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An Australian origin for the Candle Nut (*Aleurites*, Crotonoideae, Euphorbiaceae) and the fossil record of the Euphorbiaceae and related families in Australia and New Zealand.

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Abstract

A fossil seed from south east Queensland referable to the extant genus *Aleurites* (candlenut) is described as a new species, *A. australis*, and is one of the few macrofossil records of Euphorbiaceae from Australia. The new fossil data and phylogenetic studies of the biogeographical relationships of *Aleurites* based upon analysis of *rbcL* and *trnL-F* sequence data support a Gondwanic origin for the clade. The macrofossil record of Euphorbiaceae in Australia is restricted to seeds of *Aleurites*; and fruits of *Fontainocarpa* which are thought to have affinities with *Fontainea*, and both extant genera are referable to the Crotonoideae. One group of crotonoids has inaperturate spheroidal pollen, that is comparable to the dispersed pollen genus, *Crotonipollis*, which has an Oligocene to Recent range in Australia. The fossil pollen record in Australia and New Zealand of other Euphorbiaceae and related families includes species of *Malvacipollis* that have affinities to the Picrodendraceae; *Nyssapollenites endobalteus* (McIntyre) Kemp and Harris has affinities with the subfamily Acalyphoideae (Euphorbiaceae); and putative records of *Homalanthus* suggest affinities with the subfamily

Euphorbioideae (Euphorbiaceae). Fossil fruits of *Glochidion* provide possible evidence of the Phyllanthaceae. The stratigraphic range of these taxa in respect to the Weddellian Biostratigraphic Province, which includes southern South America, western Antarctica, New Zealand, and eastern Australia is also briefly reviewed.

Keywords: *Aleurites*, fossil fruits, pollen, Euphorbiaceae, Cenozoic, Australia

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1. Introduction

Candle nuts (*Aleurites* spp.) occur throughout south east Asia to India in the west and to eastern tropical Queensland (Australia), New Caledonia, and the Solomon Islands. Two species, *A. moluccanus* (L.) Willd. and *A. rockinghamensis* (Baill.) P.I.Forst., are recognized both of which occur in northern Queensland (Fig. 1) and Stuppy et al. (1999) have shown based upon a morphological study that *Aleurites*, is distinct from the Malesian genera *Reutealis* and *Vernicia*, although Webster (2014) considered these latter two genera congeneric. The fruits of *Aleurites* are typically drupaceous with 2–3 (–4) locules, which makes them variable in shape due to the number of seeds that develop, and they have a thick fleshy exocarp and thin endocarp. The fruits thus differ from those of *Reutealis* and *Vernicia* which are capsular (Stuppy et al., 1999).

Aleurites seeds are buoyant, due presumably to their high oil content, and occur as flotsam on beaches (Fortune Hopkins, 2000; Degener et al., 1978) and, presuming the embryo can survive immersion, have been widely dispersed throughout the tropics by oceanic currents. The seeds are edible, after cooking, and are rich in oils and the inner kernel (embryo plus endosperm) is used as an illuminant. The fruits/seeds have been further dispersed by humans (Fortune Hopkins, 2000) and human-mediated dispersal is thought to account for its

widespread distribution from India and China to Central America. The plant was particularly important in Polynesian culture which explains its current distribution across the Pacific through Micronesia, Polynesia, the Hawaiian Islands and Tahiti (Airy Shaw, 1966; van Balgooy, 1993). Smith (1981, p. 548) concluded that *Aleurites* was probably “indigenous to Malesia although the precise area of its nativity is probably impossible to establish”. The discovery of *Aleurites* fruits in archaeological sites in Southeast Asia (Latinis, 2000) indicates that it has been present in this region since the late Pleistocene. Fossil pollen consistent with that of *Aleurites*, and other genera in the Crotonoideae, is conformable with the dispersed pollen *Crotonipollis* de Lima, which dates back to the Early Oligocene in Australia (Macphail and Stone, 2004). This biogeographical pattern would be challenged if the identity of fossil leaves attributed to *Aleurites* from the Eocene of North America (Berry, 1930; McGinitie, 1969) was confirmed.

A fossil *Aleurites* seed is described herein from south east Queensland providing the first evidence of the genus from pre-Pleistocene deposits, and this new fossil material from Australia suggests a Gondwanic origin. The significance of this discovery is assessed, the macrofossil and pollen record of Euphorbiaceae and related families from Australia is reviewed, and the generic and familial placement of fossil leaf taxa attributed to *Aleurites* in the USA is also briefly discussed. Martin (1974) recognised that a number of pollen types in the Australian and New Zealand Cenozoic sediments have affinities with the Euphorbiaceae and related families. In this paper we have attempted to constrain, in a phylogenetic sense, the pollen record in Australia and New Zealand within the currently recognised subfamilies in the Euphorbiaceae, and previously included families such as Phyllanthaceae and Picrodendraceae (Wurdack et al., 2004, 2005; Matamoro-Vidal et al., 2012, Angiosperm Phylogeny Group IV, 2016).

2. Locality

The fossil is from the Queensland Museum collection, although this specimen was originally part of the Geological Survey of Queensland (GSQ) collection, and it is therefore prefixed with the letters 'GSQF'. The Geological Survey Collections were transferred to the Museum in 2003. The specimen was collected from Water Bore PP43, 179–204 feet [55–62 m], Portion 695, Parish North Branch, South of Pittsworth, south east Queensland, Australia. Portion 695 was an earlier land division, which is no longer current, but equates to an area in the vicinity of the property 'Argyle' near the Northern Branch of the Condamine River (Mark Thornton, Geological Survey of Queensland, pers. comm. 2016).

The seed is assumed to have been collected from a water bore as there are no geological (stratigraphic) drill cores known from the area (Mark Thornton, pers. comm., 2016). The area is mapped as Jurassic-aged Walloon Formation, with overlying Miocene volcanics of the Main Range and Quaternary sediments along current river systems (Cranfield et al. 1976). Unfortunately there is no sediment associated with the fossil seed. It is likely that the fossil seed was associated with deeply buried alluvial sediments from a palaeostream or deep lead associated with the Condamine River (North Branch) river system. Other deep leads in this area have yielded fossil fruits and seeds; Mueller (1879, p. 38; 1883, p. 14) recorded *Conchotheca* fruits (Proteaceae) collected from the Clifton Coal Mine by Mr Simson, according to Mr C. Staiger, F.L.S., analytical chemist to the Government of Queensland, but the current whereabouts of these specimens remains unknown. The stratigraphy was recorded as "2 feet (0.6 m) of volcanic black soil, then about 37 feet [12 m] of Dolerite (= basalt),... 43 feet [13 m] of drift on the bottom of which were *Conchotheca*-fruits occur with fossilised wood and drift-quartz and beneath this the coal". Further west, *Eureka* (Proteaceae) fruits were found in a bore when drilling in the Texas area, south east Queensland, at a depth of 100 m (H.T. Clifford).

pers. obs., 2015). Other fossil fruits have been recorded from Miocene-aged deposits elsewhere in Australia (Dettmann and Clifford, 2010) and carbonaceous material has not been collected, to the best of the author's knowledge, from Quaternary-Pleistocene sites in the region. Hence why we favour an older Miocene age for this specimen, but in the absence of stratigraphic information, confirmation of the age of the fossil is not possible.

