

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

Mike Pole

### 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 ‘rain-forest’ hints that its origin might not involve fire, but lie within a vegetation type no longer extant.

Mike Pole. Queensland Herbarium, Brisbane Botanic Gardens Mt Coot-tha, Mt Coot-tha Rd, Toowong, Australia. [murihiku@yahoo.com](mailto:murihiku@yahoo.com)

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## INTRODUCTION

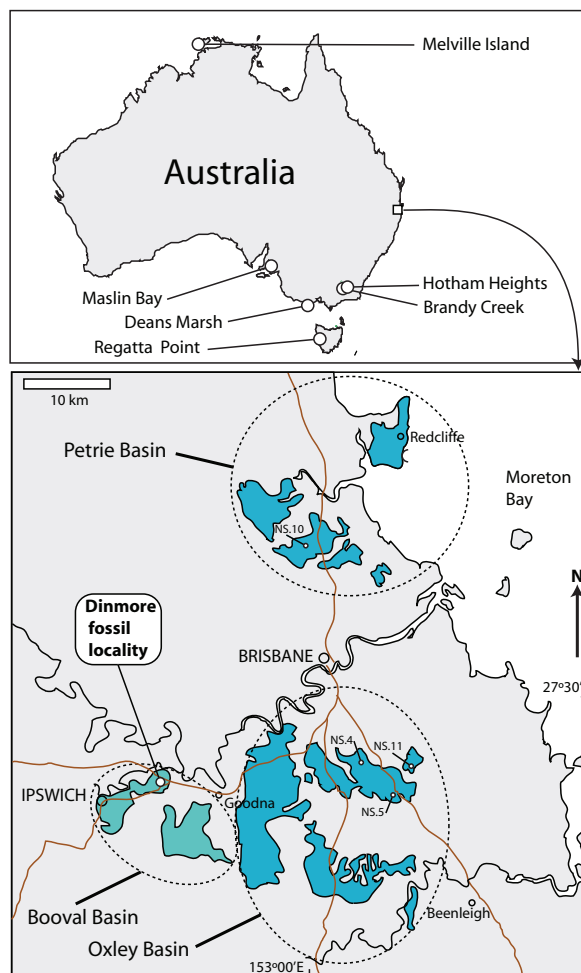
Understanding of the Cenozoic vegetation history of Australia, and of the climate and other factors which drove it, has increased dramatically over the past few decades (e.g., Hill, 1984). However, with the exception of a few far-flung studies (e.g., central Australia, Christophel et al., 1992; Carpenter 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

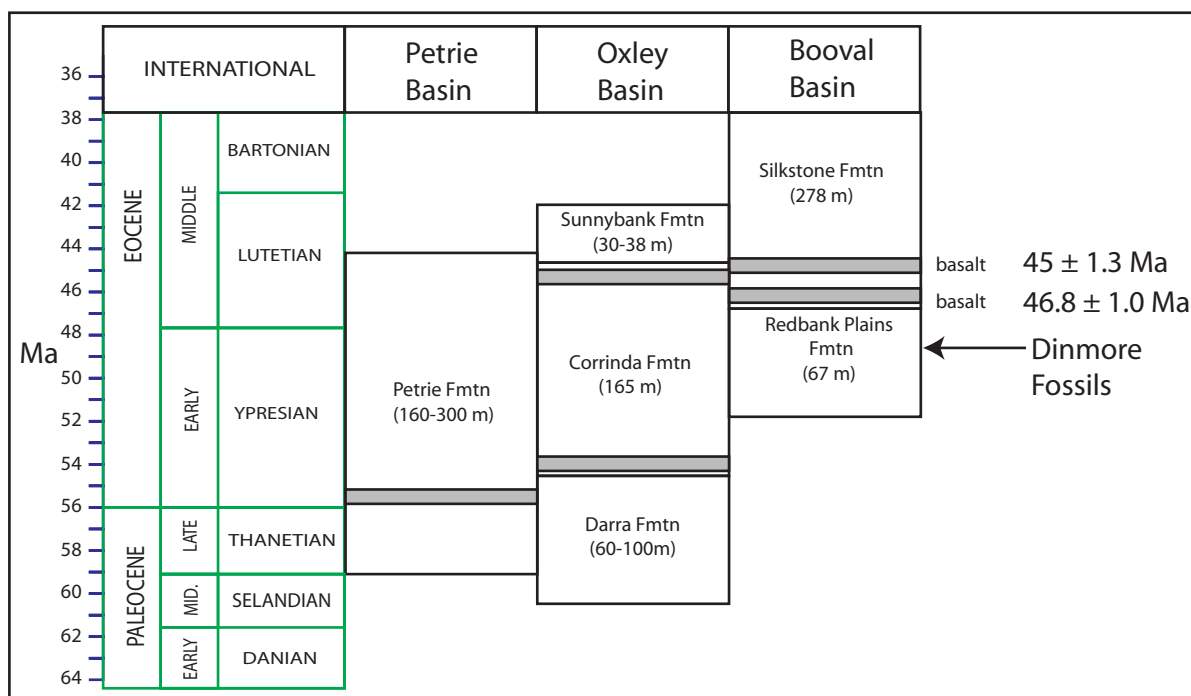
Cenozoic sediments in south east Queensland are restricted to several small basins (in the order of 10–20 km maximum dimensions) representing foci of fluvial-lacustrine activity along with some volcanicity. In the vicinity of Brisbane there are three, namely, the Oxley, Booval, and Petrie Basins (Figure 1). Sediments in the Oxley



**FIGURE 1.** Location map. Outcrop of the three Cenozoic basins near Brisbane is indicated by coloured fill and their extent schematically indicated by dashed lines. Points labelled with 'NS.' are the locations of drill holes described in Harris (1965).

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 Silkstone 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





**FIGURE 2.** Summarised stratigraphy of the three Cenozoic basins near Brisbane (see Staines, 1960; Houston 1965; Day et al., 1982; Jones, 1926), with suggested correlation with the international time scale (following Cohen et al., 2013) and subseries after Luterbacher et al. (2005) and Head et al. (2017). The position of dated basalt flows (Green and Stevens, 1975) is indicated and also the approximate level of the Dinmore leaf assemblage.

Corinda 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 Corinda 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).

**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 petioles	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

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  
Figure 3

**Reference specimen.** QMF34435A,B.

**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.  
Figure 3

**Reference specimen.** QMF14925.

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

TABLE 1 (continued).

Couplet	Criteria	Parataxon
14	Approximately one lateral vein per tooth, teeth well-spaced (c 3 per 10mm)	DINM-JBJ
14	Several small teeth per lateral, teeth numerous (c 5–6 per 10mm), pronounced, serrate 15	
15	Laterals clearly arched, fine venation dense, difficult to discern	DINM-JJC (leaflet)
15	Laterals not clearly arched 16	
16	Laterals curved, but irregular, fine venation clear, open	DINM-JJB (leaflet)
16	Laterals often forked or with many external branches, fine venation indistinct	DINM-JJA (leaflet)
17	Leaves with at least two wide looping zones	DINM-JAG (Smilacaceae)
17	Leaves without two wide looping zones 18	
18	Without domatia 19	
18	With domatia	DINM-JAC
19	Lateral veins clearly enter the petiole	DINM-JAE
19	Lateral veins do not (or not known) to clearly enter the petiole 20	
20	With intramarginal vein 21	
20	Venation externodromous 22	
21	Leaves broad (>20mm wide)	DINM -JAB (' <i>Eucalyptus</i> broad')
21	Leaves narrow	DINM -JAH (' <i>Eucalyptus</i> narrow')
22	Leaves with actinodromous development 23	
22	Leaves with normal development 24	
23	Basal laterals nearly paired, enter petiole	DINM-JAE
23	Basal laterals nearly paired, well above petiole	DINM-JAJ
24	With very drawn-out apex	DINM-JAF
24	Without very drawn-out apex 25	DINM-JBH

stricting 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  
Figure 4

**Reference specimen.** QMF34354

**Referred specimens.** 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

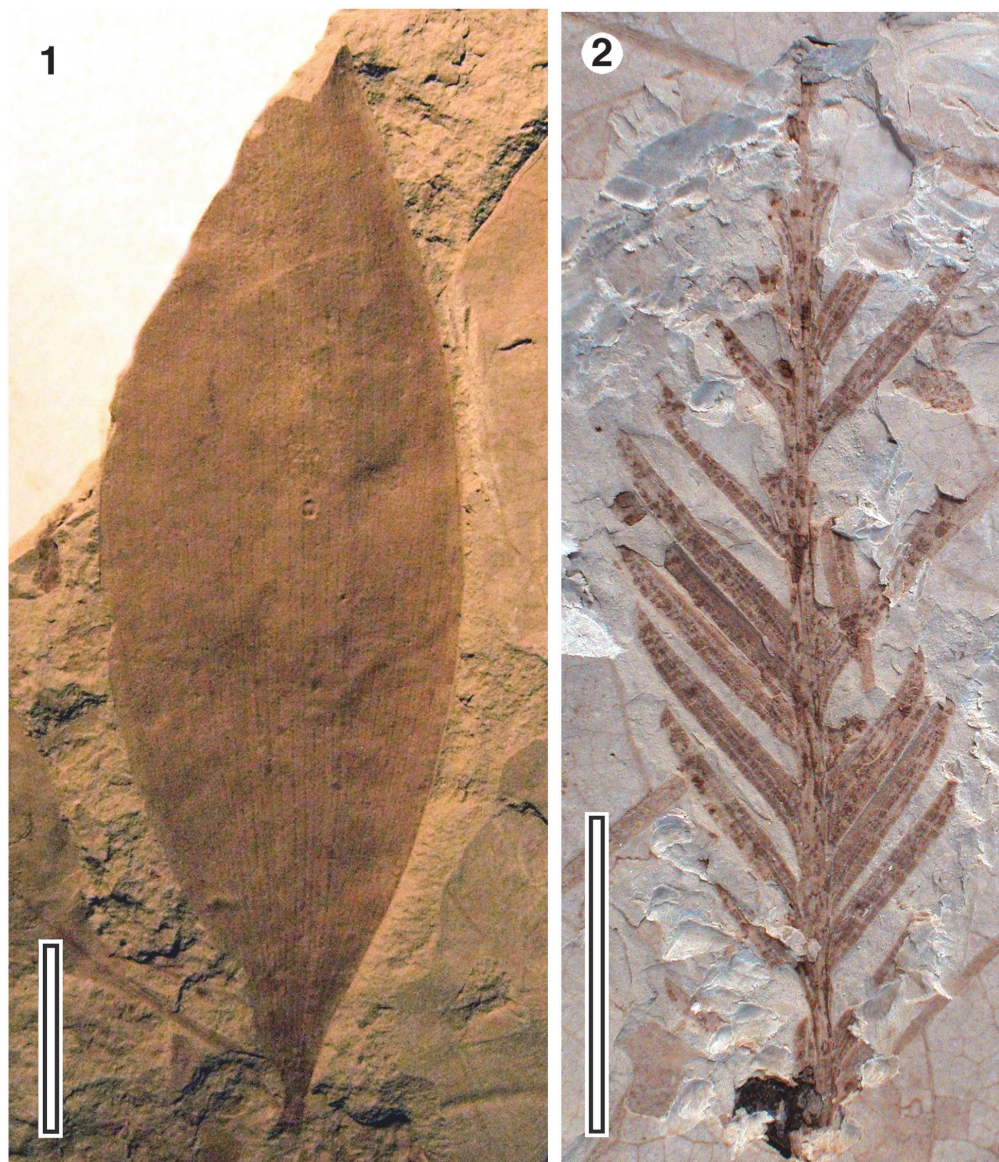
Parataxon: DINM-JJB

Figure 5

**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



**FIGURE 3.** Conifers. **1.** Multi-veined conifer leaf, QMF34435. **2.** ?Podocarpaceae shoot. QMF14925. Scale bars equal 10 mm.

