

Cunoniaceae infructescences from the early Eocene Laguna del Hunco flora, Patagonia, Argentina

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Abstract

Premise: Two distinct types of fossil infructescences from the early Eocene Laguna del Hunco flora, Chubut Province, Patagonia, Argentina, preserve features of the family Cunoniaceae. The goal of the study was to assess their affinities within Cunoniaceae and to interpret their evolutionary and biogeographical significance.

Methods: Specimens were collected from the Tufolitas Laguna del Hunco, Huitrera Formation. They were prepared, photographed, and compared morphologically with similar extant and fossil fruits and infructescences using published literature and herbarium material.

Results: The fruit and infructescence morphology place the fossil taxa within Cunoniaceae. They do not conform to any extant genus, supporting the erection of two new fossil genera. *Racemofructus* gen. nov. shares diagnostic features of the tribe Cunonieae, especially *Weinmannia* s.l., and exhibits two tribal morphological synapomorphies: a racemose inflorescence and a replum composed of a single column. *Cunoniocarpa* gen. nov. specimens are paniculate inflorescences with basipetally dehiscent, bicarpellate capsules that have persistent styles and calyces. Its replum morphology suggests an affinity to the tribe Caldcluvieae, particularly to the genus *Ackama*.

Conclusions: The new Patagonian fossils described herein constitute the oldest record of cunoniaceous capsules globally, supplementing a significant body of fossil evidence from pollen, wood, and reproductive structures from southern South America and Antarctica that suggests that the Cunoniaceae were diversified and widely distributed in the southern hemisphere by the early Eocene. *Racemofructus* and *Cunoniocarpa* are, respectively, the first fossil records from South America of reproductive structures with affinity to tribes Cunonieae and Caldcluvieae.

KEYWORDS

Ackama, Caldcluvieae, capsules, Cunoniaceae, Cunonieae, early Eocene, fossil infructescences, Laguna del Hunco, Patagonia, *Weinmannia*

The Cunoniaceae comprise about 27 extant genera and over 300 extant species of woody plants that are predominantly distributed in the southern hemisphere (Figure 1; Pillon et al., 2021). The family is well known from confirmed macrofossils of wood, leaves, and reproductive material from the Cretaceous to Paleogene of Antarctica (Poole et al., 2000, 2001, 2003) and the Cenozoic of Australia (Barnes, 1999; Barnes and Hill, 1999; Barnes and Jordan, 2000; Barnes et al., 2001) and South America (Gandolfo and Hermsen, 2017; Jud et al., 2018; Jud and Gandolfo, 2021). There are also putative macrofossil records of Cunoniaceae from the Cretaceous and Paleogene of the northern

hemisphere, including mesofossil flowers from Europe (Schönberger et al., 2001), flowers in amber from Southeast Asia (Chambers et al., 2010; Poinar and Chambers, 2017, 2019; Poinar et al., 2021), permineralized fruits from North America (Tang et al., 2022), and *Cunonioxylon*-type wood from Europe and North America (Gottwald, 1992; Wheeler and Lehman, 2009). Reports of fossil cunoniaceous capsules are rare. Until now, all have come from the Cenozoic of Australasia and are assigned to extant genera (Table 1). Occurrences include a mummified capsule of *Eucryphia* from the Oligocene of Australia (Barnes and Jordan, 2000), a capitate infructescence of *Callicoma* from the Oligocene of Australia (Barnes and



FIGURE 1 Map showing extant distribution and fossil occurrences of the tribes Caldcluvieae (squares) and Cunoniaceae (circles). From east to west, fossils shown are (1) ?*Weinmannia* sp. (Pole, 1993; Barnes, 1999; Manuherikia Formation, New Zealand; Miocene). (2,3) *Weinmanniaphyllum bernardii*, *Vesselowskyia rubifolia* (Carpenter and Buchanan, 1993; Cethana, Tasmania; Oligocene). (4) *Weinmannia* sp. (Barnes, 1999; Wilson's Creek, Tasmania; Oligocene). (5) *Caldcluvia mirabilis* (Tosolini et al., 2013; Seymour Island, Antarctica; Paleocene). (6) *Weinmannioxylon trichospermoides* (Pujana et al., 2018; James Ross Island, Antarctica; Cretaceous). (7) *Weinmannioxylon ackamoides* (Torres, 1990; Zhang and Wang, 1994; Poole et al., 2001; King George Island, Antarctica, Eocene). (8) *Weinmannioxylon nordenskjöldii* (Poole et al., 2000; Livingston Island, Antarctica, Cretaceous). (9) cf. *Weinmannia* sp./Xylotype 6 (Poole and Cantrill, 2007; West Point Island, Falkland Islands; Miocene). (10) *Weinmannioxylon multiperforatum* (Raigemborn et al., 2009; Golfo San Jorge Basin, Chubut, Argentina; Eocene). (11) *W. multiperforatum* (Petriella, 1972; Cerro Bororo, Chubut, Argentina; Paleocene). (12) *W. multiperforatum* (Brea et al., 2015; Rancagua Formation, Neuquén, Argentina; Oligocene). (13,14) *Racemofructus fasciculatus* gen. et sp. nov. and *Cunoniocarpa stylosa* gen. et sp. nov. (this paper; Laguna del Hunco, Chubut, Argentina; Eocene). (15) *Weinmannioxylon* sp. (Terada et al., 2006; Arroyo Cardenio, Aisen, Chile; Eocene). (16) *Caldcluvioxylon torresiae* (Pujana and Ruiz, 2019; Rio Turbio, Santa Cruz, Argentina).

TABLE 1 Fossil record of cunoniaceous capsules.

Genus	Age	Region	Carpel No.	Replum	Calyx	Inflorescence	Pedicels	References
<i>Eucryphia</i>	Oligocene	Tasmania	8	Free pair	Caducous	?	?	Barnes and Jordan, 2000
<i>Callicoma</i>	Oligocene	Tasmania	2	?	?	Capitulum	Absent	Carpenter and Buchanan, 1993
<i>Bauera</i>	Pleistocene	Tasmania	2	?	6 sepals	Solitary	?	Jordan et al., 1991; Barnes, 1999
<i>Weinmannia</i> sp.	Miocene	New Zealand	2	?	?	Raceme	Fascicled	Pole, 1993
<i>Racemofructus</i>	Eocene	Patagonia	2	Single	4–5 sepals	Raceme	Fascicled	This Paper
<i>Cunoniocarpa</i>	Eocene	Patagonia	2	Free pair	4–6 sepals	Panicle	Solitary	This Paper

Hill, 1999), an infructescence from the Miocene of New Zealand attributed to ?*Weinmannia* (Pole, 1993; Barnes, 1999), and a mummified capsule of *Bauera* from the Pleistocene of Tasmania (Jordan et al., 1991; Barnes, 1999).

Currently, the family Cunoniaceae is divided into six monophyletic tribes—Caldcluvieae, Codieae, Cunoniaceae, Geissoeae, Schizomerieae, and Spiraeanthemeae—with an additional seven unplaced genera: *Acrophyllum*, *Aistopetalum*, *Bauera*, *Davidsonia*, *Eucryphia*, *Gillbeea*, and *Hooglandia* (Hufford and Dickison, 1992; Bradford and Barnes, 2001; Sweeney et al., 2004; Hopkins et al., 2013; Pillon et al., 2021). These groups are broadly separated into a basal grade (comprising the genera *Aistopetalum*, *Bauera*, *Davidsonia*, *Hooglandia*, and the tribes Schizomerieae and Spiraeanthemeae) and a large Core Cunon clade (see Bradford and Barnes, 2001; Bradford et al., 2004), including four tribes

(Caldcluvieae, Codieae, Cunoniaceae, and Geissoeae) and three unplaced genera (*Acrophyllum*, *Eucryphia*, and *Gillbeea*) (Bradford and Barnes, 2001; Bradford et al., 2004; Jud and Gandolfo, 2021; Pillon et al., 2021). The Core Cunon clade is characterized by a short deletion in the *trnL-trnF* spacer (Bradford and Barnes, 2001; Jud and Gandolfo, 2021).

The recognition of most tribes and genera of Cunoniaceae using reproductive morphology requires a combination of inflorescence, flower, and fruit characters (Bradford and Barnes, 2001). Flowers are generally bisexual, with a biseriate perianth divided into a 4–5-merous calyx and a 4–5-merous corolla (Bradford et al., 2004). Syncarpous, bicarpellate ovaries are common in the family and unite all genera except for *Spiraeanthemum* (Bradford and Barnes, 2001). Genera with basipetally dehiscent bicarpellate capsules

occur nearly throughout Cunoniaceae. They include all Caldcluvieae; some members of Cunonieae (*Pterophylla*, *Vesselowskya*, *Weinmannia* s.s.) and Geissoieae (*Geissois*, *Karrabina*, *Lamanonia*); one genus each in Codieae (*Callicoma*), Schizomerieae (*Anodopetalum*), and the monotypic tribe Spiraeanthemeae (*Spiraeanthemum*); and the unplaced genera *Acrophyllum* and *Bauera* (Table 2). *Eucryphia* also produces capsulate fruits, but they have four or more carpels (Bradford and Barnes, 2001; Table 2). Inflorescence structure is variable and homoplasious among tribes but usually consistent within tribes. Panicle and cyme are the ancestral inflorescence types (Bradford and Barnes, 2001). Paniculate and thyrsoid inflorescences are common among taxa in the basal grade, but they also characterize the tribe Caldcluvieae and a few other genera in the Core Cunon clade (Bradford and Barnes, 2001). Within the Core Cunon clade, there is a general trend toward reduction from the paniculate form to less-branched inflorescence types such as racemes, capitula, or solitary flowers, and these forms generally constitute a tribal or generic apomorphy (Bradford and Barnes, 2001).

