

# Extending beyond Gondwana: Cretaceous Cunoniaceae from western North America

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## Summary

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- Cunoniaceae are important elements of rainforests across the Southern Hemisphere. Many of these flowering plants are considered Paleo-Antarctic Rainforest Lineages that had a Gondwanan distribution since the Paleocene. Fossils of several modern genera within the family, such as *Ceratopetalum*, have indicated biogeographical connections between South America and Australia in the Cenozoic.
- Here, we report a dramatic geographical range extension for *Ceratopetalum*, and Cunoniaceae as a whole, based on two exceptionally preserved fossil winged fruits from Campanian (c. 82–80 Ma old) deposits on Sucia Island, Washington, USA. The fossils were studied using physical sectioning, light microscopy, micro-computed tomography scanning and multiple phylogenetic analyses.
- The fossil fruits share diagnostic characters with *Ceratopetalum* such as the presence of four to five persistent calyx lobes, a prominent nectary disk, persistent stamens, a semi-inferior ovary and two persistent styles. Based on morphological comparisons with fruits of extant species and support from phylogenetic analyses, the fossils are assigned to a new species *Ceratopetalum suciensis*.
- These fossils are the first unequivocal evidence of crown Cunoniaceae from the Cretaceous of North America, indicating a more complicated biogeographical history for this important Gondwanan family.

## 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 before 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 floras 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 investigating the assembly and biogeographical history of these ecosystems (Barreda *et al.*, 2021). Therefore, many of these clades often are used as study systems for understanding the evolution of southern rainforests including Cunoniaceae.

Cunoniaceae today comprise 300 species and 27 genera that have a typical PARL distribution and dominate some southern rainforests (Bradford *et al.*, 2004; Kooyman *et al.*, 2014). It has

long been thought that this family has been restricted to the Southern Hemisphere since the latest Cretaceous (Santonian–Maastrichtian) as indicated by wood and pollen from South America and Antarctica (Cranwell, 1959; Askin, 1992; Baldoni & Askin, 1993; Poole *et al.*, 2000a, 2003). However, it is uncertain if these previously reported Cretaceous fossils represent crown members of Cunoniaceae, which makes it difficult to infer when the family originated.

Extant genera of the family began to appear during the Paleogene with one of the more conspicuous fossil representatives being *Ceratopetalum* Sm. (Holmes & Holmes, 1992; Barnes & Hill, 1999; Gandolfo & Hermsen, 2017). Today, this genus consists of eight species that are restricted to eastern Australia and Papua New Guinea (Rozefelds & Barnes, 2002) and can dominate rainforests in these regions (Burgess & Johnston, 1953; Baur, 1957; Webb, 1978).

Here we report two structurally preserved fruits of *Ceratopetalum* from the Northern Hemisphere, namely, the Late Cretaceous of western North America. The fossil fruits have the diagnostic character combination of the genus and comparative analysis indicates that the fossils represent a new species. Our findings indicate: (1) the diversification of Cunoniaceae was well underway during the Cretaceous; (2) *Ceratopetalum* and crown

Cunoniaceae have a biogeographical history in the Northern Hemisphere; and (3) the historical distributions of other 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 Henry Point on Sucia Island, Washington, USA. Cretaceous exposures on Sucia Island (and Little Sucia Island) belong to the Cedar District Formation of the Nanaimo Group and are Campanian in age based on biostratigraphy and magnetostratigraphy (*c.* 82–80 Ma; Ward *et al.*, 2012). The reported Cretaceous biota from these deposits include cornelian fruits, ammonites, terrestrial gastropods, inoceramid bivalves and a theropod femur (Ward, 1978; Roth, 2000; Ward *et al.*, 2012; Peacock & Sidor, 2015; Atkinson, 2016).

Specimens were imaged using a Nikon SMZ25 stereomicroscope with a Nikon DS-Fi3 camera attachment (Nikon Corp., Tokyo, Japan). One specimen (KUPB 19169) was imaged for internal morphology revealed by the initial fracture. The specimen then was glued back together for X-ray micro-computed tomography ( $\mu$ CT) and physical sectioning using cellulose acetate peeling (Joy *et al.*, 1956). Several peels were mounted on microscope slides using the mounting medium Eukitt (O. Kindler GmbH, Freiberg, Germany). All specimens are housed in the Division of Paleobotany Collections, Biodiversity Institute, University of Kansas (KUPB).

One fossil specimen (KUPB 19169) and seven fruits of five extant species of *Ceratopetalum* (Supporting Information Table S1) were  $\mu$ CT-scanned at the University of Michigan CTEES facility using a Nikon XT H 225ST industrial  $\mu$ CT system with a 1620 X-ray detector panel (Perkin Elmer, Waltham, MA, USA) and a tungsten reflection target. Scan conditions for the fossil were set at 128 KV and 145  $\mu$ A, and used a 1-mm copper filter and obtained 20.84  $\mu$ m pixel size resolution. Scan conditions for the extant fruits are presented in Table S2. The program INSPECT-X (Nikon Corp.) acquired scans that were segmented (from serial longitudinal digital sections) using the software MIMICS 22.0 (Materialise, Leuven, Belgium) to reconstruct 3D images of the fruits. AVIZO 9 LITE 3D (Thermo Fisher Scientific, Waltham, MA, USA) was used for fruit measurements. Data are archived on Morphosource (Boyer *et al.*, 2016) under the project title '3D morphology of *Ceratopetalum* fruits (Cunoniaceae).'

In order to test our systematic assignment of the Cretaceous fruits to Cunoniaceae, we analyzed them via the phyloscan method (Schönenberger *et al.*, 2020), which uses a comprehensive angiosperm floral character matrix with a molecular backbone to assess the most parsimonious position(s) of fossil flowers across the angiosperm phylogeny. This method allows us to quickly assess phylogenetic affinities of the fossils and to easily exclude angiosperm clades that may have similar (helicopter-like) fruits but a different floral plan. Because 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 did not include *Ceratopetalum*. The genus is

morphologically distinct in Cunoniaceae, so the extant species, *C. gummiferum* Sm. was added to the matrix and grafted to the backbone phylogeny with its phylogenetic position based on Bradford & Barnes (2001). The backbone phylogeny and matrix are presented in Notes S1, S2. Phyloscanning was used to assess two equivocal cunoniaceous fossils, *Tropidogyne pentaptera* Poinar & Chambers (Poinar & Chambers, 2017) and *Platydiscus peltatus* Schönenberger & Friis (Schönenberger *et al.*, 2001). Phyloscan outputs can be found in Figs S1–S6. Scoring justifications are detailed in Methods S1.

After confirming the familial assignment of the studied fossil fruits, we conducted additional phylogenetic analyses to test the systematic affinities of the Sucia Island fruits to *Ceratopetalum*. More specifically, Bayesian phylogenetic analyses that focus on relationships within Cunoniaceae were conducted using combined morphological and molecular datasets. The combined datasets have a more thorough sampling of species within the family which provides for a more precise systematic assessment of the fossils compared to the familial/ordinal level assessment of the phyloscan. Two Bayesian analyses were conducted. In the first analysis the Cretaceous fruits of this study were the only fossils included. In the second analysis, 10 additional extinct species with preserved reproductive structures were included to further test the phylogenetic position of these fruits because fossils can affect the position of other fossils in such analyses (Manos *et al.*, 2007; Ronquist *et al.*, 2012a). These analyses used a morphological dataset from Jud & Gandolfo (2020), which was modified to include the additional fossil taxa resulting in a dataset of 54 taxa (43 extant, 11 fossils) and 58 morphological characters. The modified matrix is available online via Morphobank (project P3906, matrix 27 164; O'Leary & Kaufman, 2011). The matrix then was combined with *rbcL* and *trnL-trnF* data from the sampled extant taxa. Sequences were obtained from GenBank (Table S3). Molecular data were aligned in Aliview (Larsson, 2014) using MAFFT (Katoh & Standley, 2013). PARTITIONFINDER2 (Lanfear *et al.*, 2016) was used with Aikake information criterion (AICc) model selection to search for the optimal partitioning scheme and models of molecular evolution. The most optimal scheme was a 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.*, 2012b) on the CIPRES Science Gateway (Miller *et al.*, 2011). The analysis used Markov chain Monte Carlo (MCMC) for two independent runs with four chains running for 100 million generations, sampling every 10 000 generations, with a 25% burn-in. The standard deviation of split frequencies was < 0.02; and TRACER 1.7 (Rambaut *et al.*, 2018) was used to confirm convergence with all ESS values » 200. All tree files are available in Notes S3.

