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Fossil evidence from South America for the diversification of Cunoniaceae by the earliest Palaeocene

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• **Background and Aims** Cunoniaceae are woody plants with a distribution that suggests a complex history of Gondwanan vicariance, long-distance dispersal, diversification and extinction. Only four out of ~27 genera in Cunoniaceae are native to South America today, but the discovery of extinct species from Argentine Patagonia is providing new information about the history of this family in South America.
• **Methods** We describe fossil flowers collected from early Danian (early Palaeocene, ~64 Mya) deposits of the Salamanca Formation. We compare them with similar flowers from extant and extinct species using published literature and herbarium specimens. We used simultaneous analysis of morphology and available chloroplast DNA sequences (*trnL–F*, *rbcL*, *matK*, *trnH–psbA*) to determine the probable relationship of these fossils to living Cunoniaceae and the co-occurring fossil species *Lacinipetalum spectabilum*.
• **Key Results** *Cunoniantha bicarpellata* gen. et sp. nov. is the second species of Cunoniaceae to be recognized among the flowers preserved in the Salamanca Formation. *Cunoniantha* flowers are pentamerous and complete, the anthers contain *in situ* pollen, and the gynoecium is bicarpellate and syncarpous with two free styles. Phylogenetic analysis indicates that *Cunoniantha* belongs to crown-group Cunoniaceae among the core Cunoniaceae clade, although it does not have obvious affinity with any tribe. *Lacinipetalum spectabilum*, also from the Salamanca Formation, belongs to the Cunoniaceae crown group as well, but close to tribe Schizomerieae.
• **Conclusions** Our findings highlight the importance of West Gondwana in the evolution of Cunoniaceae during the early Palaeogene. The co-occurrence of *C. bicarpellata* and *L. spectabilum*, belonging to different clades within Cunoniaceae, indicates that the diversification of crown-group Cunoniaceae was under way by 64 Mya.

Key words: Gondwana, fossil flowers, Argentina, palaeobotany, Danian, parsimony.

INTRODUCTION

The distribution of Cunoniaceae throughout tropical and southern temperate forests suggests a deep Gondwanan legacy (Raven and Axelrod, 1974; Carpenter and Buchanan, 1993; Bradford *et al.*, 2004). The family includes 28 extant genera and six tribes, but six of the genera are not assigned to a tribe (Fig. 1). Several species groups have intercontinental distributions, such as *Cunonia* L., *Eucryphia* Cav., Geissoieae, Schizomerieae and *Weinmannia* L. (Bradford and Barnes, 2001; Sweeney *et al.*, 2004; Hopkins *et al.*, 2013), but disentangling the relative importance of vicariance, long-distance dispersal, extinction and diversification in explaining these disjunctions depends on direct evidence of ancient distributions from the fossil record (Pole, 1994, 2001; Barnes *et al.*, 2001; Sanmartín and Ronquist, 2004; Wilf and Escapa, 2015).

The rich fossil record of Cunoniaceae in Australia provides evidence of at least 11 genera during the Cenozoic, but limited Cretaceous outcrops obscure the earlier history of the family on the continent (Barnes *et al.*, 2001). Elsewhere, fossil occurrences of the family are comparatively rare; therefore, new discoveries have the potential to provide valuable information about the evolution and biogeographic history of Cunoniaceae (e.g. Gandolfo and Hermsen, 2017). In South America and the Antarctic Peninsula (Fig. 2), fossil woods (Petriella, 1972; Archangelsky, 1973; Baldoni and Askin, 1993; Raigemborn *et al.*, 2009) and pollen (Archangelsky, 1973; Romero and Archangelsky, 1986; Troncoso, 1991; Zamaloa, 2000) ascribed to Cunoniaceae have been known for decades, but their possible relationships to extant tribes have not been evaluated through phylogenetic analyses.

Here, we build on an earlier study (Jud *et al.*, 2018*a*) by describing a second extinct species of Cunoniaceae from fossil flowers collected from the Salamanca Formation (earliest Palaeocene, ~64 Mya) in Patagonia, Argentina. The fossils have a combination of character states that indicates a close relationship with the syncarpous members of Cunoniaceae. We use phylogenetic analyses to explore the relationships of this new species and of *Lacinipetalum spectabilum* (Jud *et al.*, 2018*a*) to other living and extinct members of the family. Finally, we discuss the implications of the co-occurrence of these two species at an early Palaeocene site in Patagonia for understanding the diversification of Cunoniaceae.

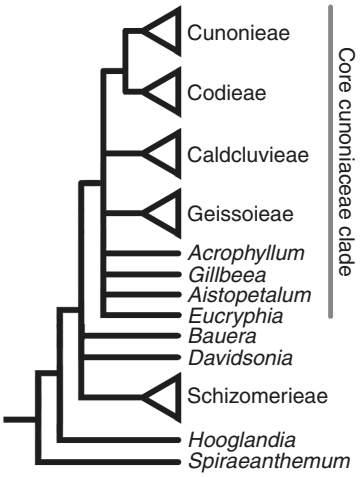

FIG. 1. Summary of phylogenetic relationships among Cunoniaceae based on previous work (Bradford and Barnes, 2001; Sweeney *et al.*, 2004; Hopkins *et al.*, 2013).

