leaf remains, many with cuticle preservation, that reported by Blackburn (1985) from the Yallourn and Morwell coal seams of the Latrobe Valley, Victoria, none of which to date have been formally described or subject to rigorous systematic treatment. Many of these taxa are given tentative identifications by Blackburn (1985), but until such a time as these fossils are formally revisited, a wealth of potential paleobiogeographic information here is wasted. It could also be very valuable to re-visit many of the original *Myrtaciphyllum* fossils described from Eocene fossil localities around Australia, all identified before molecular phylogenetic frameworks had been developed for the Myrtaceae (Christophel and Blackburn, 1978; Christophel and Lys, 1986; Christophel et al., 1992).

A wealth of untapped information also exists in the silcrete floras of Australia, notably in Central-Southern and Western Australia. While these fossil floras do not have organic preservation, there are large numbers of fossil fruits and leaves, which should be subjected to more rigorous systematic study. The major problem associated with studying these silcretes is the lack of confident age constraints, but fossils described from these deposits could still provide valuable paleobiogeographic data. For instance, capsular fruits with affinities to the Eucalypteae, Leptospermeae, Melaleuceae, Chamelauceae and possibly other capsular fruited tribes have been recovered from a number of silcrete floras, that have never been subjected to rigorous systematic study (Lange, 1978; Ambrose et al., 1979; Carpenter et al., 2011). Many of these capsular-fruited genera lack any confidently or formally described fossil representatives to date, and so the identification of potential fossil records of these groups should be considered a high priority.

Conclusions— The fossils described here represent some of the best and most thoroughly described Myrtaceae macrofossils from anywhere in the world, and demonstrate that with the significant advances in understanding the phylogeny and taxonomy of the Myrtaceae, identification of Myrtaceae macrofossils is possible with certainty not possible to earlier researchers. The fossils of *Metrosideros, M. leunigii, M. dawsonii* and *M. wrightii,* provide the first evidence for the genus *Metrosideros* in Australia, and demonstrate rare evidence for the extinction of a Tertiary rainforest angiosperm genus from Australia. These fossils contribute to our growing knowledge of extinction of elements throughout the changing Cenozoic Australian vegetation. The fossils of *Syzygium christophelii* are the most confidently identified non-eucalypt fossil Myrtaceae leaves described to date, and provide a new benchmark for the rigour with which fossil Myrtaceae leaves can be identified in a phylogenetic framework. These fossils contribute to a growing understanding of the paleobiogeography of the Myrtaceae, and suggest that the macrofossil record of the family is ripe for further study.

APPENDIX 1: Extant taxa where leaf or reproductive material was used for comparison with fossil material in Chapters 3 and 5 (with herbarium accession codes, or collection/determinant codes) Species and genera are grouped by tribe, sensu Biffin et al. (2010), genera within each tribe are listed in alphabetical order – 176 taxa. AD = State Herbarium of South Australia, LAE = Papua New Guinea National Herbarium, NSW = National Herbarium of New South Wales, and SAN = Forest Research Centre, Sabah, Malaysia.