## Results

### Systematics

Order – Oxalidales Bercht & J. Presl.

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. (Figs 1a–c, 2, 3).

Specific diagnosis. Fruit body  $\leq 4.0$  mm wide and 5.75 mm long. Calyx lobes  $\leq 3.0$ –4.0 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 45–90°. Nectary, annular ring  $\leq 0.38$ –0.60 mm tall, with conspicuous lobes bordering each stamen. Styles  $\leq 2.47$  mm long in fruit. Ovary diameter 3.62–4.0 mm.

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

Holotype. KUPB 19169 [Accession slide nos. 30 928–30 973] (Figs 1b,c, 2d–g, 3).

Paratype. KUPB 19168 (Figs 1a, 2a–c).

Type locality. Henry Point, Sucia Island, Washington, USA (lat. 48.749330°N, long. 122.900798°W).

Stratigraphy. Cedar District Formation.

Age. Early to Middle Campanian (c. 82–80 Ma).

## Description

The two fruits are radially symmetrical with an epigynous perianth and androecium (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 3.62–4.00 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, giving the fruit a helicopter-like morphology (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. Wings from both specimens range from 3.0 to 4.0 mm wide. This wing is elliptical in shape with a slightly acute apex and attenuate base that narrows gradually towards the base.

Although internal preservation is limited, calyx venation can be observed easily as dark ‘coalified’ tissue. Five primary veins can be seen entering the base of the wing with secondary veins diverging from primary veins throughout the entire wing length. The divergence of secondary veins range from 45° to 90°. The marginal veins in the wing connect to other marginal veins of adjacent wings via an interwing vein located at the outer edge of the nectary between each calyx lobe (Fig. 2b). The nectary is an annular ring (Fig. 2c) with prominent lobes that border each stamen as revealed by the  $\mu$ CT-scanned specimen and cellulose acetate peels (Figs 2d–g, 3a). The nectary is 0.38–0.60 mm tall.

Three-dimensional renderings from segmentation of  $\mu$ CT data reveal a diplostemonous androecium with abraded filaments that are 1.21–1.89 mm long. Anthers were not preserved. The outer whorl of stamens is opposite the wings (calyx lobes) whereas the inner whorl of stamens alternates with the wings (Figs 1c, 2d, 3e).

The ovary is 3.62–4.00 mm in diameter and is semi-inferior in which the apex of the ovary extends slightly above the insertion of the calyx and androecium. The  $\mu$ CT scan and sections of one specimen (KUPB 19169) reveal two free styles that are pressed against one another for most of their length (Fig. 3). In particular, Fig. 3(b) clearly shows the two separate and appressed styles. Both styles are 2.47 mm long. Stigmas are inconspicuous or not preserved.

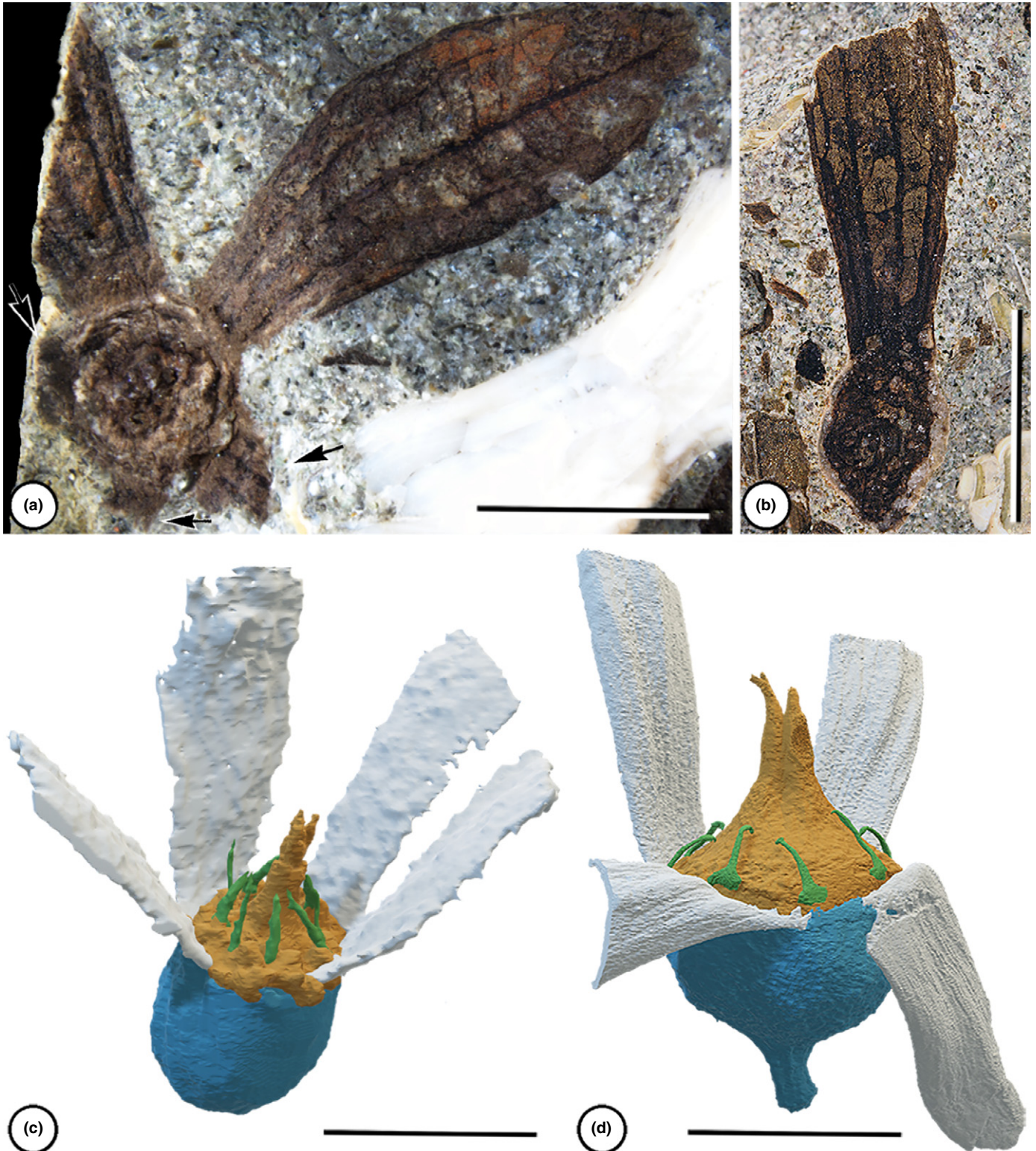
## Remarks

*Ceratopetalum suciensis* possesses a combination of wing shape and venation characters which indicate that it is a new species (Tables S4, S5). Moreover, these characters often are used to taxonomically compare fruits of extinct species to those of living ones (e.g. Barnes & Hill, 1999; Gandolfo & Hermsen, 2017). It is worth noting that *C. suciensis* is based on the most completely preserved fossil fruits of *Ceratopetalum*, to date, whereas other described fossils tend to lack preservation of other informative structures such as stamens and styles (see Table S4), which makes taxonomic comparisons straightforward.

