Int. J. Plant Sci. 180(8):902–921. 2019.

1058-5893/2019/18008-0008$15.00 DOI: 10.1086/704829

ARAUCARIA SECTION *EUTACTA* MACROFOSSILS FROM THE CENOZOIC OF SOUTHEASTERN AUSTRALIA

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Editor: Patrick S. Herendeen

Premise of research. We collate and interpret previously undescribed foliar material of *Araucaria* section *Eutacta* from Australian Cenozoic sediments.

Methodology. The fossils we describe here were collected over several decades and were identified by direct comparisons with extant and fossil species using light and scanning electron microscopy.

Pivotal results. Fossil leaves and leafy shoots of three new species of *Araucaria* section *Eutacta* (*A. macrophylla*, *A. mollifolia*, and *A. balfourensis*), along with new records of the previously described *A. planus*, are described from eight localities in southeastern Australia, spanning the early Eocene to the early Miocene.

Conclusions. These well-preserved fossils add significantly to our knowledge of *Araucaria* and confirm the dominance of the section *Eutacta* compared with other sections in the region during that time. The range of leaf morphology exhibited is similar to that seen in extant New Caledonian species and probably reflects past phases of radiation in similar wet climates.

Keywords: Araucaria, Araucariaceae, conifers, Cenozoic, Australia.

Introduction

The Araucariaceae is one of three major conifer families in the Southern Hemisphere today. There are three extant genera, *Agathis*, *Araucaria*, and *Wollemia*, and 42 species (Farjon 2001; Mill et al. 2017). Living *Araucaria* species were divided into four sections by Wilde and Eames (1952): *Eutacta*, *Araucaria* (=*Columbea*), *Intermedia*, and *Bunya*. Leslie et al. (2012) and Escapa and Catalano (2013), in recent phylogenetic analyses of living and fossil Araucariaceae, concluded that the four living sections of *Araucaria* are monophyletic. Three of these sections have relatively large, multiveined leaves, while the fourth, section *Eutacta*, is usually reported as having small, univeined leaves, although the single vein may divide in the leaf (Townrow 1967), and G. J. Jordan (unpublished data) has recorded three to seven veins in several species in section *Euctacta*. Living *Araucaria* species are highly disjunct across the land masses that constituted Gondwana. This suggests a considerable contraction through the Cenozoic of both the genus and the sections it contains. Section *Eutacta* has the highest extant species diversity in the genus by far, but today the majority of these species occur in New Caledonia, and this appears to represent relatively recent speciation (Gaudeul et al. 2012; Kranitz et al. 2014). However, the fossil record indicates a more widespread past distribution of section *Eutacta*, including recent records of leafy shoots of certain affinity with section *Eutacta* from the late Eocene Loreto Formation in southern Chile (Ohsawa et al. 2016) and a record of a bract-scale complex and associated foliage, tentatively assigned to section *Eutacta*, from the early-middle Eocene of King George Island in the Antarctic Peninsula (Shi et al. 2018). These provide potential evidence for a transantarctic link for section *Eutacta* between southern South America and Australia during the Eocene. The majority of the new *Araucaria* fossils collected from southeastern Australia belong to section *Eutacta*, and the purpose of this article is to describe these new records. Most Araucariaceae species have robust, decay-resistant wood, cones, and foliage, and many species shed their female cones or cone scales individually. The macrofossil record of the extant genera in the family was reviewed by Hill and Brodribb (1999), and more recent research has concentrated on geographical or taxonomic subsets of the extensive and complex fossil record of this family (e.g., Lee et al. 2007; Hill et al. 2008; Pole 2008; Panti et al. 2012; Wilf et al. 2014). Araucariaceae macrofossils are relatively common, and over the last few decades, many new specimens of foliage fossils of this family have been recovered from Cenozoic sediments in southeastern Australia. *Agathis* fossils have been dealt with separately (Hill et al. 2008), and *Wollemia* is excluded because no unequivocal foliage fossils of this genus were discovered as part of this research.

Material and Methods

Macrofossils of previously undescribed foliage fossils with affinities to *Araucaria* section *Eutacta* were recovered from eight

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Manuscript received December 2018; revised manuscript received April 2019; electronically published August 27, 2019.

localities in southeastern Australia (fig. 1), along with female cone scales from Balfour and a male cone from Cethana, but the relatively poor preservation of the reproductive structures yielded no characters that allowed species-level identification. All these localities have been described previously. Table 1 shows their location and age and the most critical references for establishing this information.

All fossil remains attributed to *Araucaria* section *Eutacta* in this article are vegetative. These fossils are usually isolated leaves or parts of leaves, but parts of shoots were rarely recovered. These are of most value in giving some indication of the likely variation in leaf size during a single growing season. In some *Araucaria* species, a single short shoot can contain leaves that vary significantly in size, but the fossil shoots illustrated here demonstrate little variability in leaf size, a condition that is most consistent with many living *Araucaria* species in section *Eutacta*.

Specimens from most sites were removed from the sediment by soaking large blocks in warm, dilute hydrogen peroxide. This disaggregated the sediment, and the resultant slurry was sieved through a 350-μm mesh. The retained organic fragments were sorted for recognizable plant parts. In some cases, especially Lowana Road and Cethana, specimens were too fragile to be separated from the sediment and were photographed in situ. Small blocks of the Balfour sediments were soaked in absolute ethanol and treated for several hours in an ultrasonic bath. The resultant slurry was sieved and sorted under a low-power dissecting microscope (Hill 2001).

Fossil shoots, leaves, and leaf fragments were photographed using an Olympus digital camera mounted on a Zeiss Stemi 2000C microscope. Cuticles were prepared by first soaking the fossils in 50% w/w hydrofluoric acid overnight to dissolve any adhering siliceous particles. Fragments of the leaves, taken as close to the midsection as was practicable, 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

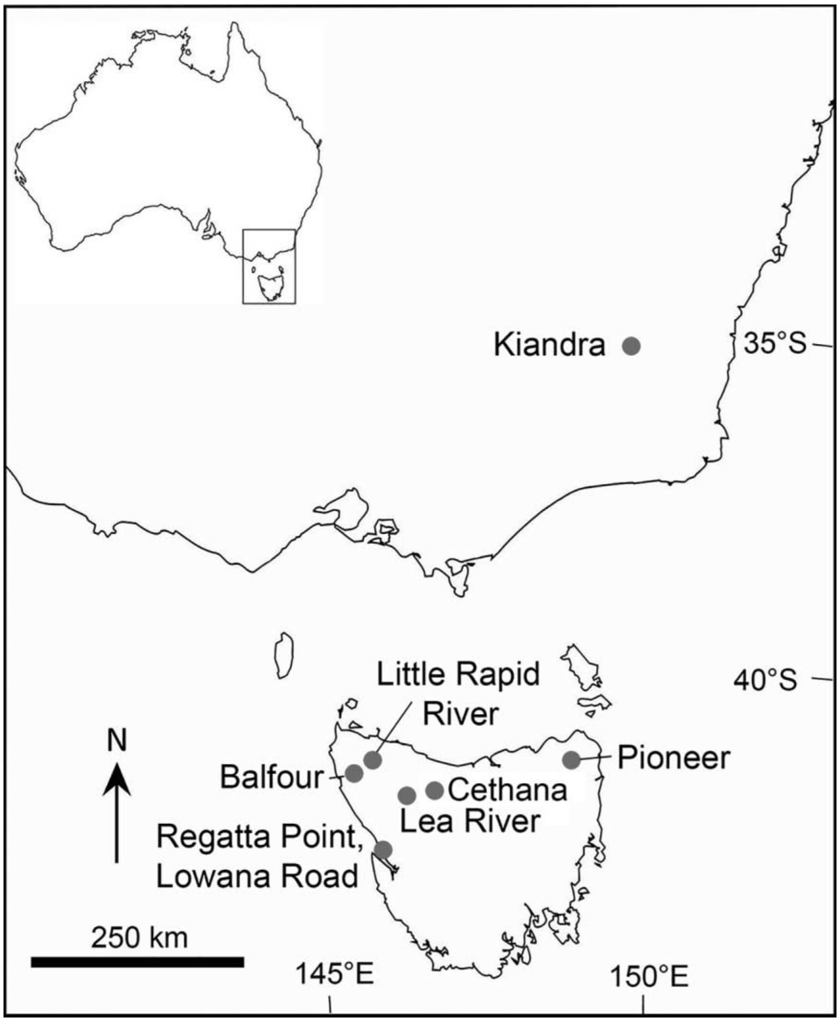

Fig. 1 Map of southeastern Australia, showing the approximate location of the eight macrofossil-bearing localities considered here. A color version of this figure is available online.

Table 1

Locations and Ages of Sediments Containing *Araucaria* Section *Eutacta* Macrofossils Considered in This Study

Site	Location (lat., long.)	Elevation (m)	Age	Reference(s)
Regatta Point	42°10′S, 145°20′E	10	Early Eocene	Bigwood and Hill 1985
Lowana Road	42°11′S, 145°22′E	30	Early Eocene	Carpenter et al. 2012
Little Rapid River	41°09′S, 145°14′E	350	Early Oligocene	Macphail et al. 1994
Lea River	41°30′S, 145°39′E	670	Early Oligocene	Macphail et al. 1994
Cethana	41°32′S, 146°07′E	300	Early Oligocene	Carpenter 1991; Macphail et al. 1994
Pioneer	41°05′S, 145°14′E	90	Late Oligocene–early Miocene	Hill and Macphail 1983; Macphail et al. 1994
Kiandra	35°88′S, 148°50′E	1400	Early Miocene	Wellman and McDougall 1974
Balfour	41°17′S, 144°54′E	260	Oligocene–late early Miocene	Hill 2001

Note. All of these sites have been described previously, and the basis of their age determinations can be found in the publications listed.

mix. They were examined using a Philips XL20 SEM or an XL30FE SEM operated at 10 kV. Leaf cuticles of living *Araucaria* species were examined from collections held at the School of Biological Sciences, University of Adelaide.

Results

Leafy shoots of *Araucaria* were recovered from Lea River, Balfour, Kiandra, and Lowana Road; leaves or leaf fragments were recovered from all sites; ovuliferous scales were recovered from Balfour; and a pollen cone was recovered from Cethana. Hill et al. (2008) noted that assigning fossil leaves of *Agathis* to species is difficult, given the general conservatism of living *Agathis* leaf morphology coupled with the variation that occurs within single living species. The situation is similar in *Araucaria*, although the range of leaf forms in that genus is greater. It is important to note that none of the fossils here can be assigned to *Wollemia*, because both juvenile and adult leaves of that genus have multiveined, flattened leaves with a round leaf apex (Chambers et al. 1998), and this is distinct from all fossil leaves considered here. However, it is notable that Chambers et al. (1998) considered that *Wollemia nobilis* has a cuticle morphology that is indistinguishable from *Araucaria* and is most similar to section *Eutacta*.

Leaves of section *Eutacta* are easily distinguished from the other extant sections by their stomatal orientation, since their stomata are typically aligned at random or at high angles approaching 90°, while in all other extant sections, the stomata are aligned predominantly parallel to the long axis of the leaf. Section *Eutacta* is by far the most species-diverse section and has probably speciated profusely on New Caledonia since its apparent arrival there in the Neogene (Hill and Brodribb 1999; Gaudeul et al. 2012; Kranitz et al. 2014). Farjon (2001) recognized 19 living species (plus one variety) of *Araucaria* section *Eutacta*, and Mill et al. (2017) have recently described another New Caledonian species in that section.

