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Fossil Celastraceae leaves from the Early Miocene Foulden Maar *Lagerstätte*, New Zealand: expanding the fossil record and biogeographic history of the family

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ABSTRACT. A new extinct fossil genus and species of Celastraceae is described, based on numerous well-preserved leaves from the Early Miocene Foulden Maar *Lagerstätte*, southern New Zealand. The leaves of *Palaeochrysa celastroides* gen. et sp. nov. are most similar in morphology and anatomy to those of several extant taxa from the proximal Austral-Pacific clade of the family, such as *Denhamia*, *Maytenus* and *Salaciopsis*. This study of leaves with excellent cuticular preservation extends the fossil record of Celastraceae to the Early Miocene of New Zealand, further expanding the past range and biogeography of this largely cosmopolitan plant family.

KEYWORDS: *Palaeochrysa*, Celastraceae, leaves, cuticles, Early Miocene, Foulden Maar, New Zealand

INTRODUCTION

Celastraceae consist of about 100 genera and 1,200 species of trees, shrubs and lianas worldwide, especially in tropical regions, although *Celastrus scandens* L. is a common woody vine (liana) in temperate deciduous forests of North America and *C. orbiculatus* Thunb., another liana, is widespread in temperate deciduous forests of China, Japan and Korea (Zhu et al., 2020).

The evolution and biogeography of the family Celastraceae and various major generic complexes has been studied extensively (e.g. Simmons et al., 2001, 2008, 2012; Simmons, 2004), with significant recent realignments of traditional subfamilial and generic concepts and dispersal patterns, with widespread morphology-based genera such as *Maytenus* and *Gymnosporia* found to be polyphyletic in molecular studies (Liang et al., 2016; Biral et al., 2017; Zhu et al., 2020). Based on clade divergence age estimates, the family arose 103–99 Ma with separation of an Austral-Pacific clade (consisting mainly of former members of subfamily Celastroideae and including *Denhamia* and *Stackhousia*) ~76 Ma as sister to most of the family, with all the major more distal clades also showing Late Cretaceous to Paleocene divergence dates (Bacon et al., 2016; Hernández-Damián et al., 2021). The family is also diverse in the long-isolated biodiversity hotspot of Madagascar and a phylogenetic study by Bacon et al. (2016) using new

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character and taxon sampling together with fossil-calibrated molecular dating found that many lineages showed an African origin followed by long-distance dispersal worldwide.

FOSSIL RECORD OF CELASTRACEAE

Reviews of the fossil record for the family by Bacon et al. (2016), Liang et al. (2016) and more recently by Hernández-Damián et al. (2018, 2021), showed that leaves, flowers, pollen and wood have been reported from the Cenozoic of most regions. However, accurate placement of leaf impression fossils is often unreliable without cuticle (Golovneva et al., 2008) and many of these records are doubtful. Cenozoic fossil leaf impressions of *Celastrinities* Saporta lacking cuticle were reported from France (de Saporta, 1865) and North America (e.g. Lesquereux, 1883; Knowlton, 1919; Bell, 1949) and numerous other fossil leaf impressions attributed to the form genus *Celastrophyllum* Heer have been described from Late Cretaceous to Miocene sediments in Asia, Europe and North America (Lesquereux, 1891), all without cuticular detail. Liang et al. (2016) described *Celastrus caducidentatus* X.Q.Liang et Z.K.Zhou from China based on leaf fossils using tooth morphology, but did not report cuticular features and Liang et al. (2016) also listed multiple leaf fossil species of *Celastrus* from North America Europe and Australia, though many of these records also lack cuticular information. Similarly, although there are Celastraceae leaf impression taxa from the Eocene and Miocene of Australia reported as *Celastrophyllum* (von Ettingshausen, 1883, 1888), *Celastrus* (three species) and *Elaeodendron* Jacq. (von Ettingshausen, 1887, 1888), the *Celastrus* fossils were considered to be unreliable by Liang et al. (2016). Cretaceous-aged Celastraceae fruits have also been reported from Central Europe (Knobloch and Mai, 1984), as well as dubious leaf impression fossils from North America (Bell, 1949, 1957; Jonsson and Hebda, 2015). Thus, despite an apparently extensive fossil record, many of these identifications are now considered unreliable and/or need further scrutiny (Hernández-Damián et al., 2021).

Celastraceae pollen grains are mostly uniform across the family (stenopalynous), tricolporate with a reticulate exine and shed as monads, tetrads, or polyad groups of four tetrads (Lobreau-Callen, 1977; Archer and Van Wyk, 1992; Simmons, 2004 and references therein). Fossil Celastraceae pollen has been reported from numerous Cenozoic sites outside Oceania (see Muller, 1981; Hernández-Damián et al., 2021), but the pollen is not always diagnostic for the family (Barreda and Caccavari, 1992; Copenhaver, 2005).

There are no definite Celastraceae fossil pollen records from New Zealand, but the in situ *Rubipollis oblatus* (Pocknall et Mildenh.) Mildenh. et Pocknall pollen of *Fouldenia staminosa* Bannister, D.E.Lee et Raine (Bannister et al., 2005) was noted as being similar to *Stackhousia* Sm. (now in Celastraceae); however, *Fouldenia* flowers lack the floral disk seen in Celastraceae. Based on extant Celastraceae pollen morphology, fossil grains would be likely assigned to the palynomorph form genus *Rhoipites* Wodehouse. There are numerous *Rhoipites* species of unknown affinity reported from Foulden Maar (Mildenhall et al., 2014), so it is possible that Celastraceae pollen may be present there, but further study is needed (J.I. Raine pers. comm., 2023).

The present-day flora of New Zealand comprises ~2,400 spp. and 115 families of flowering plants (de Lange and Rolfe, 2010), meaning that the archipelago is somewhat depauperate in angiosperm species, genera and families relative to its land area. The reason for this apparent disparity is most likely related to a series of extinctions associated with late Miocene and Plio–Pleistocene climatic cooling and there is good fossil evidence that the flora of Zealandia was once much more diverse than it is today (e.g. Lee et al., 2001, 2016b; Lee and Lee, 2015).

At least 20 families have disappeared since the early to mid-Miocene, based partly on evidence from the excellent and well-studied pollen record (Raine et al., 2011; Mildenhall and Raine, 2012; Prebble et al., 2021). However, pollen is not always able to provide a true picture of the actual vegetation, as we have shown in a detailed study of the flora of the small lake deposit of Foulden Maar where, according to the fossilised pollen, the most abundant plants were species of Nothofagaceae and Podocarpaceae (Mildenhall et al., 2014), whereas a census of thousands of the actual leaves preserved in the lake deposit shows conclusively that the forest immediately surrounding the maar lake was dominated by 10 species of Lauraceae (Bannister et al., 2012), accompanied by diverse taxa from at least 100 species representing ~35 families (Lee et al., 2016a, 2022).