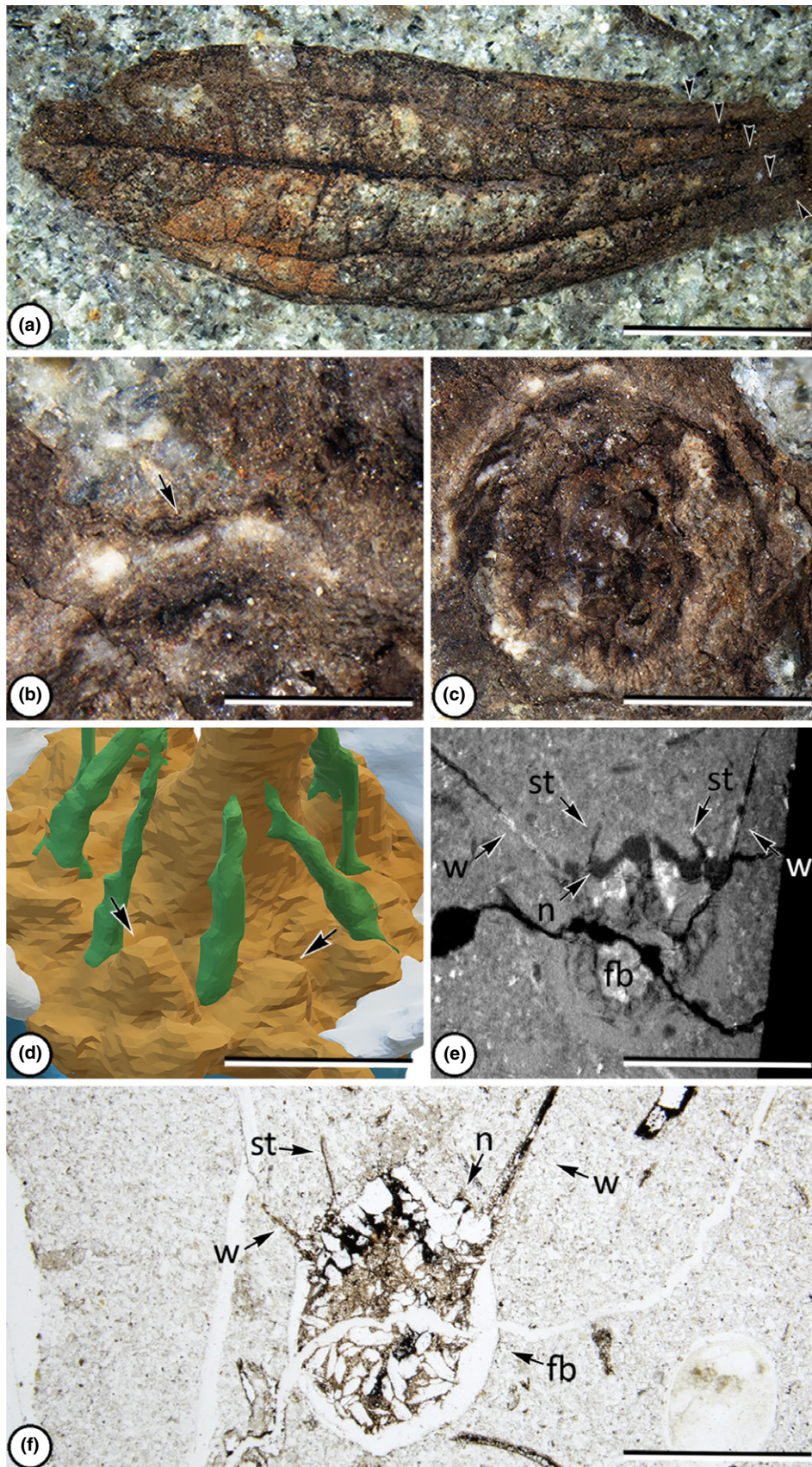
Wing shape of both extant and extinct species of *Ceratopetalum* can be oblong, obovate or elliptical. Wing bases can range from constricted to not constricted at all and wing apices range from acute to obtuse in shape. The fruit wings of *C. suciensis* fall within the range of variation seen in extant and fossil species, but the wing base is unique in being attenuate with a gradual basipetal constriction. Fruit wings of the Australian *C. virchowii* F. Muell. is the only living species in this genus with conspicuously constricted fruit wing bases (Rozeffelds & Barnes, 2002; Table S5). However, this extant species differs from *C. suciensis* by having a fruit wing shape that is typically obovate and with an abrupt constriction of the wing base rather than an elliptical wing shape with a gradually narrowing base. Therefore, based on fruit wing shape, *C. suciensis* differs from all extant species of *Ceratopetalum*.

Among reported fossil *Ceratopetalum* species, *C. edgardoromeroi* Gandolfo & Hermsen from the Eocene of Patagonia (Gandolfo & Hermsen, 2017), is the only one to have a gradually narrowing wing base that is similar to *C. suciensis*. This fossil species differs from *C. suciensis* by having a rounded wing apex (Table S4). In addition, *C. edgardoromeroi* has fruits with ovate wings (Gandolfo & Hermsen, 2017) whereas *C. suciensis* has fruit wings that are elliptical. Overall, *C. suciensis* has a unique wing shape among all reported extinct species of *Ceratopetalum*.

Additionally, fruit wing venation patterns vary and are taxonomically informative within *Ceratopetalum*. Most living species have three primary veins that enter each fruit wing (Table S5; Dickison, 1975; Barnes & Hill, 1999; Matthews *et al.*, 2001; Gandolfo & Hermsen, 2017). *Ceratopetalum succirubrum* C. T. White and *C. virchowii*, from Australia are the only two living species with more than three primary veins, which is similar to *C. suciensis*. However, these two species differ from *C. suciensis* by consistently having fruit wings with more than five primary veins. In addition, the fruits of *C. succirubrum* and *C. virchowii* have wings with secondary veins that are restricted to the distal half



**Fig. 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 (arrows). Note that the upper (superior) portion of the ovary is abraded. KUPB 19168, Bar, 5 mm. (b) Exposed specimen in oblique longitudinal view of fruit body and a wing. KUPB 19169, Bar, 5 mm (image courtesy S.R. Manchester, University of Florida). (c) Three-dimensional reconstruction of specimen in (b) showing general morphology of the fruit including two styles, diplostemonous stamens and four wings are present. KUPB 19169, 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, Bar, 5 mm. Colors: white, calyx/wings; orange, styles and nectary disk; green, stamen; blue, hypanthium.



**Fig. 2** Detailed view of wings, nectary lobes and stamens 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 at 45–90°. KUPB 19168, Bar, 2 mm. (b) Top-down view of tissue just outside of nectary lobe and between the wings showing an interwing vein (arrow). KUPB 19168, Bar, 0.3 mm. (c) Top-down view of annular nectary disk (arrow). KUPB 19168, Bar, 0.6 mm. (d) Three-dimensional reconstruction of the fossil fruit showing nectary lobes (arrows) bordering stamens. KUPB 19169, Bar, 1 mm. Colors: white, calyx/wings; orange, styles and nectary disk; green, stamen; blue, hypanthium. (e) Digital longitudinal section of micro-computed tomography scanned fruit showing persistent stamens and nectary lobes. KUPB 19169, Bar, 4 mm. (f) Longitudinal section of the fruit showing persistent stamens and nectary lobes. KUPB 19169, Slide no. 30, 939, Bar, 4 mm. w, wings; n, nectary lobe; st, stamen; fb, fruit body.

(Barnes & Hill, 1999), whereas those of *C. suciensis* have wings with secondary veins that diverge throughout their entire length. The combination of wing venation characters in *C. suciensis* is unique when compared to living species of *Ceratopetalum*.

Like their living counterparts, most extinct *Ceratopetalum* species have three primary veins in each wing (Table S4; Barnes & Hill, 1999; Gandolfo & Hermsen, 2017). Similar to *C. suciensis*, *C. priscum* Holmes and Holmes (Holmes & Holmes, 1992) and *C. wilkinsonii* (Ett.) Holmes and Holmes (Holmes & Holmes, 1992) from the Miocene and Eocene–Oligocene of Australia, are the only extinct species in this genus that have fruit wings with more than three primary veins. These two fossil species differ from *C. suciensis*, however, by having fruits with up to four primary veins in each wing rather than five. In addition, fruits of *C. priscum* and *C. wilkinsonii* lack persistent stamens, which differs from *C. suciensis* (Table S4).

It is clear that both specimens of *C. suciensis* differ from living *Ceratopetalum* species by consistently having a unique wing shape and five primary veins in each fruit wing. Known fruits of extinct *Ceratopetalum* all have wings with fewer than five primary veins and those with four veins lack persistent stamens. Owing to these differences, the *Ceratopetalum* fossils described in this study clearly have a unique combination of characters and are, therefore, assigned to a new species, *Ceratopetalum suciensis* sp.nov. Tang & Atkinson.

