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Agathis (Araucariaceae) macrofossils from Cainozoic sediments in south-eastern Australia

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Abstract. Organically preserved Cainozoic leaf fossils previously referred to *Agathis* are re-examined, and in all cases their affinity with that genus is confirmed. Previously undescribed organically preserved leaf fossils from several Cainozoic sites in south-eastern Australia are compared with *Agathis* and *Wollemia* and two new species of *Agathis* are described. Intraspecific variation in leaf cuticle morphology is examined in extant *A. macrophylla* in particular, and is found to be much higher than previously recorded. This makes assignment of fossil *Agathis* leaves to species difficult, especially when only leaf fragments are available. The new fossils extend the record of organically preserved *Agathis* macro-remains back to the Late Paleocene, but do not significantly extend the known spatial distribution.

Introduction

The Araucariaceae are an ancient family, with a bi-hemispheric macrofossil record stretching back to the Jurassic (Stockey 1994) and a pollen record extending to the Late Triassic (Kershaw and Wagstaff 2001). There are three living genera, *Agathis*, *Araucaria* and *Wollemia. Araucaria* has the most extensive macrofossil record, both spatially and temporally (Hill and Brodribb 1999), and is very common in the Australian Cainozoic. *Wollemia* has yet to be formally identified in the macrofossil record, although Chambers *et al*. (1998) drew attention to several Cretaceous fossils that may be close relatives to the single extant species and are possibly congeneric with it. The *Agathis* macrofossil record is difficult to interpret, since many descriptions of this genus in the fossil record rely on negative evidence such as the lack of an ovuliferous scale tip or 'ligule' on compression fossils of ovuliferous cones or isolated cone scales (Stockey 1982). Leaf fossils of *Agathis* are more easily identified, in part because *Agathis* leaves are constricted into a petiolate base and have Florin rings around their stomata, whereas the leaves of *Araucaria* and *Wollemia* have broad attachment to the stem and Florin rings that are poorly developed or absent entirely. *Agathis* is characterised by having stomata that are predominantly transverse or oblique to the long axis of the leaf, whereas in similarly broad-leaved *Araucaria* species they are mostly parallel (Cookson and Duigan 1951; Bigwood and Hill 1985). The extinct genus, *Araucarioides*, described by Bigwood and Hill (1985) and revised by Hill and Bigwood (1987) and Pole (1995), encompasses clearly araucarian, multi-veined strap-like leaves with stomatal orientation similar to that in *Agathis*. However, apart from their lack of Florin rings, recently recovered specimens of *Araucarioides* from near the type locality show that these leaves had a broad attachment at the base and an acute, sharply pointed apex (R. J. Carpenter, G. J. Jordan and R. S. Hill, unpubl. data), and so there is little possibility that fossils of this genus could be confused with *Agathis*.

The reliable macrofossil record of *Agathis* is confined to its extant distribution, the Australasian region. Hill and Brodribb (1999) listed six published species of *Agathis* that are based on leaf fossils and warrant consideration here (Table 1). The oldest species is *Agathis victoriensis*, described from Early Cretaceous sediments in southern Victoria by Cantrill (1992). This species has no preserved organic material on the leaf and Hill and Brodribb (1999) considered the generic identity to be doubtful. Cantrill (1992) observed that the leaves appeared petiolate, and are hypostomatic or nearly so, with stomata in rows. The stomata had left casts in the matrix, and from these Cantrill was able to determine that the stomata were variously oriented and that they were raised on the leaf surface 'perhaps forming Florin rings'. Thus, it is possible that these fossils represent a species of *Agathis*, although most extant *Agathis* species do not have raised stomata to form Florin rings, but have the Florin ring submerged into the leaf surface. With no internal cuticular detail preserved, this generic identification remains doubtful. Other doubtful records of *Agathis* were also discussed by Hill and Brodribb (1999) and will not be considered here. Organically preserved *Agathis* leaves have been recorded from across southern Australia in Eocene to Miocene sediments. Recently, Lee *et al*. (2007) reviewed the macrofossil record of *Agathis* in New Zealand. They concluded that all records before their

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Table 1. Fossil records of *Agathis* leaves in the southern hemisphere

Modified from Hill and Brodribb (1999). All fossils are from Australia unless stated otherwise. Names applied by Daniel (1989) are excluded because they have not been formally described and the identities have been questioned by Lee *et al*. (2007)

Species	Locality	Age
Agathis berwickensis Pole, R.S.Hill, Green & Macphail, Pole *et al*. (1993)	Berwick Quarry	Late Oligocene–earliest early Miocene
[A]*A. brevigongylodes* R.S.Hill, T.Lewis, R.J.Carp. & S.S.Whang	Cethana, Lea River, Pioneer	Early Oligocene–early Miocene
A. kendrickii R.S.Hill & Merrifield, Hill and Merrifield (1993)	West Dale	Middle Eocene–Oligocene
A. parwanensis Cookson & Duigan, Cookson and Duigan (1951)	Bacchus Marsh	Oligocene?
A. tasmanica R.S.Hill & Bigwood, Hill and Bigwood (1987)	Cethana, Little Rapid River	Early Oligocene
A. victoriensis Cantrill, Cantrill (1992)	Otway Basin	Early Cretaceous
[A]*A. vittatus* R.S.Hill, T.Lewis, R.J.Carp. & S.S.Whang	Cethana, Lake Bungarby	Late Paleocene–early Oligocene
A. yallournensis Cookson & Duigan, Cookson and Duigan (1951), Blackburn (1985)	Yallourn	Oligocene–Miocene
	Morwell	Oligocene–Miocene
Agathis species, Scriven (1993)	Maslin Bay	Middle Eocene
Agathis species, Carpenter and Pole (1995)	Lefroy and Cowan Palaeodrainages	Middle Eocene
Agathis species, Carpenter *et al*. (2004)	Hotham Heights	Early Eocene
Agathis sp. aff. A. Australia (D.Don) Lindl., Lee *et al*. (2007)	Newvale Mine, New Zealand	Late Oligocene–early Miocene

[A]New species described here.

description of late Oligocene–early Miocene leaves were equivocal, including organically preserved middle Cretaceous leaves published by Daniel (1989), but so far not formally described. Currently, the oldest reliable record is that of leaf fragments in the early Eocene Hotham Heights assemblage (Carpenter *et al*. 2004). Cone scales that are consistent with *Agathis* first occur (as impressions only) in late Eocene sediments in northern New South Wales (Hill 1995).

Most published records of fossil *Agathis* leaves predate the discovery of the extant *Wollemia nobilis* (Jones *et al*. 1995). Although most fossil records are of clearly petiolate leaves, they still warrant comparison with *W. nobilis*, especially at the level of cuticular morphology. Furthermore, several fossil leaves have been discovered over the past few years where the basal part of the leaf has not been preserved, and since both *Agathis* and *Wollemia* typically exhibit rounded or blunt leaf apices, identification relies mostly on the detail of cuticular morphology. The aim of this study is to re-assess the previously published species of organically preserved *Agathis* leaves from south-eastern Australia, and to determine the affinities of several previously undescribed leaf fossils that are clearly araucarian, and resemble *Agathis* and *Wollemia* in general leaf morphology.

Material and methods

Some previously described leaf fossils have been well illustrated with scanning electron micrographs of the cuticles to determine their generic affinities. These illustrations were available, along with many other photographs that have not been previously published. A list of these fossil species and their localities is provided (Table 1 and Fig. 1, respectively). New fossils that can be assigned to the Araucariaceae, but not to *Araucaria*, were recorded from four fossil localities in Tasmania and from one on mainland south-eastern Australia. The details of these sites are as follows:

(1) Lake Bungarby. The fossils were found in sub-basaltic sediments at Lake Bungarby (39°06′S, 149°08′E, at least 400 m asl) in south-eastern New South Wales. Taylor *et al*. (1990) assigned the palynoflora to the Upper *Lygistepollenites balmei* Zone of Stover and Partridge (1973), which encompasses the late Paleocene.

(2) Cethana. The fossils were found in siltstone sediments near the Cethana Dam, Tasmania (41°32′S, 146°07′E, 300 m asl). The sediments unconformably overlie Ordovician quartzose Moina Sandstone. The palynoflora has been assigned to the early Oligocene by Macphail *et al*. (1994). The presence of *Cyatheacidites annulatus* provides a confident *Proteacidites tuberculatus* Zone (Stover and Partridge 1973) maximum age, but the upper age limits are less certain owing to possible diachronism in the times of extinction of accessory species such as *Beaupreadites verrucosus*, *Granodiporites nebulosus* and *Triporopollenites ambiguus*.

(3) Lea River. The fossil-bearing sediments occur in a single large cliff, within rainforest, on the southern edge of the Lea River in north-western Tasmania (41°30′S, 145°39′E, 670 m asl). Conifer fossils are abundant in siltstone in the lower portion of the exposure and as loose blocks near the water line. The palynoflora has been assigned to the early Oligocene by Macphail *et al*. (1994), by using the same interpretation as for Cethana.

(4) Pioneer. The fossils were found in siltstone in small cut-off channels in an alluvial fan extending from granite uplands in north-eastern Tasmania (41°05′S, 145°14′E, 90 m asl). K-Ar dating fixes the upper age limit at about the early–middle Miocene boundary, although the palynoflora may be as old as late Oligocene (Hill and Macphail 1983; Macphail *et al*. 1994).

