Early Eocene plant macrofossils from the Booval Basin, Dinmore, near Brisbane, Queensland

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ABSTRACT

Early Eocene plant macrofossils are documented from Dinmore in the Redbank Plains Formation within the Booval Basin, west of Brisbane, Australia. It is one of the few Cenozoic Australian fossil macrofloras occurring outside the south-eastern corner. Angiosperms dominate the Dinmore assemblage, with 20 taxa having a mixture of simple and compound leaves, and which are almost equally distributed across the microphyll and notophyll size classes. Although cuticle is absent, gross leaf morphology and architecture suggests the taxa include: Proteaceae (probable Lomatia, Parafatsia), Myrtaceae (including Eucalyptus s.l. i.e, the clade including Angophora, Corymbia, and Eucalyptus), Smilacaceae, and probable Lauraceae. Conifers are rare with only two taxa, a multi-veined leaf consistent with Agathis (Araucariaceae) or Nageia (Podocarpaceae) and another possible Podocarpaceae. The Mean Annual Temperature predicted by a variety of leaf physiognomic methods ranges from 8–19 °C. However, average leaf size suggests 18–19 °C, and this warmer end is considered more likely. Even this may be underestimated as moisture was likely at least seasonally limited and would act to decrease leaf size. Dinmore was at a much higher latitude in the early Eocene (c. 46 °S), and the estimate of a much higher temperature is consistent with other proxies for globally warmer conditions at the time.

The presence of Eucalyptus s.l. is curious, and this additional early record of its occurrence in a vegetation community that would otherwise likely be considered ‘rainforest’ hints that its origin might not involve fire, but lie within a vegetation type no longer extant.

Keywords: paleoclimate; Eucalyptus; Lauraceae; Proteaceae; foliar physiognomy

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INTRODUCTION

Understanding of the Cenozoic vegetation history of Australia, and of the climate and other factors which drove it, has increased dramatically over the past few decades (e.g., Hill, 1984). However, with the exception of a few far-flung studies (e.g., central Australia, Christophel et al., 1992; Carpenter and Pole, 1995; Carpenter et al., 2011; Western Australia, McLoughlin and Guppy, 1993; northernmost Australia, Pole, 1998), most of the macrofossil knowledge still comes from fossil assemblages close to Australia's south-east corner (e.g., Hill, 1988, 2004; Hill et al., 1999). Cenozoic plant macrofossil localities in Queensland are rare, and leaf material is often of relatively poor quality (although fruits can be very well preserved). However, several studies have added information to this poorly-known area (e.g., Rozefelds, 1988, 1991, 1992; Rozefelds and Christophel, 1996, 2000; Clifford and Dettman, 2002; Conran and Rozefelds, 2003; Guerin and Hill, 2006; Rozefelds et al., 2014, 2017).

Plant fossils from several localities in the Oxley Basin were described by Ettingshausen (1895, who regarded the age as Cretaceous). He identified 62 species in 41 genera of angiosperms and gymnosperms, although by modern standards, most of the generic identifications are dubious. A conifer macrofossil, *Dacrycarpus*, was recorded by Selling (1950). Hill et al. (1970) illustrated a ?*Eucalyptus* sp. and “eucalypt-like” fruits were described by Rozefelds (1996). Two ferns are known; namely, *Lygodium* (Churchill, 1969; Hill et al., 1970; Rozefelds et al., 1992) and a new genus of water fern, *Tecaropteris* (Rozefelds et al., 2015).

The Booval Basin has produced a wide range of vertebrates and insects (Riek, 1952; Rix, 1991, 1992; Knezour, 1992) and through the efforts of several collectors over many years a small exposure in a clay pit near Dinmore has provided a large collection of leaf impressions. The aim of this paper is to describe the leaf macrofossils from this Dinmore locality, and investigate their climatic implications.

GEOLOGICAL SETTING

Cenozoic sediments in south east Queensland are restricted to several small basins (in the order of 10–20 km maximum dimensions) representing foci of fluvial-lacustrine activity along with some volcanicity. In the vicinity of Brisbane there are three, namely, the Oxley, Booval, and Petrie Basins (Figure 1). Sediments in the Oxley Basin are divided into the Darra, Corinda, and Sunnybank Formations (Houston, 1967). The mainly lacustrine sediments of the Booval Basin are divided into the lower Redbank Plains Formation and the upper Silkstone Formation (Staines, 1960; Day et al., 1982). Jones (1926) provided a summary of the early geological investigations of the area and concluded that the basins were Cenozoic. Basalt near the base of the Silkstone Formation (Figure 2) was isotopically dated as 45 Ma (middle Eocene) and provides an upper limit for the age of the Redbank Plains Formation (Green and Stevens, 1975). Another basalt, which probably belongs to the Silksstone Formation, was dated as 46.3 Ma. A Paleocene age was considered by Day et al. (1982), although Stephens (pers. comm. to Kemp, 1991) suggested Eocene. In the nearby
Corrida Formation the Archerfield Basalt and Eight Mile Plains Basalt were isotopically dated by Green and Stevens (1975) as 54–55 Ma and 45.7 Ma, respectively. On this basis, they concluded that the Corrida Formation (maximum thickness of 165 m) was deposited in about eight million years. If this rate of deposition is broadly applicable to the Redbank Plains Formation, which has an average thickness of 67 m (Houston, 1967; Cranfield, 1976), the base of the formation is not likely to be more than about 52 Ma. The most likely age of the Dinmore fossil leaves is therefore early Eocene.