#### X-ray micro-computed tomography of *Ceratopetalum* fruits

The  $\mu$ CT scans of the fossil fruit, KUPB 19169, revealed four calyx lobes, eight persistent stamens, a semi-inferior ovary, nectary lobes and two appressed styles (Figs 1c, 2d,e, 3a,b,e,f; Videos S1–S3, S5). The calyx lobes have abraded apices and expand out to form radiating wings (Fig. 1c). The persistent stamens form two whorls that alternate with and are opposite of the wings (Fig. 3e). Nectary lobes border each stamen (Fig. 2d).

Scans of five extant *Ceratopetalum* species display the presence of four to six calyx lobes, persistent stamens, semi-inferior ovaries, a nectary disk and two to three appressed styles on the fruits (Figs 1d, 4, 5; Videos S4, S5). The calyx lobes expand in size to form radiating wings that resemble a helicopter-like fruit morphology (Figs 1d, 4a–c). Stamens form two alternating whorls on each fruit (Figs 1d, 4b, 5). There are four wings, eight stamen, and two styles present on each *C. succirubrum* fruit (Fig. 1d). *Ceratopetalum apetalum* D. Don, *C. corymbosum* C.T. White and *C. virchowii* all have five wings present with 10 stamens and two appressed styles (Fig. 4b,c); the scans of fruits from these species reveal a morphology similar to that of *C. suciensis*. *Ceratopetalum gummiferum* is the only specimen

to have highly dissected petals persistent on the fruit (Figs 4a, 5a). There are six petals present, 12 stamens and three styles on the fruit of *C. gummiferum* (Fig. 5a,c).

#### Phylogenetic analyses

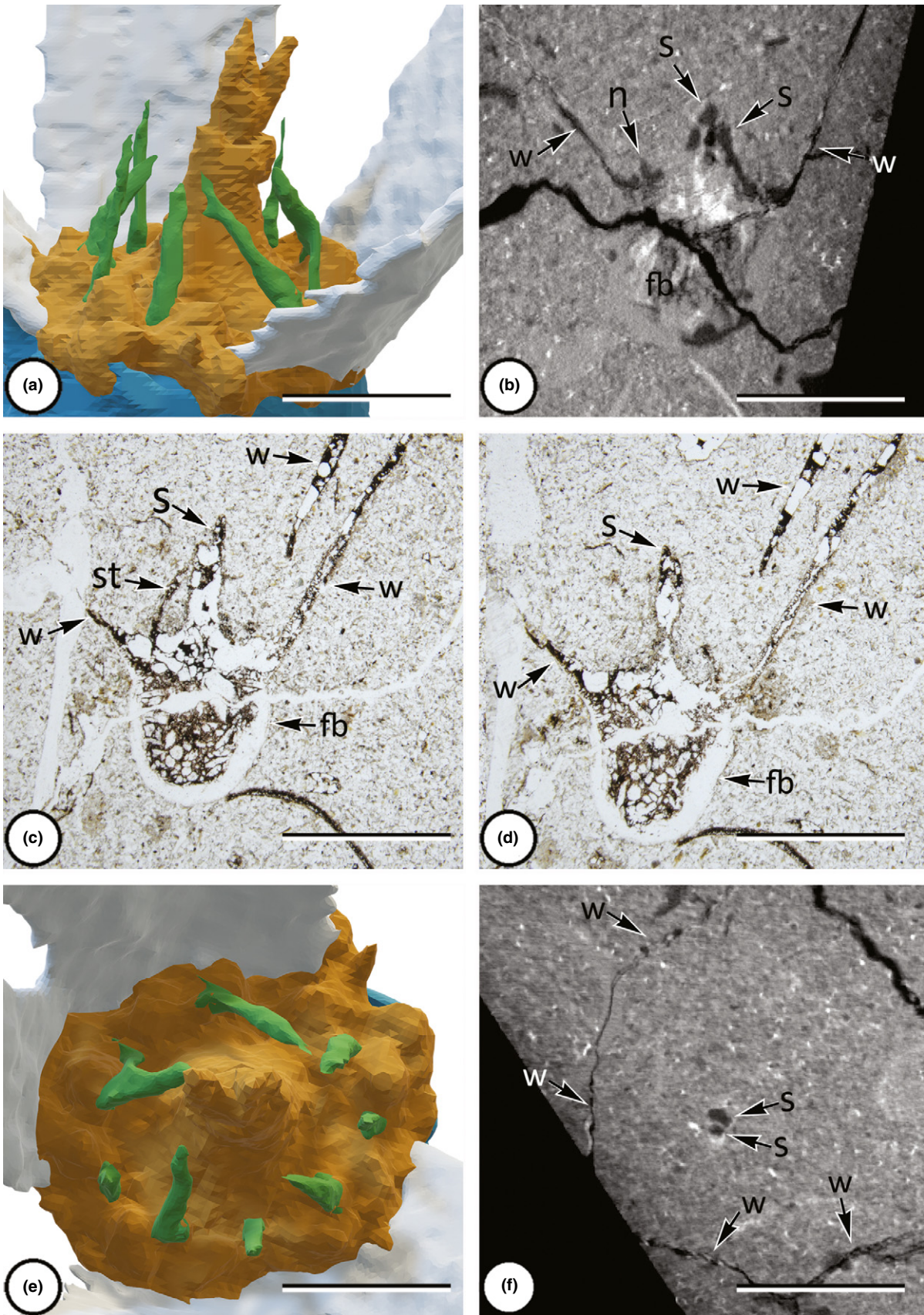
In the initial phyloscan analysis, the most parsimonious positions of *C. suciensis* were recovered on four branches leading to *Saxifraga cernua* L. (Saxifragaceae), the order Saxifragales, stem Fagales, and *C. gummiferum* (Figs S1, S2). Flowers of *Tropidogyne pentaptera* Poinar & Chambers (Poinar & Chambers, 2017) have most parsimonious positions in several distantly related taxa such as *Vahlia capensis* (L.f.) Thunb. (Vahliaceae), *Donatia fascicularis* J.R. Forst. & G. Forst. (Stylidiaceae) and the order Saxifragales (Figs S3, S4). The most parsimonious positions of *P. peltatus* Schönerberger & Friis (Schönerberger *et al.*, 2001) were recovered within the order Saxifragales, specifically on the branch leading to *Aphanopetalum resinolum* Endl. (Aphanopetalaceae) and on the branch leading to the families Tetracarpaceae, Penthoraceae and Haloragaceae (Figs S5, S6).

Both Bayesian phylogenetic analyses with increased sampling of Cunoniaceae recovered *C. suciensis* within *Ceratopetalum*. The first analysis recovered *C. suciensis* with extant *Ceratopetalum* in a trichotomy (posterior probability = 1.0; Fig. 6). The second analysis (with 10 additional fossil taxa) recovered *C. suciensis* within a clade (polytomy) comprising all other fossil and extant *Ceratopetalum* species (posterior probability = 0.72; Fig. 7).