Specimens from Lake Bungarby and Cethana are compressions on the bedding planes of the sediment. They are too fragmentary to be removed complete from the sediment surface, but small pieces of leaf can be removed for cuticular preparation. Specimens from Lea River and Pioneer were removed from the sediment by soaking large blocks in warm,

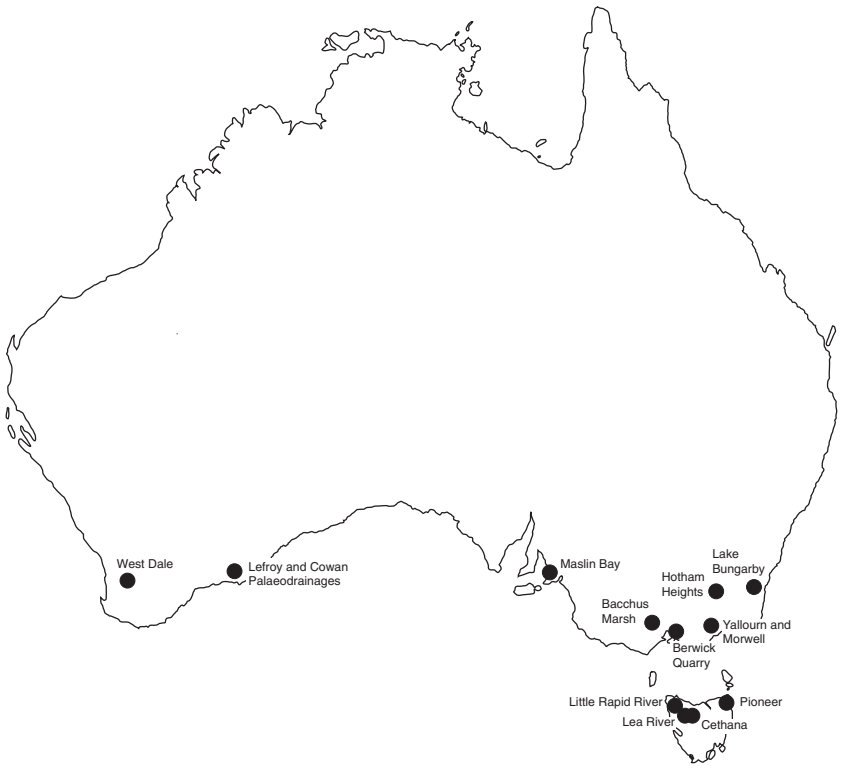


Fig. 1. Map of Australia showing all previously published organically preserved *Agathis* macrofossil locations and the sites containing the new fossil species described in the text.

dilute hydrogen peroxide. This disaggregated the sediment, and the resultant slurry was sieved through a 350-μm mesh and the retained organic fragments were sorted for recognisable plant parts.

Fossil leaves and leaf fragments were photographed with an Olympus DP11 digital camera mounted on a Zeiss Stemi 2000C microscope. Cuticles were prepared by soaking the fossils in 50% W/W hydrofluoric acid overnight to dissolve any adhering siliceous particles. Leaf fragments were then soaked in 10% aqueous chromium trioxide until all organic components except the cuticle had dissolved. The cuticles were rinsed in water and soaked briefly in 5% aqueous ammonia. Cuticles were then attached to aluminium stubs with double-sided adhesive and coated with a gold-carbon mix. They were examined with a Philips XL20 scanning electron microscope operated at 10 kV. Some cuticles were stained with aqueous safranin O and mounted on microscope slides in phenol glycerine jelly for light microscope examination. Cuticles from leaves of living *Agathis* species and *Wollemia nobilis* (Table 2) were prepared from squares of leaf cut from the margin half way along the leaf length. They were prepared in the same way as the fossils except that 20% aqueous chromium trioxide was used in the first step. Leaves of living *Agathis* species were present in the extant species collection held at the School of Earth and Environmental Sciences, University of Adelaide, and were allocated specimen numbers in that collection from E/3001 to E/3010. This was augmented by leaves from 10 different specimens of *A. macrophylla* from the New South Wales Herbarium (NSW) and five leaves (collected at different heights) from each of two living trees of *A. robusta* growing in the Adelaide Botanic Gardens. A leaf each of juvenile and adult *W. nobilis* was supplied by Ken Hill (NSW).

Results and discussion

Extant species

The cuticular micromorphology of extant *Agathis* leaves has been described in detail by Page (1980) and Stockey and Atkinson (1993) and that of *Wollemia nobilis* by Chambers *et al*. (1998), with further comments by Burrows and Bullock (1999). Stockey and Atkinson (1993) characterised the cuticle of *Agathis* leaves as having distinct Florin rings (these are unusual in often being sunken into the general leaf surface) and an undulating surface (Fig. 2). Stomata are sunken to the level of the hypodermis and are usually in discontinuous rows (Figs 3–5). Four subsidiary cells are common, although five are only slightly less so, and the range in number is three to nine. Nearly all *Agathis* species show bilobed polar extensions with two small knobs of cuticle present when the extensions are complete (Fig. 4), but these are often missing (Fig. 5), and so their absence cannot be used to exclude a fossil from *Agathis*. These polar knobs mark the position where the pair of guard cells terminate at each end of the stomatal apparatus. Most species show a deep cleft in the subsidiary cell cuticle where the cell extended to the surface of the leaf (Figs 4, 5), corresponding to the Florin ring externally (Fig. 2).

Chambers *et al*. (1998) noted that adult *W. nobilis* leaves have a smooth surface and lack Florin rings, although this is probably

Table 2. Percentage of stomata at varying angles to the long axis of the leaf in extant *Agathis* species and adult *Wollemia nobilis*
Each row represents a single specimen, except where otherwise noted

Specimen	0–30°	31–60°	61–90°
Agathis atropurpurea	45[A]	33	22
	62[B]	20	18
Agathis australis	74[A]	17	9
	42[B]	24	34
Agathis borneensis	21[B]	30	49
Agathis corbassonii	37[A]	27	36
	8[B]	12	80
	52[C]	34	14
Agathis endertii	58[B]	29	13
Agathis flavescens	9[B]	25	66
Agathis kinabaluensis	12[B]	16	72
Agathis labillardieri	3[B]	22	75
Agathis lanceolata	16[A]	23	61
	3[B]	42	55
Agathis lenticula	18[B]	22	60
Agathis macrophylla	0[A]	25	75
	2[B]	14	84
	1.8 (0–4.5)[D]	12.8 (4.5–22.0)	85.4 (74.0–92.6)
Agathis microstachya	10[A]	28	62
	11[B]	60	29
Agathis montana	16[A]	26	58
Agathis moorei	18[A]	42	40
	9[B]	37	54
	3[C]	27	70
Agathis orbicula	16[B]	23	61
Agathis ovata	7[A]	18	75
	29[B]	35	36
	22[C]	22	56
Agathis philippinensis	4[B]	31	65
Agathis robusta	4[A]	19	77
	9[B]	29	62
	6.8 (0–11.5)[D]	19.2 (5.4–36.2)	74.0 (59.5–91.9)
Agathis silbai	0[B]	8	92
Agathis spathulata	22[B]	43	35
Wollemia nobilis	79[C]	18	3

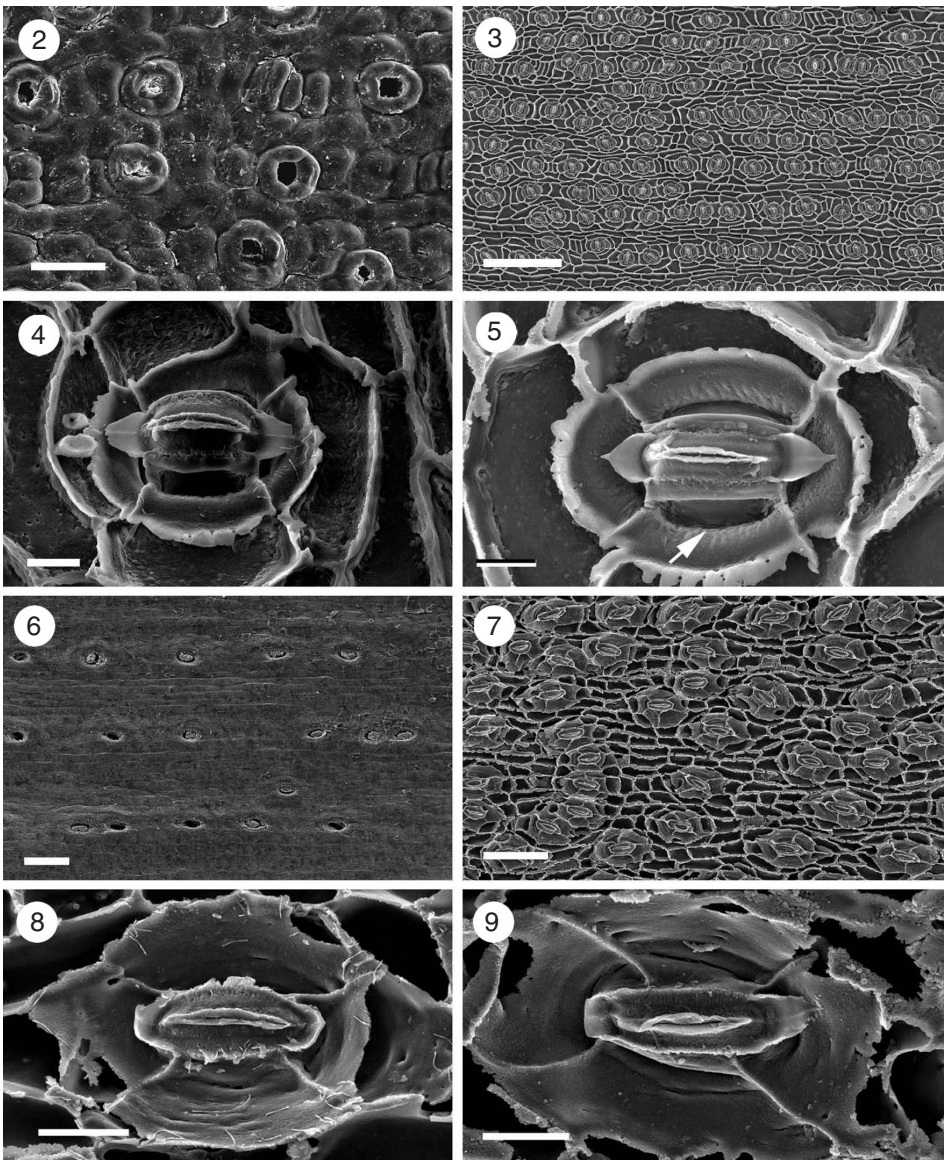
[A]Bigwood and Hill (1985).
[B]Values recorded from photos in Stockey and Atkinson (1993).
[C]The present study.
[D]Ten specimens, showing the mean value with the range in parentheses.

