Uncovering the early diversification of core eudicots in western North America: structurally preserved fruits from Late Cretaceous deposits of Sucia Island

By
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Abstract

Core eudicots are the most diverse lineage of flowering plants with a fossil record that dates back to the Late Cretaceous. Making up much of the diversity in flowering plants today, it is important to investigate the core eudicot fossil record to better understand the early diversification of angiosperms. Recent fossil discoveries from Cretaceous deposits within the western coast of North America may help shed new light on the early diversity of core eudicots and angiosperms as a whole. Late Cretaceous deposits along the western coast of North America remain relatively undersampled compared to the eastern coast or western interior. However, ongoing efforts to recover and characterize fossil flora of western North America within a phylogenetic framework will result in a better understanding of the turnover of lineages through time. Here I report two new species of core eudicots based on fossil fruits recovered from Campanian (Late Cretaceous) deposits of Sucia Island, Washington state, USA. The fossil fruits were studied using sectioning, light microscopy, X-ray micro-computed tomography, and phylogenetic analyses. Based on morphological comparisons and support from phylogenetic analyses, one fossil fruit was assigned to the extant genus *Ceratopetalum* (Cunoniaceae), as a new species *Ceratopetalum suciensis* Tang & Atkinson sp. nov., and the second fruit to the extinct genus *Esgueiria* (Esgueiriaceae), as a new species *Esgueiria aligera* Tang & Atkinson sp. nov. These fossils are the first unequivocal evidence of both genera within North America which greatly extend their distribution. Continuing to recover and describe both extant and extinct lineages will undoubtedly help us to better understand the early evolutionary patterns of flowering plants.

Acknowledgments

Table of Contents

List of Figures

List of Tables

Chapter 1: The initial diversification of core eudicots and their critical role in understanding angiosperm origins

Introduction

Angiosperms are the most diverse lineage of terrestrial plants today, but their fossil record is fairly recent only dating back to the Early Cretaceous. Drastic changes in the Earth's landscapes occurred ~100 Ma when the core eudicots begin to appear in the fossil record and diversify in rapid succession (Doyle 1969; Magallon et al. 1999; E.M. Friis et al. 2006; Friis et al. 2011). The core eudicots make up over 70% of angiosperm diversity (Magallon et al. 1999; Friis et al. 2006; Friis et al. 2011) which make them crucial in understanding the early evolution of flowering plants. Members of this clade are typically characterized by the presence of pentamerous flowers with distinct perianth whorls and their pollen is mainly tricolporate although some lineages are known to have tricolpate pollen (Wodehouse 1936; Erdtman 1952; Doyle 1969; Takhtajan 1980; Furness et al. 2007; Endress 2010; Friis et al. 2011). A majority of core eudicots comprise the rosids (~70,000 species; Magallon et al. 1999, Friis et al. 2011, APG 2016) and asterids (>80,000 species; Magallon et al. 1999, Albach et al. 2001, Friis et al. 2011, APG 2016), the largest clade within eudicots. Molecular studies recover strong support for the monophyletic groupings of rosids and asterids (Hilu et al. 2003; Moore et al. 2010; Friis et al. 2011; Soltis et al. 2011; Sun et al. 2015; APG 2016) but unifying morphological characters among the rosids and asterids remains largely understudied (Matthews et al. 2001; Endress 2010; Endress and Matthews 2012; Endress and Matthews 2006).

Additionally, several lineages lie outside the species rich rosids and asterids. The order Gunnerales is sister to all other core eudicots; Saxifragales is sister to the rosids forming the

superrosid clade; Berberidopsidales, Santalales, and Caryophyllales as successive sister lineages to the asterids forming the superastrid clade; and the monofamilial Dilleniales is placed within the core eudicots in a polytomy with the superrosids and superastrids due to conflicting positions recovered from previous studies (discussed in APG 2016). Although these orders are not as species rich as the rosids or asterids, a few lineages have fossil records dating back to the Cretaceous that can provide insight on the early evolution of the core eudicots and angiosperms as a whole.

The timing and origin of angiosperms is of considerable interest in plant evolution but remains difficult to tease apart with conflicts between molecular and fossil data as well as the angiosperm fossil record remaining grossly undersampled (Herendeen et al. 2017; Coiro et al. 2019). The large discrepancy between molecular data and the fossil data has brought on arguments against the different data types. However, the unequivocal fossil record has proven to be informative in providing minimum age constraints for molecular dating analyses as well as teasing apart diversification rates (Anderson et al. 2005; Magallón and Castillo 2009; Bell et al. 2010; Magallón et al. 2015; Ramírez-Barahona et al. 2020). In order to understand early angiosperm evolution, it is imperative to examine the fossil record. The angiosperm fossil record remains incomplete, but the recovery and characterization of fossil core eudicots in undersampled regions such as Cretaceous deposits of North America (Mindell et al. 2014; Atkinson 2016; Atkinson et al. 2016; Atkinson 2016; Atkinson et al. 2017; Jud et al. 2017; Atkinson et al. 2018; Scharfstein et al. 2020) can help shed light on early angiosperm diversity. In this review, I will examine the early fossil record of core eudicots and discuss the importance of their inclusion within phylogenetic analyses to help tease apart the early diversity and timing of angiosperms.

When do the core eudicots begin to appear? – Early core eudicot fossil record

The oldest unequivocal angiosperm fossils are dispersed monosulcate pollen from

Valanginian – Hauterivian (~132.9 Ma) deposits of Europe, Western Asia, and East Asia

(Hughes 1994; Brenner 1996; Zhang 1999) as well as tricolpate pollen from Barremian (~125

Ma) deposits of Europe, North Africa, North America, and Western Asia (Hughes and

McDougall 1990; Penny 1991; Doyle 1992; Hughes 1994; Brenner 1996). Monosulcate pollen is

characteristic of the ANA (Amborellales, Nymphaeales, Austrobaileyales) grade lineage at the

base of the angiosperm phylogeny, Magnoliids, and monocots (Wodehouse 1936; Takhtajan

1980; Doyle 2005). Tricolpate pollen, however, is present in all eudicots which have been

modified to tricolporate pollen, seen in core eudicots, and triporate pollen (Wodehouse 1936;

Takhtajan 1980; Endress 2010; Friis et al. 2011; Coiro et al. 2019). The ANA grade angiosperms

have a sparse Cretaceous meso/macro-fossil record save for a few seeds and flowers assigned to

Nymphaeaceae (Friis et al. 2001; Takahashi et al. 2007; Friis et al. 2009) and Chloranthaceae

(Crane et al. 1989; Herendeen et al. 1993; Eklund et al. 1997). Within the Magnoliids, the

Cretaceous macrofossil record largely consists of fossil flowers and wood assigned to the

families Magnoliaceae (Dilcher and Crane 1984; Frumin and Friis 1996; Frumin and Friis 1999)

and Lauraceae (Drinnan et al. 1990; Herendeen 1991; Eklund and Kvaček 1998; Eklund 2000;

Poole, Richter, et al. 2000; von Balthazar et al. 2007; Takahashi et al. 2014; Crepet et al. 2016;

Moreau et al. 2016; Friis et al. 2017; Poinar 2017). Much of the Cretaceous macrofossil record of

monocots were recovered from the Deccan Intertrappean Beds of India (Prakash 1960; Bonde

and Kumaran 1993; Bonde 1996; Bonde 2000; Manchester et al. 2016; Matsunaga et al. 2018;

Matsunaga et al. 2019). Within the eudicots, there is a rich record of dispersed leaves, fruits,

seeds, and wood from the Late Cretaceous and Cenozoic (Friis et al. 2011). Peculiarly, the

eudicot fossil record documents a sequential diversification in which lineages towards the base of the eudicot crown node, such as the families Platanaceae and Nelumbonaceae (Hickey and Doyle 1977; Crane et al. 1993; Upchurch et al. 1994), were established during the Early Cretaceous and then, major lineages of the core eudicots begin to appear afterwards throughout the Late Cretaceous and Early Cenozoic (Friis et al. 2011; Herendeen et al. 2017).

The first major core eudicot lineage that appear in the fossil record is the rosid clade. Rosids are a large and diverse group within core eudicots but the morphological diversity within the clade can make it difficult to accurately assign fossils (Matthews et al. 2001; Endress and Matthews 2006; Endress 2010; Endress and Matthews 2012). The earliest unequivocal records of rosids, and core eudicots as a whole, are pentamerous flowers, from late Albian – early Cenomanian deposits from the western interior and eastern coast of North America (Basinger and Dilcher 1984; Friis et al. 2016; Manchester et al. 2018). Fossil flowers recovered from the western interior of North America were originally dubbed the "Rose Creek flower" (Basinger and Dilcher 1984). However, careful reexamination of the specimens using X-ray micro-computed tomography (μCT) uncovered morphological characters that were not easily visible at first. The fossil flowers show great similarities with the rosid family Quillajaceae and the new genus *Dakotanthus* was erected (Manchester et al. 2018). The rosid-like flower, *Calciflora mauldinensis,* was recovered from the earliest Cenomanian of eastern North America (Friis et al. 2016) that shares diagnostic characters of core eudicots. Morphological structures of the fossil flowers indicate an affinity to the rosids although a more precise assignment is unknown due to the morphological diversity of such a large clade. Turonian deposits along the east coast of North America have also recovered a variety of rosid flowers alongside other angiosperm fossils (Crepet 2008). Beginning in the Cenomanian (~100 Ma), the Normapolles complex (order

Fagales) which is characterized by triaperturate pollen, is common throughout Late Cretaceous deposits within the Northern Hemisphere (Batten 1981; Pacltová 1981; Friis et al. 2011; Friis et al. 2006). The Normapolles pollen producing plants rapidly diversified throughout the Cretaceous until they virtually went extinct by the Oligocene. The unequivocal fossil flowers and pollen of the rosids suggest the clade's initial diversification was well underway by the Cenomanian.

Asterids are the largest clade within the core eudicots holding over 80,000 species, but their Cretaceous record is sparse and largely confined within the orders Cornales and Ericales (Magallon et al. 1999; Friis et al. 2011). Recently recovered asterid fossils indicate a radiation around the Turonian – Coniacian boundary (Martínez et al. 2016; Atkinson et al. 2018; Atkinson et al. 2019). Fossil fruits of the extinct species *Eydeia jerseyensis* within Cornales (Atkinson et al. 2019) and fossil flowers of the extinct species *Rariglanda jerseyensis* within Ericales (Martínez et al. 2016) were both recovered from Turonian deposits of eastern North America and mark the earliest unequivocal asterid fossils. Following these Turonian representatives, a variety of cornalean fruits representing extinct lineages have been described from Coniacian deposits of western North America (Atkinson et al. 2018) and Japan (Takahashi et al. 2002; Stockey et al. 2016). Cornalean representatives continue to be recovered from Campanian deposits of western North America as more Cretaceous deposits are sampled from the western coast (Atkinson 2016; Atkinson et al. 2016; Atkinson et al. 2017; Atkinson et al. 2018; Atkinson et al. 2019). The fossil fruits recovered in these studies all represent extinct lineages except for a fruit assigned to the extant genus *Cornus* (Atkinson et al. 2019). Extensive records of ericalean flowers, fruits, seeds, and wood have also been reported from Cretaceous deposits (Turonian – Campanian) of eastern North America, Europe, and Japan (Martínez-Millán 2010; Manchester et al. 2015). A variety of

these specimens represent extinct genera as well, indicating a rapid radiation of the orders

Cornales and Ericales within the Late Cretaceous. The fossil record of asterids suggests an initial

diversification near the Turonian – Coniacian boundary following the appearance of rosids. This

pattern of the rapid succession of major angiosperm lineages suggests the initial diversification

of core eudicots may have largely been comprised by rosids.

A few notable Cretaceous fossils have been recovered from other core eudicot lineages

outside of the species-rich rosids and asterids such as the orders Santalales and Saxifragales. The

Late Cretaceous record of Santalales largely consists of pollen reported from New Zealand,

North America, and East Asia (Couper 1953; Srivastava 1966; Song et al. 2004). The order

Saxifragales has a notable Late Cretaceous record which includes inflorescences/infructescences

from Santonian and Campanian deposits of North America (Magallon-Puebla et al. 1996;

Magallón et al. 2001). The described flowers represent extinct lineages within the family

Hamamelidaceae. Additional core eudicot lineages such as Gunnerales, Dilleniales, and

Caryophyllales have putative Cretaceous records of pollen or seeds while no fossil record is

known for Berberidopsidales (discussed in Friis et al. 2011). The pattern of sequential

diversification in the eudicot fossil record would suggest these orders outside the rosids and

asterids would have diversified earlier. However, taphonomic or sampling biases may play a role

in deviating from the pattern because much of the diversity within the core eudicots consist of

the rosids and asterids rather than the lineages outside of those groups. Therefore, the rosids and

asterids are more likely to be recovered from the fossil record compared to the orders outside of

those two large groups. Nonetheless, these extinct lineages will no doubt help shed light on the

early evolutionary patterns of angiosperms.

Integration of molecular data with the fossil record

While the early fossil record of core eudicots and angiosperms indicate a minimum origin age in the Early Cretaceous, several molecular dating analyses suggest a significantly older age (Smith et al. 2010; Zeng et al. 2014; Barba-Montoya 2018). However, the discrepancy between the fossil record and molecular analyses may be due to errors/biases from both molecular and fossil data. Multiple molecular dating studies estimate an origin age for angiosperms in the Triassic while and an origin age for eudicots reaching back to the Jurassic (Smith et al. 2010; Zeng et al. 2014; see table 1 in Barba-Montoya 2018). These age estimates call into question biases in the fossil record that could explain such a large discrepancy between molecular age estimates and stratigraphic age ranges. Arguments have been made suggesting the incomplete fossil record and taphonomic biases are to blame for the disagreement between the fossil record and molecular dating analyses (Smith et al. 2010). Barba-Montoya (2018) additionally argue that misinterpretation of the fossil record adds to the discrepancies and suggest the use of "key characters" to determine if fossils are crown angiosperms may be flawed due to incomplete preservation or observation. However, convincing pre-Cretaceous crown angiosperms have yet to be recovered (discussed in Herendeen et al. 2017; Coiro et al. 2019). Additionally, heterogenous rates of molecular evolution in rapidly evolving lineages or sampling biases in molecular dating analyses have been shown to cause overestimates of these origin ages (Beaulieu et al. 2015). While both the fossil record and molecular dating analyses have their flaws, both lines of evidence still play an important role in understanding the timing and age of core eudicots and angiosperms as a whole.

The angiosperm fossil record may be incomplete but the incorporation of unequivocal records with molecular data provides a more complete view of macroevolutionary patterns

within angiosperms. Using unequivocal fossils as minimum age constraints, several studies have estimated an angiosperm origin age reaching back to the Late Jurassic and core eudicots reaching back to the earliest Cretaceous which more closely reflect the fossil record (Anderson et al. 2005; Bell et al. 2010; Magallón et al. 2015; Ramírez-Barahona et al. 2020). Likewise, the use of multiple fossils within dating analyses provide a better representation of the fossil record compared to studies that use very few fossil calibrations. Compared to the studies mentioned above, Wikström et al. (2001) and Zeng et al. (2014) use very few fossil calibrations in their analysis. As a result, they estimate a much older age for angiosperms in the Mid-Jurassic. The incorporation of fossil data is key in estimating accurate ages which will help us better understand the early diversification of angiosperms. However, the early diversification of angiosperms remains difficult to tease apart due to their initial rapid radiation (Doyle 1969; Magallon et al. 1999; Friis et al. 2006; Magallón and Castillo 2009; Friis et al. 2011). Biases in molecular analyses such as heterogenous rates of molecular evolution (Beaulieu et al. 2015) due to this rapid radiation may prevent us from attaining an accurate estimation of origin ages. The fossil record, however, can provide additional data on early angiosperm diversity that may help us better understand the initial radiation of angiosperms (Donoghue et al. 1989).

The angiosperm fossil record remains grossly undersampled but the continued recovery and characterization of fossils within undersampled regions will help us gain a better understanding of angiosperm diversity in the past. Within North America, Cretaceous deposits along the western coast have remained relatively undersampled compared to the eastern coast (Herendeen 1991; Herendeen et al. 1993; Frumin and Friis 1996; Magallon-Puebla et al. 1996; Eklund 2000; Magallón et al. 2001; von Balthazar et al. 2007; Crepet 2008; Friis et al. 2011; Friis et al. 2016; Martínez et al. 2016; Atkinson et al. 2019) and western interior (Upchurch and

Dilcher 1990; Basinger and Dilcher 1984; Dilcher and Crane 1984; Ward 1986; Friis et al. 2011; Manchester et al. 2018). However, recent sampling along the western coast of North America has already revealed a great diversity of both extinct and extant genera of angiosperms (Mindell et al. 2014; Atkinson 2016; Atkinson et al. 2016; Atkinson 2016; Atkinson et al. 2017; Jud et al. 2017; Atkinson et al. 2018; Scharfstein et al. 2020). Modern methods such as extracting high resolution morphological data (Strong and Lipscomb 1999; Sereno 2007; Brazeau 2011; Simões et al. 2017), like important floral characters (Schönenberger et al. 2020; Jud and Gandolfo 2020), allow for the direct integration of fossil data and extant data within a phylogenetic framework to assess the systematic placements of fossils within the angiosperm phylogeny. However, extinct lineages such as cornalean fruits recovered from western North America (Atkinson 2016; Atkinson et al. 2017) can be difficult to place within a phylogenetic framework due to their unique character combinations. The inability to properly assign extinct taxa within modern lineages suggest those taxa represent stem lineages and will likely require additional fossil data as well as more rigorous evolutionary analyses to recover their position within the angiosperm phylogeny. The need for additional fossil data and rigorous evolutionary analyses emphasizes the importance in recovering and characterizing fossil floras from undersampled regions like Late Cretaceous deposits of western North America. The continued recovery and characterization of both extant and extinct angiosperm lineages are critical to understanding the early diversification and phylogenetic turnover of lineages through time.

References

Anderson CL, K Bremer, EM Friis 2005 Dating phylogenetically basal eudicots using rbcL sequences and multiple fossil reference points. Am J Bot 92:1737–1748.

Askin RA 1992 Late Cretaceous-Early Tertiary Antarctic Outcrop Evidence for Past Vegetation and Climates. Antarct Palaeoenvironment Perspect Glob Change 56:61–73.

Atkinson BA 2016 Early diverging asterids of the Late Cretaceous: *Suciacarpa starrii* gen. et sp. nov. and the initial radiation of Cornales. Botany 94:759–771.

Atkinson BA, C Martínez, WL Crepet 2019 Cretaceous asterid evolution: fruits of *Eydeia jerseyensis* sp. nov. (Cornales) from the upper Turonian of eastern North America. Ann Bot 123:451–460.

Atkinson BA, RA Stockey, GW Rothwell 2016 Cretaceous origin of dogwoods: an anatomically preserved *Cornus* (Cornaceae) fruit from the Campanian of Vancouver Island. PeerJ 4:e2808.

——— 2017 The Early Phylogenetic Diversification of Cornales: Permineralized Cornalean Fruits from the Campanian (Upper Cretaceous) of Western North America. Int J Plant Sci 178:556–566.

——— 2018 Tracking the Initial Diversification of Asterids: Anatomically Preserved Cornalean Fruits from the Early Coniacian (Late Cretaceous) of Western North America. Int J Plant Sci 179:21–35.

von Balthazar M, KR Pedersen, PR Crane, M Stampanoni, EM Friis 2007 Potomacanthus lobatus gen. et sp. nov., a new flower of probable Lauraceae from the Early Cretaceous (Early to Middle Albian) of eastern North America. Am J Bot 94:2041–2053.

Barba-Montoya J 2018 Constraining uncertainty in the timescale of angiosperm evolution and the veracity of a Cretaceous Terrestrial Revolution. New Phytol 218:819–834.

Basinger JF, DL Dilcher 1984 Ancient Bisexual Flowers. Science 224:511–513.

Batten DJ 1981 Stratigraphic, palaeogeographic and evolutionary significance of late cretaceous and early tertiary normapolles pollen. Rev Palaeobot Palynol 35:125–137.

Beaulieu JM, BC O'Meara, P Crane, MJ Donoghue 2015 Heterogeneous Rates of Molecular Evolution and Diversification Could Explain the Triassic Age Estimate for Angiosperms. Syst Biol 64:869–878.

Bell CD, DE Soltis, PS Soltis 2010 The age and diversification of the angiosperms re-revisited. Am J Bot 97:1296–1303.

Bonde SD 1996 *Arecoideostrobous moorei* gen. et sp. nov. a palm rachilla from the Deccan Intertrappean beds of India. The Palaeobotanist 43:102–109.

——— 2000 *Rhodospathodendron tomlinsonii* gen. et sp. nov., an araceous viny axis from the Nawargaon intertrappean beds of India. The Palaeobotanist 49:85–92.

Bonde SD, KPN Kumaran 1993 A liliaceous inflorescence from the Deccan Intertrappean beds of India. Curr Sci 65:776–778.

Brazeau MD 2011 Problematic character coding methods in morphology and their effects: Morphological Character Coding. Biol J Linn Soc 104:489–498.

Brenner GJ 1996 Evidence for the Earliest Stage of Angiosperm Pollen Evolution: A Paleoequatorial Section from Israel. In: Taylor DW, Hickey LJ, editors. Flowering Plant Origin, Evolution & Phylogeny. Boston, MA: Springer US. p. 91–115.

Coiro M, JA Doyle, J Hilton 2019 How deep is the conflict between molecular and fossil evidence on the age of angiosperms? New Phytol 223:83–99.

Couper RA 1953 Upper Mesozoic and Cainozoic spores and pollen from New Zealand. N Z Geol Surv Palaeontol Bull 22:1–77.

Crane PR, EM Friis, KR Pedersen 1989 Reproductive structure and function in Cretaceous Chloranthaceae. Plant Syst Evol 165:211–226.

Crane PR, KR Pedersen, EM Friis, AN Drinnan 1993 Early Cretaceous (Early to Middle Albian) Platanoid Inflorescences Associated with Sapindopsis Leaves from the Potomac Group of Eastern North America. Syst Bot 18:328–344.

Crepet WL 2008 The Fossil Record of Angiosperms: Requiem or Renaissance?. Ann Mo Bot Gard 95:3–33.

Crepet WL, KC Nixon, D Grimaldi, M Riccio 2016 A mosaic Lauralean flower from the Early Cretaceous of Myanmar. Am J Bot 103:290–297.

Dilcher DL, PR Crane 1984 *Archaenthus*: An Early Angiosperm From the Cenomanian of the Western Interior of North America. Ann Mo Bot Gard 71:351–383.

Donoghue MJ, JA Doyle, J Gauthier, AG Kluge, T Rowe 1989 The Importance of Fossils in Phylogeny Reconstruction. Annu Rev Ecol Syst 2:431–460.

Doyle JA 1969 Cretaceous angiosperm pollen of the Atlantic coastal plain and its evolutionary significance. J Arnold Arbor 50:1–35.

Doyle JA 1992 Revised palynological correlations of the lower Potomac group (USA) and the cocobeach sequence of Gabon (Barremian-Aptian). Cretac Res 13:337–349.

Doyle JA 2005 Early evolution of angiosperm pollen as inferred from molecular and morphological phylogenetic analyses. Grana 44:227–251.

Drinnan AN, PR Crane, EM Friis, KR Pedersen 1990 Lauraceous Flowers from the Potomac Group (Mid-Cretaceous) of Eastern North America. Bot Gaz 151:370–384.

Eklund H 2000 Lauraceous flowers from the Late Cretaceous of North Carolina, U.S.A. Bot J Linn Soc 132:397–428.

Eklund H, EM Friis, KR Pedersen 1997 Chloranthaceous floral structures from the Late Cretaceous of Sweden. Plant Syst Evol 207:13–42.

Eklund H, J Kvaček 1998 Lauraceous Inflorescences and Flowers from the Cenomanian of Bohemia (Czech Republic, Central Europe). Int J Plant Sci 159:668–686.