The reasons for such disparities include: the poor or null preservation of some pollen types such as Lauraceae (Macphail, 1980); some plants only produce small amounts of poorly dispersed pollen (e.g. many insect-pollinated taxa), whereas others (e.g. most wind-pollinated species, including Nothofagaceae and Podocarpaceae) produce large quantities of pollen that can travel long distances from the source plants; many pollen types are not distinctive/could be produced by many different families; and lastly, many described pollen types/taxa from the New Zealand Cenozoic record have not yet been assigned to a particular family (Raine et al., 2011; Mildenhall and Raine, 2012; Prebble et al., 2021). Equally, some leaves are very small, or have cuticle that preserves poorly (e.g. *Akania* Hook.f. and *Fuchsia* L.) and/or rarely detach from the parent plant and thus are often only found in exceptional circumstances, e.g. many monocots and ferns (Lee et al., 2016a, 2022).

At Foulden Maar, we have an opportunity to address some of these problems because of an excellent macrofossil record sourced from a small and highly local palaeocatchment; most leaves are from evergreen plants, flowers are often preserved with in situ pollen, enabling dispersed pollen to be associated definitively with the source plant and fruits with seeds are also preserved (Conran et al., 2014; Lee et al., 2016a, 2022).

The present study of fifty distinctive evergreen leaves with excellent cuticular preservation from the Early Miocene Foulden Maar *Lagerstätte* contributes to addressing the knowledge gap about the history of Celastraceae fossils in Australia and New Zealand, both, like Madagascar, formerly parts of Gondwana. The mesophyll-sized leaves commonly fossilise in a dark yellowish-brown (hence 'old gold') colour and have a distinctive elliptical to obovate shape, decurrent secondary venation and partially sunken, mixed laterocytic, cyclocytic and staurocytic stomata surrounded by a prominent doughnut-like cuticular ring. This combination of characters therefore supports placement of the fossil in Celastraceae. This family has not been reported from elsewhere in the New Zealand fossil record and is known only from this site. It is today represented in New Zealand only by the endemic rhizomatous herb *Stackhousia minima* Hook.f., formerly placed in Stackhousiaceae (Simmons et al., 2001). A few examples of the fossil taxon described here were also figured by Pole (1996: specimens FOLD-18 and CUT-Z-022 [OU30804], figs 33, 34, as indet.) and Lee et al. (2022: 9).

However, because these fossil leaves show similarities to several different extant Celastraceae genera and because vegetative morphology-based classifications within and between genera in the family are generally not supported (e.g. Islam et al., 2006; McKenna et al., 2011; Zhu et al., 2020), the fossils are described here as a new, extinct genus and species: *Palaeochrysa celastroides* Conran, Bannister et D.E.Lee.

GEOLOGICAL SETTING

The leaves were collected from two small mining pits in Foulden Maar on private land near Middlemarch, Otago, South Island, New Zealand (Fig. 1). Several thousand individual leaves have been collected (Pole, 1996; Lindqvist and Lee, 2009; Lee et al., 2016a) preserved in finely laminated biogenic lake sediments deposited in a small crater lake (Kaulfuss, 2017). Volcanics associated with the formation of the Foulden Maar indicate an age of earliest Miocene (~23 Ma) (Lindqvist and Lee, 2009; Fox et al., 2015; Kaulfuss, 2017). The lake sediments are mostly comprised of pennate diatom frustules (Harper et al., 2019), siliceous chrysophycean algal stomatocysts and sponge spicules, together with a small component of aeolian silt (Lindqvist and Lee, 2009; Kaulfuss, 2017). Larger fossils preserved in the *Lagerstätte* include insects (Kaulfuss et al., 2014a, b), articulated fish (Lee et al. 2007) and abundant leaves (Pole, 1996; Bannister et al., 2012; Lee et al., 2016a, 2022 and references therein), flowers and fruits (Conran et al., 2014, 2016, 2019).

MATERIALS AND METHODS

The leaves described here were mostly preserved on light-coloured (summer) bedding planes in the varved diatomite sediment. Wet paintbrushes and fine needles were used to clean debris from leaf surfaces. Selected leaves were cleared to show venation using warm 6% hydrogen peroxide and were then mounted in thymol-glycerol jelly. Cuticle preparations for both fossil and comparative living samples similarly involved soaking ~1 cm^2 leaf pieces in 6% hydrogen peroxide, warming

Figure 1. Map showing the Foulden Maar locality in Otago, South Island, New Zealand

gently until cleared, then rinsing in distilled water. Fine paintbrushes removed cell debris and separated the two layers before staining with 0.1% crystal violet for ~60 sec, rewashing and slide mounting in thymol-glycerol jelly. In total, fifty specimens out of the more than 700 well-preserved leaves examined from the site for cuticular details were identified as belonging to this taxon. All fossil specimens are held in the collections of the Department of Geology Museum (OU), University of Otago, Dunedin, New Zealand.

Fryns-Claessens and Van Cotthem (1973) and Wilkinson (1979) summarised reports of cyclocytic stomata from pteridophytes, gymnosperms, Magnoliaceae and the eudicot families Bignoniaceae, Celastraceae, Combretaceae, Rhizophoraceae and Myrtaceae, but terminology tends to be confusing, with Wilkinson (1979) noting that there can also be numerous intermediate forms with anisocytic, staurocytic and tetracytic stomata. Mixed stomatal patterns are also seen sometimes, such as Celastraceae where laterocytic, cyclocytic and staurocytic variants can all be observed on the same leaf in some taxa (den Hartog and Baas, 1978). In contrast, 'true' staurocytic stomata, defined as having three to five, usually four radially elongated subsidiary cells arranged crosswise to the guard cells (Fryns-Claessens and Van Cotthem, 1973; Baranova, 1992) are rare (Stace, 1965), are seen in some Marcgraviaceae (Fryns-Claessens and Van Cotthem, 1965), Piperaceae (Wilkinson, 1979) and a few *Eucalyptus* L'Hérit. (Myrtaceae) species (Carr and Carr, 1990).