better characterised as extremely poorly developed Florin rings (Fig. 6). Stomata are sunken to the level of the hypodermis and are in very discontinuous rows (Figs 7–9). According to Chambers *et al*. (1998) six subsidiary cells is most common, but as few as four were recorded. On our specimen, four or five subsidiary cells are much more common than six, and this was also recorded by Burrows and Bullock (1999), so this may be variable among specimens. Chambers *et al*. (1998) also noted that the subsidiary cells are deeply sunken below the rest of the epidermis and that they partly obscure a group of epidermal cells that are level with the general epidermis, giving the appearance of a cycle, or part cycle of accessory subsidiary cells. The illustrations provided by Chambers *et al*. (1998) and new preparations for this study demonstrate that the cuticle separating the subsidiary cells from these epidermal cells is often not complete, leading to a ragged appearance and sometimes a clear view of the epidermal cells (Figs 8, 9). This is quite distinct from the appearance of subsidiary cells in *Agathis* (Figs 4, 5). The cuticle of adult *W. nobilis* also lacks the bilobed polar extensions of the guard cells that are present in most *Agathis* species (Figs 8, 9 cf. Fig. 4).

In all *Agathis* species, the stomata are aligned relatively obliquely to the long axis of the leaf (Cookson and Duigan 1951; Bigwood and Hill 1985). This differs from the stomatal orientation of *W. nobilis*, where Chambers *et al*. (1998) noted that stomata of adult leaves were predominantly parallel to the leaf axis. In our study, 79% of *W. nobilis* stomata deviate by $\leq 30°$ from parallel (Table 2). The orientation of stomata relative to the long axis of the leaf does, however, appear to vary from plant to plant and in different leaves from the one plant, including in adult *v.* juvenile leaves (Chambers *et al*. 1998; Burrows and Bullock 1999). Similarly, our study shows that variability exists among extant *Agathis* species and specimens (Table 2). Among the 10 *A. macrophylla* and *A. robusta* specimens collected for this study, stomatal orientation was quite uniform, and measurements made previously, or measurements taken from earlier illustrations were consistent with these multiple measurements. However, intraspecific variation is not always so small. *Agathis corbassonii* is particularly variable, but other species also vary considerably (Table 2). The significance of this is uncertain, since it is impossible to check the identification of some of the specimens used in earlier studies and, hence, the possibility that they were misidentified cannot be dismissed.

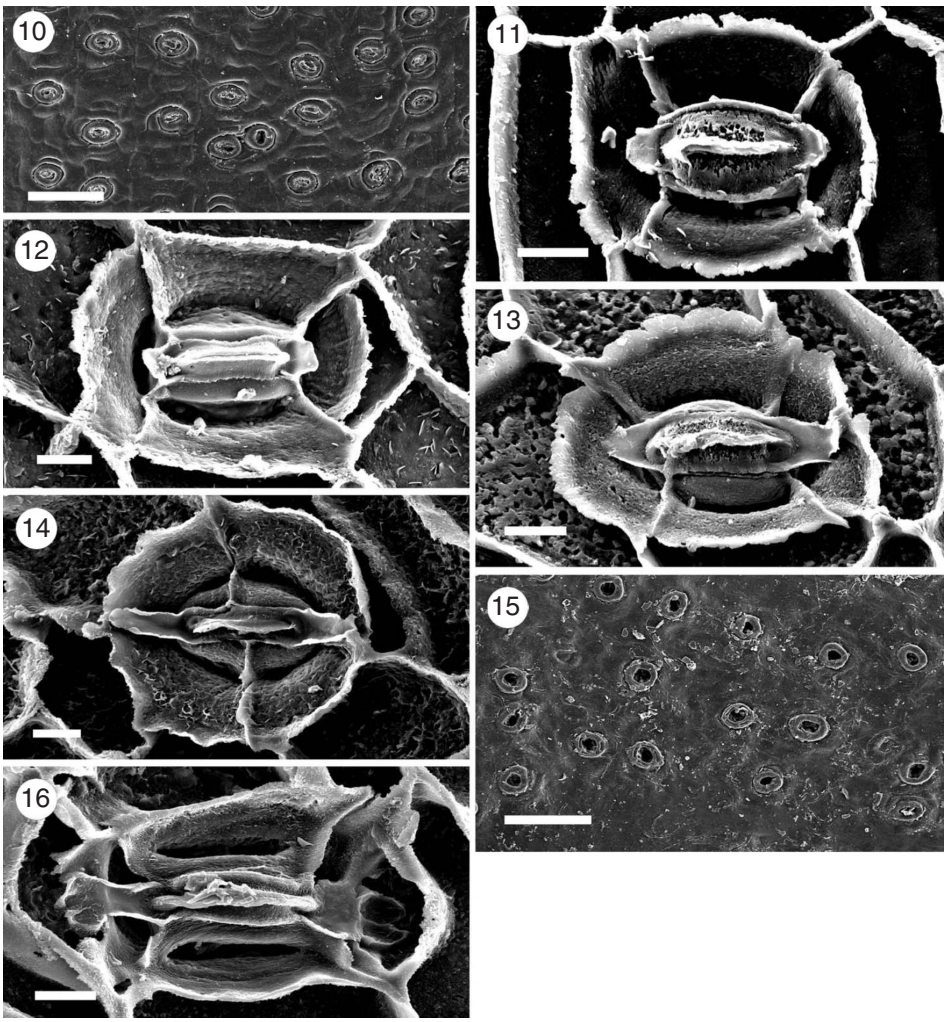
Thus, on the basis of leaf and cuticle morphology of the Araucariaceae, *Agathis* and *Wollemia* can be separated from *Araucaria* by a combination of multi-veined leaves with stomata at oblique angles to the long axis of the leaf and a blunt leaf apex. Furthermore, *Agathis* can be separated from *Wollemia* in the possession of the following character states: petiolate leaves, distinct Florin rings embedded into the leaf surface, bilobed polar extensions of the guard cells with two small knobs of cuticle present when the extensions are complete, and complete cuticular layers between the subsidiary cells and the underlying epidermal cells (as viewed from the interior surface of the cuticle). However, not all extant *Agathis* species uniformly bear these character states.

Very little is known about intraspecific variability in some of the cuticular micromorphological characters that have been used to separate leaves of *Agathis* from *Wollemia* and to differentiate species within *Agathis*. The most exhaustive leaf cuticular study of *Agathis*, by Stockey and Atkinson (1993), included all known extant species, but the majority were represented by only one specimen. In an attempt to determine the extent of intraspecific variability in cuticular micromorphology in *Agathis* leaves, leaves from 10 separate specimens of *A. macrophylla* (herbarium collections) were examined. While these demonstrated that some of the characters listed by Stockey and Atkinson (1993) were relatively invariant, many were not. For example, Stockey and Atkinson (1993) noted that in *A. macrophylla* the external cuticle surfaces are very undulating, with outlines of underlying epidermal cells clearly visible. This was not the case for the specimens examined here, which displayed only



Figs 2–9. Scanning electron micrographs (SEMs) of the cuticle of extant *Agathis* species. **Fig. 2.** The outer leaf surface of *A. corbassonii* (Specimen No. E/3001), showing the well developed but sunken Florin rings around the stomatal openings and the undulate leaf surface. Scale bar = 50 µm. **Fig. 3.** The inner surface of an *A. moorei* leaf (Specimen No. E/3002), showing the stomata in rows parallel to the long axis of the leaf. Most individual stoma are oriented oblique to the long axis of the leaf. Scale bar = 200 µm. **Figs 4, 5.** The inner surface of an *A. moorei* leaf (Specimen No. E/3003), showing single stoma. In Fig. 4, note the pair of polar knobs to the left of the stoma, which are the positions of the poles of the guard cells. These knobs are just beyond the boundary of the subsidiary cells and are largely missing from the right-hand side. In Fig. 5, there are no polar knobs preserved. Note the continuous covering of cuticle over the subsidiary cells. There are epidermal cells situated beneath these cells (towards the surface of the leaf, and hence overlying). The arrow shows the position of the deep cleft in the subsidiary cell cuticle, corresponding to the position of the Florin ring. Scale bars = 10 µm. **Figs 6–9.** SEMs of the cuticle of extant adult *Wollemia nobilis* (Specimen No. E/3004). **Fig. 6.** The outer surface showing the weak development of Florin rings and the relatively flat leaf surface. Scale bar = 100 µm. **Fig. 7.** The inner surface, showing stomata loosely aligned with the long axis of the leaf. Scale bar = 100 µm. **Figs 8, 9.** The inner surface showing single stoma. Note the absence of polar knobs of cuticle where the guard cells terminate and the ragged appearance of the cuticular layer between the subsidiary cells and the overlying epidermal cells. Scale bars = 20 µm.

minor undulations (Fig. 10). They also noted that occasionally a Florin ring will be plugged with cuticular material, but in some of our specimens almost every Florin ring is plugged (Fig. 10). Stockey and Atkinson (1993) provided a very detailed description of the inner cuticular surface of the stomatal apparatus, but in fact this is highly variable and is difficult to characterise at levels of fine detail. The four specimens of *A. macrophylla* illustrated (Figs 11–14) are well within the