Endress PK 2010 Flower Structure and Trends of Evolution in Eudicots and Their Major Subclades. Ann Mo Bot Gard 97:541–583.

Endress PK, ML Matthews 2006 First steps towards a floral structural characterization of the major rosid subclades. Plant Syst Evol 260:223–251.

Endress PK, ML Matthews 2012 Progress and problems in the assessment of flower morphology in higher-level systematics. Plant Syst Evol 298:257–276.

Erdtman G 1952 Pollen Morphology and Plant Taxonomy: Angiosperms. Stockholm: Almqvist & Wiksell.

Friis EM, PR Crane, KR Pedersen 2011 Early flowers and angiosperm evolution. Cambridge ; New York: Cambridge University Press.

——— 2017 *Saportanthus* , an Extinct Genus of Laurales from the Early Cretaceous of Portugal. Int J Plant Sci 178:650–672.

Friis Else M., A Iglesias, MA Reguero, T Mörs 2017 Notonuphar antarctica, an extinct water lily (Nymphaeales) from the Eocene of Antarctica. Plant Syst Evol 303:969–980.

Friis EM, KR Pedersen, M von Balthazar, GW Grimm, PR Crane 2009 *Monetianthus mirus* gen. et sp. nov., a Nymphaelean Flower from the Early Cretaceous of Portugal. Int J Plant Sci 170:1086–1101.

Friis EM, KR Pedersen, PR Crane 2001 Fossil evidence of water lilies (Nymphaeales) in the Early Cretaceous. Nature 410:357–360.

Friis E.M., KR Pedersen, PR Crane 2006 Cretaceous angiosperm flowers: Innovation and evolution in plant reproduction. Palaeogeogr Palaeoclimatol Palaeoecol 232:251–293.

Friis EM, KR Pedersen, PR Crane 2016 The emergence of core eudicots: new floral evidence from the earliest Late Cretaceous. Proc R Soc B Biol Sci 283:20161325.

Friis E. M., KR Pedersen, J Schönenberger 2006 Normapolles plants: a prominent component of the Cretaceous rosid diversification. Plant Syst Evol.

Frumin S, EM Friis 1999 Magnoliid reproductive organs from the Cenomanian-Turonian of north-western Kazakhstan: Magnoliaceae and Illiciaceae. Plant Syst Evol 216:265–288.

Frumin SI, EM Friis 1996 Liriodendroid seeds from the Late Cretaceous of Kazakhstan and North Carolina, USA. Rev Palaeobot Palynol 94:39–55.

Furness CA, S Magallón, PJ Rudall 2007 Evolution of endoapertures in early-divergent eudicots, with particular reference to pollen morphology in Sabiaceae. Plant Syst Evol 263:77–92.

Gandolfo MA, RN Cuneo 2005 Fossil Nelumbonaceae from the La Colonia Formation (Campanian–Maastrichtian, Upper Cretaceous), Chubut, Patagonia, Argentina. Rev Palaeobot Palynol 133:169–178.

Herendeen PS 1991 Lauraceous wood from the mid-Cretaceous Potomac group of eastern North America: *Paraphyllanthoxylon marylandense* sp. nov. Rev Palaeobot Palynol 69:277–290.

Herendeen PS, WL Crepet, KC Nixon 1993 *Chloranthus* like stamens from the Upper Cretaceous of New Jersey. Am J Bot 80:865–871.

Herendeen PS, EM Friis, KR Pedersen, PR Crane 2017 Palaeobotanical redux: revisiting the age of the angiosperms. Nat Plants 3:17015.

Hickey LJ, JA Doyle 1977 Early cretaceous fossil evidence for angiosperm evolution. Bot Rev 43:3–104.

Hilu KW, T Borsch, K Müller, DE Soltis, PS Soltis, V Savolainen, MW Chase, MP Powell, LA Alice, R Evans, et al. 2003 Angiosperm phylogeny based on *mat K* sequence information. Am J Bot 90:1758–1776.

Hughes NF 1994 The Enigma of Angiosperm Origins. Cambridge: Cambridge University Press.

Hughes NF, AB McDougall 1990 Barremian-Aptian angiospermid pollen records from southern England. Rev Palaeobot Palynol 65:145–151.

Jud NA, MA Gandolfo 2020 Fossil evidence from South America for the diversification of Cunoniaceae by the earliest Palaeocene. Ann Bot:1–11.

Jud NA, EA Wheeler, GW Rothwell, RA Stockey 2017 Angiosperm wood from the Upper Cretaceous (Coniacian) of British Columbia, Canada. IAWA J 38:141–161.

Magallón S, A Castillo 2009 Angiosperm diversification through time. Am J Bot 96:349–365.

Magallon S, PR Crane, PS Herendeen 1999 Phylogenetic Pattern, Diversity, and Diversification of Eudicots. Ann Mo Bot Gard 86:297.

Magallón S, S Gómez-Acevedo, LL Sánchez-Reyes, T Hernández-Hernández 2015 A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. New Phytol 207:437–453.

Magallón S, PS Herendeen, PR Crane 2001 *Androdecidua endressii* gen. et sp. nov., from the Late Cretaceous of Georgia (United States): Further Floral Diversity in Hamamelidoideae (Hamamelidaceae). Int J Plant Sci 162:963–983.

Magallon-Puebla S, PS Herendeen, PK Endress 1996 *Allonia decandra*: Floral remains of the tribe Hamamelideae (Hamamelidaceae) from Campanian strata of southeastern USA. Plant Syst Evol 202:177–198.

Manchester SR, SD Bonde, DS Nipunage, R Srivatava, RC Mehrotra, SY Smith 2016 Trilocular Palm Fruits from the Deccan Intertrappean Beds of India. Int J Plant Sci 177:633–641.

Manchester SR, DL Dilcher, WS Judd, B Corder, JF Basinger 2018 Early Eudicot flower and fruit: Dakotanthus gen. nov. from the Cretaceous Dakota Formation of Kansas and Nebraska, USA. Acta Palaeobot 58:27–40.

Manchester SR, F Grímsson, R Zetter 2015 Assessing the Fossil Record of Asterids in the Context of Our Current Phylogenetic Framework. Ann Mo Bot Gard 100:329–363.

Martínez C, TYS Choo, D Allevato, KC Nixon, WL Crepet, RS Harbert, CP Daghlian 2016 *Rariglanda jerseyensis*, a new ericalean fossil flower from the Late Cretaceous of New Jersey. Botany 94:747–758.

Martínez-Millán M 2010 Fossil Record and Age of the Asteridae. Bot Rev 76:83–135.

Matsunaga KKS, SR Manchester, R Srivastava, DK Kapgate, SY Smith 2019 Fossil palm fruits from India indicate a Cretaceous origin of Arecaceae tribe Borasseae. Bot J Linn Soc 190:260–280.

Matsunaga KKS, SY Smith, SR Manchester, D Kapgate, D Ramteke, A Garbout, H Villarraga-Gómez 2018 Reinvestigating an enigmatic Late Cretaceous monocot: morphology, taxonomy, and biogeography of *Viracarpon*. PeerJ 6:e4580.

Matthews M, P Endress, J Schonenberger, E Friis 2001 A Comparison of Floral Structures of Anisophylleaceae and Cunonicaeae and the Problem of their Systematic Position. Ann Bot 88:439–455.

Mindell RA, SJ Karafit, RA Stockey 2014 Bisexual Flowers from the Coniacian (Late Cretaceous) of Vancouver Island, Canada: *Ambiplatanus washingtonensis* gen. et sp. nov. (Platanaceae). Int J Plant Sci 175:651–662.

Moore MJ, PS Soltis, CD Bell, JG Burleigh, DE Soltis 2010 Phylogenetic analysis of 83 plastid genes further resolves the early diversification of eudicots. Proc Natl Acad Sci 107:4623–4628.

Moreau J-D, B Gomez, V Daviero-Gomez, D Néraudeau, P Tafforeau 2016 Inflorescences of *Mauldinia* sp. (Lauraceae) and associated fruits from the Cenomanian of Languedoc Roussillon, France. Cretac Res 59:18–29.

Pacltová B 1981 The evolution and distribution of Normapolles pollen during the Cenophytic. Rev Palaeobot Palynol 35:175–208.

Penny JHJ 1991 Early Cretaceous angiosperm pollen from the borehole Mersa Matruh 1, North West Desert, Egypt. Palaeontogr B 222:31–88.

Poinar G 2017 A mid-Cretaceous Lauraceae flower, *Cascolaurus burmitis* gen. et sp. nov., in Myanmar amber. Cretac Res 71:96–101.

Poole I, HG Richter, JE Francis 2000 Evidence for Gondwanan Origins for *Sassafras* (Lauraceae)? Late Cretaceous Fossil Wood of Antarctica. IAWA J 21:463–475.

Prakash U 1960 A survey of the Deccan Intertrappean flora of India. J Paleontol 34:1027–1040.

Ramírez-Barahona S, H Sauquet, S Magallón 2020 The delayed and geographically heterogeneous diversification of flowering plant families. Nat Ecol Evol 4:1232–1238.

Scharfstein AR, RA Stockey, GW Rothwell 2020 Evolution and Phylogeny of Altingiaceae: Anatomically Preserved Infructescences from Late Cretaceous Deposits of Vancouver Island, British Columbia, Canada. Int J Plant Sci 181:452–463.

Schönenberger J, M von Balthazar, A López Martínez, B Albert, C Prieu, S Magallón, H Sauquet 2020 Phylogenetic analysis of fossil flowers using an angiosperm-wide data set: proof-of-concept and challenges ahead. Am J Bot 107:1–16.

Sereno PC 2007 Logical basis for morphological characters in phylogenetics. Cladistics 23:565–587.

Simões TR, MW Caldwell, A Palci, RL Nydam 2017 Giant taxon-character matrices: quality of character constructions remains critical regardless of size. Cladistics 33:198–219.

Smith SA, JM Beaulieu, MJ Donoghue 2010 An uncorrelated relaxed-clock analysis suggests an earlier origin for flowering plants. Proc Natl Acad Sci 107:5897–5902.

Soltis DE, SA Smith, N Cellinese, KJ Wurdack, DC Tank, SF Brockington, NF Refulio-Rodriguez, JB Walker, MJ Moore, BS Carlsward, et al. 2011 Angiosperm phylogeny: 17 genes, 640 taxa. Am J Bot 98:704–730.

Song ZC, WM Wang, F Huang 2004 Fossil Pollen Records of Extant Angiosperms in China. Bot Rev 70:425–458.

Srivastava SK 1966 Upper Cretaceous microflora (Maestrichtian) from Scollard, Alberta, Canada. Pollen Spores 8:497–552.

Stockey RA, H Nishida, BA Atkinson 2016 Anatomically preserved fossil cornalean fruits from the Upper Cretaceous of Hokkaido: *Eydeia hokkaidoensis* gen. et sp. nov. Am J Bot 103:1642–1656.

Strong EE, D Lipscomb 1999 Character Coding and Inapplicable Data. Cladistics 15:363–371.

Sun M, DE Soltis, PS Soltis, X Zhu, JG Burleigh, Z Chen 2015 Deep phylogenetic incongruence in the angiosperm clade Rosidae. Mol Phylogenet Evol 83:156–166.

Takahashi M, PR Crane, SR Manchester 2002 *Hironoia fusiformis* gen. et sp. nov.; a cornalean fruit from the Kamikitaba locality (Upper Cretaceous, Lower Coniacian) in northeastern Japan. J Plant Res 115:463–473.

Takahashi M, EM Friis, PR Crane 2007 Fossil Seeds of Nymphaeales from the Tamayama Formation (Futaba Group), Late Cretaceous (Early Santonian) of Northeastern Honshu, Japan. Int J Plant Sci 168:341–350.

Takahashi M, PS Herendeen, X Xiao, PR Crane 2014 Lauraceous Fossil Flowers from the Kamikitaba Assemblage (Coniacian, Late Cretaceous) of Northeastern Japan (Lauraceae). Syst Bot 39:715–724.

Takhtajan AL 1980 Outline of the Classification of Flowering Plants (Magnoliophyta). N Y Bot Gard Press 46:225–359.

The Angiosperm Phylogeny Group 2016 An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Bot J Linn Soc 181:1–20.

Upchurch GR, PR Crane, AN Drinnan 1994 The megaflora from the Quantico locality (Upper Albian), Lower Cretaceous Potomac Group of Virginia. Martinsville: Virginia Museum of Natural History.

Upchurch GR, DL Dilcher 1990 Cenomanian angiosperm leaf megafossils, Dakota Formation, Rose Creek Locality, Jefferson County, southeastern Nebraska. US Geological Survey Bulletin.

Ward JV 1986 Early Cretaceous angiosperm pollen from the Cheyenne and Kiowa Formations (Albian) of Kansas, USA. Palaeontogr B 202:1–81.

Wikström N, V Savolainen, MW Chase 2001 Evolution of the angiosperms: calibrating the family tree. Proc R Soc Lond B Biol Sci 268:2211–2220.

Wodehouse RP 1936 Evolution of pollen grains. Bot Rev 2:67–84.

Zeng L, Q Zhang, R Sun, H Kong, N Zhang, H Ma 2014 Resolution of deep angiosperm phylogeny using conserved nuclear genes and estimates of early divergence times. Nat Commun 5:4956.

Zhang Y-Y 1999 The evolutionary success of Cretaceous angiosperm pollen in China. Acta Palaeobot Sin 38:435–453.

Chapter 2: Extending beyond Gondwana: Cretaceous Cunoniaceae from western North America

Introduction

Southern Hemisphere rainforests share remarkably similar plant taxonomic associations across far flung landmasses such as Australia, New Zealand, Fiji, New Guinea, and South America (Kooyman et al. 2014). Although these ecosystems currently are separated by great distances, the fossil record has shown that prior to the final break up of Gondwana, during the Eocene, important components of these southern rainforests were assembling in present day South America, Australia, and Antarctica. Thus, the plants that constitute Gondwanan ecosystems are known as Paleo-Antarctic Rainforest Lineages (PARLs), some of which include Podocarpaceae, Nothofagaceae, Myrtaceae, Proteaceae, and Cunoniaceae (Kooyman et al. 2014). Many PARLs are important components of present-day temperate to tropical rainforests in the Southern Hemisphere and their fossil records remain critical for understanding the assembly and biogeographic history of these ecosystems (Barreda et al. 2021). Therefore, many of these lineages are often used as study systems for understanding the evolution of southern rainforests and one such lineage is Cunoniaceae.

Cunoniaceae today comprise 300 species and 27 genera that have a typical PARL distribution and are important components in southern rainforests and may even dominate some ecosystems (Bradford et al. 2004; Kooyman et al. 2014). It has long been thought that this family has an exclusive southern distribution and extensive fossil record dating back to the latest Cretaceous of South America and Antarctica, which is represented by wood and pollen (Cranwell 1959; Askin 1992; Baldoni and Askin 1993; Poole et al. 2000; Poole et al. 2003).

However, due to the limited number of characters possessed by these structures it is not clear whether they represent crown members of the family. Equivocal Cretaceous records of the family include flowers from Europe and Myanmar (Schönenberger et al. 2001; Chambers et al. 2010; Poinar and Chambers 2017) that are not clearly diagnostic of the family (discussed in Gandolfo and Hermsen 2017; Jud et al. 2018; Carpenter and Rozefelds 2020). Unequivocal fossils of crown group Cunoniaceae are diverse throughout the Cenozoic of Australia (Holmes and Holmes 1992; Barnes and Hill 1999; Barnes et al. 2001; Jud and Gandolfo 2020); and recent fossil discoveries of fossil flowers representing extinct genera have been recovered from the earliest Paleocene of Patagonia (Jud et al. 2018; Jud and Gandolfo 2020). Extant genera of Cunoniaceae appear soon after with one of the more conspicuous fossil representatives being *Ceratopetalum* Sm. (Holmes and Holmes 1992; Barnes and Hill 1999; Gandolfo and Hermsen 2017).

Today, *Ceratopetalum* consists of eight species that are restricted to eastern Australia and Papua New Guinea (Rozefelds and Barnes 2002) and can dominate rainforests in these regions (Burges and Johnston 1953; Baur 1957; Webb 1978). Fossils of *Ceratopetalum* are often fruits that are easily identified by a combination of characters comprising 4-6 expanded calyx lobes that form wings, an inter-wing vein, a nectary disk, persistent stamen, semi-inferior ovary, and typically two styles. Eocene records of the genus (five extinct species) are testimony to a much wider distribution in the past that spans central Australia and Patagonia (Holmes and Holmes 1992; Barnes and Hill 1999; Gandolfo and Hermsen 2017). The past and current distribution of *Ceratopetalum,* and Cunoniaceae as a whole, are indeed typical of PARLs, which reaffirms a traditional Gondwanan history of these plants.

Here we report two three-dimensionally preserved fruits of *Ceratopetalum* from the Late Cretaceous Sucia Island locality off the coast of Washington state, USA. Comparative analysis indicates that the fossils represent a new species, *Ceratopetalum suciensis* sp. nov. Tang & Atkinson. Our findings indicate that: 1) the diversification of Cunoniaceae was well underway during the Cretaceous; 2) *Ceratopetalum* and crown Cunoniaceae have a biogeographic history in the Northern Hemisphere; and 3) the historical distributions of important PARLs may have extended beyond Gondwana in the past.

Materials and Methods

Two three-dimensionally preserved fruits are preserved within calcium carbonate concretions that were exposed along Fossil Bay on Sucia Island, Washington state, USA. Exposures along Fossil Bay belong to the Cedar District Formation of the Nanaimo Group and, based on biostratigraphy and magnetostratigraphy, are Campanian in age (~82-80 Ma; Ward et al. 2012). The fossil biota from the Sucia Island locality consist of cornalean fruits, ammonites, terrestrial gastropods, inoceramid bivalves, and a theropod femur (Ward 1978; Roth 2000; Ward et al. 2012; Peecook and Sidor 2015; Atkinson 2016).

One specimen (KUPB 19168) was imaged using a Nikon SMZ25 stereomicroscope with a Nikon DS-Fi3 camera attachment (Nikon Corporation, Tokyo, Japan). The other specimen (KUPB 19169) was imaged and then glued back together for X-ray micro-computed tomography (μCT) and physical sectioning using the cellulose acetate peeling method (Joy et al. 1956). Several peels were mounted on microscope slides using the mounting medium Eukitt (O. Kindler GmbH, Freiberg, Germany).

One specimen (KUPB 19168) and seven fruits of five extant species of *Ceratopetalum* (Appendix A, Table 3; Appendix B) were μCT scanned at the University of Michigan CTEES facility using a Nikon XT H 225ST industrial μCT system with a Perkin Elmer 1620 X-ray detector panel and a tungsten reflection target. Scan conditions for the fossils were set at 128 KV, 145 μA, and used 1 mm of copper filter with 20.84 μm pixel size resolution. Scan conditions for the extant fruits can be found in Appendix A, Table 4. The program Inspect-X (Nikon Corporation, Tokyo, Japan) acquired scans that were segmented using the software Mimics 22.0 (Materialise, Leuven, Belgium) to reconstruct three-dimensional images of the fruits. Avizo 9 Lite 3D (Thermo Fisher Scientific, Massachusetts, USA) was used for fruit measurements. Data are archived on Morphosource (Boyer et al. 2016) under project title "3D morphology of Ceratopetalum fruits (Cunoniaceae)."

In order to test our systematic assignment of the Cretaceous fruits, we analyzed them via the phyloscan method (Schönenberger et al. 2020), which uses a comprehensive angiosperm floral character matrix and molecular backbone to assess the most parsimonious position(s) of fossil flowers. Since the studied fossil fruits have a number of persistent floral structures preserved, they were easily analyzed using this method. The original floral matrix and backbone do not include *Ceratopetalum* and because it is morphologically distinct in Cunoniaceae, we added an extant species, *C. gummiferum*, to the matrix and grafted it to the backbone phylogeny based on Bradford and Barnes (2001); the revised matrix can be found in the supplementary materials. We scored 19 characters for *Ceratopetalum suciensis* and the justifications are detailed in the next section. The same method was used to assess two equivocal cunoniaceous fossils, *Tropidogyne* and *Platydiscus*. Phyloscan outputs can be found in the supplementary materials (Appendix C, Figs. 12-14).

In addition, to further test the systematic affinities of the fruits, two Bayesian phylogenetic analyses were conducted using combined morphological and molecular datasets. In the first analysis the Cretaceous fruits of this study were the only fossils included and in the second analysis ten additional fossils were included. A morphological dataset from Jud and Gandolfo (2020) was modified to include additional fossil taxa and consists of 54 taxa (43 extant, 11 fossils) and 58 characters. The modified morphological matrix is available online via Morphobank (project P3906, matrix 27164; O'Leary and Kaufman 2011). The matrix was combined with *rbcL* and *trnL-trnF* data from GenBank (Appendix A, Table 5). Molecular data were aligned in Aliview (Larsson 2014) using Mafft (Katoh and Standley 2013). PartitionFinder2 (Lanfear et al. 2016) was used with AICc model selection to search for the optimal partitioning scheme and models of molecular evolution. The most optimal scheme was GTR+G+I model for the *rbcL* data and a GTR+G model for the *trnL-trnF* data. The Mkv model (Lewis 2001) was used for the morphological data. The Bayesian phylogenetic analyses were conducted using MrBayes 3.2.7a (Ronquist et al. 2012) on the CIPRES Science Gateway (Miller et al. 2011). The analysis used Markov chain Monte Carlo for two independent runs with four chains running for 100 million generations, sampling every 10000 generations, with a 25% burn-in. The standard deviation of split frequencies was below 0.02, and Tracer 1.7 (Rambaut et al. 2018) was used to confirm convergence with all ESS values well above 200.

Phyloscan scorings justifications

Characters for *Ceratopetalum suciensis* were scored using preserved floral characters present on the specimens. Number of perianth whorls were scored as missing because the lack of petals may be due to preservation rather than the absence of petals in the species. The semi-

inferior ovary was scored as inferior due to the limited number of character states in the character matrix. Internal structures were not preserved so ovule characters were scored as missing. Additionally, anthers were not preserved so pollen characters were scored as missing.

Most of the floral characters for the fossil flowers *Platydiscus peltatus* (Schönenberger et al. 2001) and *Tropidogyne pentaptera* (Poinar and Chambers 2017) were scored according to their published descriptions. All semi-inferior ovaries were scored as inferior ovaries in the character matrix. Data that was scored as missing for the flowers were due to lack of preservation making it difficult to accurately interpret the characters in the images of the specimens. Anthers were not preserved in *P. peltatus,* so the anther characters were scored as missing. For *T. pentaptera,* the number of perianth whorls were scored as missing because the lack of petals may also be due to preservation rather than an absence in the species. Due to the preservation in amber, internal structures could not be observed so the ovule characters were scored as missing. The anther orientation of *T. pentaptera*, was scored as missing due to difficulty interpreting the image of the anther on the specimen.

Results

Systematics

Order – Oxalidales

Family – Cunoniaceae R. Br. 1814

Tribe – Schizomerieae J.C. Bradford & R. W. Barnes 2001

Genus – *Ceratopetalum* Sm. 1793

Species – *Ceratopetalum suciensis* Tang & Atkinson, sp. nov.

Specific diagnosis. Fruit body up to 4.0 mm wide and 5.75 mm long. Calyx lobes up to 3.0 mm wide and 11.0 mm long, oblong with slightly acute apex and up to five vascular bundles. Secondary bundles in calyx lobes diverging throughout the entire length of wing at ca. 45-90⁰. Nectary, annular ring with conspicuous lobes. Stamen filaments ca. 1.0 mm long.

Etymology. The specific epithet, *suciensis*, refers to Sucia Island where the fossils were recovered.

Holotype. KUPB 19169 (Figs. 1B, 1C, 2D, 2E).

Paratype. KUPB 19168 (Figs. 1A, 2A, 2B, 2C).

