

Biogeography of Araucariaceae

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Introduction

The Araucariaceae, with an extensive fossil record dating to the Mesozoic, has long been of interest to palaeobotanists and plant geographers. Extant members of the family (*Araucaria* Juss., *Agathis* Salisbury, and *Wollemia* WG Jones, KD Hill & JM Allen) are confined predominantly to southern regions but as first recognised nearly a century ago (Seward and Ford 1906), the family was formerly distributed over wide areas of both hemispheres. At that time, the family comprised two extant genera—*Araucaria* and *Agathis*—and was considered to occupy an isolated position amongst the conifers. Following the discovery of living *Wollemia* (Jones et al. 1995), molecular sequence data of extant members have provided some understanding of the inter-relationships within the family and of its relationships with the other ‘southern’ conifer family, Podocarpaceae (Setoguchi et al. 1998).

The incorporation of whole plant data, including morphological and anatomical characters of living and fossil members, may be expected to provide a robust basis for plotting the distribution of the family in time and space thereby yielding meaningful insights into its evolution. In this context morphological and anatomical analyses of recently discovered fossil araucarians have provided further insights into the past diversity and distribution of the family (Stockey 1982, 1994).

The most recent catalogue of extant Araucariaceae (Farjon 1998) lists 41 species grouped into three genera. Although no modern detailed taxonomic treatment of the Araucariaceae is available, several general works (Silba 1986, Page 1990) provide useful accounts of the family, notwithstanding that all predate the discovery of *Wollemia*. An extensive literature is available for fossil taxa assigned to the family, but many of the specimens are impressions or poorly preserved compressions lacking diagnostic characters and so must be treated with caution. In what follows, only reliably identified material is considered unless otherwise specified.

Extant representatives

Agathis Salisbury

Agathis, usually a forest emergent, extends from New Zealand and eastern Australia along the frontal arc to Malesia and Fiji. Species number from at least 13 (Page 1990) to 21 (Laubenfels 1988, Farjon 1998), depending on criteria used to delimit species. Sectional classifications based on external cuticle characters (Page 1980) or on the shapes of microsporophylls, cone scale tips, and seeds (Laubenfels 1988) are not confirmed by cuticle micromorphology (Stockey & Atkinson 1993). Moreover, neither classification is supported by clades generated from cladistic analyses of the plastid gene, *rbcL*, sequence data (Setoguchi et al. 1998, Stöckler et al. 2002).

***Araucaria* Juss.**

Araucaria is the most geographically widespread genus of the Araucariaceae, with a range from South America to eastern Australia and islands in the southwest Pacific. It contains 18-20 extant species, most of which are forest emergents, grouped into four sections as outlined in Table 1.

Table 1: The sections of extant *Araucaria*, their defining characters, and geographic distribution

Section	Characters	Distribution
<i>Eutacta</i> Endlicher	Adult leaves small, awl-like, often keeled, imbricate, erect; juvenile leaves acicular; stomatal orientation oblique or horizontal; seed cone scales thinly winged and shed with seed; vascular trace to bract-scale single; germination epigeal.	New Caledonia, New Guinea, Norfolk Island, Australia
<i>Araucaria</i> Juss. (= <i>Columbea</i> Salisb.)	Adult leaves large, flat, generally thin; juvenile leaves not acicular; stomatal orientation vertical; seed cone-scales nut-like, wings absent, seed retained on scale at shedding; vascular trace to bract-scale single; germination hypogeal.	South America
<i>Intermedia</i> White	Adult leaves large, flat, generally thin; juvenile leaves not acicular; stomatal orientation vertical; seed cone-scales with broad wings; seed retained on scale at shedding; germination epigeal.	New Guinea
<i>Bunya</i> Wilde & Eames	Adult leaves large flat, spreading, imbricate; juvenile leaves not acicular; stomatal orientation vertical seed cone-scales large, woody' wingless; seed shed from scale at maturity; trace to bract-scale double; germination hypogeal	Australia

Note: Adapted from Stockey 1982, Stockey & Ko 1986. The sectional name *Araucaria* replaces *Columbea* to satisfy nomenclatural requirements.

***Wollemia* WG Jones, KD Hill & JM Allen**

Wollemia is a monotypic genus (Jones et al. 1995) with little morphological or genetic variation observable between the less than 100 known trees that grow in three stands along the floor of a gorge in the Wollemi National Park, New South Wales (Royal Botanic Gardens Sydney 2005).