Two-thirds of the species in Cunoniaceae belong to the Cunonieae, a monophyletic tribe comprising the genera *Cunonia*, *Pancheria*, *Pterophylla* (formerly in *Weinmannia*

s.l.), *Vesselowskya*, and *Weinmannia* s.s. (Pillon et al., 2021). The monophyly of this tribe is supported by a long deletion in the *trnL-trnF* spacer and three morphological synapomorphies: racemose inflorescences, capsules with a single vertical, seed-bearing replum (column or partition between the carpels), and tricolporate pollen (Bradford and Barnes, 2001). *Vesselowskya* includes two species that are restricted to the subtropical rainforests of eastern Australia (Figure 1) and is easily recognized by its trimerous perianth and decurrent styles that persist on mature capsules (Rozefelds et al., 2001). *Pancheria* comprises about 30 species endemic to New Caledonia; it bears flowers in a capitulum instead of a raceme and produces follicles instead of capsules (Hopkins et al., 2009). *Cunonia* comprises about 25 species endemic to New Caledonia and one species endemic to South Africa (Figure 1), and it is the only genus in Cunoniaceae with acropetally dehiscent capsules (Bradford, 2002). *Weinmannia* s.s. includes about 90 species that occur in moist temperate forests of Chile and Argentina, tropical montane forests of Central America, and tropical forests of the Mascarene Islands (Bradford, 1998, 2001; Pillon et al., 2021). *Pterophylla* has 68 species and is divided into four sections that were previously included in *Weinmannia* s.l.: *Pterophylla* (formerly *Weinmannia* sect. *Fasciculata*, 20 species),

TABLE 2 Genera of Cunoniaceae with dehiscent capsulate fruits.^a

Genus	Tribe	Inflorescence	Dehiscence	Replum ^b
<i>Ackama</i> ^c	Caldcluvieae	Thyrse	Basipetal	Absent, free pair
<i>Caldcluvia</i>	Caldcluvieae	Cyme	Basipetal	Free pair
<i>Opocunonia</i>	Caldcluvieae	Cyme	Basipetal	Absent
<i>Callicoma</i>	Codieae	Capitulum	Basipetal	Absent
<i>Cunonia</i>	Cunonieae	Raceme	Acropetal	Solitary
<i>Pterophylla</i> ^d	Cunonieae	Raceme or spike	Basipetal	Solitary
<i>Vesselowskya</i>	Cunonieae	Raceme	Basipetal	Solitary
<i>Weinmannia</i> s.s. ^d	Cunonieae	Raceme	Basipetal	Solitary
<i>Geissois</i>	Geissoieae	Raceme	Basipetal	Free pair
<i>Karrabina</i>	Geissoieae	Raceme	Basipetal ^e	Free pair
<i>Lamanonia</i>	Geissoieae	Raceme	Basipetal	Free pair
<i>Anodopetalum</i>	Schizomerieae	Solitary flower or 3-flowered cyme	Basipetal ^f	Absent
<i>Spiraeanthemum</i> ^g	Spiraeanthemeae	Panicle	Basipetal	Absent
<i>Acrophyllum</i>	NA	Panicle	Basipetal	Absent
<i>Bauera</i>	NA	Solitary flower	Basipetal	Solitary
<i>Eucryphia</i>	NA	Solitary flower	Basipetal	Free pair

^aSources: Godley (1983), Dickson (1984), Bradford (1998, 2001), Barnes and Hill (1999), Barnes and Rozefelds (2000), Bradford and Barnes (2001), de Lange et al. (2002), Hopkins and Hoogland (2002), Bradford et al. (2004), Hopkins et al. (2013), Pillon et al. (2021).

^bAbsent includes fruits described as having no replum or scored as inapplicable or having an adnate-pair replum in Bradford and Barnes (2001).

^cIncludes *Spiraeopsis* after Pillon et al. (2021).

^dThe circumscriptions of *Pterophylla* and *Weinmannia* s.s. follow Pillon et al. (2021).

^eBased on an illustration of the capsule in Hopkins et al. (2013, see fig. 4H).

^fCapsule dehiscence recorded as septicidal (Barnes and Rozefelds, 2000), inferred to be the typical basipetal type in Cunoniaceae.

^gIncludes *Acsmithia* after Pillon et al. (2009).

Leiospermum (18 species), *Inspersae* (9 species), and *Spicatae* (21 species); *Pterophylla* occurs in tropical montane forests of Malesia and the West Pacific and tropical lowland and montane forests in Madagascar and the Comoros Islands (Bradford, 1998, 2001; Pillon et al., 2021). *Pterophylla* and *Weinmannia* s.s. have hairy seeds and often bear flowers in fascicles (Bradford, 1998; Pillon et al., 2021).

The *Caldcluvieae* are a monophyletic tribe with 12 species that have been grouped into as many as four distinct genera (*Ackama*, *Caldcluvia*, *Opocunonia*, *Spiraeopsis*; Bradford and Barnes, 2001) or lumped into the single genus *Caldcluvia* s.l. (Hoogland, 1979). In the most recent treatment of the *Caldcluvieae*, Pillon et al. (2021) suggested that the tribe should comprise three genera—*Ackama* (including the species formerly placed in *Spiraeopsis* and *Ackama* s.s.), *Caldcluvia*, and *Opocunonia*—and we follow their circumscription hereafter. Bradford and Barnes (2001) identified tuft domatia on the underside of leaves as a morphological synapomorphy for *Caldcluvieae*. Some reproductive characters—such as valvate sepals, loosely connate carpels, and thickened axile placentae that are either adnate to the endocarp or that form a free-pair replum (i.e., two bifurcating columns between the capsule valves that occur on either side of the fruit; see Godley, 1983; Bradford and Barnes, 2001; Hopkins and Hoogland, 2002; Pillon et al., 2021)—have been used to unite the species in the *Caldcluvieae* (Hoogland, 1979; Pillon et al., 2021), but they are neither exclusive to nor ubiquitous within the group. *Ackama* comprises 10 species and occurs in New Guinea (5 spp.), the Philippines and Solomon Islands (1 sp.), Australia (2 spp.), and New Zealand (2 spp.); it can be distinguished from the other genera in the tribe by its large, paniculate or thyrsoid inflorescences with small (1–2 mm) flowers that are sessile or borne on short (1–2.5 mm) pedicels (Pillon et al., 2021). *Opocunonia* and *Caldcluvia* are both monotypic genera with small, cymose inflorescences bearing large (2–4 mm) flowers on long (3–8 mm) pedicels (Bradford et al., 2004; Pillon et al., 2021). *Caldcluvia* occurs in Chile, and its capsules have a replum and caducous sepals; *Opocunonia* occurs in New Guinea, and its capsules lack a replum and have persistent sepals (Pillon et al., 2021).

The goal of our contribution is to describe two new monotypic fossil genera based on infructescences bearing bicarpellate, basipetally dehiscent capsules that have characters consistent with placement in Cunoniaceae. Both are from the diverse early Eocene Laguna del Hunco flora of north-central Chubut Province, Argentina, the same assemblage that yielded the cunoniaceous samaroid fruit *Ceratopetalum edgardoromeroi* of tribe Schizomerieae (Gandolfo and Hermsen, 2017). One of the new taxa includes racemose infructescences bearing capsules in fascicles; its structural characteristics clearly indicate that it has affinities to tribe Cunoniaceae. The second includes a paniculiform infructescence with capsules bearing long, persistent styles; although the structural features of this taxon are not as conclusive, it likely has affinities to *Caldcluvieae*. These early Eocene fossils are the earliest known record of cunoniaceous capsules and infructescences and the first fossils with affinities to the tribe Cunoniaceae and *Caldcluvieae* from South America.

MATERIALS AND METHODS

The taxa described in this paper are based on fossil infructescences collected from five of 32 quarried localities of the Tufolitas Laguna del Hunco, Huitrera Formation, Chubut Province, Patagonia, Argentina, paleolatitude ~47°S (Wilf et al., 2003, 2005; Figure 1). The Tufolitas Laguna del Hunco are fossiliferous caldera-lake deposits within a volcanoclastic depositional sequence consisting of tuffaceous mudstones to sandstones (Wilf et al., 2003, 2005; Gosses et al., 2021). The fossils occur throughout the most densely sampled and fossiliferous 60-m interval of the 170-m local stratigraphic section (Wilf et al., 2003, 2005; Hermsen and Gandolfo, 2016). The horizon that yielded the youngest of the fossils (containing localities LH6, LH22, LH25, and LH27) sits 23.05 m above, and in the same paleomagnetic polarity interval as, Ash 2211A, which yielded an $^{40}\text{Ar}/^{39}\text{Ar}$ age on sanidine of 52.22 ± 0.22 Ma (early Eocene) (Wilf et al., 2003; Wilf, 2012). Other fossil material is from the lower part of the section, below and thus older than Ash 2211A. The maximum age of the fossils comes from the youngest beds of the underlying, caldera-forming Barda Colorada Ignimbrite, which yielded an $^{40}\text{Ar}/^{39}\text{Ar}$ age on sanidine of 52.54 ± 0.17 Ma (Gosses et al., 2021). Thus, the age of all the fossils is close to 52 Ma, within the Early Eocene Climatic Optimum. The paleoflora includes leaf, flower, fruit, pollen, and wood fossils (Zamaloa et al., 2006, 2020; Gonzalez et al., 2007; Wilf et al., 2009, 2014, 2017a, 2017b, 2019; Gandolfo et al., 2011; Hermsen et al., 2012; Wilf, 2012; Knight and Wilf, 2013; Carpenter et al., 2014; Hermsen and Gandolfo, 2016; Deanna et al., 2020; Barreda et al., 2020; Brea et al., 2021) and is considered to be one of the most diverse Eocene fossil compression floras ever discovered (Wilf et al., 2003, 2005). The paleoflora also has extensive, significant biogeographic connections to the West Pacific, particularly the extant montane rainforests of the Malay Archipelago and subtropical notophyll forests of eastern Australia (Wilf et al., 2013; Kooyman et al., 2014; Merkhofer et al., 2015). In addition to the fossil *Ceratopetalum* fruits (see Introduction), the flora has an abundant, undescribed leaf morphotype (TY116, “*Cupania*” *latifolioides* Berry of Wilf et al., 2005) reported as similar to *Caldcluvia* and *Ackama* that occurs at nearly all the individual fossil quarries, including those studied here (Wilf et al., 2005; Merkhofer et al., 2015; authors' unpublished field data).