Type locality. Fossil Bay, Sucia Island, Washington State, USA (48.749330°N, 122.900798°W).

Stratigraphy. Cedar District Formation.

Age. Early to Middle Campanian (ca. ~82-80 Ma).

Description

The two three-dimensionally preserved fruits are epigynous and radially symmetrical with a semi-inferior ovary (Fig. 1A-B). The calyx, nectary, androecium, and styles are persistent; petals and internal tissues are not preserved. The width of the fruit body, excluding the wings, is 4.0 mm and the length of the fruit body is 5.75 mm from the base to the tip of the styles. There are four to five calyx lobes per fruit that extend outward forming wings (Fig. 1A, C). Most wings are abraded; however, one specimen has an entire wing preserved (Fig. 1A) with smooth margins and it is 11.0 mm long and 3.0 mm wide. This wing is elliptic in shape with a slightly acute apex and attenuate base. Internal structures were not preserved.

Although anatomical preservation is limited, details on calyx venation are easily observed as dark "coalified" tissue. Five primary veins can be seen entering the base of the wing with
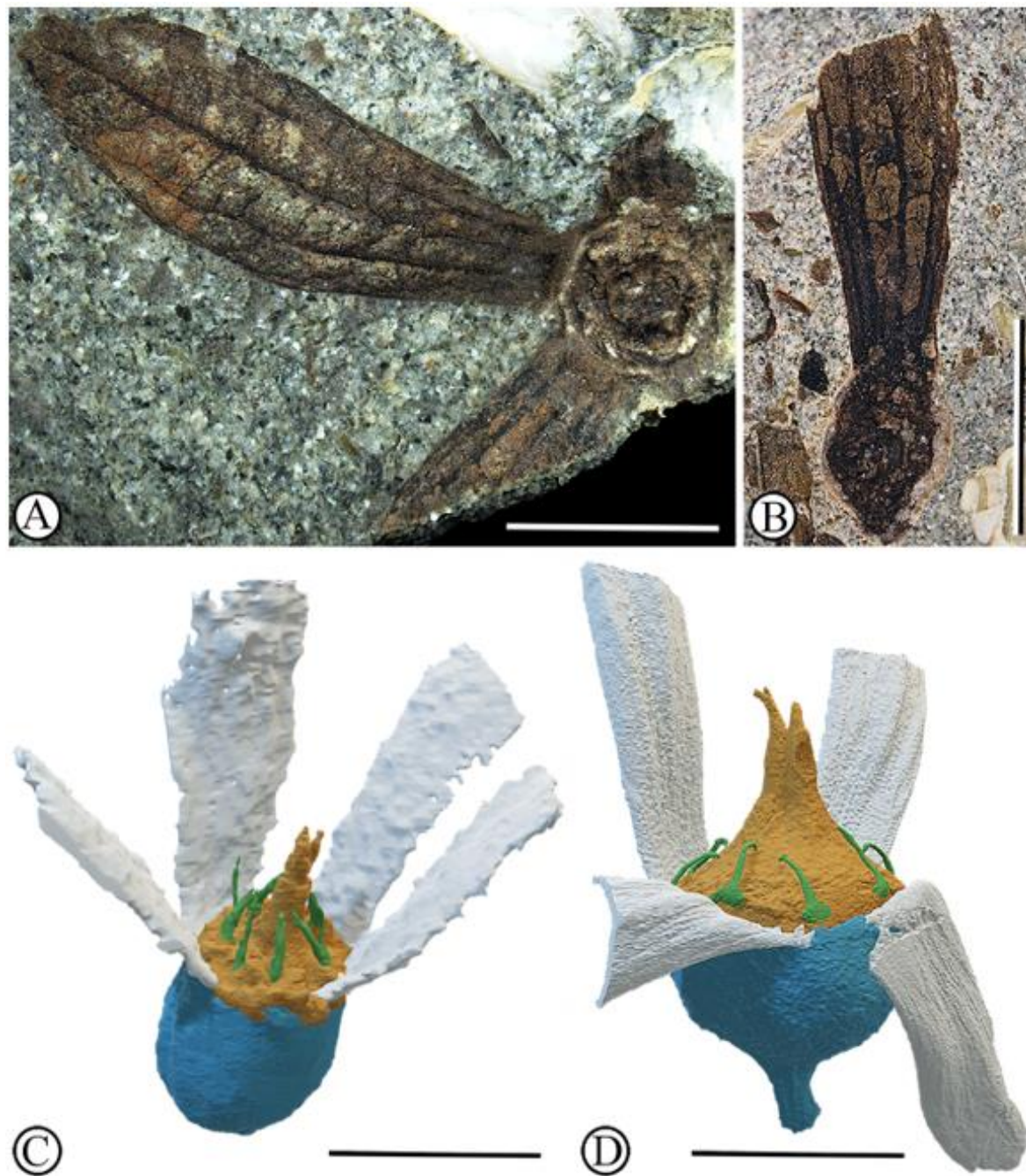
Figure 1. Structure of *Ceratopetalum suciensis* Tang & Atkinson sp. nov. (A-C) and extant *Ceratopetalum succirubrum* (in D). (A) Exposed rock showing top-down view of fruit with an annular nectary, one entire wing, a partial wing, and three abraded wings. Specimen KUPB 19168, scale bar = 2 mm. (B) Exposed specimen in oblique longitudinal view of fruit body and a wing, courtesy of S. R. Manchester. Specimen KUPB 19169, scale bar = 5 mm. (C) Three-dimensional reconstruction of specimen in B showing general morphology of the fruit including two styles, diplostemonous stamens, and four wings are present. Specimen KUPB 19169, scale bar = 5 mm. (D) Three-dimensional reconstruction of extant fruit of *C. succirubrum* showing general morphology including two styles, diplostemonous stamens, and four wings (apices are cropped). BH 95696, scale bar = 5 mm. White = calyx/wings; Orange = styles and nectary disk; Green = stamen; Blue = hypanthium.
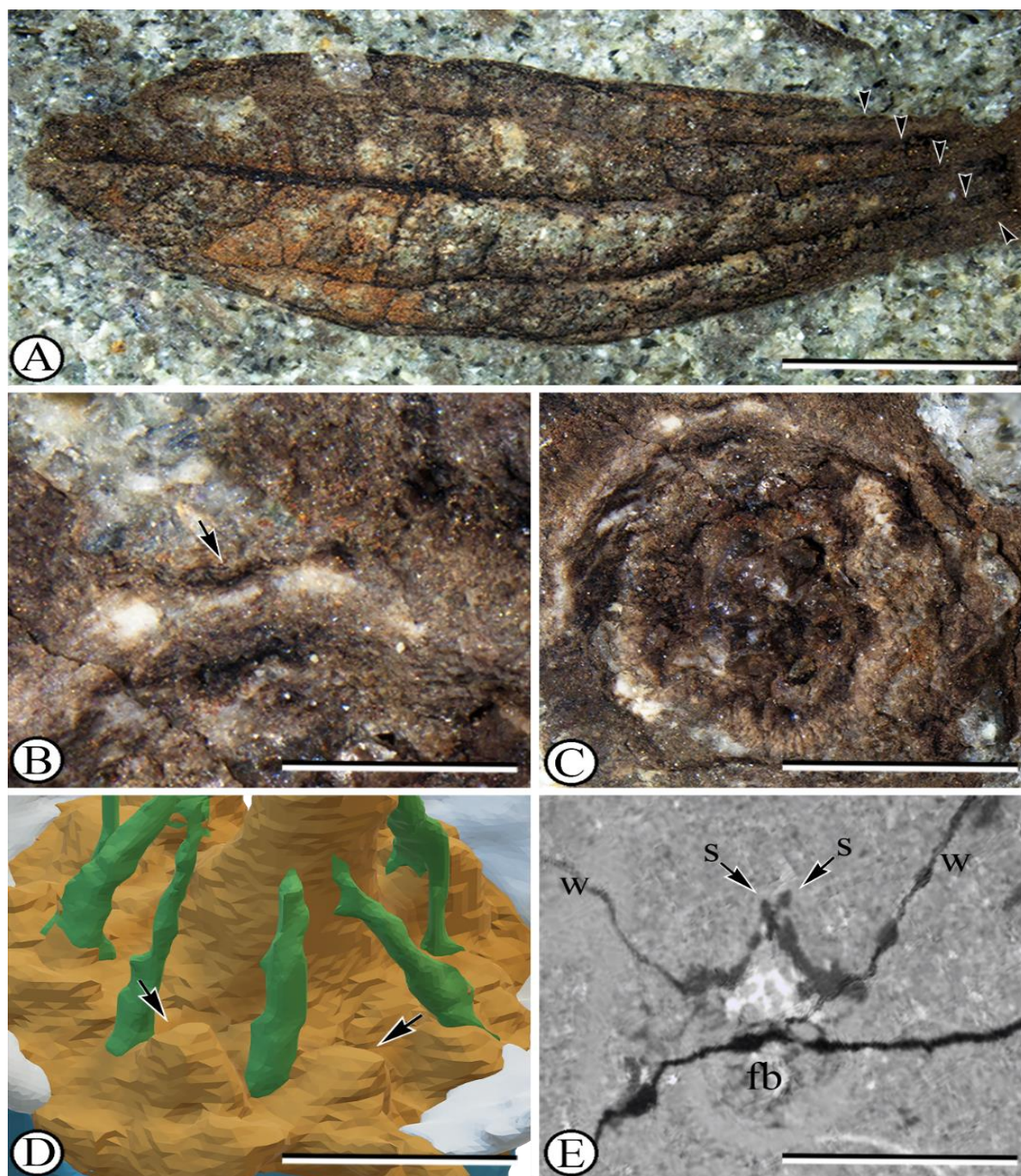
Figure 2. Detailed view of wings, nectary lobes, and styles of *Ceratopetalum suciensis* Tang & Atkinson sp. nov. (A) Detailed view of wing with five primary veins (arrowheads) and secondary veins that diverge from the primary veins 45-90°. Specimen KUPB 19168, scale bar = 2 mm. (B) Top-down view of tissue just outside of nectary lobe and between the wings showing an inter-wing vein (arrow). Specimen KUPB 19168, scale bar = 0.3 mm. (C) Top-down view of annular nectary disk. Specimen KUPB 19168, scale bar = 0.6 mm. (D) Three-dimensional reconstruction of the fossil fruit showing nectary lobes bordering stamens. Specimen KUPB 19169, scale bar = 1 mm. White = calyx/wings; Orange = styles and nectary disk; Green = stamen; Blue = hypanthium. (E) Digital longitudinal section of micro-CT scanned fruit showing two appressed styles. Specimen KUPB 19169, scale bar = 6 mm. w = wings; s = styles; st = stamen; fb = fruit body.

secondary veins diverging from the primary veins at about 45-90⁰ throughout the entire length. The marginal veins in the wing connect to adjacent ones via an inter-wing vein located at the outer edge of the nectary between each calyx lobe (Fig. 2B). As revealed by the μCT-scanned specimen, the nectary is an annular ring (Fig. 2C) with prominent nectary lobes (Fig. 1C).

The androecium is diplostemonous and consists of filaments that are ca. 1.0 mm long. Anthers are not preserved. The outer whorl of stamens is opposite of the wings (calyx lobes) while the inner whorl of stamens alternates with the wings (Fig. 1C, 2D). Each filament is nestled between two nectary lobes (Fig. 1C).

The gynoecium is well preserved in one specimen. The ovary is semi-inferior and 4.0 mm in diameter. The μCT scan reveals two free styles that are pressed against one another for most of their length (Figs. 1C, 2E).

X-ray micro-computed tomography (μCT) of extant fruits

Scans of five *Ceratopetalum* species display the presence of 4 – 6 calyx lobes, persistent stamens, semi-inferior ovaries, a nectary disk, and 2-3 appressed styles on the fruits (Appendix B). The calyx lobes expand in size to form radiating wings that resemble a "helicopter" fruit morphology. Stamens form two alternating whorls on each fruit. There are four wings, eight stamens, and two styles present on each *C. succirubrum* fruit. Scanned specimens of *Ceratopetalum apetalum, C. corymbosum,* and *C. virchowii* all have five wings present with 10 stamens and two appressed styles. *Ceratopetalum gummiferum* is the only specimen to have highly dissected petals persistent on the fruit. There are six petals present, 12 stamens, and three styles.

Phylogenetic analyses

In the phyloscan analyses, the most parsimonious positions of *Ceratopetalum suciensis* were recovered on the branch leading to *C. gummiferum* and stem Fagales (Appendix C, Fig. 12). *Platydiscus peltatus* was recovered within the order Saxifragales and Myrtales (Appendix C. Fig. 13). Flowers of *Tropidogyne pentaptera* were recovered in several distantly related groups such as Proteales, Saxifragales, and Apiales (Appendix C, Fig. 14).

Both Bayesian phylogenetic analyses resulted in *C. suciensis* within crown Cunoniaceae. The first analysis recovered *C. suciensis* with extant *Ceratopetalum* in a trichotomy (posterior probability = 1.0; Fig. 3). The second analysis (with nine additional fossil taxa) recovered *C. suciensis* within a clade (polytomy) comprising all other fossil and extant *Ceratopetalum* species (posterior probability = 0.72; Fig. 4).

Discussion

Cretaceous Ceratopetalum

Based on multiple lines of evidence, the Sucia Island fruits are assigned to the genus *Ceratopetalum* as *C. suciensis* sp. nov. The multiple phylogenetic analyses in this study support the systematic assignment of the Sucia Island fruits to the genus *Ceratopetalum*. Using the recent phyloscan method (Schönenberger et al. 2020), two most parsimonious positions of *Ceratopetalum suciensis* were recovered, one being along the branch leading to extant *Ceratopetalum gummiferum* Sm. (crown group Cunoniaceae) and the other along the stem lineage of Fagales. Fruits of Fagales, however, are typically nuts or samaras (Kubitzki et al. 1993; Larson-Johnson 2016), which differ from the multi-winged "helicopter" fruit morphology of *C. suciensis*. In addition, no reported stem Fagales have a fruit morphology similar to *C.*
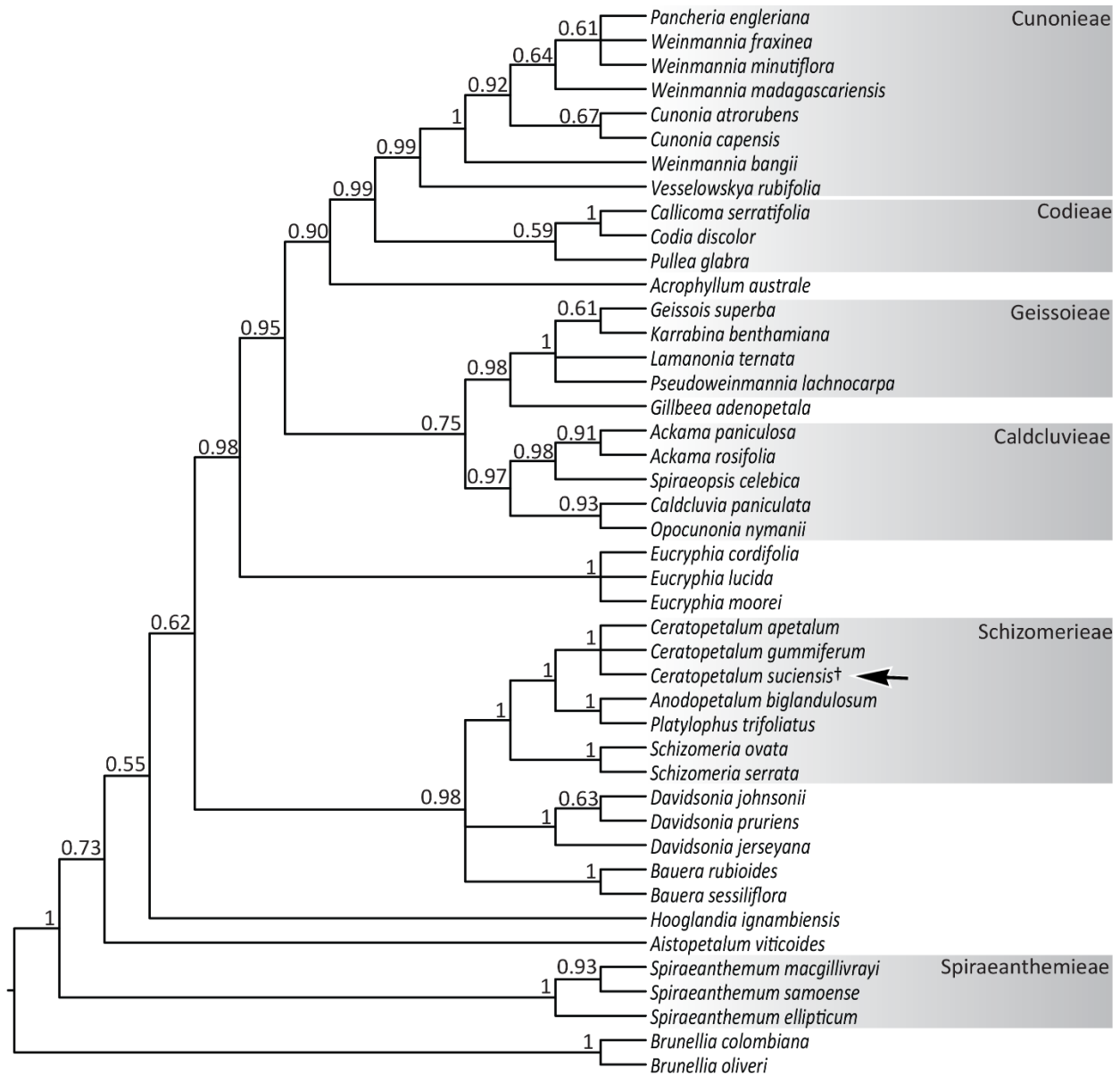
Figure 3. Majority rules consensus tree from Bayesian phylogenetic analysis showing relationship of *Ceratopetalum suciensis* **within Cunoniaceae.** Numbers above the branches are posterior probability value. Tribes are indicated by the gray shading.
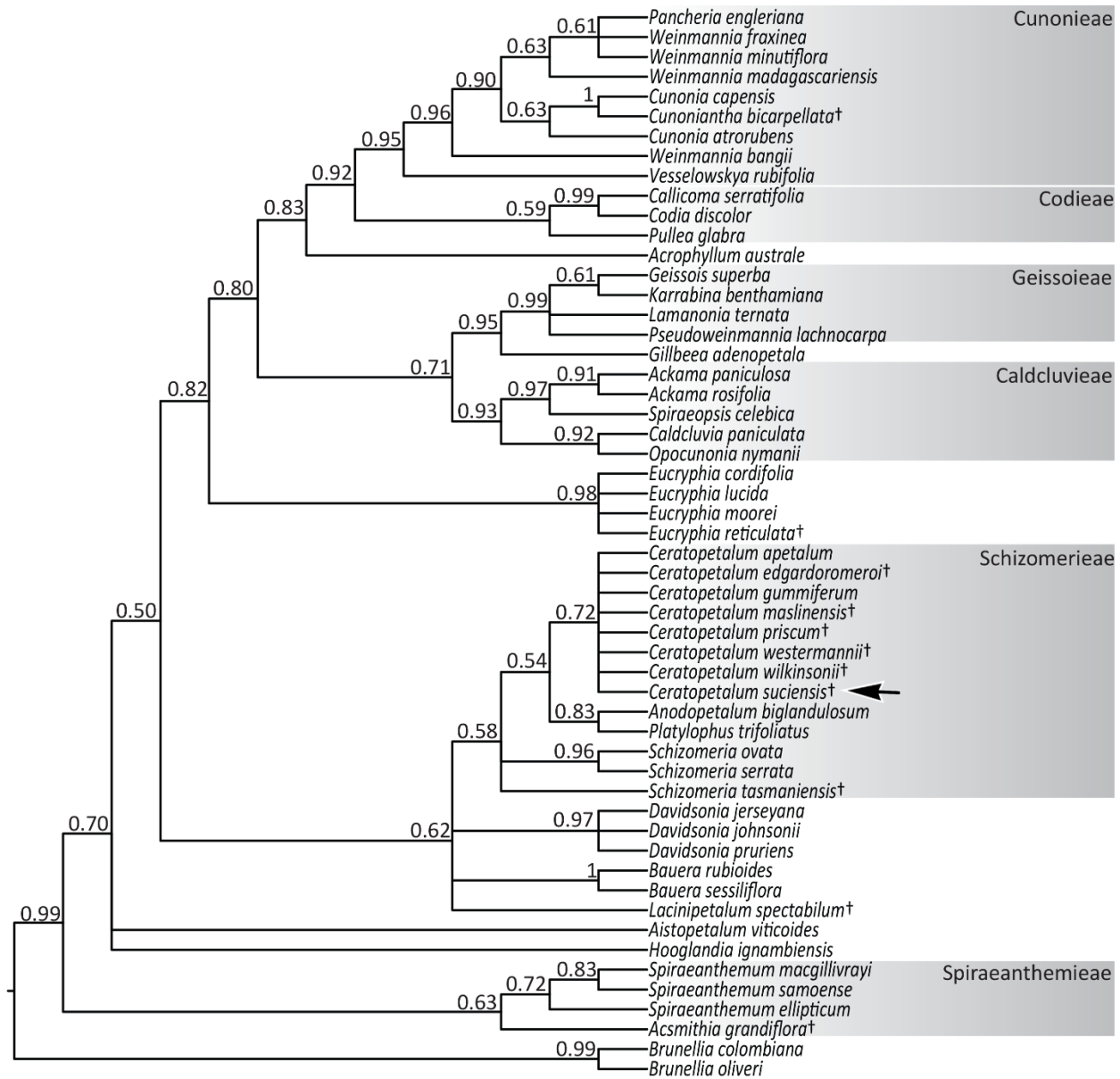
Figure 4. Majority rules consensus tree from Bayesian phylogenetic analysis including ten additional fossils. Fossils are marked by the daggers (†). Numbers above the branches are posterior probability values. Tribes are indicated by the gray shading.

suciensis, as they are mostly drupaceous (see Larson-Johnson 2016). Therefore, stem Fagales is excluded from taxonomic consideration. Our Bayesian phylogenetic analyses that focused on Cunoniaceae also support the placement of *C. suciensis* fruits within the genus *Ceratopetalum*.

The morphology of *C. suciensis* is clearly diagnostic of the genus *Ceratopetalum.* As shown in our CT scans and in previous studies, extant *Ceratopetalum* fruits are characterized by the presence of four to six persistent calyx lobes, a prominent nectary disk, persistent stamens, a semi-inferior ovary, and two persistent styles (Hoogland 1960; Dickison 1984; Barnes and Hill 1999; Fortune Hopkins and Hoogland 2002; Rozefelds and Barnes 2002). Persistent petals on the fruits are absent in the genus with the exception of *C. gummiferum*. The calyx lobes are extensively expanded giving the fruit a "helicopter"-like morphology and have three to many primary veins. In addition, located between each calyx lobe there are inter-wing veins that connect lateral veins of adjacent wings (Barnes and Hill 1999; Gandolfo and Hermsen 2017). The androecium is diplostemonous with two alternating whorls of eight to ten (less often twelve) stamens. The two styles are closely appressed to one another. These characters are used to identify *Ceratopetalum* in the fossil record (Holmes and Holmes 1992; Barnes and Hill 1999; Gandolfo and Hermsen 2017) and, as documented in the description, *C. suciensis* clearly has all of these characters.