MATERIALS AND METHODS

Geological setting

The Salamanca Formation crops out in the San Jorge Basin in Patagonia, Argentina. It consists primarily of estuarine and shallow marine deposits and yields abundant plant micro- and megafossils (Berry, 1937; Romero, 1968; Petriella, 1972; Iglesias *et al.*, 2007; Brea *et al.*, 2008; Zucol *et al.*, 2008; Futey *et al.*, 2012; Jud *et al.*, 2017, 2018*a*, *b*; Ruiz *et al.*, 2017; Andruchow-Colombo *et al.*, 2019; Hermsen *et al.*, 2019). The Salamanca Formation overlies the Cretaceous Chubut Group and underlies the Palaeocene–Eocene Río Chico Group (Clyde *et al.*, 2014; Comer *et al.*, 2015). The fossils described here were collected from the Palacio de los Loros-2 (PL-2) locality in the lower part of the formation in south-eastern Chubut Province (Iglesias *et al.*, 2007). The age of the PL-2 locality is constrained to geomagnetic polarity chron C28n. Comer *et al.* (2015) dated this chron to 64.67–63.49 Ma (early Danian) on the 2012 Geomagnetic Polarity Timescale, but the age of the lower boundary was revised to 64.535 ± 0.040 Ma by Clyde *et al.* (2016). This site yields an allochthonous assemblage of leaves, fruits and flowers, but so far Cunoniaceae have not been identified among the dicot leaves (Iglesias *et al.*, 2007). The fossils are preserved in a grey clay shale that is interpreted as a swale between point-bar ridges of a tidally influenced fluvial channel that meandered across the coastal flats (Comer *et al.*, 2015).

All necessary permits were obtained for this study, which complied with all relevant regulations. Coordinates for the locality are on file at the Museo Paleontológico Egidio Feruglio (MEF), Trelew, Chubut, Argentina.

FIG. 2. Map of southern South America and the Antarctic Peninsula showing the occurrences of macrofossils identified to Cunoniaceae. (1) Williams Point Beds (Upper Cretaceous), Williams Point, Antarctica (Poole *et al.*, 2000). (2) Salamanca Formation (Palaeocene), Chubut Province, Argentina (Jud *et al.*, 2018*a*; this study). (3) Peñas Coloradas Formation (Palaeocene), Chubut Province, Argentina (Raigemborn *et al.*, 2009). (4) Cerro Bororó Formation (Palaeocene), Chubut Province, Argentina (Petriella, 1972). (5) Fossil Hill Formation (Eocene), King George (25 de Mayo) Island, Antarctica (Zhang and Wang, 1994). (6) Sobral Formation (Palaeocene), Seymour (Marambio) Island, Antarctica (Poole *et al.*, 2003). (7) Lopez de Bertodano Formation (Palaeocene), Seymour Island, Antarctica (Poole *et al.*, 2003). (8) La Meseta Formation (Eocene), Seymour Island, Antarctica (Poole *et al.*, 2003). (9) Fildes Formation (Eocene) King George Island, Antarctica (Poole *et al.*, 2001, Francis and Poole, 2002). (10) Huitrera Formation (Eocene), Chubut Province, Argentina (Hermsen *et al.*, 2010; Gandolfo and Hermsen, 2017). (11) Ligorio Márquez Formation (Eocene), Chile (Terada *et al.*, 2006). (12) Ligorio Márquez Formation (Eocene), Chile (Carpenter *et al.*, 2018) (13) 'Forest Bed' (Miocene), West Point Island, Falkland (Malvinas) Islands (Poole and Cantrill, 2007). (14) Seymour Island (Cretaceous), Antarctica (Pujana *et al.*, 2018).

Fossil preparation

The fossils were collected over the course of four field seasons (2005, 2009, 2011 and 2012) and are curated at the Palaeobotanical Collection of the Museo Paleontológico Egidio Feruglio (MPEF-Pb), Trelew, Chubut, Argentina. We captured images of macroscopic features with a Canon EOS 7D DSLR camera and microscopic details were photographed with a Nikon DS Fi1 camera mounted on a Nikon SMZ1000 stereoscope at the MEF. We used epifluorescence microscopy to examine the anthers for preserved pollen grains. We captured images of fossil and modern pollen grains with a Jeol NeoScope JCM-5000 scanning electron microscope at the Paleontological

Research Institute (PRI), Ithaca, NY, USA. We processed the images using whole-image manipulations only with Adobe Photoshop CC 2017 (San Jose, CA, USA).

Molecular data

We began by obtaining the *trnL–F* and *rbcL* sequence data used by Bradford and Barnes (2001) from GenBank. We modified the dataset to include additional *trnL–F* and *rbcL* sequence data from GenBank. We also modified the dataset to reflect changes to the taxonomy since the work of Bradford and Barnes (2001), including the synonymy of *Acsmithia* Hoogland with *Spiraeanthemum* A.Gray (Pillon *et al.*, 2009), the segregation of *Karrabina* Rozefelds & H.C.Hopkins from *Geissois* Labill. (Hopkins *et al.*, 2013) and the rediscovery of *Hooglandia ignambiensis* (McPherson and Lowry, 2004). We used one exemplar species for each section of *Weinmannia* (Bradford, 2002). Next, we searched for additional informative sequences available on GenBank using the BLAST search tool and obtained *matK* and the *trnH–psbA* intergenic spacer region sequences for nine and seven species, respectively (Table 1).

We used Brunelliaceae (represented by *Brunellia colombiana* Cuatrec. and *B. oliveri* Britton) as the outgroup. Cunoniaceae form a clade with Brunelliaceae, Cephalotaceae and Elaeocarpaceae (Moody and Hufford, 2000; Bradford and Barnes, 2001; Sun *et al.*, 2016; Valencia *et al.*, 2020), but the sister taxon of Cunoniaceae is unclear. We did not use Cephalotaceae because they are morphologically specialized herbaceous pitcher plants and we did not use Elaeocarpaceae because the alignment of the *trnL–F* sequences with Cunoniaceae was ambiguous.

We aligned each locus independently using MUSCLE v. 3.8.31 in Aliview v. 1.18 (Larsson, 2014). The final concatenated matrix of sequence data (Supplementary Data NEXUS file) consists of the *trnL* intron (36 species, positions 1–618), the *trnL–F* intergenic spacer (36 species, positions 619–1167), *rbcL* (31 species, positions 1168–2638), *matK* (9 species, positions 2639–4151) and *trnH–psbA* (7 species, positions 4152–4752).