The assignment of the vegetative fossils examined here to *Araucaria* followed the protocol described by Stockey and Ko (1986), who, following an examination of all the extant species, concluded that they could characterize the epidermal patterns of the genus in this way: (1) The outer cuticular surface is smooth, with no surface ornamentation. (2) All species have wax stomatal plugs. (3) Stomata are sunken to the level of the hypodermis and are in discontinuous rows in all species, especially those with relatively small leaves. (4) Stomatal orientation varies greatly. (5) Although three to seven subsidiary cells have been reported, four is the common number, with five slightly less so, particularly in the smaller-leaved species. (6) The cuticle on the internal surfaces of subsidiary cells is usually slightly pitted, and the cuticle on the guard cell surface is the most diagnostic character for distinguishing araucarian species. (7) Polar extensions are common, especially in the smaller-leaved section *Eutacta* species. (8) The cuticular flange between subsidiary cells and guard cells is usually serrated, but a few species show a smooth edge.

The fossils described here have cuticular morphology that is consistent with this description and have leaves that are apetiolate, with a broad base for the attachment to the stem. The only discrepancy is that polar extensions are not common among the fossils. This may be a preservational artifact, but it is also possible that polar extensions are generally not as common as Stockey and Ko (1986) reported. When combined, these characters identify the fossils as belonging to *Araucaria*. Also, where it could be observed, the leaves are usually strongly keeled, suggesting that one major leaf vein is present, and in all specimens, the stomata are aligned at random or at high angles, allowing designation to section *Eutacta* for all of these fossils. There is a high degree of variability in stomatal orientation among specimens of the same species in section *Eutacta*, so measuring stomatal orientation precisely is of little value in discriminating species.

Araucaria leaf fossils have been recorded previously from some of these sites (table 2), but at each site, only those fossils regarded as being new records were considered. *Araucaria* leaf fossils ranged from common (e.g., Lowana Road) to rare (e.g., Pioneer, Little Rapid River, and Cethana). One potential new species of *Araucaria* section *Eutacta* was recorded from Pioneer, Kiandra, Balfour, Cethana, Lowana Road, and Regatta Point. Two were recorded from Lea River, and at Little Rapid River, the two individual leaves examined differed significantly in morphology (see later discussion).

Section *Eutacta* is not only by far the most species-diverse living section; it is also relatively common in Cenozoic sediments in Australasia (Hill and Brodribb 1999). Hence, the fossils recovered here must be compared with each other and also with previously described species in the fossil record and with the living species in section *Eutacta*.

How Many Fossil Species of Section Eutacta *Are Preserved in These Sediments?*

Lowana Road/Regatta Point. These two localities are considered together because the fossil *Araucaria* leaves recovered

Table 2

List of Fossil Species of *Araucaria* Section *Eutacta* Previously Described from Australia Based on Foliar Remains

Araucaria species	Locality	Age	Reference(s)
A. annulata (Bigwood & R.S. Hill) Pole	Hasties, Tasmania	Mid-late Eocene	Bigwood and Hill 1985; Pole 1992
A. carinatus Cantrill	Otway Basin, Victoria	Early Cretaceous	Cantrill 1992
A. crassa (Tenison-Woods) Townrow	Booval Group, Queensland	Cenozoic?	Townrow 1967
A. derwentensis Selling	Hobart Town, Tasmania	Cenozoic?	Selling 1950
A. falcatus Cantrill	Otway Basin, Victoria	Early Cretaceous	Cantrill 1992
A. fletcheri Selling	Rocky River, New South Wales	Cenozoic	Selling 1950
A. sp. cf. *A. heterophylla* (Salisb.) Franco	Koonwarra, Victoria	Early Cretaceous	Drinnan and Chambers 1986
A. lignitici (Cookson & Duigan) emend. R.S. Hill	Yallourn, Morwell, Victoria	Oligocene–Miocene	Cookson and Duigan 1951; Hill 1990
A. otwayensis Cantrill	Otway Basin, Victoria	Early Cretaceous	Cantrill 1992
A. planus R.S. Hill	Monpeelyata, Tasmania	Latest Oligocene–early Miocene	Hill 1990
A. prominens R.S. Hill	Monpeelyata, Tasmania	Latest Oligocene–early Miocene	Hill 1990
A. readiae (R.S. Hill & Bigwood) emend. R.S. Hill	Regatta Point, Tasmania	Early Eocene	Hill and Bigwood 1987; Hill 1990
A. uncinatus R.S. Hill	Monpeelyata, Tasmania	Latest Oligocene–early Miocene	Hill 1990

from them are morphologically similar and are thus regarded as a single species. They are geographically and stratigraphically close to one another and have previously been regarded as containing some taxa in common (e.g., *Bowenia johnsonii*; Hill et al. 2019). This is probably at least in part because sedimentary facies in the region indicate the presence of a range of near-coastal depositional environments, including tidal channels and mangrove and freshwater swamps, indicating a complex of overlapping vegetation types (Pole 1998).

The fossil leaves recovered from these sites are usually individually preserved (fig. 2*A*–2*C*, 2*E*), but some shoots with spirally arranged leaves were recovered (fig. 2*D*). The leaves are all relatively large for section *Eutacta*, and their lengths and length-to-width ratios vary considerably (fig. 2*C* vs. 2*E*). Stomata vary from being in poorly defined rows (fig. 2*F*) to being in quite well-defined rows (fig. 2*G*). Individual stomata are randomly aligned (fig. 2*F*), but most are aligned at close to 90° (fig. 2*G*), with typically four to six subsidiary cells with smooth cuticular surfaces (fig. 2*F*, 2*H*). The external leaf surface lacks ornamentation, and the stomata are sunken into the leaf surface, sometimes with the remnants of wax plugs present (fig. 2*I*). These characters are diagnostic of *Araucaria* section *Eutacta*, with the leaves being at the large-size end for that section.

Lea River. Two species of section *Eutacta* leaves are present at Lea River. One is known from several relatively large individual leaves (fig. 3*A*–3*C*), each appearing to have the same broad attachment. The stomata are in relatively well-developed rows (fig. 3*D*, 3*E*). Individual stomata are often randomly aligned, but most are aligned near parallel to the long axis of the leaf (fig. 3*D*, 3*E*), with typically four or five subsidiary cells with smooth cuticular surfaces (fig. 3*F*, 3*G*), all characters diagnostic of section *Eutacta*. These leaves, like those from Lowana Road and Regatta Point, are at the large-size end for section *Eutacta*. The probable adaxial external leaf surface is relatively smooth, and the stomata possibly have remnants of wax plugs present (fig. 3*H*). The epidermal cells on the probable abaxial leaf surface often have relatively thick cuticular walls (fig. 3*I*).

The second Lea River species is best represented by a single well-preserved shoot (fig. 4*A*; see also Carpenter et al. 1994, fig. 12.3*b*), with relatively small, spirally arranged leaves more typical of the usual leaf size range seen in extant section *Eutacta* species. Several other individual leaves were also recovered (e.g., fig. 4*B*). The stomata are in relatively well-developed rows (fig. 4*C*) or much more randomly placed (fig. 4*D*). The possible position of the leaf vein can be seen in figure 4*C* at the bottom, where stomata are absent. Individual stomata are randomly aligned (fig. 4*C*, 4*D*), and there are usually four to six subsidiary cells (fig. 4*E*, 4*F*) with smooth (fig. 4*E*) to slightly granular (fig. 4*F*) surfaces, all characters that are diagnostic of section *Eutacta*. Abaxial epidermal cells often have relatively thick cuticular walls (fig. 4*G*). The main distinguishing feature of the two Lea River species is the significant difference in leaf size and shape.

Little Rapid River. The circumscription of *Araucaria* species at Little Rapid River is difficult because only a few leaf specimens have been recovered. Hill (1990) described *A. fimbriatus* from a leafy shoot and some individual leaves, all from a single block of sediment and thus possibly from a single tree. He was unable to place this species in a section, and it is certainly not in section *Eutacta*.

The new specimens recovered since that time are all individual leaves and appear to represent three taxa. The first taxon is represented by two specimens, which we have assigned to the previously described *A. fimbriatus*, although these specimens are smaller leaved and are from a stratigraphically distinct part of the Little Rapid River sediments than the original specimens of this species (see Hill 1990). These specimens will not be considered further here.