Celastraceae leaf venation patterns and epidermal anatomy were investigated using living and herbarium collections at the Adelaide Botanic Gardens, The University of Adelaide Waite Arboretum, South Australian Herbarium (AD), Allan Herbarium (CHR) and Atherton Tropical Herbarium (QRS). Images of X-rayed Celastraceae, Balanopaceae and Marcgraviaceae leaves on the Australian Tropical Rainforest Plants website (CSIRO, 2020), the cleared leaf collection image databases of Hickey and Hu (2015) and Wilf et al. (2021) and published accounts such as von Ettingshausen (1857), Jessup (1984) and Simmons (2004) were also examined, as appropriate, with leaf morphology and venation terminology following Ellis et al. (2009). Additionally, Dressler (2004, 2017, 2020) was used for cuticular data on Marcgraviaceae and Carlquist (1980), Baranova (1983) and Kubitzki (2014) for Balanopaceae. Living taxa were compared for features such as leaf attachment, shape, margin, venation and cuticles. Cuticular preparation followed the same method as the fossils. The Celastraceae classification used here largely follows the phylogenies of Bacon et al. (2016) and Hernández-Damián et al. (2021), though some traditional subfamilial and generic concepts are also mentioned to allow comparison with older literature. Cuticular and stomatal terminology follows den Hartog and Baas (1978) and Wilkinson (1979).

SYSTEMATIC PALAEOBOTANY

Order: CELASTRALES Link

Family: CELASTRACEAE R.Br.

Palaeochrysa celastroides Conran, Bannister et D.E.Lee **gen. et sp. nov.**

Figs 2–4

Holotype here designated. OU33079 (Fig. 2A).

Paratypes. OU32472 (Fig. 2H), OU35625 (Fig. 2C), OU32397a (slide; Fig. 4C), OU32397b (SEM stub; Fig. 4D–I).

Other material examined. OU30804, OU32251, OU32252, OU32269, OU32305, OU32311, OU32315, OU32324, OU32330, OU32369, OU32370, OU32378, OU32388, OU32392, OU32399, OU32439, OU32455, OU32468, OU32473, OU32481, OU32482, OU32509, OU32535, OU32543, OU32576, OU32589, OU32595, OU32597, OU32628, OU32632, OU32648, OU32709, OU32712, OU32727, OU32779, OU32815, OU32821, OU32857, OU32886, OU33062, OU33069, OU33073, OU32675, OU32777, OU32788, OU32242, OU32470, OU32264, OU32259, OU32306.

Repository. Collections of the Department of Geology Museum (OU), University of Otago, Dunedin, New Zealand.

Locality. Foulden Maar, Middlemarch, Otago, South Island, New Zealand.

Stratigraphy. Foulden Hills Diatomite.

Age. Early Miocene (~23 Ma).

Etymology. The generic epithet comes from the Greek words *palaios* (old) and *chrysos* (gold) in reference to the characteristic deep yellow to pale brown colour of most of the fossil leaves of this taxon upon excavation. The specific epithet indicates the resemblance of the fossil leaves to those of several extant genera of Celastraceae.

Diagnosis. Leaves obovate elliptical, decurrent, margins entire; petiole short, base wide, sheathing; secondary vein course long, running into petiole, angle to midrib narrow and decurrent to petiole. Abaxial gland-like structures with cuticular flanges present. Stomata mixed laterocytic, staurocytic and cyclocytic and slightly sunken with a prominent smooth overhanging ring of cuticle, often with a squarish ring of narrow subsidiary cells and sometimes a second adjacent ring of narrow epidermal cells (bicyclic).

Description. Leaves simple, alternate (Fig. 2C) or in more or less terminal clusters (Fig. 2B), shortly petiolate; petioles 8–41 mm long, flat to semi-terete; petiole base wide, not pulvinate (Fig. 2H). Lamina notophyll, at least 37–160 × 28–72 mm, L:W ratio 4:3–3:1, narrow to widely elliptic or obovate, medially symmetrical to asymmetrical; margins entire; apex symmetrical, rounded to convex, apical angle obtuse to shortly acute (Figs 2, 3); base cuneate to decurrent, symmetrical to asymmetrical, basal angle acute (Fig. 3); lamina surface smooth; surficial glands or hairs not obvious. Primary venation pinnate; midvein stout proximally, tapering distally. Secondary and higher venation orders relatively weak. Major secondaries simple-brochidodromous, spacing inconsistent, decreasing proximally, attachment basally decurrent, angle acute, course long, almost parallel to midrib; interior secondaries absent; minor secondary course simple brochidodromous, proximal course parallel to major secondaries. Intersecondary veins <50% length of subjacent secondary; distal course parallel to subjacent major secondary; ~1 per intercostal area. Intercostal tertiary veins percurrent to irregular reticulate; acute to midvein; vein angle increasing proximally; epimedial tertiaries reticulate; proximal course parallel to intersecondary; distal course parallel to intercostal tertiary; exterior tertiary course looped. Quaternary veins irregularly reticulate. Quinternary veins freely ramifying. Areolation development moderate; freely ending veinlets mostly dichotomously one-branched, with simple termination. Marginal ultimate veins incomplete (Fig. 2I). Stipules not observed.

Cuticles. Leaves hypostomatic. Adaxial cuticle thin, epidermal cells irregularly polygonal, isodiametric to elongate, 29–63 × 20–42 µm (average 42 ± 7.4 × 31 ± 5.9 SD, n = 20); anticlinal walls rounded to slightly sinuous (Fig. 4A). Abaxial cuticle thin, cuticle over the veins not differentiated, smooth; anticlinal epidermal cells irregularly polygonal, isodiametric to elongate, 25–50 × 15–27 µm (35 ± 6.8 × 20 ± 3.8 µm); outer surface of periclinal walls smooth (Fig. 4D, E), inner surface finely granular (Fig. 4H, I); anticlinal walls rounded to slightly sinuous (Fig. 4G). Abaxial gland-like structures similar to cork warts (sensu Joffily and Cardoso Vieira, 2010) very rare, sunken with overlapping cuticular flanges (Fig. 4C), 25–50 × 15–27 µm (35 ± 6.8 × 20 ± 3.8 µm). Hair bases, hydathodes and colleters not observed.