Parataxon: DINM-JBD  
Figure 6

**Reference specimen.** QMF35317.

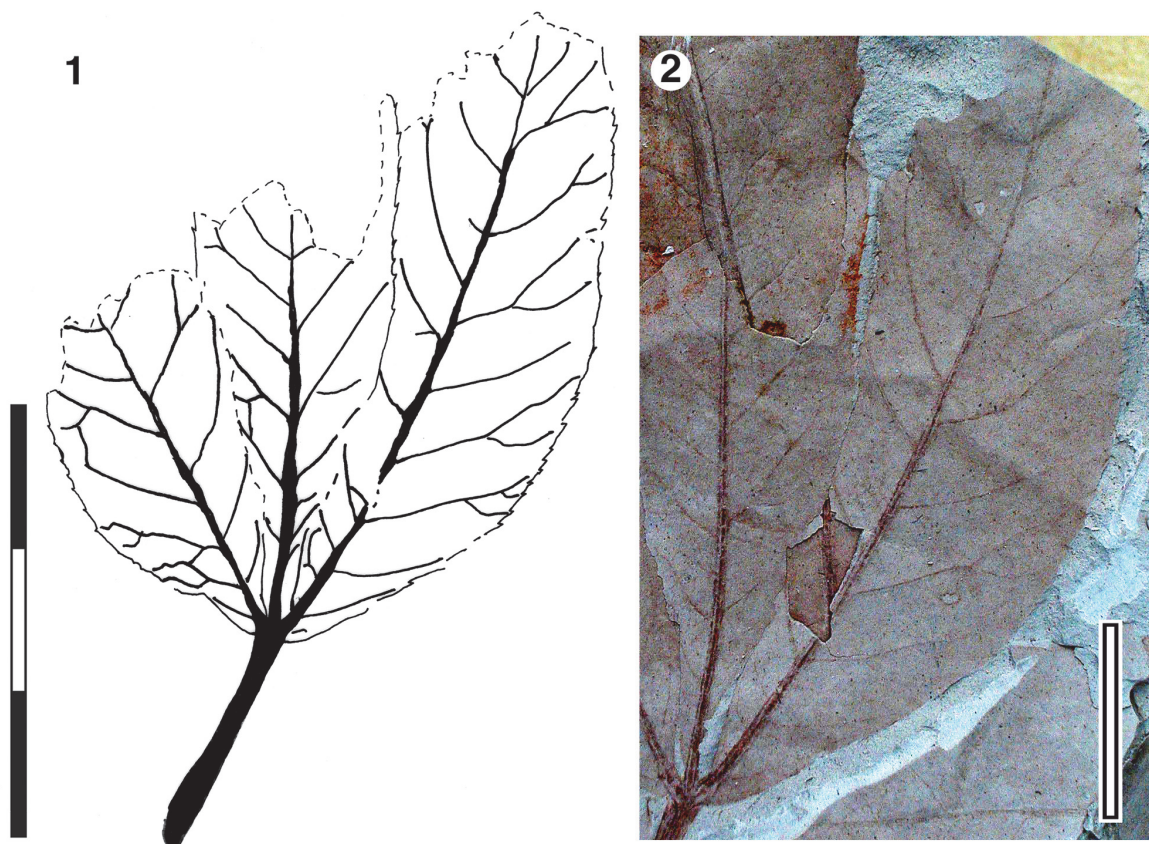
**Referred specimen.** QMF34487.

**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).





**FIGURE 4.** Parataxon: DINM-JJA, reference specimen QMF34354. **1.** Line drawing. **2.** Photographic detail. Scale bars equal 10 mm long or in 10 mm intervals.

Leaves pinnately 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

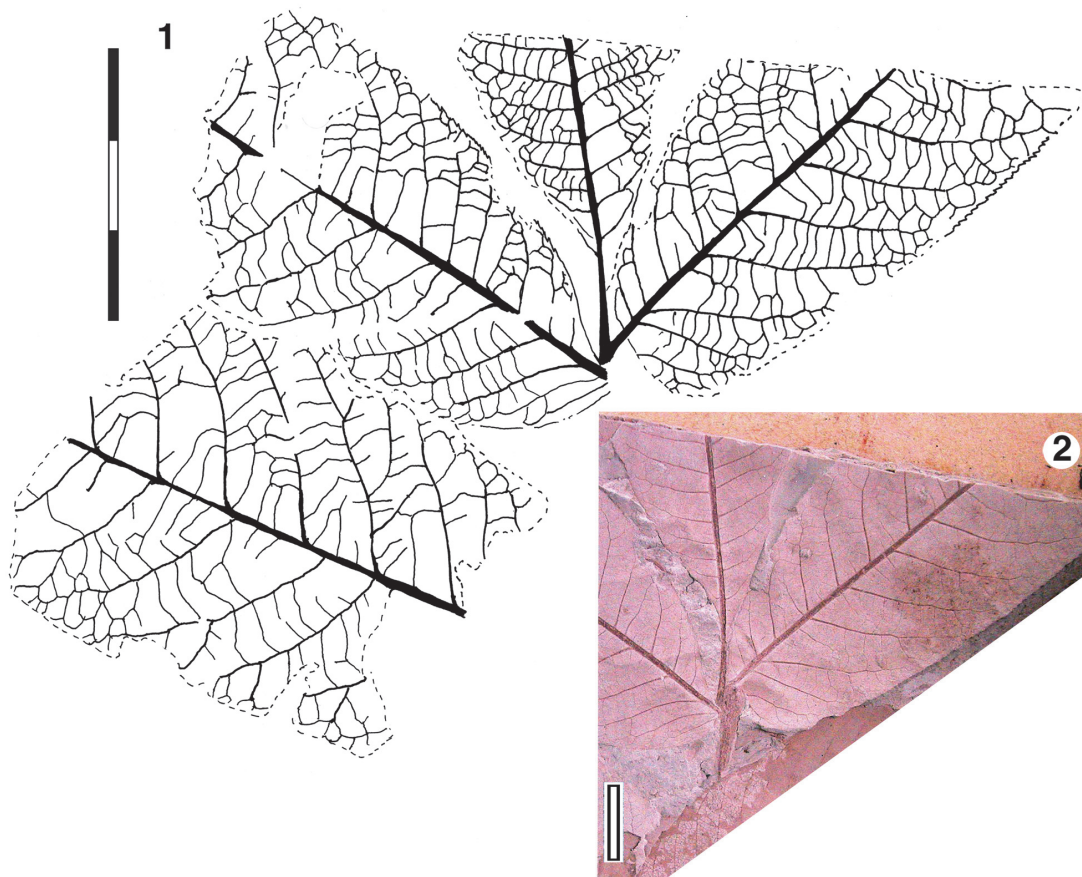
**Reference specimen.** QMF15322.

**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-





**FIGURE 5.** Parataxon: DINM-JJB, reference specimen QMF34356. **1.** Line drawing. **2.** Photographic detail. Scale bars equal 10 mm long or in 10 mm intervals.

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

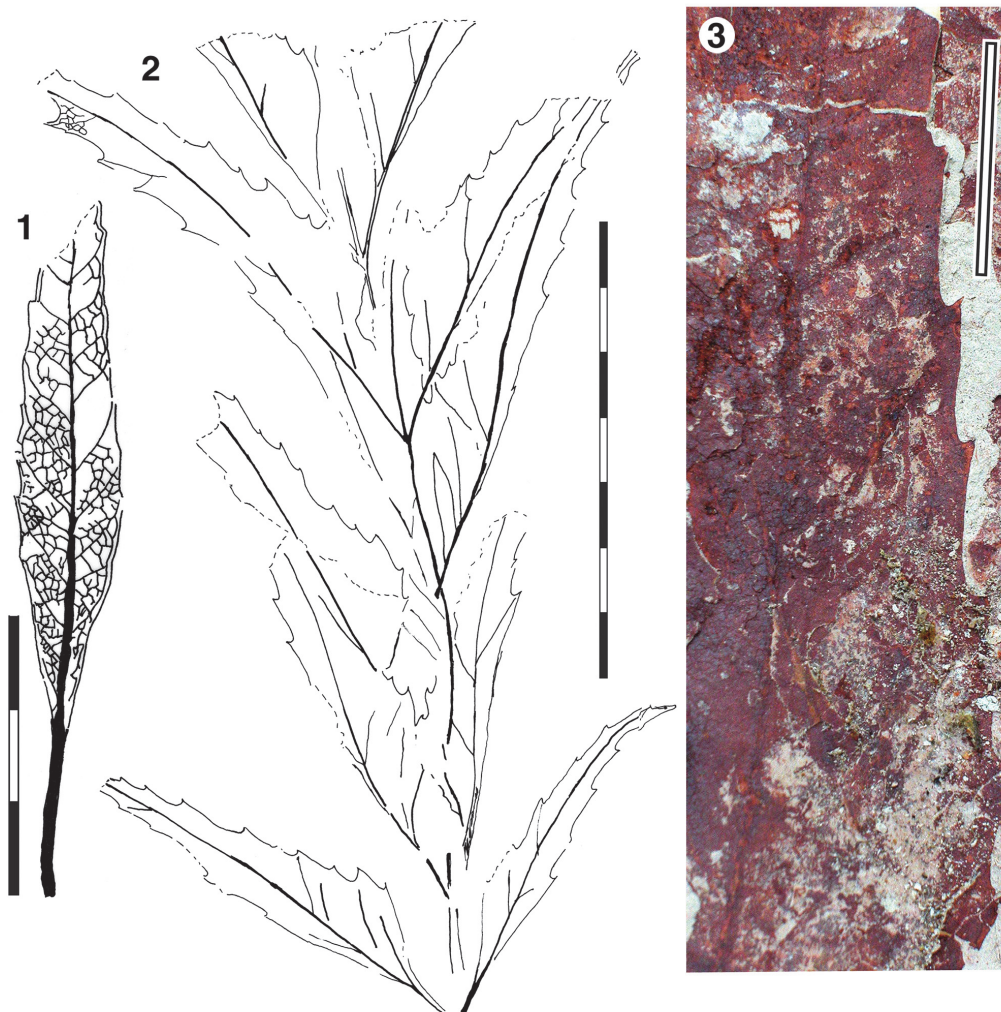
Parataxon: DINM-JJG

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.