The fossils were trimmed in the field, then prepared as necessary by the staff at Museo Paleontológico Egidio Feruglio (MEF; Trelew, Chubut Province, Argentina), where the fossils are housed permanently in the paleobotanical collection under specimen number prefix MPEF-Pb. Fossils were photographed at MEF using Nikon D90 and D700 cameras (Nikon, Melville, NY, USA). Fossils loaned to Cornell from MEF were studied and photographed at the L.H. Bailey Hortorium, Plant Biology Section, School of Integrative Plant Science, Cornell University, using a Nikon SMZ18 stereomicroscope and Nikon DS-Ri2 Digital Camera.

Extant material of 10 capsular genera of Cunoniaceae (*Ackama*, *Callicoma*, *Cunonia*, *Eucryphia*, *Geissois*, *Lamania*, *Opocunonia*, *Vesselowskyia*, *Pterophylla*, and *Weinmannia*

s.s.) were compared with the fossil specimens, using herbarium sheets held at the L.H. Bailey Hortorium Herbarium (BH). Images of extant material were taken at BH with a Nikon D800e camera.

Descriptions of extant and fossil material follow the terminology used by Bradford (1998, 2002) and Bradford and Barnes (2001) in coding character states for phylogenies. We consider the replum (columella sensu Spjut, 1994 or column sensu Bradford and Barnes, 2001) to be a persistent partition between the carpels that occurs in the capsules of some Cunoniaceae that is formed from the fusion of marginal vascular bundles (Dickison, 1975; Godley, 1983; Bradford and Barnes, 2001; Hopkins and Hoogland, 2002). The single and free-pair replum types are defined as in character 41 of Bradford and Barnes (2001), although their adnate-pair replum is here considered equivalent to a replum being absent (see Pillon et al., 2021). Delimitation of genera in Cunoniaceae and use of the terms *Weinmannia* s.s. and *Weinmannia* s.l. follows Pillon et al. (2021).

RESULTS

Systematics

Family

Cunoniaceae R.Br.

Tribe

Cunonieae (R.Br.) Schrank & Mart.

Genus

Racemofructus Matel, Gandolfo, Hermsen, & Wilf, gen. nov.

Generic diagnosis

Racemose infructescence bearing pedicellate capsules; capsules in fascicles of three; calyx persistent, 4- or 5-merous, sepals basally connate; capsule syncarpous, bicarpellate, dehiscence septifragal; replum present, single; styles free.

Type species

Racemofructus fasciculatus Matel, Gandolfo, Hermsen, & Wilf, sp. nov.

Holotype here designated

MPEF-Pb 11025. Figure 2C, E, and G.

Paratypes

MPEF-Pb 11021–11028 (11027, Figure 2A), MPEF-Pb 11030, MPEF-Pb 11031, and MPEF-Pb 11033–11037 (MPEF-Pb 11035, Figure 2B; MPEF-Pb 11037, Figure 2D).

Etymology

The generic name *Racemofructus* is a compound word combining the botanical Latin terms *racemus* (raceme) and *fructus* (fruit), referring to the racemose infructescence morphology of the fossils; the species epithet *fasciculatus* describes the fasciculate attachment of fruits to the infructescence axis.

Repository

Paleobotanical collection of the Museo Paleontológico Egidio Feruglio (MPEF-Pb), Trelew, Chubut, Argentina.

Type locality

Laguna del Hunco quarry LH22, Huitrera Formation, early Eocene (Ypresian), Chubut Province, Argentina.

Other localities

Laguna del Hunco quarries LH6 (MPEF-Pb 11021), LH13 (MPEF-Pb 11022–11024), LH25 (MPEF-Pb 11026–11028), and LH27 (MPEF-Pb 11030, MPEF-Pb 11031, MPEF-Pb 11033–11037), Huitrera Formation, early Eocene (Ypresian), Chubut Province, Argentina.

Specific diagnosis

As for the genus *Racemofructus*.

Informal prior reference

Morphotype TY093 “Unknown dicot sp.” (exemplar LH22-29 = MPEF-Pb 11025) of Wilf et al. (2005: appendix table A2, p. 8).

Description

The fossils are segments of racemose infructescences bearing pedicellate, dehiscent capsules. The infructescence segments are 3.17–13.97 cm long and often broken and missing both ends. The arrangement and spacing of fruits in relation to the main axis is variable among and within specimens (Figure 2A, B). Most commonly, the fruits are in fascicles of three, with the fascicles spirally arranged on the axis of the raceme

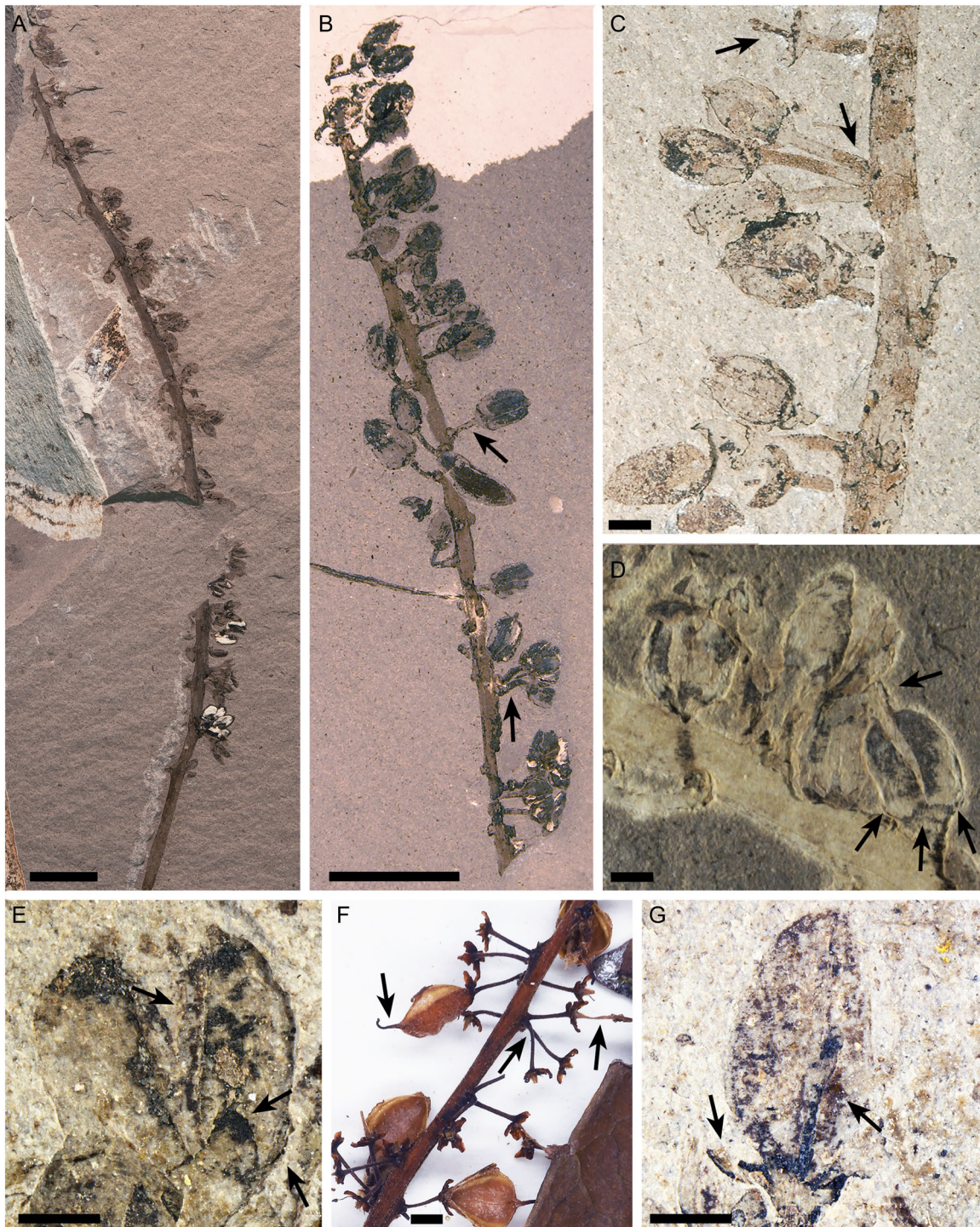


FIGURE 2 *Racemofructus fasciculatus* Matel, Gandolfo, Hermesen, & Wilf, gen. et. sp. nov. (A) MPEF-Pb 11027; racemose infructescence with fascicled pedicels bearing open and closed capsules with persistent calyxes and style bases. Scale bar = 1 cm. (B) MPEF-Pb 11035; specimen showing a racemose infructescence with arrows pointing to a fascicle of three pedicellate capsules (lower arrow) and a solitary, pedicellate, closed bivalvate capsule with a persistent calyx and three visible sepal lobes (upper arrow). Scale bar = 1 cm. (C) MPEF-Pb 11025 (holotype); detail of an infructescence axis showing a single replum attached to the receptacle after valve dehiscence and detachment (upper arrow), and a fascicle of three fruits (lower arrow). Scale bar = 1 mm. (D) MPEF-Pb 11037; detail of an open bivalvate capsule showing two valves with basipetal dehiscence, one valve retaining a long style (upper arrow), and a persistent calyx with three sepal lobes (lower arrows). Scale bar = 1 mm. (E) MPEF-Pb 11025; a capsule of the holotype showing a single replum (upper arrow) free from style bases while both valves remain attached to the receptacle. The calyx is persistent and shows two sepal lobe (lower arrows). Scale bar = 1 mm. (F) BH54023; image of a *Weinmannia* sp. (Cunoniaceae) specimen showing a single replum attached to the receptacle after valve dehiscence and detachment (right arrow), a fascicle of three pedicels (center arrow), and a single capsule valve with a persistent style (left arrow). Scale bar = 1 mm. (G) MPEF-Pb 11025; view of a capsule with one valve showing septifragal dehiscence, a single replum (right arrow), and a calyx with a single persistent sepal lobe (left arrow). Scale bar = 1 mm.