3. Methods

The specimens, both herbarium and fossil, were photographed with a Canon camera using a Zerene stacker with the software, 'portable imaging' by Visionary Digital Photographic System, and also with a Nikon camera with a 105 mm macro lens. Photographs of the seed coat microstructure were taken without coating, using a Hitachi TM 1000 SEM.

Data for modern plant records is from the *Atlas of Living Australia* (ala.org.au), and the abbreviations, BRI and MEL, refer to herbarium collections held in the Queensland Herbarium (Brisbane) and Herbarium of Victoria (Melbourne) respectively. Comparative material also includes specimens held by the senior author which are figured in this paper. Authorities to extant plant taxa are available at the International Plant Names index website, (<http://www.ipni.org/>). Information on the ecology and distribution of modern *Aleurites*, from both the literature and records in the *Atlas of Living Australia*, <http://www.ala.org.au/>, are used to interpret the habitat in which the plant grew. The seed coat terminology and seed microstructure generally follows that of Schmid (1986) and Corner (1976) respectively. The 3D scatter plots were prepared using PAST (Hammer, 2016).

4. Systematics

Family Euphorbiaceae Juss.

Subfamily Crotonoideae Beilschm.

Aleurites J.R.Forst. and G. Forst.

Type species *Aleurites moluccanus* (L.) Willd.

Aleurites australis Rozefelds, M.E.Dettmann & H.T.Clifford sp. nov. (Pl. I, 1, 3, 5, 7, 9; Pl. II, 1-3).

Macadamia seed – Hill et al., 1970 (Pl. Cx X11, fig. 4).

Diagnosis: Seed obovoid, dorsiventrally compressed with slightly raised longitudinal ridges, length 27.2 mm long, width 28.7 mm wide, thickness 20.5 mm, length/thickness ratio 1:3, seed coat mainly formed by exotegmen, 2.0–2.7mm thick, consisting of radially arranged, prismatic cells.

Etymology: *australis* for southern, by implication inferring a southern origin for the species.

Holotype: GSQF11642.

Repository: Geosciences Collection, Queensland Museum, Brisbane, Australia.

Type Locality: Bore PP43, 179–204 feet [= 55–62 m], Portion 695, Parish North Branch, South of Pittsworth, south east Queensland, Australia.

Stratigraphy: Derived from buried alluvial deposits, probably deep leads.

Description. Seed, obovoid, cordate in dorsal view, dorsiventrally compressed, truncate at the micropylar end, tapering to the obtusely acuminate chalazal end; dorsal surface with low (slightly raised) longitudinal ridges; ventral surface with a smooth depression down the centre of the seed. Seed bitegmic, seed coat thick, consists of a poorly preserved outer thin-walled layer (interpreted as endotesta) overlying a thick woody layer (exotegmen), 2.0–2.7 mm thick consisting of regular, radially-arranged, parallel-sided, heavily lignified, narrow (columnar) prismatic cells.

Remarks: Fruit and seed morphology of *Aleurites*, and Euphorbiaceae more generally, has been described and illustrated by various authors (Wichmann, 1880; Gram, 1896; Mandl, 1926; Netoliztky, 1926; Landes, 1946; Wunderlich, 1967; Corner, 1976; Tokuoka and Tobe, 1998, 2002). The fruits in the family are usually capsules, the seeds are bitegmic and often there is evidence of vascular tissue in the outer integument while the inner integument forms the hard mechanical layer of the seed coat.

The fossil is interpreted as being a bitegmic seed comprising an outer thin endotesta and an inner thick woody exotegmen. The fossil has no preserved vasculature, but has a poorly preserved endotesta (derived from outer integument) and a well preserved exotegmen (from inner integument), which forms a protective layer around the embryo (Corner, 1976; Webster, 1994). The arrangement of lignified cells in the exotegmen, is similar in overall appearance to that in extant *Aleurites moluccanus* in being long thin, parallel sided, and radially arranged (pl. II, 1-6). At higher magnification, the cells in modern *A. moluccanus* consist of radially cylindrical cells, the walls of which are composed of helical structures (Fig. 2.6), while in the fossil specimen the seed coat is homogenous and there is no evidence of similarly arranged

structures. It is possible that the palisade cells in the exotegmen in the fossil were indurated with minerals from the ground water, which might obscure the finer structures in the seeds.

Radially-arranged, narrow prismatic cells in the exotegmen are present in many genera in the Euphorbiaceae (Gram, 1896; Mandl, 1926; Netoliztky, 1926; Landes, 1946; Corner, 1976; Tokuoka and Tobe, 1998, 2002). This fossil was initially identified as a *Macadamia* (Proteaceae) seed (Hill et al., 1970), but it differs from *Macadamia*, which has globose or hemispherical seeds, and in that the thick woody testa lacks a prismatic cell structure (Strohschen, 1986; Gross, 1995). In *Aleurites* the seeds are dorsiventrally compressed and broadly obovoid (cordate) in dorsal view, and the exotegmen consists of thick walled, radially arranged, parallel-sided prismatic cells. The fossil closely matches the seeds of modern *Aleurites* in overall appearance and in the structure of the exotegmen but differs in being less strongly furrowed on the dorsal surface, and in being near the lower range of size for the seeds of *Aleurites* (Fig. 2).

Two extant species of *Aleurites* are recognised (Forster, 1996; Stuppy et al., 1999), *A. moluccanus* and *A. rockinghamensis*. Stuppy et al. (1999, p. 78) described the seeds of *Aleurites moluccanus* as “broadly obovoid, dorsiventrally compressed, cordate in dorsal view, truncate or rarely minutely tipped at the micropylar end and always tapering towards the obtusely acuminate chalazal end, while the seeds of *A. rockinghamensis* are subglobose to obovoid, truncate at the micropylar end and obtuse at the chalazal end”. While (Forster 1996) recorded seed length in *A. rockinghamensis* as 20–25 mm, and seed diameter 20–25 mm; *A. moluccanus* was slightly larger, with a seed length of 23–32 mm and seed diameter of 23–32 mm. A sample of *A. moluccanus* seeds from Biak, Cendarawasih Bay (as Geelvink Bay), Western New Guinea showed a range (length: 23.6–30.5 mm, mean 28.1; width: 24.8–30.0 mm, mean 27.9 mm;

height: 21.4–25.1; mean 23.4 mm). A three dimensional scatter plot of these data shows that *Aleurites australis* seed is proportionally smaller than those of the sample studied (Fig. 2). The surface of the modern seeds may be irregularly wrinkled to smooth and may be greyish or brownish in colour but the fossil seed appears to be more dorsiventrally compressed than the extant species, and the wrinkling is less conspicuous.