Ceratopetalum suciensis possesses a combination of characters that indicate it is a new species (Tables 1 and 2). Each extant and fossil species typically have their own unique pattern of wing venation. Most species have three primary veins that enter each calyx wing (Dickison 1975; Barnes and Hill 1999; Matthews et al. 2001; Gandolfo and Hermsen 2017), but a few species have more than three including extant *C. succirubrum* C. T. White and *C. virchowii*, F. Muell. from Australia as well as extinct *C. priscum* Holmes and Holmes (Holmes and Holmes

1992) and *C. wilkinsonii* (Ett.) Holmes and Holmes (Holmes and Holmes 1992) from the

Miocene and Eocene-Oligocene of Australia, respectively. This is similar to *C. suciensis*, and,

therefore, it is most comparable to the above taxa. Fruits of *C. succirubrum* and *C. virchowii*

have more than five primary veins per calyx wing whereas fruits of *C. suciensis* consistently

have five primary veins per wing. In addition, the secondary veins within the calyx wings of *C.*

succirubrum and *C. virchowii* are restricted to the distal half while those of *C. suciensis* extend

throughout the entire length of the wing (Table 1). The extinct *C. priscum* and *C. wilkinsonii* also

differ from *C. suciensis* in venation by only having four primary veins per wing. In addition,

these two fossil Australian species have fruits that lack persistent stamens while *C. suciensis* has

fruits with persistent stamens (Table 2). It is worth noting that *C. suciensis* is based on the most

completely preserved fruits of *Ceratopetalum*, to date, while other described fossils tend to lack

preservation of informative structures such as stamen and styles (see Table 2). Furthermore,

some data on informative characters are lacking for a few extant species as well (see Table 1).

Such missing data makes a more thorough comparative analysis difficult, but it is clear that *C.*

suciensis differs from other *Ceratopetalum* species that have more complete morphological data

recorded. Thus, it is more conservative to assign the Cretaceous fruits to a new species,

Ceratopetalum suciensis sp. nov. Tang & Atkinson, rather than assigning them to a previously

described one.

Origin and evolution of Cunoniaceae

There is much uncertainty surrounding the age and early evolution of Cunoniaceae.

Divergence time estimates of stem ages for the family range from 90.9 to 66.55 Ma (Magallón et

al. 2015; Ramírez-Barahona et al. 2020). Moreover, reported crown ages of Cunoniaceae range

Table 1. Modified data table from Gandolfo and Hermsen 2017 for extant species of *Ceratopetalum*. gum, *C. gummiferum*; ape, *C. apetalum*; cor, *C. corymbosum*; hyl, *C. hylandii*; suc, *C. succirubrum*; vir, *C. virchowii*; tet, *C. tetrapterum*; iug, *C. iugumensis*; mac, *C. macrophyllum*; suci, *C. suciensis*.

Wing width (mm)	Primary veins	Petals	Disk height	Ovary diameter (mm)	Style branch length (mm)	Stamens on fruit	Stamen filament length (mm)
2.7-6.7	3	Present	~0.7	**3.4-4.8**	~1.5	**Present**	2.6-3.0
2.1-4.3	3	Absent	**0.4-0.5**	**3-4.4**	~1.5	**Present**	~2
?	3	Absent	**~0.4**	?	~1.5	**?**	**1.8-2.3**
2.2-3	3	Absent	**0.3-0.4**	**3.6-4**	0.6-1.0	Present	1.9
2.4-4.1	Many (>5)	Absent	**~0.4**	**3.6-4.2**	~1.5	**Present**	**0.6-1.4**
3.4-4.9	Many (>5)	Absent	**~0.6**	6.1-7.3	~1.5	**Present**	**1.5-2.3**
3.8-5.1	3	Absent	**~0.4**	6-8	~1.6	**Present**	**1.5**
4.8-5	3	Absent	**~0.4**	?	~1.5	**Present**	**~1.5**
3.2-4.5	3	Absent	0.04-0.08	5.4-5.9	1.1-2.1	**Present**	**1.5-3.0**
~3-4	**5**	**Absent**	**0.38-0.60**	**3.62-4**	**2.47**	**Present**	**1.21-1.89**

	No. of wings	Wing shape	Wing apex	Wing base	Wing length (mm)
gum	**4-6**	Narrowly to broadly obovate	**Acute**	Not constricted	**9.8-16.1**
ape	**4-6**	Obovate to ovate	**Acute**	Slightly constricted	6.3-8.9
cor	**4-6**	Obovate to ovate	**Acute**	Slightly constricted	At least 7
hyl	**4**	Narrowly obovate to lanceolate	**Acute** to obtuse	Slightly constricted	**6.6-11.2**
suc	**4-5**	**Elliptical** to obovate	**Acute**	Slightly constricted	**8.3-12.6**
vir	**4-6**	Obovate to lanceolate	**Acute**	Slightly constricted	11.5-13.5
tet	**4**	Ovate to obovate	**Acute**	Slightly constricted	**8.8-17**
iug	**4**	Narrowly to broadly obovate	**Acute**	Not constricted	4.8-5
mac	**4-5**	Obovate to lanceolate	**Acute**	Constricted	**10-13**
suci	**4-5**	**Elliptic**	**Acute**	**Attenuate (gradual constriction)**	**11**

Table 2. Modified table from Gandolfo and Hermsen 2017 for fossil species of *Ceratopetalum*. pri, *C. priscum*; wes, *C. westermannii*; mas, *C. maslinensis*; wil, *C. wilkinsonii*; edg, *C. edgardoromeroi*; suci, *C. suciensis*.

Age	Stamens on fruit	Ovary diameter (mm)	Nectary disk	Petals	Secondary veins	Primary veins	Wing width (mm)	Wing length (mm)
Middle Miocene	Absent	**3-5**	**Present**	Present	**Diverge throughout wing**	4	**3-4**	7-10
Early - Late Miocene	**Present**	1-1.2	Absent?	**Absent**	**Diverge throughout wing**	3	1.8-2.2	6-9
Middle Eocene	Absent	~2.1	Absent?	**Absent**	Diverge at distal half	3	~1.5-2	5-5.5
Late Eocene – Early Oligocene	Absent	6.5	**Present**	Present	**Diverge throughout wing**	4	4-5.5	~10
Ypresian (Early Eocene)	Absent	**4-5**	**Present**	**Absent**	Diverge at distal half	3	2-4	10
Campanian (Late Cretaceous)	**Present**	**3.62-4**	**Present**	**Absent**	**Diverge throughout wing**	**5**	**3-4**	**11**

	No. of wings	Wing shape	Wing apex	Wing base
pri	**5**	Narrow oblong	Obtuse	Not constricted
wes	**5**	Narrow obovate	Rounded	Not constricted
mas	**5-6**	Narrow oblong	**Acute** to obtuse	Not constricted
wil	**5**	Ovate to **elliptical**	Obtuse	Not constricted
edg	**5**	Narrow obovate	Rounded	**Constricted gradually**
suci	**4-5**	**Elliptic**	**Acute**	**Attenuate (gradual constriction)**

from 83.32 to 63.49 Ma (Heibl and Renner 2012; Ramírez-Barahona et al. 2020). Much of this uncertainty is rooted in a lack of Cretaceous fossils that can be unequivocally assigned to the crown group of the family.

Cunoniaceae have an extensive fossil record that extends back to the Late Cretaceous of Antarctica and Patagonia (Cranwell 1959; Askin 1992; Baldoni and Askin 1993; Poole et al. 2000; Poole et al. 2003; Carpenter and Rozefelds 2020). Prior to this study, the only unequivocal Cretaceous fossils for the family were pollen and wood from Antarctica and Patagonia; however, due to the limited taxonomic resolution of these particular structures, it is unclear whether those fossils are stem or crown members of the family. There have been a few equivocal records of cunoniaceous flowers from Late Cretaceous deposits including *Tropidogyne* Chambers, Poinar &

R.T. Buckley from the Cenomanian of Myanmar (Chambers et al. 2010; Poinar and Chambers

2017) and *Platydiscus* Schönenberger & Friis from the Santonian-Campanian of Europe

(Schönenberger et al. 2001). However, these fossils are not often accepted as being

cunoniaceaous (see Gandolfo and Hermsen 2017; Jud et al. 2018; Carpenter and Rozefelds 2020)

because their floral morphology is not entirely consistent with the crown group of the family;

and, therefore, need to be analyzed in a phylogenetic framework. Our phyloscan analysis

recovered multiple most parsimonious positions for *Tropidogyne pentaptera* Poinar & Chambers

among several eudicot families, none of which are Cunoniaceae. In addition, crown Cunoniaceae

was not recovered as a most parsimonious position for *Platydiscus peltatus* Schönenberger &

Friis. Overall, the phyloscan analyses suggests that *Tropidogyne* and *Platydiscus* are not

assignable to crown (or stem) Cunoniaceae or even Oxalidales.

Recent studies have described extinct genera assignable to crown Cunoniaceae based on

fossil flowers from the lowermost Paleocene (Danian) of Patagonia (Jud et al. 2018; Jud and

Gandolfo 2020). These reports clearly indicate that the diversification of the family was well

underway by the Cretaceous-Paleogene boundary. The age and phylogenetic position of

Ceratopetalum suciensis, however, is the first unequivocal evidence of crown Cunoniaceae in the

Cretaceous, affirming that the initial diversification of the family was well underway by the

Campanian.

Paleobiogeographic implications

Paleo-Antarctic Rainforest Lineages (PARLs) and their fossil record play an important

role in understanding the assembly and biogeographic history of Southern Hemisphere

rainforests. These lineages were once part of a near continuous rainforest biome that extended

across much of Gondwana during the Mesozoic and Paleogene (discussed in Kooyman et al. 2014; Wilf et al. 2019). Today, rainforest communities in Australia, New Zealand, Fiji, New Guinea, and South America are remarkably similar to one another in floral composition and PARLs comprise much of the floral diversity. This biogeographic disjunction of similar floras is largely due to the separation of Gondwana. While some PARLs, such as Araucariaceae and Winteraceae, were nearly cosmopolitan during the Mesozoic (Kunzmann 2007; Kooyman et al. 2014; Brea et al. 2021), most PARLs are traditionally thought to have been restricted to the Southern Hemisphere; this includes *Ceratopetalum* and other Cunoniaceae, which are important elements of modern southern rainforests.

Prior to this study, the entire reported biogeographic history of Cunoniaceae was restricted to the Southern Hemisphere (discussed in Carpenter and Rozefelds 2020). Cunoniaceous fossil pollen and wood have been recovered from the Santonian-Maastrichtian of Patagonia and Antarctica (Cranwell 1959; Askin 1992; Baldoni and Askin 1993; Poole et al. 2000; Poole et al. 2003) and at the onset of the Cenozoic Cunoniaceae were diverse in South America and Australia (Holmes and Holmes 1992; Barnes and Hill 1999; Barnes et al. 2001; Gandolfo and Hermsen 2017; Jud et al. 2018; Jud and Gandolfo 2020). These, along with slightly younger records, reflect that the family was part of the expansive Gondwanan rainforests during the Late Cretaceous and Paleogene (Kooyman et al. 2014; Barreda et al. 2021). This biogeographic pattern is particularly seen in *Ceratopetalum*. Previously, fossil *Ceratopetalum* was only known from the Cenozoic of Patagonia and much of Australia (Holmes and Holmes 1992; Barnes and Hill 1999; Gandolfo and Hermsen 2017) and today is restricted to eastern Australia and Papua New Guinea. However, our report of *Ceratopetalum* fruits from the Campanian of western North America dramatically expands the family's paleogeographic range

and provides a Northern Hemisphere occurrence for what was once considered a strictly Southern Hemisphere lineage.

This dramatic geographic range expansion is consistent with the hypothesis of a North American-South American-Antarctic (NA-SA-A) biotic exchange that occurred during the Late Cretaceous and the Paleogene (Case et al. 2000; Case et al. 2005; Goin et al. 2006). This hypothesis is largely supported by reports of primarily Northern Hemisphere vertebrates, such as hadrosaurs and nodosaurids, from Coniacian-Maastrichtian deposits in Antarctica. Based on stratigraphic and biogeographic occurrences it has been suggested that these vertebrates expanded their ranges into South America from North America and later into Antarctica (Case et al. 2000; Lamanna et al. 2019). Some fossil marsupials show a similar pattern as well (Case et al. 2005; Goin et al. 2006). Concerning this biotic exchange hypothesis, fossil plants have been discussed to a limited degree (Wilf et al. 2013) with some lineages showing a North America to South America-Antarctica migration during the Cretaceous and Paleogene, including *Regnillidium* (Batten et al. 2011; Cúneo et al. 2013) and some nymphaealeans (Gandolfo and Cuneo 2005; Friis et al. 2017). Poole et al. (2000) reported *Sassifrassoxylon* from Late Cretaceous deposits in Antarctica and cautiously discussed that *Sassafras*, which today is restricted to the Northern Hemisphere, may have had a Gondwanan origin.

Considering that cunoniaceous wood and pollen from Antarctica are nearly contemporaneous with *C. suciensis*, the Cretaceous distribution of Cunoniaceae fits well within the NA-SA-A scenario. However, it is also reasonable to suggest that *Ceratopetalum* and Cunoniaceae as a whole were cosmopolitan in the past, as seen in Araucariaceae and Winteraceae (Kunzmann 2007; Brea et al. 2021). However, it is striking that there are no other reliable fossil records of Cunoniaceae elsewhere in the Northern Hemisphere. It is probably

premature to infer whether *Ceratopetalum* and Cunoniaceae originated in the Northern Hemisphere or the Southern Hemisphere. As more fossils are recovered from undersampled regions across the world, more light will be shed on these biogeographic patterns. Nonetheless, given the previously recorded modern and Cenozoic distribution of *Ceratopetalum*, the recovery of *C. suciensis* from the Cretaceous of the west coast of North America suggests a more complicated biogeographic history for important Paleo-Antarctic Rainforest Lineages.

Summary

Based on three-dimensionally preserved fruits, we report a new species of *Ceratopetalum*, *C. suciensis*. These fossils are the only unequivocal evidence for Cunoniaceae from the Cretaceous so far. The age of *C. suciensis* clearly indicates that the initial diversification of the family was well underway by the Campanian. Furthermore, its occurrence in the Northern Hemisphere dramatically expands the paleogeographic range of the genus and Cunoniaceae as a whole. Although, today, the genus and other Cunoniaceae have a typical PARL distribution, the occurrence of these fossils paint a more complicated biogeographic history that extends well beyond Gondwana for Cunoniaceae and we suspect other flowering PARLs as more fossil data is collected from undersampled regions.

References

Askin RA 1992 Late Cretaceous-Early Tertiary Antarctic Outcrop Evidence for Past Vegetation and Climates. Antarct Palaeoenvironment Perspect Glob Change 56:61–73.

Atkinson BA 2016 Early diverging asterids of the Late Cretaceous: *Suciacarpa starrii* gen. et sp. nov. and the initial radiation of Cornales. Botany 94:759–771.

Baldoni AM, RA Askin 1993 Palynology of the Lower Lefipan Formation (Upper Cretaceous) of Barranca De Los Perros, Chubut Province, Argentina Part II. Angiosperm Pollen and Discussion. Palynology 17:241–264.

Barnes R, R Hill 1999 Ceratopetalum Fruits from Australian Cainozoic Sediments and their Significance for Petal Evolution in the Genus. Aust Syst Bot 12:635–645.

Barnes R, R Hill, J Bradford 2001 The history of Cunoniaceae in Australia from macrofossil evidence. Aust J Bot 49:301–320.

Barreda VD, L Palazzesi, RR Pujana, C Panti, MJ Tapia, DA Fernández, S Noetinger 2021 The Gondwanan heritage of the Eocene–Miocene Patagonian floras. J South Am Earth Sci 107:103022.

Batten DJ, ME Collinson, APR Brain 2011 Megaspores and Microspores of the Extant and Paleogene Marsileaceous Fern *Regnellidium* and Cretaceous *Molaspora* : Evolutionary and Phytogeographic Implications. Int J Plant Sci 172:1087–1100.

Baur G 1957 Nature and distribution of rain-forests in New South Wales. Aust J Bot 5:190–233.

Boyer DM, GF Gunnell, S Kaufman, TM McGeary 2016 Morphosource: Archiving and sharing 3-D digital specimen data. Paleontol Soc Pap 22:157–181.

Bradford J, R Barnes 2001 Phylogenetics and Classification of Cunoniaceae (Oxalidales) Using Chloroplast DNA Sequences and Morphology. Syst Bot 26:354–385.

Bradford J, H Fortune Hopkins, R Barnes 2004 Cunoniaceae. In: Flowering Plants Dicotyledons. Vol. 6. The Families and Genera of Vascular Plants. Springer. p. 91–111.

Brea M, A Iglesias, P Wilf, E Moya, MA Gandolfo 2021 First South American Record of *Winteroxylon*, Eocene of Laguna del Hunco (Chubut, Patagonia, Argentina): New Link to Australasia and Malesia. Int J Plant Sci 182:000–000.

Burges A, RD Johnston 1953 The Structure of a New South Wales Subtropical Rain Forest. J Ecol 41:72–83.

Carpenter RJ, AC Rozefelds 2020 Gondwanan or global? A commentary on: 'Fossil evidence from South America for the diversification of Cunoniaceae by the earliest Palaeocene.' Ann Bot:i–iii.

Case JA, FJ Goin, MO Woodburne 2005 "South American" Marsupials from the Late Cretaceous of North America and the Origin of Marsupial Cohorts. J Mamm Evol 12:461–494.

Case JA, JE Martin, DS Chaney, M Reguero, SA Marenssi, SM Santillana, MO Woodburne 2000 The first duck-billed dinosaur (Family Hadrosauridae) from Antarctica. J Vertebr Paleontol 20:612–614.

Chambers KL, G Poinar, R Buckley 2010 *Tropidogyne*, a New Genus of Early Cretaceous Eudicots (Angiospermae) from Burmese Amber. Novon J Bot Nomencl 20:23–29.

Cranwell LM 1959 Fossil Pollen from Seymour Island, Antarctica. Nature 184:1782–1785.

Cúneo RN, EJ Hermsen, MA Gandolfo 2013 *Regnellidium* (Salviniales, Marsileaceae) Macrofossils and Associated Spores from the Late Cretaceous of South America. Int J Plant Sci 174:340–349.

Dickison W 1984 Fruits and seeds of the Cunoniaceae. J Arnold Arbor 65:149–190.

Dickison WC 1975 Studies on the Floral Anatomy of the Cunoniaceae. Am J Bot 62:433–447.

Fortune Hopkins H, R Hoogland 2002 Cunoniaceae. In: Flora Malesiana. Vol. 16. 1. p. 53–165.

Friis EM, A Iglesias, MA Reguero, T Mörs 2017 *Notonuphar antarctica*, an extinct water lily (Nymphaeales) from the Eocene of Antarctica. Plant Syst Evol 303:969–980.

Gandolfo MA, RN Cuneo 2005 Fossil Nelumbonaceae from the La Colonia Formation (Campanian–Maastrichtian, Upper Cretaceous), Chubut, Patagonia, Argentina. Rev Palaeobot Palynol 133:169–178.

Gandolfo MA, EJ Hermsen 2017 *Ceratopetalum* (Cunoniaceae) fruits of Australasian affinity from the early Eocene Laguna del Hunco flora, Patagonia, Argentina. Ann Bot 119:507–516.

Goin FJ, R Pascual, MF Tejedor, JN Gelfo, MO Woodburne, JA Case, MA Reguero, M Bond, GM Lopez, AL Cione, et al. 2006 The earliest Tertiary Therian mammal from South America. J Vertebr Paleontol 26:505–510.

Heibl C, SS Renner 2012 Distribution Models and a Dated Phylogeny for Chilean *Oxalis* Species Reveal Occupation of New Habitats by Different Lineages, not Rapid Adaptive Radiation. Syst Biol 61:823–834.

Holmes W, F Holmes 1992 Fossil flowers of *Ceratopetalum* Sm. (family Cunoniaceae) from the Tertiary of Eastern Australia. Proc Linn Soc New South Wales 113:265–270.

Hoogland R 1960 Studies in the Cunoniaceae. I. The genera *Ceratopetalum, Gilbeea, Aistopetalum*, and *Calycomis*. Aust J Bot 8:318–341.

Joy KW, AJ Willis, WS Lacey 1956 A Rapid Cellulose Peel Technique in Palaeobotany. Ann Bot 20:635–637.

Jud NA, MA Gandolfo 2020 Fossil evidence from South America for the diversification of Cunoniaceae by the earliest Palaeocene. Ann Bot:1–11.

Jud NA, MA Gandolfo, A Iglesias, P Wilf 2018 Fossil flowers from the early Palaeocene of Patagonia, Argentina, with affinity to Schizomerieae (Cunoniaceae). Ann Bot 121:431–442.

Katoh K, DM Standley 2013 MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. Mol Biol Evol 30:772–780.

Kooyman RM, P Wilf, VD Barreda, RJ Carpenter, GJ Jordan, JMK Sniderman, A Allen, TJ Brodribb, D Crayn, TS Feild, et al. 2014 Paleo-Antarctic rainforest into the modern Old World tropics: The rich past and threatened future of the "southern wet forest survivors." Am J Bot 101:2121–2135.

Kubitzki K, JG Rohwer, V Bittrich eds. 1993 Flowering Plants · Eudicots. The Families and Genera of Vascular Plants. Springer.

Kunzmann L 2007 Araucariaceae (Pinopsida): Aspects in palaeobiogeography and palaeobiodiversity in the Mesozoic. Zool Anz 246:257–277.

Lamanna MC, JA Case, EM Roberts, VM Arbour, RC Ely, SW Salisbury, JA Clarke, DE Malinzak, AR West, PM O'Connor 2019 Late Cretaceous non-avian dinosaurs from the James Ross Basin, Antarctica: description of new material, updated synthesis, biostratigraphy, and paleobiogeography. Adv Polar Sci 30:228–250.

Lanfear R, PB Frandsen, AM Wright, T Senfeld, B Calcott 2016 PartitionFinder 2: New Methods for Selecting Partitioned Models of Evolution for Molecular and Morphological Phylogenetic Analyses. Mol Biol Evol 34:772–773.

Larson-Johnson K 2016 Phylogenetic investigation of the complex evolutionary history of dispersal mode and diversification rates across living and fossil Fagales. New Phytol 209:418–435.

Larsson A 2014 AliView: a fast and lightweight alignment viewer and editor for large datasets. Bioinformatics 30:3276–3278.

Lewis PO 2001 A Likelihood Approach to Estimating Phylogeny from Discrete Morphological Character Data. Syst Biol 50:913–925.

Magallón S, S Gómez-Acevedo, LL Sánchez-Reyes, T Hernández-Hernández 2015 A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. New Phytol 207:437–453.

Matthews M, P Endress, J Schonenberger, E Friis 2001 A Comparison of Floral Structures of Anisophylleaceae and Cunonicaeae and the Problem of their Systematic Position. Ann Bot 88:439–455.

Miller MA, W Pfeiffer, T Schwartz 2011 The CIPRES science gateway: a community resource for phylogenetic analyses. In: Proceedings of the 2011 TeraGrid Conference: extreme digital discovery. Salt Lake City, Utah: ACM Press. p. 1–8.

O'Leary MA, S Kaufman 2011 MorphoBank: phylophenomics in the "cloud." Cladistics 27:529–537.

Peecook BR, CA Sidor 2015 The First Dinosaur from Washington State and a Review of Pacific Coast Dinosaurs from North America. Evans DC, editor. PLOS ONE 10:1–15.

Poinar GO, KL Chambers 2017 *Tropidogyne pentaptera,* sp. nov., a new mid-Cretaceous fossil angiosperm flower in Burmese amber. Palaeodiversity 10:135–140.

Poole I, DJ Cantrill, P Hayes, J Francis 2000 The fossil record of Cunoniaceae: new evidence from Late Cretaceous wood of Antarctica? Rev Palaeobot Palynol 111:127–144.

Poole I, AMW Mennega, DJ Cantrill 2003 Valdivian ecosystems in the Late Cretaceous and Early Tertiary of Antarctica: further evidence from myrtaceous and eucryphiaceous fossil wood. Rev Palaeobot Palynol 124:9–27.

Poole I, HG Richter, JE Francis 2000 Evidence for Gondwanan Origins for *Sassafras* (Lauraceae)? Late Cretaceous Fossil Wood of Antarctica. IAWA J 21:463–475.