Figs 10–16. Scanning electron micrographs (SEMs) of the cuticle of leaves of *Agathis macrophylla* provided by the NSW Herbarium. **Fig. 10.** The outer surface of Specimen No. E/3005, showing well developed Florin rings embedded in the surface and a moderately undulate surface. Scale bar = 100 µm. **Figs 11–14.** The inner surface showing a single stoma in four different specimens (Specimen Nos E/3006–3009, respectively). Note the variation in guard-cell morphology and cell-surface pitting in particular. Scale bars = 10 µm. **Figs 15, 16.** SEMs of the cuticle of a leaf of *A. robusta* (Specimen No. E/3010). **Fig. 15.** The outer surface showing well developed Florin rings embedded in the leaf surface and a relatively smooth surface. Scale bar = 10 µm. **Fig. 16.** The inner surface showing a single stoma. Note the well developed pairs of polar knobs at each end of the stoma, which are the positions of the poles of the guard cells. These seem to be positioned within the boundary of the subsidiary cells, but the preservation makes that difficult to determine with certainty. Scale bar = 10 µm.

range of what was observed, but quite distinct from each other in many details (cf. the descriptions and illustrations of Stockey and Atkinson 1993). The other species with multiple specimens available for this study was *A. robusta*, where five leaves were collected from different heights on each of two living trees to determine the amount of variation in cuticular micromorphology within individual trees. The specimen of *A. robusta* examined by Stockey and Atkinson (1993) differs considerably from the specimens examined here, particularly in having aborted stomata, lobed Florin rings, and marking of the outer cuticular surface with epidermal cell outlines (cf. Fig. 15). However, the inner cuticular morphology of the stomatal apparatus, while quite fragile in preservation, is relatively uniform in morphology within individuals (Fig. 16), and demonstrates little of the variation observed in *A. macrophylla*. This leads to the following four possible conclusions:

(1) There is much more variation in cuticular micromorphology within *Agathis* species than has been previously recognised.
(2) *A. macrophylla* is unusual in having highly variable cuticular micromorphology.
(3) Herbarium specimens of *Agathis* are difficult to identify reliably, and the 10 specimens of *A. macrophylla* available for this study may represent more than one species.
(4) *Agathis* has distinct juvenile and adult foliage and some of the variation observed may be due to an unidentified mixture of these two leaf forms in the collection. This could be tested by further examination of living specimens in their natural habitat.

Previously described fossil species

Agathis berwickensis was described by Pole *et al*. (1993) from late Oligocene–earliest early Miocene sediments at Berwick Quarry in southern Victoria. One specimen consists of a nearly complete leaf that appears to constrict into a petiole at the basal end (fig. 20 in Pole *et al*. 1993). The cuticle is relatively poorly preserved, but Florin rings of the *Agathis* type are clearly present (fig. 3 in Pole *et al*. 1993). The inner cuticular surface is poorly preserved and no diagnostic characters can be observed. However, the presence of a petiole and Florin rings means that this fossil species can confidently be assigned to *Agathis*, although the poor cuticular preservation limits comparison with other fossil and living species.

Agathis kendrickii was described by Hill and Merrifield (1993) from middle Eocene–Oligocene sediments at West Dale in south-western Australia. Preservation at this site is unusual, and while surface detail of the leaves is often excellent, the inner cuticular surface cannot be observed. The leaves taper towards the base, but no complete leaf bases have been observed and so it is not certain whether or not the leaves are petiolate. Stomata occur in loosely defined rows between the veins and have random orientation. The stomata have Florin rings of the *Agathis* type (fig. 2*D* in Hill and Merrifield 1993) and an undulating leaf surface. The presence of these characters means that this fossil species can be confidently assigned to *Agathis*, but the lack of inner cuticular morphology limits comparison with other fossil and living species.

Agathis tasmanica was described by Hill and Bigwood (1987) from early Oligocene sediments at Little Rapid River in north-western Tasmania. Leaves of this species are abundant and many are complete, demonstrating the presence of a petiole (fig. 4*A*–*C*, *E*, *F* in Hill and Bigwood 1987). The cuticle is not well preserved on these leaves, but Florin rings of the *Agathis* type are obvious (fig. 4*G*, *H* in Hill and Bigwood 1987), and on the inner cuticular surface the guard cells have bilobed polar extensions with two small knobs of cuticle present (fig. 4*J* in Hill and Bigwood 1987). These polar knobs sit on, or just outside the outer boundary of the subsidiary cells (cf. Fig. 4 here). There is no doubt that these fossils represent a species of *Agathis*. Further cuticular preparations were attempted during the present study, but no improvement in cuticular preservation was observed.

Agathis yallournensis was described by Cookson and Duigan (1951) from the Latrobe Valley coal in south-eastern Victoria. This species ranges through the Oligocene and Miocene (Blackburn 1985). The leaves are relatively common and petiolate (figs 29 and 32 in Cookson and Duigan 1951). The cuticle is well preserved, and examination by scanning electron microscopy (not available to Cookson and Duigan) demonstrated the presence of Florin rings of the *Agathis* type (Figs 17, 18), and a typical undulating surface. On the inner cuticular surface, there is a relatively complete coverage of cuticle between the subsidiary cells and the underlying epidermal cells (Fig. 19). One of the stomatal complexes appears to have guard cells with bilobed polar extensions with two small knobs of cuticle present (one still present, the other having been dislodged, Fig. 20). This polar knob occurs inside the margin of the subsidiary cells. There is no doubt that these fossils represent a species of *Agathis*.

Agathis parwanensis was described by Cookson and Duigan (1951) from probable Oligocene (redated as early Miocene by Holdgate and Gallagher (2003)) brown coals at Bacchus Marsh near Melbourne. This species is only known from leaf fragments with multiple parallel veins, so the overall leaf size and shape is uncertain. Scanning electron micrographs of the cuticle demonstrate probable Florin rings of the *Agathis* type, although even the best example has apparently collapsed (Fig. 21). More importantly, the inner cuticular surface is well preserved and some of the guard cells have prominent bilobed polar extensions with two small knobs of cuticle present, on or outside the outer margins of the subsidiary cells (Fig. 22). Where preserved, there is a relatively complete coverage of cuticle between the subsidiary cells and the underlying epidermal cells (Fig. 22). There is no doubt that these fossils represent a species of *Agathis*.

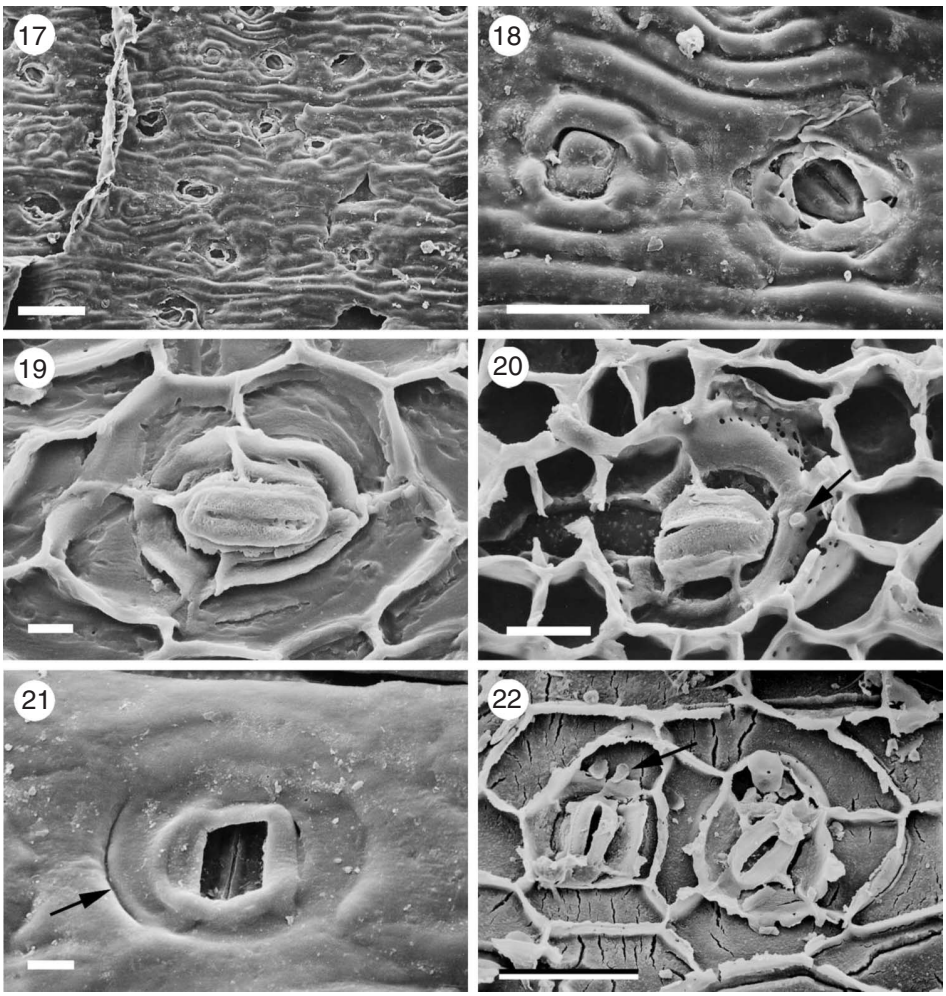
Agathis has also been previously reported as dispersed leaf fragments and cuticular remains from Eocene sites in Western Australia (Carpenter and Pole 1995) and Victoria (Carpenter *et al*. 2004). Although there is no doubt that this material represents *Agathis*, the fossils were considered too limited or poorly preserved for adequate assessment in the present study.

New fossil specimens

Complete and fragmentary araucarian leaves that are multi-veined and petiolate were recovered from Cethana. A few fragments of araucarian leaves were recovered from Lake Bungarby, Pioneer and Lea River. These leaf fragments are recognisably araucarian because they have multiple, parallel veins, and possess large, individually sunken stomata within rows, with the individual stoma usually oblique to the long axis of the leaf. The subsidiary cell number varies usually between four and six in all specimens, with four being the most common number.