(Figure 2A, C). Solitary fruits occur sporadically on axes predominantly bearing fascicled fruits (Figure 2B). Based on the apparently consistent maturity of fruits attached to the same axis as determined by the degree of dehiscence (Figure 2A, C), fruits are interpreted as maturing synchronously on axes.

Capsules are borne on pedicels 1.6–3.0 mm long and 0.4–0.5 mm wide. Pedicels are slender and apparently flexible, as they frequently occur wrapped around the main infructescence axis (Figure 2B, C). Capsules are 2.8–4.2 mm long. Each capsule is subtended by a calyx of basally connate sepals. Although the calyx is interpreted as persistent (i.e., not caducous), the presence of sepals is variable, and their eventual loss appears to be related to the maturity of the capsule. Sepal lobes are most conspicuous on capsules with fused valves or with valves separated only by a narrow opening (Figure 2D, E, G). When sepal lobes are present, only two or three are visible on each capsule; the total number of sepal lobes is inferred to be four or five based upon symmetry (Figure 2D, E, G). Sepal lobes are triangular with an acute or obtuse apex (Figure 2D, E, G). Capsules have two valves that open basipetally along a longitudinal suture aligned with the septum (Figure 2D, E). A persistent, terminal style 0.1–0.9 mm long (Figure 2D) is attached to the apex of each valve. The capsules are thus interpreted to have developed from a syncarpous, bicarpellate ovary with two free and persistent styles (Figure 2D, E, G). Open capsules and capsules in which one or both valves have broken away from the receptacle reveal a single replum 1.1–1.8 mm long between the valves; the replum is free from the style bases (Figure 2C, E, G). The retention of valves on dehiscent capsules is variable (Figure 2C); however, based on the persistence of the replum after valve separation (Figure 2C), capsules are interpreted as septifragally dehiscent.

Tribe

Caldcluvieae.

Genus

Cunoniocarpa Matel, Gandolfo, Hermsen, & Wilf, gen. nov.

Generic diagnosis

Paniculate infructescence bearing spirally arranged, pedicellate capsules borne singly on axes; calyx persistent, 4–6-merous, sepals basally connate; capsule syncarpous, bicarpellate, dehiscence septicidal and basipetal; replum present, of the free-pair type; styles free, sometimes splitting apically and appearing bifid.

Type species

Cunoniocarpa stylosa Matel, Gandolfo, Hermsen, & Wilf, sp. nov.

Holotype here designated

MPEF-Pb 11029. Figure 3A, B, E.

Paratypes

MPEF-Pb 11032 and MPEF-Pb 11038 (Figure 3C).

Etymology

The name *Cunoniocarpa* is a combination of *Cunonio*-, a reference to Cunoniaceae, and *-carpa*, from the Greek for fruit. The species epithet *stylosa* denotes the prominent, persistent styles on the fossil fruits.

Repository

Paleobotanical collection of the Museo Paleontológico Egidio Feruglio (MPEF-Pb), Trelew, Chubut, Argentina.

Type locality

Laguna del Hunco quarry LH27, Huitrera Formation, early Eocene (Ypresian), Chubut Province, Argentina.

Other localities

Laguna del Hunco quarry LH25 (MPEF-Pb 11038) and LH27 (MPEF-Pb 11032), Huitrera Formation, early Eocene (Ypresian), Chubut Province, Argentina.

Specific diagnosis

As for the genus *Cunoniocarpa*.

Description

This species is represented by three specimens: a panicle (MPEF-Pb 11029), a panicle fragment bearing capsules (MPEF-Pb 11038), and a pair of dispersed capsules (MPEF-Pb 11032). The holotype is a 2.50 cm segment of an infructescence with at least three pairs of lateral branches 0.35–0.74 cm long. These lateral branches emerge from the main axis in opposite pairs except for a solitary branch in between the basal and apical pairs (Figure 3A). A fourth pair of lateral branches is interpreted to have been present based on the presence of a pair of scars on opposite sides of the main axis at a node below the lowest pair of lateral branches. Each branch is subtended by an inflorescence bract 1.2–1.4 mm long and bears numerous bracteate fruits. Fruits

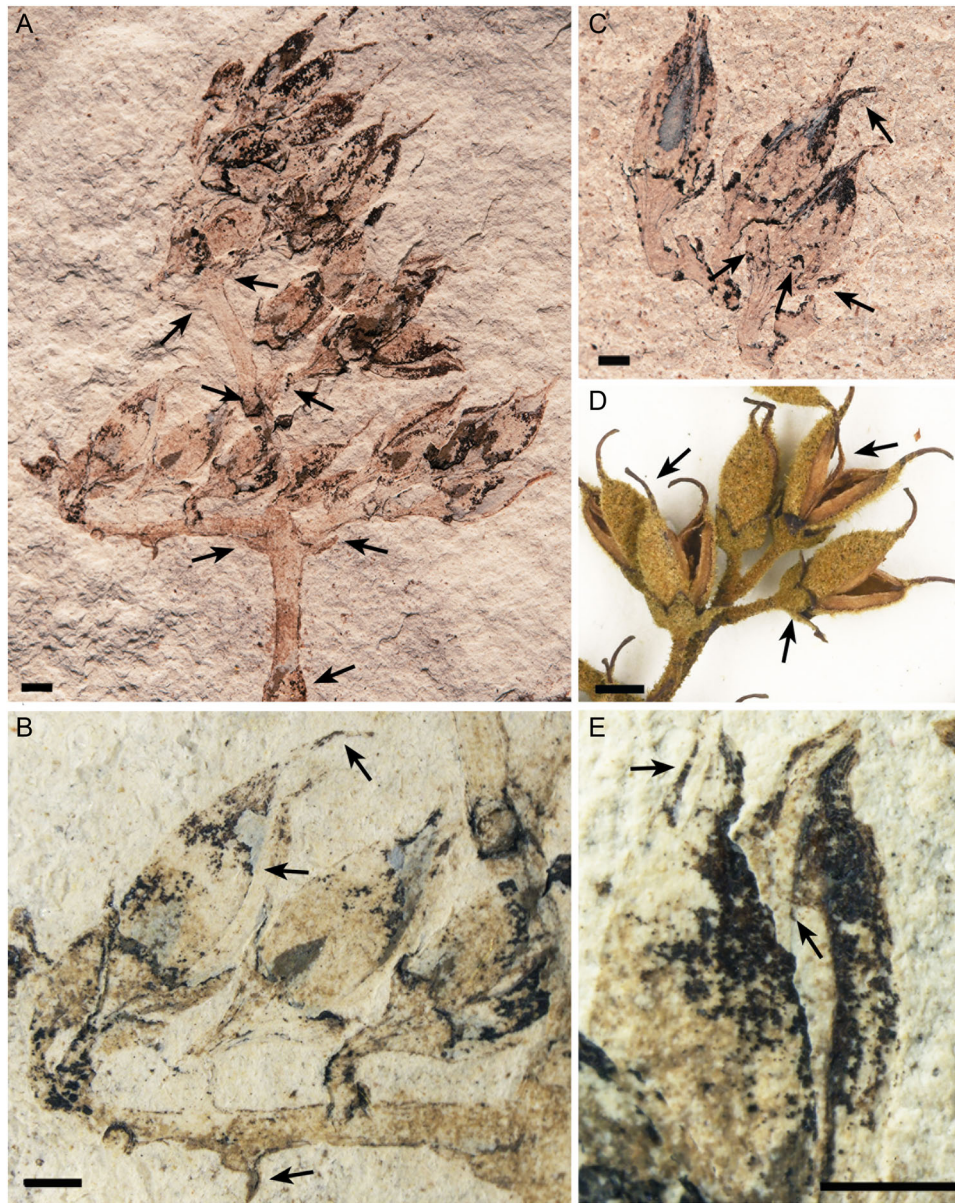


FIGURE 3 *Cunoniocarpa stylosa* Matel, Gandolfo, Hermesen, & Wilf, gen. et. sp. nov. Scale bar = 1 mm. (A) MPEF-Pb 11029 (holotype); overall view showing a paniculate infructescence with at least three pairs of lateral branches subtended by bracts and scars at a lower node where lateral branches have been lost. Uppermost pair of arrows points to a pair of opposite lateral branches; the second pair of arrows from the top point to a lateral branch (right) and an opposite scar (left); the third pair of arrows from the top point to opposite lateral branches, each subtended by a bract; the lowermost arrow points to a scar. (B) MPEF-Pb 11029; bivalvate capsules with elongate, persistent styles (upper arrow), and basipetal dehiscence (center arrow) borne on solitary pedicels attached to a lateral branch; a persistent floral bract (lower arrow) subtends a pedicel scar. (C) MPEF-Pb 11038; detail of capsules with elongate, persistent styles (upper arrow), and valves divided by a narrow suture; capsules are separate from an infructescence axis and show three lobes of a persistent calyx (lower arrows). (D) BH46252; image of an *Ackama celebica* (Caldcluvieae) specimen showing bivalvate capsules with persistent, elongate styles (left arrow), a bifurcating replum fused to style bases (right arrow), and a persistent calyx with three visible sepal lobes (lower arrow). (E) MPEF-Pb 11029; partially opened capsule showing bifid styles (upper arrow) and a replum fused to the style base of one valve (lower arrow).

are borne singly (i.e., not in fascicles) and are pedicellate, the pedicels 1.6–1.9 mm long and 0.4–0.5 mm wide (Figure 3B). Fruits are attached to at least two sides of the lateral branches, and their arrangement is interpreted as spiral or distichous (Figure 3A). The fruit apices are all pointed in the same direction and are at an angle nearly perpendicular to the main infructescence axis (Figure 3A), suggesting that the fruiting axis was plagiotropic. Orbicular scars circa 0.5 mm long occur

sporadically on the lateral axes (Figure 3A) and are interpreted as pedicel scars left by abscised flowers or fruits.