Rambaut A, AJ Drummond, D Xie, G Baele, MA Suchard 2018 Posterior Summarization in Bayesian Phylogenetics Using Tracer 1.7. Susko E, editor. Syst Biol 67:901–904.

Ramírez-Barahona S, H Sauquet, S Magallón 2020 The delayed and geographically heterogeneous diversification of flowering plant families. Nat Ecol Evol 4:1232–1238.

Ronquist F, M Teslenko, P van der Mark, DL Ayres, A Darling, S Höhna, B Larget, L Liu, MA Suchard, JP Huelsenbeck 2012 MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice Across a Large Model Space. Syst Biol 61:539–542.

Roth B 2000 Upper Cretaceous (Campanian) land snails (Gastropoda: Stylommatophora) from Washington and California. J Molluscan Stud 66:373–381.

Rozefelds AC, RW Barnes 2002 The Systematic and Biogeographical Relationships of *Ceratopetalum* (Cunoniaceae) in Australia and New Guinea. Int J Plant Sci 163:651–673.

Schönenberger J, M von Balthazar, A López Martínez, B Albert, C Prieu, S Magallón, H Sauquet 2020 Phylogenetic analysis of fossil flowers using an angiosperm-wide data set: proof-of-concept and challenges ahead. Am J Bot 107:1–16.

Schonenberger J, E Friis, M Matthews, P Endress 2001 Cunoniaceae in the Cretaceous of Europe: Evidence from Fossil Flowers. Ann Bot 88:423–437.

Ward P, J Haggart, R Mitchell, J Kirschvink, T Tobin 2012 Integration of macrofossil biostratigraphy and magnetostratigraphy for the Pacific Coast Upper Cretaceous (Campanian-Maastrichtian) of North America and implications for correlation with the Western Interior and Tethys. GSA Bull 124:957–974.

Ward PD 1978 Revisions to the stratigraphy and biochronology of the Upper Cretaceous Nanaimo Group, British Columbia and Washington State. Can J Earth Sci 15:405–423.

Webb LJ 1978 A structural comparison of New Zealand and south-east Australian rain forests and their tropical affinities. Aust J Ecol 3:7–21.

Wilf P, NR Cúneo, IH Escapa, D Pol, MO Woodburne 2013 Splendid and Seldom Isolated: The Paleobiogeography of Patagonia. Annu Rev Earth Planet Sci 41:22.1-22.43.

Wilf P, KC Nixon, MA Gandolfo, NR Cúneo 2019 Eocene Fagaceae from Patagonia and Gondwanan legacy in Asian rainforests. Science 364:1–9.

Chapter 3: A structurally preserved fin-winged fruit from the Late Cretaceous of western North America

Introduction

The Late Cretaceous deposits of North America successfully capture the early diversification of angiosperms which is largely dominated by core eudicots. Core eudicots make up over 70% of angiosperm diversity and begin to appear in the fossil record ~100 Ma and rapidly diversifying throughout the Late Cretaceous (Doyle 1969; Magallon et al. 1999; Friis et al. 2006; Friis et al. 2011). Two large clades, the rosids and asterids, make up much of the diversity within the core eudicots (Magallon et al. 1999; Friis et al. 2011), which are well represented within Late Cretaceous floras sampled from the eastern coast and western interior of North America (Upchurch and Dilcher 1990; Basinger and Dilcher 1984; Magallon-Puebla et al. 1996; Magallón et al. 2001; Crepet 2008; Friis et al. 2011; Friis et al. 2016; Martínez et al. 2016; Manchester et al. 2018; Atkinson et al. 2019). However, this leaves the western coast of North America relatively undersampled which could hinder our understanding of early angiosperm diversity. Ongoing efforts to sample the region has already uncovered a diverse assemblage of both extinct and extant genera within the core eudicots (Mindell et al. 2014; Atkinson 2016; Atkinson et al. 2016; Atkinson et al. 2017; Atkinson et al. 2018; Scharfstein et al. 2020). More attention is given to extant genera of angiosperms, but extinct genera play an important role in helping us understand early angiosperm diversity. Continued efforts to sample these deposits are crucial as we recover fossil data that will help us tease apart early angiosperm diversity and the turnover of genera through time.

Here, I report a three-dimensionally preserved fin-winged fruit from Late Cretaceous deposits of Sucia Island, off the coast of Washington state, USA. The fin-winged fruit shares diagnostic characters with the extinct genus *Esgueiria* Friis, Pedersen & Crane and the placement of the fossil within the genus is clearly supported by the phyloscan method (Schönenberger et al. 2020). Additionally, the systematic placement of *Esgueiria* was tested and recovered within the core eudicot clade. However, a precise placement within the core eudicots was not recovered with the phyloscan method which suggests the genus likely is a member of an extinct angiosperm family. Based on morphological differences, the fin-winged fruit represents a new species *Esgueiria aligera* sp. nov. Tang & Atkinson and a new family Esgueiriaceae comb. nov. is erected for this extinct lineage. The recovery of *E. aligera* indicates *Esgueiria* may have had a widespread distribution (or circum-polar distribution) within the Northern Hemisphere during the Late Cretaceous and that fossil assemblages along the western coast of North America likely holds a great diversity of extinct genera and species waiting to be described.

Materials and Methods

One structurally preserved fruit was recovered within a calcium carbonate concretion from Fossil Bay on Sucia Island, Washington state, USA. Cretaceous exposures along Fossil Bay belong to the Cedar District Formation of the Nanaimo Group and, based on biostratigraphy and magnetostratigraphy, are Campanian in age (~82-80 Ma) (Ward et al. 2012). Fossil fauna recovered from Sucia Island includes ammonites, terrestrial gastropods, inoceramid bivalves, and a theropod femur (Ward 1978; Roth 2000; Ward et al. 2012; Peecook and Sidor 2015). Described fossil flora from the locality includes *Ceratopetalum suciensis* (see previous chapter) and cornalean fruits (Atkinson 2016).

The fossil counterparts were imaged using a Canon EOS 5DS camera with a macro lens attached (Canon Inc., Tokyo, Japan). Additional detailed images of the specimen were taken using a Nikon SMZ25 stereomicroscope with a Nikon DS-Fi3 camera attachment (Nikon Corporation, Tokyo, Japan). Both counterparts of the specimen were glued back together for X-ray micro-computed tomography (µCT). The specimen was µCT scanned at the University of Michigan CTEES facility using a Nikon XT H 225ST industrial µCT system. A Perkin Elmer 1620 X-ray detector panel and a tungsten reflection target were used with scan conditions set at 128 KV and 133 µA. The scans used 1.1 mm of copper filter with a 17.13 µm pixel size resolution. Scans were acquired using the program Inspect-X (Nikon Corporation, Tokyo, Japan) and segmented using the software Mimics 22.0 (Materialise, Leuven, Belgium) to reconstruct a three-dimensional image of the fruit. The software Avizo 9 Lite 3D (Thermo Fisher Scientific, Massachusetts, USA) was used to take measurements of the reconstruction. Data are archived on Morphosource (Boyer et al. 2016) under project title "Fin-winged fruit of *Esgueiria*."

The phyloscan method (Schönenberger et al. 2020) was used to test the systematic positions of *Esgueiria* and the fin-winged fruit. This method uses a floral character matrix and angiosperm molecular backbone to assess the most parsimonious position(s) of fossil flowers. Persistent floral characters preserved on the fin-winged fruit were scored in order to analyze the most parsimonious position of the fossil using the phyloscan method. The systematic placement of *Esgueiria* within the angiosperm phylogeny had not been previously tested in a phylogenetic framework so *E. adenocarpa* was analyzed first since it is the most complete specimen compared to other previously described *Esgueiria* species. Once the results were obtained, *E. adenocarpa* was grafted onto the backbone phylogeny at its most parsimonious position as sister to all other

core eudicots, excluding Gunnerales. Using the modified backbone phylogeny, we scored characters for the fin-winged fruit and *E. futabensis*.

Phyloscan scorings justifications

Twenty characters were scored out of 30 floral and pollen traits for the fin-winged fruit based on persistent floral parts preserved on the fossil. Petals are not present on the fruit which may be due to preservation or absence in the species so number of perianth whorls were scored as missing. Both anther and pollen characters were scored as missing due to lack of preservation of these structures. Additionally, internal structures were not preserved so ovule characters were scored as missing.

Fossil flowers of *E. adenocarpa* and *E. miraensis* were scored according to their published descriptions. In total, 26 characters were scored for *E. adenocarpa* and 24 characters for *E. miraensis*. Anther dehiscence and the presence of a connective extension of anthers were not described or imaged for *E. adenocarpa* so those characters were scored as missing. Likewise, anther characters for *E. miraensis* were scored as missing because anthers were not described and cannot be seen clearly in published images. Ovules in *E. adenocarpa* were preserved but the placentation was scored as missing. The specimens were described to have apical placentation but the only character states available within the character matrix were axile, parietal, free-central, or laminar placentation. Ovule characters were scored as missing for *E. miraensis* as they were not preserved in the specimens. Aperture shape for *E. adenocarpa* was scored as missing due to uncertainty in the interpretation of the pollen. Pollen characters scored for *E. miraensis* are based on the description of the most abundant pollen type observed on the styles.

Twenty-two characters for *E. futabensis* were scored according to the published description. Anther, pollen, and ovule characters were not described or observed in the specimen so related characters in the matrix were scored as missing. Styles appear to be free but were described as proximally fused so they were scored as >5% fused.

Results

Systematics

Family – Esgueiriaceae comb. nov. Tang & Atkinson

Familial diagnosis. As for genus.

Genus – *Esgueiria* Friis, Pedersen and Crane, 1992

Emended generic diagnosis. Flowers small, epigynous, and bisexual with five free calyx lobes and five free sepals, triangular in shape. Two whorls of stamens with tricolporate or tricolpate pollen. Gynoecium with unilocular ovary and three, free or partially fused styles. Simple stiff hairs and peltate glandular trichomes on flowers. Fruit unilocular with up to five pairs of fin-wings on fruit body and persistent calyx lobes, stamens, and styles.

Species – *Esgueiria aligera* Tang & Atkinson, sp. nov.

Specific diagnosis. Fruit body including fin wings up to 8 mm wide and 20 mm long. Five free calyx lobes up to 5 mm long, triangular in shape with acute-obtuse apex and anastomosing veins. Five pairs of fin wings fused with calyx margins extending longitudinally on fruit body. Vascular bundles entering base of the locule and surrounding ovary. Receptacle mounds opposite of calyxes and surrounding androecium. At least four stamen bases up to 1.5 mm long. Three styles fused for half their proximal length.

Etymology. The specific epithet, *aligera,* refers to the wings present on the fruit.

Holotype. C2056A, C2056B

Type locality. Fossil Bay, Sucia Island, Washington State, USA (48.749330°N, 122.900798°W).

Stratigraphy. Cedar District Formation.

Age. Early to Middle Campanian (ca. ~82-80 Ma).

Description

      The three-dimensionally preserved fruit is epigynous and radially symmetrical with a unilocular ovary (Figs. 5A-D). Persistent calyx lobes, stamens, and styles are present on the fossil (Figs. 5D, 6A). The fruit is 20 mm long from the base of the pedicel to the tip of the calyx lobes and 8 mm wide, including the fin-wings. Without the fin-wings, the fruit measures 6 mm wide. Five free calyx lobes persist on the fruit which are triangular in shape with acute-obtuse apices (Fig. 5C, 5D). The calyx lobes measure up to 4 mm wide at the base and up to 6 mm long. The proximal margins of the calyx lobes expand and form pairs of wings that extend longitudinally along the entire fruit body (Figs. 5C, 5D, 6B). The fin-wings fan out distally at the center of the fruit body before meeting with the adjacent wing at the base of the fruit (Figs. 5C, 5D, 6C). Internal structures of the fruit were not preserved.

      Venation patterns can be observed on the fossil fruit as dark "coalified" tissue. These dark vascular bundles are present in the pedicel (Figs. 7A, 7B) and approach the base of the locule (Fig. 7C). Additional vasculature can be seen surrounding the unilocular ovary (Fig. 7C). Multiple veins can be seen, when submerged under ethanol, entering the calyx and immediately anastomose at the base (Fig. 7).
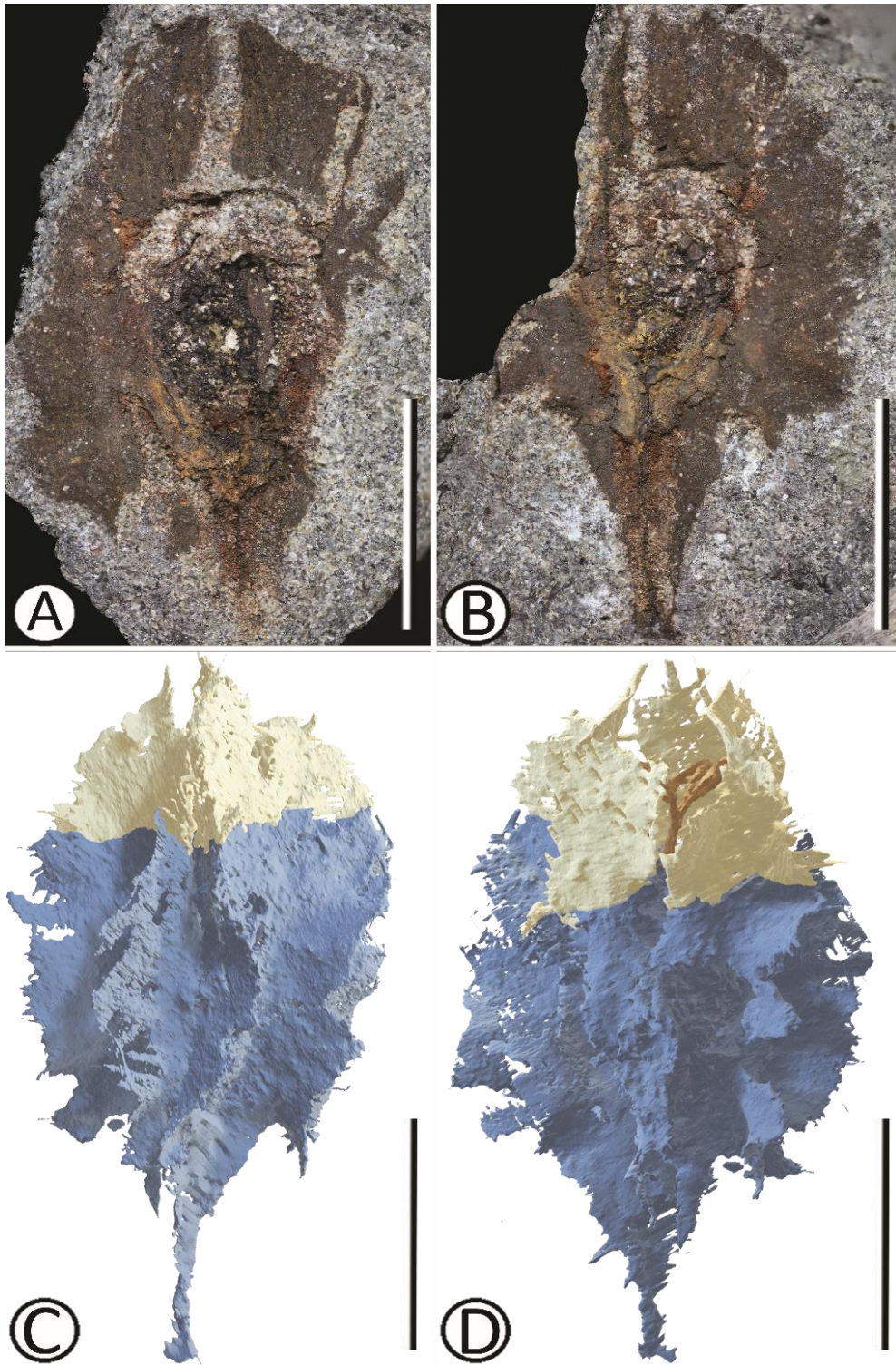
Figure 5. General morphology of *Esgueiria aligera* sp. nov. Tang & Atkinson. (A) Exposed rock shows fossil counterpart A with fin-wings and unilocular ovary. Scale bar = 8 mm. **(B)** Exposed rock shows fossil counterpart B with a pedicel, fin-wings, and unilocular ovary. Scale bar = 8 mm. **(C)** Three-dimensional reconstruction of the fruit showing fin-wing morphology. Scale bar = 7 mm. **(D)** Three-dimensional reconstruction of the fruit in a different angle showing the persistent styles and fin-wing morphology. Scale bar = 7 mm. Blue = fruit body, white = calyx lobes, orange = styles.
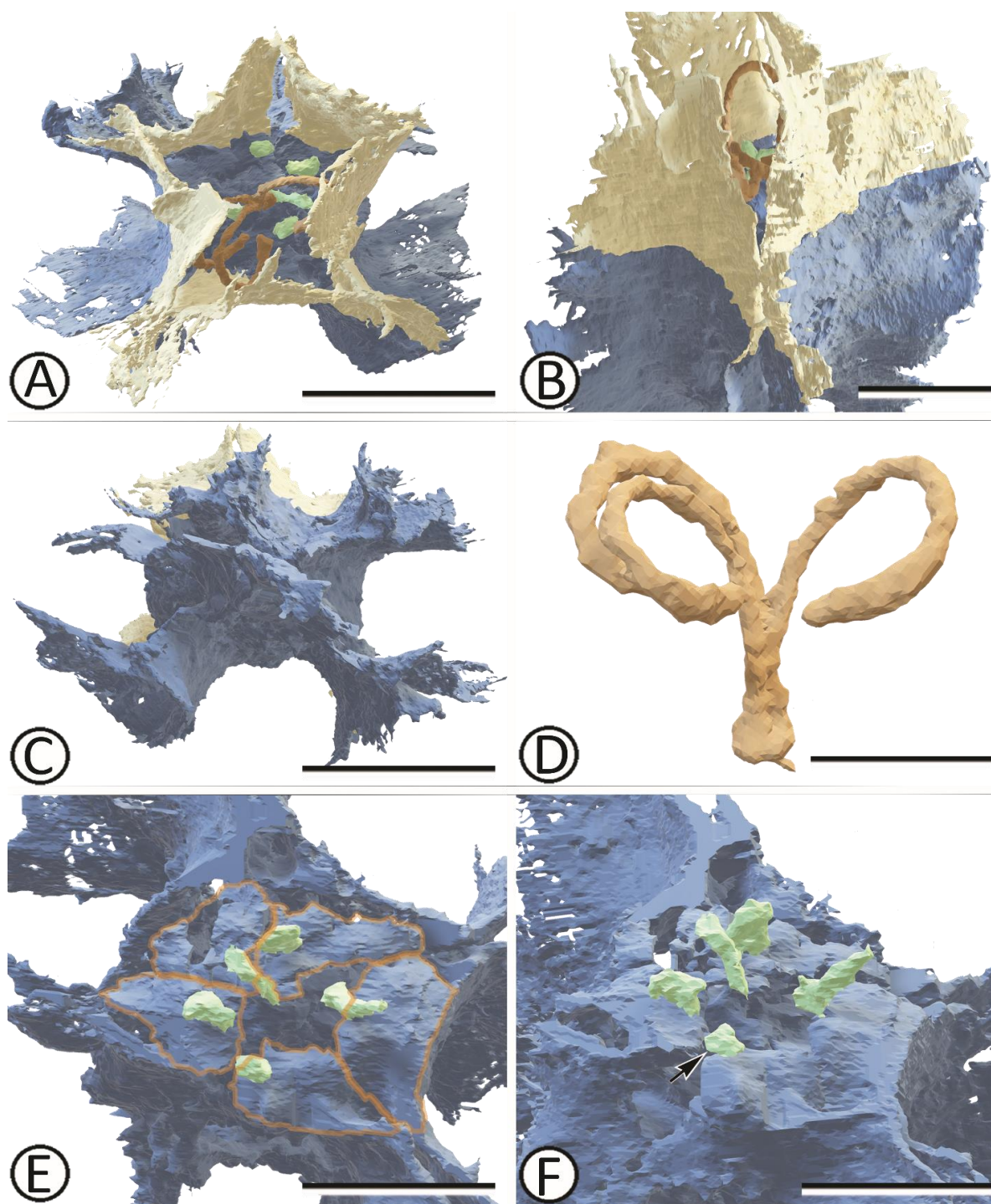
Figure 6. Detailed morphology on the three-dimensional reconstruction of *Esgueiria aligera*. (A) Top-down view of the fin-winged fruit with persistent styles and stamen bases apparent. Scale bar = 6 mm. **(B)** Magnified view of calyx margins that form part of the fin-wings. Scale bar = 3 mm. **(C)** View of base of the fruit where adjacent fin-wings meet. Scale bar = 6 mm. **(D)** Magnified view of the extracted styles of the fin-winged fruit. Scale bar = 1.5 mm. **(E)** Magnified top-down view of the fin-winged fruit with calyxes and styles removed for a better view of the receptacular mounds (traced in orange) and persistent stamen bases. Scale bar = 3 mm. **(F)** Magnified view of the androecium with calyxes and styles removed showing four stamen bases and a potential fifth stamen base (arrow). Scale bar = 3 mm. Blue = fruit body, white = calyx lobes, green = stamen bases, orange = styles.
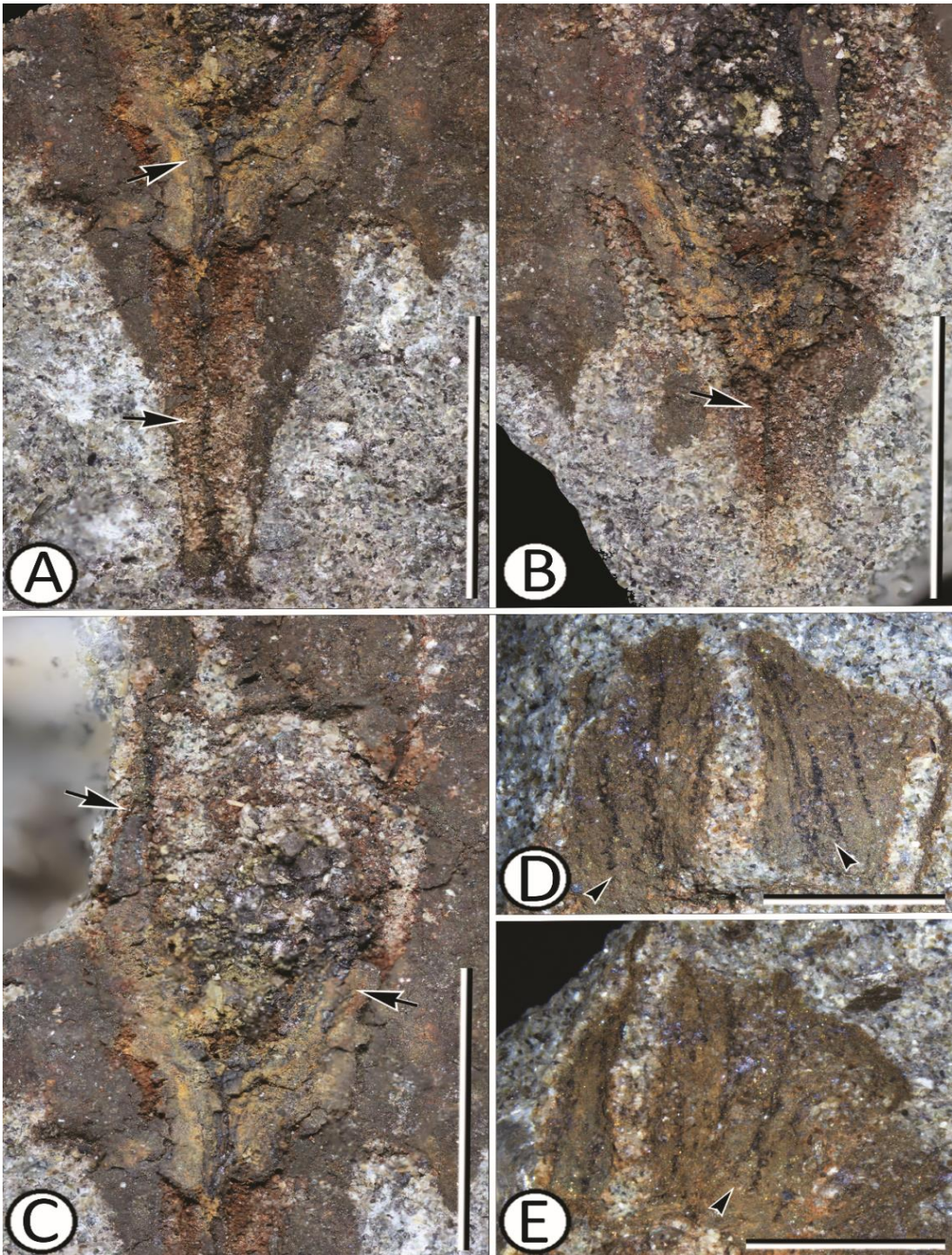
Figure 7. Detailed view of *Esgueiria aligera* fossil counterparts. (A) Magnified view of the fruit base in fossil counterpart B showing dark vascular bundles (arrows) in the pedicel and approaching base of locule. Scale bar = 5 mm. **(B)** Magnified view of fossil counterpart A showing vascular bundles (arrow) approaching base of the locule. Scale bar = 5 mm. **(C)** Unilocular ovary in fossil counterpart B showing vascular bundles surrounding the locule (arrows). Scale bar = 6 mm. **(D)** Calyx lobes of fossil counterpart A in magnified view showing anastomose veins (arrows). Scale bar = 5 mm. **(E)** Calyx lobes of fossil counterpart B in magnified view showing anastomose veins (arrow). Scale bar = 4 mm.