Syzygieae: *Syzygium gustavioides* NSW674598, *Syzygium claviflorum* NSW426207, *Syzygium pringlei* NSW520411, *Syzygium alatoramulum* NSW528106, *Syzygium angophoroides* NSW845167, *Syzygium angophoroides* (2) NSW835455*, Syzygium apodophyllum* NSW528117, *Syzygium branderhorstii* NSW533070 *Syzygium canicortex* NSW528132, *Syzygium cordatum* AD97603008, *Syzygium cumini* AD98575252, *Syzygium erythrodoxum* NSW682786, *Syzygium eucalyptoides* NSW528126, *Syzygium eucalyptoides* (2) ssp. *bleeseri* AD98141173, *Syzygium fibrosum* NSW293731, *Syzygium fratris* NSW8359952*, Syzygium hemilamprum* AD97808262, *Syzygium longipes* NSW245595, *Syzygium minutiflorum* NSW528786, *Syzygium nervosum* NSW528788, *Syzygium porphyrocarpum* NGF46428 J. Womersley 1973, *Syzygium puberulum*, NSW533058, *Syzygium rubrimolle* NSW529232, *Syzygium subaubiculare* NSW533052*, Syzygium wesa* NSW834934*, Syzygium xerampelinum* NSW683562, *Syzygium anisatum* NSW447023, *Syzygium paniculatum* M. Tarran Adelaide Botanic Gardens, **Backhousieae:** *Backhousia bancroftii* NSW529578, *Backhousia citriodora* NSW835510, *Backhousia sciadaphora* NSW518234, *Backhousia kingii* NSW531697, *Backhousia myrtifolia* NSW530929, *Backhousia myrtifolia* (2) NSW530933, *Backhousia oligantha* NSW669324, *Backhousia hughesii* NSW541378, *Backhousia angustifolia* NSW593087, *Backhousia enata* NSW684447, *Decaspermum urvillei* NGF18494 J.R. Croft 1973, **Myrteae:** *Archirhodomyrtus beckleri* NSW578959, *Decaspermum prunoides* H Streimann 1972, *Decaspermum vitis-idaea* SAN15251, *Eugenia stricta* NSW536534, *Eugenia reinwardtiana* NSW840686, *Eugenia capensis*, AD98403423, *Eugenia biflora* AD99340199, *Gossia alaternoides* J. Jaffre 2367, *Gossia (Myrtus) versteeghii* LAE7218, *Lenwebbia lasioclada*, NSW466610, *Lenwebbia prominens* NSW406575, *Lithomyrtus kakaduensis* NSW467733, *Lithomyrtus grandifolia* NSW461883, *Lithomyrtus hypoleuca* NSW578598, *Myrtella beccarii* NSW772997, *Pilidiostigma papuanum* NSW673562, *Pilidiostigma rhytispermum* NSW540544, *Rhodomyrtus sericea* NSW592771, *Rhodamnia rubescens* NSW460628, *Rhodamnia pauciovulata* NSW462420, *Rhodomyrtus locellata* G.McPherson 5238, *Rhodomyrtus pervagata,* NSW843018, *Rhodomyrtus efusa* NSW624218, *Uromyrtus archboldiana* A. Kairo NGF44105, *Uromyrtus artensis* I. Franc 1907, *Uromyrtus tenella* NSW835721, *Uromyrtus lamingtonensis* NSW576237, *Uromyrtus australis* NSW540485, *Uromyrtus metrosideros* NSW521834, **Kanieae:** *Barongia lophandra* B.Gray 618 13/7/1997, *Cloezia artensis* H.S.McKee 35.381 197, *Cloezia aquarum* H.S. McKee 12245 1965, *Kania eugenioides* NGF3724 J.S. Womersley 1996, *Kania eugenioides* (2) LAE55700 P.F.Stevens 1972, *Kania eugenioides* (3) NSW507902, *Kania eugenioides* (4) NSW779223, *Kania platyphylla* CANB128223, *Kania platyphylla* (2) CANB14186, *Kania hirsutula* CANB73763, *Kania nettotensis* CANB129209, *Kania sp.*, NSW870234, *Lysicarpus angustifolius* NSW531527, *Mitrantia bilocularis* CANB00396458, *Ristantia pachysperma* NSW530547, *Ristantia waterhousei* NSW530554, *Sphaerantia discolor* NSW410055, *Sphaerantia chartacea* B. Hyland 12516, *Tristaniopsis reticulata* G. Mcpherson 3571, *Tristaniopsis glauca* (2) NSW299091, *Tristaniopsis collina* NSW529538, *Tristaniopsis collina* (2) M. Tarran 2014, *Tristaniopsis laurina* NSW531466, *Tristaniopsis exiliflora* NSW835468, *Tristaniopsis capitulata* R. Schlecter 26 1902, *Tristaniopsis calobuxus* G. McPherson 20811979, *Tristaniopsis guillainii* J. Jaffre 3462 2000, *Tristaniopsis mcphersonii* G. McPherson 5513 1983, *Tristaniopsis glauca* NSW211172, *Xanthomyrtus montivaga* J.S. Womersley NGF24859 1967, *Xanthomyrtus flavida* SAN152562 2010, **Metrosidereae:** *Carpolepis elegans* H.S. McKee 25999, *Carpolepis laurifolia* J. Munzinger 594, *Carpolepis tardiflora* G. McPherson 2538, *Metrosideros robusta* P.I. Knightbridge PK42 may 2001, *Metrosideros bartlettii* R. Drummond 1998, *Metrosideros bartlettii* (2) AK236084, *Metrosideros sclerocarpa* NSW255743, *Metrosideros sclerocarpa* (2) NSW299059, *Metrosideros sclerocarpa* (3) CBG8800534, *Metrosideros brevistylis* G. McPherson 2415 1980, *Metrosideros salomonensis* LAE82142, *Metrosideros salomonensis* (2) S.F. Kajewski 1755, *Metrosideros* *salomonensis* (3) CANB144493, *Metrosideros salomonensis* (4) CANB99120, *Metrosideros paniensis* G. McPherson 2386, *Metrosideros paniensis* (2) H.S. McKee 19132, *Metrosideros operculata* I. Franc 703, *Metrosideros operculata* (2) G. McPherson 3594, *Metrosideros operculata* (3) Le Boucher 1383, *Metrosideros operculata* (4) H.S. McKee 30804, *Metrosideros operculata* (5) K.L. Wilson 7200, *Metrosideros operculata* (6) G. McPherson 1525, *Metrosideros patens* H.S. McKee 41753, *Metrosideros patens* (2) G. McPherson 2747, *Metrosideros tetrasticha* CANB00547979, *Metrosideros longipetiolata* CANB00548054, *Metrosideros nervulosa* NSW787363, *Metrosideros nitida* G. McPherson 1568, *Metrosideros nitida* (2) G. McPherson 6424, *Metrosideros polymorpha* O. Degener 19,720, *Metrosideros cacuminum* H.S. McKee 18795, *Metrosideros fulgens* NSW237486, *Metrosideros perforata* R. Melville 6857, *Metrosideros albiflora* R. Gardner 1974, *Metrosideros angustifolia* J.P. Rourke 1804, *Metrosideros angustifolia* (2) P. Goldblatt 1309, *Metrosideros macropus* G.A. Pearsall 1958, *Metrosideros ramiflora* AK256202, *Metrosideros cherrieri* CANB00568204, *Metrosideros oreomyrtus* CANB00449468, *Metrosideros parkinsonii* CHR468333, *Metrosideros humboldtiana* J. Munzingr 3446, *Metrosideros halconensis* Elmer 13759, *Metrosideros porphyrea* R. Schlechter 15302, *Metrosideros engleriana* CANB00547926, *Metrosideros dolichandra* G. McPherson 5170, *Metrosideros dolichandra* (2) G. McPherson 1970, *Metrosideros punctata* G. McPherson 2693, *Metrosideros cordata* J.S. Womersley 4722, *Metrosideros microphylla* CANB00547976, *Metrosideros kermadecensis* CANB00703819, *Metrosideros scandens* CANB128225