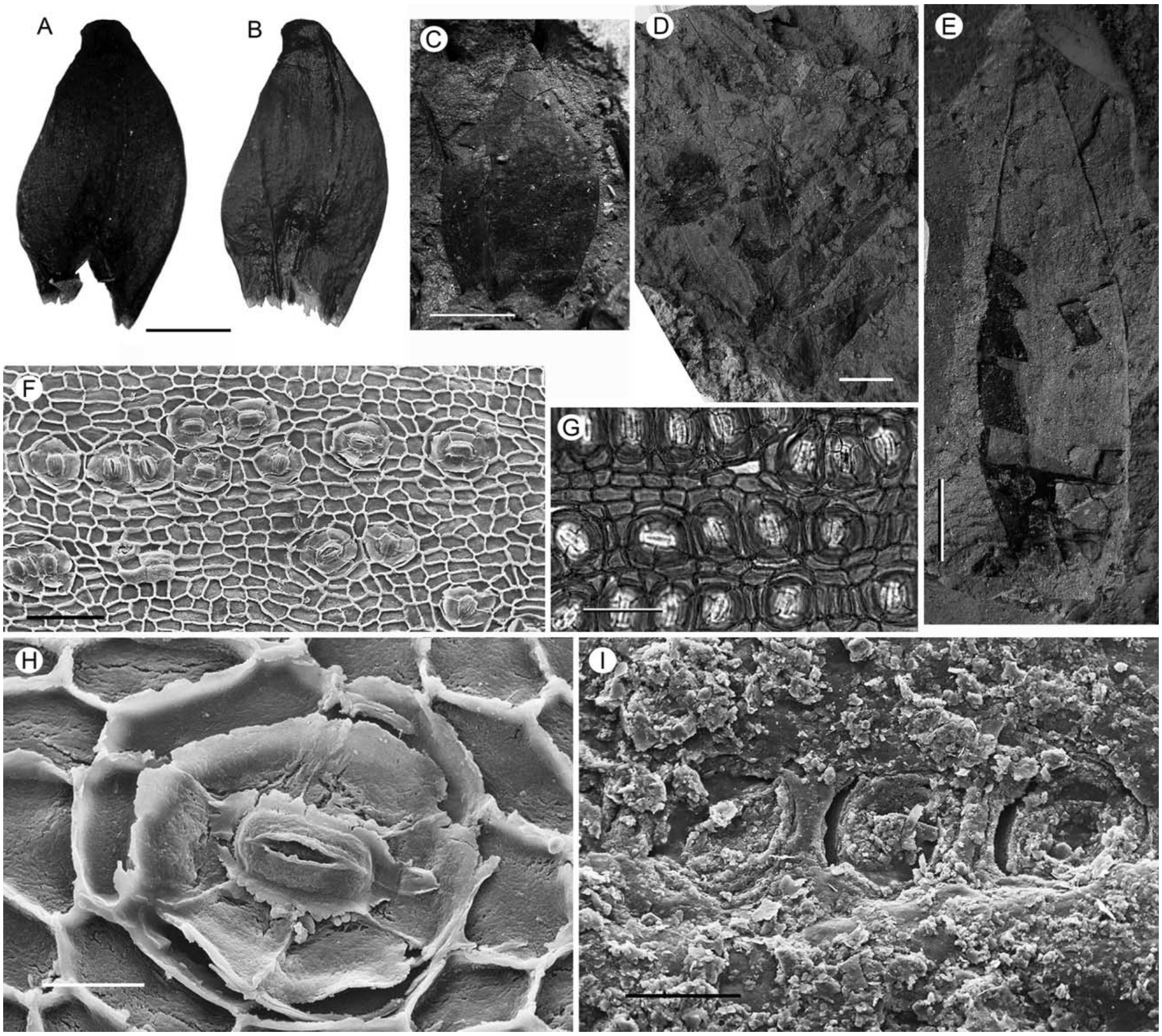

Fig. 2 Fossils of *Araucaria macrophylla*. *A*, *B*, Single mummified leaf from Regatta Point (RPE-294), showing the abaxial (*A*) and adaxial (*B*) surfaces. *C*, Compression fossil leaf from Lowana Road with a relatively broad lamina that tapers to an acute apex (LO-0104). *D*, Compression fossil of a leafy shoot from Lowana Road (LO-0132), showing several spirally arranged leaves. *E*, Compression fossil leaf from Lowana Road that is relatively long and narrow compared with other specimens (LO-0227). *F*, SEM of the inner cuticular surface of the leaf, showing relatively sparse stomata in poorly defined rows, arranged at a variety of angles to the long axis of the leaf (RPE-295). *G*, Light micrograph of the leaf cuticle, showing stomata in rows oriented mostly at close to 90° to the long axis of the leaf (LO-0132). *H*, SEM of the inner cuticular surface of an individual stoma. Note the relatively ragged cuticular margin between the guard and the subsidiary cells and the thin, tapering cuticle separating subsidiary and epidermal cells. A small polar extension can be seen at the right-hand end of the stoma (RPE-295). *I*, SEM of the outer leaf surface, showing three moderately sunken stomata, possibly with remnants of a wax plug in the stomatal pore (RPE-057). Scale bars = 5 mm (*A*–*E*), 100 μm (*F*, *G*), 20 μm (*H*), 50 μm (*I*).

The second taxon is represented by a single relatively large leaf, about 1.5 cm long (fig. 5*A*, 5*B*) and narrowing toward the base. The stomata are in well-developed rows within broad stomatal bands (fig. 5*C*). Individual stomata are randomly aligned, and there are usually four to six subsidiary cells (fig. 5*C*, 5*D*) with smooth inner surfaces (fig. 5*D*), all of which is diagnostic of section *Eutacta*. This specimen has a cuticle with a smooth outer surface and with slightly sunken stomata (fig. 5*E*).

The third taxon (fig. 5*F*) is represented by a single smaller leaf (less than half the length of the first specimen), with a much more three-dimensional structure and a very prominent point of attachment to the stem. The leaf clearly narrows toward the base before it flares out into the point of attachment. The stomata are in relatively well-developed rows (fig. 5*G*), and individual stomata are randomly aligned, with usually four or, less commonly, five subsidiary cells (fig. 5*G*, 5*H*) and with slightly granular surfaces (fig. 5*H*). Stomata do not occur over the midvein (fig. 5*G*). All of these characters are diagnostic of section *Eutacta*.

Balfour. The single species from Balfour is represented by a shoot bearing spirally arranged leaves (fig. 6*A*), as well as

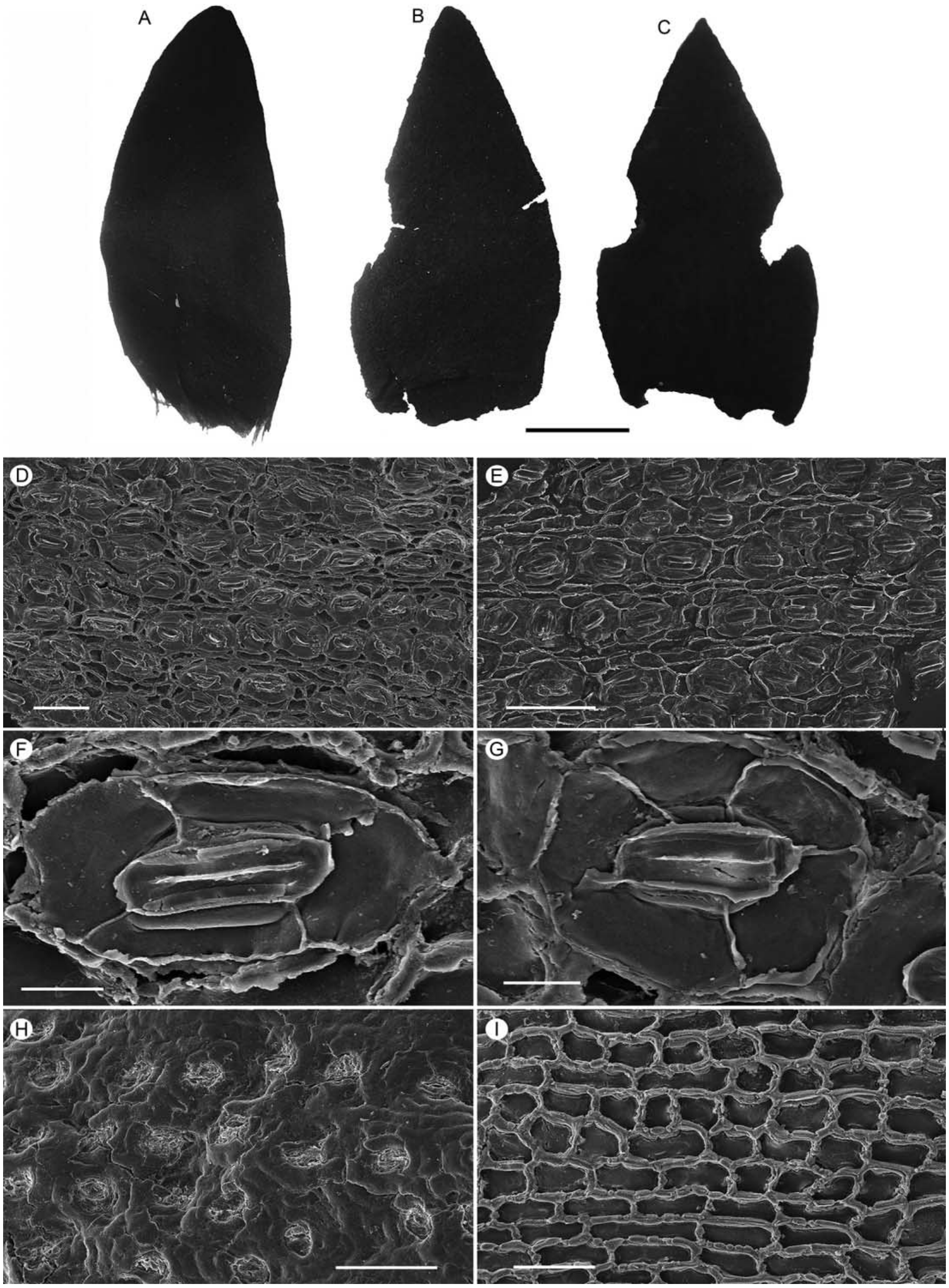

Fig. 3 Fossils of *Araucaria mollifolia* from Lea River. *A–C*, Mummified leaves with broad attachment and a moderately acute apex (*A* = Lea-2904; *B* = Lea-4257; *C* = Lea-4258). *D–I*, SEMs of the leaf cuticle. *D*, *E*, Inner stomatal surface, showing densely packed stomata in well-defined rows, individual stomata with random orientation. Many stomata are close to parallel to the long axis of the leaf (*D* = Lea-4257; *E* = Lea-2904). *F*, *G*, Inner surface of single stomata, showing that the cuticle does not extend between the guard and the subsidiary cells and that the smooth cuticle covering the subsidiary cells ends quite abruptly at the margin with epidermal cells. Polar extensions are poorly developed or absent (Lea-1258). *H*, Outer stomatal surface, showing undulating epidermal cells and rows of partly sunken stomata, with possible traces of stomatal plugs (Lea-1258). *I*, Inner nonstomatal surface, showing regular, thick-walled epidermal cells (Lea-1258). Scale bars = 5 mm (*A–C*), 100 μm (*D*, *E*, *H*), 20 μm (*F*, *G*), 50 μm (*I*).