Raised semicircular mounds of tissue are present opposite of each calyx lobe and surround the androecium (Fig. 6E). Based on the position and raised structure, the mounds of tissue are possibly nectary lobes. The androecium appears to be diplostemonous, although only four stamen bases are observed as well as an unattached structure that may be a fifth stamen base (Figs. 6E, 6F). Two stamen bases appear to form a whorl that is opposite of the calyx lobes and the other two stamen bases form another whorl that alternate with the calyx lobes (Fig. 6E). Based on the diplostemonous pattern of the stamen bases, a total of ten stamens are inferred. Three of the persistent stamens have a typical narrow filament shape but the fourth stamen has a laminar shape (Fig. 6F).

The gynoecium is well preserved with an inferior, unilocular ovary (Figs. 5A, 5B). The ovary measures 5 mm in diameter and 8 mm long. Micro CT scans revealed three curved styles (Fig. 5D, 6A, 6B, 6D). The three style branches are curved downwards and fused for about half their length (Fig. 6D). Seeds or ovules were not observed because the internal structure of the ovary was not preserved.

Phyloscan results

In the initial phyloscan analysis, one most parsimonious position for *Esgueiria adenocarpa* was recovered on the branch leading to the core eudicot clade (Fig. 8). Two most parsimonious positions for *E. miraensis* were recovered on branches leading to the core eudicot clade and stem Fagales (Appendix C, Fig. 15). In the second phyloscan analysis with *E. adenocarpa* grafted as sister to the core eudicot clade, three most parsimonious positions for *E. futabensis* were recovered on branches leading to *E. adenocarpa*, the core eudicot clade, and

stem Fagales (Appendix C, Fig. 16). The same three most parsimonious positions were recovered

for *E. aligera* with an additional branch leading to *Hevea brasiliensis* (Euphorbiaceae) (Fig. 9).

Figure 8. Phyloscan results of *Esgueiria adenocarpa.* "Fan" shaped phyloscan tree shows most parsimonious positions indicated by the black branches on the tree. Most parsimonious positions +1 are indicated by the green branches while a gradient from yellow to gray show subsequent parsimonious positions.
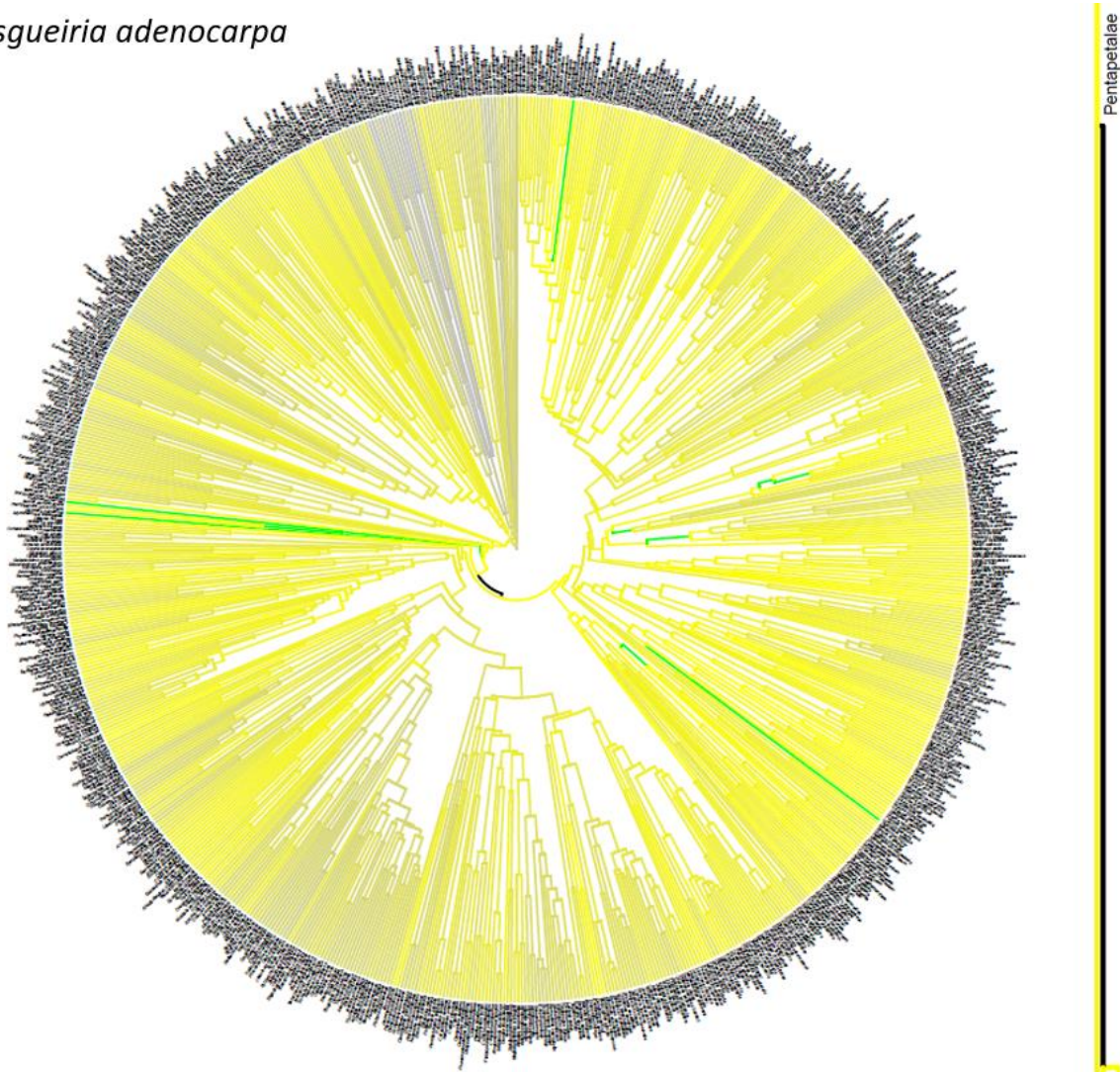
Figure 9. Phyloscan results of *Esgueiria aligera*. "Fan" shaped phyloscan tree shows most parsimonious positions indicated by the black branches on the tree. Most parsimonious positions +1 are indicated by the green branches while a gradient from yellow to gray show subsequent parsimonious positions.
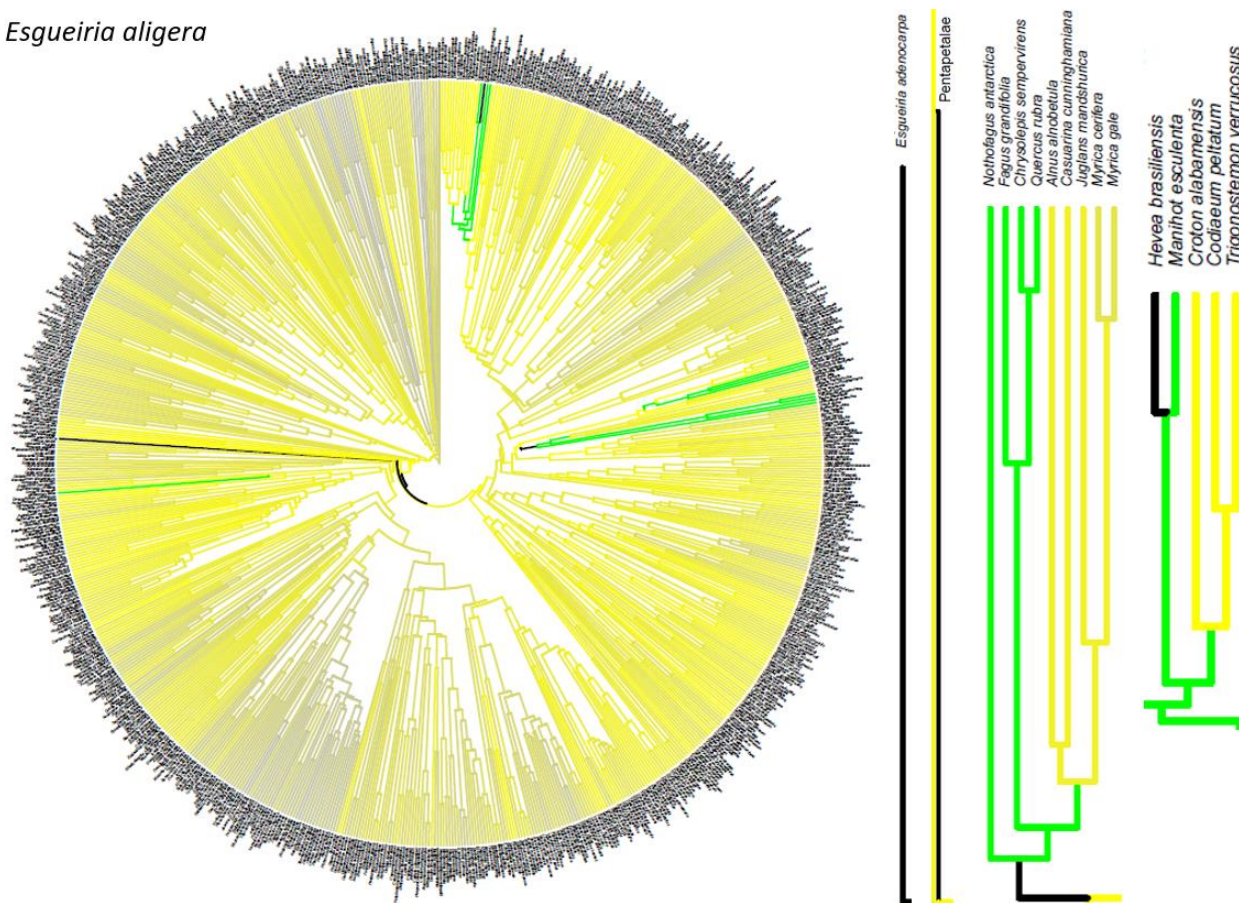
Discussion

New species of Esgueiria

Diagnostic characters of the fossil genus *Esgueiria* are clearly observed in the persistent floral structures present on the fin-winged fruit of *Esgueiria aligera*. The genus is described from fossil flowers recovered in Campanian-Maastrichtian deposits of Europe and Coniacian deposits of Japan (Friis et al. 1992; Takahashi et al. 1999). Two species, *E.* adenocarpa and *E.* miraensis, are described from Europe (Friis et al. 1992) and one species, *E.* futabensis, is described from Japan (Takahashi et al. 1999). The fossil flowers are characterized by the presence of a

pentamerous perianth, two whorls of stamens, an inferior unilocular ovary and three styles (Friis et al. 1992; Takahashi et al. 1999). Simple stiff hairs and peltate glandular trichomes are also present on the fossil flowers. Perianth whorls consist of a corolla and calyx, although the corolla tends to be poorly preserved or not preserved at all within the specimens. Five free calyx lobes are observed in specimens from deposits of both Europe and Japan and are triangular in shape (Friis et al. 1992). Two whorls of stamens are present within the previously described species although the total number of stamens present is difficult to interpret due to incomplete preservation. A total of eight stamens are observed in *E. adenocarpa* and form an obdiplostemonous pattern, although the interpretation is uncertain because the stamen arrangement is not consistent among specimens (Friis et al. 1992). Up to ten stamens are estimated in *E. futabensis* based on stamen remnants that were observed in a diplostemonous pattern with one whorl opposite of the calyx lobes and another whorl alternate with the calyx lobes (Takahashi et al. 1999). The three styles present in each species vary in the degree of fusion. Three free styles are observed in *E. adenocarpa* and *E. miraensis* while the styles of *E. futabensis* are partially fused at the base but free for much of their length. Additionally, receptacular mounds are observed in *E. futabensis* that surround the androecium and alternate with the stamen bases. The receptacular mounds are interpreted to be potential nectary lobes (Takahashi et al. 1999). The characters listed here, save for the trichomes, are all observed in the persistent floral characters of *E. aligera* which supports its placement within the genus.

Morphological differences in the receptacular mounds and styles of *E. aligera* indicate it is a new species. The degree of fusion in the styles vary among the previously described fossil flowers which range from completely free styles to partially fused at the base. The styles of *E. aligera* are fused for half of their length which differ from previously described species.

Receptacular mounds present on *E. aligera* differ in shape and number compared to the

receptacular mounds present on *E. futabensis*. Five receptacular mounds are observed on the fin-

winged fruit of *E. aligera* that are semicircular in shape, but up to ten receptacular mounds that

are ellipsoidal in shape are observed on *E. futabensis*. Although the difference in shape may be

due to the number of receptacular mounds present. Additional morphological differences, such as

presence/absence of trichomes or ovary size, are difficult to compare with previously described

fossil flowers of *Esgueiria* because *E. aligera* is in the fruiting stage. These morphological

differences may be due to the different life stages observed between the specimens. Due to the

difference in life stage and morphological difference in receptacular mounds and styles, it is

most conservative to assign the fin-winged fruit as a new species, *Esgueiria aligera* sp. nov.

Tang & Atkinson.

Additionally, phyloscan results support the placement of the fin-winged fruit within

Esgueiria. The phyloscan analysis recovered four most parsimonious positions for *E. aligera*

along branches leading to *E. adenocarpa*, crown core eudicots, stem Fagales, and *Hevea*

brasiliensis (Euphorbiaceae). However, fruits of both Fagales and *Hevea* differ in morphology of

the fin-winged fruit. Fruits of Fagales are typically nuts or samaras (Kubitzki et al. 1993; Larson-

Johnson 2016) and fruits of reported stem Fagales are mostly drupaceous (Larson-Johnson

2016). Fruits of Euphorbiaceae lack wings and are typically dehiscent capsules with three locules

(Webster 2014). The fruit morphology of both Fagales and Euphorbiaceae differ greatly from the

fin-winged fruit of *E. aligera* and, therefore, can be excluded from taxonomic consideration. The

recovery of the branches leading to *E. adenocarpa* and the core eudicot clade, however, do

support the placement of the fin-winged fruit within the genus *Esgueiria,* as the new species *E.*

aligera sp. nov. Tang & Atkinson.

The recovery and characterization of the new species *E. aligera* from Campanian deposits of Sucia Island contributes important insights on the fruit morphology and distribution of the genus. While several fragmentary fossils interpreted to be fruits associated with *E. adenocarpa* and *E. miraensis* were recovered from Cretaceous deposits of Europe, much of the species descriptions were based on fossil flowers (Friis et al. 1992). Likewise, the species description of *E. futabensis* is based on flowers as no associated fruits were described. The structurally preserved fruit of *E. aligera,* however, provides a more complete record of fruit morphology for the genus. Additionally, *Esgueiria* was previously only known from Late Cretaceous deposits of Europe and Japan (Friis et al. 1992; Takahashi et al. 1999). The report of *E. aligera* from Late Cretaceous deposits of western North America greatly expands the geographic range and suggests a circumpolar distribution of *Esgueiria* within the Northern Hemisphere.

Systematic position of Esgueiria

The genus *Esgueiria* was placed as a stem lineage of the family Combretaceae based on unique shared morphological characters such as the presence of glandular trichomes (Friis et al. 1992), but had yet to be tested within a phylogenetic framework. Combretaceae, within the order Myrtales and part of the rosids, is characterized by the presence of small bisexual flowers, distinct stiff hairs and glandular trichomes, a pentamerous perianth, two whorls of stamens, and an inferior unilocular ovary (Exell and Stace 1965; Friis et al. 1992; Stace 2007). *Esgueiria* differs morphologically in having three styles and receptacular mounds, so the genus was tentatively placed as a stem lineage (Friis et al. 1992). Using the recent phyloscan method (Schönenberger et al. 2020), a single most parsimonious position was recovered along the branch

leading to the core eudicot clade for *E. adenocarpa*. The core eudicots are known to have pentamerous perianths with distinct whorls and tricolporate, or tricolpate, pollen (Wodehouse 1936; Erdtman 1952; Doyle 1969; Takhtajan 1980; Furness et al. 2007; Endress 2010; Friis et al. 2011). The pentamerous perianth and triaperturate pollen observed in *E. adenocarpa* and *E. miraensis* clearly place the genus within the core eudicots. Results of the phyloscan method indicate *Esgueiria* is not assignable to a modern angiosperm family, but likely is a member of an extinct family.

It should be noted that the character matrix within the phyloscan uses floral and pollen traits that can be applied broadly amongst all described angiosperms (Sauquet et al. 2017; Schönenberger et al. 2020). In doing so, unique morphological characters such as the peltate glandular trichomes were not assessed and may have prevented the recovery of Combretaceae as a most parsimonious position for *Esgueiria*. However, all extant members within the order Myrtales only have one style present (Friis et al. 1992; Endress 2010). The branch leading to *Terminalia catappa* (Combretaceae) was recovered as a green branch accounting for one additional step in the phyloscan analysis. The placement of *Esgueiria* within Combretaceae would have suggested multiple independent evolutions of a single style and so was not recovered as a most parsimonious position. Members of the order Saxifragales, such as the families Peridiscaceae and Saxifragaceae, have three free styles present (Bayer 2007; Soltis 2007) but *Esgueiria* differs in the number of ovules as well as the fruit morphology (Friis et al. 1992).

Core eudicots include over 70% of angiosperm diversity and are largely grouped within the rosids and asterids (Magallon et al. 1999; Friis et al. 2006; Friis et al. 2011; APG 2016). The order Gunnerales is typically placed within the clade as sister to all other core eudicots based on molecular data, although the two groups differ in morphology (Soltis et al. 2003; Friis et al.

2006; Endress 2010; Friis et al. 2011; APG 2016). The general floral morphology of Gunnerales consist of dimerous whorls and an inconspicuous perianth that more closely resemble the floral morphology of eudicots outside of the core eudicots (Endress and Igersheim 1999; Wanntorp and Craene 2005; Ronse De Craene and Wanntorp 2006; González and Angélica Bello 2009; Endress 2010). The phyloscan results recovered the branch leading to all other core eudicots, excluding Gunnerales due to the difference in floral morphology, as the single most parsimonious position for *Esgueiria adenocarpa.* This position indicates the genus is part of stem group core eudicots as they are unable to be placed within a modern lineage. Generally, the core eudicots are characterized by the presence of a pentamerous perianth with distinct whorls and tricolpate or tricolporate pollen (Wodehouse 1936; Erdtman 1952; Doyle 1969; Takhtajan 1980; Furness et al. 2007; Endress 2010; Friis et al. 2011). The general floral morphology of Esgueiriaceae clearly indicate the family belongs to the total group of core eudicots (Friis et al. 1992; Takahashi et al. 1999). Disc shaped nectaries are also a prominent character found within the core eudicots (Smets 1986; Bernardello 2007; Endress 2010). These disc shaped nectaries can form a continuous or fragmented ring and are typically positioned between the androecium and gynoecium (Smets 1986; Bernardello 2007; Endress 2010). Receptacular nectaries, meaning the nectary is associated with the receptacle rather than the perianth or gynoecium, are commonly seen in the core eudicots (Smets 1986; Bernardello 2007). These receptacular nectaries can be categorized within three types: extrastaminal, intrastaminal, or interstaminal nectaries (Schmid 1988; Bernardello 2007). The receptacular mounds observed in *E. futabensis* and *E. aligera* are potentially receptacular nectaries that are extrastaminal, meaning the nectaries surround the androecium. Extrastaminal receptacular nectaries are common in several core eudicot lineages including Berberidopsidaceae, Oleaceae, and several families within the rosid

clade (Cronquist 1981; Ronse De Craene 2004; see Bernardello 2007). If our interpretations of the receptacular mounds are correct, the floral morphology of Esgueiriaceae and the phyloscan results indicate the family is assignable to the core eudicots as a stem lineage as their unique character combinations are not seen in modern lineages. Therefore, it is more appropriate to erect the new family Esgueiriaceae comb. nov. Tang & Atkinson within the core eudicot clade. The recovery of a stem lineage of core eudicots will help further our understanding of morphological evolution.

Late Cretaceous angiosperm diversity of western North America

Sampling from Late Cretaceous deposits of the eastern coast and western interior of North America has uncovered a diverse fossil flora that were placed within modern core eudicot families (Basinger and Dilcher 1984; Magallon-Puebla et al. 1996; Magallón et al. 2001; Crepet 2008; Friis et al. 2011; Manchester et al. 2018). However, less attention has been given to Late Cretaceous deposits of western North America and extinct genera. Recent sampling along the western coast of North America has already uncovered a diverse flora of extinct core eudicot genera within the asterids (Atkinson 2016; Atkinson et al. 2017; Atkinson et al. 2018). These extinct taxa are placed within the order Cornales but are unassignable to modern families due to their unique character combinations. The continued characterization of fossil floras will likely reveal additional extinct angiosperm lineages, such as *Esgueiria aligera*. The discovery of *E. aligera* and the systematic placement of Esgueiriaceae as a stem core eudicot lineage stresses the importance of continued efforts to recover and characterize fossil flora within the region. The recovery of additional fossil data will result in more precise systematic assignments of extinct lineages within the angiosperm phylogeny. Assessing fossil flora within a phylogenetic

framework is critical to understanding early angiosperm diversity and the phylogenetic turnover of extinct lineages through time.

Summary

Here, I report a new species of *Esgueiria*, *E. aligera*, based on a structurally preserved fin-winged fruit. Additionally, the phyloscan results indicate the fossil genus *Esgueiria* is a stem core eudicot lineage and so the new family Esgueiriaceae was erected. The recovery and characterization of a stem core eudicot within Late Cretaceous deposits of western North America emphasizes the need to continue sampling within the region. Early angiosperm diversity is not fully understood but ongoing efforts to characterize fossils will result in additional fossil data that can be applied within a phylogenetic framework to uncover extinct lineages and their turnover through time.

References

Atkinson BA 2016 Early diverging asterids of the Late Cretaceous: *Suciacarpa starrii* gen. et sp. nov. and the initial radiation of Cornales. Botany 94:759–771.

Atkinson BA, C Martínez, WL Crepet 2019 Cretaceous asterid evolution: fruits of *Eydeia jerseyensis* sp. nov. (Cornales) from the upper Turonian of eastern North America. Ann Bot 123:451–460.

Atkinson BA, RA Stockey, GW Rothwell 2016 Cretaceous origin of dogwoods: an anatomically preserved *Cornus* (Cornaceae) fruit from the Campanian of Vancouver Island. PeerJ 4:e2808.