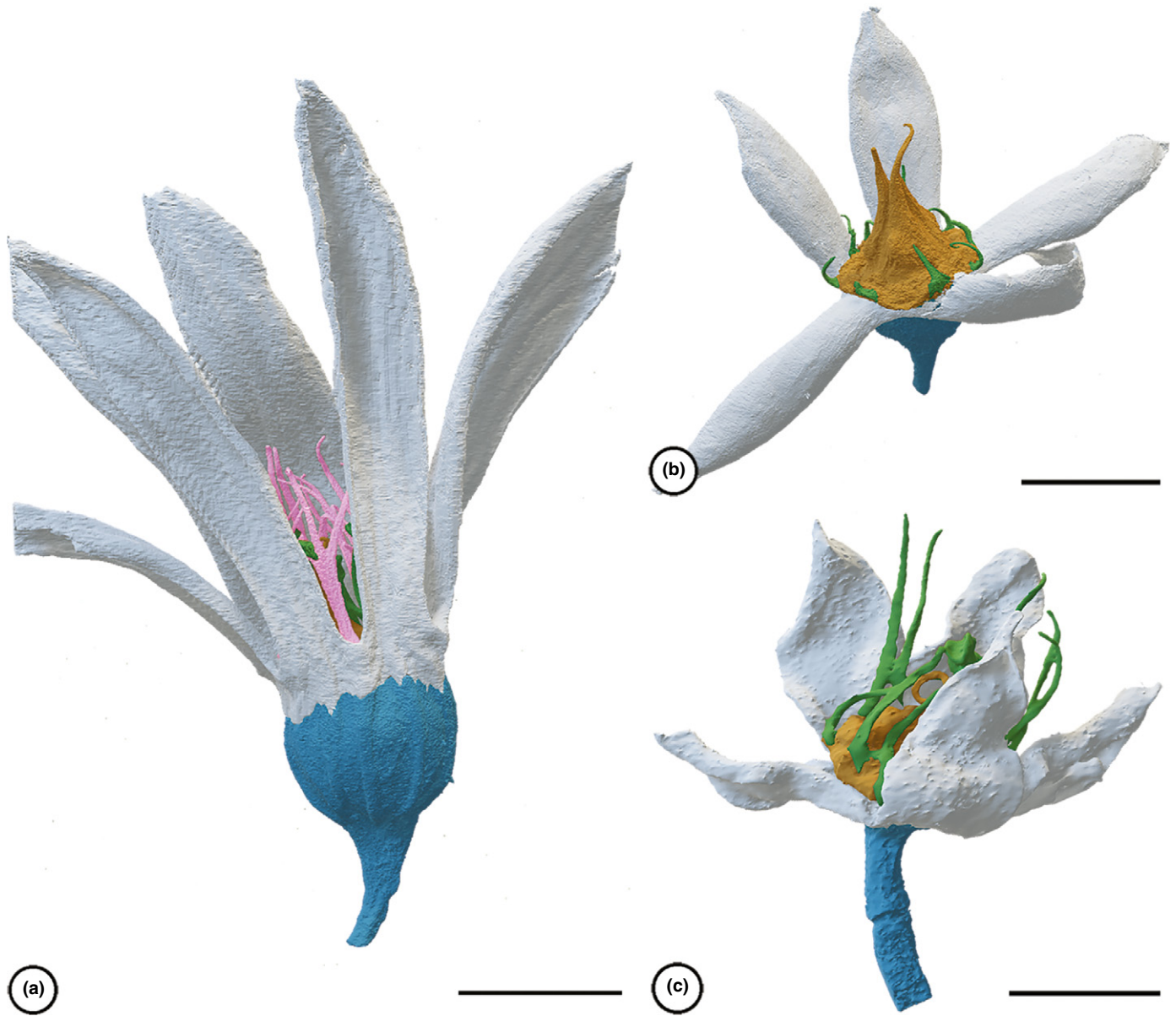
#### Discussion

##### Cretaceous *Ceratopetalum*

Based on multiple lines of evidence, the Sucia Island fruits are assigned to *Ceratopetalum* as a new species, *C. suciensis*. Phylogenetic analyses in this study support the systematic assignment of the Sucia Island fruits to the genus *Ceratopetalum*. Using the recent phyloscan method (Schönerberger *et al.*, 2020), four most parsimonious positions of *C. suciensis* were recovered along branches leading to Saxifragales, *Saxifraga cernua* (Saxifragaceae), the stem lineage of Fagales, and *Ceratopetalum gummiferum* (crown group Cunoniaceae). Helicopter-like fruits with expanded calyx lobes are not present in the order Saxifragales (Soltis, 2007; Carlswald *et al.*, 2011) and fruits of Fagales typically are nuts or samaras (Kubitzki *et al.*, 1993; Larson-Johnson, 2016). Some fagalean taxa have helicopter-like fruits such as the juglandaceous *Cruciptera* Manchester and *Polyptera* Manchester et Dilcher and the betulaceous *Asterocarpinus* Manchester and Crane, but the fruit wings in these genera are derived from bracts (Manchester & Dilcher, 1982, 1997; Manchester & Crane,



**Fig. 3** Detailed view of two styles of *Ceratopetalum suciensis* Tang & Atkinson sp.nov., KUPB 19169. (a) Three-dimensional reconstruction of the fossil fruit showing persistent stamens and two styles. Bar, 1 mm. (b) Digital longitudinal section showing the two styles. Bar, 4 mm. (c, d) Longitudinal sections of fruit, each section shows one of two styles. Slide nos. 30 959, 30 964, Bar, 5 mm. (e) Top-down view of the 3D reconstruction. Bar, 1 mm. (f) Digital cross-section showing the two styles. Bar, 4 mm. Colors: white, calyx/wings; orange, styles and nectary disk; green, stamen; blue, hypanthium. w, wings; n, nectary lobe; st, stamen; s, styles; fb, fruit body.

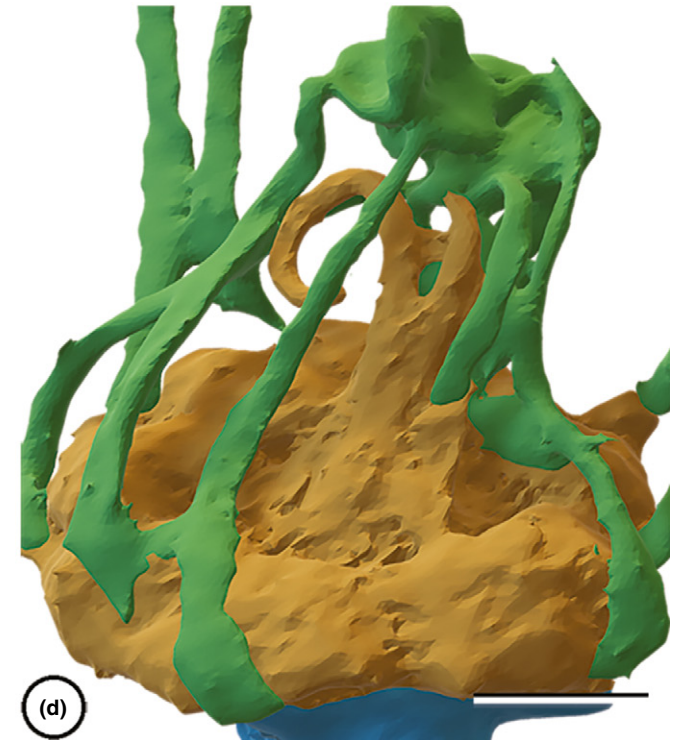
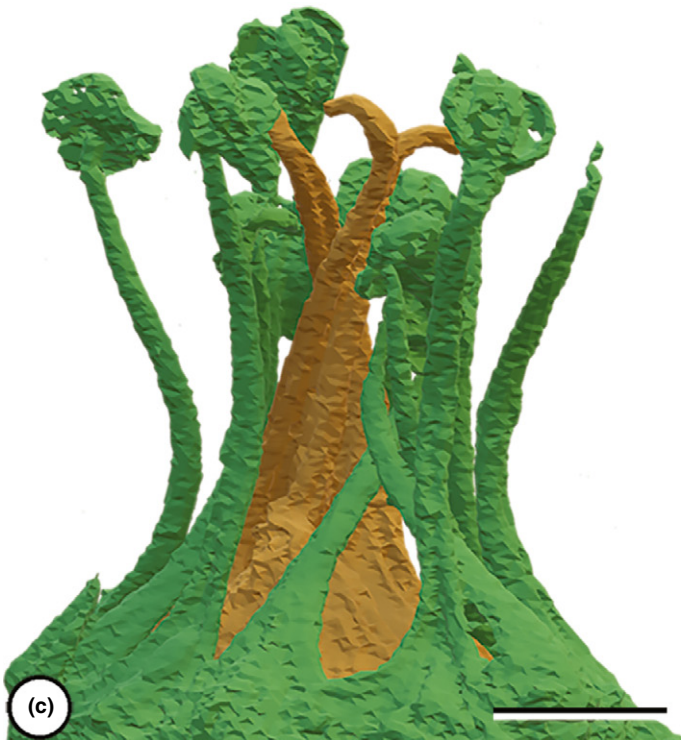
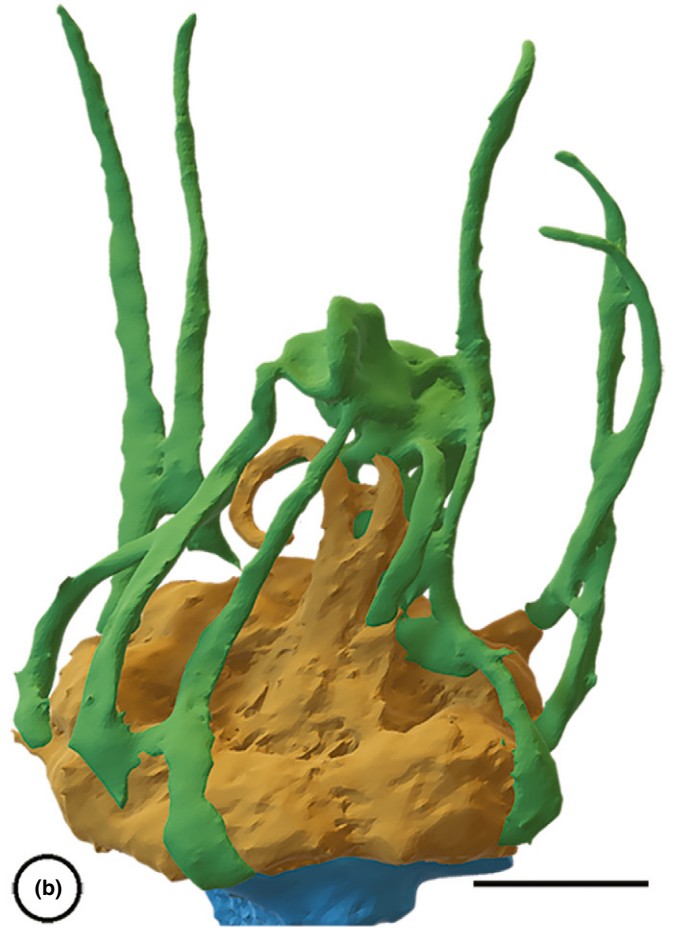
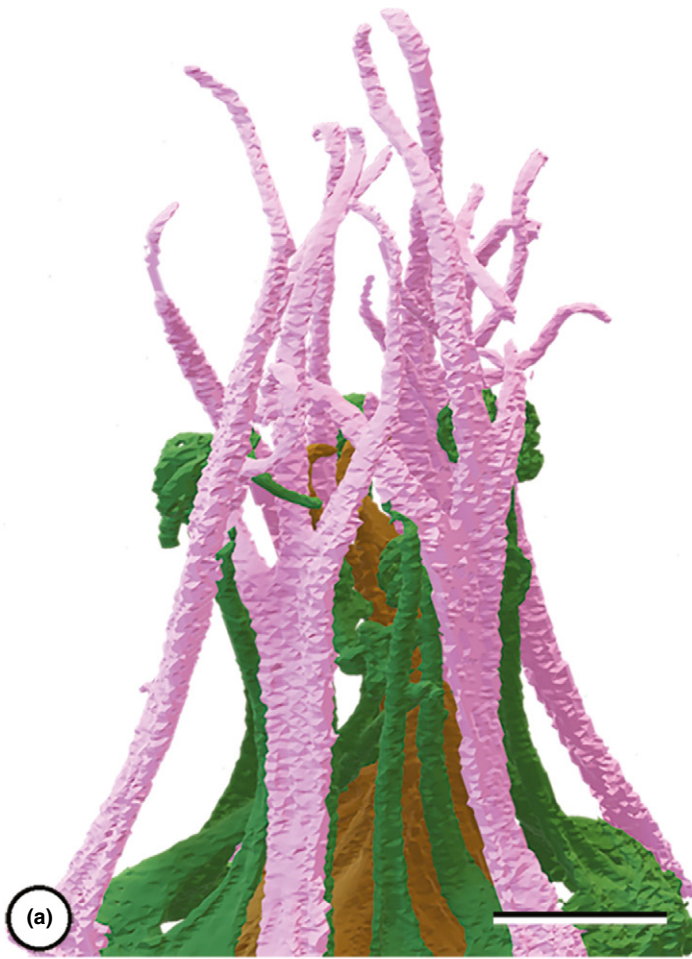