Lake Bungarby

Two specimens were recovered from the Lake Bungarby sediments. One of these specimens (LB-197 and its counterpart LB-198) is relatively long and narrow and tapers asymmetrically towards one end. It is uncertain whether this is the base or the apex of the leaf, although compared with other fossil and living Araucariaceae taxa, it is more likely to be an apex (Fig. 23). The leaf fragment is relatively small compared with extant *Agathis* leaves. The outer surface of the leaf is poorly preserved and it is difficult to determine whether Florin rings are present, although there are some indications that they may be. The inner cuticular surface is very well preserved. One obvious feature of this surface is that stomata are not in clear rows (Figs 24, 25), but are in bands more or less between the veins. The guard cells sometimes have prominent bilobed polar extensions with two small knobs of cuticle present inside the outer boundary of the subsidiary cells (Fig. 26 cf. Fig. 27). There is also a relatively complete coverage of cuticle between the subsidiary cells and the underlying epidermal cells (Figs 26, 27). These characters in combination confirm that this fossil can be assigned to *Agathis*, although the lack of stomatal rows and the elongate and tapering, asymmetrical leaf apex (or, less likely, base) are not typical features of the genus.



Figs 17–22. Scanning electron micrographs (SEMs) of the cuticle of *Agathis yallournensis*. **Fig. 17.** The outer surface showing the well developed but sunken Florin rings around the stomatal openings and the undulate leaf surface (Museum of Victoria Specimen No. P15266). Scale bar = 100 µm. **Fig. 18.** Close up of part of Fig. 17, showing two stomatal openings. The one on the left has a stomatal plug still in place. Scale bar = 50 µm. **Figs 19, 20.** The inner surface of P15266 showing a single stoma. A single polar knob is present on the right-hand side of the stoma in Fig. 20 (arrowed), within the boundary of the subsidiary cells, but otherwise they are absent. Scale bars = 10 µm (Fig. 19) and 25 µm (Fig. 20). **Figs 21, 22.** SEMs of the cuticle of *A. parwanensis* (Museum of Victoria Specimen No. P15272). **Fig. 21.** The outer surface showing a single stoma. A sunken Florin ring was present here, but it has partially collapsed. The arrow shows the crease where the Florin ring has sunken. Scale bar = 10 µm. **Fig. 22.** The inner surface showing two stomata. A pair of polar knobs are present at the top of the stoma on the left (arrowed), on the outer edge of the subsidiary cell cuticle. Scale bar = 50 µm.

The second specimen from Lake Bungarby (LB-156) is missing both the base and apex (Fig. 28) and it is uncertain whether it tapers like the specimen shown in Fig. 23. This leaf fragment is also relatively small compared with extant *Agathis* leaves. The outer surface of this leaf is quite poorly preserved, but Florin rings of the *Agathis* type are present (Fig. 29). The inner cuticular surface is very well preserved, showing that the stomata are in better defined rows than for the other Lake Bungarby specimen (Fig. 30 cf. Figs 24, 25). This is probably an artefact of vein density, since only one row of stomata can fit between veins in this specimen. The general stomatal morphology is very similar to the first specimen (Fig. 31 cf. Figs 26, 27), except that the two small knobs of cuticle that characterise the bilobed polar extensions of the guard cells have not been observed. The stomatal orientations of the two specimens are very different (Table 3) and although this might be expected if the cuticle of one specimen came from part of the leaf where veins are crowded, thus forcing the stomata into a longitudinal alignment, the trend here is the opposite to this (LB-156 has many more stomata aligned obliquely to the long axis of the leaf but has no leaf base or apex preserved to contribute cuticle). The difference in stomatal orientation, in combination with differences in development of stomatal rows, suggests these two specimens may represent different taxa, but the similar small leaf size, asymmetrical shape and the very similar stomatal morphology support the conclusion that they are conspecific. However, it must be acknowledged that there is great morphological variation in some characters within this taxon. Further collections from

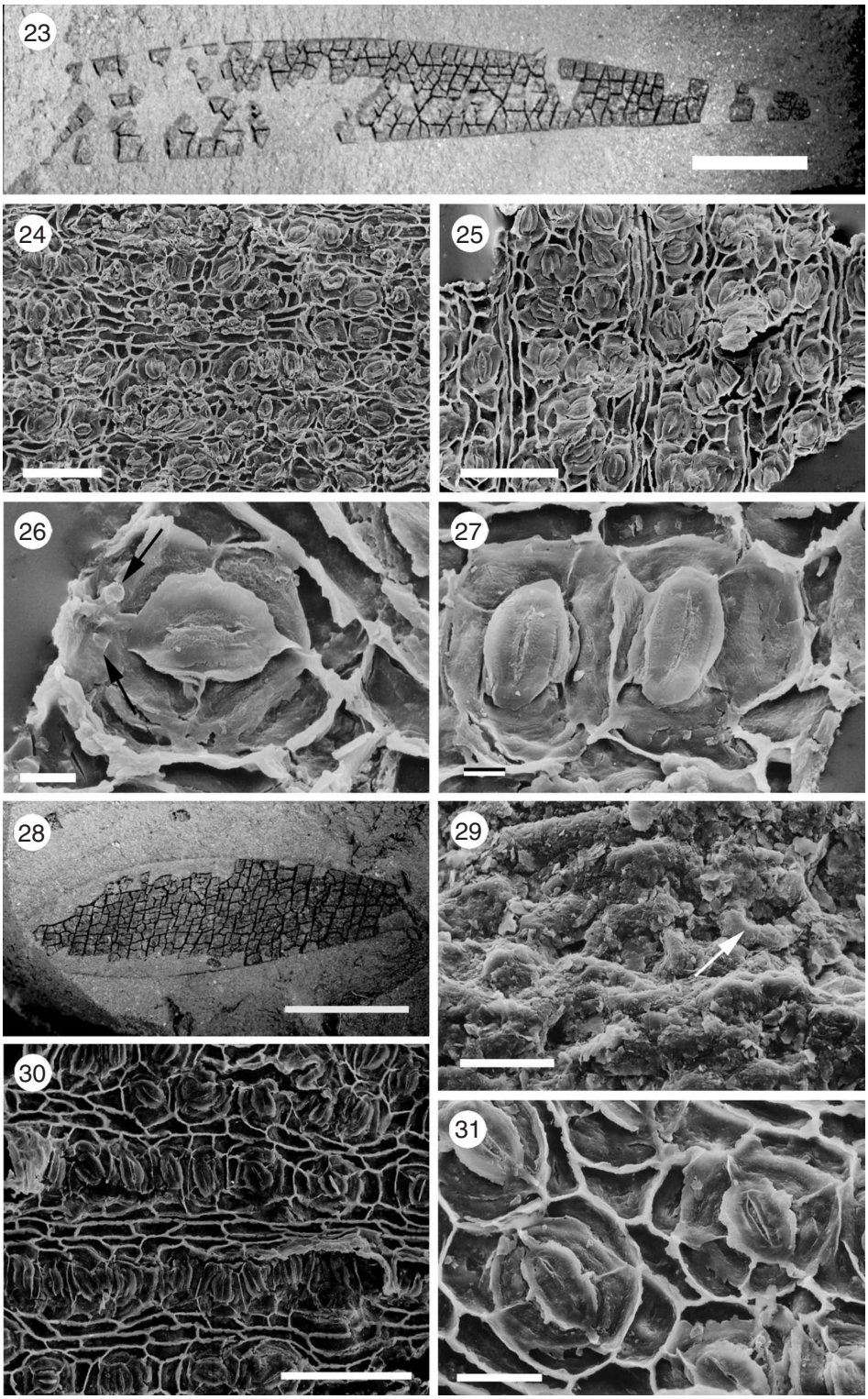

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Table 3. Cuticular details for fossil *Agathis* specimens
*small sample—values considered unreliable

Specimen	Stomatal alignment (%)			No. of stomata examined
	0–30°	31–60°	61–90°	
Agathis parwanensis[A]	0	11	89	*
A. tasmanica[B]	13	45	42	*
A. yallournensis[A]	12	19	69	*
C-478	54	36	10	90
C-489	13	25	62	180
C-534	4	8	88	70
C-468	43	32	25	138
C-491	44	36	20	114
C-484	24	39	37	68
C-622	14	30	56	50
LB-156	14	33	53	63
LB-197/8	52	28	20	90
P-707	29	47	24	34
P-710	14	25	61	28
P-709	13	21	66	70
Lea-2299	58	29	13	52

[A]Bigwood and Hill (1985). [B]Hill and Bigwood (1987).

Lake Bungarby may resolve the magnitude of this variation. It is also possible that new collections may demonstrate that this taxon represents an extinct araucarian genus, since some of the characters displayed are very unusual for *Agathis*.

Cethana

Carpenter (1991) reported *Agathis* leaf fossils from the Cethana sediments, but the number of species present was uncertain. One complete leaf is petiolate, with an acuminate apex, and is 43 mm long and 15 mm wide (Fig. 32). There are ~15 parallel veins, and stomata occur between these veins. The outer surface is not well preserved and Florin rings are present but indistinct. Stomata are widely separated from each other (Fig. 33), but only small cuticle fragments are preserved and so it is impossible to extrapolate this to more general stomatal density and distribution over the whole leaf surface. The guard cells sometimes have prominent bilobed polar extensions with two small knobs of cuticle present on, or just outside the outer boundary of the subsidiary cells (Fig. 34), but preservation is not good enough to be certain of the coverage of cuticle between subsidiary cells and underlying epidermal cells. Nevertheless, this specimen can clearly be assigned to *Agathis*, and is distinct front the Lake Bungarby species.