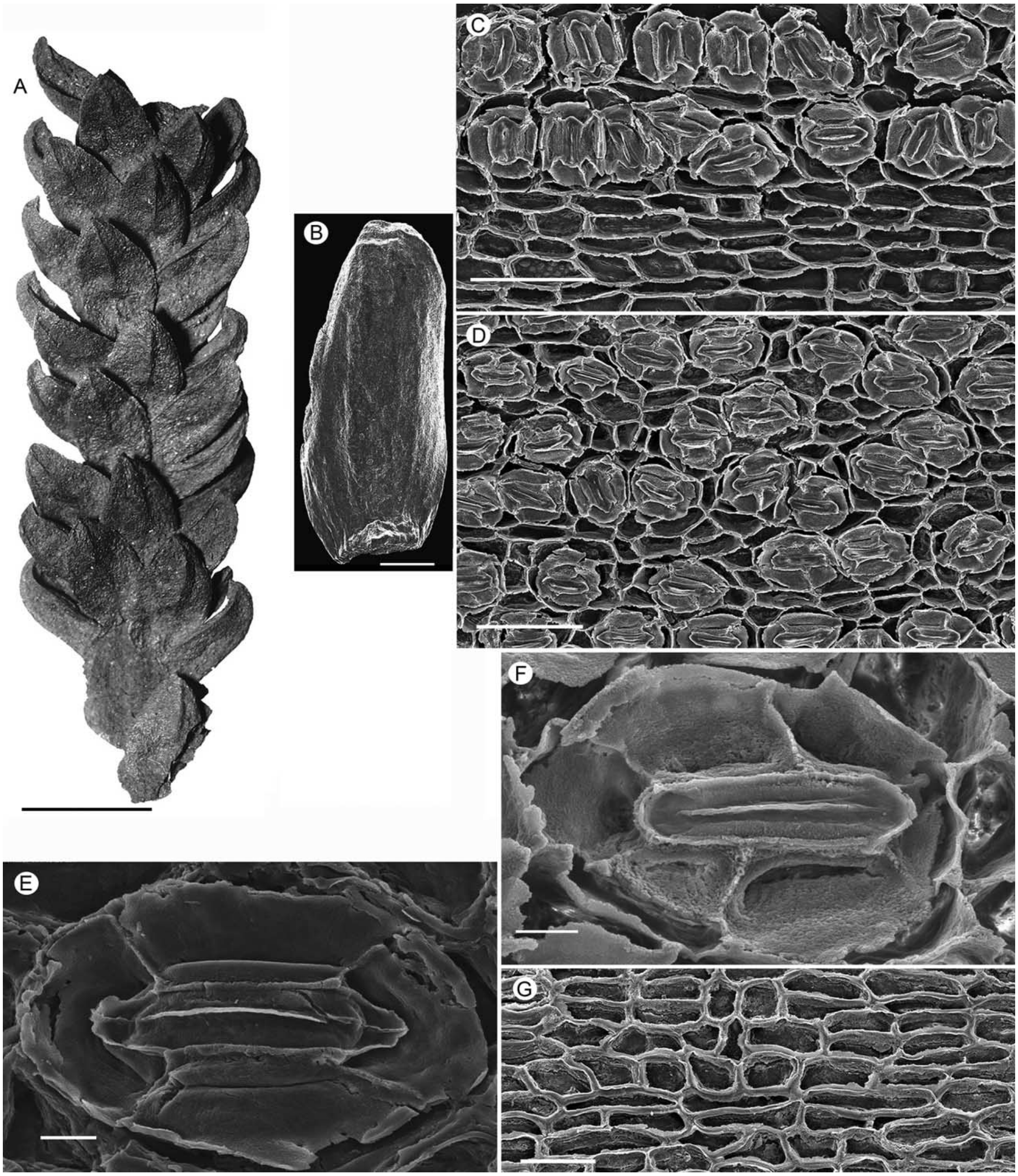

Fig. 4 Fossils of *Araucaria planus* from Lea River. *A*, Leafy shoot with spirally arranged leaves (Lea-4337). *B*, SEM of a single leaf, showing the abaxial leaf surface and the broad attachment at the base (Lea-5221). *C–G*, SEMs of the leaf cuticle. *C*, *D*, Inner stomatal surface, showing densely packed stomata in well-defined (*C*) or loosely defined (*D*) rows and individual stomata with random orientation (*C* = Lea-5222; *D* = Lea-5223). *E*, *F*, Inner surface of single stomata, showing that the cuticle does not extend between the guard and the subsidiary cells. The somewhat granular cuticle covering the subsidiary cells ends quite abruptly at the margin with epidermal cells. Polar extensions are moderately developed (*E*) or absent (*F*; *E* = Lea-5132; *F* = Lea-3984). *G*, Inner nonstomatal surface, showing regular, thick-walled epidermal cells (Lea-5223). Scale bars = 5 mm (*A*), 1 mm (*B*), 100 μm (*C*, *D*), 10 μm (*E*, *F*), 50 μm (*G*).

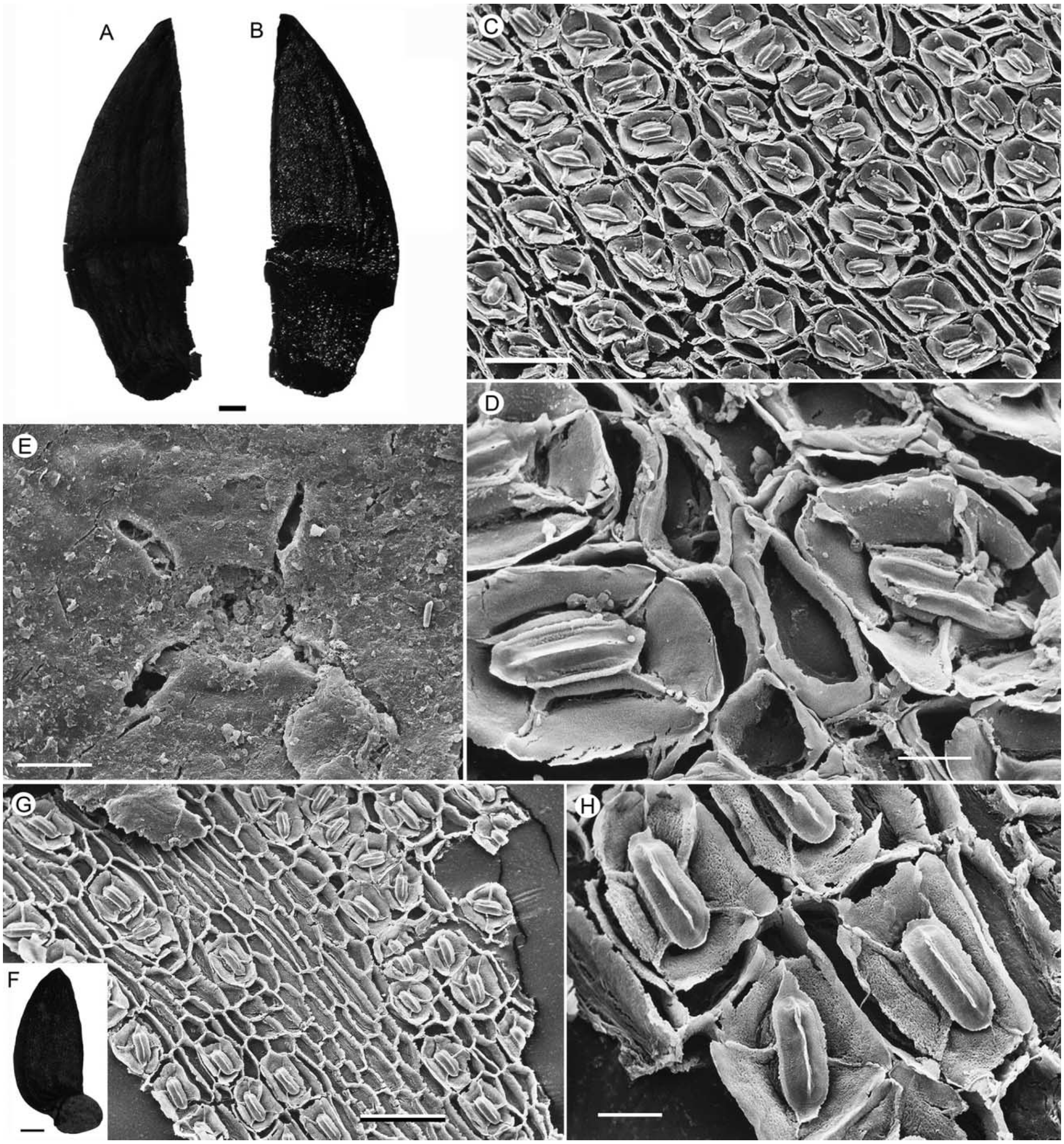

Fig. 5 Fossils of *Araucaria balfourensis* (*A–E*) and *A. planus* (*F–H*) from Little Rapid River. *A*, *B*, Single mummified leaf of *A. balfourensis*, showing the adaxial (*A*) and abaxial (*B*) surfaces (LRR2-5367). *C–E*, SEMs of the leaf cuticle. *C*, Inner stomatal surface, showing densely packed stomata in well-defined rows and individual stomata with random orientation to the long axis of the leaf, which runs from top left to bottom right (LRR2-5367). *D*, Inner surface of stomata, showing that the cuticle extends only a relatively short distance between the guard and the subsidiary cells and that the relatively smooth cuticle covering the subsidiary cells ends quite abruptly at the margin with epidermal cells. Polar extensions are absent (LRR2-5367). *E*, Outer surface over a single stoma, showing the moderately sunken stomatal opening, which may contain the remnants of a wax plug (LRR2-5367). *F*, Single mummified leaf of *A. planus*, showing the well-developed and slightly swollen point of attachment at the base (LRR2-871). *G*, SEM of the inner stomatal surface, showing densely packed stomata in moderately well-defined rows and individual stomata with random orientation to the long axis of the leaf, which runs from top left to bottom right (LRR2-871). *H*, SEM of the inner stomatal surface, showing that the cuticle does not extend between the guard and the subsidiary cells and that the relatively granular cuticle covering the subsidiary cells tapers at the margin with epidermal cells. Polar extensions are absent or moderately developed when they occur over the boundary of two subsidiary cells (LRR2-871). Scale bars = 1 mm (*A*, *B*, *F*), 100 μm (*C*, *G*), 20 μm (*D*, *E*, *H*).

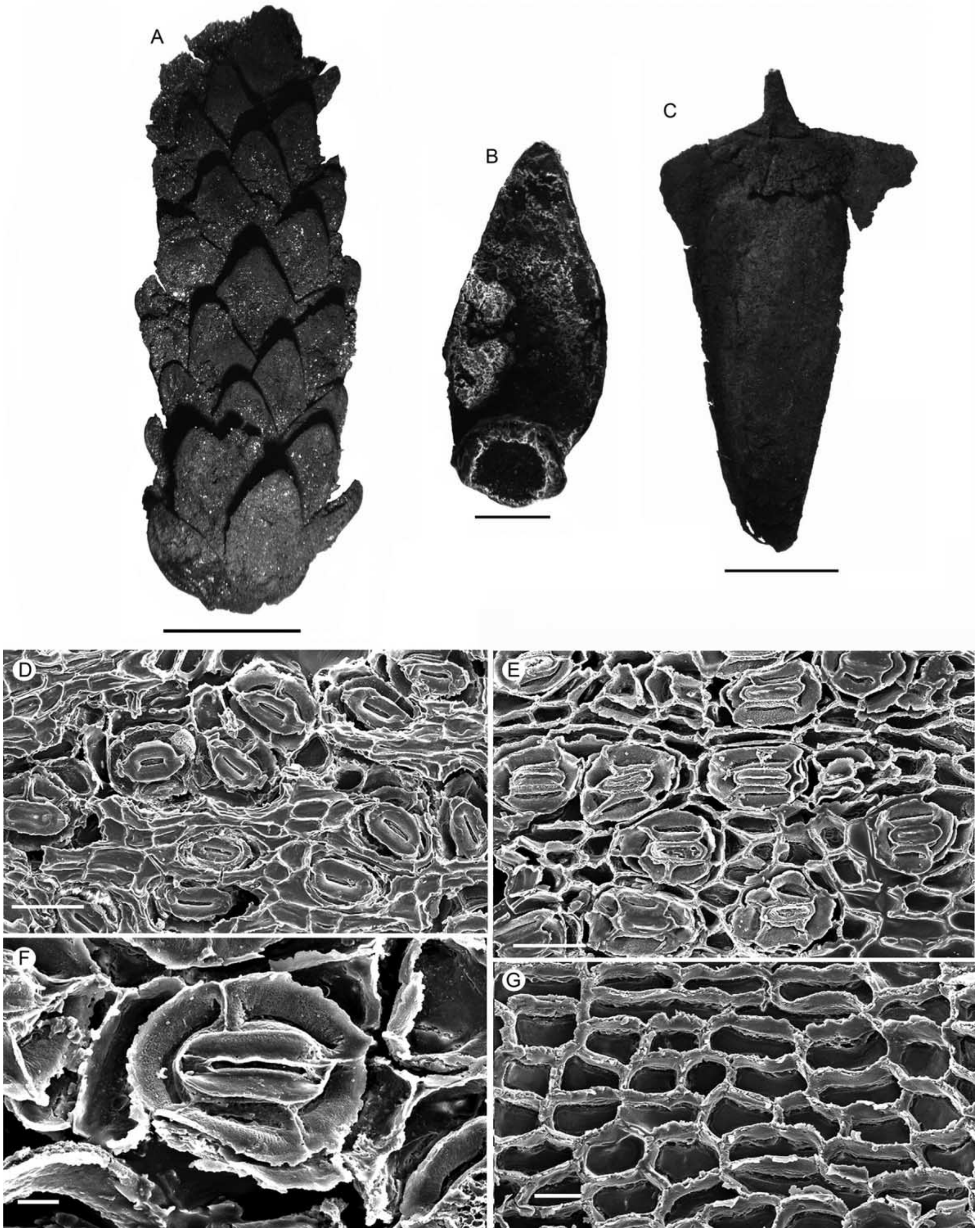

Fig. 6 Fossils of *Araucaria balfourensis* from Balfour. *A*, Leafy shoot with spirally arranged leaves. Note the slightly rounded leaf apexes (B-700). *B*, Single leaf, showing the adaxial surface and the slightly swollen leaf base (B-029). *C*, An ovuliferous cone scale. As there is no organic connection with the leaf fossils, the species identity of this specimen is uncertain (B-929). *D–G*, SEMs of the leaf cuticle. *D*, *E*, Inner stomatal surface, showing stomata in poorly defined rows and individual stomata with random orientation to the long axis of the leaf. The stomata in *D* have a cuticular envelope surrounding the guard cells (*D* = B-028; *E* = B-613). *F*, Inner surface of single stoma, showing that the cuticle does not extend between the guard and the subsidiary cells and that the somewhat granular cuticle covering the subsidiary cells ends moderately abruptly at the margin with epidermal cells. Polar extensions are usually absent but may be moderately developed (B-028). *G*, Inner nonstomatal surface, showing regular, thick-walled epidermal cells (B-497). Scale bars = 1 cm (*A*), 2 mm (*B*), 5 mm (C), 50 μm (*D*, *E*), 10 μm (*F*), 25 μm (*G*).