**FIGURE 6.** Parataxon: DINM-JBD. **1.** QMF34487 line drawing. **2.** Reference specimen QMF35317 line drawing. **3.** Photographic detail of reference specimen QMF35317. Scale bars equal 10 mm long or in 10 mm intervals.

Leaves simple, with toothed margin, not lobed

Parataxon: DINM-JJH

Figure 11

**Reference specimen.** QMF35370.

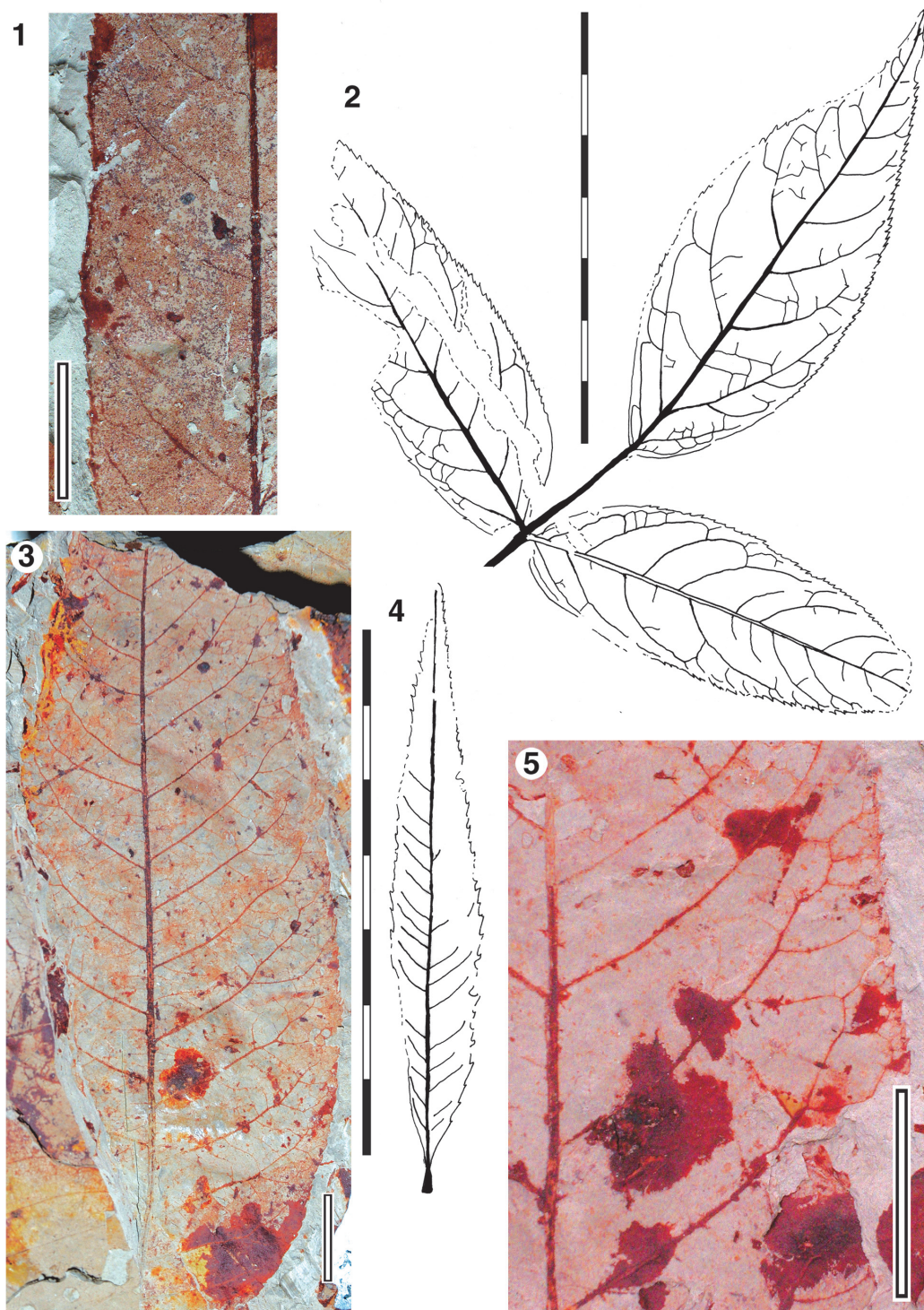
**Referred specimens.** QMF35303.

**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 *Banksiaephyllum* and *Banksiaaeformis* (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 *Banksiaephyllum* 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)



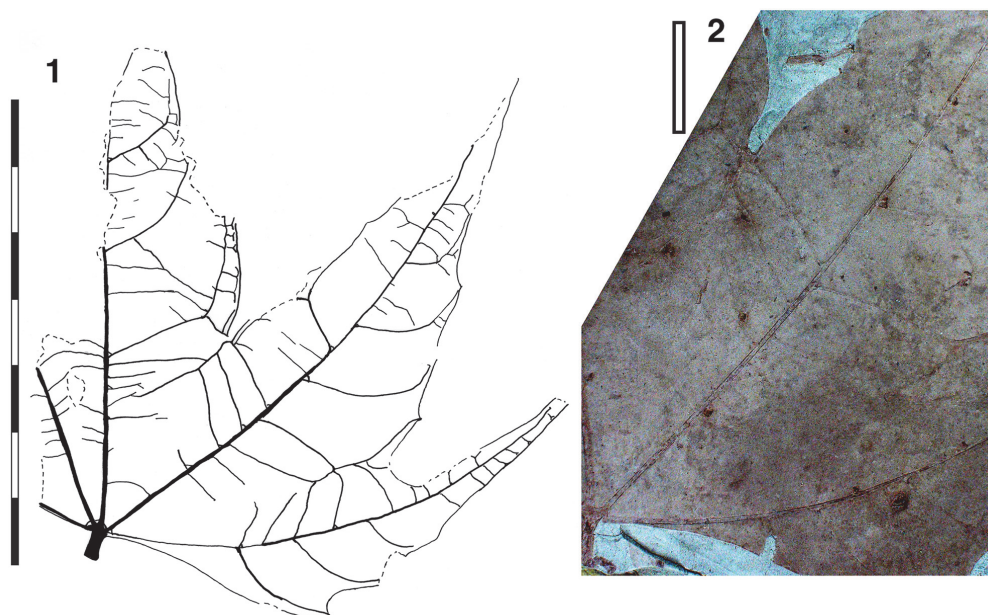


**FIGURE 7.** Parataxon: DINM-JJC. **1.** QMF49460, photographic detail of margin. **2.** Reference specimen QMF15325, line drawing. **3.** Specimen QMF55797. **4.** Specimen QMF35371. **5.** Specimen QMF55789. Scale bars equal 10 mm long or in 10 mm intervals.



**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.





**FIGURE 9.** Parataxon: DINM-JJE, reference specimen QMF34330. **1.** Line drawing **2.** Photographic detail. 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