Table 1. *GenBank accession numbers for each sequence used in the phylogenetic analyses*

Term	tRNA-Leu (*trnL*) *trnL c–d*	*trnL–F* intergenic spacer *trnL e–F*	*rbcL*	*matK*	*trnH–psbA*
Ackama rosifolia	AF299162	AF299215	KT626660	NA	NA
Acrophyllum australe	AF299168	AF299221	AF291926	NA	NA
Anodopetalum biglandulosum	AF299175	AF299228	AF291932	NA	NA
Bauera rubioides	AF299183	AF299236	L11174.2	NA	NA
Bauera sessiliflora	AF299184	AF299237	NA	NA	NA
Brunellia colombiana	AF299181	AF299234	AF291937	NA	NA
Brunellia oliveri	AF299182	AF299235	AF291938	NA	NA
Caldcluvia paniculata	AF299163	AF299216	AF291922	NA	NA
Callicoma serratifolia	AF299170	AF299223	AF291928	KM894952	NA
Ceratopetalum apetalum	NA	NA	KM895900	KM894747	KM895248
Ceratopetalum gummiferum	AF299176	AF299229	L01895	NA	NA
Codia discolor	AF299171	AF299224	AF291929	NA	NA
Cunonia atrorubens	AF299154	AF299207	AF291918	NA	NA
Cunonia capensis	AF299156	AF299209	NA	JX517913	NA
Davidsonia jerseyana	AF299185	AF299238	AF206759	AY935930	NA
Davidsonia johnsonii	AF299186	AF299239	KM895905	NA	KM895252
Eucryphia cordifolia	AF299173	AF299226	AF291931	KF224980	NA
Eucryphia moorei	AF299174	AF299227	NA	NA	NA
Geissois superba	AF299166	AF299219	NA	NA	NA
Gillbeea adenopetala	AF299169	AF299222	AF291927	NA	NA
Hooglandia ignambiensis	AY549639	AY549640	AY549641	NA	NA
Karrabina benthamiana	AF299165	AF299218	AF291924	NA	KM895230
Lamanonia ternata	JX236029	JX236029	JX236032	MG833493	KF421056
Opocunonia nymanii	NA	NA	MH826693	NA	MH826497
Pancheria engleriana	AF299158	AF299211	AF291919	NA	NA
Platylophus trifoliatus	AF299177	AF299230	AF291933	JX517817	NA
Pseudoweinmannia lachnocarpa	AF299167	AF299220	AF291925	NA	NA
Pullea glabra	AF299172	AF299225	AF291930	NA	NA
Schizomeria ovata	AF299178	AF299231	KM895629	KM894933	KM895087
Schizomeria serrata	JX236028	JX236028	JX236031	NA	NA
Spiraeanthemum samoense	AF299180	AF299233	AF291936	NA	NA
Spiraeanthemum ellipticum	EU867222	EU867222	AF291935	NA	NA
Spiraeopsis celebica	AF299164	AF299217	AF291923	NA	NA
Vesselowskya rubifolia	AF299160	AF299213	AF291920	NA	NA
Weinmannia bangii	AF299145	AF299198	AF291915	NA	NA
Weinmannia fraxinea	AF299149	AF299202	NA	AM889750	GQ248402
Weinmannia madagascarensis	AF299152	AF299205	AF291916	NA	NA
Weinmannia minutiflora	AF299150	AF299203	NA	NA	NA
Weinmannia raiateensis			AF291917	NA	GQ248402
Lacinipetalum spectabilum	NA	NA	NA	NA	NA
Cunoniantha bicarpellata	NA	NA	NA	NA	NA

Morphological data

We examined the matrix of morphological characters used by Bradford and Barnes (2001) and modified several characters. Leaf arrangement is treated as unordered to remove any assumption about how this character evolves. Marginal tooth vascularization was replaced with secondary vein framework following Ellis *et al.* (2009). The stipule characters are modified from present/absent and lateral/interpetiolar/axillary to a single character where the various stipule types are considered alternative states along with the absence of stipules (Rutishauser and Dickison, 1989; Dickison and Rutishauser, 1990). We replaced the character of petal morphology (entire/incised) with a more complex set of four states to reflect the diversity of venation, shape, and type of incision across the family: ovate to obovate and single veined/large multiveined–obovate/flabellate incised/retuse. We used these new character states because we doubt the homology between the pattern of petal incision in Schizomerieae (Barnes and Rozefelds, 2000; Rozefelds and Barnes, 2002; Hopkins, 2018) and the retuse glandular petals of *Gillbeea* F.Muell. (Endress and Matthews, 2006). We also added new characters. These include winged rachis (absent/present), diffuse axial parenchyma in the wood (absent/present), irregular discontinuous bands of axial parenchyma in the wood (absent/present), regular bands of axial parenchyma in the wood (absent/present), number of parts per perianth whorl, number of stamens, anther attachment, number of carpels, texture of the ovary, type of stigma and accrescent calyx. We circumscribed character states with the aims of limiting polymorphic terminals and identifying clear discontinuities in interspecific variation. We coded the character states using descriptions and illustrations available in the literature and with herbarium specimens at the L. H. Bailey Hortorium Herbarium (BH), Cornell University, Ithaca, NY, USA (Supplementary Data Table S1). Missing data associated with the fossil taxa are unknown because the flowers have not yet been matched to co-occurring fossilized leaves, wood or fruits. All characters are treated as unordered. The final dataset comprises 41 taxa and 58 morphological characters. The character descriptions and morphological matrix are available online at the Morphobank website (www.morphobank.com; project P2600, matrix 26123).