Most of the surficial Cenozoic sediments in the Brisbane region have been too deeply weathered for preservation of pollen. Although no productive palynological samples are known from the Booval Basin, Harris (1965) reported on productive bore-hole samples from all three formations of the Oxley Basin. The oldest sample from the Darra Formation was dominated by *Myrcipites harrisii* pollen (often considered to be Casuarinaceae) and had rare *Nothofagus* (trace amounts). However, there is also a similarity with the New Zealand palynological zonation in which Zone MH1 of the *Myrcipites harrisii* Assemblage is “characterised by the abundance, and frequent dominance of *M. harrisii* (Raine, 1984, p. 24), and in which *Nothofagus* is typically very rare or absent. Zone MH1 extends from about the start of the early Eocene until the earliest middle Eocene and thus broadly correlates with the early Eocene Climatic Optimum.

**MATERIAL AND METHODS**

Most of the plant fossils described here were collected by R. Knezour, A. Rozefelds, and S. McLoughlin. They are preserved as impressions (no pollen or cuticle is preserved) on the bedding surfaces of clay-rich sediment. Preparation involved further excavation of selected specimens using a vibrating chisel. Most investigation used a binocular microscope, as surface details which might have been visible using a scanning electron microscope are absent. Specimens were photographed using low angle light. Specimens were drawn with a camera lucida at about five to seven times full size, reduced to two times, then traced onto architectural paper using Indian ink. All material is catalogued and stored in the Queensland Museum. Leaf architecture terminology mostly follows Hickey (1973) and Dilcher (1974) and Ellis et al. (2009), but with the modifications of Pole (1991).
The leaves are described as parataxa (an arbitrary string of three letters prefixed with 'DINM') and a key (Table 1) is provided to help clarify the distinctions.

Leaf physiognomic techniques, including univariate (based on Wolfe, 1979), and the multivariate 'CLAMP' (Wolfe, 1990; Yang et al., 2011) are used to estimate the mean annual temperature. Following normal practise, leaflets of compound leaves are treated as leaves.

**DESCRIPTIONS**

Multi-veined conifer

**Description.** Isolated leaf flattened, scale-like, multi-veined, almost elliptical, expanding from a false petiole (about 3.0 mm long, 1.0 mm wide, slightly expanded at the base) to a maximum width of 19 mm, and around 38 veins, then contracting. The apex is missing and the preserved length is 54 mm.

**Remarks.** The expanding, multi-veined blade is consistent with *Agathis* and *Nageia* (Offler, 1984; Jin et al., 2010)

?Podocarpaceae gen. indet.

**Reference specimen.** QMF14925.

**Description.** Shoot: flattened into two dimensions, leaves single-veined, bilaterally flattened, not con-

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**TABLE 1. Key to distinguish the Dinmore leaf parataxa.**

| Couplet | Criteria | Parataxon |
|---------|----------|-----------|
| 1       | Leaves lobed 2 |  |
| 1       | Leaves not lobed 4 |  |
| 2       | Leaves palmately lobed 3 |  |
| 2       | Leaves trilobed | DINM-JJG |
| 3       | Palmately Lobed (4–6 lobes), no domatia | DINM-JJD |
| 3       | Palmately Lobed (4–6 lobes), multiple domatia | DINM-JJE |
| 4       | Leaves compound 5 |  |
| 4       | Leaves simple or appearing so 8 |  |
| 5       | Leaves palmately trifoliate, toothed | DINM-JJA |
| 5       | Leaves pinnate 6 |  |
| 6       | Pinnately trifoliate | DINM–JJC |
| 6       | Pinnately compound 7 |  |
| 7       | Teeth many and small (c 10 mm apart), lateral leaflets sessile or with very short petoles | DINM-JJB |
| 7       | Teeth large and well-spaced (c 3–8 mm apart), lateral leaflets petiolate | DINM-JBD |
| 8       | Toothed-margined 9 |  |
| 8       | Entire-margined 17 |  |
| 9       | Craspedodromous 10 |  |
| 9       | Externodromous 13 |  |
| 10      | Lateral veins all travel to teeth 11 |  |
| 10      | Lateral veins alternate between tooth apex and sinus 12 |  |
| 11      | Lamina elliptical, prominent teeth, sinuses mostly sharp | DINM-JBB |
| 11      | Lamina ovate-lanceolate, teeth shallow, sinuses smooth | DINM-JBD (single leaflet) |
| 12      | Broad leaved | DINM-JJH |
| 12      | Narrow-leaved | DINM-JJI |
| 13      | Teeth regular 14 |  |
| 13      | Teeth irregular, minute | DINM-JAD |
striking towards the base, length 8 mm, width 1 mm, straight to slightly sinusoidal.