Figure 12

**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

Figure 13

**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 Ettingshausen's (1895) *Myrica*.

Parataxon JBJ

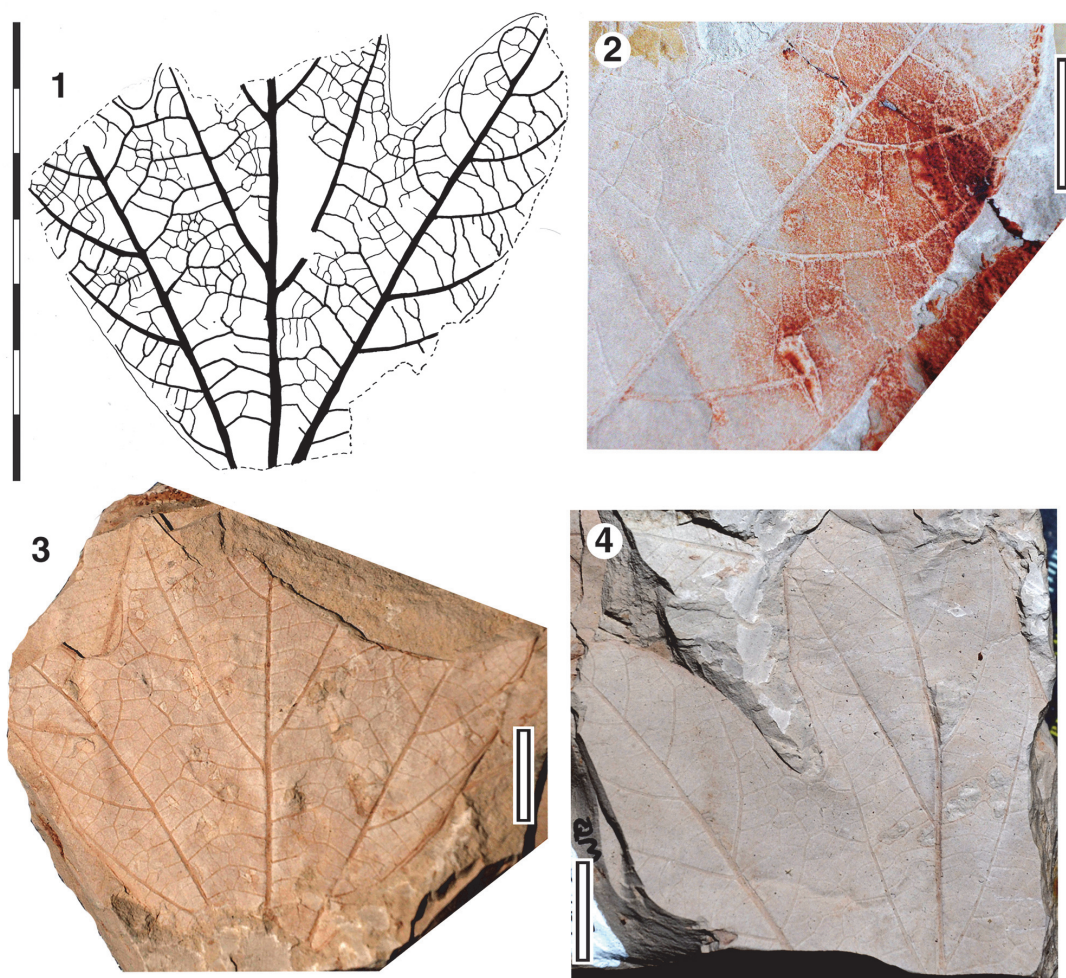
Figure 14

**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-





**FIGURE 10.** Parataxon: DINM-JJG. **1.** Line drawing of reference specimen QMF34352. **2.** Photographic detail of reference specimen QMF34352. **3.** Specimen QMF35311. **4.** Specimen QMF35343. Scale bars equal 10 mm long or in 10 mm intervals.

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.

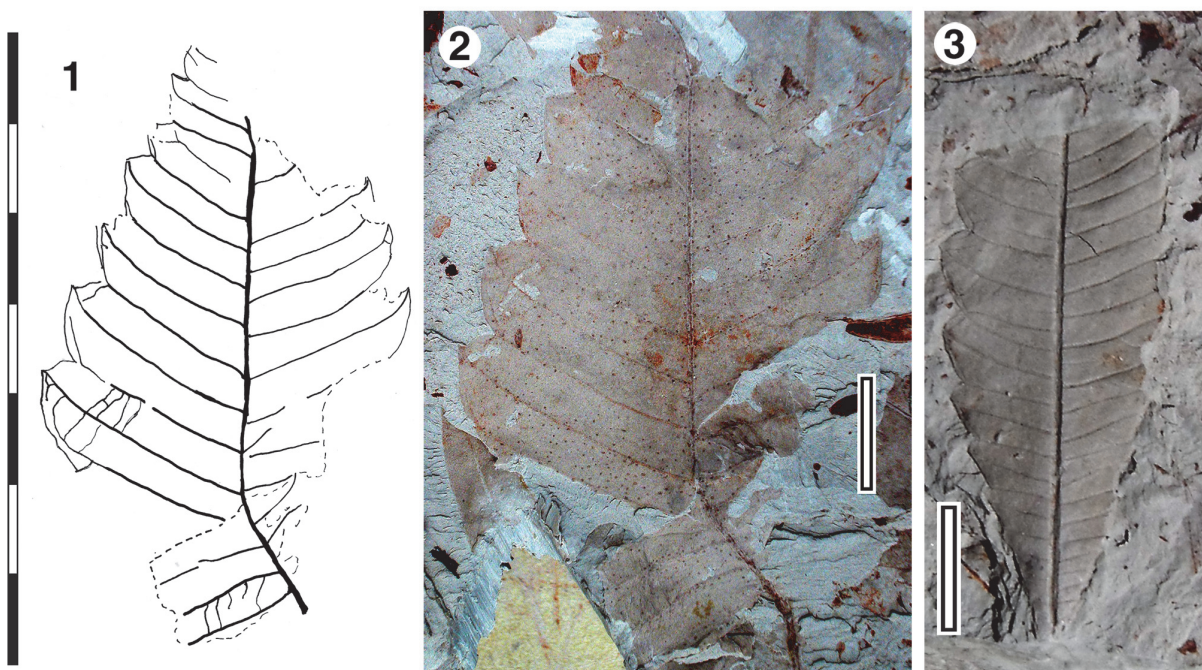
**Referred specimens.** QMF34293, QMF34298A,B, QMF34308, QMF34372, QMF34381, QMF35299, QMF35330, QMF35331, QMF35336, QMF35337, QMF35359, QMF35340, QMF49465, QMF49475A,B, QMF49476, QMF49478.

**Description.** Organisation: simple. Size: length 80–110 mm, width 21–45 (perhaps >60) mm, microphyll–notophyll. Shape: elliptical-obovate, 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.



**FIGURE 11.** Parataxon: DINM-JJH. **1.** Line drawing of reference specimen QMF35370. **2.** Photograph of reference specimen QMF35370. **3.** Specimen QMF35303. Scale bars equal 10 mm long or in 10 mm intervals.

**Referred 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  
Figure 17

**Reference specimen.** QMF34319.

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

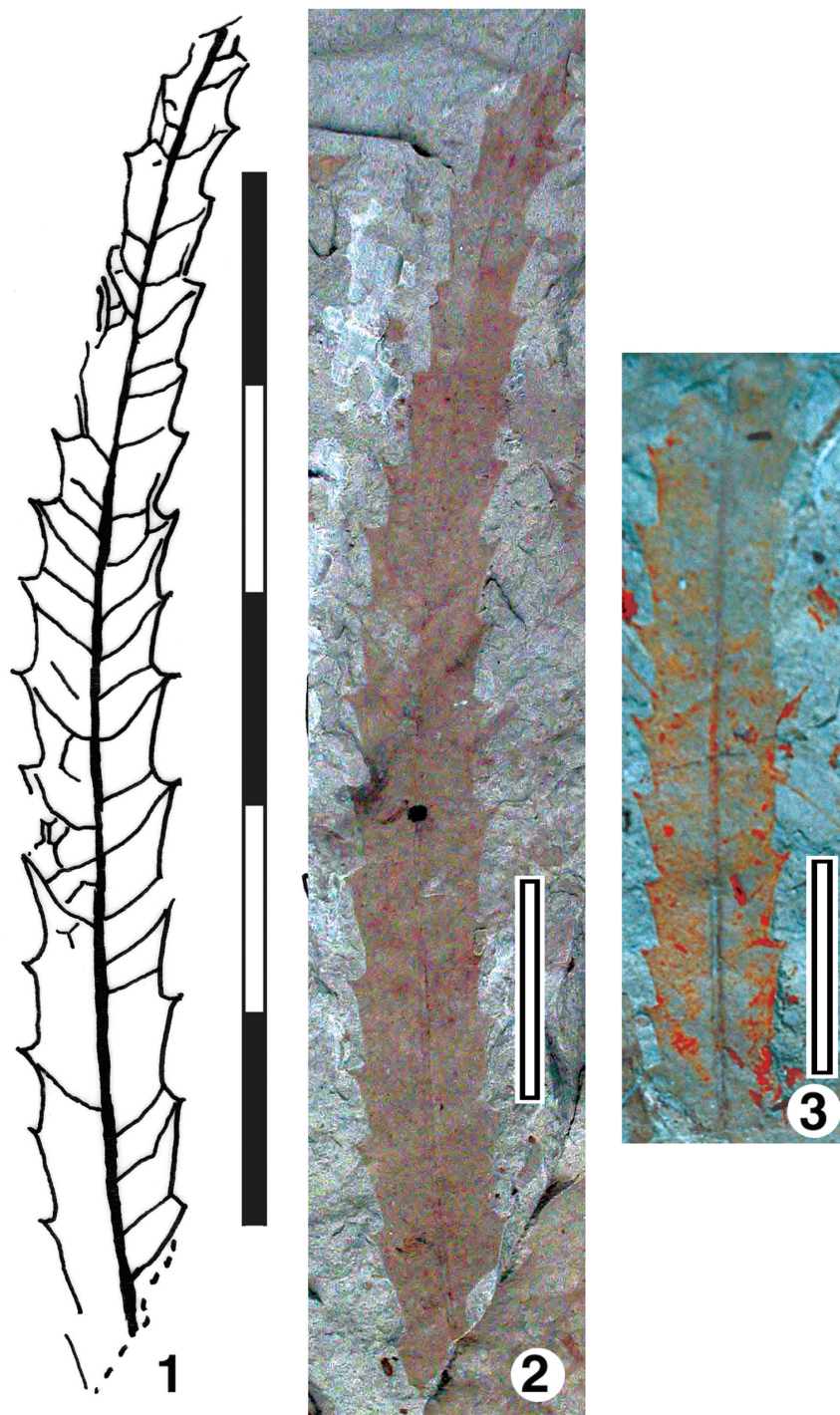
**Description.** Organisation: simple. Size: length 45–67 mm, width 7.5–8 mm, microphyll. Shape: narrow elliptic to narrow ovate, unlobed, apex acute, base decurrent, acute. Margin entire. Venation with intramarginal vein, no looping zone. Development normal. Lateral veins closely-spaced, not decurrent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