Search strategy: parsimony analysis

We concatenated the molecular and morphological matrices using the 'new matrix merge' function in Winclada v. 1.99 spawned through ASADO version 1.99 (Nixon, 2008). The resulting matrix includes 41 taxa and 4810 total characters. Of these, 340 characters are parsimony-informative. We omitted all non-informative characters to optimize calculation of branch support values. To minimize *a priori* assumptions about character evolution and character importance, all characters were equally weighted and unpolarized. We conducted a tree search using NONA version 2.0 (Goloboff, 1999) spawned through ASADO version 1.99 (Nixon, 2008) using the following parameters: 'hold 1000; mult*100; hold/100', using the unconstrained 'mult*max*' search strategy. Bootstrap support values and jackknife values for branches were estimated by employing 1000 replicates, ten search pseudoreplicates and ten starting trees per pseudoreplicate. We then mapped the support values onto those branches also present in the strict consensus of the the most parsimonious trees.

RESULTS

Systematics

Order. Oxalidales Heintze.

Family. Cunoniaceae R.Br.

Genus. ***Cunoniantha*** **Jud & Gandolfo gen. nov.**

Type species. ***Cunoniantha bicarpellata*** **Jud & Gandolfo sp. nov.** (Figs 3 and 4A, B).

Generic diagnosis. Flowers pedicellate, perfect, hypogynous, actinomorphic, with two perianth whorls of five organs; sepals ovate, inserted at the margin of the floral disc; petals obovate, entire, and equal to or greater than the length of the sepals; androecium of five stamens in one cycle, alternipetalous, anthers dorsifixed, without a connective extension, thecae with longitudinal dehiscence, pollen tricolpate, prolate and reticulate; gynoecium superior, bicarpellate, syncarpous with two free styles; stigmas non-capitate, ovary pubescent.

Specific diagnosis. As for the genus *Cunoniantha*.

Etymology. The name *Cunoniantha* refers to the morphology of the flowers typical of the syncarpous Cunoniaceae, and the epithet refers to the bicarpellate gynoecium.

Holotype. 35MPEF-Pb 8523a, b.

Repository. Museo Paleontológico Egidio Feruglio Paleobotany Collection (MPEF-Pb), Trelew, Chubut, Argentina.

Type locality. Palacio de Los Loros-2 (PL-2), Chubut, Argentina.

Stratigraphic position and age. Lower Salamanca Formation; Palaeocene, early Danian (Clyde *et al.*, 2014; Comer *et al.*, 2015).

Description. The flowers are perfect, actinomorphic, and borne on a pedicel ~5.8 mm long (5.0–7.9 mm) (Fig. 3). Most flowers were recovered isolated, but one is attached to an axis with sub-opposite lateral scars (Fig. 3C) indicating that the flowers were borne on an inflorescence. Inflorescence type is variable in Cunoniaceae, but this fragment is more consistent with a thyrsoid or cymiform inflorescence structure than a capitate, racemose or paniculiform structure. The perianth is composed of calyx and corolla, each with five parts and whorled phyllotaxis. The sepals are free and ovate, their bases are broadly attached at the rim of the floral cup and their apices are acute and straight. Sepals are 4.5 mm long by 2.0 mm wide (n = 9) (Fig. 3A). The petals are alternisepalous, narrow, 0.8–1.5 mm wide and 3.4–3.8 mm long, slightly obovate, and entire with a