Relationships between and within extant genera of Araucariaceae

Taxa can be classified into hierarchical groups by 'cladistical analysis' on the basis of shared characters. Relationships between the three extant genera of the Araucariaceae and the Podocarpaceae, as suggested by four cladistic analyses, confirm the two families to be sister groups (Stefanović et al. 1998, Fig. 1). However, interrelationships of the three genera of the Araucariaceae are ambiguous. Three cladistic analyses based on gene sequences (Gilmour & Hill 1997, Stefanović et al. 1998, Wagstaff 2004) and one based on morphological/anatomical data place *Wollemia* and *Agathis* in the same 'clade', showing them to be descended from a common ancestor (Figure 2B). A fourth family tree, or 'cladogram' based on gene sequences (Setoguchi et al. 1998) has *Araucaria* and *Agathis* as sister taxa (Figure 2A).

Support for the presently recognized Sections within *Araucaria* is afforded by the analyses that include at least one species from each Section in the sampling protocol (Setoguchi *et al.* 1998, Stöckler *et al.* 2002). However, in each instance the resulting cladogram suggests there are three, not

four, groupings in the genus. This reduction in grouping number results from Sections *Intermedia* and *Bunya* being treated as sister groups—i.e. derived from an immediate common ancestor—in the gene sequence analyses (Gilmour & Hill 1997, Setoguchi *et al.* 1998) and *Araucaria* and *Bunya* being sister groups in the morphological based analyses presented herein.

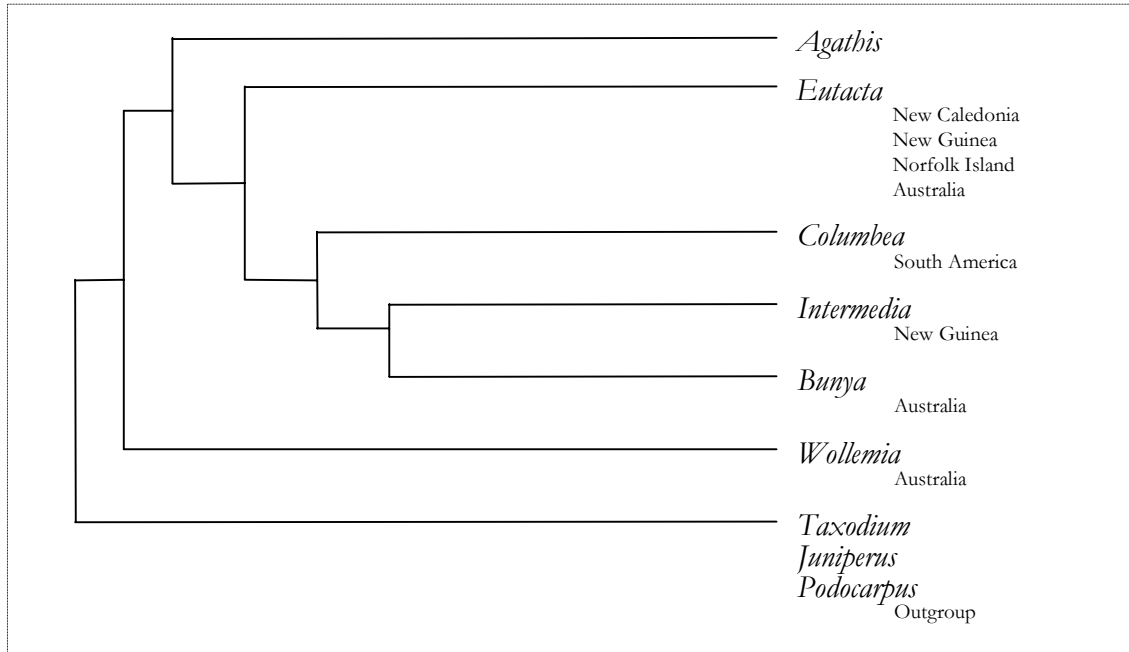


Figure 1: Consensus tree showing the relationships of the genera of Araucariaceae, based on rbcL sequences, with the geographical distributions of each Section of *Araucaria* superimposed. Adapted from Setoguchi *et al.* (1998).