Aleurites in northern Australia occurs in a range of rainforest communities from dry and semi-deciduous notophyll vine forest to complex mesophyll communities from near sea level to 1000 metres (Atlas of Living Australia.org.au).

5. Discussion

5.1 Archaeological records and historical use of candlenuts in south east Asia and Australia

The oldest previous evidence of fossil candlenuts comes from late Pleistocene archaeological sites (13,000 yrs B.P.) in Indonesia and Timor, South East Asia (Latinis, 2000). There is also evidence from younger sites in New Ireland, New Guinea and the Bismarck Archipelago which demonstrates that the genus *was* widespread throughout the region at this time (Latinis, 2000). Roth (1901, p. 9) recorded, according to the Indigenous people of north eastern Queensland, that the fruits of *Aleurites* were “roasted in a slow fire and when the nut cracked, it was fit to eat”. Archaeological evidence of Aboriginal use of the seeds in Australia is limited, although *Aleurites* nutshells have been collected from a site, MR1, just south of Cairns in the Mulgrave River Valley, north eastern Queensland (Nicky Horsfall, pers. comm. 2016); but she noted that the site was disturbed through quarrying and inverted dates (modern below 240 +/-60 B.P.) were obtained.

Airy Shaw (1966) concluded that the introduction of *Aleurites* to neighbouring areas, including India and Ceylon as well as Melanesia and Polynesia was through its movement by indigenous communities. The kernels of the seeds are recorded as being used as illuminants in Otaheiti, French Polynesia (Miller, 1833). In more recent times the plant has also been introduced to Madagascar and North America, through Europeans trading the fruits and propagating the seed (Fortune Hopkins, 2000). In Australia, because of their horticultural and potential industrial uses, they were available through the Australian Horticultural and Agricultural Society as early as 1859 (*Maitland Mercury and Hunter River General Advertiser*, 17 May 1859) and fruits were being imported for sale into Australia in 1871 (*The Sydney Morning Herald*, 18 September 1871).

Modern *Aleurites* seeds, that were thought to be fossilised, have been lodged in both Herbarium and Museum collections in Australia. The reason for this is that modern drift fruits/seeds of candlenuts (*Aleurites*) become black in colour when immersed in water (Fortune Hopkins, 2000). Fruits/seeds found associated with mining operations in both States of Victoria and New South Wales are black due to immersion in water, and were erroneously interpreted to be fossils. Those lodged in the Museum of Victoria fossil collections were thought to be associated with other fruits/seeds from the Oligocene-Miocene Deep Leads in that State (A. Rozefelds, pers. obs.). Labels on modern fruits of *Aleurites* in the Melbourne Herbarium (MEL) from Newcastle in New South Wales record that they were found with coals, but were recognized as living fruits (e.g. MEL 232491A); i.e. "Embryo of *Aleurites triloba* [= *A. moluccanus*] nuts from the Sydney coal or (mixed?) with the coals; Among coals near Sydney (Newcastle); among Sydney coal, in a perfectly edible state".

5.2 Evidence of *Aleurites* from Paleogene sites in North America

Although originally assigned to *Cucurbita* (Cucurbitaceae) by Brown (1934) fossil leaves from the Eocene Green River Formation in the United States were referred to *Aleurites* based upon minute punctuation distributed over the surface, palmate venation, decurrent vein near leaf base, quadrangular meshes of tertiary venation, and details of areolation (McGinitie, 1969). McGinitie (1969) also suggested that some leaves originally assigned to *Aralia*, by Berry (1930) from the Middle Eocene Tipperary and Kisinger Lakes Floras of the Wild River Basin may also be assignable to *Aleurites*. Referral of these leaves to *Aleurites* was accepted by Graham (1999). Webster (1967) who was working on the systematics of modern Euphorbiaceae genera, however, considered the identifications as unreliable as the assessments were based solely upon gross morphology of leaf remains without detailed reference to venation or cuticular features (Dilcher and Manchester, 1988); moreover, no reproductive material was associated with the leaves. Crepet and Daghljan (1992) also alluded to the unreliability of the Euphorbiaceae fossil leaf record.

There are a large number of genera in the Euphorbiaceae and related families, such as the Malvaceae and Sterculiaceae that have somewhat similar generalised (palmate) leaf shapes and venation (Klucking, 1995, 1997, 2003). The decurrent vein, that McGinitie (1969) drew particular attention to, is a variable feature in *Aleurites* and other genera in the Euphorbiaceae being absent in younger leaves but present in older (palmate) foliage, so its expression can be a factor of both leaf size and hence leaf maturity. In the absence of cuticular and anatomical evidence, or associated reproductive material, leaf morphology must be treated with caution. Webster (1967) also alludes to records of *Aleurites* based upon fossil wood samples, but the authors are unaware if, or where, these records were published.

A phylogenetic analyses of Euphorbiaceae using *rbcl* and *trnL-F* sequence data places *Aleurites* as a weakly supported sister to a subclade with austral genera *Beyeria*, *Baloghia*, *Ricinocarpos* and *Fontainea* (Wurdack et al. 2005; Matamoro-Vidal et al., 2012) which makes referral of the North American fossil leaves to *Aleurites* unlikely, and also suggests, a southern origin for the genus. In a recent description of a new crotonoid genus from Africa, this molecular support linking *Aleurites* to the other Australian genera collapses (Cheek et al., 2016). A robust phylogenetic placement of *Aleurites* will require more complete generic sampling for the tribe along with sequence data that is faster evolving and more informative (Ken Wurdack, pers. comm. 2016),

5.3 Phylogenetic relationships and stratigraphic ranges of Euphorbiaceae and related families pollen types in the Weddellian Biogeographical Province

Pollen of the Euphorbiaceae, including Picrodendraceae and Phyllanthaceae, has been studied by Erdtman (1952); Punt (1962); Köhler (1965); Nowicke (1994); Simpson and Levin (1994); Nowicke et al. (1998, 1999); Takahashi et al. (2000), and Nowicke and Takahashi (2002). These studies have collectively shown great variation and therefore demonstrate the taxonomic significance of pollen morphology in distinguishing various families or subfamilies in Euphorbiaceae (Webster, 2014). There is also a significant, but scattered, literature on dispersed fossil pollen with euphorbiaceous affinities from Cenozoic sediments in Australia, New Zealand and South America. The stratigraphic range and the phylogenetic significance of these records is reviewed below and tabulated in Table 1 and Fig. 3.