**Remarks.** This is probably the same taxon are that described by Selling (1950) from the same or nearby locality, as *Podocarpus* (sect. *Dacrycarpus*) sp.

Leaves palmately trifoliate and toothed

**Parataxon:** DINM-JJA

**Reference specimen.** QMF34354

**Referred specimen.** QMF34306, QMF34332, QMF34333.

**Description.** Organisation: palmately trifoliate. Leaflet size: length 50 mm, width 18 mm, microphyll. attachment sessile. Leaflet shape: elliptic, unlobed, apex unknown, base convex. Margin serrate, teeth simple, irregularly-spaced, close to distant, several teeth per lateral, sinuses sharp. Venation externodromous (sensu Pole, 1991), development normal. Lateral veins well-spaced, not decurrent on midrib, forking where externals branch-off.

Leaves pinnately compound with a terminal leaflet and toothed

**Parataxon:** DINM-JJB

**Reference specimen.** QMF34356.

**Referred specimen.** QMF34342A,B.

**Description.** Organisation: pinnate with a terminal leaflet. Size: length probably c. 100 mm, width c. 40 mm, microphyll–notophyll. Leaflet shape: not clear, unlobed. Lateral leaflet attachment sessile, terminal leaflet with petiolule. Apex unknown, base possibly concave and asymmetrical. Margin serrate, teeth simple, several teeth per lateral, sinuses sharp. Venation externodromous, development normal. Lateral veins closely-spaced, not decurrent on midrib, gradually losing distinction towards the margins, no clear lateral loops. Finer venation prominently percurrent
**Parataxon: DINM-JBD**

**Reference specimen.** QMF35317.

**Referred specimen.** QMF34487.

**Description.** Organisation: pinnate, unclear whether with a terminal leaflet or not. Size: leaflets length 55–85 mm, width 11–19 mm, microphyll. Shape: ovate-lanceolate, unlobed. Leaflet attachment with petiolule. Apex acute. Base cuneate-decurrent, asymmetrical. Margin serrate, teeth simple, distantly-spaced, sinuses smooth. Venation craspedodromous or cemicraspedodromous, development normal. Lateral veins well-spaced, not decurrent on midrib. First order lateral veins running direct to apices of teeth or becoming tangential with the margin, losing distinction towards the margins, no clear lateral loops. Finer venation indistinct.

**Remarks.** Identification: Compares with “Lomatia preferruginea” (Proteaceae) from the early Eocene of the Laguna del Hunco flora, Patagonia (Wilf et al., 2003; Gonzalez et al., 2007).
Leaves pinately trifoliate
Parataxon: DINM-JJC

Figure 7
Reference specimen. QMF15325.
Referred specimens. QMF34326, QMF35280, QMF35285, QMF35290, QMF35296, QMF35310, QMF35324, QMF35338, QMF35341, QMF35348, QMF35350, QMF35351, QMF35352, QMF34355.

Description. Organisation: pinnately trifoliate. Size: length 55–150 mm, width 11–43 mm, microphyll–notophyll. Shape elliptic, unlobed. Leaflet attachment lateral leaflets sessile, terminal leaflet with petiolule. Apex acute, base cuneate, rounded-acute. Margin serrate, teeth simple, closely-spaced, several teeth per lateral, sinuses sharp. Venation externodromous. Development normal. Lateral veins well-spaced, not decurrent on midrib, strongly arched, gradually losing coherence towards the margins, as more external veins branch off, no clear lateral loops.

Leaves simple, palmately lobed, and toothed, no domatia

Parataxon: DINM-JJD

Figure 8
Reference specimen. QMF15322.
Referred specimens. QMF34366, QMF49484.

Description. Organisation: simple. Size: lobe length c. 130–170 mm, width c. 26–34 mm, mesophyll. Shape: palmately lobed, five to six lobes, lobes broadest in the middle (elliptical), apex acute. Whole leaf base cordate. Margin serrate, teeth simple, distantly-spaced, irregular, probably about one lateral vein per tooth, a vein runs from the lateral loop to the sinus or apical margin of the tooth. Venation externodromous. Development normal. Lateral veins well-spaced, not decurrent on midrib, lateral loops fine but distinct, looping zone narrow. Domatia absent.

Remarks. This leaf is probably conspecific with Ettingshausen's (1895) Aralia subformosa, and similar, if not identical to Parafatsia subpeltata, which was initially described from the middle Eocene of Maslin Bay, South Australia by Blackburn (1981) as Araliaceae. Subsequent reinvesti-
gation of this species and its cuticular anatomy by Carpenter et al. (2006) resulted in its reassignment to the Proteaceae. This may also apply to the similar ‘cf. Cochlospermum’ recorded from central Australia by Greenwood (1996). A more broadly similar form from the early Eocene Laguna del Hunco flora of Argentina was placed in Cochlospermum by Berry (1935). More illustrations of this taxon and a wider comparison would be welcome.