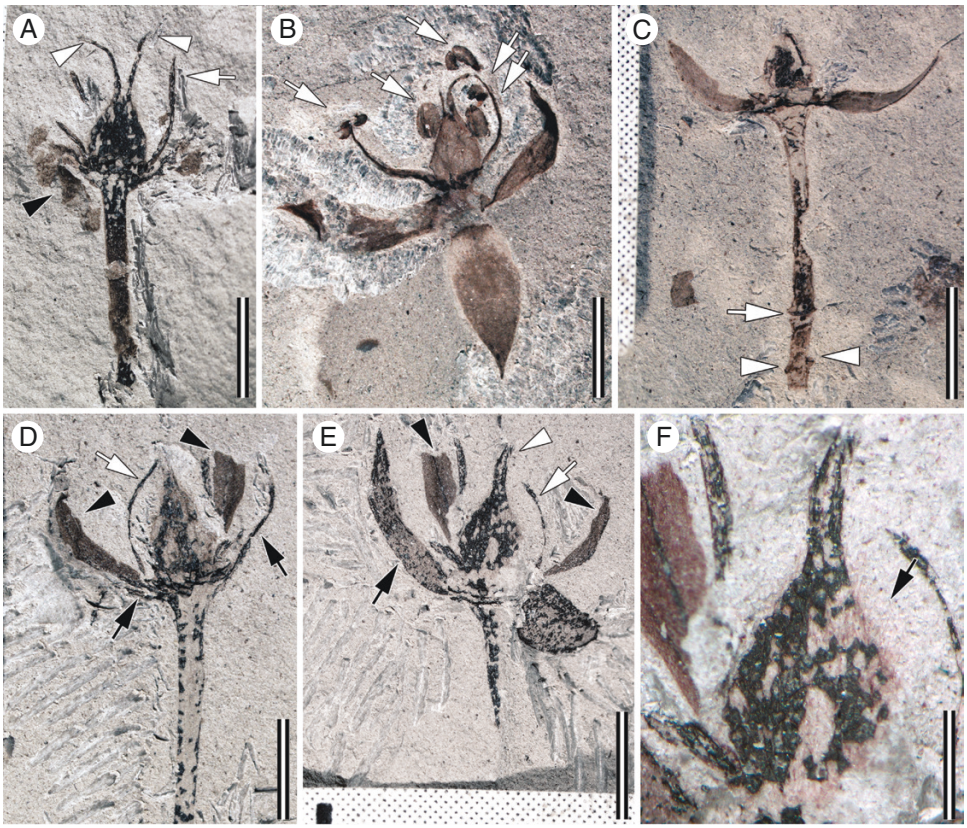

FIG. 3. Longitudinal views of 35T*Cunoniantha bicarpellata* Jud & Gandolfo gen. et sp. nov.35T specimens from PL-2 locality, Salamanca Formation. (A) Flower with pedicel, remains of petals (black arrowhead), filaments (white arrow), and a superior syncarpous ovary with two diverging styles (white arrowheads). MPEF-Pb 8523a. (B) Flower showing five anthers (arrows). MPEF-Pb 8545. (C) Flower attached to a partial possible thyrsoid/cymiform inflorescence. Note the abscission zone where the terminal flower is attached (at arrow) and the scars where other flowers or bracts were attached (at arrowheads). MPEF-Pb 8533. (D) Flower showing the pedicel, calyx (black arrows), petals (black arrowheads), filaments (white arrow) and a superior ovary. MPEF-Pb 8530b. (E) Counterpart of (D) showing pedicel, calyx (black arrow), petals (black arrowheads), filaments (white arrow) and a superior ovary with two parallel styles (white arrowhead). MPEF-Pb 8530a. (F) Close-up of (E) showing the pubescent ovary (black arrow). Scale bars: A–E = 3.0 mm; F = 1.0 mm.

single midvein (Fig. 3D, E). Individual specimens have up to five stamens preserved (Fig. 3B); the stamen filaments taper from the base towards the anther and are 2.8–3.9 mm long (Fig. 3B); the anthers are dorsifixed, introrse, and versatile with longitudinal dehiscence along a ventral slit, ~1.1 mm long by 0.9 mm wide (n = 5) (Figs 3A and 4A). They contain prolate, tricolpate pollen grains (18 µm × 12 µm; n = 3) with a reticulate tectum (Fig. 4A, B). The gynoecium is superior, bicarpellate, and syncarpous with two free diverging styles (Fig. 3A, B). The ovary is pubescent (Fig. 3F), 2.4 mm long by 1.7 mm wide (n = 7). The styles are ~2.1 mm long (n = 5) and have indistinct stigmas (Fig. 3A, B, D). At the base of the gynoecium in many specimens there are abundant coalified remains, suggestive of an annular or segmented floral disc (Fig. 3A, B, D). Floral formula: *Ca^5 Co^5 A^5 $G^{(2)}$.

Material examined. MPEF-Pb 8522, 8523, 8527, 8529, 8530, 8533, 8534, 8536, 8540, 8541, 8542, 8545, 9731, 9732, 9733.

Phylogenetic analyses

Parsimony analysis yielded 92 equally short trees of 748 steps (Fig. 5). The consistency index is 0.56 and the retention index is 0.69. In all trees, *Cunoniantha* is nested in the 'core Cunoniaceae' clade of Bradford and Barnes (2001), but outside the tribes. *Lacinipetalum* is sister to extant members of Schizomerieae in all trees. Bootstrap support values are generally low around the position of the fossil species, but this is typical when including taxa with a high proportion of missing data (Fig. 5).

DISCUSSION

The position of Cunoniantha

Character states that support the placement of *Cunoniantha* within Cunoniaceae include a pentamerous, actinomorphic perianth with free sepals and petals, dorsifixed versatile anthers with longitudinal dehiscence, reticulate tricolpate pollen <20 µm long in maximum diameter (e.g. Fig. 4C–E), and a superior syncarpous bicarpellate gynoecium with two free styles and non-capitate stigmas (Bradford *et al.*, 2004). Cunoniaceae are morphologically diverse; identification of morphological synapomorphies that apply to flowers across the entire family is challenging. Nonetheless, the combination of character states preserved in *Cunoniantha* falls within the range of variation for