Stomata mixed laterocytic, staurocytic and bicyclic cyclocytic (Fig. 4B, G), irregularly spaced and oriented, 90–116 per mm^2 (n = 10), slightly sunken with a prominent smooth overhanging ring of cuticle (Fig. 4D–F);

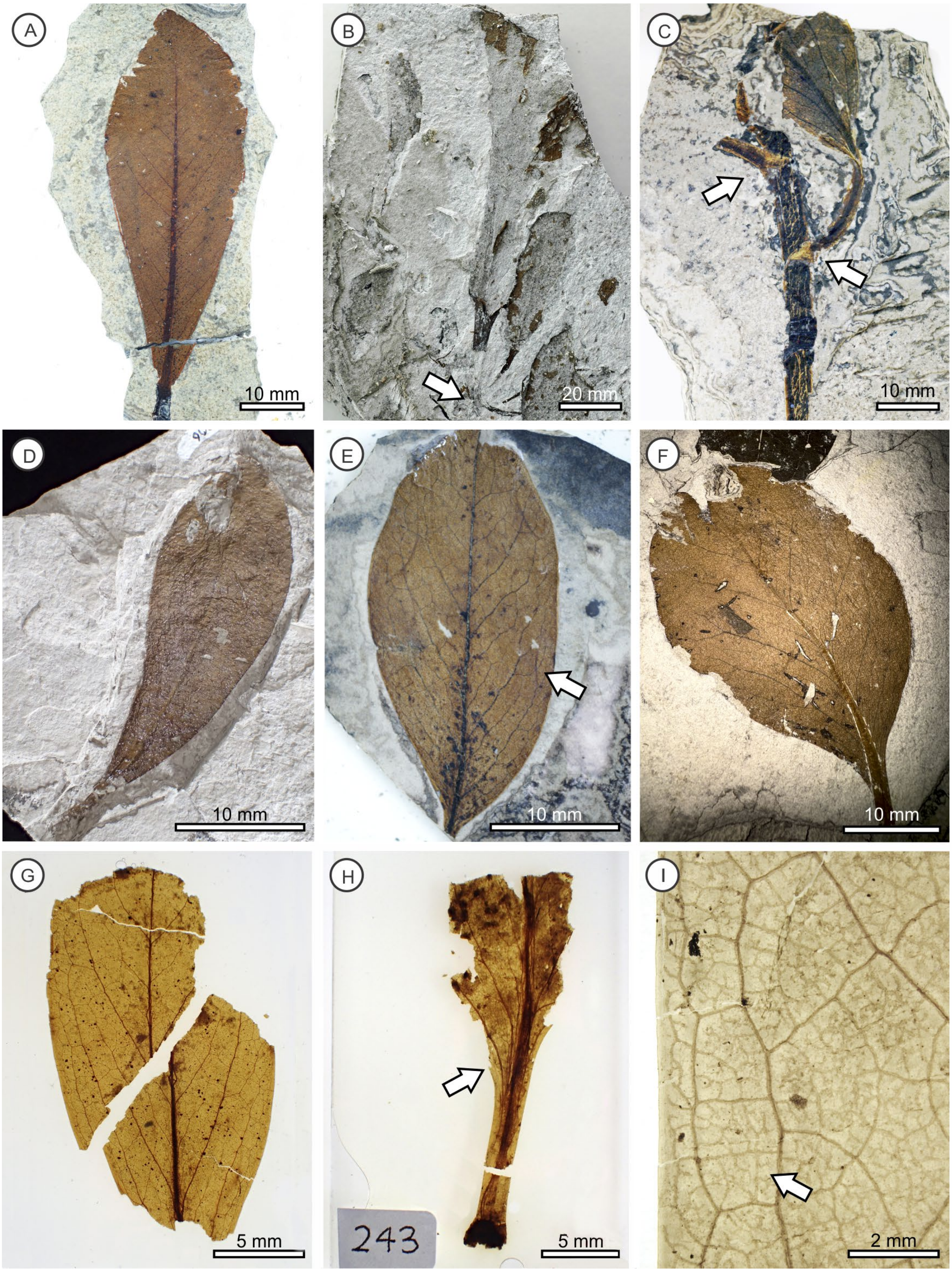

Figure 2. Fossil leaves of *Palaeochrysa celastroides* showing variation in leaf shape from obovate (A, D) to ovate (E, F), a well-developed petiole (A–D, H) and looped brochidodromous secondary venation (E, G, I). **A**. OU33079, HOLO showing obovate leaf form; **B**. OU32324 showing stem leaf cluster (arrow); **C**. OU35625 PARA showing alternate leaf attachment (arrows); **D**. OU30906; **E**. OU32886 with looped brochidodromous secondary venation (arrow); **F**. OU35616; **G**. OU32369, cleared leaf showing venation detail; **H**. OU32472 PARA showing detail of petiole and decurrent leaf base (arrow); **I**. OU32370 showing close-up of higher order venation and areoles with dichotomously 1-branched veinlets (arrow). Scale bars as indicated