many individually preserved leaves, most of which preserve a clear point of attachment (fig. 6*B*). There is also a single ovuliferous cone scale preserved (fig. 6*C*), which is morphologically consistent with section *Eutacta* and hence may belong to the same taxon. The leaves of this species are not prominently keeled and have a relatively rounded leaf apex. They are larger than those of many species of section *Eutacta*, but they do not approach the extremely large size seen in other fossil taxa reported here. The stomata are not in well-developed rows (fig. 6*D*, 6*E*). Individual stomata are randomly aligned, but this varies across the leaf (e.g., fig. 6*D* vs. 6*E*). There are usually four or, less commonly, five subsidiary cells (fig. 6*D*–6*F*) with slightly granular surfaces (fig. 6*F*), all characters diagnostic of section *Eutacta*. Abaxial epidermal cells often have relatively thick cuticular walls (fig. 6*G*).

Pioneer. Three fragments of individual leaves have been recovered from the Pioneer sediments. Two of these include the broad basal attachment (fig. 7*A*, 7*B*), and one has the acute apex (fig. 7*C*). The base is slightly less than the maximum width of the leaves. The stomata are in relatively well-developed rows (fig. 7*D*), and individual stomata are randomly aligned, many at close to 90° to the long axis of the leaf (fig. 7*D*). There are usually four or, less commonly, five subsidiary cells (fig. 7*D*–7*F*) with smooth to very slightly granular surfaces (fig. 7*E*, 7*F*), all characters diagnostic of section *Eutacta*. On the external leaf surface, many stomatal openings appear to contain a stomatal plug (fig. 7*G*).

Cethana. Several fossils referable to *Araucaria* were recorded by Carpenter (1991) from Cethana, but only a single detached leaf (fig. 8*A*) with a preserved (although extremely fragmentary) cuticle (fig. 8*B*, 8*C*) has been recovered. A fossil pollen cone is also known (fig. 8*D*), which may belong to the same taxon, but this cannot be confirmed at present. The leaf is slightly less than 10 mm long and about 4 mm wide and has a broad point of attachment preserved at the base. The stomata are randomly aligned (fig. 8*B*), and the two preserved stomata have four and five subsidiary cells, respectively. The cuticle between the guard and the subsidiary cells tapers to a slightly irregular fringe, and the cuticle covering the subsidiary cells is slightly granular. All of these characters are consistent with section *Eutacta*.

Kiandra. A single shoot with spirally arranged leaves has been recovered from the Kiandra sediments (fig. 8*E*), along with a few smaller shoot fragments. The leaves are relatively small, although they may come from a shoot apex and hence not be representative of the species as a whole. The cuticle of this specimen is relatively poorly preserved. The stomata are randomly oriented, with usually four or, less commonly, five subsidiary cells (fig. 8*F*), and they occur in short but relatively well-defined rows. The cuticle has a smooth outer surface, with sunken stomata containing the remnants of wax plugs in the stomatal pores (fig. 8*G*). While this specimen is not as well-preserved as some others, it represents an important record of the genus at a high-altitude, relatively northern site.

Taxonomic Descriptions

A comparison of the fossil remains from these deposits leads to the conclusion that three new *Araucaria* species are present, with the remaining fossils able to be assigned to a previously described species, *A. planus*.

Order—Coniferales

Family—Araucariaceae

*Genus—*Araucaria *Juss., Gen. Pl.: 413 (1879)*

*Species—*Araucaria macrophylla *R.S. Hill, G.J. Jordan, R.J. Carpenter et R. Paull (Fig. 2)*

Holotype. RPE-294 (fig. 2*A*, 2*B*), housed in the David T. Blackburn Palaeobotany Collection, University of Adelaide.

Other specimens examined. LO-014, 082, 085, 101, 124, 132, 146, 159, 160, 163, 164, 169, 170, 227. RPE-053, 057, 295, 888.

Diagnosis. Leaves 16–37 mm long, 9.5–10.5 mm wide, length-to-width ratio 1.7–3.8. Stomata in rows or isolated singly or in small groups with variable orientation, often up to 90° to the long axis of the leaf. Four to six subsidiary cells, with smooth cuticular surfaces. Polar extensions may be present. Cuticle between guard and subsidiary cells extensive and with a ragged outline. Cuticle between subsidiary and epidermal cells tapers to a well-defined margin.

*Species—*Araucaria mollifolia *R.S. Hill, G.J. Jordan, R.J. Carpenter et R. Paull (Fig. 3)*

Holotype. Lea-4257 (fig. 3*B*), housed in the David T. Blackburn Palaeobotany Collection, University of Adelaide.

Other specimens examined. Lea-1258, 2904, 2948, 4258.

Diagnosis. Leaves 20–21 mm long, 9–10.5 mm wide, length-to-width ratio 1.9–2.4. Stomata in well-developed rows and with variable orientation but rarely more than 30° from the long axis of the leaf. Four or five subsidiary cells, with smooth cuticular surfaces. Polar extensions usually absent. Cuticle between guard and subsidiary cells truncated and smooth in outline. Cuticle between subsidiary and epidermal cells with a distinct and slightly thickened margin.

*Species—*Araucaria balfourensis *R.S. Hill, G.J. Jordan, R.J. Carpenter et R. Paull (Figs.* 5A–5E, 6A, 6B, 6D–6G, *7)*

Holotype. B-700 (fig. 6*A*), housed in the David T. Blackburn Palaeobotany Collection, University of Adelaide.

Other specimens examined. B-028–037, 131, 275, 499, 615–617, 689. LRR2-5367. P-513, 514, 708, 710.

Diagnosis. Leaves 7–10 mm long, 4.5–5.5 mm wide, length-to-width ratio 1.6–2.3. Stomata in bands, each stoma with highly variable orientation, often parallel to the long axis of the leaf. Four or, less commonly, five subsidiary cells, with slightly granular cuticular surfaces. Polar extensions absent. Cuticle between guard and subsidiary cells truncated and smooth in outline. Cuticle between subsidiary and epidermal cells tapering to a slightly ragged margin.

Discussion

How Many Species Are Present?

We conclude that six locations (Lowana Road, Regatta Point, Balfour, Cethana, Pioneer, and Kiandra) each contain

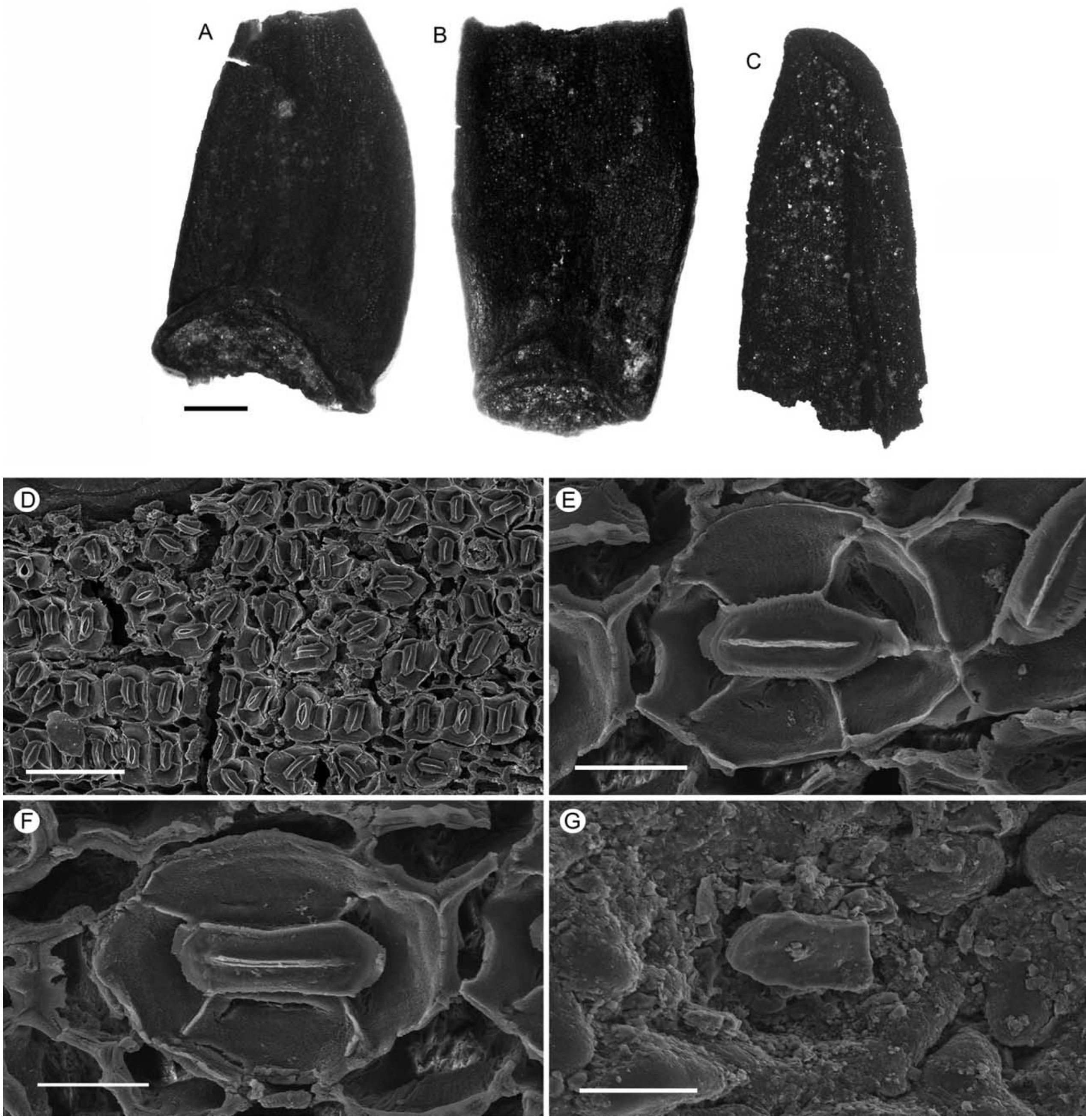

Fig. 7 Fossils of *Araucaria balfourensis* from Pioneer. *A–C*, Leaf fragments. *A*, The most complete leaf with the broad attachment preserved and about two-thirds of the leaf length. *B*, Approximately the basal half of a leaf, including the attachment. *C*, Side-on view (*left*) of approximately half a leaf, clearly showing the leaf apex, the leaf margin (about two-thirds of the way to the right-hand side), and the abaxial (*right*) and adaxial (*left*) leaf surfaces (*A* = P-708; B = P-710; C = P-513). *D–G*, SEMs of the leaf cuticle. *D*, Inner stomatal surface, showing densely packed stomata, in many cases in well-defined rows, with individual stomata randomly oriented, typically at approximately 90° to the long axis of the leaf (P-513). *E*, *F*, Inner surface of stomata, showing the cuticle extending only a relatively short distance between the guard and the subsidiary cells and the relatively smooth cuticle covering the subsidiary cells that ends quite abruptly at the margin with epidermal cells. Polar extensions are moderately developed when they occur over the boundary of two subsidiary cells (*E*), or they are absent (*F*; P-513). *G*, Outer leaf surface, showing a moderately sunken stoma and possibly wax plug remnants in the stomatal pore (P-513). Scale bars = 1 mm (*A–C*), 100 μm (*D*), 20 μm (*E–G*).