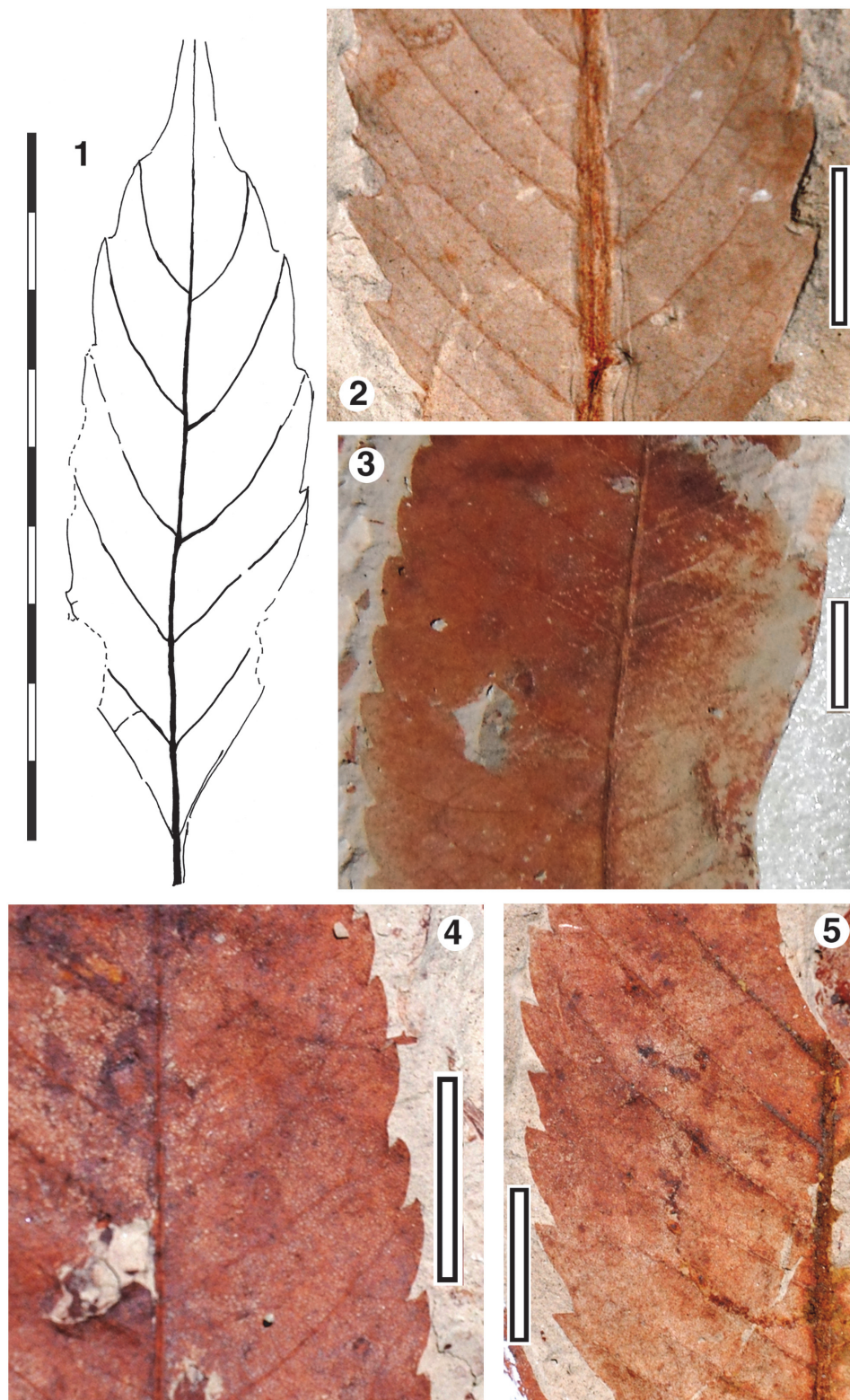
Parataxon: DINM-JAC  
Figure 18

**Reference specimen.** QMF35279.



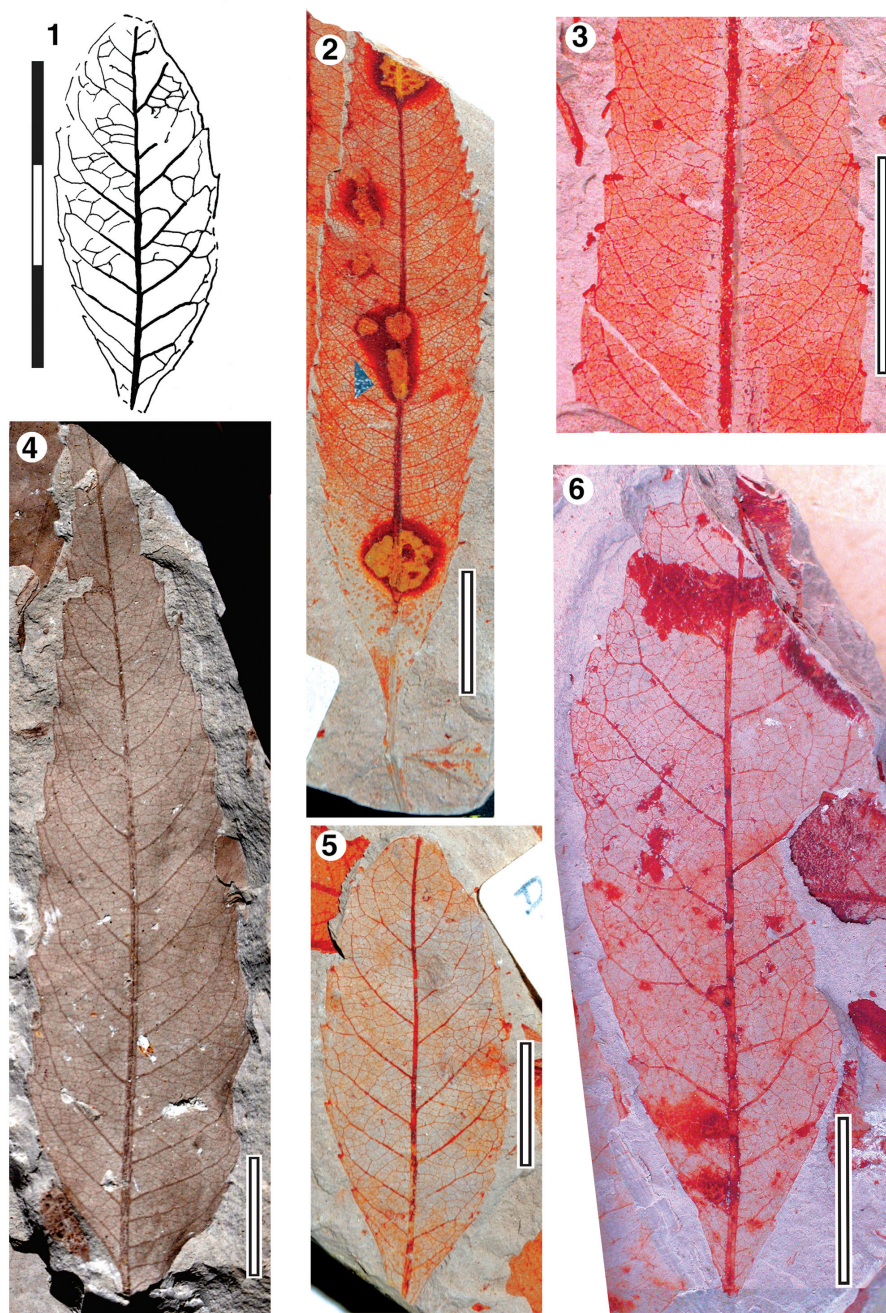


**FIGURE 12.** Parataxon: DINM-JJI. **1.** Line drawing of reference specimen QMF34351. **2.** Photograph of reference specimen QMF34351. **3.** Specimen QMF35362. Scale bars equal 10 mm long or in 10 mm intervals.



**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.





**FIGURE 14.** Parataxon: DINM-JBJ. **1.** Specimen QMF34316. **2.** Specimen QMF34315. **3.** Specimen QMF34318. **4.** Specimen QMF35289. **5.** Specimen QMF34316. **6.** Specimen QMF49458. 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-JAD