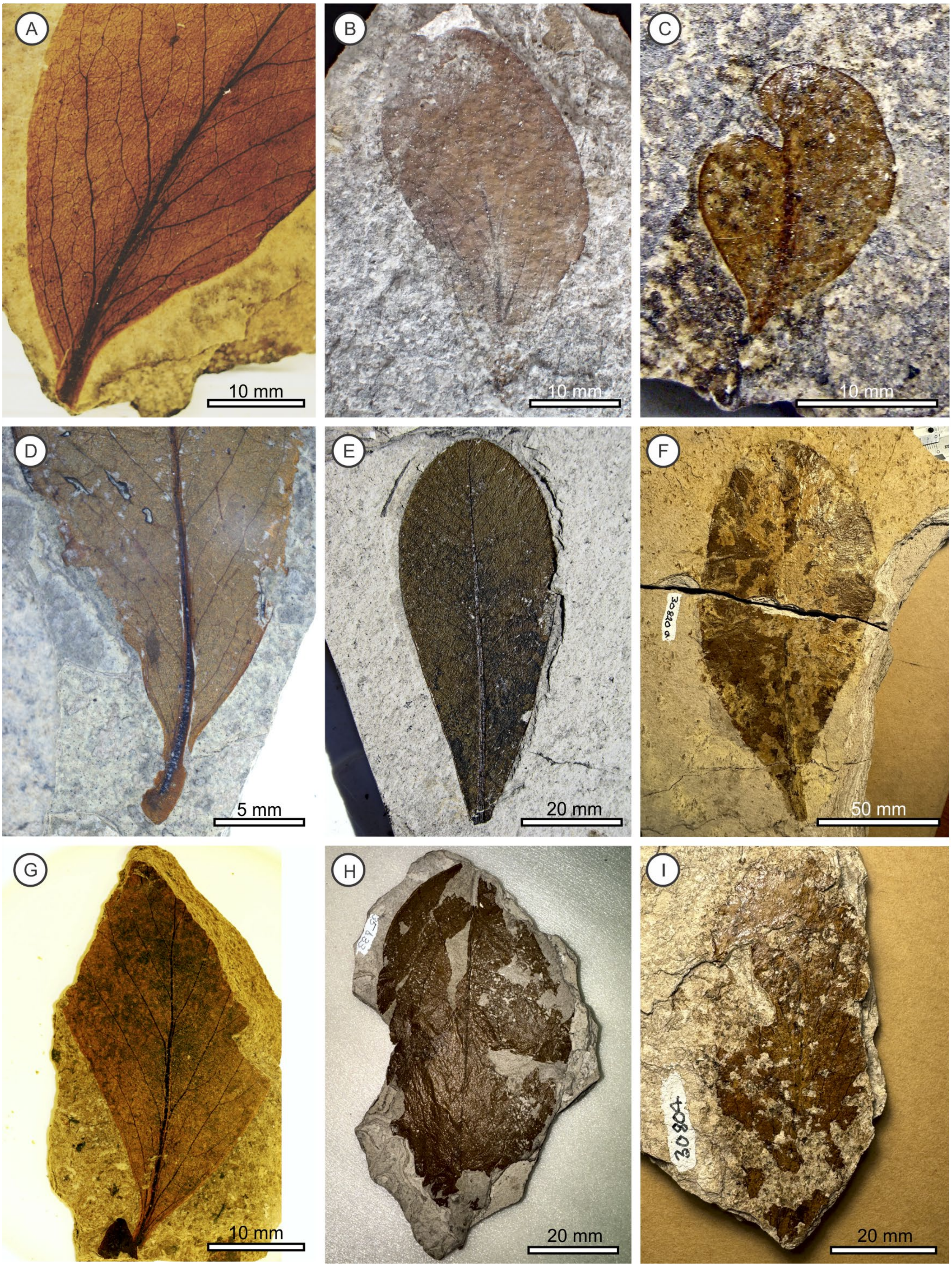

Figure 3. Additional specimens of *Palaeochrysa celastroides* showing variation in leaf form and size from obovate (E) to ovate (C), a well-developed petiole with decurrent leaf base (D) and looped brochidodromous secondary venation (A). **A**. OU32779; **B**. OU35602; **C**. OU13539; **D**. OU35930; **E**. OU35931; **F**. OU 30820a; **G**. OU32712; **H**. OU35633; **I**. OU30804. Scale bars as indicated

subsidiary cells 3–4(–7), 24–35 × 15–27 µm (29 ± 3.2 × 23 ± 2.9 µm), sometimes with a second adjacent ring of narrow subsidiary-like epidermal cells (bicyclic) 38–56 × 31–45 µm (46 ± 4.1 × 37 ± 3.4 µm) (Fig. 4I); guard cells 5–9 µm (7 ± 1.3 µm) wide; stomatal pores 7–13 × 5–9 µm (9 ± 1.7 × 7 ± 1.2 µm); polar rods prominent, t-shaped (Fig. 4H, I).

Remarks. Celastrales generally possess brochidodromous secondary veins and percurrent tertiary veins are also common (Hickey and Wolfe, 1975). Upchurch and Dilcher (1990: 15) further suggested that features which characterise modern Celastraceae leaves include “a distinct petiole, teeth with a glandular, nondeciduous seta directed into the sinus (a celastroid tooth), and subparallel tertiary venation with low-angle branching and perpendicular orientation to the midvein”. However, not all Celastraceae have toothed leaves and Liang et al. (2016) noted that some *Celastrus* L. species have camptodromous, craspedodromus or semicraspedodromus secondary venation.

Comparisons of leaf venation patterns for Celastraceae found that genera containing species with similar characteristics to *Palaeochrysa* include *Denhamia* Meisn., *Gymnosporia* (Wight et Arn.) Benth. et Hook.f., *Maytenus* Molin, *Salaciopsis* Baker f. and *Elaeodendron*, although this last genus has opposite, toothed leaves. The brochidodromous venation, subparallel tertiary venation with low-angle branching and perpendicular orientation to the midvein and incomplete ultimate marginal veins are all features shared with the fossil (e.g. Fig. 5A–D). However, in most genera the leaf base is generally not decurrent, the secondary veins do not run into the midrib and their course and angle to the midrib do not match the fossil, therefore there is no clearly supported placement into a modern genus.

Laterocytic stomata are regarded as the most common type in Celastraceae (den Hartog and Baas, 1978), although some taxa also have stomata with distinctive staurocytic to cyclocytic subsidiary cells that are partially sunken under the guard cells (Pant and Kidwai, 1966; den Hartog and Baas, 1978; Gomes and Lombardi, 2010) and with the 3–7 subsidiary cells described as being arranged in one to two or more narrow rings, generally of four cells (Van Cotthem, 1970; Wilkinson, 1979). Similarly, Pant and Kidwai (1966) noted that in some Celastraceae the ring of subsidiary cells has an additional outer ring of adjacent ‘encircling cells’, creating the impression of a double ring of guard cells. This distinctive pattern was later termed bicyclic by den Hartog and Baas (1978), who noted that it has arisen independently in *Denhamia*, *Tricerma phyllanthoides* (Benth.) Lundell (as *Maytenus texana* Lundell) and *Robsonodendron maritimum* (Bolus) R.H.Archer (as *Cassine maritima* L.Bolus); all formerly members of subfamily Celastroideae, though some are now placed in a proximal Austral-Pacific clade within the family (Bacon et al., 2016; Hernández-Damián et al., 2021). Additionally, Gomes and Lombardi (2010) reported this stomatal pattern in *Peritassa dulcis* Miers (subfam. Salacioideae). In particular, *Denhamia* has a mixture of bicyclic to tricyclic and/or cyclocytic to complex cyclocytic stomata (den Hartog and Baas, 1978; Biral et al., 2017) and many taxa possess a mixture of stomatal types (Fig. 6B–H).

Accordingly, the presence in *P. celastroides* of partially sunken, mainly bicyclic and cyclocytic to staurocytic stomata, described by Pole (1996: 28) as “amphicyclocytic, with two or sometimes three rings of elongate subsidiary cells”, as well as a prominent doughnut-like cuticular ring surrounding the stomata, supports its placement in Celastraceae, possibly close to the clade within Celastroideae that contains *Denhamia*. Although the leaves of *P. celastroides* do not show obvious stipules or scars, the stipules in Celastraceae are often tiny and caducous, therefore it is unlikely they would have been preserved on the fossils.