A second, more fragmentary specimen has an undulating leaf surface and Florin rings of the *Agathis* type are well developed (Figs 35, 36). Stomata occur on what is probably the abaxial surface in discontinuous rows (Fig. 37). Many stomatal complexes have prominent bilobed polar extensions of the guard cells that are present well within the outer boundary of the subsidiary cells (Fig. 38), and complete coverage of cuticle between subsidiary and underlying epidermal cells. This specimen has distinctly different stomatal orientation, placement of the bilobed polar extensions, and higher stomatal density than the first specimen and is regarded here as a separate species of *Agathis* at Cethana. This species is also distinct from the Lake Bungarby species.

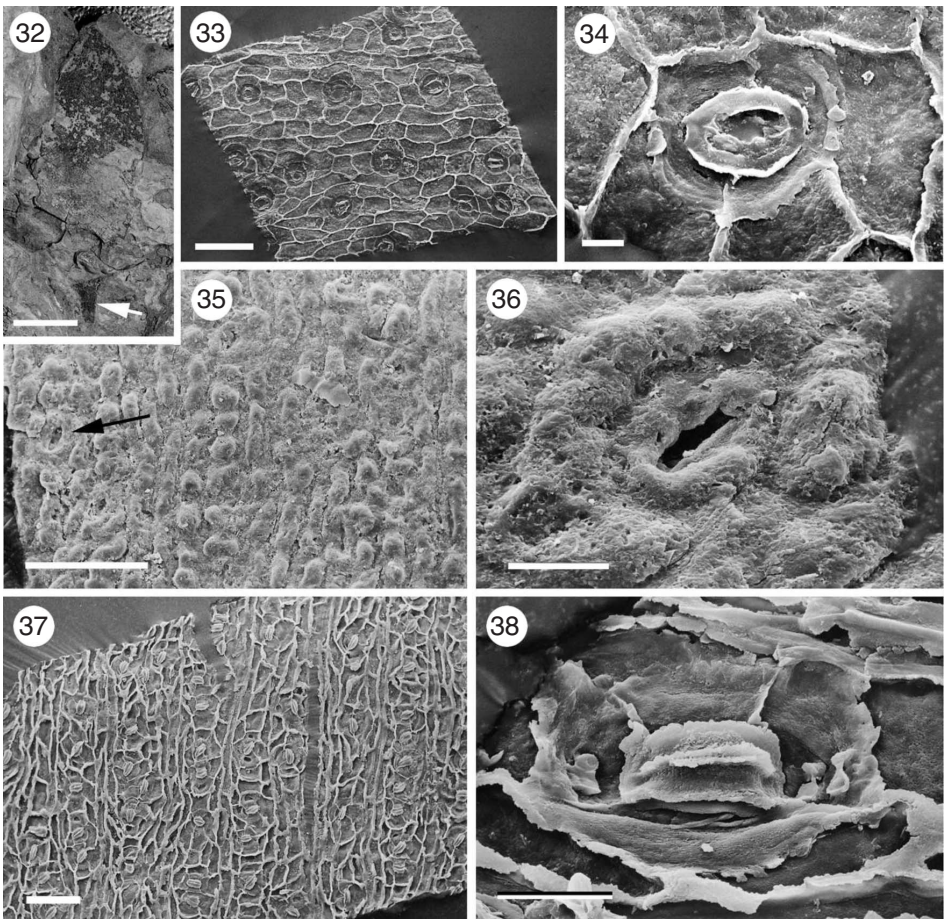
A third specimen is of a linear leaf, tapering asymmetrically, probably towards the apex and ~8 mm at its widest point (Fig. 39). About 10 parallel veins are visible. The leaf surface is undulating and Florin rings of the *Agathis* type are well developed (Fig. 40). There are a few stomata on one (adaxial?) surface, but most occur on the other (abaxial?) surface in discontinuous rows (Fig. 41). The prominent bilobed polar extensions of the guard cells have not been observed on this specimen, but there is a well developed coverage of cuticle between the subsidiary cells and overlying epidermal cells (Fig. 42). Similar stomatal morphology has been observed on other specimens (e.g. Fig. 43). These specimens can also be clearly assigned to *Agathis*, although to a third species at Cethana because of the absence of the bilobed polar knobs and a distinct stomatal orientation (Table 3). This specimen is considered to be conspecific with the Lake Bungarby species.

Three other less complete specimens were recovered from Cethana and all have enough characters preserved to be sure that they belong to *Agathis*, and they can each be assigned to one of the three species described above. In addition to leaves, cone scales conforming to *Agathis* also occur at Cethana (Carpenter 1991; fig. 12.3c in Carpenter *et al*. 1994).

Pioneer

Four specimens that could be compared with *Agathis* and *Wollemia* were recovered from the Pioneer sediments. All specimens are leaf fragments, but all are multiple and parallel veined (Figs 44, 45) and bear stomata in discontinuous rows with individual stomata at oblique angles to the long axis of the leaf. They have Florin rings of the *Agathis* type, although they are

Figs 23–31. *Agathis vittatus* sp. nov. from Lake Bungarby. **Fig. 23.** LB-197 (holotype), showing the complete, tapering leaf. The apex is probably towards the right, but this is uncertain. Scale bar = 5 mm. **Figs 24, 25.** Scanning electron micrographs (SEMs) of the inner cuticular surface of LB-198, showing the obliquely oriented stomata that are not in rows, but in broad bands (in Fig. 24, the long axis of the leaf runs left to right, in Fig. 25, it runs from top to bottom). Scale bars = 100 μm. **Fig. 26.** SEM of the inner cuticular surface of LB-198, showing a single stoma. Note the well developed pair of polar knobs at the left hand end of the stoma (arrowed), which are the positions of the poles of the guard cells. These polar knobs are probably within the boundary of the subsidiary cells. The covering of cuticle over the subsidiary cells is not continuous, but this is probably an artefact of preservation (cf. Fig. 27). Scale bar = 10 μm. **Fig. 27.** SEM of the inner cuticular surface of LB-197 showing two stomata. Polar knobs are absent from these stomata, but the cuticle covering the subsidiary cells is complete as in extant *Agathis*. Scale bar = 10 μm. **Figs 28–31.** *A. vittatus* from Lake Bungarby (LB-156). **Fig. 28.** The leaf fragment with both base and apex missing. Scale bar = 1 cm. **Fig. 29.** SEM of the outer cuticular surface, showing a well developed Florin ring embedded in the surface (arrow) and the undulate surface. Scale bar = 25 μm. **Fig. 30.** SEM of the inner cuticular surface, showing the obliquely oriented stomata in rows. It is difficult to determine whether the epidermal cell bands between these rows represent closely spaced veins or files of interveinal epidermal cells. Scale bar = 100 μm. **Fig. 31.** SEM of the inner cuticular surface showing several stomata. Pairs of polar knobs appear to be absent, although several fragments that could be interpreted this way are present. The cuticle covering the subsidiary cells is complete as in extant *Agathis*. Scale bar = 25 μm.