——— 2017 The Early Phylogenetic Diversification of Cornales: Permineralized Cornalean Fruits from the Campanian (Upper Cretaceous) of Western North America. Int J Plant Sci 178:556–566.

——— 2018 Tracking the Initial Diversification of Asterids: Anatomically Preserved Cornalean Fruits from the Early Coniacian (Late Cretaceous) of Western North America. Int J Plant Sci 179:21–35.

Basinger JF, DL Dilcher 1984 Ancient Bisexual Flowers. Science 224:511–513.

Bayer C 2007 Peridiscaceae. In: Flowering Plants Eudicots. The Families and Genera of Vascular Plants. Vol. 9. Kubitzki K, editor. Berlin, Heidelberg: Springer. 297-300.

Bernardello G 2007 A systematic survey of floral nectaries. In: Nectaries and Nectar. Nicolson SW, Nepi M, Pacini E, editors. Dordrecht: Springer. p. 19–128.

Boyer DM, GF Gunnell, S Kaufman, TM McGeary 2016 Morphosource: Archiving and sharing 3-D digital specimen data. Paleontol Soc Pap 22:157–181.

Crepet WL 2008 The Fossil Record of Angiosperms: Requiem or Renaissance?. Ann Mo Bot Gard 95:3–33.

Cronquist A 1981 An integrated system of classification of flowering plants. New York: Columbia University Press.

Doyle JA 1969 Cretaceous angiosperm pollen of the Atlantic coastal plain and its evolutionary significance. J Arnold Arbor 50:1–35.

Endress PK, A Igersheim 1999 Gynoecium diversity and systematics of the basal eudicots. Bot J Linn Soc 130:305–393.

Endress PK 2010 Flower Structure and Trends of Evolution in Eudicots and Their Major Subclades. Ann Mo Bot Gard 97:541–583.

Erdtman G 1952 Pollen Morphology and Plant Taxonomy: Angiosperms. Stockholm: Almqvist & Wiksell.

Exell A, C Stace 1965 Revision of the Combretaceae. Bol Soc Broteriana 40:5–26.

González F, M Angélica Bello 2009 Intra-individual variation of flowers in *Gunnera* subgenus *Panke* (Gunneraceae) and proposed apomorphies for Gunnerales. Bot J Linn Soc 160:262–283.

Friis E, K Pedersen, P Crane 1992 Esgueiria gen. nov., fossil flowers with combretaceous features from the Late Cretaceous of Portugal. Biol Skr 41:1–45.

Friis EM, PR Crane, KR Pedersen 2011 Early flowers and angiosperm evolution. Cambridge ; New York: Cambridge University Press.

Friis EM, KR Pedersen, PR Crane 2006 Cretaceous angiosperm flowers: Innovation and evolution in plant reproduction. Palaeogeogr Palaeoclimatol Palaeoecol 232:251–293.

Friis EM, KR Pedersen, PR Crane 2016 The emergence of core eudicots: new floral evidence from the earliest Late Cretaceous. Proc R Soc B Biol Sci 283:20161325.

Furness CA, S Magallón, PJ Rudall 2007 Evolution of endoapertures in early-divergent eudicots, with particular reference to pollen morphology in Sabiaceae. Plant Syst Evol 263:77–92.

Kubitzki K, JG Rohwer, V Bittrich eds. 1993 Flowering Plants · Eudicots. The Families and Genera of Vascular Plants. Springer.

Larson-Johnson K 2016 Phylogenetic investigation of the complex evolutionary history of dispersal mode and diversification rates across living and fossil Fagales. New Phytol 209:418–435.

Magallon S, PR Crane, PS Herendeen 1999 Phylogenetic Pattern, Diversity, and Diversification of Eudicots. Ann Mo Bot Gard 86:297.

Magallón S, PS Herendeen, PR Crane 2001 *Androdecidua endressii* gen. et sp. nov., from the Late Cretaceous of Georgia (United States): Further Floral Diversity in Hamamelidoideae (Hamamelidaceae). Int J Plant Sci 162:963–983.

Magallon-Puebla S, PS Herendeen, PK Endress 1996 *Allonia decandra*: Floral remains of the tribe Hamamelideae (Hamamelidaceae) from Campanian strata of southeastern USA. Plant Syst Evol 202:177–198.

Manchester SR, DL Dilcher, WS Judd, B Corder, JF Basinger 2018 Early Eudicot flower and fruit: *Dakotanthus* gen. nov. from the Cretaceous Dakota Formation of Kansas and Nebraska, USA. Acta Palaeobot 58:27–40.

Martínez C, TYS Choo, D Allevato, KC Nixon, WL Crepet, RS Harbert, CP Daghlian 2016 *Rariglanda jerseyensis* , a new ericalean fossil flower from the Late Cretaceous of New Jersey. Botany 94:747–758.

Mindell RA, SJ Karafit, RA Stockey 2014 Bisexual Flowers from the Coniacian (Late Cretaceous) of Vancouver Island, Canada: *Ambiplatanus washingtonensis* gen. et sp. nov. (Platanaceae). Int J Plant Sci 175:651–662.

Peecook BR, CA Sidor 2015 The First Dinosaur from Washington State and a Review of Pacific Coast Dinosaurs from North America. Evans DC, editor. PLOS ONE 10:1–15.

Ronse De Craene LP 2004 Floral Development of *Berberidopsis corallina*: a Crucial Link in the Evolution of Flowers in the Core Eudicots. Ann Bot 94:741–751.

Ronse De Craene LP, L Wanntorp 2006 Evolution of Floral Characters in *Gunnera* (Gunneraceae). Syst Bot 31:671–688.

Roth B 2000 Upper Cretaceous (Campanian) land snails (Gastropoda: Stylommatophora) from Washington and California. J Molluscan Stud 66:373–381.

Sauquet H, M von Balthazar, S Magallón, JA Doyle, PK Endress, EJ Bailes, E Barroso de Morais, K Bull-Hereñu, L Carrive, M Chartier, et al. 2017 The ancestral flower of angiosperms and its early diversification. Nat Commun 8:16047.

Scharfstein AR, RA Stockey, GW Rothwell 2020 Evolution and Phylogeny of Altingiaceae: Anatomically Preserved Infructescences from Late Cretaceous Deposits of Vancouver Island, British Columbia, Canada. Int J Plant Sci 181:452–463.

Schmid R 1988 Reproductive versus extra-reproductive nectaries—historical perspective and terminological recommendations. Bot Rev 54:179–227.

Schönenberger J, M von Balthazar, A López Martínez, B Albert, C Prieu, S Magallón, H Sauquet 2020 Phylogenetic analysis of fossil flowers using an angiosperm-wide data set: proof-of-concept and challenges ahead. Am J Bot 107:1–16.

Smets E 1986 Localization and Systematic Importance of the Floral Nectaries in the Magnoliatae (Dicotyledons). Bull Jard Bot Natl Belg/Bull Van Natl Plantentuin Van Belg 56:51–76.

Soltis DE, AE Senters, MJ Zanis, S Kim, JD Thompson, PS Soltis, LP Ronse De Craene, PK Endress, JS Farris 2003 Gunnerales are sister to other core eudicots: implications for the evolution of pentamery. Am J Bot 90:461–470.

Soltis DE 2007 Saxifragaceae. In: Flowering Plants Eudicots. The Families and Genera of Vascular Plants. Vol. 9. Kubitzki K, editor. Berlin, Heidelberg: Springer. 418-435.

Stace C 2007 Combretaceae. In: Flowering Plants · Eudicots. The Families and Genera of Vascular Plants. Vol. 9. Springer. p. 67–82.

Takahashi M, P Crane, H Ando 1999 *Esgueiria futabensis* sp. nov., a new angiosperm flower from the Upper Cretaceous (lower Coniacian) of northeastern Honshu, Japan. Paleontol Res 3:81–87.

Takhtajan AL 1980 Outline of the Classification of Flowering Plants (Magnoliophyta). N Y Bot Gard Press 46:225–359.

The Angiosperm Phylogeny Group 2016 An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Bot J Linn Soc 181:1–20.

Upchurch GR, DL Dilcher 1990 Cenomanian angiosperm leaf megafossils, Dakota Formation, Rose Creek Locality, Jefferson County, southeastern Nebraska. US Geological Survey Bulletin.

Wanntorp L, LPRD Craene 2005 The *Gunnera* Flower: Key to Eudicot Diversification or Response to Pollination Mode? Int J Plant Sci 166:945–953.

Ward PD 1978 Revisions to the stratigraphy and biochronology of the Upper Cretaceous Nanaimo Group, British Columbia and Washington State. Can J Earth Sci 15:405–423.

Ward PD, JW Haggart, R Mitchell, JL Kirschvink, T Tobin 2012 Integration of macrofossil biostratigraphy and magnetostratigraphy for the Pacific Coast Upper Cretaceous (Campanian-Maastrichtian) of North America and implications for correlation with the Western Interior and Tethys. Geol Soc Am Bull 124:957–974.

Webb LJ 1978 A structural comparison of New Zealand and south-east Australian rain forests and their tropical affinities. Aust J Ecol 3:7–21.

Webster GL 2014 Euphorbiaceae. In: Kubitzki K, editor. The Families and Genera of Vascular Plants. Vol. 11. Berlin, Heidelberg: Springer Berlin Heidelberg. p. 51–216.

Wodehouse RP 1936 Evolution of pollen grains. Bot Rev 2:67–84.

Chapter 4: Conclusion

Angiosperms have a fairly recent fossil record dating back to the Early Cretaceous and are greatly represented by the core eudicots. Making up more than 70% of angiosperm diversity (Magallon et al. 1999; Friis et al. 2006; Friis et al. 2011), core eudicots provide important insight to the early evolution of angiosperms. However, there is much work that still needs to be done in order to uncover the timing and origin of core eudicots and angiosperms as a whole. While the fossil record indicates an Early Cretaceous origin, at minimum, for eudicots and angiosperms, molecular dating analyses continue to recover significantly older ages (Smith et al. 2010; Zeng et al. 2014; Barba-Montoya 2018). Incorporating fossils and their stratigraphic data with molecular dating analyses prove to be crucial in understanding the timing and evolution of flowering plants (Anderson et al. 2005; Bell et al. 2010; Magallón et al. 2015; Ramírez-Barahona et al. 2020). The continued integration of fossil and molecular data will allow us to combine multiple lines of evidence to obtain a more accurate view of early core eudicot and angiosperm evolution.

My thesis describes two new fossil fruit species recovered from Late Cretaceous deposits on the western coast of North America. More specifically, the fossil fruits were recovered from Campanian deposits of Sucia Island, Washington state, USA that represent an extant and extinct lineage within the core eudicots. Phylogenetic analyses have assigned one fruit to the extant genus *Ceratopetalum* Sm., within the rosids, and the second fruit to the extinct genus *Esgueiria* Friis, Pederson & Crane, an extinct lineage that falls within the core eudicots. The new species *Ceratopetalum suciensis* (Chapter 2) and *Esgueiria aligera* (Chapter 3) are the first unequivocal representatives of these respective genera within North America. The recovery of *C. suciensis* is the first unequivocal evidence of the family Cunoniaceae within the Northern Hemisphere and greatly expands the geographic range of a predominantly Southern Hemisphere family.

Likewise, the recovery of *E. aligera* within western North America is the first evidence of the genus within the region which expands their geographic range of Europe and Japan, indicating a wide distribution within the Northern Hemisphere. The phyloscan method also indicates that the fossil genus *Esgueiria* is a stem core eudicot so the family Esgueiriaceae was erected for this fossil lineage. The recovery and characterization of these fossil fruits reveal that the fossil flora assemblage within western North America have much more to reveal.

Only one fossil fruit has been described from Sucia Island and placed within the order Cornales (Atkinson 2016). Further investigation of the Campanian deposits on Sucia Island is crucial because the locality may provide a unique snapshot of angiosperm diversity approaching the mass extinction at the end of the Cretaceous. This unique insight will better inform our understanding of early angiosperm diversification and how it may have been impacted by the approaching mass extinction. Sucia Island reveals itself to be an important locality holding extant and extinct lineages of core eudicots which will undoubtedly provide a better look into the early evolutionary patterns of angiosperms.

References

Anderson CL, K Bremer, EM Friis 2005 Dating phylogenetically basal eudicots using rbcL sequences and multiple fossil reference points. Am J Bot 92:1737–1748.

Atkinson BA 2016 Early diverging asterids of the Late Cretaceous: *Suciacarpa starrii* gen. et sp. nov. and the initial radiation of Cornales. Botany 94:759–771.

Barba-Montoya J 2018 Constraining uncertainty in the timescale of angiosperm evolution and the veracity of a Cretaceous Terrestrial Revolution. New Phytol 218:819–834.

Bell CD, DE Soltis, PS Soltis 2010 The age and diversification of the angiosperms re-revisited. Am J Bot 97:1296–1303.

Friis EM, PR Crane, KR Pedersen 2011 Early flowers and angiosperm evolution. Cambridge ; New York: Cambridge University Press.

Friis EM, KR Pedersen, PR Crane 2006 Cretaceous angiosperm flowers: Innovation and evolution in plant reproduction. Palaeogeogr Palaeoclimatol Palaeoecol 232:251–293.

Magallon S, PR Crane, PS Herendeen 1999 Phylogenetic Pattern, Diversity, and Diversification of Eudicots. Ann Mo Bot Gard 86:297.

Magallón S, S Gómez-Acevedo, LL Sánchez-Reyes, T Hernández-Hernández 2015 A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. New Phytol 207:437–453.

Ramírez-Barahona S, H Sauquet, S Magallón 2020 The delayed and geographically heterogeneous diversification of flowering plant families. Nat Ecol Evol 4:1232–1238.

Smith SA, JM Beaulieu, MJ Donoghue 2010 An uncorrelated relaxed-clock analysis suggests an earlier origin for flowering plants. Proc Natl Acad Sci 107:5897–5902.

Zeng L, Q Zhang, R Sun, H Kong, N Zhang, H Ma 2014 Resolution of deep angiosperm phylogeny using conserved nuclear genes and estimates of early divergence times. Nat Commun 5:4956.

Appendix A: Data tables for *Ceratopetalum*

Table 3. Extant *Ceratopetalum* fruits that were μCT scanned and segmented for morphological comparison.

Species	Collector	Herbarium	Accession #
C. succirubrum	Schodde 2178	L.H. Bailey Hortorium Herbarium	BH 95696
C. succirubrum	T.G. Hartley 10967	Harvard University Herbarium	A00969699
C. succirubrum	B. Hyland 10185	Harvard University Herbarium	A00969700
C. apetalum	F.A. Rodway 2668	Harvard University Herbarium	A00969698
C. corymbosum	T.G. Hartley 14046	Harvard University Herbarium	A00969697
C. gummiferum	R. Coveny 11751	Harvard University Herbarium	A00969696
C. virchowii	R. Booth 2772	Harvard University Herbarium	A00969701

Table 4. Scan parameters for extant fruits.

Species	Collector	KV	Current (μA)	Effective pixel size (μm)	Filter
C. succirubrum	Schodde 2178	78	87	6.81	None
C. succirubrum	T.G. Hartley 10967	92	130	12.03	None
C. succirubrum	B. Hyland 10185	92	130	12.03	None
C. apetalum	F.A. Rodway 2668	85	125	10.67	None
C. corymbosum	T.G. Hartley 14046	85	125	10.67	None
C. gummiferum	R. Coveny 11751	85	125	10.7	None
C. virchowii	R. Booth 2772	94	101	10.05	None

Table 5. GenBank accession numbers for rbcL and trnL sequences used in the Bayesian phylogenetic analyses.

Family	Species	*rbcL*	*trnL c-d* (intron)	*trnL e-F*
Brunelliaceae	*Brunellia colombiana*	AF291937.1	AF299181.1	AF299234.1
Brunelliaceae	*Brunellia oliveri*	AF291938.1	AF299182.1	AF299235.1
Cunoniaceae	*Ackama paniculosa*	AF291921.1	AF299161.1	AF299214.1
Cunoniaceae	*Ackama rosifolia*	-	AF299162.1	AF299215.1
Cunoniaceae	*Acrophyllum australe*	AF291926.1	AF299168.1	AF299221.1
Cunoniaceae	*Anodopetalum biglandulosum*	AF291932.1	AF299175.1	AF299228.1
Cunoniaceae	*Bauera rubioides*	L11174.2	AF299183.1	AF299236.1
Cunoniaceae	*Bauera sessiliflora*	-	AF299184.1	AF299237.1
Cunoniaceae	*Caldcluvia paniculata*	AF291922.1	AF299163.1	AF299216.1
Cunoniaceae	*Callicoma serratifolia*	AF291928.1	AF299170.1	AF299223.1
Cunoniaceae	*Ceratopetalum apetalum*	KM895900.1	-	-
Cunoniaceae	*Ceratopetalum gummiferum*	L01895.1	AF299176.1	AF299229.1
Cunoniaceae	*Codia discolor*	AF291929.1	AF299171.1	AF299224.1
Cunoniaceae	*Cunonia atrorubens*	AF291918.1	AF299154.1	AF299207.1
Cunoniaceae	*Cunonia capensis*	-	AF299156.1	AF299209.1
Cunoniaceae	*Davidsonia jerseyana*	-	AF299185.1	AF299238.1
Cunoniaceae	*Davidsonia johnsonii*	-	AF299186.1	AF299239.1
Cunoniaceae	*Davidsonia pruriens*	AF291934.2	-	-
Cunoniaceae	*Eucryphia cordifolia*	AF291931.1	AF299173.1	AF299226.1
Cunoniaceae	*Eucryphia lucida*	L01918.2	-	-
Cunoniaceae	*Eucryphia moorei*	-	AF299174.1	AF299227.1
Cunoniaceae	*Geissois superba*	-	AF299166.1	AF299219.1
Cunoniaceae	*Gillbeea adenopetala*	AF291927.1	AF299169.1	AF299222.1
Cunoniaceae	*Hooglandia ignambiensis*	AY549641.1	AY549639.1	AY549640.1
Cunoniaceae	*Pancheria engleriana*	-	AF299158.1	AF299211.1
Cunoniaceae	*Platylophus trifoliatus*	AF291933.1	AF299177.1	AF299230.1
Cunoniaceae	*Pseudoweinmannia lachnocarpa*	AF291925.1	AF299167.1	AF299220.1

Cunoniaceae	*Pullea glabra*	AF291930.1	AF299172.1	AF299225.1
Cunoniaceae	*Schizomeria ovata*	-	AF299178.1	AF299231.1
Cunoniaceae	*Schizomeria serrata*	JX236031.1	-	JX236028.1
Cunoniaceae	*Spiraeanthemum ellipticum*	AF291935.1	AF299179.1	AF299232.1
Cunoniaceae	*Spiraeanthemum samoense*	AF291936.1	AF299180.1	AF299233.1
Cunoniaceae	*Spiraeopsis celebica*	AF291923.1	AF299164.1	AF299217.1
Cunoniaceae	*Vesselowskya rubifolia*	AF291920.1	AF299160.1	AF299213.1
Cunoniaceae	*Weinmannia bangii*	AF291915.1	AF299145.1	AF299198.1
Cunoniaceae	*Weinmannia fraxinea*	-	AF299149.1	AF299202.1
Cunoniaceae	*Weinmannia madagascariensis*	AF291916.1	AF299152.1	AF299205.1
Cunoniaceae	*Weinmannia minutiflora*	-	AF299150.1	AF299203.1

Appendix B: Additional images of *Ceratopetalum*
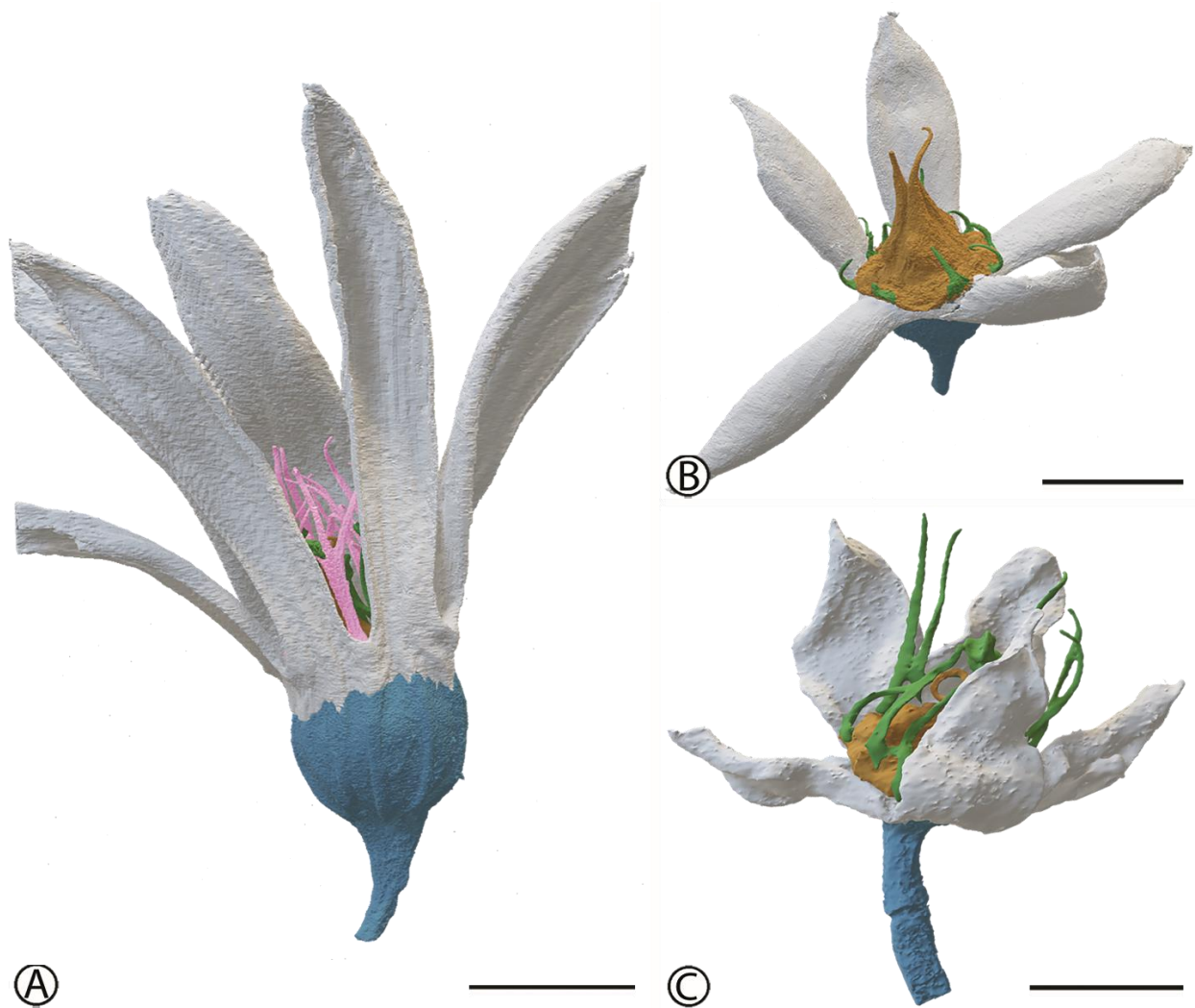
Figure 10. Three-dimensional reconstructions of extant fruits of *Ceratopetalum gummiferum*, *C. apetalum*, and *C. corymbosum*. White = calyx/wings; Pink = petals; Orange = styles and nectary disk; Green = stamens; Blue = hypanthium. (**A**) General fruit morphology of *C. gummiferum*, the only living species to have petals. Scale bar = 4mm. (**B**) General fruit morphology of *C. apetalum* showing two styles, diplostemonous stamens, and five wings. Scale bar = 4 mm. (**C**) General fruit morphology of *C. corymbosum*. Scale bar = 2 mm.
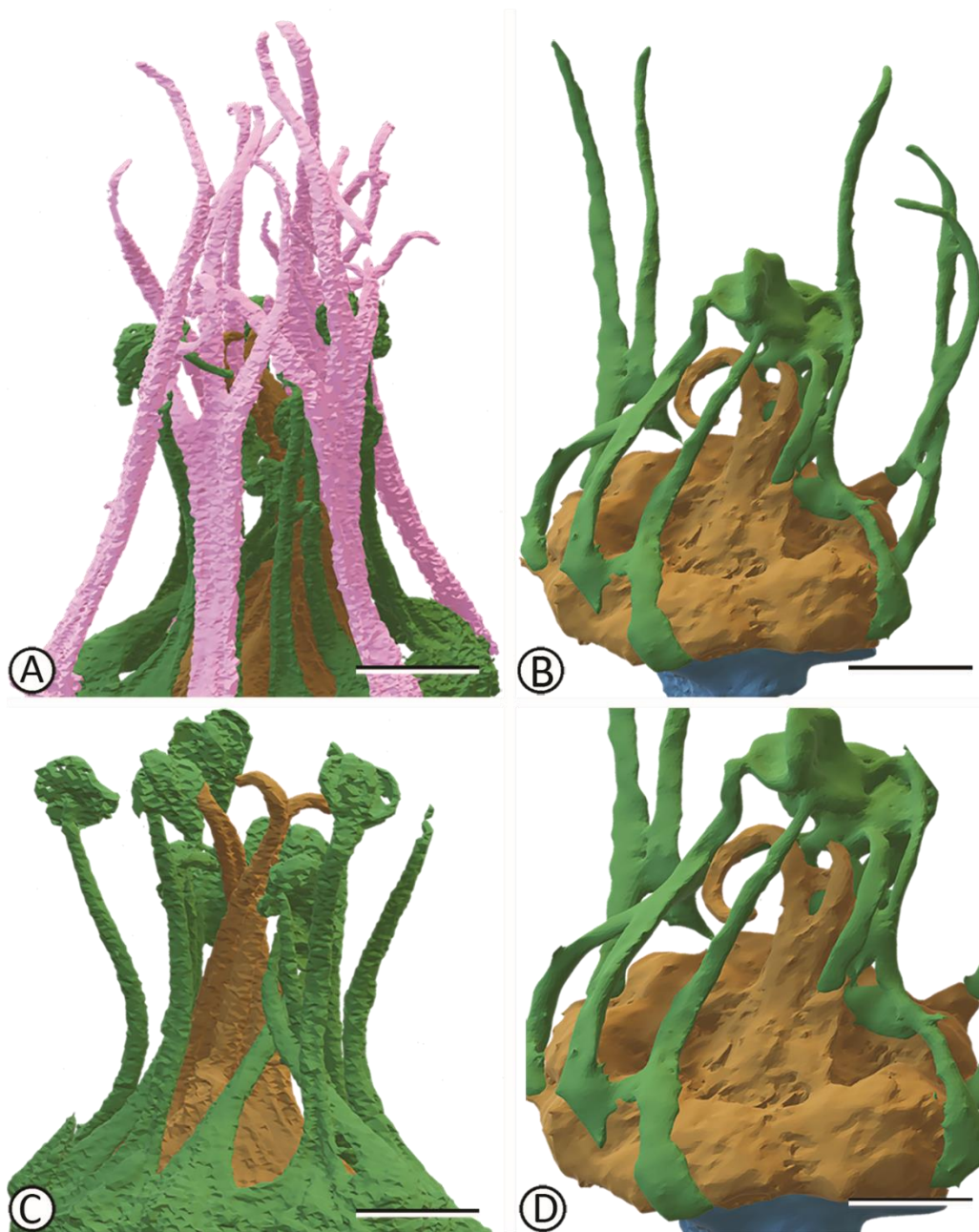
Figure 11. Detailed view of *C. gummiferum* and *C. corymbosum* fruits with the wings removed for a better view of the androecium and gynoecium. White = calyx/wings; Pink = petals; Orange = styles and nectary disk; Green = stamens; Blue = hypanthium. **(A)** *C. gummiferum* fruit with persistent petals on the fruit. Scale bar = 1.0 mm. **(B)** *C. corymbosum* fruit with persistent stamens and two styles. Scale bar = 0.68 mm. **(C)** *C. gummiferum* fruit with persistent stamens and three styles present. Scale bar = 0.8 mm. **(D)** A magnified view of *C. corymbosum*. Scale bar = 0.57 mm.