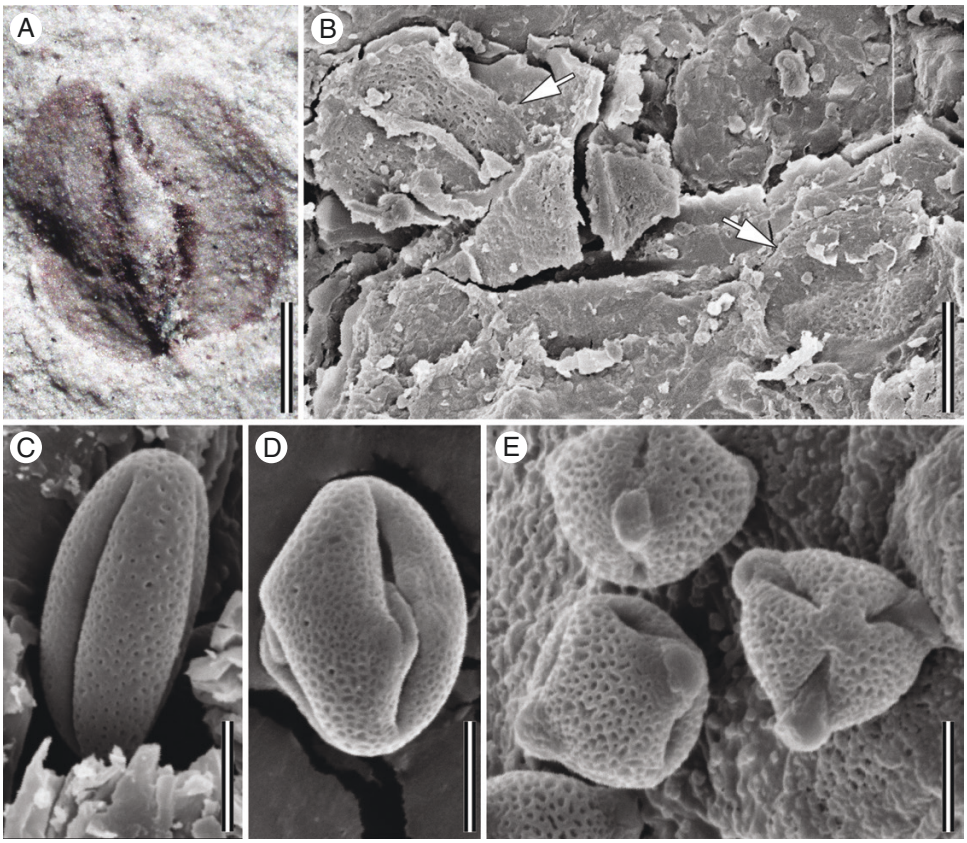

Fig. 4. Anther of 35T*Cunoniantha bicarpellata* Jud & Gandolfo, gen et sp. nov. 35Tand scanning electron micrographs of fossil and pollen of modern Cunoniaceae. (A) Close-up of an anther showing the longitudinal dehiscence slits and the absence of a connective extension. MPEF-Pb 8541a. (B) Two pollen grains 35Twith finely reticulate tectum35T (at arrows) preserved within the anthers of 35T*Cunoniantha bicarpellata*. MPEF-Pb 35T97335T. (C) Prolate, tricolpate pollen grain *Weinmannia glabra* L.f. Note the perforate tectum. BH 000 054 033. (D) Prolate, tricolpate pollen grain *Weinmannia glabra*. Note the finely reticulate tectum. BH 000 054 033. (E) Oblate, tricolpate pollen grains of *Opocunonia nymanii* Schultr. See the finely reticulate tectum. BH 000 046 024. Scale bars: A = 0.5 mm, B = 10 µm, C35T–E = 5 µm.

Cunoniaceae. Similar flowers occur in Saxifragaceae (Hideux and Ferguson, 1976; De Craene, 2010); however, Saxifragaceae are characterized by some combination of clawed petals, basifixed anthers and capitate stigmas (Soltis, 2007). These features are not present in *Cunoniantha*. Saxifragaceae are also less likely to be fossilized because they are herbaceous, and they are relatively recent arrivals to Patagonia (Deng *et al.*, 2015). Matthews *et al.* (2001) found numerous similarities between Cunoniaceae and Anisophylleaceae, but flowers with bicarpellate gynoecia are exceptional in Anisophylleaceae, whereas this is the typical condition in most Cunoniaceae and in *Cunoniantha*.

The combination of undissected petals, only five stamens per flower, anthers without a thecal connective protuberance, and a thyrsoid/cymiform inflorescence structure observed in *Cunoniantha* does not match any extant genus. Nor does it match any of the previously described fossil genera that have been compared with Cunoniaceae (Matthews *et al.*, 2001; Schönenberger *et al.*, 2001; Poinar *et al.*, 2008; Chambers *et al.*, 2010; Poinar and Chambers, 2017, 2019; Jud *et al.*, 2018*a*). Nonetheless, the results of our phylogenetic analysis indicate that *Cunoniantha* is nested within the syncarpous Cunoniaceae (Supplementary Data Fig. S1) and among the predominantly bicarpellate lineages (Supplementary Data Fig. S2). Bradford and Barnes (2001) recognized a 'core Cunoniaceae' clade that excludes Schizomerieae, *Davidsonia* and *Bauera*, but includes *Eucryphia* and is united by a shared deletion in the *trnL–F* spacer region (Fig. 1). More recent analyses also resolve this clade using maximum likelihood and Bayesian inference (Sweeney *et al.*, 2004; Hopkins *et al.*, 2013). Our analysis places *Cunoniantha* among this 'core Cunoniaceae' clade (Fig. 5).

The position of Lacinipetalum

Jud *et al.* (2018*a*) included the fossil *Lacinipetalum spectabilum* in a phylogenetic analysis of Schizomerieae with *Davidsonia* as the outgroup. In that analysis, *Lacinipetalum* was recovered as sister to Schizomerieae. We included *Lacinipetalum* in this broader analysis for three reasons. First, we updated some of the characters in this new analysis based on available data from the literature and a broader examination of morphological variation in the family (see Materials and methods section). Second, the absence of petals in *Davidsonia* means that it does not provide polarization for the characters related to the corolla that are preserved in the *Lacinipetalum* (Supplementary Data Fig. S3). Third,