Fruits are dehiscent capsules 3.7–4.4 mm long. Each capsule retains a persistent calyx with 4–6 triangular sepal lobes with acute or narrowly acute apices (Figure 3B, C). Because each capsule has two valves (Figure 3A–C, E), capsules are interpreted as developing from bicarpellate, syncarpous ovaries. Capsules dehisce basipetally by means

of a longitudinal primary suture about 2.6–2.9 mm long; the suture is interpreted as parallel to the septum dividing the carpels, and thus dehiscence is considered septicidal. Upon dehiscence, the fruit divides into two concave valves of equal size; a single persistent style 0.6–1.7 mm long extends from the apex of each valve (Figure 3A–C). In some fruits, a loculicidal suture extending the length of the style divides the stylar beak of each valve in two, making the valve apices appear bifid (Figure 3E). Some dehiscent capsules preserve the distal arm of an apically bifurcating replum between the carpels, with the arm of the bifurcation fused to the style base of the adjacent capsule valve (Figure 3E); thus, the capsules are interpreted as having repla of the free-pair type sensu Bradford and Barnes (2001). The bases of the repla are obscured by intact valves but are inferred to emerge from the fruit receptacle based on comparison with modern taxa (Figure 4A, C, E, F; for more details, see Discussion).

DISCUSSION

To explore the taxonomic position of the Patagonian fossils, we compared them with several families that produce infructescences bearing bicarpellate, loculicidal, septicidal, and septicidal. Some of them were promptly rejected for their large character dissimilarities with the fossils; among these were families that produce flowers with inferior ovaries, a well-developed hypanthium, and globose, spherical, subspherical, obovoid, and oblong capsules with loculicidal and/or septicidal dehiscence, such as Buxaceae (Köhler, 2007), the monotypic Vahliaceae (Thiv, 2016), Hydrangeaceae (Hufford, 2004), Saxifragaceae (Soltis, 2007), and Iteaceae (Kubitzki, 2007). There is no indication that the Patagonian fossil fruits were developed from an inferior ovary nor that there is a hypanthium; the type of dehiscence (septicidal) of the capsules is very different from those of the aforementioned families. Some members of the family Celastraceae also produce capsules (Simmons, 2004); however, their capsules tend to be ovoid or pyriform and compressed (e.g., *Dicarpellum*, *Celastrus*), 5-lobed and fusiform (e.g., *Bhesa*, *Canotia*), or trilocular (*Kokoona* and *Menepetalum*), thus completely differentiating them from the Patagonian fossils. The fossils are different from Escalloniaceae capsules as well. Escalloniaceae, a small family comprising four genera, produce dry indehiscent or septicidally dehiscent capsules on terminal racemes and panicles (Lundberg, 2016). Fruits of *Escallonia* are characterized by their persistent calyx, but differ from the Patagonian fossils in having an inferior ovary and a hypanthium. Capsules of the other genera in Escalloniaceae, *Forgesia* and *Anopterus*, dehisce from the top to the base and are 2–3 locular; *Valdivia* capsules are indehiscent (Lundberg, 2016).

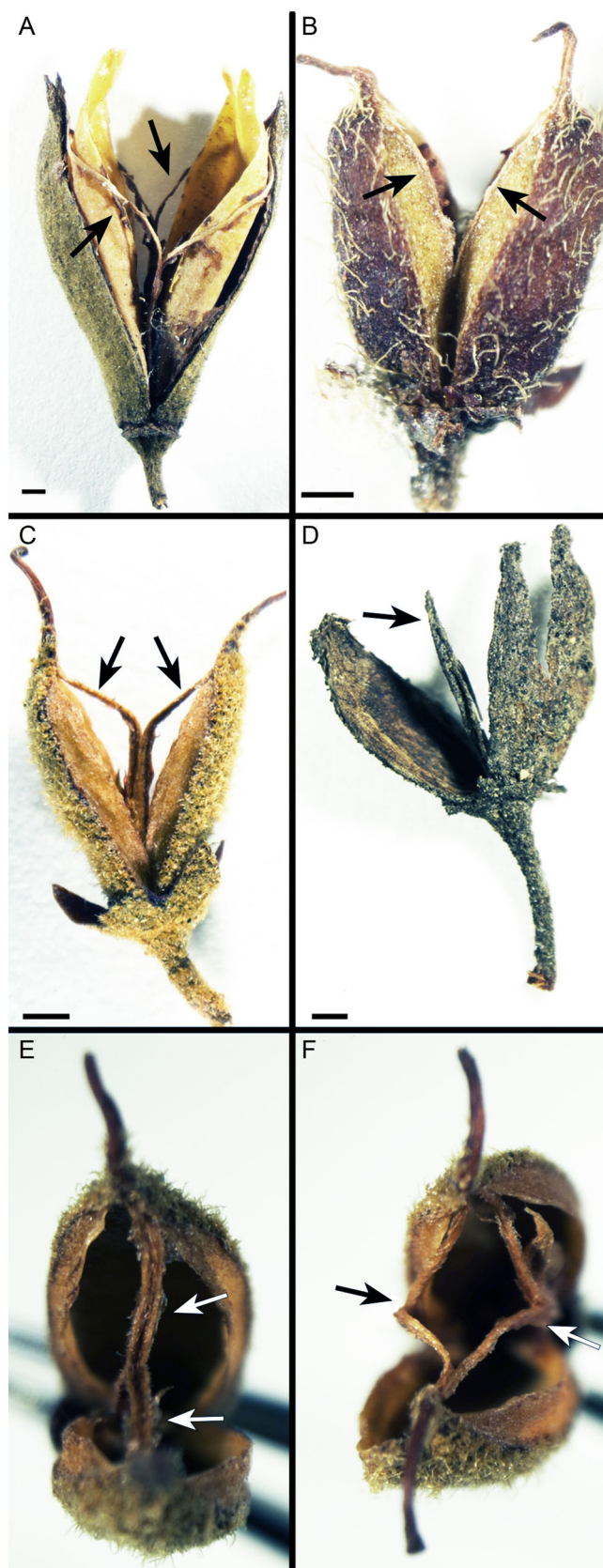


FIGURE 4 (See caption on next page)

The fossils were also compared with the families Clethraceae, Clusiaceae, Ericaceae, Geraniaceae, Loganiaceae, and Brassicaceae, which all have a replum in their capsules. Geraniaceae were discarded because their flowers are solitary or form pseudumbellate inflorescences (Albers and Van der Walt, 2007). *Clethra* capsules are always 3-valved and loculicidal and are enclosed by a persistent calyx (Schneider and Bayer, 2004). Capsules of Ericaceae can be either septicidal or loculicidal and very rarely septifragal; they develop from a (1–) 4–5 (–12)-carpellate ovary (Stevens et al., 2004). Within Ericaceae, only the genera *Diplarche* and *Calluna* have septifragal capsules; however, both were discarded. *Calluna* flowers are solitary (Gimingham, 1960), and *Diplarche* capsule valves split into two layers (Gillespie and Kron, 2010). Capsules of Clusiaceae can be septicidal or septifragal (e.g., members of the tribe Clusieae), but they are mostly 3–5-valvate. *Mesua* septifragal capsules are bivalvate, but its ramiflorous inflorescences bear only 2–6 flowers. In Loganiaceae, members of the tribe Antonieae have capsules that are elliptical to obovoid, septicidal, and bivalved with persistent styles and subtended by a series of scale-like bracts (Struwe et al., 2018). The family Brassicaceae usually produce 2-valved capsules with a false septum (considered a persistent replum at maturity) that divides the fruit into two locules. Major differences between the fruits of this family and the Patagonian fossils are the number of sepals (always four for the Brassicaceae) and the shape of the capsule. Fruits of Brassicaceae are known as siliques (e.g., *Diptychocarpus*, *Arabidella*,) and silicles, which are differentiated by their dimensions; these vary in shape from terete to quadrangular depending on the degree and plane of the compression (right angle, angustiseptate, and latiseptate; Appel and Al-Shehbaz, 2003). Clearly, Brassicaceae fruits are rather different from the ones described here. All the families considered for comparison have combinations of characters (such as presence or absence of infructescence and flower bracts, type of styles and stigmas, number and connation of sepals, shape of the capsules, number of valves and locules

per capsule, etc.) that are not consistent with the character suite observed in the Patagonian fossils.

The fossil infructescences described herein were also compared with the family Cunoniaceae because they share numerous characters with members of this family. Characters that support their placement in the Cunoniaceae are the type of inflorescence, pedicellate fruits, persistent and basally connate sepals, and bicarpellate, syncarpous capsules with valves separating distally from the base. Although these characters are not individually unique to the family, their combination in the fossils justifies their placement within the Cunoniaceae. This is not the first time that a combination of characters has been used for placing fossils within Cunoniaceae (see, e.g., Schönenberger et al., 2001; Gandolfo and Hermsen, 2017). The fruits of both new fossil genera are bicarpellate, basipetally septifragal, dehiscent capsules with a persistent calyx of mostly five (sometimes four) sepals, persistent styles, and a persistent replum inside the fruit. We interpreted the capsules as septifragal because they are incompletely opened along the dorsal or ventral sutures by a break in the partition, leaving a persistent replum.

The key characteristics that can be used to distinguish among Cunoniaceae with basipetally dehiscent bicarpellate capsules that are relevant to the analysis of *Racemofructus* and *Cunoniocarpa* are the branching pattern of the infructescence—whether a cyme, thyse, raceme, panicle, capitulum, or solitary flower—and the structure of the replum in the capsule (Table 2). The replum is a persistent partition between the carpels that occurs in the capsules of some Cunoniaceae; it is thought to be formed by the fusion of the marginal vascular bundles (placentae) in the carpels and occurs in a few configurations based on the number of columns (one or two) present per capsule and whether they are attached to the margins of the carpels or completely free of them (Figure 4A–F; Godley, 1983; Bradfield and Barnes, 2001; Hopkins and Hoogland, 2002; Pillon et al., 2021).