**Fig. 4** Three-dimensional reconstructions of extant fruits of *Ceratopetalum gummiferum*, *C. apetalum* and *C. corymbosum*. Colors: white, calyx/wings; orange, styles and nectary disk; green, stamen; blue, hypanthium. (a) *Ceratopetalum gummiferum* with persistent petals. A00969696, Bar, 4 mm. (b) *Ceratopetalum apetalum* showing two styles, diplostemonous stamens, and five wings. A00969698, Bar, 4 mm (c) *Ceratopetalum corymbosum* with five calyx lobes. A00969697, Bar, 2 mm.

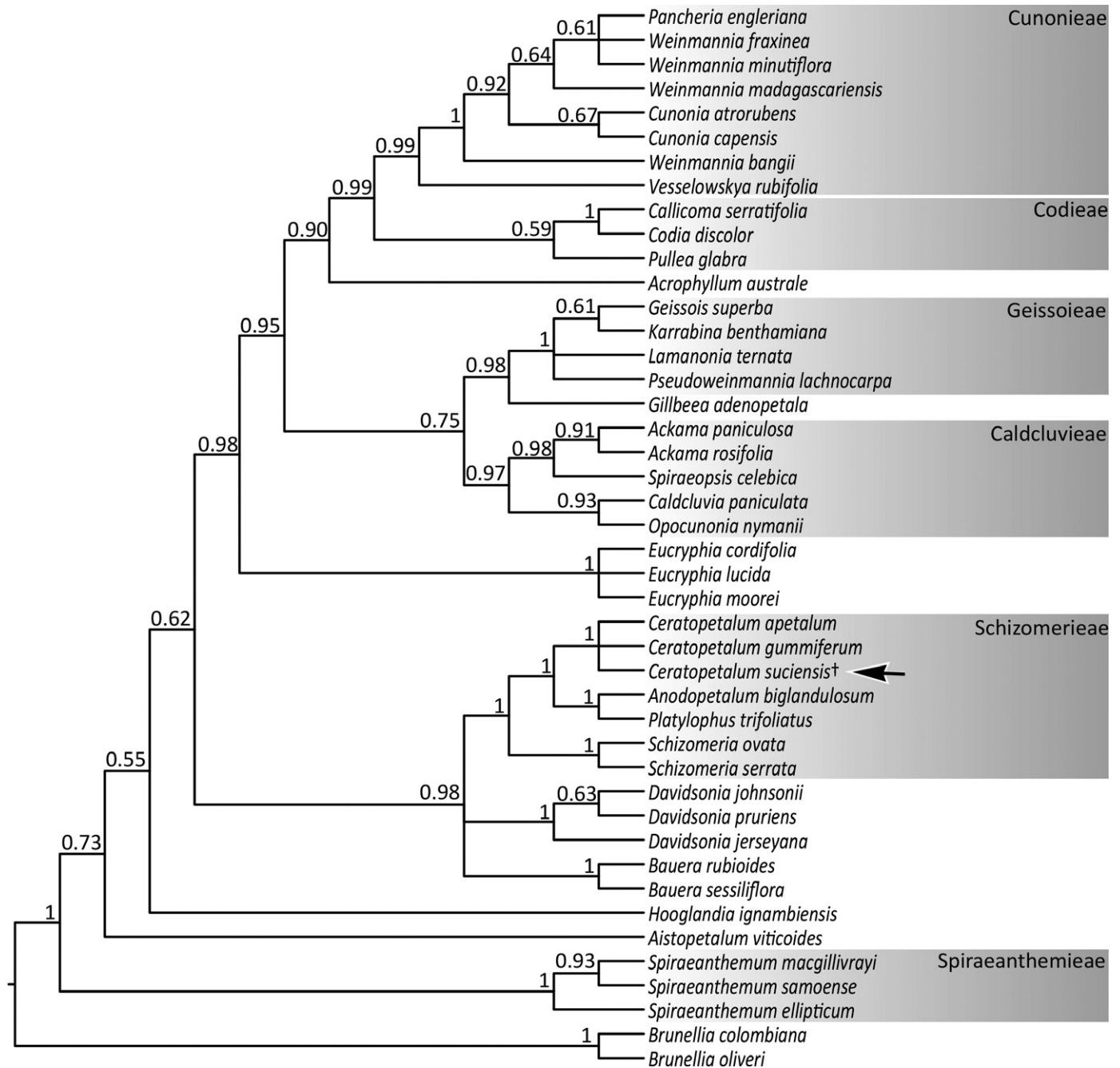
1987; Manchester, 1991), rather than perianth as seen in *C. suciensis*. In addition, no reported stem Fagales have a fruit morphology similar to *C. suciensis* (see Larson-Johnson, 2016). Therefore, Saxifragales and stem Fagales are excluded from taxonomic consideration. The extinct genus *Calycites* Massalongo, of unknown familial affinity, also has an epigynous perianth and produces helicopter-like fruits (Crane, 1988). Distinct midribs

on the fruit wings and longitudinal ribbing present on the ovary of *Calycites* differentiates this genus from *C. suciensis*. Furthermore, persistent floral characters other than calyx lobes are not known for *Calycites*. Additionally, as branches leading to other angiosperm families that produce helicopter fruits such as Caprifoliaceae (see Crane, 1988), Malpighiaceae and Dipterocarpaceae were not recovered as most parsimonious positions for