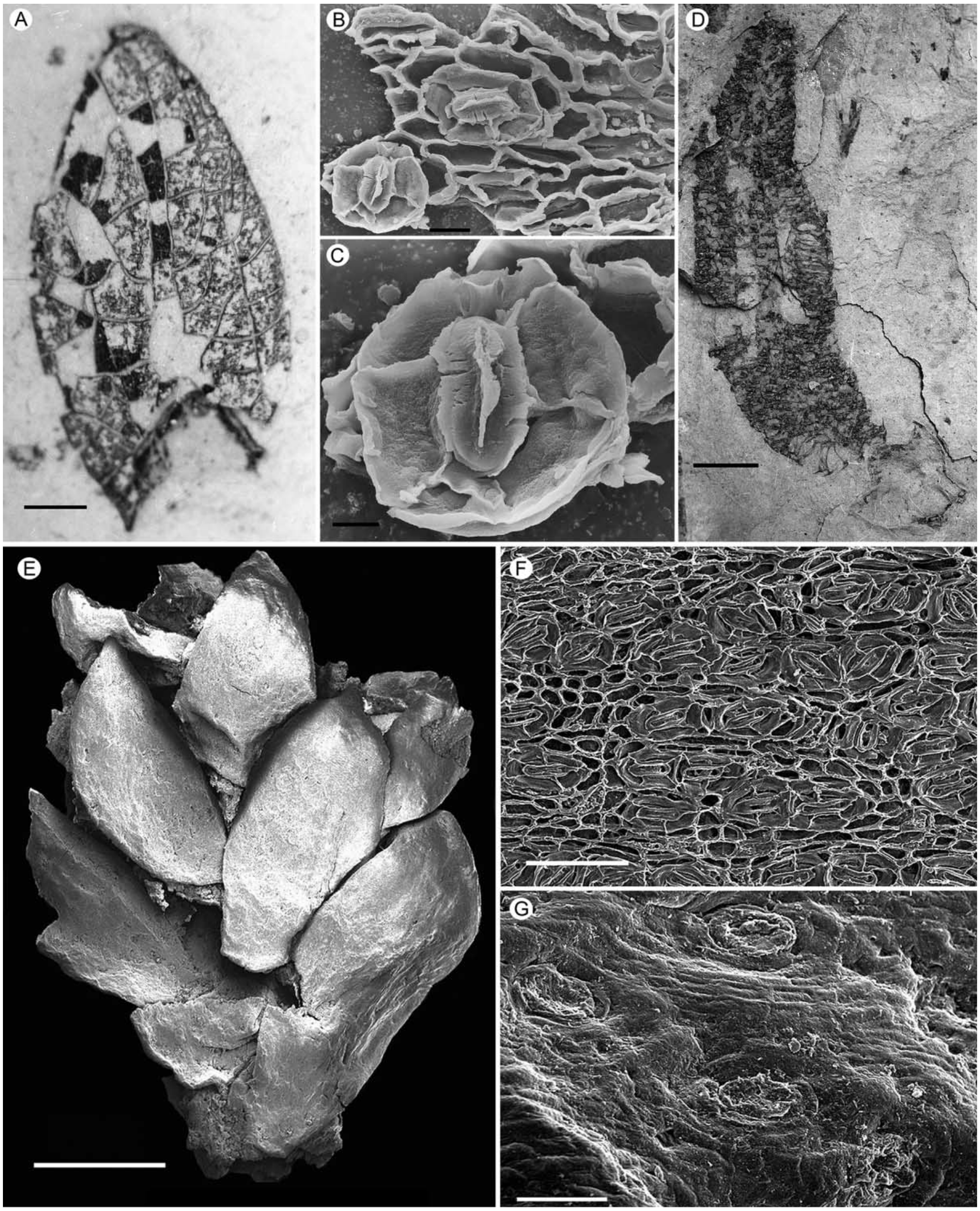

Fig. 8 Fossils of *Araucaria planus* from Cethana (*A–C*; C-632) and Kiandra (*E–G*; K-1006) and a male araucarian cone from Cethana (*D*; C-647). *A*, Single leaf with the broad attachment shown at the base. *B*, SEM of the inner cuticular surface, showing two randomly oriented stomata. *C*, SEM of the inner surface of a stoma, showing that the cuticle extends only a relatively short distance between the guard and the subsidiary cells and that the granular cuticle covering the subsidiary cells tapers at the margin with epidermal cells. Polar extensions are moderately developed. *D*, Male araucarian cone from Cethana (C-647). *E*, SEM of a leafy shoot with spirally arranged leaves. *F*, SEM of the inner stomatal surface, showing moderately dense stomata in loosely defined rows and individual stomata with random orientation. *G*, SEM of the outer leaf surface, showing moderately sunken stomata, with possible remnants of a wax plug in the stomatal pore. Scale bars = 1 mm (*A*), 25 μm (*B*), 10 μm (*C*), 5 mm (*D*), 2 mm (*E*), 100 μm (*F*), 50 μm (*G*).

one unrecorded species of *Araucaria* section *Eutacta* and that Lea River and Little Rapid River each contain two. The next issue is to determine whether there are any species in common among these fossil localities. The Lowana Road/Regatta Point taxon is distinct from all others in having very large leaves, and it is assigned to *A. macrophylla*. It is approached in leaf size by only one of the Lea River taxa (figs. 2*A*–2*E*, 3*A*–3*C*), but the cuticular pattern of this Lea River taxon is quite distinct from that of *A. macrophylla* in which the stomata are mostly aligned transversely, whereas stomata in the Lea River taxon, here assigned to *A. mollifolia*, are mostly aligned near parallel to the long axis of the leaf. *Araucaria macrophylla* also has a cuticle covering the stomata, with a ragged margin between the guard cells and the subsidiary cells, compared with the smooth margin in *A. mollifolia* (fig. 2*H* vs. fig. 3*F*, 3*G*). Additionally, the cuticular flange between the guard cells and the subsidiary cells in *A. macrophylla* tapers out in a much less defined way than that in *A. mollifolia* (fig. 2*H* vs. fig. 3*F*, 3*G*). In total, these differences strongly indicate the presence of two distinct species.

The Balfour taxon has a leaf shape similar to that of *A. macrophylla* and *A. mollifolia* (fig. 6*A*, 6*B* vs. figs. 2*A*–2*E*, 3*A*–3*C*), and while its cuticular morphology is distinct from *A. macrophylla* (fig. 6*D*–6*G* vs. fig. 2*F*–2*I*), it is very similar to *A. mollifolia* from Lea River (fig. 6*D*–6*G* vs. fig. 3*D*–3*I*). The leaves of the Balfour taxon are only about half the length of those from Lea River, and while leaf length is not necessarily a useful species-level diagnostic character for *Araucaria*, all of the isolated leaves recovered from Balfour were of a similar size, while no smaller leaves similar to those in figure 3 were recovered from the Lea River site. We conclude that the Balfour specimens represent a distinct species from *A. mollifolia*, and they are assigned to *A. balfourensis*.

The largest-leaved specimen from Little Rapid River is in the same size range as *A. balfourensis* (fig. 5*A*, 5*B* vs. fig. 6*A*, 6*B*), and its cuticular morphology is very similar (fig. 5*C*–5*E* vs. fig. 6*D*–6*G*). While the leaf shape is somewhat different, and the stomatal density and arrangement in rows are not identical, we cannot conclude that these differences are enough to warrant recognition of a distinct species. Hence, we propose to place this specimen from Little Rapid River in *A. balfourensis*.

The fragmentary leaves at Pioneer are closest in size to *A. balfourensis*, and they share a similar shape and stomatal morphology (fig. 7*A*–7*C* vs. fig. 6*A*, 6*B*). Also, the cuticular morphologies of these sets of specimens are similar without being identical (fig. 7*D*–7*G* vs. fig. 6*D*–6*G*). Given the fragmentary nature of these fossils, we assign them to *A. balfourensis*, although that may change if better-preserved specimens are located.

The smaller-leaved taxon from Lea River has much smaller leaves than any of the species described above, and this, along with the robust three-dimensional nature of the strongly keeled leaves (fig. 4*A*), warrants separate specific status from any of them. However, the small leaf preserved at Little Rapid River (fig. 5*F*) may belong to the same taxon. The leaf size and shape are similar, and they have similar cuticular morphology, including the pitted nature of the cuticle over the guard and subsidiary cells (fig. 4*C*–4*F* vs. fig. 5*G*, 5*H*), although this is less evident in the Lea River specimens.

The Cethana specimen is similar in leaf size and shape to this taxon shared by Lea River and Little Rapid River (fig. 8*A* vs. figs. 4*A*, 5*F*), but it has a slightly different cuticular pattern over the stomata (fig. 8*B*, 8*C* vs. figs. 4*C*–4*F*, 5*G*, 5*H*) and may represent a distinct species, but in the absence of more and better-preserved specimens, we assign it here to the same species as at Lea River and Little Rapid River. We note that these sites are palynologically coeval.

Finally, the Kiandra shoot is closest in leaf size and shape and stomatal morphology to the small-leaved Lea River taxon (fig. 8*E* vs. fig. 4*A*, 4*B*), and again in the absence of any better-preserved specimens from Kiandra, it is assigned to the same species. However, better-preserved specimens in the future may lead to a reassessment of the affinities of the Kiandra specimens, and we note that there is a temporal and spatial gap between the sites. These specimens from four sites (Lea River, Little Rapid River, Cethana, and Kiandra) are not distinguishable from the previously described *A. planus* (Hill 1990) and are assigned here to that species.

Hence, we conclude that there are four species of *Araucaria* section *Eutacta* among the fossils reported here, three of which are new species.

How Do the Fossil Species Recognized Here Compare with Previously Described Species from Southeastern Australia?

Prior to this study, 12 fossil species of *Araucaria* section *Eutacta* had been described from southeastern Australia based on foliar remains (table 2), and one species had been compared with an extant species. We will consider these published fossil species in alphabetical order:

Araucaria annulata. Known only from dispersed cuticle. Its stomatal morphology is distinct from the species considered here.

Araucaria carinatus. Leaves are 4–17 mm long, 2–12 mm wide. Its cuticular morphology is distinct from any of the species described here, especially the prominent flange of the cuticle that in some cases extends over the lateral subsidiary cells (see Cantrill 1992, fig. 11*C*) and the very distinctive broad polar extensions (see Cantrill 1992, fig. 10*F*). Another distinctive feature of this species is that stomatal bands appear to be separated by stoma-free regions (see Cantrill 1992, fig. 11*A*). The leaves are similar in size and shape to the Lowana Road/Regatta Point species, *A. macrophylla*.