Aleurites, and a large group of genera within the Crotonoideae, have inaperturate, spheroidal pollen with an exine sculpture which consists of triangular-rounded structures in

regular arrays, known as “croton (or crotonoid) pattern” (Webster, 2014); and this pollen type is a synapomorphy for this “inaperturate” clade (Nowicke, 1994; Wurdack et al., 2005; Tokuoka, 2007; Matamoro-Vidal et al., 2012). Similar inaperturate pollen are recorded from early Oligocene of Western Australia (Macphail and Stone, 2004), from Late Miocene-Early Pliocene sites in the Murray Basin, southern Australia and have been referred to several informal species of *Crotonipollis* that have been compared with pollen of *Croton* and *Beyeria* (Truswell et al., 1985; Macphail and Truswell, 1993; Macphail, 1996; Macphail and Stone, 2004) (Fig. 3). This pollen type is not restricted to these two genera but occurs in the tribes Aleuritideae, Codieae, Crotoneae, Jatropeae, Ricinocarpeae, and Ricinodendreae, in the Crotonoideae (Wurdack et al. 2005; Webster, 2014).

Other evidence of the Euphorbiaceae in the Weddellian Province includes the tricolporate/tetracolporate *Nyssapollenites endobalteus* (McIntyre) Kemp and Harris, often recorded as *Triporopollenites endobalteus* McIntyre 1973, which has affinities with the subfamily Acalyphoideae, and has been compared to extant pollen of *Macaranga* and *Mallotus* (Martin, 1974; Lee et al., 2010; Conran et al., 2015). Martin (1974) also included *Triorites introlimbatus* McIntyre 1968 here. It appears in the Late Eocene in Australia (Martin, 1974) and *N. endobalteus*, as *Triporopollenites endobalteus*, was recorded from the Oligo-Miocene Morwell and Yallourn Coal Measures of south eastern Australia and Oligocene-Miocene sediments at Little Bay, New South Wales (Blackburn and Sluiter, 1994; Macphail et al., 1994) (Fig. 3). It is recorded from the Paleogene to Neogene sediments in New Zealand (Raine et al., 2011), and dominates some early middle Miocene pollen assemblages in the South Island (Conran et al., 2010) (Fig. 3). In South America, *N. endobalteus* is recorded from Late Oligocene–Early Miocene Chenque Formation (Barreda, 1996, 1997a) and the Oligocene San

Julian Formation, Patagonia (Barreda, 1997b) and has a late Oligocene to Miocene range in Patagonia (Palazzesi and Barreda, 2007) (Fig. 3).

Martin (1974) also recorded *Psilatricolporites operculatus* van der Ham. & Wijmstra from the Murray Basin which was thought to have affinities with *Alchornea* (Germeraad et al., 1968; Palazzesi and Barreda, 2007) in the Acalyphoideae (Fig. 3). Martin (1974) infers an Oligocene–Miocene age for this pollen type in Australia. Palazzesi and Barreda (2007) also indicated a late Oligocene–Early Mid Miocene range for *Psilatricolporites operculatus* van der Ham. & Wijmstra in southern South America (Barreda, 1997a). Barreda et al. (2009) recorded *Psilatricolporites operculatus* from the Paleogene Río Leona Formation, Patagonia.

Luly et al. (1980) recorded *Homalanthus* (as *Omalanthus* complex) subfamily Euphorbioideae pollen from the Miocene, Latrobe Valley Coal Measures (Fig. 3).

Some of the fossil pollen is referred to the Picrodendraceae which in the older literature were cited as Euphorbiaceae, subfamily Oldfieldioideae, or more broadly, Euphorbiaceae. Picrodendraceae is characterised as having mostly echinate and reduced apertures (porate) pollen (Simpson and Levin, 1994), although the spines can be reduced or absent in some taxa. Martin (1974) recorded two distinct pollen types that were compared to genera in the Picrodendraceae. Type 1, which includes the dispersed pollen type, *Polyorificites oblatum* Martin, 1973 (including *Helicoporites astrus* Partridge 1973) is oblate, five to six equatorial pores, thickened annulus has a surface pattern consisting of very fine to granular reticulum, but lacks spines; and was compared to species in extant *Austrobuxus* and *Dissilaria* (Martin, 1974). It is recorded from Oligocene to Miocene sediments in the Murray Basin, Australia (Martin, 1974).

Martin (1974) recognized a second type, that includes a number of species of *Malvacipollis*, which have been compared with pollen of several genera in the Picrodendraceae. The pollen is oblate, echinate with four to nine equatorial pores with a thickened annulus (Martin, 1974). While Martin (1974) recorded differences in both the appearance of the exine stratification and the base of the spines between Malvaceae and Picrodendraceae pollen, she drew attention to a small basal cushion at the base of spines which was absent from the latter family. Simpson and Levin (1994) illustrated the sculpture and pollen structure in Picrodendraceae using transmission and scanning electron microscopy confirming that the radially elongate, sharp tapering spines are continuous with the exine and they considered this character a synapomorphy for the family.

In Australia, *Malvacipollis* has first appearances in the Paleocene (Martin, 1974; Macphail, 1994). While the literature, particularly the biostratigraphic literature in the past, includes references to various dispersed pollen taxa of *Malvacipollis* based on the generalised appearance of the pollen, *Malvacipollis subtilis* Stover in Stover and Partridge 1973 has been compared with the Picrodendraceae (Martin, 1974; Macphail et al., 1994) and some records have been compared with the Malvaceae (Raine et al., 2011). Blackburn and Sluiter (1994) recorded *M. subtilis* pollen from the Oligocene-Miocene Morwell and Yallourn series, and they thought this taxon had affinities with modern *Austrobuxus* sp. aff. *swainii*. However, comparative studies of modern pollen (Simpson and Levin, 1994) indicate that resolution beyond Picrodendraceae, generally, is currently not possible. *Malvacipollis subtilis* has a Paleogene to Neogene range in New Zealand (Raine et al., 2011) and has also been recorded from Eocene sequences in Wilkes Land Margin, Antarctica (Contreras et al., 2013) (Fig. 3).

Malvacipollis diversus Harris emend., Stover and Partridge 1973 was compared with *Austrobuxus*, *Petalostigma* and *Dissilaria* (Martin, 1974) in the Picrodendraceae, but as she indicated this pollen type, which was referred to as the *Tetracoccus* pollen type (sensu Köhler, 1965), occurs in other genera, such as *Tetracoccus*, *Oldfieldia*, *Aristogeitonia*, *Piranhea*, *Mischodon*, *Hyaenanche* and *Richeria* in this family. This dispersed pollen has a Paleogene to Neogene range in New Zealand (Raine et al., 2011) (Fig. 3). It is also recorded from Eocene Estancia Laguna Manantiales, Patagonia and has an Eocene range in southern South America (Zamaloa and Andreis, 1995; Palazzesi and Barreda, 2007). Another species of *Malvacipollis*, *M. spinyspora* (Martin 1973) Mildenhall and Pocknall has been compared with *Micrantheum* (Macphail et al., 1994) or more widely to *Micrantheum* and *Neoroepera* (Martin, 1974, 1994). Both genera are placed in the subtribe Pseudanthinae (Picrodendraceae) (Webster, 2014). It first appeared in the Middle Eocene in Australia (Macphail et al., 2014), and it has a Neogene range in New Zealand (Raine et al., 2011) (Fig. 3).