APPENDIX 2 – *Carpolepis*, *Metrosideros & Tepualia* sp. where reproductive material was examined for comparison with fossil fruits in Chapter 4- *52 specimens,* 33 species – With herbarium accession codes or collector & coll. Number. AK = Museum of Auckland, CANB = Herbarium of Canberra, LAE = Papua New Guinea National Herbarium NSW = Harbarium of New South Wales

***Carpolepis** elegans* (Montrouz.) J.W.Dawson, H.S. McKee 25999, *C. laurifolia* (Brongn. & Gris) J.W.Dawson, J. Munzinger 594 , *C. tardiflora* J.W.Dawson, G. McPherson 2538, ***Metrosideros** albiflora* Sol. ex Gaertn., R. Gardner 1974, *M. angustifolia* (L.) Sm., J.P. Rourke 1804, *M. angustifolia* (2), P. Goldblatt 1309, *M. bartlettii* J.W.Dawson, R. Drummond 1998, *M. bartlettii* (2), AK236084, *M. brevistylis* J.W.Dawson, G. McPherson 2415 1980, *M. cherrieri* J.W.Dawson, CANB00568204, *M. cordata* (C.T.White & W.D.Francis) J.W.Dawson, J.S. Womersley 4722, *M. dolichandra* Schltr. ex Guillaumin, G. McPherson 5170, *M. dolichandra* (2), G. McPherson 1970, *M. engleriana* Schltr., CANB00547926, *M. fulgens* Sol. ex Gaertn., NSW237486, *M. fulgens* (2), CANB128225, *M. halconensis* (Merr.) J.W.Dawson, Elmer 13759, *M. humboldtiana* Guillaumin, J. Munzingr 3446, *M. kermadecensis* W.R.B.Oliv., CANB00703819, *M. longpetiolata* J.W.Dawson, CANB00548054, *M. macropus* Hook. & Arn., G.A. Pearsall 1958, *M. microphylla* (Schltr.) J.W. Dawson, CANB00547976, *M. nervulosa* C.Moore & F.Muell., NSW787363, *M. nitida* Brongn. & Gris, G. McPherson 1568, *M. nitida* (2), G. McPherson 6424, *M. operculata* Labill., I. Franc 703, *M. operculata* (2), G. McPherson 3594, *M. operculata* (3), Le Boucher 1383, *M. operculata* (4), H.S. McKee 30804, *M. operculata* (5), K.L. Wilson 7200, *M. operculata* (6), G. McPherson 1525, *M. oreomyrtus* Däniker, CANB00449468, *M. parkinsonii* Buchanan, CHR468333, *M. patens* J.W.Dawson, H.S. McKee 41753, *M. patens* (2), G. McPherson 2747, *M. perforata* (J.R.Forst. & G.Forst.) Druce, R. Melville 6857, *M. paniensis* J.W.Dawson, G. McPherson 2386, *M. paniensis,* (2),H.S. McKee 19132, *M. polymorpha* Gaudich., O. Degener 19,720, *M. porphyrea* Schltr., R. Schlechter 15302, *M. punctata* J.W.Dawson, G. McPherson 2693, *M. ramiflora* Lauterb., AK256202, *M. robusta* A.Cunn., P.I. Knightbridge PK42, *M. solomonensis*

C.T.White, LAE82142, *M. solomonensis*, (2), S.F. Kajewski 1755, *M. solomonensis*, (3), CANB144493, *M. solomonensis*, (4), CANB99120, *M. sclerocarpa* J.W.Dawson, NSW255743, *M. sclerocarpa* (2), NSW299059, *M. sclerocarpa* (3), CBG8800534, *M. tetrasticha* Guillaumin, CANB00547979, ***Tepualia*** *stipularis* (Hook. & Arn.) Griseb., NSW777995.

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