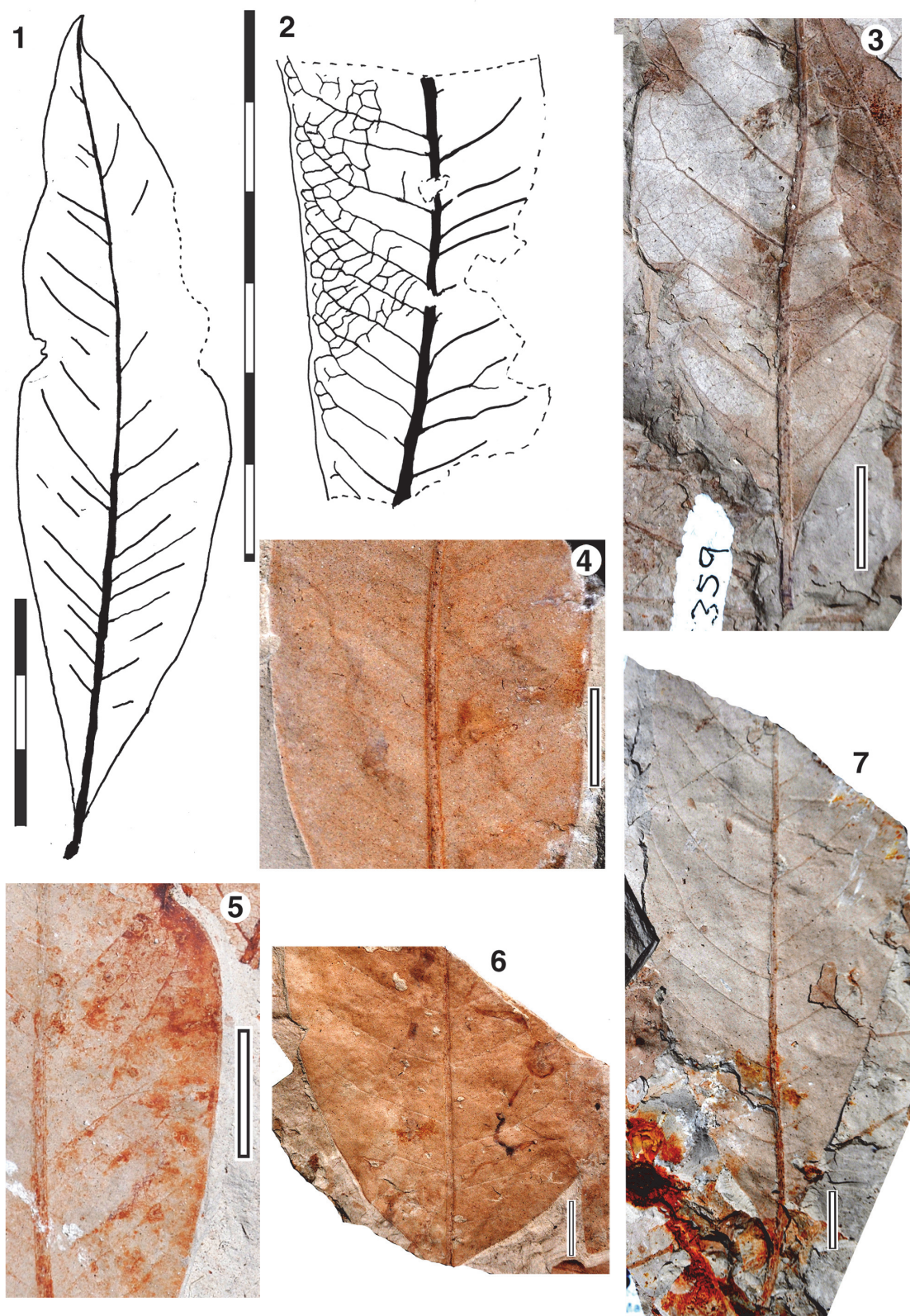
Figure 19

**Reference specimen.** QMF34303.

**Referred specimen.** QMF49485.

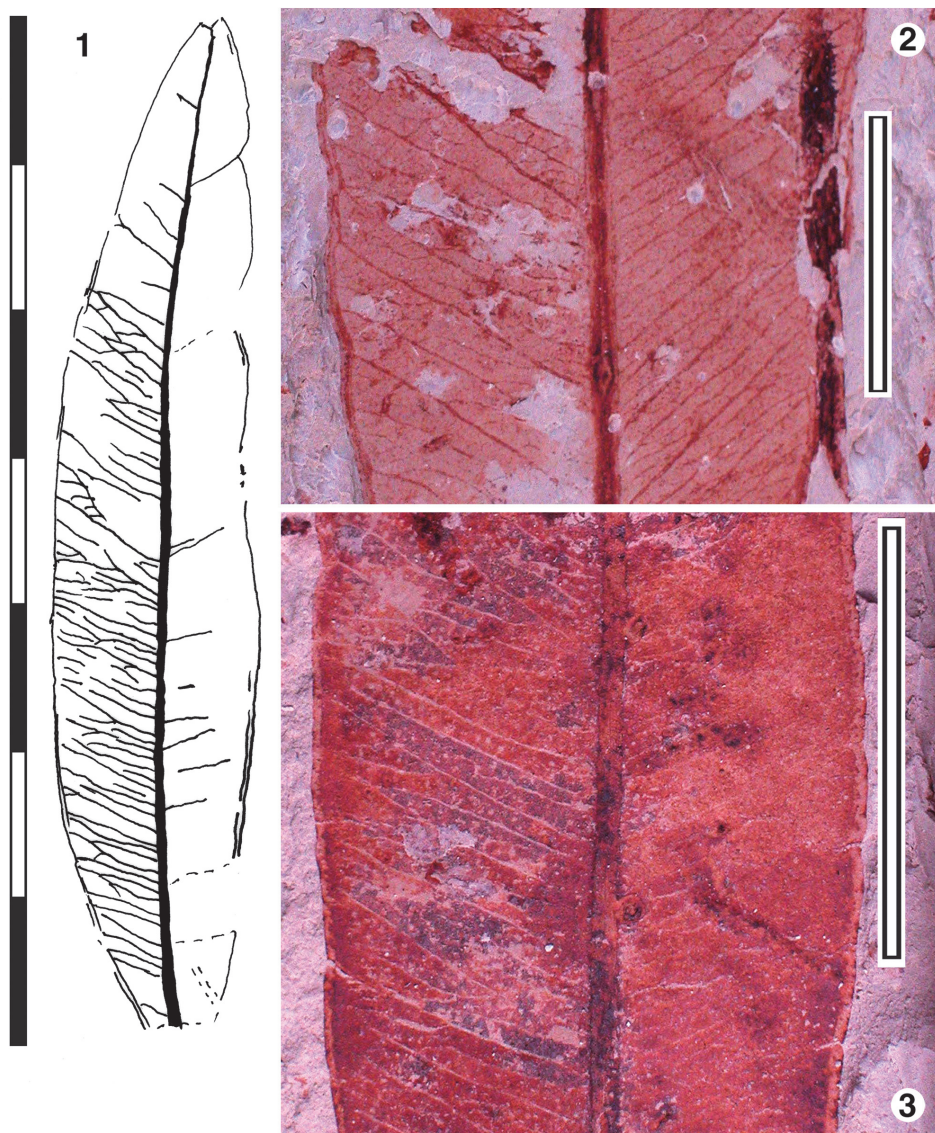
**Description.** Organisation: Size: length 85–c. 148 mm, width 35–45 mm, notophyll. Shape ovate,





**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.





**FIGURE 16.** Parataxon: DINM-JAB. **1.** Line drawing of reference specimen QMF34373. **2.** Specimen QMF35295. **3.** Specimen QMF34373. Note numerous oil-glands and compare with Pole (1993c, fig. 4A). 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.

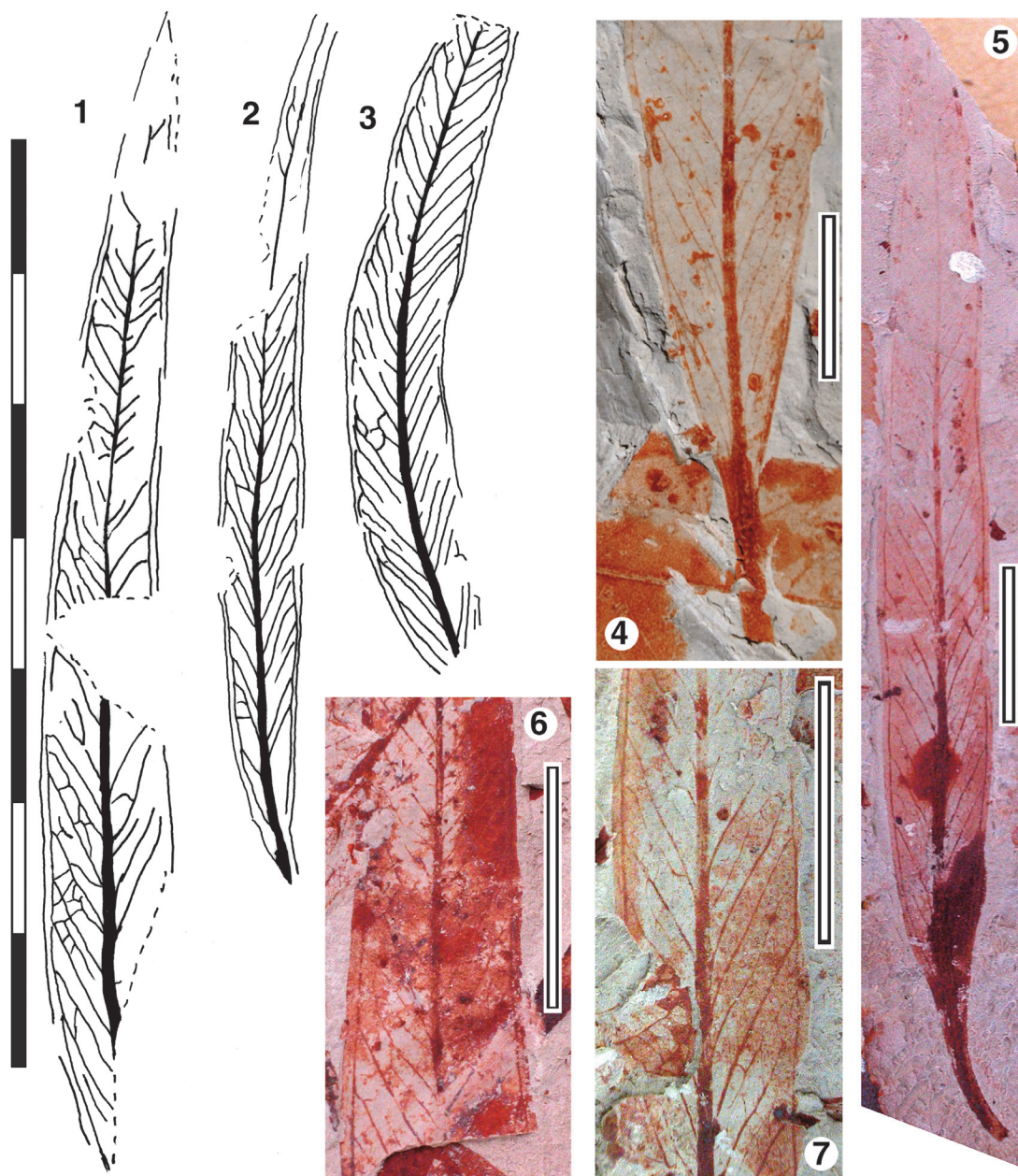
Parataxon: DINM-JAE  
Figure 20

**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 17.** Parataxon: DINM-JAH. **1.** Specimen QMF49456. **2.** Specimen QMF35313. **3.** Specimen QMF34319. **4.** Specimen QMF55800. **5.** Specimen QMF49492A. **6.** Specimen QMF49456. **7.** Specimen QMF49492B. Scale bars equal 10 mm long or in 10 mm intervals.

Parataxon: DINM-JAF  
Figure 21

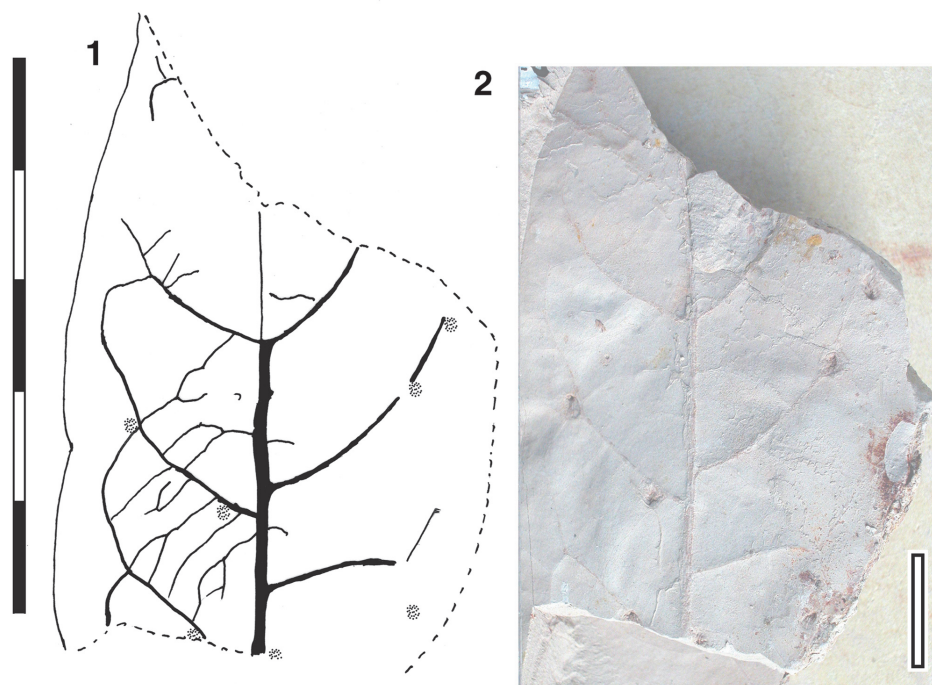
**Reference specimen.** QMF34478.