The phylogenetic affinities of other dispersed pollen taxa that have been compared to the Euphorbiaceae is less clear. *Rhoipites alveolatus* (Couper) Pocknall and Crosbie from Australia and New Zealand have been compared with the pollen from a range of families including the Avicenniaceae (*Avicennia*), Euphorbiaceae (*Excoecaria*, Norfolk Island), Caesalpiniaceae/Verbenaceae (Macphail, 1999); or Euphorbiaceae (El-Ghazaly and Chaudhary, 1993; Mautino and Anzotegui, 2002; Raine et al., 2011). *Rhoipites cienaguensis* (Ducnas) Barreda is thought to have affinities with the Euphorbiaceae (Palazzesi and Barreda, 2007), and it has a Late Oligocene-Early Mid Miocene range in southern South America (Barreda, 1976; Barreda 1977b; Palazzesi and Barreda, 2007). *Rhoipites ampereaformis* Macphail and Truswell from the late Miocene to Recent has been compared with *Amperea* (Euphorbiaceae) but

similarities to pollen of other angiosperm families, e.g. *Avicennia* (Verbenaceae) were also noted (Macphail and Truswell, 1993).

Conclusion

Herein an attempt has been made to place with modern families Australian fossil pollens, albeit with the uncertainty of the affinities of some palynomorphs, and the macrofossil records referred to the Euphorbiaceae and related families (Wurdack et al., 2004, 2005; Matamorovidal *et al.*, 2012; Angiosperm Phylogeny Group IV, 2016). As Martin (1974) pointed out some of pollen assigned to Euphorbiaceae cannot be confirmed without checking the exine stratification. While there is uncertainty about the referral of some *Malvacipollis* spp. to the Picrodendraceae, the family is best developed in Australasia (Webster, 2014) and fossil pollen (Martin, 1974; Macphail et al., 1994; Blackburn and Sluiter, 1994) assigned to this family has a Paleocene through Recent range in Australia (Table 1, Martin 1974; Macphail et al., 1994). This family is absent from the contemporary New Zealand flora but a number of species of *Malvacipollis* are known from Cenozoic sediments where it has a Paleogene-Neogene range (Raine et al., 2011). *Malvacipollis* is also recorded from Eocene sediments in southern South America (Palazzesi and Barreda, 2007). Collectively this data suggests that the family was widespread throughout the Weddellian Biogeographical Province. The affinities of these *Malvacipollis* species, at least in Australia, appear to lie with the Tribe Caletieae (sensu Webster, 2014), which is an austral clade within the Picrodendraceae. *Polyorificites oblatum* Martin, 1973 is known from Eocene-Recent sediments in Australia (Macphail, 1996), but it has not been recorded with certainty from southern South America or New Zealand, although pollen of uncertain affinities from the San Julian Formation, Argentina was questionably compared with *Polyorificites* by Heredia et al. (2012).

Subfamily Acalyphoideae based upon the dispersed pollen type, *Nyssapollenites endobalteus*, has a Late Eocene-Recent range in Australia, and affinities with Acalypheae have been suggested (Lee et al. 2010). Associated macrofossils and pollen from New Zealand link the form genus *Malloranga* for leaves, that were considered to have affinities with *Mallotus* or *Macaranga*, with fruits (*Euphorbiotheca*) and staminate inflorescences with *N. endobalteus* pollen (Lee et al., 2010; Conran et al., 2015). Based upon photos supplied by Jennifer M. Bannister, Nucete et al. (2012) interpreted the staminate inflorescences as having 2-thecate stamens, which indicate affinities to *Mallotus*. This subfamily, based upon pollen data, has a Paleogene-Neogene range in New Zealand, but is no longer represented in their contemporary flora (Raine et al., 2011). *Nyssapollenites endobalteus* has a Late Oligocene to Miocene range in Patagonia, South America (Palazzesi and Barreda, 2007), although older leaf fossils from the Eocene Laguna del Hunco flora in Argentina (Wilf et al., 2007) were compared with *Macaranga/Mallotus*, even though these genera are not represented in the contemporary South American flora (Nucete et al., 2012). The subfamily is also recorded from Late Oligocene sediments in North western Ethiopia plateau, and the material was referred to *Macaranga* (Garcia Massini et al., 2010), a view supported by Nucete et al. (2012), and which is also consistent with the current distribution of this genus.

Inaperturate spheroidal pollen, is considered a synapomorphy for a group within the Crotonoideae and the pollen genus *Crotonipolis* is known from sediments as old as the Oligocene in Australia (Truswell et al., 1985; Macphail, 1996; Macphail and Stone, 2004). Macrofossil evidence in Australia is limited but Rozefelds (1990) described indehiscent fossil fruits *Fontainocarpa*, that he suggested were closely related to modern *Fontainea* (inaperturate crotonoid) from Oligocene-Miocene sediments; its affinities are currently being

re-examined (Rozefelds et al. in prep.). There is no fossil record of this subfamily from New Zealand and records from Cenozoic sites in South America are unsubstantiated (Fig. 3).

Combined analysis of *rbcL* and *trnL-F* sequence data by Wurdack et al. (2005) and Matamoro-Vidal et al. (2012) identified *Aleurites* as the weakly supported sister of a subclade in a largely Australian clade in the “inaperturate” crotonoids consisting of *Baloghia*, *Beyeria*, *Ricinocarpos* and *Fontainea*, although further, more complete generic sampling is needed to confirm these relationships. *Aleurites* has a widespread contemporary and past distribution, based upon archaeological records in south east Asia, and northern Australia. The new fossil evidence, although limited, supports an Australian origin for the genus and indicates that it may have been present in Australia since the Miocene. The extant genus in Australia is restricted to north eastern Queensland, so the new fossil record from south eastern Queensland is outside the modern range of the genus (Fig. 1). Previous museum and herbarium collection records of “fossil” *Aleurites* fruits from more southern fossil deposits in Australia are shown to be modern fruits as the commercial trade in the seeds of the plant was widespread by the 19th century. We accept Webster’s (1967) view that the records of *Aleurites* leaves from North America were not described in sufficient detail to warrant referral to an extant genus or for placement in the Euphorbiaceae.