Another, albeit rare, feature on the fossils supporting placement in Celastraceae is the presence of occasional leaf epidermal glands comparable in structure to the cork-warts reported on the leaves of several Celastroideae (Joffily and Cardoso Vieira, 2010; Chin et al., 2013). In contrast, there is no evidence of leaf colleters, but those are only known to date from subfamily Salacioideae (Mercadante-Simões and Paiva, 2013).

Comparison of the fossil with living families with alternate, obovate leaves, cuneate decurrent bases, brochidodromous secondary venation and distinctive epidermal and stomatal features suggest placement in Celastraceae (e.g. von Ettingshausen, 1857; Jessup, 1984; Simmons, 2004). Based on leaf shape and venation, an alternative candidate family is Marcgraviaceae, a South American family of lianas

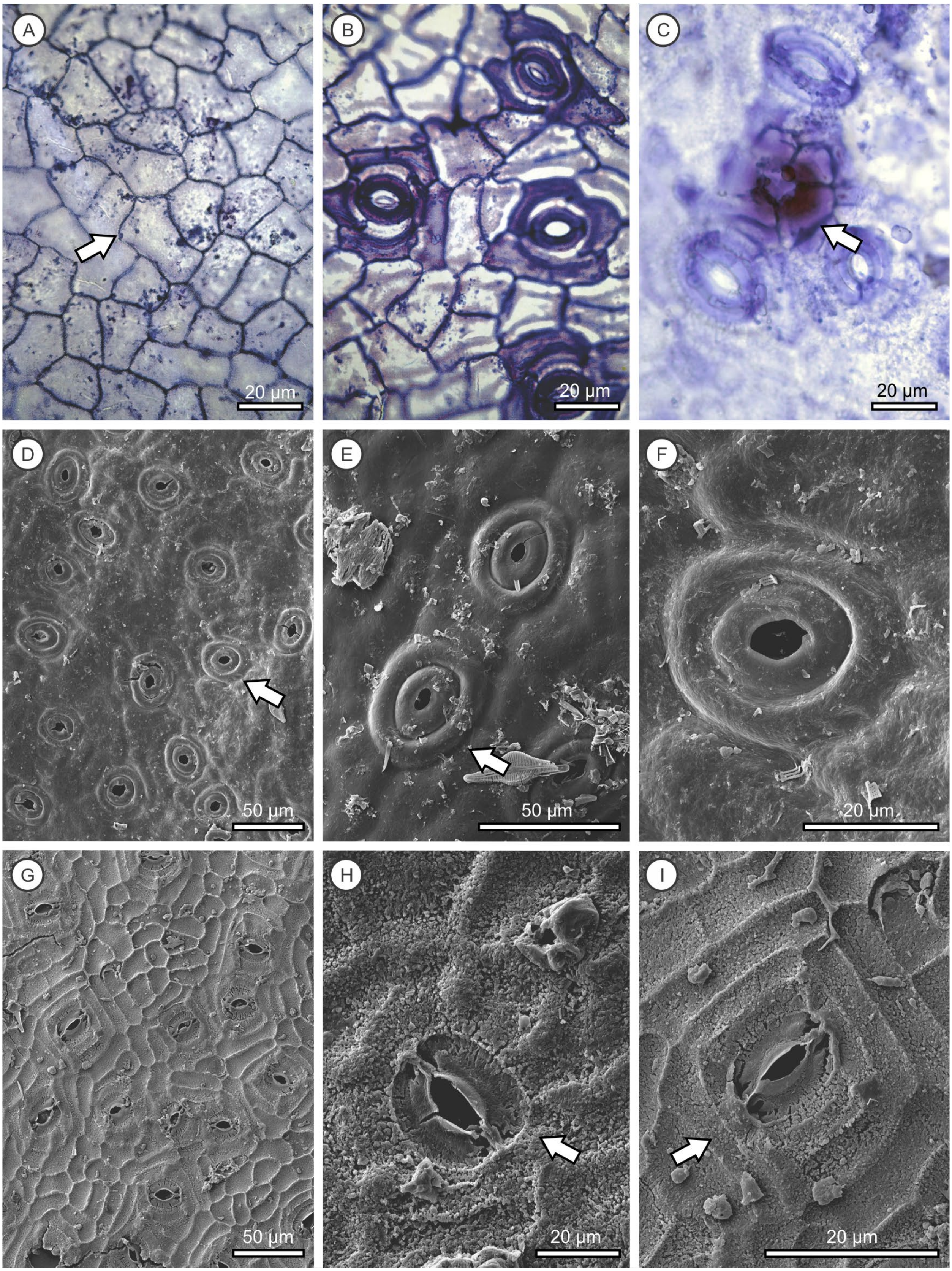

Figure 4. Fossil cuticles of *Palaeochrysa celastroides*. **A**. OU32857, adaxial surface with slightly sinuous anticlinal walls (arrow); **B**. OU32543, abaxial surface showing mixed stomatal types; **C**. OU32397, abaxial surface showing sunken gland-like structure with overlapping cuticular flanges (arrow); **D**, **E**. OU32397, outer abaxial surface showing smooth periclinal walls and prominent stomatal rings (arrow); **F**. OU32397, outer abaxial surface showing detail of stomatal ring; **G**. OU32397, inner abaxial surface showing mixed stomatal types; **H**. OU32397, inner abaxial surface showing granular periclinal walls and cyclocytic stomate (arrow); **I**. OU32397, inner abaxial surface showing bicyclic stomate (arrow). A–C from transmitted / reflected light, D–I from SEM. Scale bars as indicated