Assignment of *Racemofructus* to Cunoniaceae

Racemofructus fasciculatus has fruit and inflorescence morphology that is consistent with placement in Cunoniaceae. *Racemofructus* shares two tribal synapomorphies suggested by Bradford and Barnes (2001): (1) fruits borne in a raceme and (2) capsules with a single replum. The single replum is a solitary, unbranched columnar structure that occurs between the carpels of the capsule; this type of replum is characteristic only of Cunoniaceae and *Bauera* among Cunoniaceae (Figures 4D, 5A; Table 2; Godley, 1983; Bradfield and Barnes, 2001; Pillon et al., 2021). However, according to Hopkins et al. (2013), the free-pair replum in capsules of Geissoieae can become detached so that the capsules appear to have a single replum. *Bauera* differs from *Racemofructus* in having solitary flowers rather than inflorescences (Bradford et al., 2004). Geissoieae are different from *Racemofructus* in having flowers borne singly in the inflorescences (i.e., the flowers are not in fascicles;

FIGURE 4 Replum morphology of extant members of the Cunoniaceae. Scale bar = 1 mm. (A) BH54000; capsule of *Geissois pruinosa* (Geissoieae) with a free-pair replum composed of two apically bifurcating columns (arrows), which are free from the endocarp and adnate to style bases. (B) BH46258; capsule of *Ackama rosifolia* (Caldcluvieae) with an adnate-pair replum (equivalent to the replum being absent in this study) composed of two apically bifurcating columns; arrows point to the bifurcating arms of the proximal column; the column is completely adnate to the inner walls of adjacent carpels. (C) BH46252; capsule of *Ackama celebica* (Caldcluvieae) with a free-pair replum composed of a single bifurcating column (arrows) adnate to style bases and free from endocarp. (D) BH54025; capsule of *Weinmannia racemosa* with a single replum composed of a single central column (arrow) free from style bases and endocarp. (E) Top-down view of a capsule of *A. celebica* at an early stage with arrows pointing to the arms of the bifurcating central column; the arms are fused to style bases and free from endocarp. (F) Top-down view of an *A. celebica* capsule at a late stage in which the central column has divided to produce a pair of apically bifurcating columns (arrows) adnate to style bases and free from endocarp.

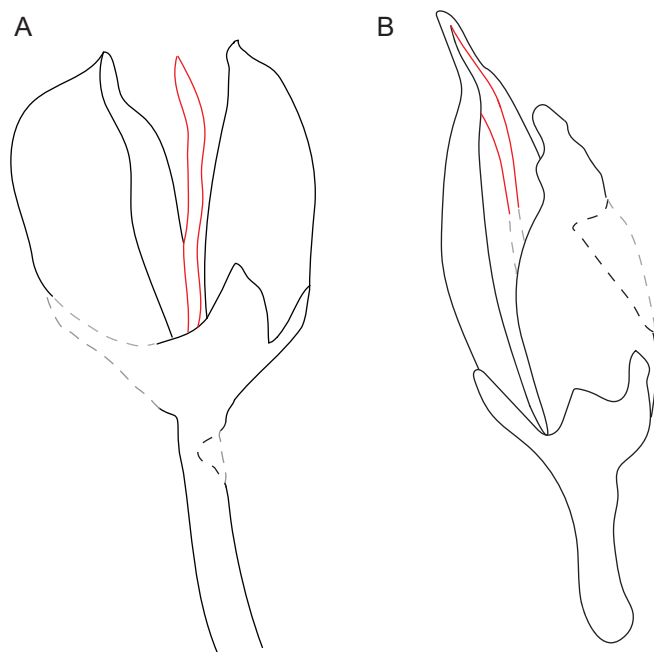


FIGURE 5 Fossil fruit reconstructions. Not to scale. Solid lines represent the outline of the fossil, with the replum of each capsule outlined in red. Dashed black lines outline areas in which the fossil is broken or obscured. Gray dashed lines indicate inferred outlines of broken or obscured structures. (A) Drawing of a capsule from *Racemofructus* (MPEF-Pb 11025; Figure 2C) showing the solitary replum. (B) Drawing of a capsule from the holotype of *Cunoniocarpa* (MPEF-Pb 11029, Figure 3A) showing one apical arm of the free-pair replum.

Schimanski and Rozefelds, 2002; Rozefelds and Pellow, 2011; Hopkins et al., 2013; Hopkins, 2018).

Racemofructus lacks the diagnostic features that define three of the genera in Cunoniaceae: a capitate inflorescence (*Pancheria*), acropetal capsule dehiscence (*Cunonia*), and a trimerous perianth (*Vesselowskyia*) (Bradford, 1998; Bradford and Barnes, 2001; Rozefelds et al., 2001; Bradford et al., 2004; Hopkins et al., 2009; Pillon et al., 2021). Although the characters present in *Racemofructus* are largely consistent with *Pterophylla* and *Weinmannia* s.s., placement within either genus is weakly supported because many of the features of *Racemofructus*—such as its racemose inflorescence structure, basipetal capsule dehiscence, and 4- or 5-merous calyx—are plesiomorphic within Cunoniaceae (see Bradford, 1998, 2002; Bradford and Barnes, 2001). The strongest character linking *Racemofructus* to *Pterophylla* and *Weinmannia* s.s. is the fasciculate arrangement of the fruits; among Cunoniaceae and outside of those genera, fruit in fascicles only occurs in some species of *Cunonia* (Bradford, 1998; Bradford et al., 2004; Pillon et al., 2021). The morphological characters which reliably distinguish *Pterophylla* and *Weinmannia* s.s. at the generic level pertain to inflorescence architecture (Pillon et al., 2021). Because *Racemofructus* is based on fossils of unbranched, capsule-bearing axes (Figure 2A, B), its complete inflorescence architecture cannot be compared with those of *Pterophylla* and *Weinmannia* s.s., and it therefore lacks diagnostic characters of either genus.

Although not diagnostic at generic level, some characters observed in *Racemofructus* are useful for distinguishing sections or species of extant *Pterophylla* and *Weinmannia* s.s. These include whether fruits (1) are solitary or in fascicles on the ultimate inflorescence axis; (2) are pedicellate or sessile; (3) are subtended by a persistent bract or lack an associated bract (i.e., are associated with caducous bracts); and (4) have a persistent or caducous calyx (Bradford, 1998; Hopkins, 1998; Pillon et al., 2021). In *Racemofructus*, fruits are in fascicles, pedicellate, lack associated persistent bracts, and have an attached calyx (Figure 2C). These character traits occur in *Weinmannia* s.s. and *Pterophylla* sections *Pterophylla*, *Inspersae*, and *Spicatae* (Bradford, 1998; Hopkins and Hoogland, 2002). *Racemofructus* can be distinguished from *Pterophylla* section *Leiospermum* because their flowers are borne singly and have caducous calyxes (Bradford, 1998; Hopkins and Hoogland, 2002). *Racemofructus* may differ from *Pterophylla* section *Spicatae* in having pedicellate fruits, although pedicels sometimes develop on fruits in *Spicatae* even though flowers are sessile (Bradford, 1998, 2001). Thus, the combination of characters present in *Racemofructus* clearly suggests an affinity to the Cunoniaceae—and to *Weinmannia* s.s. and *Pterophylla* in particular—but does not support its placement in any extant genus. Notably, *Weinmannia*-type pollen (*Tricolporites* sp. 2; Barreda et al., 2020) occurs in some of the layers yielding *Racemofructus* fossils (LH6, LH22). The co-occurrence of *Racemofructus* and the *Weinmannia*-type pollen in the same layers supports the idea that *Racemofructus* could belong to *Weinmannia* s.l.

Assignment of *Cunoniocarpa* to *Caldcluvieae*

Cunoniocarpa stylosa exhibits a combination of characters that are not found in any extant genus of Cunoniaceae and does not include any tribal or generic apomorphies. Among bicarpellate, capsular Cunoniaceae, the presence of a persistent, 4- to 6-merous calyx and long, persistent styles suggests an affinity to the tribes *Caldcluvieae* and Cunoniaceae (Hoogland, 1979; Bradford, 1998; Bradford and Barnes, 2001; Hopkins and Hoogland, 2002). Interestingly, the genera included in *Caldcluvieae* lack tribal synapomorphies based on reproductive structures and share many features of their fruit morphology with *Pterophylla* and *Weinmannia* s.s. (Hoogland, 1979; Bradford and Barnes, 2001; Table 2). Cunoniaceae and *Caldcluvieae* can be reliably distinguished, however, based on their inflorescence structure and replum morphology. Inflorescences of *Caldcluvieae* are compound and cymose or paniculate/thyrsoïd, whereas inflorescences of Cunoniaceae are racemose (most genera) or capitate (*Pancheria*) (Bradford, 1998, 2001; Bradford and Barnes, 2001; de Lange et al., 2002; Hopkins and Hoogland, 2002; Bradford et al., 2004; Pillon et al., 2021). The structure of the paniculate or thyrsoïd inflorescences of *Ackama* (*Caldcluvieae*) is, however, like some species in *Pterophylla* sect.

Leiospermum in which inflorescence modules are composed of a terminal raceme and multiple pairs of opposite racemes (Bradford, 1998, 2002; de Lange et al., 2002; Hopkins and Hoogland, 2002; Pillon et al., 2021).