Seeds of dehiscent fruits often have thickened seed coats. In the Euphorbiaceae most genera have trilocular, capsular fruits, and the thickened seed coat is derived from the exotegmen. It is therefore surprising that even through the seeds of this and related families often have a strongly developed mechanical layer there is so little macrofossil evidence of the family in the fossil record worldwide. This record of *Aleurites* and *Fontainocarpa* are the only fossil Euphorbiaceae fruits, and the only macrofossil evidence of the family to date, from

Australia. Fossil wood from the Canning Basin, Western Australia, of likely Paleogene age, was compared with *Bridelia* (Phyllanthaceae) by Bamford and McLoughlin (2000) but a comparative analysis of the wood characters recognised, using Insidewood (<http://insidewood.lib.ncsu.edu/>), did not support placement in this family. Fossil fruits similar to *Glochidion* from the Miocene, Yallourn Series, Latrobe Valley Coal Measures have also been seen (A. Rozefelds, pers. obs.), and provide possible evidence of the Phyllanthaceae. None of the fossil fruits from the Deep Leads in Victoria (i.e. Mueller, 1879, 1883) appear referable to the family but as some of these taxa remain little studied there is still a need for further assessment of their affinities. Our newly established record of *Aleurites* is therefore significant as it provides additional information on the fossil record of the Crotonoideae in Australia, and it is a significant addition to knowledge of the Euphorbiaceae fossil record internationally.

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Dr Ken Wurdack (Smithsonian Institution) provided both helpful comments on the ms, and insights into the phylogenetic relationships within the crotonoid Euphorbiaceae. Dr Gordon Guymer (Queensland Herbarium BRI) provided access and loans of modern material of Euphorbiaceae for study. Dr Pinna Milne provided information and photographs on specimens in the Herbarium of Victoria. Dr Nicky Horsfall provided advice on the archaeological record of *Aleurites* from north eastern Queensland. Peter Waddington and Geoff Thompson provided detailed photographs of the fossil and modern material. Advice on regional drill bores in the Pittsworth area of Queensland was provided by Ashley Crank, Steve Reynolds and Ian Sobbe. Mark Thornton (Geological Survey of Queensland) provided advice on interpreting the original site data, in terms of current regional mapping of the area, and confirmed that the specimen was likely to have come from a water bore rather than through geological drilling. June

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Plate I. *Aleurites moluccanus* (L.) Willd. modern fruit (1) and seeds (2-6); and fossil seed, *A. australis* (7-12). 1. Section through an immature tri-carpellate fruit of *A. moluccanus* showing axile placentation, and the single seed in each carpel of the fruit. The fruit wall (FW) consists of soft tissues, and the carpel walls (CW) enclose each seed (O), note the linear indentation on the inside carpel which is evidence of a tardily dehiscent, loculicidal suture (S), the seed coat consists of an outer brown layer formed by the testa (T) and an off-white in colour, inner, thicker layer, the exotegmen (Ex) which consists of prismatic cells. Cultivated plant BR1AQ793753. 2. Section through *A. moluccanus* seed, specimen senior author's collection, showing the thick seed coat (exotegmen, Ex) and seed kernel (embryo + endosperm, K). 3. Detail of seed coat showing the exotegmen layer (Ex) consisting of radially-arranged, narrow (columnar) prismatic cells, from 2. Scale bar = 1 mm. 4-5. External views of seed showing the furrowed appearance of the seed coat, with remnants of the endotesta (T) overlying exotegmen. 6. Distal end of seed showing broadly oval outline. 7-8. *Aleurites australis* n. sp. External views of fossil seed (exotegmen) showing the furrowed appearance and the position of the micropyle (M) in GSQF11642. 9. Distal end of seed showing broadly oval outline. 10-11. Broken seed showing distinctive exotegmen (Ex) layer of the seed coat. 12. Detail of seed coat

showing the thick exotegmen (Ex) and well preserved radially-arranged narrow (columnar) prismatic cells. Scale bar = 1 mm. Scale bar = 1 cm, except where otherwise indicated.

Plate II. SEM showing cellular structure of the seed coat (exotegmen) in fossil and living *Aleurites*. 1-3. fossil *Aleurites australis*, 1. Showing the regular arrangement of narrow prismatic cells in the exotegmen. Scale bar = 300 μm . 2. Detail of the arrangement of cells. Scale bar = 500 μm . 3. Detail of cellular structure showing the uniform angled appearance of the cell walls. Scale bar = 50 μm . 4-6. *Aleurites moluccanus*. 4. Showing the regular arrangement of narrow prismatic cells in the exotegmen. Scale bar = 300 μm . 5. Detail of the arrangement of cells. Scale bar = 500 μm . 6. Detail of cellular structure showing the helical thickenings on the cell walls. Scale bar = 50 μm .

Fig. 1. Modern distribution of *Aleurites* in eastern Australia and the fossil locality near Pittsworth is indicated.

Fig. 2. Scatter plot showing the variation in length, width and height of a sample of extant *Aleurites moluccanus* seeds (in blue) from Biak, Cendarawasih Bay (as Geelvink Bay), Western New Guinea and the single seed of the fossil *Aleurites australis* (in red).

Fig. 3. Comparison of the recorded stratigraphic ranges of selected Euphorbiaceae and Picrodendraceae pollen from Australia, New Zealand and South America.

Table 1. Fossil pollen taxa that have been compared with extant pollen of the Euphorbiaceae, Picrodendraceae, and Phyllanthaceae and recorded from Cenozoic sediments in Australia, New Zealand, and southern South America.

Appendix A

Comparative material illustrated: BRIAQ 793753 *Aleurites moluccanus* (L.) Willd. Cultivated tree, Darwin Botanical Gardens, Northern Territory, Coll. A.A. Mitchell 8242, 30 Oct. 2004.

BRIAQ 87682, Biak, Cendarawasih Bay (as Geelvink Bay), Western New Guinea (as Netherlands New Guinea), coll. H. Weygers.