Araucaria crassa. Very small leaves, 3–4.5 mm long, and slightly less than this in width. They have a distinctly different leaf shape from any of the fossils considered here. The storage location of these fossils is unknown to us, and the cuticle is reported only from line drawings and not in enough detail to allow critical comparison with the species reported here.

Araucaria derwentensis. Leaves are broadly ovate, ~7 mm × 5.5 mm, and slightly keeled. The absence of organic preservation in these fossils does not allow critical comparison with the fossil species described here, other than that they fall within the leaf size range of some of them and may prove to be conspecific if more specimens can be located for examination in the future.

Araucaria falcatus. Leaf dimensions are 9–15 mm × 2–4 mm. Cuticle preservation is poor, but stomata are clearly aligned at random. No other comparison is possible. The leaves are almost at right angles to the axis that bears them, and they are long and thin and clearly distinct from any of the newly described fossil species considered here.

Araucaria fletcheri. This species is preserved as shoots that contain leaves that are ~4.5 mm × 3 mm in size, keeled on the lower side, and amphistomatic. The cuticle is preserved and confirms the assignment to section *Eutacta*. However, published light micrographs do not allow for close comparison with the new fossil species. We were unable to locate any specimens of this species for further examination.

Araucaria* sp. cf. *A. heterophylla. This fossil was not described as a new species but instead was compared with a living species. It is considered in the next section, where the fossil taxa are compared with living species.

Araucaria lignitici. Leaf dimensions are 3–8 mm × 1 mm. Whole shoots are preserved, and the leaf morphology is clearly distinct from any of the new fossil species considered here. Polar extensions of the guard cells are absent, and stomatal plugs are usually prominent.

Araucaria otwayensis. Leaves are 20 mm long, and the width is uncertain. They are described as "leaves not well defined, appearing thornlike or stretched against axis, keeled, lanceolate, base broad, margins entire" (Cantrill 1992, p. 635). The small cuticular fragments show a very thick cuticle, unlike any of the new fossil species considered here.

Araucaria planus. Leaves are preserved in a shoot and are individually 4 mm × 2 mm. They appear to be broadest just above the base. Although not identical, they are difficult to separate from the Lea River shoot and individual small leaves, the small-leaved taxon at Little Rapid River, the single leaf from Cethana, and the Kiandra shoot. The Monpeelyata specimen has relatively poor cuticle preservation, but every character that can be observed is consistent with assigning these new fossils to *A. planus*. There are some minor differences among specimens from different sites, but we consider these to fall within acceptable levels for within-species variation and hence identify these new fossils as *A. planus*.

Araucaria prominens. This species is represented by only a single detached leaf, 5 mm × <2 mm in dimension, which has a distinctly acute and incurving keel. Although the cuticle is fragmentary, it clearly demonstrates the species's affinity with section *Eutacta*. The leaf shape is distinct from all the new fossil species considered here, as is the presence of prominent, extruded wax plugs in each stomatal opening.

Araucaria readiae. This is the only species of *Araucaria* section *Eutacta* that has previously been described from one of the fossil sites considered here—Regatta Point. The holotype of this species consists of a leafy shoot, with spirally arranged and relatively small leaves about midway in size between the leaves on the Balfour and Lea River shoots. The cuticular morphology of *A. readiae* appears to be distinct from all the taxa considered here. In particular, it has usually clear polar extensions, indicating where the guard cells ended over the subsidiary cells. These are common in *A. readiae* but are rarely preserved in the new fossil species described here.

Araucaria uncinatus. This species consists of a single detached leaf, 5 mm × <2 mm in dimension, strongly keeled, with an acute, incurving apex. The cuticle is fragmentary, and overall stomatal distribution is unknown. Stomatal plugs are absent, and stomata are randomly oriented, confirming the affinity to section *Eutacta*. The leaf size and shape of this species are distinct from the new fossil species described here.

How Do the Fossil Species Recognized Here Compare with Previously Described Fossil Species from Other Parts of the World?

Macrofossils of *Araucaria* section *Eutacta* are most commonly found in Australia (Hill and Brodribb 1999), but there are important records elsewhere. Table 3 shows published records from outside of Australia that must be compared with the fossil species reported here. We will consider these species in the order shown in table 3.

Table 3

List of Fossil Species of *Araucaria* Section *Eutacta* Previously Described from Outside Australia Based on Foliar Remains

Araucaria species	Locality	Age	Reference(s)
A. desmondii	Eastern Otago, New Zealand	Late Cretaceous	Pole 1995
Araucaria sp. 1	Manuherikia Group, New Zealand	Early Miocene	Pole 1992
Araucaria sp. 2	Manuherikia Group, New Zealand	Early Miocene	Pole 2008
Araucaria? sp.	Manuherikia Group and Gore Lignite Measures, New Zealand	Early Miocene	Pole 2007
A. fibrosa	Vega Island, Antarctica	Late Cretaceous	Cesari et al. 2001; Cesari et al. 2009
A. fildensis	King George Island, Antarctica	Early–middle Eocene	Shi et al. 2018
A. pararaucana	Sloggett Bay, Tierra Del Fuego Province, Argentina	Eocene–early Oligocene	Panti et al. 2007
Araucaria sp. cf. *A. nathorstii*	Loreto Formation in Río de las Minas, Punta Arenas, Chile	Late Eocene	Ohsawa et al. 2016
A. pichileufensis	Río Pichileufú, Argentina	Eocene	Berry 1938

Table 4

Summary of Key Morphological Characters of Living *Araucaria* Section *Eutacta* Species and the Four Fossil Species Considered Here

Araucaria species	Leaves (length × width, mm)	Stomatal distribution	Stomatal orientation	No. subsidiary cells	Stomatal dimensions (length × width, μm)
A. bernieri J. Buchholz	1–3.5 × 1–2.5	2 bands adaxially, 2 basal groups abaxially extending to thin bands to apex; discontinuous irregular rows	Oblique, rarely parallel or perpendicular	4 common, 5 occur, 3 rare	66 × 47
A. biramulata J. Buchholz	5–9 × 4–6	Discontinuous rows on either side of midrib with variable spacing between rows, on both leaf surfaces	Perpendicular, few oblique, rarely parallel	4 common, 5 occur, 6 rare	83 × 55
A. columnaris (J.R. Forst.) Hook.	5–7 × 4–5 4–7 × 2–3 (J)	Adult foliage: discontinuous rows on adaxial surface, 2 basal groups abaxially; juvenile foliage: 2 bands of discontinuous rows adaxially, 2 basal groups abaxially	Most perpendicular, some oblique, rarely parallel	4 common, 5 occur, 6 rare	60 × 41
A. cunninghamii Aiton ex D. Don	5–6 × 1.5–2 7–9 × 1.5–2 (J)	Adult foliage: 2 groups on both surfaces, only basal on abaxial; juvenile foliage: 2 extensive groups both surfaces	Most oblique, few parallel, rarely perpendicular	4 common, 5 occur, 6 rare	60 × 52
A. heterophylla (Salisb.) Franco	6 × 5–6	2 extensive groups adaxially, 2 basal groups abaxially	Most oblique, few parallel or perpendicular	4 common, 5 occur, 6 rare	66 × 59
A. humboldtensis J. Buchholz	5–6 × 4–5	2 basal groups abaxially, 2 elongate bands adaxially	Most oblique, few parallel or perpendicular	4 common, 5 occur, 3 rare, 6 rare	89 × 78
A. laubenfelsii Corbasson	12–20 × 8–10	Discontinuous rows on both surfaces with more on adaxial	Most perpendicular, some oblique, few parallel	4 common, 5 occur, 6 rare	79 × 55
A. luxurians (Brongn. & Gris) de Laub.	5–7 × 4–5 6–12 × 1 (J)	2 distinct bands on both surfaces with more adaxially, some leaves with fewer stomata adaxially near tip	Most oblique, some parallel, few perpendicular	4 common, 5 occur, 3 rare, 6 rare	75 × 52
A. montana Brongn. & Gris	11–14 × 7–8	2 basal groups on abaxial surface, 2 broad bands on adaxial surface	Most oblique, perpendicular common, rarely parallel	4 common, 5 occur, 6 rare	96 × 78

A. muelleri (Carriere) Brongn. & Gris	30–35 × 15–20 18–20 × 7–8 (J)	Discontinuous rows on both leaf surfaces of adult foliage and on adaxial of juvenile; 2 basal groups on abaxial juvenile	Most perpendicular, some oblique, and parallel	4 common, 5 occur, 3 rare, 6 rare	80 × 75
A. nemorosa de Laub.	6–10 × 1.5–3 4–8 × 0.8–1.2 (J)	2 continuous bands on both surfaces	Most perpendicular, several oblique, few parallel	4 common, 5 occur, 3 rare, 6 rare	66 × 35
A. rulei F. Muell.	15–25 × 11–14	2 basal groups on abaxial surface, discontinuous rows cover adaxial surface	Most oblique, few parallel and perpendicular	4 common, 5 occur, 6 rare	93 × 81
A. schmidii de Laub.	7–10 × 1.5–2	2 basal groups on adaxial, 2 wide bands on abaxial surface	Most perpendicular and oblique, rarely parallel	4 common, 5 occur, 3 rare	58 × 45
A. scopulorum de Laub.	3–4 × 2.5–3	2 basal groups, widely spaced rows abaxially, 2 broad bands adaxially	Most oblique, rarely perpendicular and parallel	4 common, 5 occur	77 × 64
A. subulata Vieill.	4–6 × 2–2.5 2–7 × 1–1.5 (J)	2 basal groups on abaxial surface, 2 elongate bands adaxially; juvenile foliage with more regular rows	Most oblique, rarely perpendicular or parallel	4 common, 5 occur, 3 rare	55 × 44
A. macrophylla: Lowana Road/ Regatta Point	20–36 × 11–12	Stomata in poorly defined rows	Parallel, oblique and perpendicular in approximately equal numbers	4, 5, and 6 about equal	63 × 53
A. mollifolia: Lea River, large leaf	20–22 × 10–12	Stomata is several clearly defined rows	Mostly parallel, with some oblique, and none perpendicular	4 common, 5 occur, 6 rare	72 × 47
A. balfourensis: Balfour, medium leaf shoot; LRR, large leaf; Pioneer	8–15 × 4–5	Some row development	Ranges from typically perpendicular or nearly so, less typically oblique or parallel	4 common, 5 occur, 6 rare	51–86 × 42–61
A. planus: Lea River, small leaf; LRR, small leaf; Cethana; Kiandra	4–7 × 2–3	Some clear row development, but also sometimes in patches	Most oblique or parallel; some specimens perpendicular dominates	4 common, 5 occur, 6 rare	62–73 × 43–54

Note. Juvenile foliage characters are labeled (J). Most data from Stockey and Ko (1986), with some from Silba (1986) and Kranitz (2005).

***Araucaria desmondii*.** This is a particularly enigmatic species, included here because the stomata are oriented well away from parallel to the long axis of the leaf. Pole (1995, p. 1069) placed this species in a new section of *Araucaria*, mostly because he believed the stomatal orientation was closer to *Agathis* than to *Araucaria*, but the leaves were clearly *Araucaria* because the "triangular morphology of these leaves with broad attachment clearly places them in *Araucaria* and not *Agathis*." However, the two specimens illustrated as drawings (Pole 1995, figs. 2–4) show leaf fragments without a preserved base and with a rounded leaf apex. It is unclear why these leaves were referred to *Araucaria* rather than to *Agathis*. The multiple veins, in combination with the rounded leaf apex and the stomata at highly oblique angles, separate them from any of the new fossil species considered here.