**Referred specimens.** QMF34294, QMF34320, QMF34321, QMF35325, QMF34379,, QMF35325, QMF35374, QMF49477.

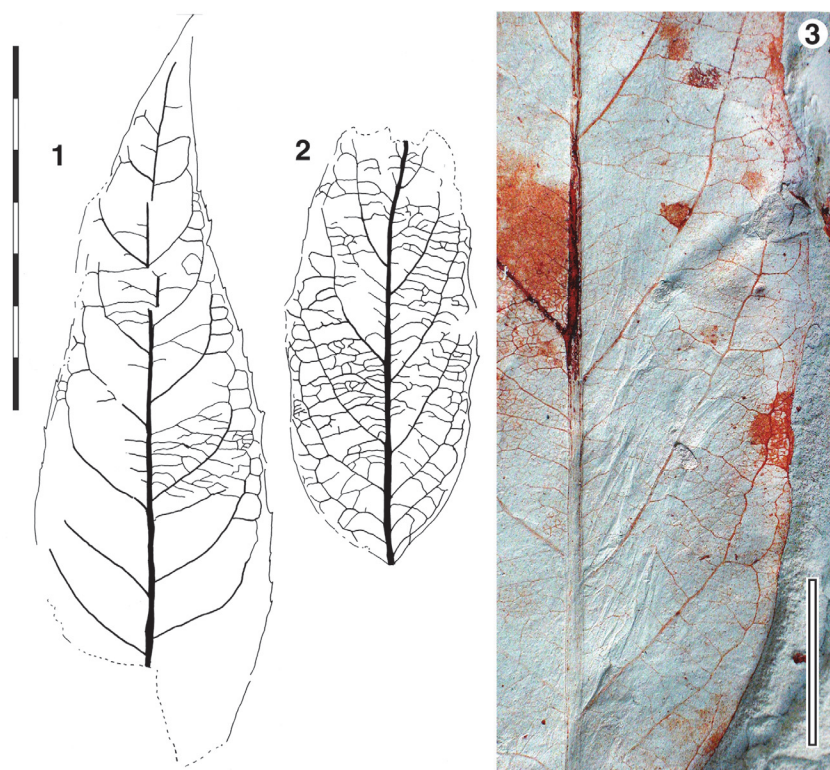
**Description.** Organisation: probably simple. Size: length 100–c. 110 mm, width 14–c. 32 mm, micro-

phyll 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

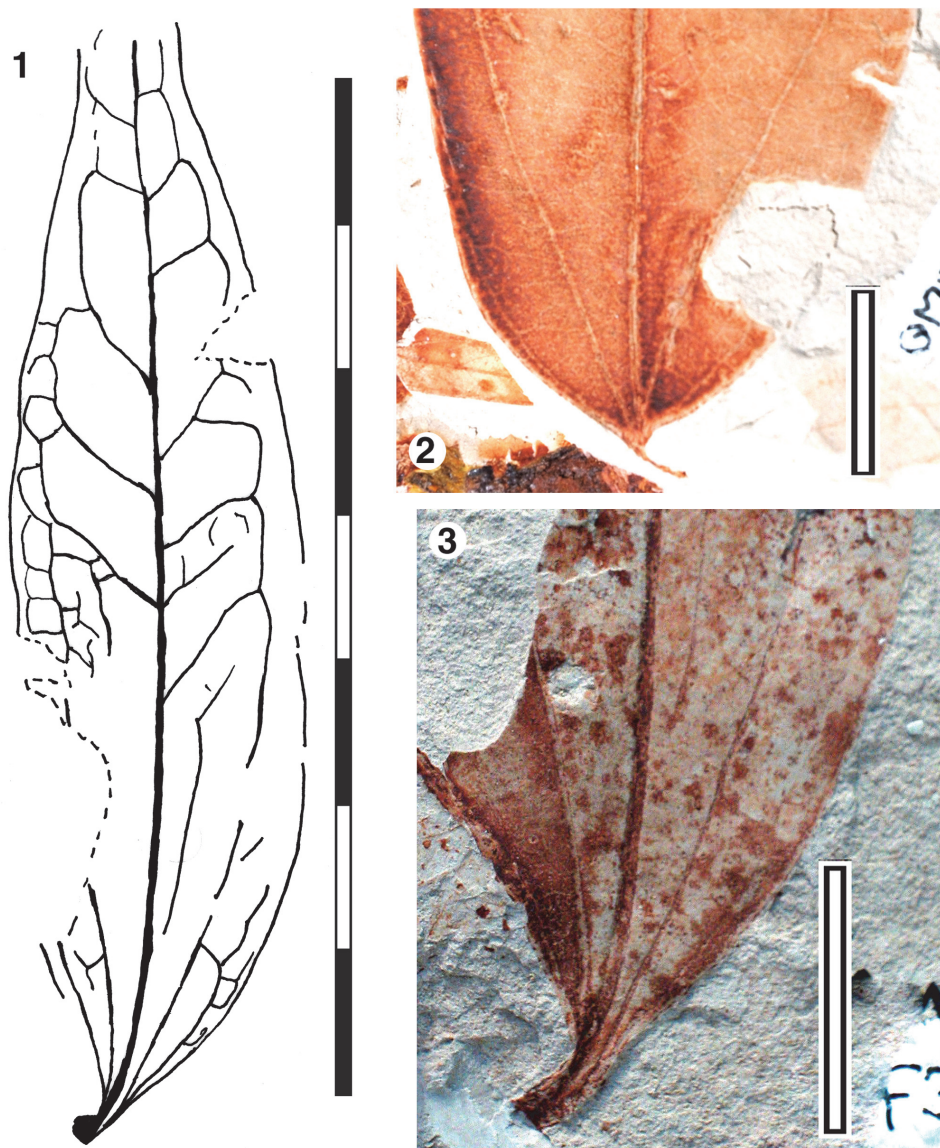




**FIGURE 18.** Parataxon: DINM-JAC, reference specimen QMF 35279. **1.** Line drawing, putative domatia indicated by stipple. **2.** Photographic detail, note putative domatia-pits. Scale bars equal 10 mm long or in 10 mm intervals.



**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.



**FIGURE 20.** Parataxon: DINM-JAE. **1.** Line drawing of reference specimen QMF35368. **2.** Specimen QMF55801. **3.** Photographic detail of reference specimen QMF35368. 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.

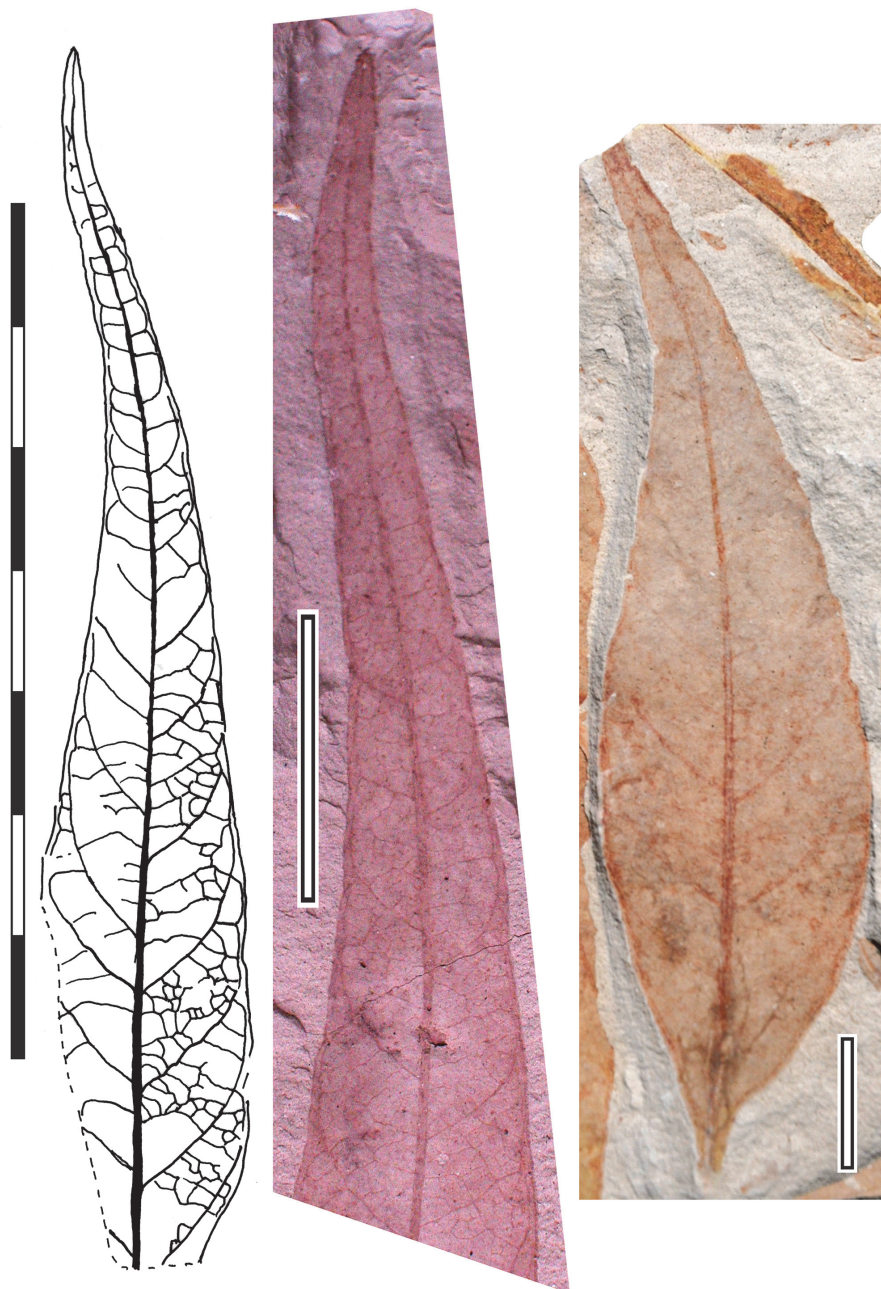
**Remarks.** The venation pattern suggests Smilacaceae, although to no specific extant genus (Inamdar et al., 1983; Pole, 1993a, 1996; Carpenter et al., 2014).