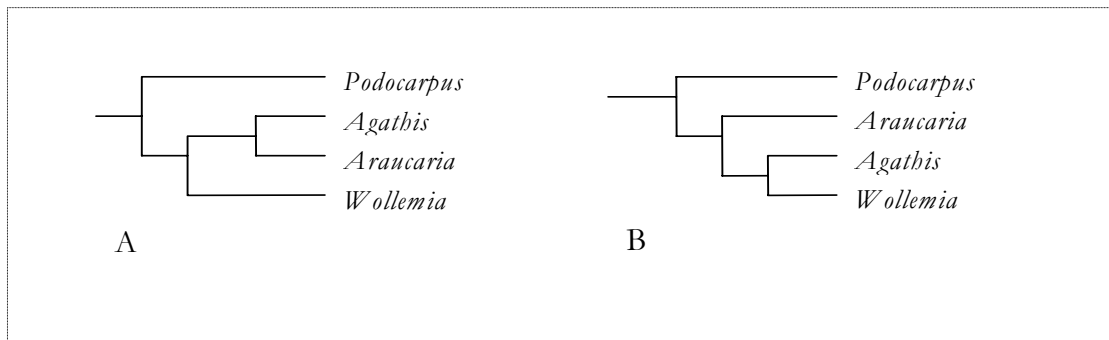


Figure 2. Cladograms, based on molecular sequences, expressing relationships between the genera of Araucariaceae. A. Cladogram resolved by Setoguchi *et al.*(1998); B. Cladogram resolved by Gilmour and Hill (1997), Stefanović *et al.* (1998), and Wagstaff (2004).

Formal taxonomic groupings based on morphological criteria have not been upheld for *Agathis*. However, cladistic analysis of rbcL sequences (Stöckler *et al.* 2002) segregate the genus into two, with the New Zealand endemic, *A. australis*, as sister taxon to the remainder. This, in turn, resolves into three clades, one of which is restricted to New Caledonia, one with species in Australia and one in Borneo, and the other with one species in each of Australia, Fiji, and Vanuatu (Fig.3).

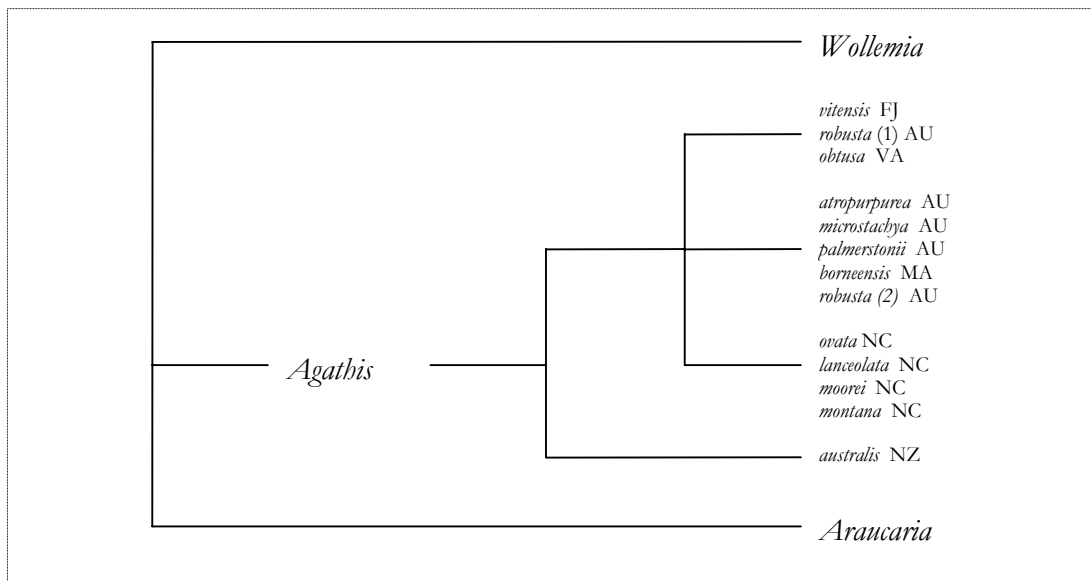


Figure 3: The relationships between the species of *Agathis* along with their geographical distributions. Adapted from Stöckler et al. (2002). AU, Australia; FJ, Fiji; MA, Malesia and Philippines; NC, New Cledonia; NZ, New Zealand; VA, Vanuatu.