Appendix C: Additional phyloscan results
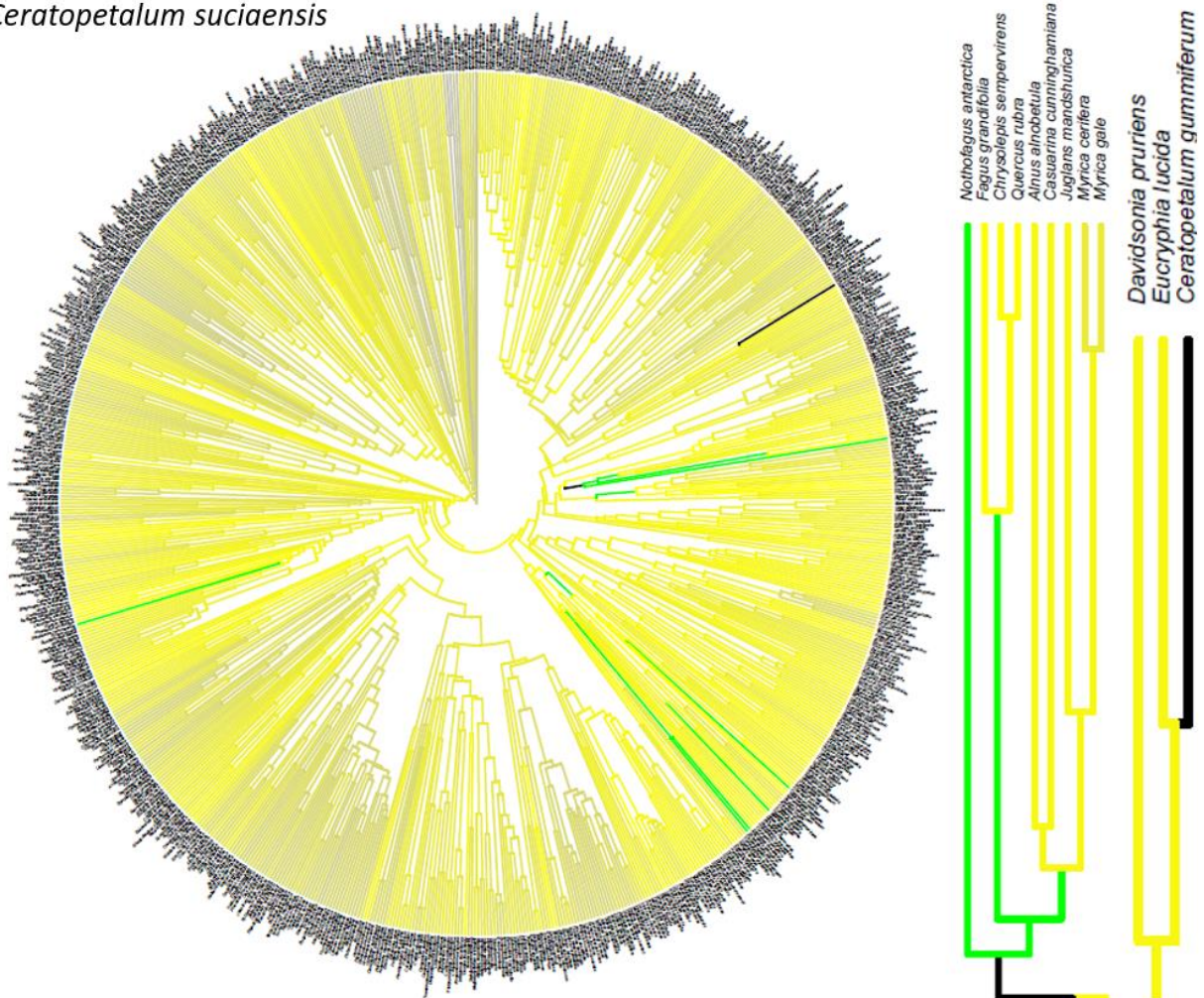
Figure 12. Phyloscan results for *Ceratopetalum suciensis*. "Fan" shaped phyloscan tree shows most parsimonious positions indicated by the black branches on the tree. Most parsimonious positions +1 are indicated by the green branches while a gradient from yellow to gray show subsequent parsimonious positions.
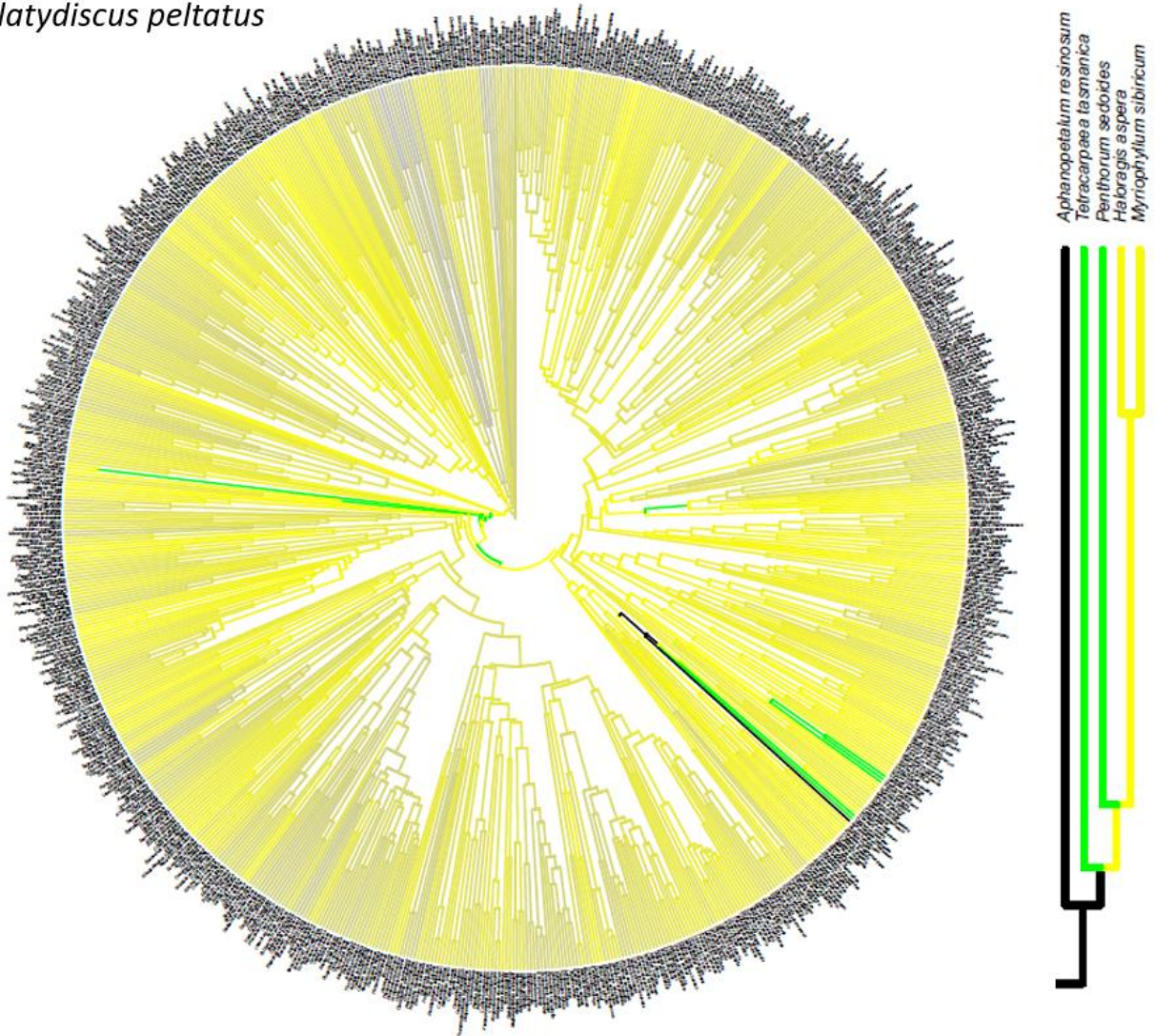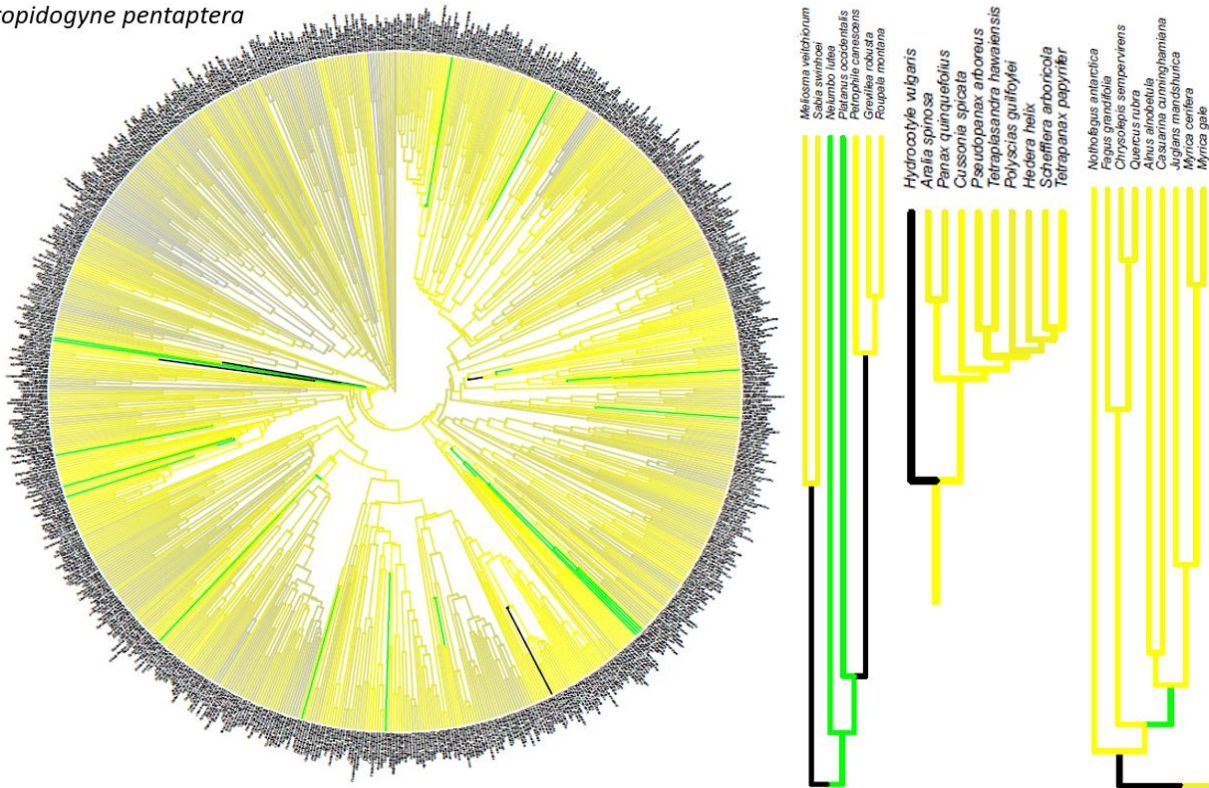
Figure 13. Phyloscan results for *Platydiscus peltatus*. "Fan" shaped phyloscan tree shows most parsimonious positions indicated by the black branches on the tree. Most parsimonious positions +1 are indicated by the green branches while a gradient from yellow to gray show subsequent parsimonious positions.

Figure 14. Phyloscan results of *Tropidogyne pentaptera*. "Fan" shaped phyloscan tree shows most parsimonious positions indicated by the black branches on the tree. Most parsimonious positions +1 are indicated by the green branches while a gradient from yellow to gray show subsequent parsimonious positions.
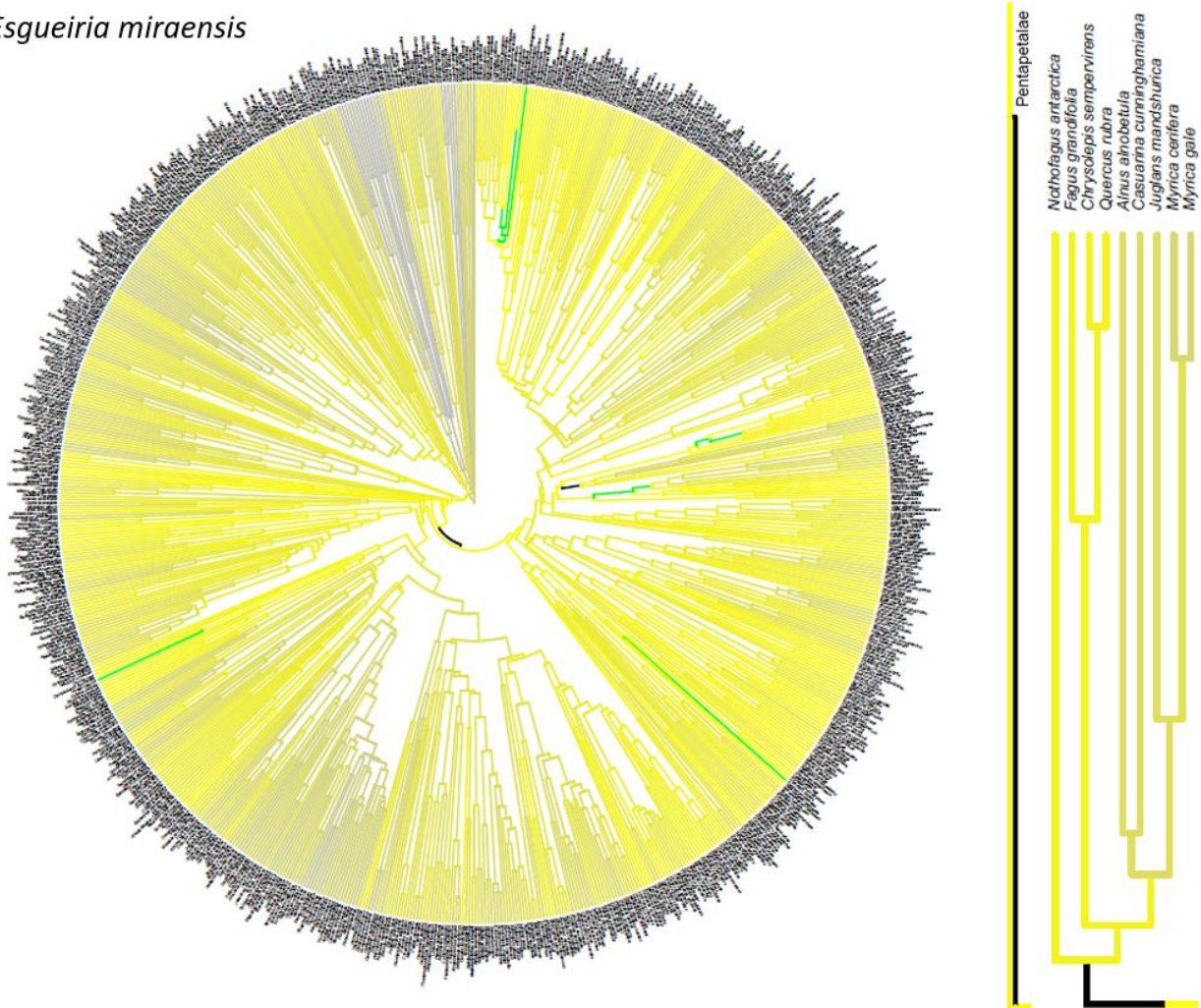
Figure 15. Phyloscan results of *Esgueiria miraensis*. "Fan" shaped phyloscan tree shows most parsimonious positions indicated by the black branches on the tree. Most parsimonious positions +1 are indicated by the green branches while a gradient from yellow to gray show subsequent parsimonious positions.
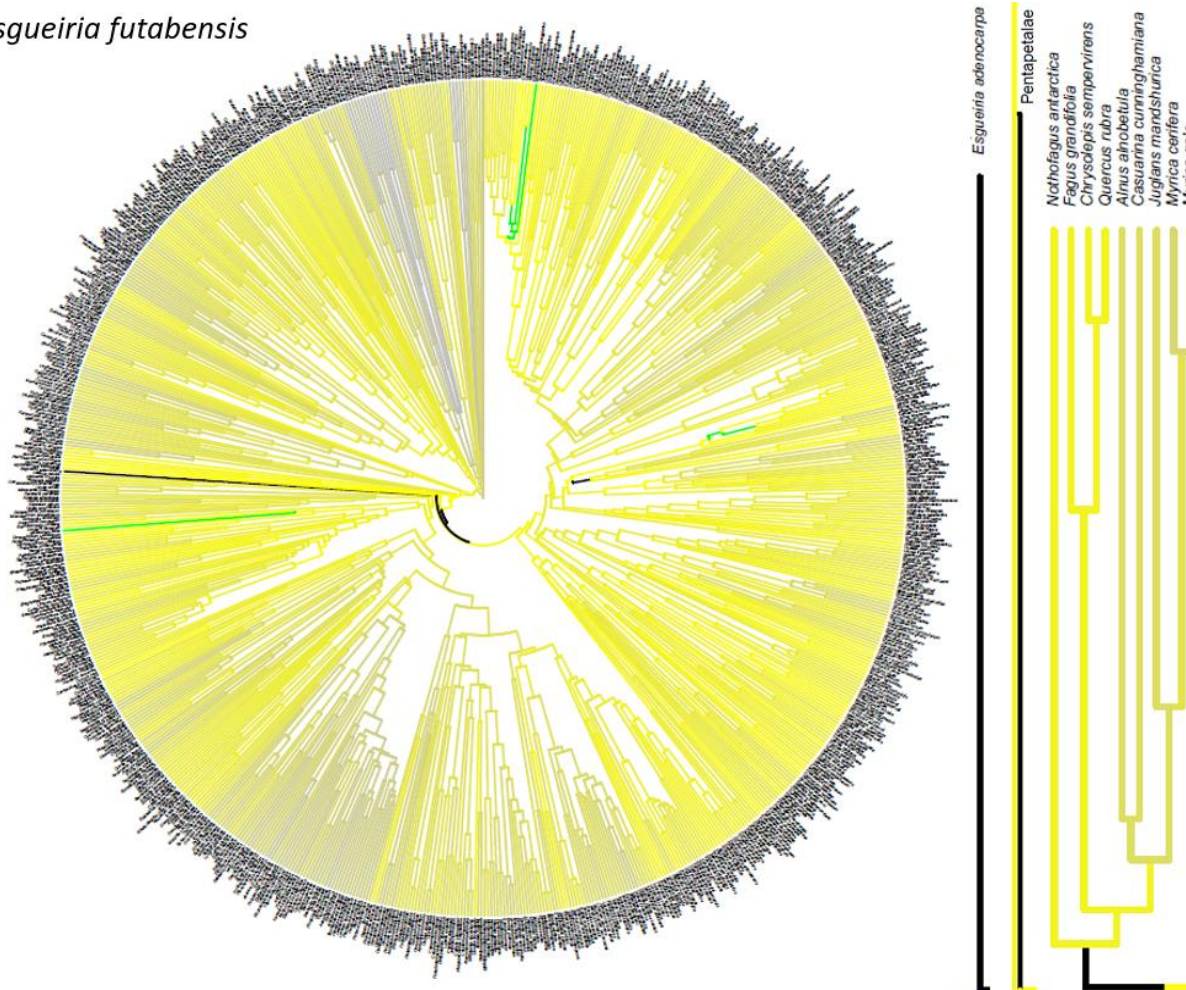
Figure 16. Phyloscan results of *Esgueiria futabensis*. "Fan" shaped phyloscan tree shows most parsimonious positions indicated by the black branches on the tree. Most parsimonious positions +1 are indicated by the green branches while a gradient from yellow to gray show subsequent parsimonious position