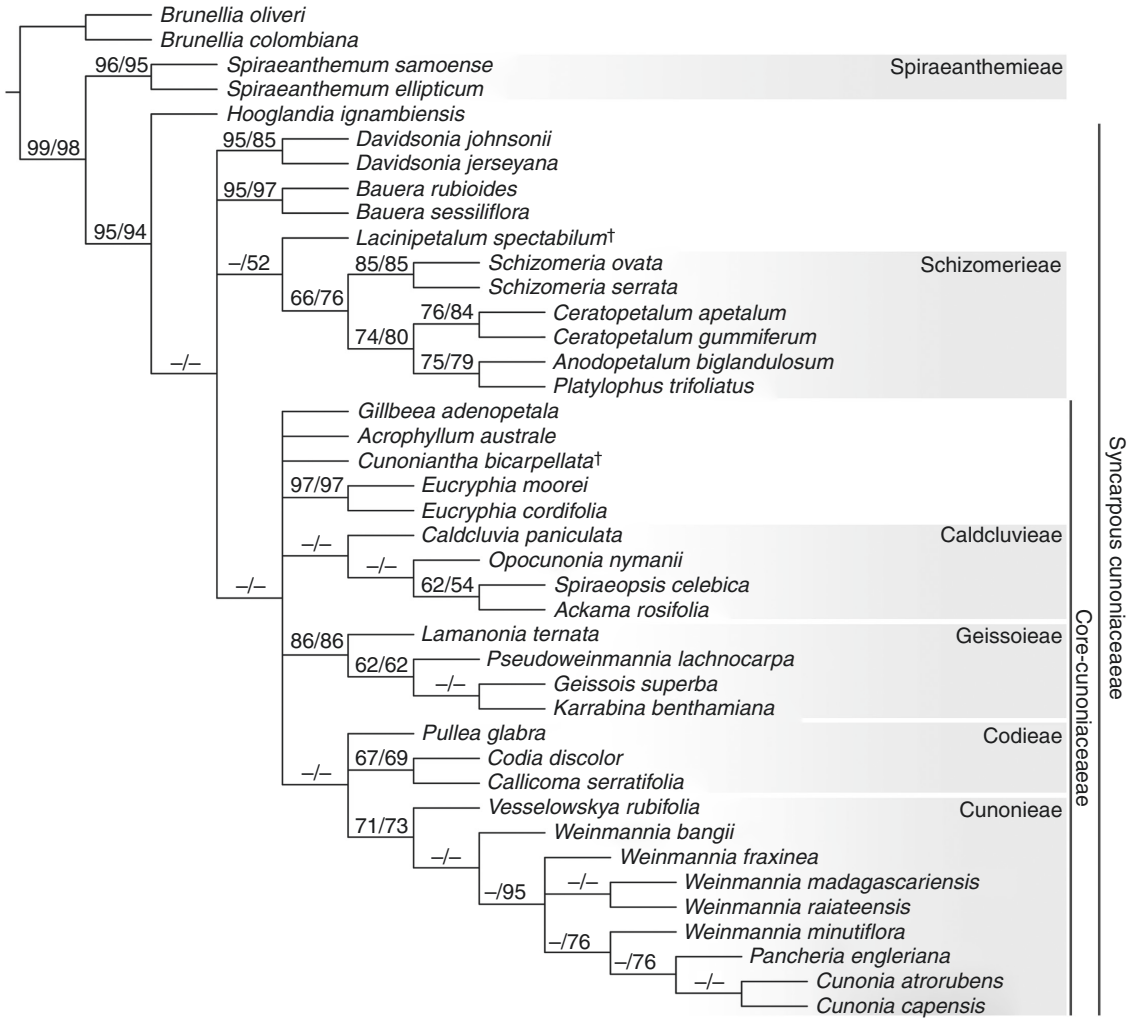

FIG. 5. Strict consensus of 92 most parsimonious trees based on simultaneous analysis of *rbcL*, *trnL–F*, *matK* and *trnH–psbA* sequence data and morphology. Note the positions of the fossil taxa within crown-group Cunoniaceae indicated by the daggers (†). Numbers above the branches are bootstrap support values followed by jackknife support values. Clades indicated by grey shading are tribes.

by using an ingroup consisting only of the fossil and extant Schizomerieae, Jud *et al.* (2018*a*) evaluated the most parsimonious position of *Lacinipetalum* within Schizomerieae, not the hypothesis that *Lacinipetalum* is more closely related to Schizomerieae than to other tribes. Indeed, this new analysis confirms a close relationship between *Lacinipetalum* and Schizomerieae (Fig. 5).

Biogeography and diversification of Cunoniaceae

Several extant genera in Cunoniaceae likely had broader distributions during the Palaeogene when the climate was warmer and wetter in Patagonia and when Australia was further south. These include *Ceratopetalum* Sm. (Holmes and Holmes, 1992; Barnes and Hill, 1999*a*; Gandolfo and Hermsen, 2017), *Callicoma* Andrews (Barnes and Hill, 1999*b*), *Codia* J.R.Forst & G.Forst (Barnes and Hill, 1999*b*), *Eucryphia* (Hill, 1991; Barnes and Jordan, 2000), *Spiraeanthemum* (Carpenter and Pole, 1995; Barnes *et al.*, 2001) and *Weinmannia* (Carpenter and Buchanan, 1993; Barnes *et al.*, 2001). The presence of *Ceratopetalum*, *Eucryphia* and *Spiraeanthemum* by the middle Eocene implies either a Cretaceous origin of crown-group Cunoniaceae or rapid diversification during the Palaeogene. Heibl and Renner (2012) presented the results of an analysis calibrated with early Eocene *Eucryphia* fossils (Barnes and Jordan, 2000) showing a late Eocene or younger divergence for most of the tribes in Cunoniaceae (except Spiraeanthemieae); however, given the Eocene–early Oligocene fossil occurrences discussed above, their ages are likely underestimates.

With the exception of the early Eocene *Ceratopetalum* (Gandolfo and Hermsen, 2017), most Upper Cretaceous and Palaeogene fossils from Patagonia and Antarctica assigned to Cunoniaceae are not included in any extant genus (Table 2). Nonetheless, fossil pollen from Upper Cretaceous and early Palaeogene sites across South America (Archangelsky, 1973; Romero and Archangelsky, 1986; Troncoso, 1991; Baldoni and Askin, 1993; Zamaloa, 2000; Barreda *et al.*, 2020), Antarctica (Cranwell, 1959; Cantrill and Poole, 2012) and Australia (Kershaw and Sluiter, 1982; Hill and MacPhail,

1983; Christophel *et al.*, 1987; Sluiter, 1991; Macphail, 1997; Alley, 1998; Barnes and Jordan, 2000) indicate that the family was widespread when floristic interchange was still possible without invoking trans-oceanic long distance dispersal. Similarly, fossil woods of *Weinmannioxylon* Petriella and *Eucryphioxylon* Poole Mennega & Cantrill are widespread in Upper Cretaceous and Palaeocene deposits in Patagonia (Petriella, 1972; Terada *et al.*, 2006; Raigemborn *et al.*, 2009) and Antarctica (Chapman and Smellie, 1992; Zhang and Wang, 1994; Poole *et al.*, 2000, 2001, 2003; Cantrill and Poole, 2012; Pujana *et al.*, 2018). However, these genera may or may not belong to the crown group. They have suites of plesiomorphic character states for the family including diffuse porosity, scalariform perforation plates, vessel-ray parenchyma pits that are scalariform to opposite, and diffuse axial parenchyma (Ingle and Dadswell, 1956; Dickison, 1980). Fossil leaves similar to Cunoniaceae have also been reported from the Eocene Ligorio Márquez Formation in South America, but these were not identified to genus (Carpenter *et al.*, 2018).