Parataxon: DINM-JAJ  
Figure 23

**Reference specimen.** QMF34358.

**Referred specimens.** QMF34329, QMF49531.

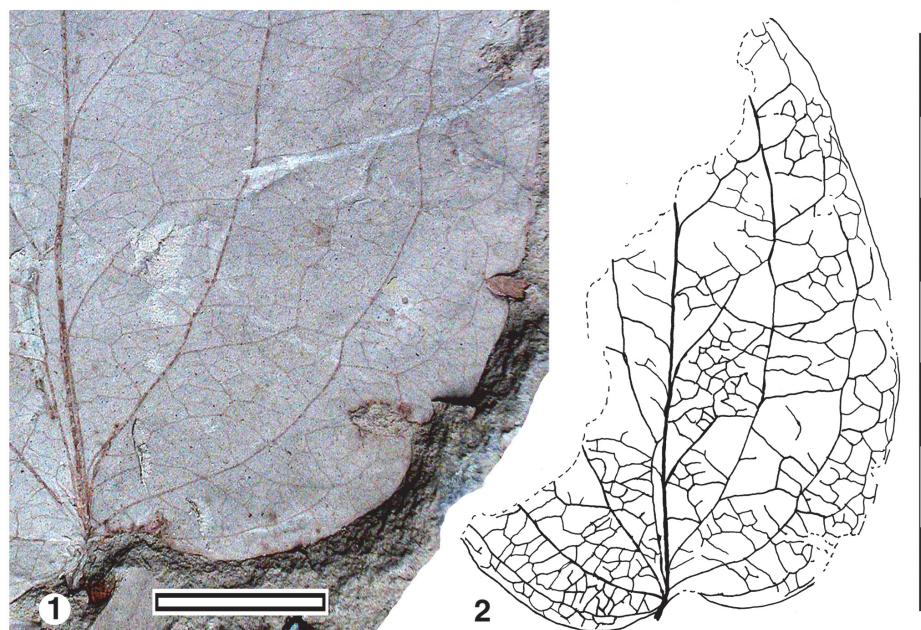




**FIGURE 21.** Parataxon: DINM-JAF. **1.** Line drawing of reference specimen QMF34478. **2.** Photographic detail of reference specimen QMF34478. **3.** Specimen QMF34379. Scale bars equal 10 mm long or in 10 mm intervals.

**Description.** Organisation: simple. Size: length c. 28–c. 120 mm, width 24–45 mm, microphyll–notophyll. 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



**FIGURE 22.** Parataxon: DINM-JAG, reference specimen QMF34376. **1.** Line drawing. **2.** Photographic detail. Scale bars equal 10 mm long or in 10 mm intervals.

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 Roze-feld'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

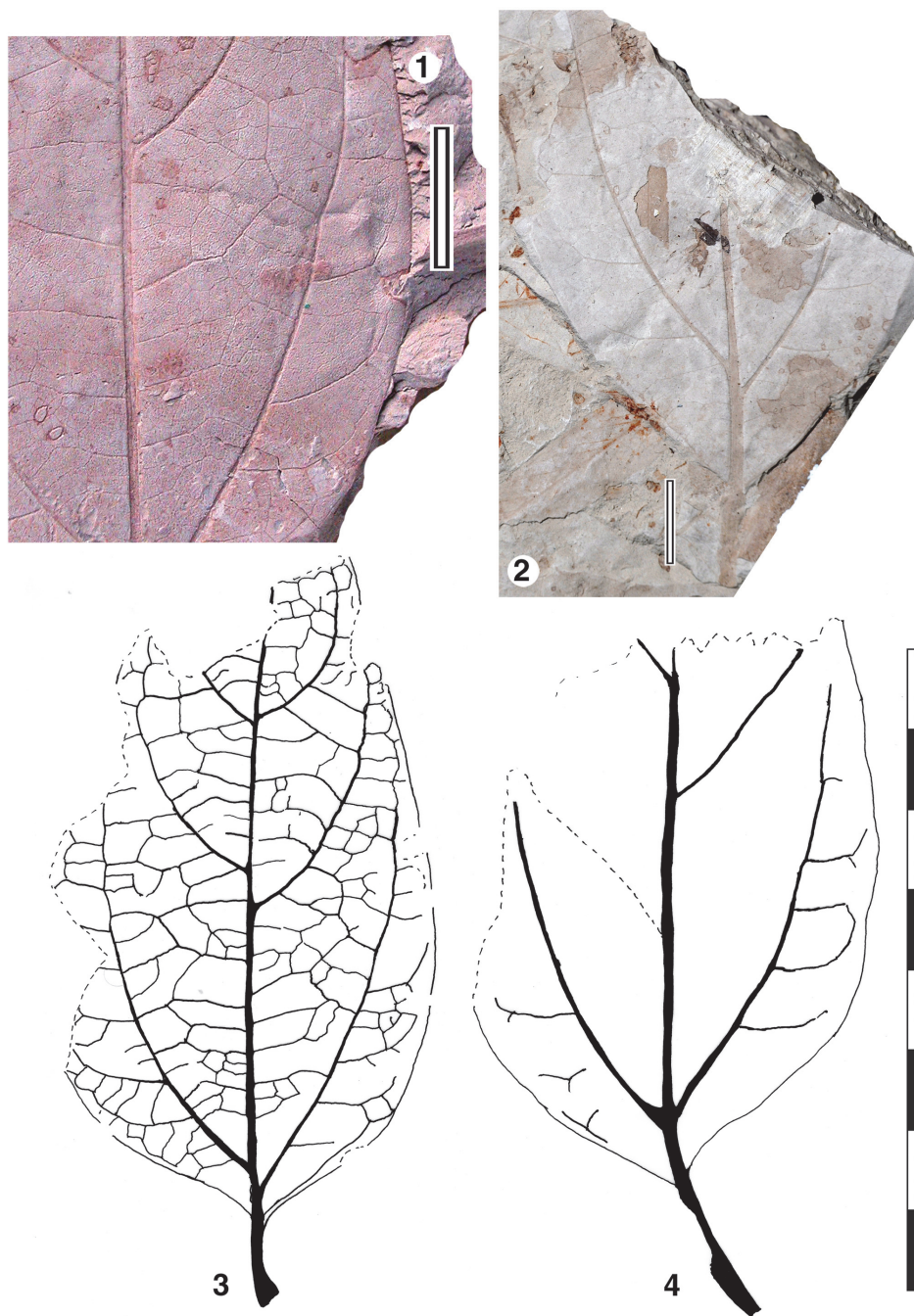
Foliar physiognomy is a well-established source of climatic information. However, the accuracy and most appropriate methods to extract it are subject to vigorous debate. Because Dinmore is distant from other floras of similar age, it provides a potentially useful window into the paleoclimate.

**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  $\pm 5^{\circ}\text{C}$  (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

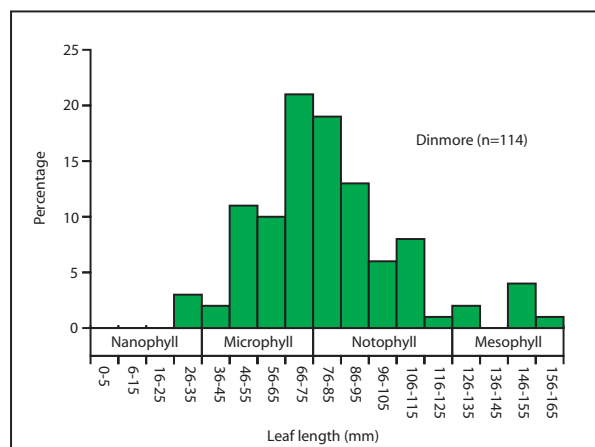




**FIGURE 23.** Parataxon: DINM-JAJ. **1.** Photographic detail of reference specimen QMF34358. **2.** Specimen QMF55816. **3.** Line drawing of reference specimen QMF34358. **4.** Specimen QMF34329. Scale bars equal 10 mm long or in 10 mm intervals.

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-



**FIGURE 24.** Leaf length histogram.

blage is therefore marginal for the technique. Some entire margined taxa may have been grouped, and thus their overall proportion underestimated (entire-margined taxa are probably more likely to be grouped than toothed ones). An entire-margined proportion of about 60% is needed for the leaf margin MAT predictions to match those of leaf area. In that case, a revision of the assemblage would need to describe an additional nine entire-margined taxa (and no more toothed ones). This is regarded as unlikely.

Average leaf area is specimen-based and avoids the potential problem of an incorrect taxonomy (Greenwood, 1992). However, despite the higher MAT indicated by average leaf size, this is likely to still be a minimum. Factors other than temperature are known to affect leaf size; a dry season and/or low nutrient soils will tend to decrease it (e.g., Webb, 1959; Adam, 1992) and thus result in a lower than predicted MAT.

It is unlikely that the Dinmore assemblage represents a type of vegetation that is currently extant, but not yet sampled by the various researchers of leaf physiognomy. The high proportion of teeth, but relatively large leaves, suggests a physiognomy, and perhaps a climate, that is not represented today. The presence of three prominently lobed taxa (15%) in a small flora is also curious, and appears to be outside the range for evergreen rainforest as represented in the various calibration datasets of CLAMP lodged online (<http://clamp.ibcas.ac.cn>). In these datasets, comparable proportions of lobed species occur only in dry/open or deciduous vegetation (although it is noted that some of the South African datasets treat compound leaves, e.g., *Acacia*, as lobed). Other factors argue that Dinmore was likely either relatively

dry or had a dry season. These include both the presence of elongate leaves (with Length: Width >4) and their identification of *Eucalyptus*, as well as the general absence of coal in the region and rarity of *Nothofagus* pollen (Harris, 1965, proposed a geographical control for this genus from southern to central Australia in the early Cenozoic). Dinmore was possibly a form of dry rainforest, and therefore with moisture at least seasonally limited, leaf size would under-represent MAT. The results reinforce a previous observation that MAT based on leaf-litter size and inventory-based margin proportions were slightly different (Pole, 2010). Note that this is a different issue too where Dinmore, dominated by microphyll and notophyll leaves, would likely be classified as a 'notophyll' forest if it grew in Australia today (Webb, 1959; Greenwood, 1992; Pole, 2014).

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., Brodribb 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 floras 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 *Eucalyptopsis*, 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.

## ACKNOWLEDGEMENTS

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