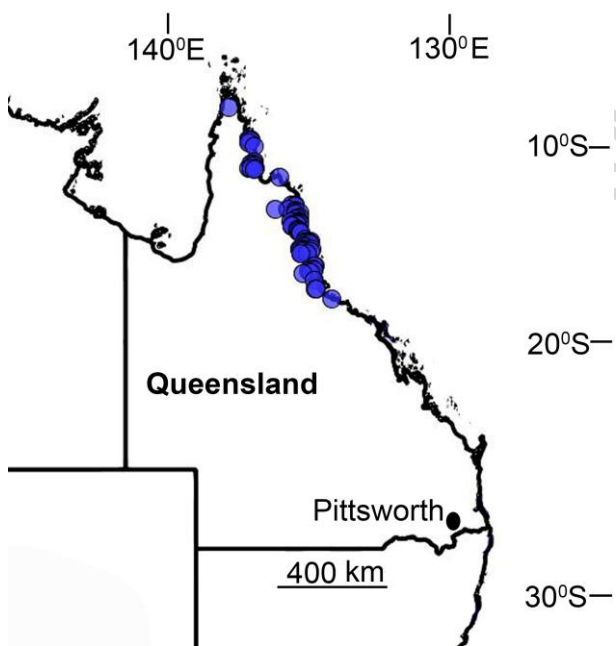


Fig. 1

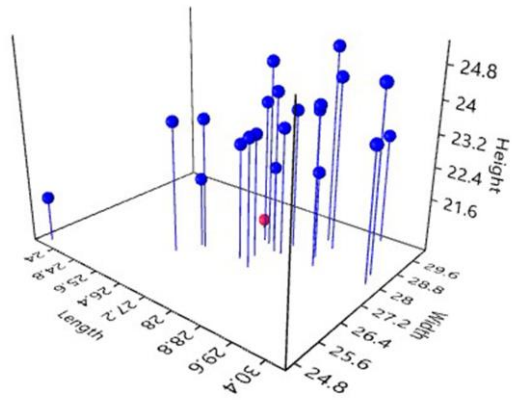


Fig. 2

ACCEPTED MANUSCRIPT

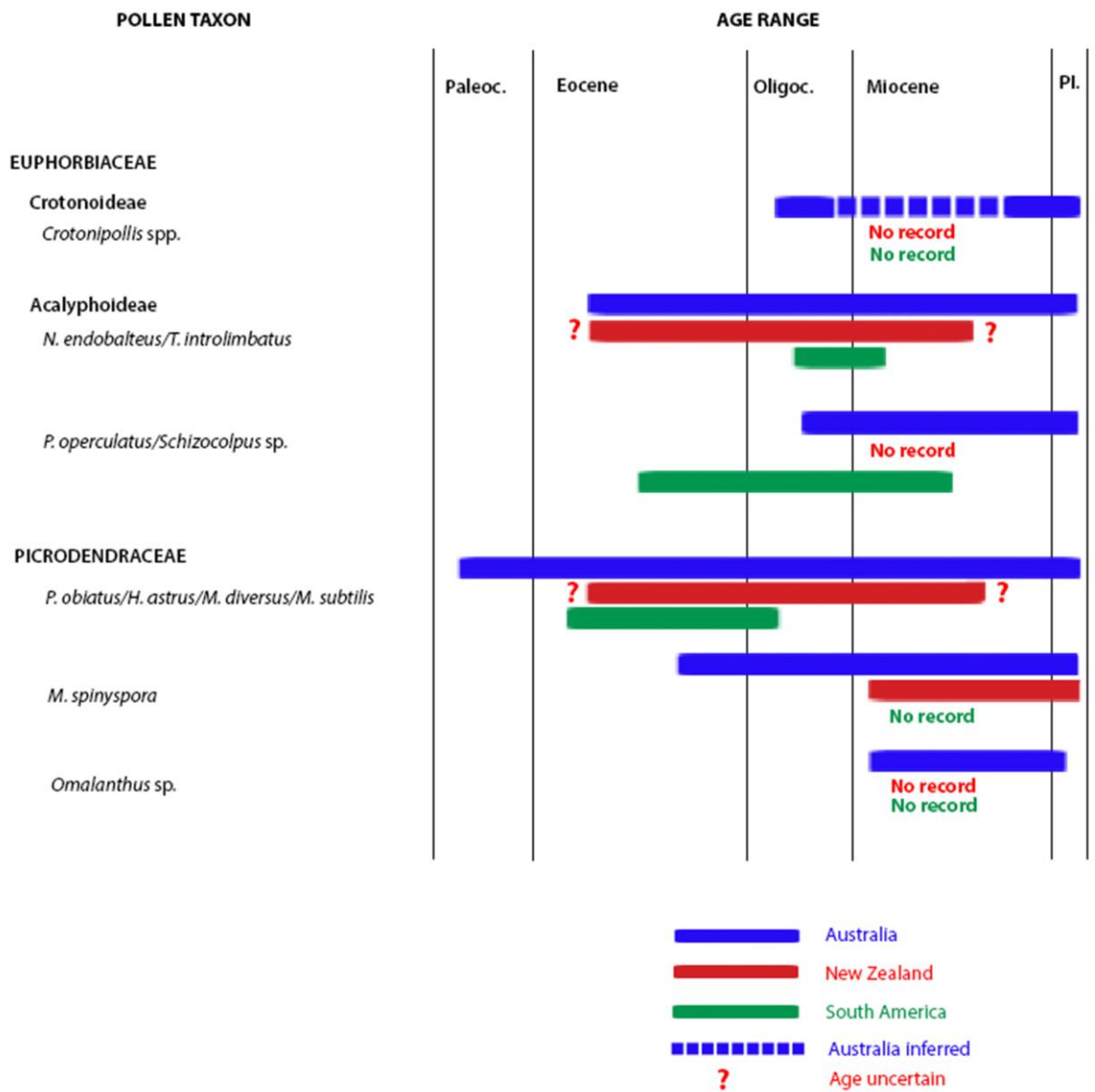


Fig. 3

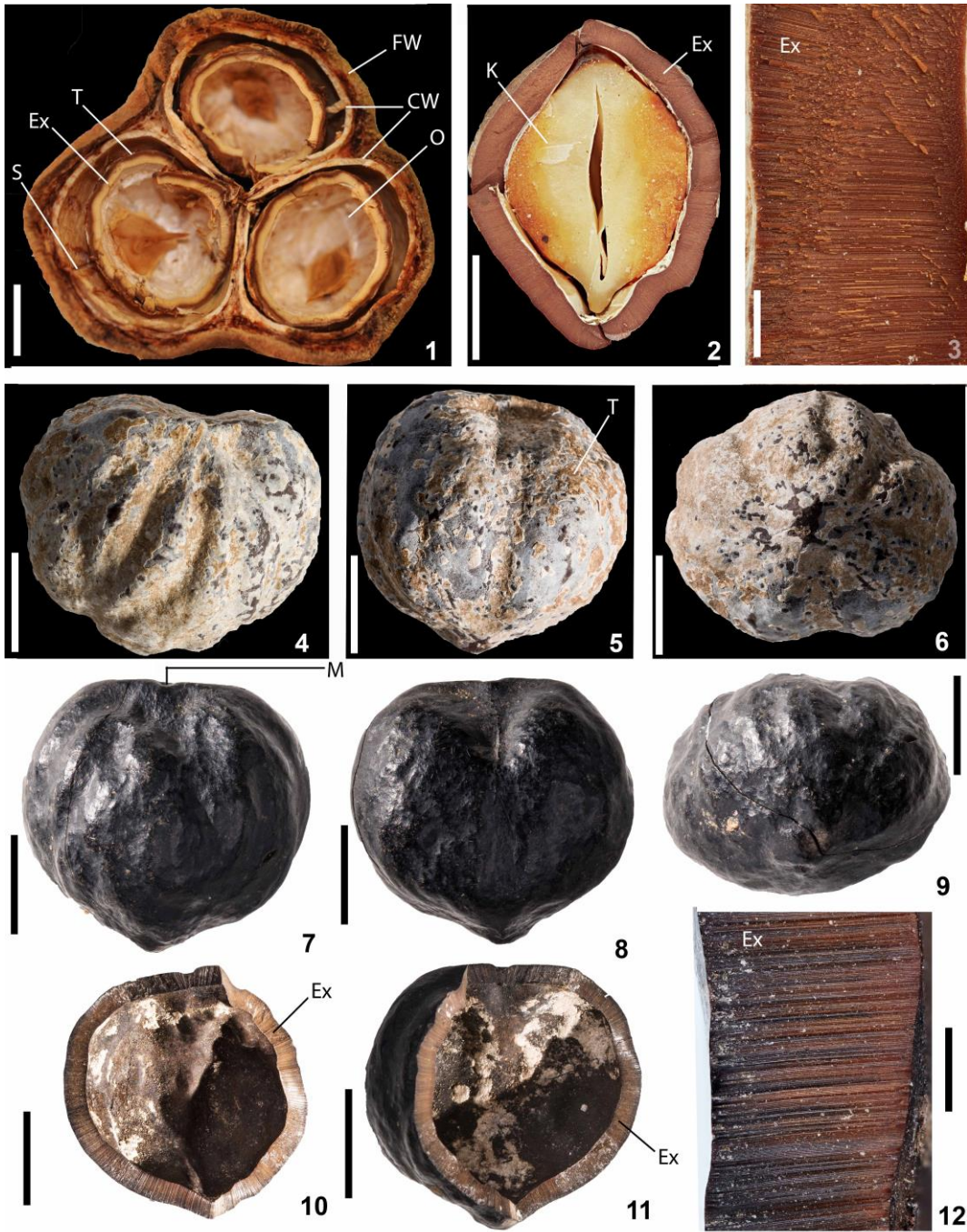


Plate 1

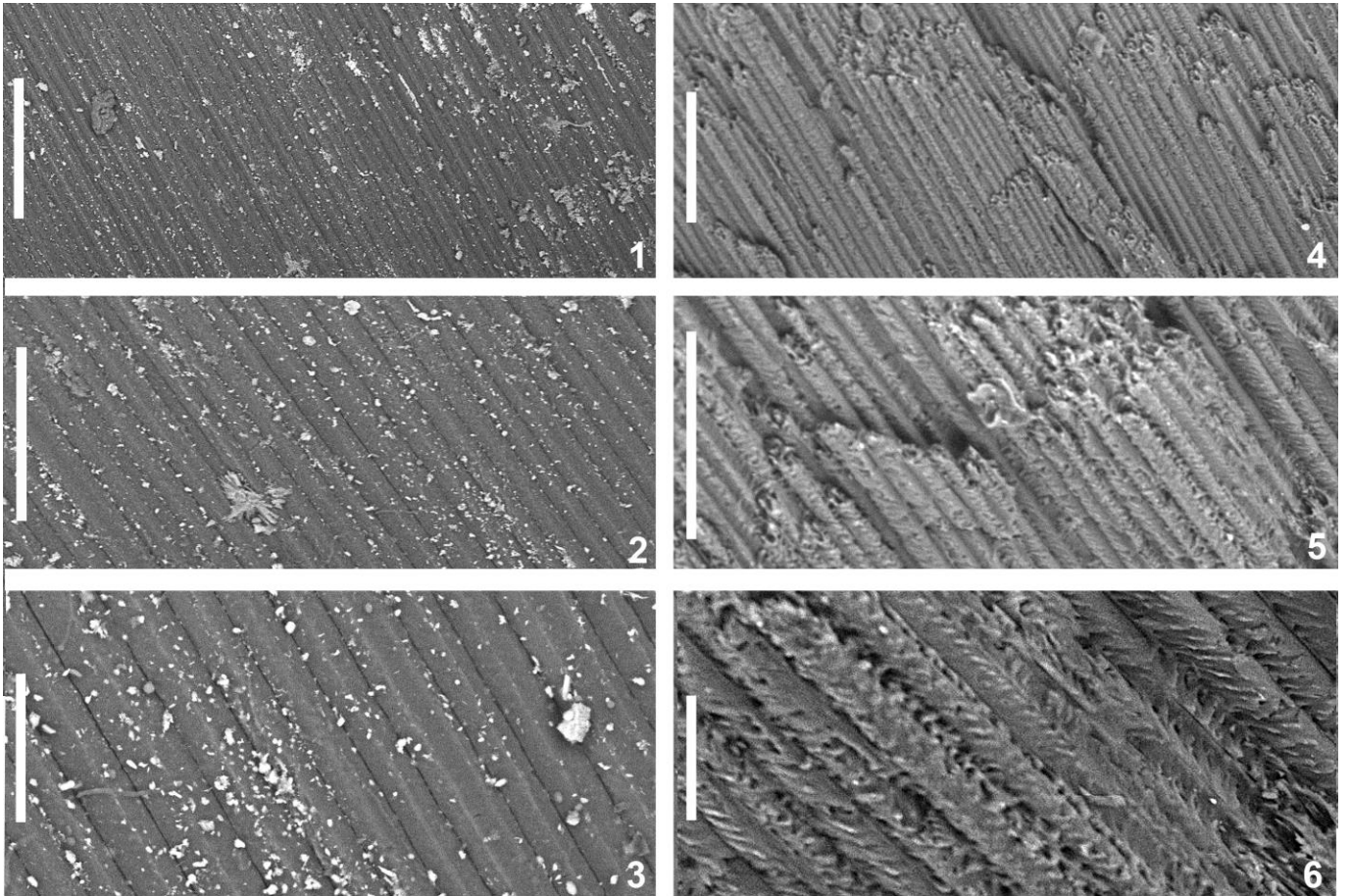


Plate 2

Picrodendraceae	<i>Polyorificites oblatius</i> Martin	Oligocene–Miocene (Murray Basin); Note Macphail (1999) records <i>P. oblatius</i> as unidentified angiosperm In Eocene–Pleistoc. Murray Basin	Paleocene–Neogene Raine et al. (2011)	Eocene Zamaloa and Andreis (1995) Palazzesi and Barreda (2007)
<i>Austrobuxus</i>	<i>Helicoporites astrus</i> Partridge			
<i>Dissiliaria</i>	<i>Malvacipollis diversus</i> (pars) Harris emend. Stover and Partridge 1973 and <i>M. subtilis</i> Stover	Paleocene–Miocene (Murray, Gippsland and Otway Basins)		
<i>Micrantheum</i>			Neogene Raine et al. (2011)	
<i>Neorepera</i>	<i>Malvacipollis spinyspora</i> (Martin) Mildenhall and Pocknall	Middle Eocene–Pleistocene (Murray Basin), Macphail et al. (2014)		

Highlights

- New species of fossil *Aleurites* described
- Previous records of *Aleurites* leaf fossils from USA dismissed
- The oldest fossil of *Aleurites* is from Australia
- Fossil record of Euphorbiaceae in the Southern Hemisphere reviewed
- Fossil pollen record of Picrodendraceae in the Southern Hemisphere examined