Capsules of *Cunoniocarpa* can be separated from Cunoniaceae and linked to Caldcluvieae based on their replum morphology. Caldcluvieae either lack a replum (Figure 4B) or have a replum in a free-pair configuration (Figure 4C, E, F; also shown in *Geissois* of tribe Geissoieae in Figure 4A), whereas Cunoniaceae have a solitary replum (Figure 4D; Godley, 1983; Bradford and Barnes, 2001; Hopkins and Hoogland, 2002; Pillon et al., 2021). The replum observed in capsules of *Cunoniocarpa* consists of a single apically bifurcating column, with each arm of the column adnate to the nearest style base (Figures 3E, 5B). The free-pair configuration was first illustrated by Godley (1983) and was defined by Bradford and Barnes (2001); a free-pair replum is composed of two apically bifurcating columns with distal arms adnate to the style bases. Bradford and Barnes (2001) scored the free-pair replum type as occurring in *Ackama* (sometimes), *Spiraeopsis* (here included in *Ackama* after Pillon et al., 2021), *Caldcluvia*, *Eucryphia*, *Geissois* s.l., and *Lamanonia*. *Ackama celebica* capsules may have free-pair repla with the replum columns distinct (Figure 4F) or connate in the dorsal-ventral plane (Figure 4E), perhaps representing different stages of capsule maturation or variation in carpellary vascular anatomy. Similar variation in the free-pair replum configuration also occurs in *Ackama brassii* fruits (Fig. 27D of Hopkins and Hoogland, 2002) but has not been recorded from species of any other genera in the Cunoniaceae. Dickison (1975) noted that two species of *Ackama* (as *Spiraeopsis* in Dickison, 1975), *A. celebica* and *A. rufa*, deviate from the pattern of carpellary vasculature typically associated with the free-pair replum type and instead share a pattern of carpellary vasculature with species of the Cunoniaceae that have a single replum. Further study may reveal that this variation of the free-pair configuration is in fact diagnostic of the Caldcluvieae. Morphological features of *Cunoniocarpa* clearly differentiate the genus from Cunoniaceae taxa that have capsules with a free-pair replum but are not in Caldcluvieae. Geissoieae differ from *Cunoniocarpa* in having racemose inflorescences (Bradford et al., 2004; Hopkins et al., 2013); furthermore, elongated styles are not persistent on the capsules in Geissoieae (Figure 4A; Hopkins et al., 2013; Hopkins, 2018). *Eucryphia* is easily distinguished from *Cunoniocarpa* because it bears solitary flowers and produces capsules with four or more carpels (Bradford and Barnes, 2001; Bradford et al., 2004).

Capsules of *Cunoniocarpa* are pedicellate and borne singly, as in some species in all three genera of Caldcluvieae (Bradford, 1998; Bradford and Barnes, 2001; Hopkins and Hoogland, 2002). They are borne on a compound infructescence that consists of a central axis with at least three pairs of lateral branches (Figure 3A). The triangular shape of the infructescence suggests that this form may represent a fragment from a large panicle or thyrsoid

inflorescence like that of *Ackama* (de Lange, 2002; Hopkins and Hoogland, 2002; Pillon et al., 2021). The pedicels of *Cunoniocarpa* are less than 2 mm long, putting them in the size range of *Ackama* (Pillon et al., 2021). The floral bracts and the calyx are persistent in the holotype specimen of *Cunoniocarpa stylosa* (Figure 3A, B). Among extant genera of Caldcluvieae, *Caldcluvia* has persistent bracts and a caducous calyx, whereas *Ackama* (Figures 3D, 4B, 4C) and *Opocunonia* have a persistent calyx and caducous bracts (see appendices 2 and 4 of Bradford, 1998; Pillon et al., 2021). The capsules of *Cunoniocarpa* have styles that divide at the apex and appear bifid (Figure 3E). Some species of *Ackama* (documented in *A. australiensis*, *A. paniculosa*, and *A. rosifolia*) have capsules that divide up to one half their length loculicidally (de Lange et al., 2002), which can make the valves appear bifid at the apex (illustrated in Maiden, 1917; Harden, 2021).

In summary, although *Cunoniocarpa* lacks apomorphies for Caldcluvieae, it does exhibit characteristics that strongly suggest a relationship to the tribe, particularly the presence of a free-pair replum type. *Cunoniocarpa* cannot be placed within a modern genus with confidence, but it does share multiple features with *Ackama*, such as its branching, triangular inflorescence, short pedicels, and bifid styles in fruit. Notably, abundant, co-occurring, undescribed compound leaves and leaflets from Laguna del Hunco were reported as an unpublished species of *Caldcluvia* or *Ackama* based on the presence of hairy domatia in secondary vein axils, among other characters (morphotype TY116 of Wilf et al., 2005; Merkhofer et al., 2015). Additional study is necessary, however, to confirm their taxonomic placement.

Fossil record of Cunoniaceae and Caldcluvieae

Several reports of Cunoniaceae in the macrofossil record of Antarctica and South America are based on wood assigned to *Weinmannioxylon*, some species of which share similarities to *Weinmannia* s.l. or Cunoniaceae more broadly. It should be noted, however, that Jud and Gandolfo (2021) expressed reservations about the assignment of Cretaceous and Paleogene *Weinmannioxylon* wood to crown Cunoniaceae; furthermore, not all species of *Weinmannioxylon* are thought to be related to *Weinmannia* s.l. or other genera of Cunoniaceae (discussed further below). The earliest potential macrofossil records of Cunoniaceae are two species of *Weinmannioxylon* from the Late Cretaceous of James Ross and Livingston islands, Antarctica (Poole et al., 2000; Pujana et al., 2018; Jud and Gandolfo, 2021; Figure 1). Poole et al. (2000) compared *Weinmannioxylon nordenskjöldii* to multiple genera of Cunoniaceae including *Weinmannia* s.l. (Poole et al., 2000), while Pujana et al. (2018) considered *Weinmannioxylon trichospermoides* similar to wood of several species in *Weinmannia* s.l. *Weinmannioxylon multiperforatum* (the type species) and *Weinmannioxylon pluriradiatum*, also considered similar to wood of *Weinmannia* s.l. and *Cunonia* (Petriella, 1972; Brea et al., 2015),

have been found at several Paleogene localities in Chubut and Neuquén provinces in Argentina (Petriella, 1972; Raigemborn et al., 2009; Brea et al., 2015; Jud and Gandolfo, 2021). One Neogene occurrence of wood from the Falkland (Malvinas) Islands has been assigned to cf. *Weinmannia* (Poole and Cantrill, 2007, equivalent to *Weinmannia* s.l. in this study).

Cunoniaceae are represented by leaf and infructescence records in Australasia beginning in the Paleogene (Barnes, 1999; Barnes et al., 2001). A leaf macrofossil of *Weinmannia* s.l. and leaf macrofossils of *Weinmanniaphyllum bernardii*—which has affinities to either *Weinmannia* s.l. or *Cunonia*—are known from Paleogene deposits of Tasmania, Australia, where neither *Weinmannia* s.l. nor *Cunonia* occurs presently (Carpenter and Buchanan, 1993; Barnes, 1999; Barnes et al., 2001; Carpenter and Rozefelds, 2021). *Vesselowskyia* is known from a leaf macrofossil from the Oligocene Cethana flora, Tasmania (Carpenter and Buchanan, 1993; Barnes, 1999; Barnes et al., 2001). Pole (1993) reported a fossil infructescence bearing bicarpellate capsules in fascicles from the Miocene of New Zealand and assigned it to ?*Weinmannia racemosa* (*Pterophylla racemosa* in section *Leiospermum* in Pillon et al., 2021). Barnes (1999) assigned the infructescence only to ?*Weinmannia* (*Weinmannia* s.l. of this study); he excluded it from section *Leiospermum* because it has fruits in fascicles whereas *Leiospermum* has flowers borne singly. The New Zealand infructescence is the only previous report of a reproductive macrofossil with putative affinities to the Cunoniaceae.

There are additional reports of Cunoniaceae fossils outside of the Patagonia–Antarctica–Australasia region, although most are dubious (see review by Barnes, 1999). Some occurrences of *Cunonioxylon*, a wood taxon that has been reported from the Paleogene of North America and Europe, may have affinities to Cunoniaceae (Gottwald, 1992; Schönenberger et al., 2001; Wheeler and Lehman, 2009). Although the type species, *Cunonioxylon weinmannioides*, probably does not belong in Cunoniaceae (see Gregory et al., 2009; Wheeler and Lehman, 2009), two other occurrences are considered similar to genera in Cunoniaceae. The older is an unnamed wood type from the Paleocene of Texas, United States, that Wheeler and Lehman (2009) described as “cf. *Cunonioxylon sensu* Gottwald” (1992); they compared it to wood of *Weinmannia* s.l. Gottwald (1992) described the younger, *Cunonioxylon parenchymatosum* from the Eocene of Germany, as similar to wood of *Cunonia* (see also Wheeler and Lehman, 2009).

Macrofossil evidence of the *Caldcluvieae* is limited. Wood of *Weinmannioxylon ackamoides* (which includes species assigned to the genus *Caldcluvioxylon*) has been reported from the Late Cretaceous of Livingston Island (Chapman and Smellie, 1992; Poole and Cantrill, 2001) and the Paleogene of King George Island (Torres, 1990, 2003; Zhang and Wang, 1994; Poole and Cantrill, 2001; Oh et al., 2020) in Antarctica; it has been compared to the wood of *Ackama* (Chapman and Smellie, 1992; Poole and Cantrill, 2001) and *Caldcluvia* (Torres, 1990; Zhang and

Wang, 1994). Pujana and Ruiz (2019) rejected the inclusion of *Caldcluvioxylon* within *Weinmannioxylon* and introduced a new species, *Caldcluvioxylon torresiae*, from the Eocene Río Turbio formation in Patagonia; they considered *C. torresiae* comparable to wood of *Caldcluvia paniculata*. Leaves from the Paleocene of Seymour Island, Antarctica, have been assigned to *Caldcluvia mirabilis* (Dusén, 1908; Tosolini et al., 2013); additional material of *C. mirabilis* has been reported from the Paleogene of King George Island (Czajkowski and Rösler, 1986; Li, 1994; Torres, 2003; Budantsev, 2012). No putative fossil infructescences of *Caldcluvieae* have been previously reported.