Leaves simple, palmately lobed, not toothed, no domatia
Parataxon: DINM-JJE
Figure 9

Reference specimen. QMF34330.
Description. Organisation: simple. Size: length c. 88 mm, width c. 138 mm, mesophyll. Shape: palmately lobed, probably five lobes, tapering to a point (acute-triangular), apex straight, base truncate-cordate. Margin serrate, teeth simple, distantly-spaced, irregular, probably about one lateral vein per tooth. Venation externodromous with the veins becoming tangential to the margin, or perhaps also craspedodromous. Lateral veins well-spaced, not decurrent on midrib. Domatia scattered along the primary and first-order laterals at the junction of the tertiary veins.

Leaves simple, trilobed, and entire
Parataxon: DINM-JJG
Figure 10

Reference specimen. QMF34352.
Referred specimens. QMF35311, QMF35343.
Description. Organisation: simple. Size: length c. 95 mm, width c. 100 mm, mesophyll. Shape: palmately lobed, three–five lobes, lobes narrowing to a rounded apex, base unknown, probably acute. Margin entire. Venation externodromous. Basal lateral veins prominent, probably paired or nearly so, near the base, with prominent external and thinner counter-external veins. Lateral veins well-spaced, not decurrent on midrib. Second order venation markedly percurrent.
Leaves simple, with toothed margin, not lobed
Parataxon: DINM-JJH

Reference specimen. QMF35370.
Referred specimens. QMF35303.

Description. Organisation: simple. Size: length c. 56 mm-unclear, width c. 18–44 mm, microphyll–notophyll. Shape: probably elliptical, unlobed, apex unknown, base acute. Margin dentate-serrate to mucronate, teeth simple, closely-spaced, mostly one tooth per two laterals, convex on both margins, sinuses sharp. Venation craspedodromous. Development normal. Lateral veins well-spaced, regular, not decurrent on midrib. First order lateral veins alternately running to sinuses and tooth apices.

Remarks. Identification: Possibly Proteaceae. The alternation of veins running to teeth and sinuses is found in extant Banksia and in the fossil taxa Banksiaphyllum and Banksiaeformis (Cookson and Duigan, 1950; Hill and Christophel, 1988). Some of these fossil taxa are clearly Proteaceae, but Carpenter et al. (2016) have pointed out that some do not have epidermal details typical of Proteaceae, and are therefore unlikely to belong in the family. Of relevance here is a taxon that was first described as Banksia fastigata (Deane, 1925), which is smaller, but has a similar venation and margin as the Dinmore material. This was placed in Banksiaphyllum by Cookson and Duigan (1950), a genus accepted as Proteaceae by Hill and Christophel (1988). Carpenter et al. (2016) reconsidered the material and concluded that the stomata “do not appear brachyparacytic,” and both the form and location (restricted to epidermal cell junctions)
FIGURE 7. Parataxon: DINM-JJC. 1. QMF49460, photographic detail of margin. 2. Reference specimen QMF15325, line drawing. 3. Specimen QMF55797. 4. Specimen QMF35371. 5. Specimen QMF55789. Scale bars equal 10 mm long or in 10 mm intervals.
FIGURE 8. Parataxon: DINM-JJD. 1. Line drawing of reference specimen QMF15322. 2. Photographic detail of reference specimen margin QMF15322. 3. Specimen QMF34366 line drawing. Scale bars equal 10 mm long or in 10 mm intervals.
of the trichome bases were not typical of the Proteaceae. They moved the species into a new genus, *Pseudobanksia*, of unknown affinity. The absence of brachyparacytic stomata does not clearly rule out identification as Proteaceae, as extant *Bellendena* does not have them either (Carpenter et al., 2005). But the combination of stomatal and trichome details are a compelling argument that the Dinmore material should not automatically be considered Proteaceae.

**Parataxon: DINM-JJI**

**Reference specimen.** QMF34351.
**Referred specimens.** QMF35362.
**Description.** Organisation: simple. Size: length c. 75 mm, width c. 7 mm, microphyll. Shape: lanceolate, unlobed, straight to slightly curved, apex probably acute, base unknown, assumed acute. Margin serrate-spinose, teeth simple, sinuses smooth. Venation craspedodromous. Development normal. Lateral veins well-spaced, not decurrent on midrib. First order lateral vein termination alternately running to sinuses and tooth apices.

**Parataxon: DINM-JBB**

**Reference specimen.** QMF35373A,B.
**Referred specimens.** QMF22638, QMF34292, QMF34302, QMF34305, QMF34311, QMF34344, QMF34349, QMF34357, QMF34358, QMF34361, QMF34365, QMF34369, QMF34370, QMF34374, QMF34376, QMF34377, QMF34378, QMF35282, QMF35297A,B, QMF35320, QMF35322, QMF35323, QMF35333, QMF35364, QMF49459, QMF49467A,B, QMF49472A,B, QMF55781A,B, QMF55786, QMF55791, QMF55792, QMF55801, QMF55815.