Fossil representatives

The fossil record confirms a rich history of the Araucariaceae dating to the Mesozoic when the family was represented in both the Northern and Southern Hemispheres. Well-preserved reproductive structures and foliage date to the Jurassic in England, the United States, India and South America and to the Cretaceous of Japan and Saghalien (an adjacent Russian island), New Zealand, South Africa, Antarctica, and Australia (Stockey 1990, 1994; Hernandez-Castillo & Stockey 2002). Less certainly of araucarian affinities are many of the pre-Jurassic fossils of 'araucarian' foliage and wood (Stockey 1982). For instance, although leaf form of *Brachyphyllum* Lindley & Hutton resembles that of *Araucaria*, only a few of the fossils referred to that category have cuticle diagnostic of the family, while others have been shown to be consistent with the extinct conifer family Cheirolepidaceae (Stockey 1982). *Araucarioxylon* Kraus accommodates fossil wood consistent with the Araucariaceae and also of other disparate groups including that of cordaites (Stockey 1982).

Jurassic and younger reproductive and foliage fossils unquestionably of araucarian affinities include representatives of all extant as well as extinct sections of *Araucaria* (Stockey et al. 1992, Ohsawa et al. 1995, Pole 1995, Hill & Brodribb 1999). *Agathis* has been reliably traced to the Early Cretaceous (Albian), based on organically preserved foliage, but lacking cuticle (Cantrill 1992), and *Wollemia* to the Turonian on the basis of *Dilwynites*, a fossil pollen taxon that replicates pollen of extant *Wollemia* (Chambers et al. 1998, Dettmann & Jarzen 2000). There are foliage fossils of Late Mesozoic and Tertiary of undoubted araucarian affinity, but distinct from *Araucaria*, *Agathis*, and *Wollemia* and believed to represent extinct members of the family. In this category are several species of *Araucarioides* Hill & Bigwood. The pollen taxon, *Araucariacites* Cookson, which is widespread in Mesozoic and Tertiary sediments, accommodates pollen of the *Agathis*- and *Araucaria*-type; pollen of *Agathis* and *Araucaria* are morphologically similar and difficult to discriminate between in the fossil pollen record.

Fossil *Araucaria*

As noted above there is a fossil record of all four sections of extant *Araucaria*; selected fossil taxa representing each of the sections are mentioned and/or discussed below. Also represented in the

fossil record are taxa that have been allocated to two extinct sections that combine characters of several extant sections or have features not known in living members of the genus. Additionally there are several taxa that include fossils possessing features of *Araucaria*, but whose sectional affinities are indeterminate.

Section *Eutacta*

The section, which today is widespread in the southwest Pacific, is known as fossil in Mesozoic sediments from both hemispheres. Northern Hemisphere representatives include the Jurassic cones and cone scales of *Araucaricites phillipsi* Kendall as well as leaves and pollen cones referred to *Brachyphyllum mamillare* Lindley & Hutton from England (Stockey 1994), and the Early Cretaceous cones of *Araucaria cutchensis* (Feistmantel) from the Early Cretaceous of India (Stockey 1994). Foliage with preserved cuticle has been confirmed from the Early Cretaceous of Victoria, Australia (Cantrill 1992) and there are numerous records of foliage and cuticle from the Tertiary of Australia and New Zealand (Hill and Brodribb 1999).

Section *Araucaria* (= *Columbea*)

Foliage remains from the Tertiary of Rio Negro, Argentina and Victoria, Australia assigned to *Araucaria nathorstii* Dusén and to *A. balcombensis* (Selling) respectively are considered representatives of this section (Stockey 1994, Hill & Brodribb 1999). The cone taxon, *A. nipponensis* Stockey, Nishida & Nishida reported from the Upper Cretaceous of Hokkaido, Japan and nearby Saghalien, Russia, is similar to those of Section *Araucaria*, but also possesses characters of Sections *Eutacta* and *Intermedia* (Stockey et al. 1994).

Section *Intermedia*

Fossil leaves of *Araucaria haastii* Ettingshausen and cone scales from the Late Cretaceous of New Zealand conform with this section (Stockey 1994, Pole 1995).

Section *Bunya*

Araucaria mirabilis (Spegazzini), based on permineralised cones from the Jurassic Petrified Forest at Cerro Cuadrado, Argentina, conforms with Section *Bunya*, which today is represented by a single species, *A. bidwillii*, in eastern Queensland. Exceptionally preserved anatomical detail of the fossil cones reveals that two vascular strands lead from the axis to the cone scale complexes, which have winged bracts and vascularized ovuliferous scale tips free from the bract for about half their length. Embryos are similar to those of *A. bidwillii*. 'Seedlings' with swollen hypocotyls were described, but these woody corm-like structures have been reinterpreted as lignotubers and similar to the burls that develop under the bark on living Bunya pines (Stockey 1994, Hernandez-Castillo & Stockey 2002, Stockey 2002). Cones included in *A. sphaerocarpa* Carruthers, from the Middle Jurassic of England, have seeds borne on ovuliferous scales that are anatomically similar to the seeds of living Bunyas (Hernandez-Castillo & Stockey 2002).