***Araucaria* sp. 1.** Pole (1992) recorded *Araucaria* section *Eutacta* from the early Miocene Manuherikia Group at Bannockburn but did not provide a species description, and the cuticle is not preserved.

***Araucaria* sp. 2.** Pole (2008) illustrates the cuticle from a probable second species of section *Eutacta* from the same locality. Although he provided light microscope images of this taxon, there is not enough information to make a detailed comparison with the new fossil species described here.

***Araucaria*? sp.** Pole (2007) described a small portion of a leafy shoot as an *Araucaria* species, and the very fragmentary cuticle showed stomata with oblique orientation. However, there is no species description, and the leaves are very small, just over 2 mm long, which is unusual for *Araucaria*. In our opinion, there is some doubt about the familial placement of this fossil, and it may also be considered as a possible member of the Podocarpaceae. It is clearly distinct from the new fossil species considered here.

***Araucaria fibrosa*.** Cesari et al. (2001) described *A. antarctica* (later changed to *A. fibrosa* by Cesari et al. [2009]) from the late Cretaceous of Vega Island, Antarctica. The leaves are preserved on shoots and are individually 55–70 mm × 25 mm. These relatively large leaves are similar in shape to the leaves preserved at Lowana Road/Regatta Point, but they are significantly larger. It is clear that the stomata, while not well preserved, are oblique to the long axis of the leaves, a condition unique to section *Eutacta* among living *Araucaria* species. The fossil leaves have several bundles of longitudinally placed fibers within the hypodermis of the leaves, but it is not apparent whether the leaves are genuinely multiveined. Cesari et al. (2001, 2009) compare *A. fibrosa* most closely with extant *A. araucana* (section *Araucaria*). *Araucaria fibrosa* appears to be distinct from any of the new fossil species considered here, but its sectional affiliation requires further research.

***Araucaria fildensis*.** Shi et al. (2018) described *A. fildensis* from the early-middle Eocene of King George Island, Antarctica, based on a broad bract-scale complex. Closely associated shoots, described as juvenile foliage, were assigned to *Araucaria* sp., because they lacked organic connection to the bract-scale complex. These shoots have leaves that are 10–14 mm × ~1 mm, and the cuticle is not preserved. These very narrow leaves are distinct from all the fossils described here, but that may be because this is juvenile foliage that is being compared with adult foliage. Shi et al. (2018) illustrate two isolated leaves that may represent the adult foliage of this species, but they were not in such close association with the bract-scale complex, and hence, better-preserved specimens are required to resolve this.

***Araucaria pararaucana*.** Panti et al. (2007) described *A. pararaucana* from the Eocene–early Oligocene of Sloggett Bay in Tierra Del Fuego Province in Argentina. The leaves vary from 17 mm × 7 mm to 59 mm × 24 mm, and their size and shape are very similar to those from Lowana Road/Regatta Point. Stomata are in parallel and discontinuous rows, in some cases with perpendicular orientation (Panti et al. 2007). Panti et al. (2007) noted that section *Eutacta* is characterized by stomata that are mostly oblique or perpendicular, distributed in two bands or groups. On the basis of this definition, they excluded *A. pararaucana* from section *Eutacta*. However, it does have stomata with variable orientation, and Stockey and Ko (1986) noted that the largest-leaved species of extant section *Eutacta*, *A. muelleri*, does not obviously have stomata in two bands on either side of the midvein. Unfortunately, Panti et al. (2007) do not mention the venation of this species, but given that they conclude it is most similar to extant *A. araucana*, they must believe it to be multiveined. Their illustrations certainly confirm the similarity of *A. pararaucana* to *A. araucana*, and thus, we assume it is distinct from all the new fossil species reported here. The sectional affiliation of this species also requires further research.

***Araucaria* cf. *nathorstii*.** *Araucaria nathorstii* was first described by Dusén (1899) from the late Eocene Loreto Formation, near Punta Arenas in the Magellan Region of southern Chile, and was regarded as belonging to section *Columbea* by Menendez and Caccavari (1966) and Del Fueyo and Archanglesky (2002). Ohsawa et al. (2016) re-collected this locality and described cone scales and leaves with cuticular preservation. This included leafy shoots that probably best reflect the original description of *A. nathorstii*, with multiple veins and stomata oriented parallel to the long axis of the leaf, but also included leafy shoots with much smaller, apparently univeined leaves, with stomata clearly demonstrating random orientation. While Ohsawa et al. (2016) conclude that Dusén's original collections of *A. nathorstii* included both of these leaf forms, they attribute the section *Eutacta* shoots to "*Araucaria* sp.," and hence, it is best to regard this convincing record of section *Eutacta* as being an undescribed species. In the absence of scanning electron micrographs of the cuticle of this species, no further comparison can be made with the new species described here.

***Araucaria pichileufensis*.** Berry (1938) described *A. pichileufensis* from the Rio Pichileufu in Argentina. The leafy twigs bear leaves that are about 7 mm long and 2.5 mm in maximum width. There is no record of organic preservation. Berry notes that this species appears to be intermediate in character between sections *Colymbea* (now *Columbea*) and *Eutacta*, but he considers it closest in form to the extant *Eutacta* species *A. excelsa* (now *A. heterophylla*) and *A. cookii* (now *A. columnaris*). Florin (1940, p. 39) strongly supported an affinity within section *Eutacta*. The leaf dimensions are distinct from any of the new fossil species described here, and this species can be disregarded as a likely identity for them.

Are the Fossil Species Recognized Here Distinct from All Living Species of Section Eutacta?

In order to determine the morphological similarity of the newly reported fossils to the extant species of section *Eutacta*, the general leaf characters that were measured in the fossils are summarized in table 4. One issue arising from this literature search was that in *Araucaria*, juvenile leaves are quite persistent, often typically different in size from adult leaves, and they can potentially fossilize well, adding a complication to the comparisons. However, it is apparent from table 5 that three of the four *Araucaria* species considered here are distinct from any living species. *Araucaria mollifolia* matches *A. laubenfelsii* in four of the five characters presented, and *A. balfourensis* matches *A. biramulata*, and these two comparisons require further consideration.

The leaves of *A. mollifolia* preserve as flattened in two dimensions and hence appear to have had very little three-dimensional structure to them, whereas *A. laubenfelsii* leaves are quite robust and three-dimensional. Similarly, the leaves of *A. balfourensis* appear to be quite two-dimensional and flattened compared with *A. biramulata*, and the cuticle at the margins of the guard cell is not thickened at all in the fossil, but it is clearly thickened in *A. biramulata*. In more general terms, the extant New Caledonian species appear to be the result of a relatively recent radiation of the genus on that land mass (Gaudeul et al. 2012; Kranitz et al. 2014). Hence, finding a close morphological match between a New Caledonian extant species and a Paleogene fossil is more likely to be an example of reradiation and convergence than to represent a true nearest living relative.

Conclusions

A large number of leaf and shoot specimens from eight southeastern Australian Cenozoic localities are assigned here to three new species of *Araucaria* section *Eutacta*, along with some new specimens of the previously described species *A. planus* (table 6). These new discoveries add significantly to the already substantial macrofossil record of *Araucaria* at high southern latitudes and confirm the significance of the section *Eutacta* in the Cenozoic vegetation of southeastern Australia. Such a large number of records of fossil *Araucaria* foliage from across the Southern Hemisphere should allow some general conclusions to be made about how this genus evolved in this region through the Cenozoic. This is hampered to some degree by the difficulty encountered in applying species limits to *Araucaria* fossils based solely on foliage. Nevertheless, for southeastern Australia, two trends appear to be emerging: (1) Although spread over tens of millions of years, the high diversity of species is similar to that currently observed in New Caledonia, and it appears likely that there was a high

Table 5

Characters Shown in Table 4 with the Closest Matches for the Fossil Species, with Extant Species Indicated

Fossil taxon	Leaves (length × width)	Stomatal distribution	Stomatal orientation	No. subsidiary cells	Stomatal dimensions
A. macrophylla: Lowana Road/Regatta Point	*A. rulei* *A. muelleri* *A. laubenfelsii* *A. montana*	Not well enough defined in fossil	*A. muellleri*	No extant match	*A. heterophylla* *A. cunninghamii*
A. mollifolia: Lea River	*A. rulei* *A. laubenfelsii* *A. muelleri*	Matches most extant species	No extant match	*A. biramulata* *A. columnaris* *A. cunninghamii* *A. heterophylla* *A. laubenfelsii* *A. montana* *A. rulei*	*A. bernieri* *A. laubenfelsii* *A. luxurians*
A. balfourensis: Balfour; Little Rapid River; Pioneer	*A. biramulata*	Matches most extant species	*A. biramulata* *A. laubenfelsii* *A. muelleri* *A. nemorosa* *A. schmidii*	*A. biramulata* *A. columnaris* *A. cunninghamii* *A. heterophylla* *A. laubenfelsii* *A. montana* *A. rulei*	Most species. Not: *A. humboldtensis* *A. montana* *A. rulei*
A. planus: Lea River; Little Rapid River; Cethana; Kiandra	*A. columnaris* (J) *A. cunninghamii* *A. nemorosa* *A. schmidii* *A. scopulorum* *A. subulata*	Matches most extant species	Matches most extant species	*A. biramulata* *A. columnaris* *A. cunninghamii* *A. heterophylla* *A. laubenfelsii* *A. montana* *A. rulei*	*A. bernieri* *A. luxurians*

Table 6

Distribution in Time and Space of *Araucaria* Section *Eutacta* Species Identified in This Study

Locality	*A. macrophylla*	*A. mollifolia*	*A. balfourensis*	*A. planus*
Lowana Road	X			
Regatta Point	X			
Lea River		X		X
Little Rapid River			X	X
Cethana				X
Balfour			X	
Pioneer			X	
Kiandra				X

species diversity of *Araucaria* in southeastern Australia at times during the Eocene to Miocene, similar to that observed in other conifer genera (Hill and Brodribb 1999). (2) The wide range of fossil leaf morphology is also similar to that currently observed in New Caledonia, where species are broadly split into large-leaved species and small-leaved species (Gaudeul et al. 2012; Escapa and Catalano 2013), with the latter further subdivided into coastal and inland species. Gaudeul et al. (2012) speculate on the possible reasons for the significant differences in leaf size in the extant New Caledonian species but acknowledge that more research is required to resolve this. This is even more complicated for the fossil *Araucaria* species, which existed over a much greater spatial and temporal range and hence were subject to many variables that could have impacted leaf size.

Overall, the Cenozoic macrofossil record of the Araucariaceae is in need of revision. Although many fossils have been reported, many of these remain undescribed or unnamed, adding considerable confusion to an already complex problem.

The excellent organic preservation of the macrofossils described here has provided much-needed new information. There is no doubt that more *Araucaria* leaf fossils will be described in the future, and we may begin to understand the evolutionary drivers for this common but ecologically unusual genus (it is typically a canopy emergent tree). It is possible that the many organically preserved leaves will soon provide data that will allow a more detailed reconstruction of the environments in which these trees once grew and flourished.

Acknowledgments

This research was funded in part by the Australian Research Council (grant DP130104314).

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