**Fig. 5** Detailed view of *Ceratopetalum gummiferum* (A00969696) and *C. corymbosum* (A00969697) fruits with the wings removed for a better view of the androecium and gynoecium. Colors: white, calyx/wings; orange, styles and nectary disk; green, stamen; blue, hypanthium. (a) *Ceratopetalum gummiferum* fruit with persistent petals on the fruit. Bar, 1.0 mm. (b) *Ceratopetalum corymbosum* fruit with persistent stamens and two styles. Bar, 0.68 mm. (c) *Ceratopetalum gummiferum* fruit with persistent stamens and three styles present. Bar, 0.8 mm. (d) A magnified view of *C. corymbosum*. Bar, 0.57 mm.



**Fig. 6** Majority rules consensus tree from Bayesian phylogenetic analysis showing position of *Ceratopetalum suciensis* (arrow) within Cunoniaceae. Numbers above the branches are posterior probability values. † Indicates fossil taxon. Tribes are indicated by the gray shading.

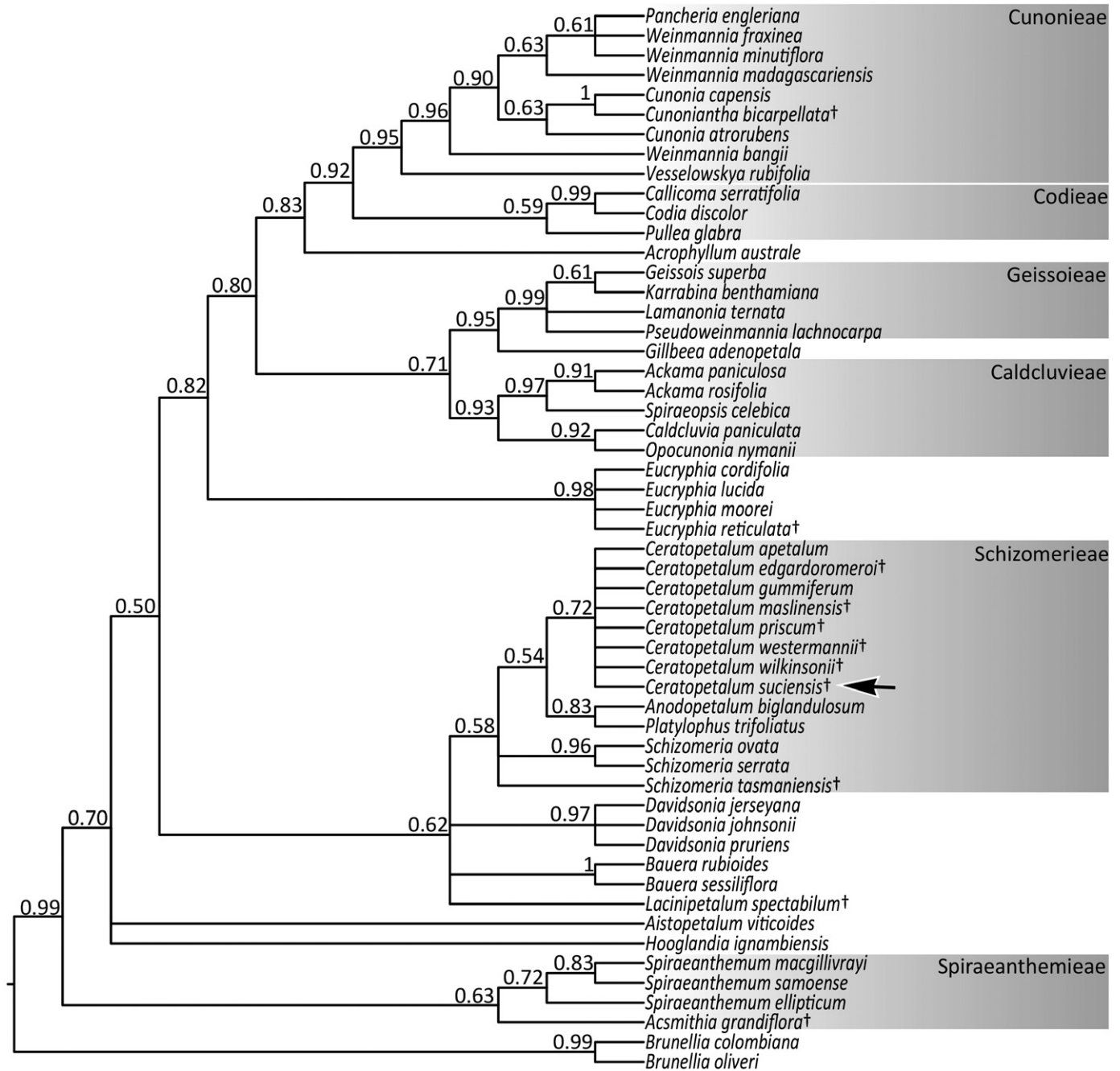
*C. suciensis*, these families were excluded from taxonomic consideration. This is a consequence of differences in overall floral morphology: for instance, Caprifoliaceae flowers are typically

zygomorphic with a fused perianth (Hofmann & Bittrich, 2016), flowers in Malpighiaceae have superior ovaries (Anderson, 1979), and most Dipterocarpaceae flowers have a superior ovary and a

single style with a stylopodium (Ashton, 2003). Our Bayesian phylogenetic analyses that focused on Cunoniaceae also support the placement of *C. suciensis* fruits within the genus *Ceratopetalum*.

The fruit morphology of *C. suciensis* is clearly diagnostic of the genus *Ceratopetalum*. As shown in our micro-computed tomography ( $\mu$ 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, interwing veins, persistent stamens, a semi-inferior ovary that slightly extends above the attachment of the perianth, and two (rarely three) persistent styles

(Hoogland, 1960; Dickison, 1984; Barnes & Hill, 1999; Fortune Hopkins & Hoogland, 2002; Rozefelds & 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 (Dickison, 1975; Barnes & Hill, 1999; Table S5). In addition, located in the sinus area between adjacent calyx lobes, there are interwing veins that connect lateral veins of adjacent wings (Barnes & Hill, 1999; Gandolfo & Hermsen, 2017). The androecium is diplostemonous with two alternating whorls of 8–10 stamens. The two styles are closely appressed to



**Fig. 7** Majority rules consensus tree from Bayesian phylogenetic analysis including 10 additional fossils. Arrow indicates position of *Ceratopetalum suciensis*. Numbers above branches are posterior probability values. † Indicates fossil taxon. Tribes are indicated by the gray shading.

one another. These characters are used to identify *Ceratopetalum* in the fossil record (Holmes & Holmes, 1992; Barnes & Hill, 1999; Gandolfo & Hermsen, 2017) and, as documented in the description, *C. suciensis* clearly has all of these characters.

### 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 Myr ago (Ma) (Magallón *et al.*, 2015; Ramírez-Barahona *et al.*, 2020). Moreover, reported crown ages of Cunoniaceae range from 83.32 to 63.49 Ma (Heibl & Renner, 2012; Ramírez-Barahona *et al.*, 2020). Much of this uncertainty in the age of the family comes from the difficulty of distinguishing stem and crown members from Cretaceous deposits.