Cunoniaceae Patagonian macrofossil record

The macrofossil record of Patagonia indicates the existence of multiple lineages of Cunoniaceae by the Paleogene; it was recently summarized by Jud and Gandolfo (2021) and is briefly updated here. The earliest Cunoniaceae macrofossil records from the southern hemisphere are Late Cretaceous wood assigned to the genera *Eucryphiaceoxylon* and *Weinmannioxylon* from Antarctica (Pujana et al., 2018; Poole et al., 2000; Poole and Cantrill, 2001; Jud and Gandolfo, 2021; Figure 1) whereas the Patagonian record begins in the early Paleocene (early Danian) (Jud et al., 2018; Iglesias et al., 2021; Jud and Gandolfo, 2021). Most Paleocene to Eocene macrofossil reports of Cunoniaceae from Patagonia are from Chubut Province, Argentina. They include wood (*Weinmannioxylon*: Petriella, 1972; Raigemborn et al., 2009), flowers (*Lacinipetalum spectabilum* and *Cunoniantha bicarpellata*: Jud et al., 2018; Jud and Gandolfo, 2021), samaroid fruits (*Ceratopetalum edgardoromeroi*, Gandolfo and Hermesen, 2017), and unnamed leaf remains (Merkhofer et al., 2015; Iglesias et al., 2021). Other Eocene occurrences are farther to the south, in Santa Cruz Province, Argentina, and adjacent to the Chilean Aysén XI Region; these include a ?Cunoniaceae leaf (Carpenter et al., 2018), cf. *Weinmannioxylon* wood (Terada et al., 2006), and *Caldcluvioxylon torresiae* wood (Pujana and Ruiz, 2019). Younger macrofossil records in Patagonia are sparse and include occurrences of the wood taxa *Eucryphiaceoxylon eucryphioides* and *Weinmannioxylon multiperforatum* in the Oligocene of Neuquén Province (Brea et al., 2015), *E. eucryphioides* from the Miocene of Santa Cruz Province (Brea et al., 2012), and cf. *Weinmannia* wood from the Neogene of the Falkland Islands/Islands Malvinas (Xylotype 6 of Poole and Cantrill, 2007).

The early Paleocene flower *Cunoniantha bicarpellata* was resolved in the Core Cunon clade but not placed within a tribe (Jud and Gandolfo, 2021). The other two reproductive structures—the Paleocene flower *Lacinipetalum spectabilum* and the Eocene samaroid fruit *Ceratopetalum edgardoromeroi*—are in tribe Schizomerieae (Gandolfo and Hermesen, 2017; Jud et al., 2018; Jud and Gandolfo, 2021). Cladistic analyses suggest that *Lacinipetalum* is a stem taxon to the extant Schizomerieae clade (Jud et al., 2018; Jud and

Gandolfo, 2021); *Ceratopetalum* is an extant Australasian genus within Schizomerieae (Gandolfo and Hermsen, 2017). At least some of the fossil wood occurrences are possibly related to their namesake genera, all of which are in the Core Cunon clade; among these are the unplaced genus *Eucryphia* (*Eucryphiaceoxylon*, Brea et al., 2012, 2015), *Caldcluvia* in *Caldcluvieae* (*Caldcluvioxylon*, Pujana and Ruiz, 2019), and *Weinmannia* s.l. in *Cunonieae* (cf. *Weinmannia* and *Weinmannioxylon*, Petriella, 1972; Poole and Cantril, 2007; Raigemborn et al., 2009; Brea et al., 2015). Thus, the Core Cunon clade and tribe Schizomerieae are strongly supported as being present in Patagonia by the Paleocene to early Eocene based on analysis of reproductive structures (Jud et al., 2018; Jud and Gandolfo, 2021), and *Caldcluvieae*, *Cunonieae*, and the *Eucryphia* lineage may have been present in the Paleogene based on fossil wood. The new fossil infructescences, *Cunoniocarpa* and *Racemofructus*, described in this study provide additional evidence for the presence of tribes *Caldcluvieae* and *Cunonieae* by the early Eocene and suggest that the Core Cunon clade was represented by as many as three genera and two tribes in Patagonia by the early Eocene (52 Ma).

Biogeography

Cunoniocarpa and *Racemofructus* grew in a moist subtropical-like climate with a diverse community of plants that included ferns, gymnosperms, and angiosperms (Wilf et al., 2005; Barreda et al., 2020). Many constituents of this paleoflora currently are absent from or have a limited distribution in South America, but they have extensive distributions in the tropical and subtropical aseasonal rainforests of Australasia and Malesia. Among gymnosperms, examples include *Podocarpus*, *Dacrycarpus*, *Acropyle*, and *Retrophyllum* (*Podocarpaceae*; Wilf, 2012; Wilf et al., 2009, 2017b); *Papuacedrus* (*Cupressaceae*; Wilf et al., 2009); and *Agathis* and *Araucaria* (*Araucariaceae*; Wilf et al., 2014; Rossetto-Harris et al., 2020). Among angiosperms, examples include *Atherospermaphyllum* and *Monimiophyllum* (*Atherospermataceae* and *Monimiaceae*; Wilf and Knight, 2013), *Gymnostoma* (*Casuarinaceae*; Zamaloa et al., 2006), *Ceratopetalum* (*Cunoniaceae*; Gandolfo and Hermsen, 2017), *Winteroxylon* (*Winteraceae*; Brea et al., 2021), several *Proteaceae* (Gonzalez et al., 2007), *Castanopsis* (*Fagaceae*; Wilf et al., 2019a, b), and the monocot *Ripogonum* (*Ripogonaceae*; Carpenter et al., 2014). The noted floristic similarity between the Laguna del Hunco paleorainforest, the modern rainforests of Australasia and the Malay Archipelago, and the paleorainforests of Australia and Antarctica supports the interpretation of the early Eocene Laguna del Hunco paleoflora as the westernmost reach of a trans-Antarctic paleorainforest biome, for which the ranges of its taxa have relocated and contracted in response to loss of favorable climates in southern South America and the development of substantial oceanic barriers beginning later in the Eocene (Wilf et al., 2013, 2019; Kooyman et al., 2014).

However, the presence of lineages with New World affinities such as *Physalis* (*Solanaceae*; Wilf et al., 2017a; Deanna et al., 2020), at Laguna del Hunco suggest that the composition of the LH paleoflora is not entirely contained in any single modern region (Merkhofer et al., 2015).

The extant distributions of genera in *Cunonieae* and *Caldcluvieae* are consistent with the dominant biogeographic pattern among lineages present in the Laguna del Hunco paleoflora (Figure 1). Structural evidence suggests that *Racemofructus* is likely related to *Weinmannia* s.l., and its likely biogeographic allies within *Weinmannia* s.l. are *Weinmannia* s.s. or *Pterophylla* sect. *Pterophylla*. *Weinmannia* s.s. is disjunct in the southern hemisphere (see Pillon et al., 2021), with the majority of its species occurring in Central and South America; only two species occur in the Mascarene Islands east of Madagascar. *Pterophylla* sect. *Pterophylla* is distributed predominantly in the Malay Archipelago to as far east as Fiji (Pillon et al., 2021). On the basis of morphological evidence, *Cunoniocarpa* belongs in *Caldcluvieae*; it has the most similarities to the genus *Ackama*, although it also shares features with *Caldcluvia*. Thus, the likely biogeographical allies of *Cunoniocarpa* are either *Caldcluvia*, a monotypic genus that occurs in temperate rainforests of Chile and Argentina, or *Ackama*, which occurs on islands of the Malay Archipelago and Australia and New Zealand (Hopkins and Hoogland, 2002; de Lange, 2002; Pillon et al., 2021).

CONCLUSIONS

The presence of fossil *Cunoniaceae* in Patagonia is corroborated by wood, pollen, and reproductive remains. *Cunoniocarpa* and *Racemofructus* strongly support the hypothesis that the *Cunoniaceae* had diversified by the early Eocene as at least three tribes (*Schizomerieae*, *Caldcluvieae*, and *Cunonieae*) were represented in the southern South American fossil record at Laguna del Hunco. These new Patagonian fossil genera have morphological similarities and plausible biogeographic links to *Ackama* and *Caldcluvia*, and to *Weinmannia* s.s. and *Pterophylla* sect. *Pterophylla*, respectively. Thus, both fossil taxa can plausibly be linked biogeographically to the living flora of humid lower montane rainforests of Australasia and Malesia, and *Ackama* and *Weinmannia* s.l. should be added to the long list of Laguna del Hunco survivor lineages that occur in these associations (Kooyman et al., 2014; Merkhofer et al., 2015; Wilf et al., 2019a).

Currently, extant *Cunoniaceae* are represented in South America by four genera: *Eucryphia* (unplaced Core Cunon clade), *Lamanonia* (*Geissoieae*), *Caldcluvia* (*Caldcluvieae*), and *Weinmannia* s.s. (*Cunonieae*), and their combined distribution on the continent spans from southern South America (Santa Cruz province) to Central America and from the Andes to the Atlantic coast of Brazil (Barnes et al., 2001). Based on the Patagonian fossil record, the breadth of phylogenetic diversity of the *Cunoniaceae* in

South America has decreased since the Paleogene, as shown by the loss of tribe Schizomerieae, which is in the basal grade of Cunoniaceae; this loss likely occurred due to the regional constriction of areas with an equable and everwet climate following the Early Eocene Climatic Optimum and cooling associated with the opening of the Drake Passage and the formation of the Antarctic Circumpolar Current.

AUTHOR CONTRIBUTIONS

T.P.M. and M.A.G. conceived the study, described the fossils, and analyzed the data; T.P.M. led the writing of the manuscript with contributions from M.A.G., E.J.H., and P.W., who all contributed to fieldwork, and sorting, inventorying, and photographing the fossils.

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DATA AVAILABILITY STATEMENT

The fossil specimens are curated at the Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina. Extant material used in this study is curated and housed at BH, Bailey Hortorium, Cornell University, Ithaca, NY, US.

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