**Description.** Organisation: simple. Size: length 46–102 mm, width 16–45 mm, microphyll–notophyll. Shape: elliptic, unlobed, apex attenuate, base acute-cuneate. Margin serrate to slightly crenate, teeth simple, closely to distantly-spaced, mostly one tooth per lateral, sinuses mostly sharp. Venation craspedodromous. Development normal. Lateral veins well-spaced, not decurrent on midrib, sometimes forking, running to tooth apex.

**Remarks.** Without cuticle information this remains unclear, but is probably conspecific with Ettinghausen’s (1895) *Myrica*.

**Parataxon JBJ**

**Reference specimen.** QMF34316.
**Referred specimens.** QMF34309, QMF34315, QMF34318, QMF34337, QMF34359, QMF49458A,B, QMF49461A,B, QMF49494A,B, QMF55788, QMF55799A,B, QMF55798.

**Description.** Organisation: simple. Size: length 41–73 mm, width 12–42 mm, microphyll. Shape: elliptic, unlobed, apex unclear, probably acute but one specimen appears rounded, base acute-
cuneate. Margin serrate, teeth simple, closely to distantly spaced, sometimes glandular-tipped, mostly one or two teeth per lateral, sinuses sharp. Venation externodromous. Development normal. Lateral veins well-spaced, not decurrent on midrib, course irregular, straight, or curving towards the margin, frequently forking where external veins branch off, running to sinus or most apical margin of tooth.

Remarks. The elliptical shape with a relatively rounded apex and acute-cuneate base, in combination with frequently forking lateral veins, suggest Cunoniaceae or Elaeocarpaceae (compare with a range of figures in Hyland et al., 2003).

Leaves simple, with entire margin, not lobed
Parataxon JBH
Figure 15

Reference specimen. QMF35337.
Referred specimens. QMF34293, QMF34298A,B, QMF34308, QMF34372, QMF34381, QMF35299, QMF35330, QMF35331, QMF35336, QMF35337, QMF35359, QMF35340, QMF49465, QMF49475A,B, QMF49476, QMF49478.

Description. Organisation: simple. Size: length 80–110 mm, width 21–45 (perhaps >60) mm, microphyll–notophyll. Shape: elliptical-ovate, unlobed, apex acute, base acute. Margin entire. Venation externodromous. Development normal. Lateral veins well-spaced, not decurrent on midrib, losing coherence towards the margins, lateral loops poorly distinct.

Parataxon: DINM-JAB
Figure 16
Reference specimen. QMF35295.
Referenced specimens. QMF34373, QMF35329.

Description. Organisation: simple. Size: length 70–c. 110 mm, width 13–24 mm, microphyll. Shape: elliptic, unlobed, apex acute, base assumed acute. Margin entire. Venation with intramarginal vein. Development normal. Lateral veins closely-spaced, not decurrent on midrib, running either direct to the intramarginal vein, or branching first. Oil glands numerous in inter-venal areas.

Remarks. Identification: Eucalyptus s.l., on the basis of the intramarginal vein and laminar oil glands. It is the wider of two Eucalyptus taxa at Dinmore. These will be conspecific with some of Ettingshausen's (1895) five species of Eucalyptus.

Parataxon: DINM-JAH

Reference specimen. QMF34319.

Referenced specimens. QMF35287, QMF35283, QMF35293, QMF35298, QMF35313, QMF34334, QMF49456, QMF49492, QMF55800.

Description. Organisation: simple. Size: length 45–67 mm, width 7.5–8 mm, microphyll. Shape: narrow elliptic to narrow ovate, unlobed, apex acute, base decurrent, acute. Margin entire. Venation with intramarginal vein, no looping zone. Development normal. Lateral veins closely-spaced, not decurrent on midrib. Oil glands scattered over lamina.

Remarks. Identification: DINM-JAH is regarded as Eucalyptus s.l. (i.e. falling within the clade which includes Eucalyptus, Corymbia and Angophora, e.g., Hill and Johnson, 1995; Ladiges et al., 1995; Brooker, 2000) on the basis of the narrow and sometimes falcate shape and the presence of an intramarginal vein, or more specifically, a longitudinal vein. Pole (1991), drawing on Carr et al., 1986) discussed how a longitudinal vein differs from the typically broad usage of an intramarginal vein. A longitudinal vein appears as a single entity, thicker than other veins, which may anastomose with it. The term 'intramarginal' vein does not distinguish between an individual vein and one which has formed from the loops of succeeding lateral (or secondary) veins. The later can be identified by close observation. Longitudinal veins (see Carr et al., 1986) are a feature of Eucalyptus s.l. leaves, distinguishing them from leaves of Eucalyptus 'look-alikes', such as Syzygium eucalyptoides, which have an intramarginal vein, formed of thickened loops. DINM-JAH is the narrower of two Eucalyptus taxa at Dinmore. Similar forms were recorded by Ettingshausen (1895) as Eucalyptus from the Oxley Basin.