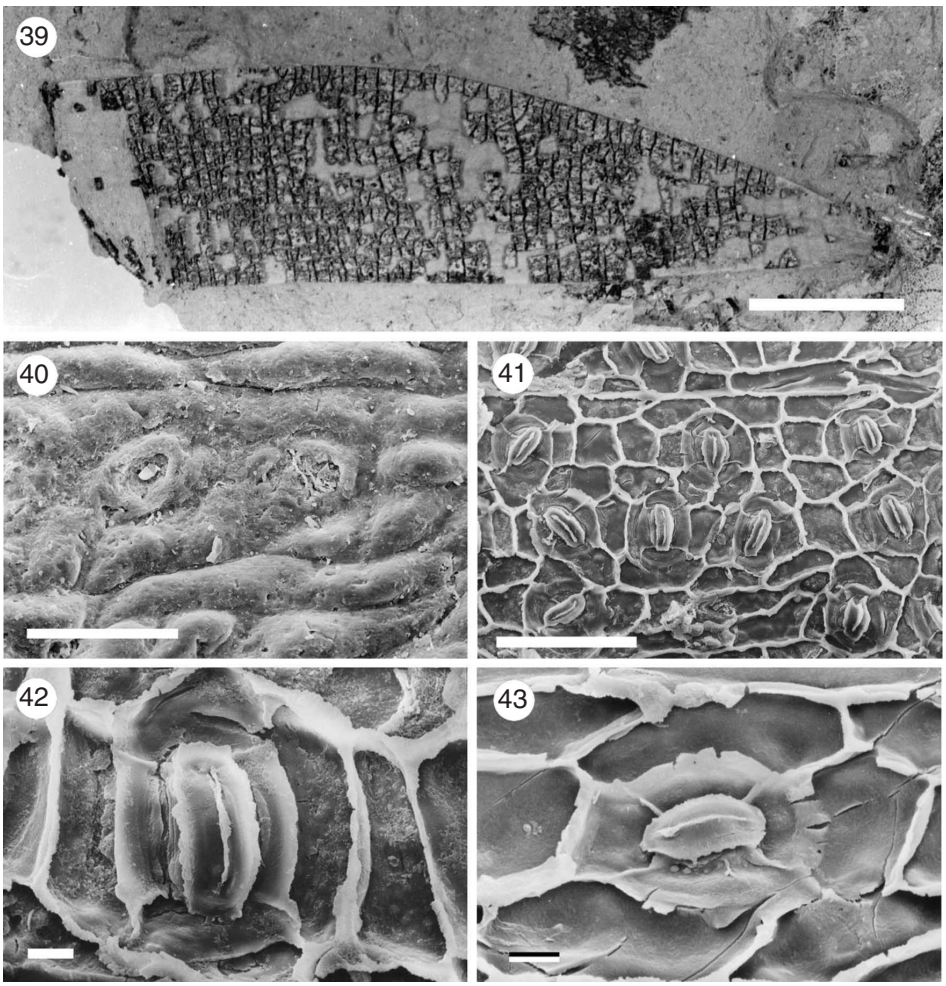


Figs 32–38. *Agathis tasmanica* from Cethana (C-478). **Fig. 32.** The whole leaf, with the petiole at the base (arrowed). Part of the middle of the leaf has not been preserved, but the apex is in place. Scale bar = 1 cm. **Fig. 33**. Scanning electron micrograph (SEM) of the inner cuticular surface, showing sparse stomata, more or less in rows. Scale bar = 100 µm. **Fig. 34.** SEM of the inner cuticular surface showing a single, poorly preserved stoma. A pair of well developed polar knobs are present on the right-hand side of the stoma and one is present on the left-hand side. These are positioned on the outer margin of the subsidiary cell cuticle. Scale bar = 10 µm. **Figs 35–38.** *A. brevigongylodes* sp. nov. from Cethana (C-491). **Fig. 35.** SEM of the outer cuticular surface, showing the well developed but sunken Florin rings (one arrowed) around the stomatal openings and the undulate leaf surface. Scale bar = 100 µm. **Fig. 36.** SEM of the outer cuticular surface, showing a single stomatal opening with a well developed but sunken Florin ring. Scale bar = 25 µm. **Fig. 37.** SEM of the inner cuticular surface, showing the obliquely oriented stomata arranged in rows. The long axis of the leaf runs from top to bottom. Scale bar = 100 µm. **Fig. 38.** SEM of the inner cuticular surface, showing a single stoma with a pair of well developed polar knobs at each end, well within the boundary of the subsidiary cells. The covering of cuticle over the subsidiary cells is complete as in extant *Agathis*. Away from the stoma, the cuticle extends partially between the epidermal and hypodermal cells. Scale bar = 25 µm.

not strongly developed (Fig. 46). On the inner cuticular surface, the guard cells have prominent bilobed polar extensions with two small knobs of cuticle present, well inside the subsidiary cell boundary (Figs 47–49), although in other cases they extend to the boundary. There is also a relatively complete coverage of cuticle between the subsidiary cells and the underlying epidermal cells (Figs 48, 49). The cuticle between the epidermal cells extends over the hypodermis (Fig. 50), sometimes completely enclosing the epidermal cells. There is no doubt that these specimens belong to *Agathis*, and can be assigned to a single species, which is conspecific with one of the Cethana species.

Lea River

A single leaf fragment has been recovered from the Lea River sediments. The fragment includes the blunt leaf apex and several parallel veins (Fig. 51). Florin rings may be present on the outer leaf surface, but are very poorly developed or absent in most cases, and the surface is slightly undulate, in a very similar fashion to the leaf surface of extant *Wollemia* (Fig. 52 cf. Fig. 6). Stomata are in discontinuous rows (Fig. 53). On the inner cuticular surface, *Agathis* type polar extensions of the guard cells have not been observed, but the cuticle between the subsidiary cells and the underlying epidermal cells is well formed (Figs 54, 55). The cuticle between the epidermal cells extends partially over the hypodermis (Fig. 56). Of all the specimens considered in the present study, this is the one that is most difficult to assign to a genus in isolation. However, this specimen compares very closely with those from Pioneer and one specimen from Cethana described above, with the exception of its stomatal orientation, which may be an artefact of the very fragmentary cuticle



Figs 39–43. *Agathis vittatus* from Cethana. **Fig. 39.** C-534, showing part of a leaf, tapering asymmetrically towards what is probably the apex. Scale bar = 5 mm. **Fig. 40.** SEM of the outer cuticular surface of C-489, showing the well developed but sunken Florin rings around the stomatal openings and the undulate leaf surface. Scale bar = 25 µm. **Fig. 41.** SEM of the inner cuticular surface, showing obliquely oriented stomata in loose rows (the long axis of the leaf runs from left to right). Scale bar = 100 µm. **Figs 42, 43.** SEM of the inner cuticular surface showing single stoma (42 = C-489, 43 = C-484). Polar knobs are absent but there is a complete covering of cuticle over the subsidiary cells. Scale bars = 10 µm.

preserved, meaning it may have come from an extreme part of the leaf. All these specimens are considered to be conspecific. Several thousand specimens have been curated from Lea River and this is the only specimen of this species recorded. Hence, it is unlikely that more specimens will be discovered in the near future.

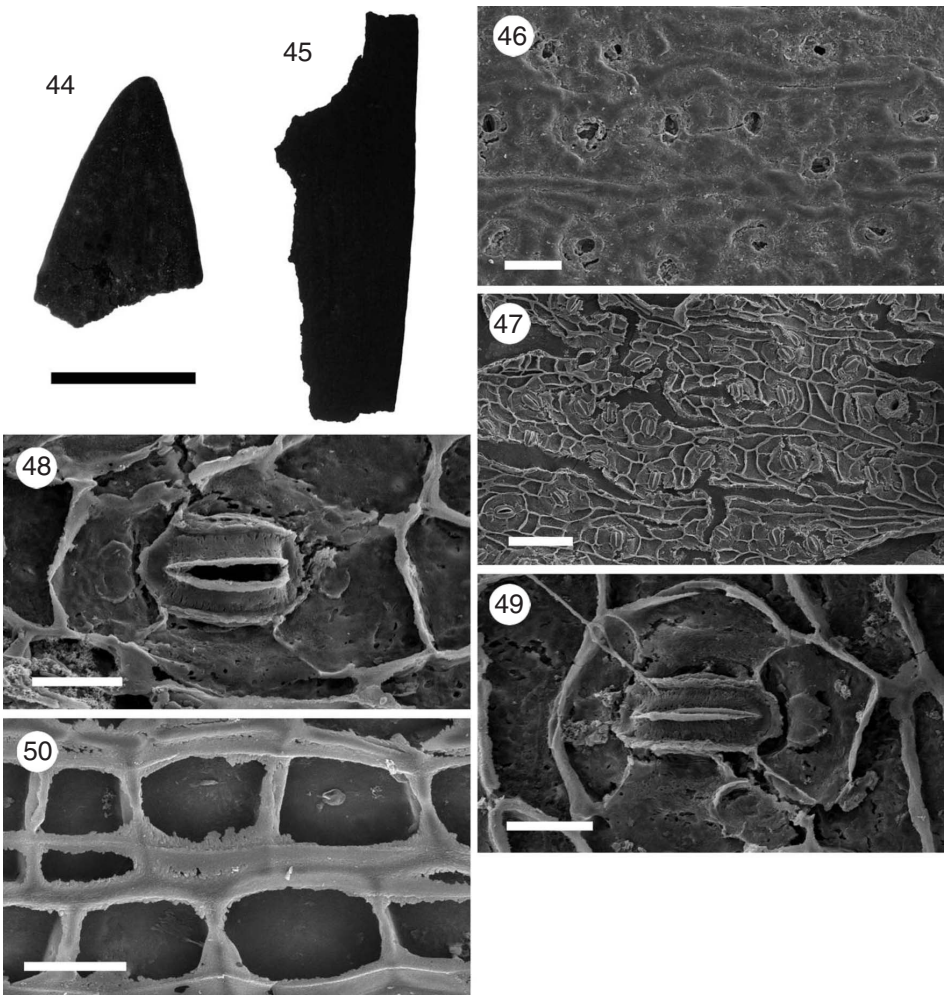
Comparison of the fossil and living species

As a result of this investigation, one fossil *Agathis* species has been recognised as occurring at both Lake Bungarby and Cethana, one at Cethana, Pioneer and Lea River and one only at Cethana. Determining species limits was difficult for the following two reasons:

(1) The multiple specimens of *A. macrophylla* examined suggested that there is much more intraspecific variation in *Agathis* leaf morphology than has been previously recognised. This is complicated by the well known difficulty of placing living *Agathis* specimens into species (at least in some instances) and thus the potential that some of the replicates of *A. macrophylla* examined do not belong to the same species.

(2) It is difficult to place species limits around the morphological variation exhibited by the fossil specimens examined, and it must be recognised that other interpretations of species limits are plausible. However, it is important to note that while species limits are difficult to define, the identification of the genus is not in dispute, and that is valuable information for reconstructing vegetation, and phylogeny and biogeography of the family.

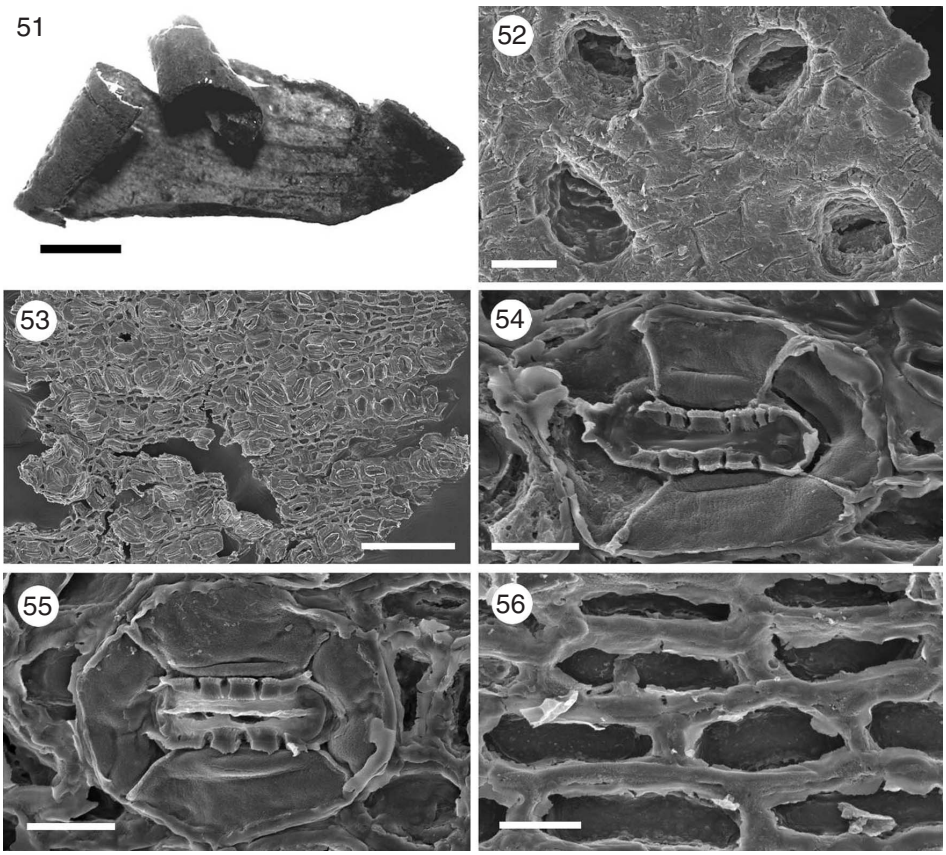
It is difficult is to compare these new species with existing *Agathis* fossil species, since some of the previously described fossil species lack adequate cuticular preservation. *A. victoriensis* is the most difficult species in this regard, since no cuticular detail has been preserved. *A. kendrickii* will also be excluded from this comparison since, although there is no doubt that this is an *Agathis*