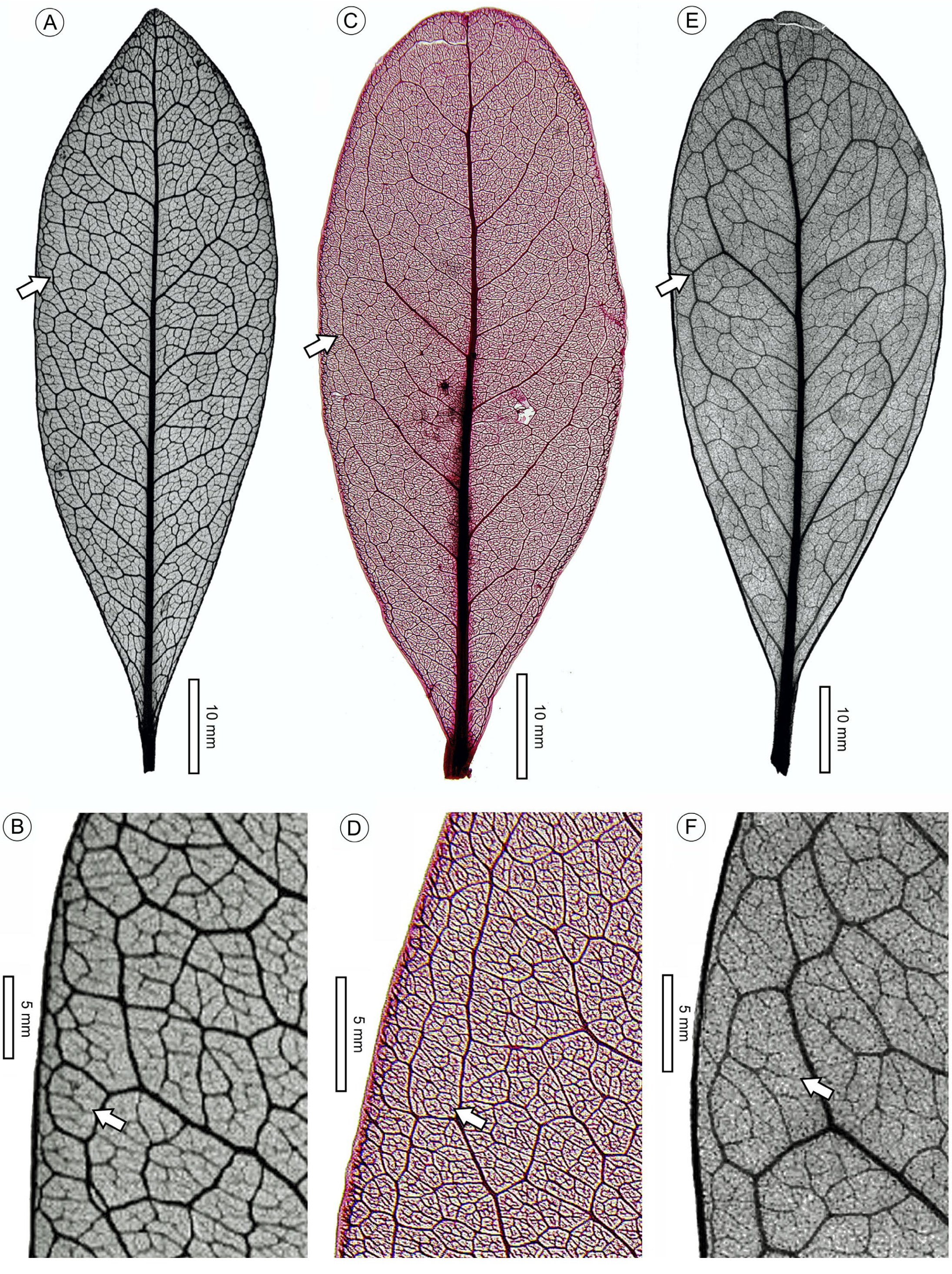

Figure 5. Leaves and venation details of genera with showing venation similarities to the fossil. **A**, **B**. *Denhamia viridissima* F.M.Bailey et F.Muell. ex F.M.Bailey, **A**. leaf showing looped brochidodromous venation (arrow), **B**. close-up of higher order venation and areoles with dichotomously 1-branched veinlets (arrow); **C**, **D**. *Salaciopsis neocaledonica*, **C**. leaf showing looped brochidodromous venation (arrow), **D**. close-up of higher order venation and areoles with dichotomously 1-branched veinlets (arrow); **E**, **F**. *Balanops australiana*, **E**. leaf showing looped brochidodromous venation (arrow), **F**. close-up of higher order venation and areoles with irregularly branched veinlets (arrow). Image sources A, B, E, F Australian Tropical Rainforest Key (CANBR 2020); C, D (Wilf et al. 2021), used with permission. Scale bars as indicated

or small trees with alternate, coriaceous, entire or revolute-margined leaves with obscure brochidodromous secondary venation and which, when sterile, can be mistaken for Celastraceae (Biral and Lombardi, 2020). However, Marcgraviaceae are characterised by the presence of specialised hypophyllous glands arranged in patterns on the petioles and lamina (Dressler, 2004, 2017), T-shaped hairs (Biral and Lombardi, 2020) and predominantly staurocytic stomata in at least *Marcgravia* (Fryns-Claessens and Van Cotthem, 1965).