Parataxon: DINM-JAC

Reference specimen. QMF35279.
FIGURE 12. Parataxon: DINM-JJ1. 1. Line drawing of reference specimen QMF34351. 2. Photograph of reference specimen QMF34351. 3. Specimen QMF35362. Scale bars equal 10 mm long or in 10 mm intervals.
FIGURE 13. Parataxon: DINM-JBB. 1. Line drawing of reference specimen QMF35373B. 2. Specimen QMF34349. 3. Specimen QMF49459. 4. Specimen QMF49472. 5. Specimen QMF55781A. Scale bars equal 10 mm long or in 10 mm intervals.
Description. Organisation: simple. Size: length unknown, width c. 36 mm, probably notophyll. Shape: not clear. Apex and base unknown. Margin entire. Venation externodromous. Development normal. Lateral veins well-spaced, not decurrent on midrib. Domatia apparently present along lateral veins.

Parataxon: DINM-JBJ

Reference specimen. QMF34303.
Referred specimen. QMF49485.

Description. Organisation: simple. Size: length 85–c. 148 mm, width 35–45 mm, notophyll. Shape ovate,

Parataxon: DINM-JAD
FIGURE 15. Parataxon: DINM-JBH. 1. Line drawing of reference specimen QMF49475. 2. Specimen QMF35337. 3. Specimen QMF35359. 4. Specimen QMF49476. 5. Specimen QMF49475. 6. Specimen QMF34298. 7. Specimen QMF49478. Scale bars equal 10 mm long or in 10 mm intervals.
unlobed, apex acute, base possibly rounded. Margin irregularly serrate-entire, teeth simple, distantly-spaced, irregular, sometimes up to three teeth per lateral, Sinuses smooth. Venation externodromous. Development normal. Lateral veins well-spaced, furthest apart in mid lamina, decreasing towards apex and base, decurrent, or often decurrent, on midrib, losing coherence towards the margins as many external veins branch off.

Parataxon: DINM-JAE
Figure 20

Reference specimen. QMF35368.
Referred specimens. QMF34325, QMF35294, QMF35306, QMF35369, QMF55801.

Description. Organisation: simple. Size: length 26–90 mm, width 22–25 mm, microphyll. Shape: ovate, unlobed, apex unknown, base cuneate-decurrent to rounded. Margin entire. Development acrodromous, basal lateral veins paired, entering the leaf base/petiole. Lateral veins well-spaced, not decurrent on midrib, well-defined lateral loops. Domatia absent.

Remarks. Identification: Lauraceae.
FIGURE 21. Reference specimen. QMF34478. Referred specimens. QMF34294, QMF34320, QMF34321, QMF35325, QMF34379, QMF35325, QMF35374, QMF49477.

Description. Organisation: probably simple. Size: length 100–c. 110 mm, width 14–c. 32 mm, microphyll or notophyll. Shape: ovate, unlobed, slightly flexuous, apex attenuate, base unknown. Margin entire. Venation externodromous, with an apparent intramarginal vein, at least near the base. Development normal. Lateral veins well-spaced, not decurrent on midrib, relatively thin, running towards and almost tangential with the margin, resulting in little or no looping zone. Higher order venation consists...
FIGURE 18. Parataxon: DINM-JAC, reference specimen QMF 35279. 1. Line drawing, putative domatia indicated by stipple. 2. Photographic detail, note putative domatia-pits. Scale bars equal 10 mm long or in 10 mm intervals.

FIGURE 19. Parataxon: DINM-JAD. 1. Line drawing of specimen QMF49485. 2. Line drawing of specimen QMF34303. 3. Photographic detail specimen QMF34303. Scale bars equal 10 mm long or in 10 mm intervals.
of a loose network broadly oriented at a higher angle to the midrib than the lateral veins. Laminar glands possibly present.

Remarks. Identification: possibly Myrtaceae.

Parataxon: DINM-JAG

Figure 22

Reference specimen. QMF34376.

Description. Organisation: simple. Size: length c. 86 mm, width c. 60 mm, microphyll–notophyll. Shape: probably ovate, unlobed, apex unknown, base cordate. Margin entire. Lateral veins well-spaced, two to three sets of longitudinal veins (sensu Pole, 1991) on each side of the midrib, decurrent on midrib. Well-developed looping zone outside the outermost longitudinal veins.

Remarks. The venation pattern suggests Smilaceae, although to no specific extant genus (Inamdar et al., 1983; Pole, 1993a, 1996; Carpenter et al., 2014).

Parataxon: DINM-JAJ

Figure 23

Reference specimen. QMF34358.

Referred specimens. QMF34329, QMF49531.
Description. Organisation: simple. Size: length c. 28–c. 120 mm, width 24–45 mm, microphyll–noto-phyll. Shape: ovate, unlobed, apex unknown, base cuneate. Margin entire. Venation externodromous. Development acrodromous with the basal lateral veins almost paired, well above (c. 5–10 mm) the base of the leaf. Lateral veins well-spaced, slightly decurrent on midrib, strongly arched.