Before this study, the only accepted Cretaceous fossils for the family were pollen and wood from the Santonian–Maastrichtian of Antarctica and Patagonia (Cranwell, 1959; Askin, 1992; Baldoni & Askin, 1993; Poole *et al.*, 2000a, 2003; Carpenter & Rozefelds, 2020); however, owing to the limited taxonomic resolution of these particular structures, it is unclear whether those fossils are stem or crown members. Moreover, there are a few equivocal reports of cunoniaceous flowers from Late Cretaceous deposits including *Tropidogyne* Chambers, Poinar & R.T. Buckley from the Cenomanian of Myanmar (Chambers *et al.*, 2010; Poinar & Chambers, 2017, 2019; Poinar Jr. *et al.*, 2021) and *Platydiscus* Schönenberger & Friis from the Santonian–Campanian of Europe (Schönenberger *et al.*, 2001). These fossils have been challenged as being cunoniaceous (see Gandolfo & Hermsen, 2017; Jud *et al.*, 2018; Carpenter & Rozefelds, 2020) because their floral morphology is not entirely consistent with the crown group of the family. Our phyloscan analysis recovered multiple most parsimonious positions for *Tropidogyne pentaptera* among several eudicot families, none of which are Cunoniaceae. In addition, crown Cunoniaceae were not recovered as a most parsimonious position for *Platydiscus peltatus*. Overall, the phyloscan analyses suggest 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 & Gandolfo, 2020). These reports clearly indicate that the diversification of the family was well underway by the Cretaceous–Paleogene boundary. Until now, extant genera have yet to be identified before the Eocene, suggesting that the early evolution of crown Cunoniaceae primarily comprised a diversification of extinct genera near the Cretaceous–Paleogene boundary of Gondwana. However, our report of *C. suciensis* provides the first unequivocal evidence for crown Cunoniaceae in the Cretaceous, which indicates that the initial diversification of the family was well underway by the Campanian and comprised at least one extant genus as well. Based on this report, a conservative minimal clade age for the family can be considered as 80 Ma.

### Paleobiogeographical implications

Although the breakup of Gondwana began during the Jurassic, many of the landmasses that made up the southern super continent were still united or in sufficiently close proximity to one another to allow dispersal and migration across one another throughout the Mesozoic and into the Paleogene. As detailed by the fossil record, biogeographical connections between Australia, South America and Antarctica were the last to persist until the Eocene (discussed in Wilf *et al.*, 2013). These connections facilitated a nearly continuous rainforest biome across these three continents with constituent plants known as Paleo-Antarctic Rainforest Lineages (PARLs; discussed in Kooyman *et al.*, 2014; Wilf *et al.*, 2019). Although some PARLs, such as Araucariaceae and Winteraceae, were nearly cosmopolitan during the Mesozoic (Kunzmann, 2007; Kooyman *et al.*, 2014; Brea *et al.*, 2021), most are traditionally thought to have been restricted to the Southern Hemisphere throughout their evolutionary history; this includes *Ceratopetalum* and other Cunoniaceae.

Before this study, the entire reported biogeographical history of Cunoniaceae was restricted to the Southern Hemisphere (discussed in Carpenter & Rozefelds, 2020). Cunoniaceous fossil pollen and wood have been recovered from the Late Cretaceous (Santonian–Maastrichtian) of Patagonia and Antarctica (Cranwell, 1959; Askin, 1992; Baldoni & Askin, 1993; Poole *et al.*, 2000a, 2003) and at the onset of the Cenozoic Cunoniaceae were diverse in South America and Australia (Holmes & Holmes, 1992; Barnes & Hill, 1999; Barnes *et al.*, 2001; Gandolfo & Hermsen, 2017; Jud *et al.*, 2018; Jud & Gandolfo, 2020). These, along with slightly younger records, reflect that the family was part of the expansive Gondwanan rainforest biome during the Late Cretaceous and Paleogene (Kooyman *et al.*, 2014; Barreda *et al.*, 2021), before the final breakup of the supercontinent. This biogeographical pattern is well-exemplified by *Ceratopetalum*. Previously, fossil *Ceratopetalum* was known only from the Cenozoic of Patagonia and Australia (Holmes & Holmes, 1992; Barnes & Hill, 1999; Gandolfo & Hermsen, 2017), and today the genus 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 paleogeographical range and provides a Northern Hemisphere legacy for what was formerly considered a strictly Southern Hemisphere lineage.

This dramatic geographical range expansion is somewhat 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, 2005; Goin *et al.*, 2006). This hypothesis is based largely on reports of primarily Northern Hemisphere vertebrates, such as hadrosaurs and nodosaurids, recovered from Coniacian–Maastrichtian deposits in Antarctica. Based on stratigraphic and biogeographical 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 to this (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 *Regnellidium* (Batten *et al.*, 2011; Cúneo *et al.*, 2013) and some nymphaleans (Gandolfo & Cuneo, 2005; Friis *et al.*, 2017). Poole *et al.* (2000b) reported *Sassafrasoxylon* Brezinová et Süss from Late Cretaceous deposits in Antarctica and cautiously discussed that *Sassafras* J. Presl, which today is restricted to the Northern Hemisphere, may have had a Gondwanan origin. Recent work by Viñola-López *et al.* (2021) revealed terrestrial plant and animal assemblages from Campanian–Maastrichtian deposits in Cuba indicating that islands in the Caribbean Seaway may have facilitated NA-SA–A biotic exchanges during the Late Cretaceous.

Considering that Cunoniaceae wood and pollen from Antarctica are nearly contemporaneous with *C. suciensis*, the Cretaceous distribution of Cunoniaceae fits well within the NA-SA–A scenario. This distribution could be explained by long-distance dispersal and/or migration, similar to the vertebrates discussed above. However, it also is 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). Regional extinctions within northern regions since the Cretaceous likely restricted the family's geographical range to the Southern Hemisphere, but it is striking that there are no other reliable fossil records of Cunoniaceae elsewhere in the Northern Hemisphere. We also note that 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 biogeographical patterns. Nonetheless, given the previously recorded current and Cenozoic distribution of *Ceratopetalum*, the recovery of *C. suciensis* from the Cretaceous of the western coast of North America suggests a more complicated biogeographical history for this important Paleo-Antarctic Rainforest Lineage and potentially others.

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## Author contributions

KKT and BAA conceptualized the project; BAA designed the methodology; SYS collected micro-CT data and KKT prepared 3D reconstructions and datasets to carry out analyses; and KKT wrote the original draft of the manuscript. All authors contributed to the review and edits of subsequent drafts of the manuscript.

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## Data availability

*Ceratopetalum suciensis* fossils are curated at the University of Kansas Paleobotanical Collections (Biodiversity Institute) on behalf of the Washington State Parks Commission. Extant fruits were provided by L.H. Bailey Hortorium Herbarium and Harvard University Gray Herbarium (Table S1). All  $\mu$ CT scans can be accessed on Morphosource under the project title '3D Morphology of *Ceratopetalum* fruits (Cunoniaceae)'. GenBank accession numbers can be found in the Supporting Information (Table S3). Data associated with phylogenetic analyses can be found on Morphobank (project P3906, matrix 27 164) or in the Supporting Information.

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Fig. S1** ‘Fan’-shaped phyloscan output for *Ceratopetalum suciensis*.

**Fig. S2** ‘Long’-shaped phyloscan output for *Ceratopetalum suciensis*.

**Fig. S3** ‘Fan’-shaped phyloscan output for *Tropidogyne pentaptera*.

**Fig. S4** ‘Long’-shaped phyloscan output for *Tropidogyne pentaptera*.

**Fig. S5** ‘Fan’-shaped phyloscan output for *Platydiscus peltatus*.

**Fig. S6** ‘Long’-shaped phyloscan output for *Platydiscus peltatus*.

**Table S1** List of scanned fruits and herbarium accession numbers.

**Table S2** List of scan parameters.

**Table S3** List of taxa and GenBank accession numbers.

**Table S4** Floral characters for fossil species of *Ceratopetalum*.

**Table S5** Floral characters for extant species of *Ceratopetalum*.

**Notes S1** Tree file used in phyloscan.

**Notes S2** Character matrix used for phyloscan.

**Notes S3** MRBAYES tree files.

**Video S1** Digital cross-sections of *Ceratopetalum suciensis*.

**Video S2** Digital longitudinal sections of *Ceratopetalum suciensis*.

**Video S3** 3D model of *Ceratopetalum suciensis*.

**Video S4** 3D model of *Ceratopetalum succirubrum*.

**Video S5** *Ceratopetalum suciensis* and *C. succirubrum* in comparison.

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