Figs 44–50. *Agathis brevigongylodes* sp. nov. from Pioneer. **Fig. 44.** P-050, showing the leaf apex. **Fig. 45.** P-707, showing part of the mid-leaf region, with a margin preserved on the right-hand side. Scale for both specimens = 5 mm. **Figs 46–50.** Scanning electron micrographs (SEMs) of P-710 (holotype). **Fig. 46.** The outer cuticular surface, showing the moderately developed but sunken Florin rings. Scale bar = 50 µm. **Fig. 47.** The inner cuticular surface showing obliquely oriented stomata in loosely defined rows (the long axis of the leaf runs from left to right). Scale bar = 100 µm. **Figs 48, 49.** The inner cuticular surface over a single stoma, with pairs of well developed polar knobs at each end, well within the boundary of the subsidiary cells. The covering of cuticle over the subsidiary cells is complete as in extant *Agathis*. Scale bar = 20 µm. **Fig. 50.** The inner cuticular surface, showing the cuticle extending partially between the epidermal and hypodermal cells. Scale bar = 20 µm.

species, the lack of internal cuticular preservation makes comparison with other fossil and living species relatively superficial. *A. berwickensis* is also difficult to compare with these new fossils because of limited illustration of the cuticular morphology. The species that must be considered for comparison are *A. parwanensis*, *A. yallournensis* and *A. tasmanica*. *A. yallournensis* shares some similarities with the species present at Lake Bungarby and Cethana, but differences in leaf symmetry (which cannot be assessed for *A. parwanensis*, because it is only known from a leaf fragment), stomatal orientation, formation of stomatal rows, and cuticular morphology over the guard cells, are enough to warrant their separation. *A. parwanensis* is similar in many respects to the species that only occurs at Cethana, but the extreme difference in stomatal orientation, along with the very sparse nature of the stomata in the Cethana specimens (e.g. Fig 33), precludes their conspecificity. However, *A. tasmanica* is very similar in aspects to these Cethana specimens except for the stomatal orientation, which is based on a small sample size. The relatively sparse stomata (Fig. 33 cf. fig. 4*I* in Hill and Bigwood (1987)), guard cells with polar knobs on or near the outer wall of the subsidiary cells (Figs 34, 38 cf. fig. 4*J* in Hill and Bigwood (1987)) and the generally smooth cell surfaces are virtually identical. Therefore, these Cethana specimens (Figs 32–38) are assigned to *A. tasmanica*.

Recently, Lee *et al*. (2007) described abundant and beautifully preserved *Agathis* leaves from the late Oligocene–early Miocene



Figs 51–56. *Agathis brevigongylodes* from Lea River (Lea-2299). All except Fig. 51 are Scanning electron micrographs (SEMs). **Fig. 51.** The whole specimen, showing a leaf apex with some of the parallel veins clearly visible. Scale bar = 2 mm. **Fig. 52.** The outer cuticular surface, showing the near absence of Florin rings and the relatively smooth surface. Scale bar = 25 µm. **Fig. 53.** The inner cuticular surface, showing obliquely oriented stomata, sometimes in well defined rows. The long axis of the leaf runs from left to right. Scale bar = 200 µm. **Figs 54, 55.** The inner cuticular surface, showing single stoma, lacking polar knobs, but with a complete covering of cuticle covering the subsidiary cells. Scale bar = 20 µm. **Fig. 56.** The inner cuticular surface, showing the cuticle extending partially between the epidermal and hypodermal cells. Scale bar = 20 µm.

from the Newvale Mine in the far south of the South Island of New Zealand as having affinities with the extant *A. australis*. These fossils are quite distinct from any of those described here and are unusual for *Agathis* in having a relatively acute leaf apex, and the cuticle separating the subsidiary cells from the epidermal cells above them (i.e. towards the leaf surface) is often not complete, leading to a ragged appearance, as in extant *W. nobilis*.

The fossils must also be compared with living *Agathis* species. The relatively few replicates among both the fossil and living species hinders this process, and where replicates are present the degree of variability does not inspire confidence in setting clear morphological limits to species. By concentrating on the form of polar extensions, stomatal orientation and Florin ring development, it is clear that very few of the extant species match the fossils and in no case was there a good reason for assigning fossil specimens to an extant species. Therefore, the two new species recognised here are distinct from all other described fossil and living *Agathis* species.

Systematics

Order Coniferales

Family Araucariaceae

Genus ***Agathis*** Salisb. (1807)

Agathis vittatus R.S.Hill, T.Lewis, R.J.Carp. & S.S.Whang, *sp. nov*. (Figs 39–42)

Diagnosis

Leaf small, 5–8 mm wide, length unknown, asymmetrical, tapering towards apex. Florin rings weakly developed, leaf surface undulate, polar knobs of guard-cell extensions, when present, well developed and present on or outside of the subsidiary cell margins.

Holotype: LB-197, LB-198 (part and counterpart), stored in the School of Earth and Environmental Sciences, University of Adelaide.

Type locality: Lake Bungarby, south-eastern New South Wales (39°06′S, 149°08′E, at least 400 m asl).

Etymology: named for the longitudinal bands of stomata that occur between the parallel veins.

Specimens examined

C-484, C-489, C-534, C-622, LB-156, LB-197, LB-198.

Agathis brevigongylodes R.S.Hill, T.Lewis, R.J.Carp. & S.S.Whang, *sp. nov.* (Figs 45–50)

Diagnosis

Florin rings weakly developed or absent, leaf surface undulations weakly developed, polar knobs of guard-cell extensions well developed and present well inside of the subsidiary cell margins, cuticle extends significantly over the hypodermis.

Holotype: P-710, stored in the Palaeobotany Collection, School of Earth and Environmental Sciences, University of Adelaide.

Type locality: Pioneer, north-eastern Tasmania (41°05′S, 145°14′E, 90 m asl).

Etymology: named for the cuticular knob-like polar extensions of the guard cells that fall short of the edge of the subsidiary cells.

Specimens examined

C-491, P-050, P-707, P-709, P-710, Lea-2299.

Conclusions

The organically preserved fossil leaves described here can all be assigned to the extant araucarian genus *Agathis*. These fossils do not extend the known spatial distribution of *Agathis* in the fossil record, but they do extend the time range for well preserved *Agathis* leaf fossils back to the late Paleocene. *A. victoriensis*, from the Early Cretaceous of Victoria, predates this record by more than 40 million years, but this species cannot yet be confirmed as a definite member of the genus. Organically preserved leaves ascribed to *Agathis* from the middle Cretaceous of New Zealand by Daniel (1989) cannot be considered further until they are formally described, although Lee *et al*. (2007) noted that the cuticle illustrations do not show the bilobed polar extensions on the stomata that characterise *Agathis*.

The major problem with the leaf fossil record of *Agathis* is that there is a great deal of uncertainty over species limits. The present study is the first to attempt to determine the amount of intraspecific variation in leaf micromorphological characters in extant *Agathis*. The results suggest that either this variation is enormous, or the identification of species is extremely difficult and it is not intraspecific variation that is being assessed. This, in combination with the very few characters that are applicable to determining species limits in fossil leaves, makes the task of setting fossil species limits very difficult. The fossils considered here have been separated into two new species, and some have been assigned to an existing species; however, further collection and assessment of variation among the extant species could change this.

An important conclusion from the present study is that all of the previously described organically preserved *Agathis* fossil species based on leaves remain within that genus and hence have no generic affinity with *Wollemia*. Hill and Scriven (1997) compared the mesothermal taxa present in five Tasmanian macrofossil localities spanning the Oligocene–early Miocene. One of the genera considered was *Agathis*, which at that stage had been recorded from Cethana, Little Rapid River and Pioneer, but not Lea River. On the basis of this, and several other taxa, it was concluded that the Lea River macrofossils represented the remains of a more microthermal vegetation than the other sites. The single *Agathis* leaf fragment from Lea River does not particularly alter that conclusion, since the genus was very rare in the vegetation, with one specimen in more than 5000 recorded, compared, for example, with the relatively common occurrence of well preserved *Agathis* leaves in the lowland Little Rapid River sediments.

Acknowledgements

We thank Ken Hill from the Royal Botanic Gardens, Sydney, for providing leaf material of *Wollemia nobilis* and providing leaves of 10 specimens of *Agathis macrophylla*, Colin Harris, Acting Director of the Adelaide Botanic Gardens, for allowing us to collect leaves from living species of *Agathis*, and Tom Rich at the Victorian Museum for loaning the holotypes of *A. parwanensis* and *A. yallournensis*. This research was funded by a grant from the Australian Research Council.

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