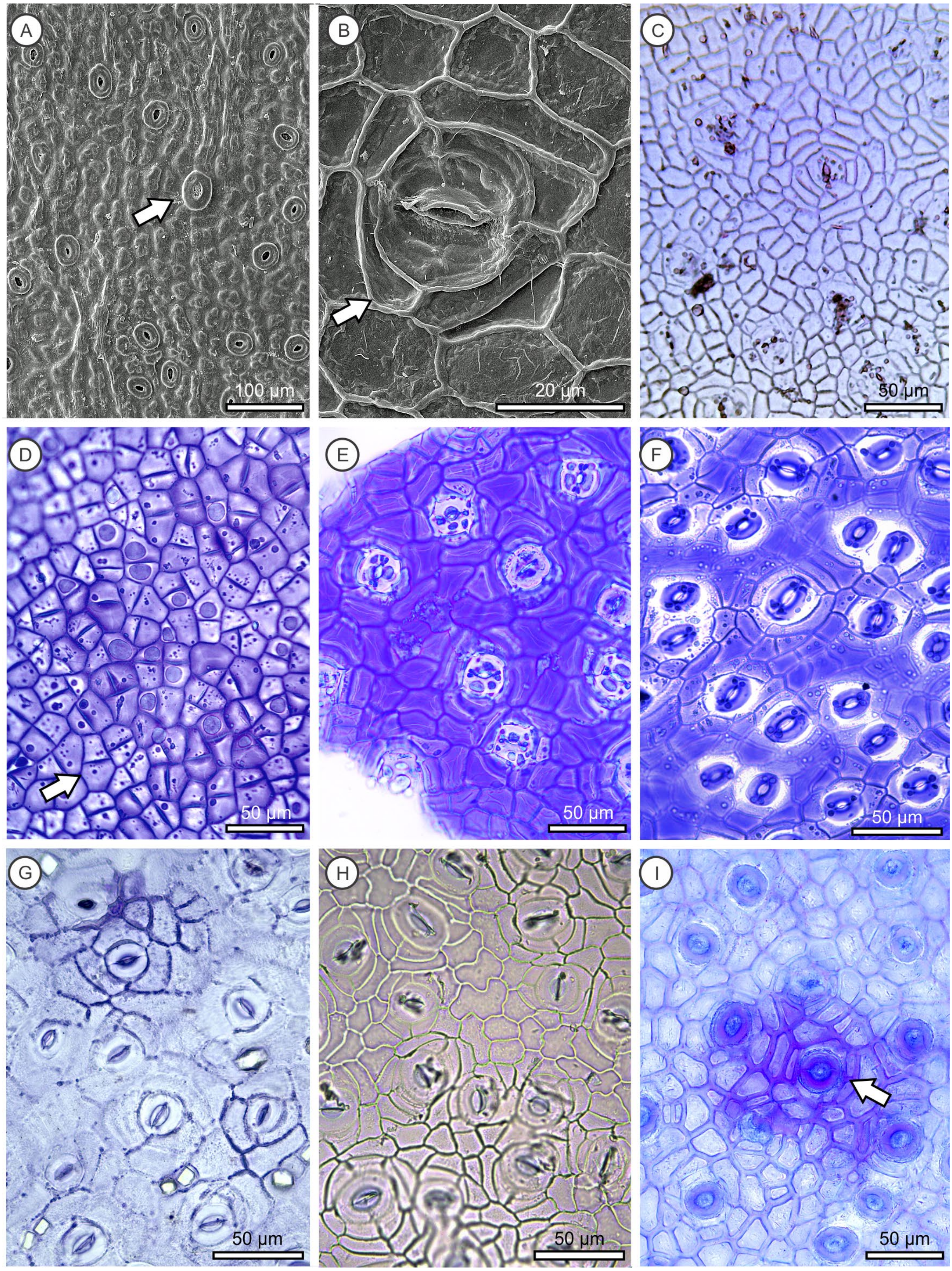

Figure 6. Comparative leaves and cuticles for extant Celastraceae and Balanopaceae with similar features to the fossil. **A**, **B**. *Denhamia cunninghamii* (Hook.) M.P.Simmons, **A**. Outer abaxial surface showing smooth periclinal walls and prominent stomatal rings (arrow), **B**. Inner abaxial surface showing laterocytic stomate (arrow); **C**. *D. bilocularis* (F.Muell.) M.P.Simmons, abaxial surface showing mixed stomatal types; **D**, **E**. *D. pittosporoides* F.Muell., **D**. Adaxial surface showing curved anticlinal walls (arrow), **E**. Abaxial surface showing mixed stomatal types; **F**. *D. silvestris* (Lander et L.A.S.Johnson) M.P.Simmons, abaxial surface showing mixed stomatal types; **G**. *Elaeodendron australe* Vent., abaxial surface showing mixed stomatal types; **H**. *Maytenus boaria* Molina; **I**. *Balanops australiana*, abaxial surface showing heavily thickened anticlinal cell walls and anomocytic stomata (arrow). Vouchers: A, B. QRS 97354.1; C. Waite Arboretum 73-H14; D, E. Adelaide BG G831221; F. Adelaide BG G910244; G. CHR 407267; H Adelaide BG G881352; I. CHR 550990. Scale bars as indicated

Similarly, the leaves of the Australian and Pacific Island rainforest tree family Balanopaceae also share some characteristics with the fossils, as the leaves of many *Balanops* Baill. species are elliptic to obovate with brochidodromous secondary veins, superficially resembling the fossil (Fig. 5E, F). However, the leaves of *Balanops* possess a marginal vein, are often toothed and their cuticles are strongly thickened (Fig. 5I) (Guillaumin, 1925). Balanopaceae stomata are classed as anomocytic (Carlquist, 1980; Kubitzki, 2014) or laterocytic (Baranova, 1983) and although they possess a prominent overarching cutinized dome (Carlquist, 1980), they lack the distinctive doughnut-like cuticular ring surrounding the sunken stomata seen in the Foulden fossil.

DISCUSSION

Given the age of the lineages in the family and presence of *Palaeochrysa* fossils in the Early Miocene of New Zealand, the obvious candidates for possible living relatives would be with taxa from the Australian–New Guinean land mass and former parts of Zealandia such as New Caledonia, especially given the postulated long history of floristic exchanges between these land masses (Pole, 1994, 2010). *Denhamia* is an Australian, New Guinean and New Caledonian genus of 17 species of shrubs and small trees (Jessup, 1984; Müller et al., 1996; Halford and Jessup, 2020) which was expanded recently to include former members of the Austro-Pacific clade of the cosmopolitan Celastroideae genus *Maytenus* (McKenna et al., 2011). Comparison of extant members of both genera with the fossil shows that there are clear similarities in the venation and cuticle patterns, particularly the apparent double ring of subsidiary-like cells surrounding some of the guard cells and occasional cork-warts. However, as these features are not unique to these genera (den Hartog and Baas, 1978; Gomes and Lombardi, 2010) and there are other taxa with similar leaves but unknown cuticles, such as the phylogenetically isolated ~72 Ma divergent New Caledonian endemic *Salaciopsis* and particularly given the evidence for past long distance dispersal of multiple lineages within the family (Bacon et al., 2016), many of which are bird dispersed (Simmons, 2004; Zhu et al., 2020), the fossils were placed into their own genus.

Celastraceae occur in a wide range of habitats from tropical rainforest to cool temperate forests and semi-arid environments, suggesting strong adaptability. The climatic conditions at Foulden Maar 23 million years ago were estimated to be much warmer than southern New Zealand is today and possibly warm temperate to almost subtropical with rainfall seasonality, although the results vary between different climate proxy methods (Reichgelt et al., 2013; Pole, 2014). Nevertheless, estimates for the palaeoenvironment at Foulden are still well within the modern climatic envelopes of possible relatives, such as Maytenus and Denhamia, both of which have species that grow in seasonally dry conditions (e.g. Simmons, 2004; Pérez-Latorre et al., 2010; Halford and Jessup, 2020).

This now extinct Celastraceae taxon with similarities to modern Australian and Pacific genera, such as Denhamia, Maytenus and Salaciopsis was therefore common in the seasonally dry mesothermal rainforest that grew on the basalt-derived soils around Foulden Maar at the beginning of the Miocene. If dispersed pollen from the site can be matched definitively to Celastraceae in the future, this might help to determine how long the lineage persisted in New Zealand before going extinct, presumably due to cooling in the Late Miocene or Plio-Pleistocene.

This study represents the first record of fossil Celastraceae leaves with excellent cuticular preservation, extending the fossil record to the Early Miocene of New Zealand and expanding the past biogeographic range of the family. This precisely dated Celastraceae record from southern New Zealand also provides an important additional robust fossil calibration point for future studies of the family.

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ADDITIONAL INFORMATION

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