Remarks. Identification: probably Lauraceae. This taxon is probably conspecific with Ettingshausen’s (1885) *Cinnamomum* species. This genus was once applied widely to acrodromous leaves in the past but it occurs in several Lauraceae genera and even other families. Without cuticle details (e.g., Hill, 1986; Christophel and Rowett, 1996), a generic name is unwarranted, although the taxon
exhibits basal lateral veins which are almost paired, but well above the leaf base, and a modest amount of development above the basal laterals—a combination suggesting Cryptocarya (see the range of figures in Christophel and Rowett, 1996).

**DISCUSSION**

**Floristics**

Most of Ettingshausen’s (1895) identifications are either unlikely (e.g., Quercus) or are probably taxonomically close, though not warranted by the poor preservation (e.g., Cinnamomum), or on the basis of his figures, cannot reliably be related to the material here. However, his record of Eucalyptus s.l. leaves is accepted. It is supported by Rozefeld’s (1996) Myrtaceae fruits, which appear more similar to Eucalyptus than any other genus. The Dinmore specimens therefore seem to represent some of the oldest Eucalyptus known, although they probably post-date those from Laguna del Hunco in Patagonia (Gandolfo et al., 2011).

**Climatic Interpretation**

Foliar physiognomy is a well-established source of climatic information. However, the accuracy and most appropriate methods to extract it are subject to vigorous debate. Because Dinmore is distant from other floras of similar age, it provides a potentially useful window into the paleoclimate.

**Leaf physiognomy.** Of the 20 species described from Dinmore, eight (40 %) have entire margins. Based on a range of forest-inventory based univariate regression equations (Wolfe, 1979; Greenwood, 1992; Wing and Greenwood, 1993; Wilf, 1997; Greenwood et al., 2004; Gregory-Wodzicki, 2000; Traiser et al., 2005; Miller et al., 2006; Steart et al., 2010; Su et al., 2010; Kennedy et al., 2014) a MAT of around 8–14 °C is suggested.

The multivariate CLAMP method (CLAMP online http://clamp.ibcas.ac.cn; Yang et al., 2011, using both Physg3brcAZ and PhysgAsia2 calibration sets) predicts a similar MAT to the leaf margin approach of around 12–15 °C, but with strong seasonality (a Cool Month Minima c. 0–3 °C). The CLAMP analysis predicts just 16–17 mm precipitation for the three driest months, and around 140–166 mm for the entire growing season. Realistic errors for both the univariate and CLAMP methods may be around ± 5°C (e.g., Royer, 2012), and the accuracy of CLAMP precipitation figures is probably far less than for temperature. But the broad indication is that seasonal dryness may have been a significant factor.

**Leaf size.** The average length of the Dinmore leaves is around 82 mm (Figure 24). Assuming an approximately elliptical shaped leaf where the area is two-thirds of the rectangular area of length times width (Cain et al., 1956; Webb, 1959) the average leaf size therefore lies close to the boundary of the
microphyll-notophyll size classes (Webb, 1959). Average leaf size in Australian rainforest litter is closely correlated with MAT (Greenwood, 1992; Carpenter et al., 1994) and based on this correlation, the average Dinmore leaf size suggests a MAT of around 18–19 °C.

The overall range of MAT results, 8–19 °C, is remarkably wide, and the large difference between leaf physiognomy and leaf area results prompts some discussion. Wolfe (1979) suggested that leaf margin analysis requires at least 20 taxa to be reasonably accurate. At 20 taxa, the Dinmore assem-
The study recognised 20 leaf taxa out of 169 fossil specimens, which were considered identifiable to taxa. On a number of specimens versus number of taxa graph, this plots on a moderately steep line (see Pole, 2014, fig. 11), and this diversity is consistent with the Dinmore assemblage accumulating under relatively warm conditions. Currently the Dinmore area has a mean annual temperature (MAT) of c. 20 °C and lies at about 27 °S latitude. Thus the leaf area results suggest an early Eocene MAT at least as high as today. However, around 50 Ma Dinmore would have lain in significantly higher latitudes – about 46 °S (using GPlates with the Muller et al., 2008, rotation model). That latitude is higher than Tasmania today and is equivalent to southernmost New Zealand. Coastal MATs in both areas today are around 10 °C. The results are consistent with a wide range of other proxies for significantly elevated sea surface temperatures at mid-latitudes in the Southern Ocean early Eocene (e.g., Davies et al., 1989; Feary et al., 1991; Ivany et al., 2008; Creech et al., 2010; Contreras et al., 2013; Pancost et al., 2013) and globally (e.g., Greenwood and Wing, 1995; Huber, and Caballero, 2011). Hollis et al. (2009, fig. 2) modelled sea surface temperatures of 20–25 °C offshore the Brisbane region in the early Eocene. Given the inherent error, the Dinmore results compare favourably with the cooler end of this range. However, some predictions for mid-latitude temperatures at this time (e.g., Naafs et al., 2018) are higher still.