There are no reliable fossil records of the section from Australian sediments, and thus far, no record from the Tertiary worldwide.

Section *Perpendiculares* Pole

Pole (1995, p. 1074) proposed the section on the basis of fossil leaves 'having stomate orientation predominantly transverse to the long axis'. The section is represented by a single foliage taxon, *Araucaria desmondii* Pole, from the early Late Cretaceous of New Zealand.

Section *Yezonia* Ohsawa, Nishida & Nishida

This section was proposed for araucarian plants that bore *Brachyphyllum*-like foliage and *Eutacta*-like seed cones, and is based on permineralised vegetative and reproductive fossils of *Araucaria vulgaris*

(Stopes & Fuji) from the Late Cretaceous of Japan (Ohsawa et al. 1995). The single taxon includes foliage originally described as *Yezonia vulgaris* Stopes & Fuji and cones allocated to *A. nibongii* Stockey, Nishida & Nishida. The helically arranged leaves are imbricate with stomates in discontinuous rows restricted to the abaxial surface. Cones are spherical with winged bracts and thin ovuliferous scales. The cones combine features of those of Section *Entacta* (scales with thin wings) and of Section *Araucaria* (cone-scale complexes with vasculature in a single arched row) and Section *Bunya* (double vasculature to the scales at axis).

Araucaria Section unknown

Cones similar to, but larger than, those of *Araucaria mirabilis* have been collected recently from the Lower Cretaceous of Chubut, Argentina. These, which are referred to *A. 'alvarezii'*, have ligulate scales typical of the genus but await systematic documentation (Dernbach & Jung 2002). Foliage fossils referred to *Araucaria*, many with preserved cuticle, but of indeterminate sectional affiliation, occur frequently in Cretaceous and Tertiary sediments of Australia, New Zealand, and Antarctica (Hill & Brodribb 1999, Pole 2000, Cantrill & Falcon-Lang 2001). From the same region, cone scales and impressions of pollen cones occur at some localities, and some of the Australian foliage and cone fossils were considered to compare favourably with *Wollemia* (Chambers et al. 1998). However, arguments against identifying these fossils with *Wollemia* have been outlined by Hill & Brodribb (1999) and Pole (2000).

Fossil *Agathis*

In their review of fossil Araucariaceae, Hill and Brodribb (1999) consider the oldest reliably identified remains to be those from the Middle Eocene of Australia. Thus, they question the generic placement of *A. jurassica* White, a foliage taxon associated with seed cone scales, but without organic preservation, from the Jurassic Fish Beds, Talbragar, New South Wales; this taxon has also been compared with *Wollemia*, but detailed analysis has not yet been undertaken. Also without cuticle preservation is *Agathis victoriensis* Cantrill (1992) from the Albian of Victoria, a record accepted by Stockey (1994). Mid-Cretaceous foliage from New Zealand has been identified as *Agathis*, but this awaits systematic documentation (Daniel et al. 1989). According to Stöckler et al. (2002) the fossil foliage closely resembles that of extant *A. australis*, which they argue evolved from a New Zealand ancestor rather than from a migrant Australian taxon.

Securely identified compression fossils of *Agathis* are all from Middle Eocene and later sediments of southern Australia. Most are of foliage, but ovulate cone scales have been reported from the Oligocene of Tasmania (Carpenter 1991).

Fossil *Wollemia*

No macrofossils have been reliably identified as representing *Wollemia*, but *Agathis jurassica* (noted above), leaf fossils included in *Araucarioides* Bigwood & Hill, and various Cretaceous leaves, ovuliferous cone scales and pollen cones from Australia have been nominated as potential candidates (Chambers et al. 1998, Hill & Brodribb 1999). The latter authors note important differences between Tertiary *Araucarioides* and *Wollemia*, and Pole (2000, p.156) considers that Queensland Winton Formation impression fossils assigned to *Araucaria* are 'unlikely to represent *Wollemia*'. Nevertheless, reassessment of araucarian macrofossils may provide evidence of *Wollemia* foliage/reproductive structures in the fossil record.