The discovery of *Cunoniantha* and *Lacinipetalum* from the early Palaeocene of Argentine Patagonia provides strong evidence that the diversification of crown-group Cunoniaceae was under way by 64 Mya. Although both genera are extinct, our phylogenetic analysis indicates that they belong to two different clades within the syncarpous Cunoniaceae. Together with other occurrences of fossil wood, pollen and *Eucryphia* leaves discussed above (Table 2), these fossils also indicate that the family was widespread across Gondwana by the Palaeocene, when warm climates permitted floristic exchange between South America and Australia via Antarctica (Hallam, 1995; Sanmartín and Ronquist, 2004; Cantrill and Poole, 2012; Wilf *et al.*, 2013).

Evidence from fossil mammals suggests the land connection between South America and Antarctica was severed during the late Palaeocene or early Eocene (Reguero *et al.*, 2014). Climate deterioration associated with global cooling and eventually deep-water currents through the Drake Passage (Lawver and Gahagan, 2003; Livermore *et al.*, 2007; Eagles and Jokat, 2014) rendered the Antarctic peninsula inhospitable to Cunoniaceae by the mid-Eocene (Anderson *et al.*, 2011). It appears that Cunoniaceae grew on the Falkland (Malvinas) Islands until at least the Miocene, but the age of these fossils is poorly constrained (Poole and Cantrill, 2007). During the late Palaeogene and Neogene, much of Patagonia also became increasingly moisture-limited (Palazzesi *et al.*, 2014; Dunn *et al.*, 2015). Suitable habitat for Cunoniaceae in South America retreated northward with the montane forests of the rising Andes. This dramatic reduction in available habitat area could explain the loss of some Cunoniaceae from South America, whereas *Lamanonia*, *Weinmannia*, *Eucryphia* and *Caldcluvia* survive.

Table 2. *Macrofossils attributed to Cunoniaceae from Antarctica, South America (Australian record summarized by Barnes et al., 2001)*

Taxon	Organs	Age	Locality	Continent	Reference	Latitude	Longitude
Eucryphiaceoxylon eucryphioides	Wood	Eocene	King George Island (8)	Antarctica	Poole *et al.*, 2001	−62.17	−59.07
Eucryphiaceoxylon eucryphioides	Wood	Cretaceous-Eocene?	Seymour Island (7)	Antarctica	Poole *et al.*, 2003	−64.2784	−56.7324
Eucryphiaceoxylon eucryphioides	Wood	Upper Cretaceous	James Ross Island (14)	Antarctica	Pujana *et al.*, 2018	−63.898	−57.948
Weinmannioxylon ackamoides	Wood	Palaeocene	King George Island (5)	Antarctica	Zhang and Wang, 1994	−62.33	−58.45
Weinmannioxylon nordenskjoeldii	Wood	Upper Cretaceous	Williams Point (1)	Antarctica	Poole *et al.*, 2000	−62.475	−60.137
Weinmannioxylon trichospermoides	Wood	Upper Cretaceous	James Ross Island (14)	Antarctica	Pujana *et al.*, 2018	−63.876	−57.906
Weinmannioxylon sp.	Wood	Neogene	Falkland Island (13)	South America	Poole and Cantrill, 2007	−51.35	−60.66
cf. Weinmannioxylon	Wood	Middle Eocene	Arroyo Cardenio River (11)	South America	Terada *et al.*, 2006	−46.763	−71.775
Weinmannioxylon multiperforatum	Wood	Palaeocene	Peñas Coloradas (3)	South America	Raigemborn *et al.*, 2009	−46.82	−69
Weinmannioxylon multiperforatum	Wood	Palaeogene	Chubut (4)	South America	Petriella, 1972	−43.65	−67.71
Weinmannioxylon pluriradiatum	Wood	Palaeogene	Chubut (4)	South America	Petriella, 1972	−43.65	−67.71
Ceratopetalum edgaroromeroi	Fruit	Eocene	Laguna del Hunco (10)	South America	Gandolfo and Hermsen, 2017	−42.461	−70.037
undetermined Cunoniaceae	Leaf	Middle Eocene	Río Zeballos (12)	South America	Carpenter *et al.*, 2018	−46.834	−71.856
Cunoniantha bicarpellata	Flower	Palaeocene	PL-2, Chubut (2)	South America	This study	−45.912	−69.214
Lacinipetalum spectabilum	Flower	Palaeocene	LF, Chubut (2)	South America	Jud *et al.*, 2018*a*	−45.69	−68.611
Lacinipetalum spectabilum	Flower	Palaeocene	PL-2, Chubut (2)	South America	Jud *et al.*, 2018*a*	−45.912	−69.214
Lacinipetalum spectabilum	Flower	Palaeocene	PL-5, Chubut (2)	South America	Jud *et al.*, 2018*a*	−45.909	−69.226

Numbers following each locality correspond to points on the map in Fig. 2.

Conclusions

Cunoniantha bicarpellata exhibits a mosaic of features consistent with Cunoniaceae. Phylogenetic analysis of morphological and molecular characters supports its position within crown-group Cunoniaceae among the syncarpous lineages. This is the second genus of Cunoniaceae from the Salamanca Formation described from fossilized flowers. Based on our phylogenetic analysis, *Cunoniantha* and *Lacinipetalum* together provide the oldest evidence of crown-group Cunoniaceae worldwide and show that the diversification was under way by 64 Mya.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following. Table S1: herbarium specimens at the L. H. Bailey Hortorium Herbarium, Cornell University, Ithaca, NY, USA, examined for this study. NEXUS file: character matrix (*trnL* intron, *trnL–F* intergenic spacer, *rbcL*, *matK*, *trnH–psbA*). Figure S1: one of the most parsimonious trees showing the distribution of carpel number in Cunoniaceae. Figure S2: one of the most parsimonious trees showing the distribution of apocarpy and syncarpy in Cunoniaceae. Figure S3: one of the most parsimonious trees showing the distribution of petal type in Cunoniaceae.

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