**Comparison with Other Fossil Floras**

The Dinmore assemblage, with just two conifer taxa, is highly distinct from the higher latitude
early Eocene assemblage of Regatta Point, in Tasmania where they are abundant and diverse (Wells and Hill, 1989; Hill and Carpenter, 1991). Lower paleolatitude early Eocene assemblages from Victoria include Hotham Heights and Brandy Creek, and Deans Marsh (Greenwood et al., 2003; Carpenter et al., 2004). In those assemblages conifers appear to have been less diverse than Tasmania, but still much more prominent than Dinmore. This broad gradient is likely to be another reflection of drier conditions in Queensland (e.g., Brodrribb and Hill, 1998).

Closer physiognomic comparison with Dinmore is difficult, as the Victorian and Tasmanian fossil assemblages tend to be known from dispersed cuticle rather than leaf impressions. *Eucalyptus* is not yet known from any of them.

The general physiognomy of the Dinmore assemblage is comparable to lower latitude fossil assemblages of Melville Island, in northernmost Australia (White, 1976; Pole and Bowman, 1996; Pole, 1998). The Melville assemblages are also angiosperm dominated with minor conifers (including *Araucaria*), also have prominent lobed, compound and very narrow leaves (*Eucalyptus* s.l. is potentially present, but venation details are lacking). They are of an unknown age but were suggested to be early Cenozoic by Pole (1998). The similarity with Dinmore is consistent with that conclusion. Eocene material in central Australia also includes some of these morphologies (Greenwood, 1996).

In New Zealand, broadly similar foliar physiognomies (lobed and narrow leaves) are seen in the early Eocene of Kakahu (Pole, 1997, 2010, work in progress has also recovered *Eucalyptus* s.l.) and the mid Eocene of Livingstone, New Zealand (Pole, 1994). Further afield, the early Eocene flora of Laguna del Hunco, Patagonia (Wilf et al., 2003, 2005; Carpenter et al., 2014) lay at approximately the same paleolatitude as Dinmore. It has a far higher diversity than Dinmore, and with more conifers, but has a more prominent microphyll component. Despite these differences, it has several angiosperm leaf forms similar to Dinmore, including *Eucalyptus* (Gandolfo et al., 2011).

The leaf assemblages at Dinmore and Melville Island in Australia, Livingstone in New Zealand, and Laguna del Hunco, in Patagonia suggest a remarkably similar flora over a what would have been the mid latitudes of the Southern Hemisphere. All florae hint at seasonal dryness, and perhaps all contain *Eucalyptus* s.l. To account for the light-demanding *Eucalyptus* at Lajuna del Hunco, Gandolfo et al. (2011) proposed a mosaic, with *Eucalyptus* dominating on disturbed areas related to volcanism, with "intact rainforest" adjacent on more stable areas. This is certainly possible, and the argument has been used (e.g., New Zealand: Pole, 1993b; Australia: Pole et al., 1993) to account for *Eucalyptus* fossils co-occurring with *Nothofagus* in situations interpreted in terms of modern-day fire and wet-rainforest interaction in Tasmania (Jackson, 1968). However, at least in an early Miocene New Zealand deposit (Pole, 1993b,c), *Eucalyptus* was prominent in one assemblage, while in associated assemblages representing unmixed rainforest, it appeared absent. Finding *Eucalyptus*-dominated assemblages as well as those where it was a minor component amongst rainforest taxa would be expected under a fire-disturbance model. But the repeated presence of fossil *Eucalyptus* s.l. leaves in diverse assemblages of an otherwise, ‘rainforest’ aspect in the early Cenozoic should give pause for thought. These might rather be taken at face-value, as indicating *Eucalyptus* s.l. as a ‘normal’ component of the vegetation. There is little doubt that the group of plants which gave rise to the *Angophora-Corymbia-Eucalyptus* clade (i.e., *Arillastrum* and the clade currently including *Allosyncarpia*, *Stockwellia*, and *Eucalytopsis*, Macphail and Thornhill, 2016) were rainforest plants. However, the current paper suggests that even the ecology of early members of the *Angophora-Corymbia-Eucalyptus* clade may not have been fire-based. This conflicts with evidence that *Eucalyptus* s.l. origins were intimately connected with fire (see Crisp et al., 2011), but is more consistent with the later spread of fire (Scott, 2000; Belcher et al., 2013) triggering its expansion. Perhaps something about early Eocene conditions allowed early *Eucalyptus* s.l. to perpetuate in non-burning, rainforest and not be reliant on fire. A minority of extant taxa, e.g., *Eucalyptus deglupta*, may perpetuate such a lifestyle.

**CONCLUSIONS**

The early Eocene Dinmore leaf fossil assemblage is important as being one of the few of Cenozoic age located away from the south-eastern corner of Australia. As such it provides an important data point for what the vegetation and climate were doing in this more northerly region, in the early Eocene. It records an angiosperm-dominated flora, including one of the oldest records of *Eucalyptus* s.l. in the world (consistent with the results of Macphail and Thornhill, 2016), along with probable rainforest taxa, and a minor conifer component.
Despite being at a significantly higher latitude at around 50 Ma, the MAT was probably much higher than at that latitude today. The assemblage has broad physiognomic and floristic similarity with the poorly-dated, most northern assemblages in Australia, on Melville Island, as well as with New Zealand and Patagonia.

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