Pollen evidence provides a fossil record of *Wollemia*. The distinctive pollen of *Wollemia* replicates the fossil pollen taxon, *Dihymnites* Harris, which has oldest occurrences in the Late Cretaceous (Turonian) of Australia and Antarctica and a Late Cretaceous-Early Tertiary distribution range that encompasses Australia, New Zealand and Antarctica. Youngest recorded records of *Dihymnites* are in the Miocene of New Zealand and late Pliocene of Australia (Macphail et al 1995, Dettmann & Jarzen 2000).

Extinct and indeterminate Araucariaceae

Araucariooides Bigwood & R.Hill

The genus was proposed for Araucariaceae leaf fossils that cannot be unequivocally be placed in an extant genus (Bigwood & Hill 1985). Although instituted without knowledge of leaf form/anatomy of *Wollemia*, the fossil genus is considered distinct from *Wollemia*, *Agathis*, and *Araucaria* (Hill & Brodribb 1999, Pole 2000). Described species of *Araucariooides* are from Albian and Eocene sediments of southeastern Australia and the Campanian of New Zealand (Hill & Brodribb 1999).

Araucarites Presl

Araucarites is a fossil genus with araucarian-like cones and cone scales which cannot be assigned with certainty to extant members of the family. Thus, *Araucarites* has been the repository of Mesozoic and Tertiary araucarian cones (and cone scales) lacking diagnostic characters or requiring further detailed investigation. These have been reported from Mesozoic sediments in both hemispheres and are common in Jurassic-Tertiary sediments of austral areas.

Biogeographic implications

Records of reliably identified araucarian fossils demonstrate that the family has a history extending to at least the Early Jurassic. Of extant taxa, *Araucaria* has the longest history dating to the Early Jurassic, and the genus persisted and diversified in both hemispheres during the Late Mesozoic. By latest Cretaceous-earliest Tertiary times all extant sections of *Araucaria* had differentiated, and in addition there were representatives of groups that are now extinct. Tertiary fossil occurrences imply restriction of the distribution range of the genus to the Southern Hemisphere encompassing the southern Gondwanan region of South America, Antarctica, New Zealand, and Australia. By latest Tertiary times, *Araucaria* was extinct on Antarctica and New Zealand, and in Australia was represented only along the continent's northeastern coastal margin having contracted from Western and southern Australia during sustained periods of climatic drying and increased seasonality (Kershaw & Wagstaff 2001). Today, the genus occupies cloud forests in South America and 'drier' rainforests of northeastern Australia and New Guinea. The area to the east, encompassing New Caledonia and subjacent islands, is the present centre of diversity of the genus.

Within *Araucaria*, Sections *Bunya* and *Eutacta* have the longest histories, both dating to the Jurassic and both occurring in the two hemispheres during the Mesozoic. Mesozoic records of *Bunya* include beautifully preserved cones, *A. mirabilis*, from the Jurassic of Patagonia, but there are scant records of its Tertiary history. Today the section is represented by a single species, *A. bidwillii*, in eastern Queensland. Section *Eutacta*, which today contains the most species, is concentrated in the southwest Pacific region. It is known from diverse Mesozoic fossils in both hemispheres, but Tertiary macrofossils are known only from Australia and New Zealand. These include numerous foliage taxa that are common at some localities in southern Australia and New Zealand.

Section *Araucaria*, which is represented by two living species in South America, has a history extending to the Early Tertiary in South America and southern Australia, and may have differentiated earlier if the cone taxon, *A. nipponensis*, proves to be an early member (Late Cretaceous) of this section. As mentioned above, the cone taxon is not entirely conformable with cones of present day members of the section. The fossil record of Section *Intermedia* is limited, being known only from foliage and cone scales from the Late Cretaceous of New Zealand. Extant members are restricted to Papua New Guinea.

Amongst the fossils allocated to *Araucaria* are foliage and cone taxa that possess character combinations not known in living members of the genus. These fossils are believed to have expressed higher diversity levels in the past than at present, and have provided the basis for adding extinct sections to the genus. On macrofossil evidence presently accrued, it would appear that

diversification of *Araucaria* accelerated during Cretaceous-Early Tertiary times, a time period during which the other two extant araucarian genera, *Wollemia* and *Agathis*, enter the fossil record.

Undisputed fossils of *Agathis* occur in Middle Eocene and later sediments of southern Australia, but, if records of Victorian *Agathis victoriensis* are confirmed as belonging to the genus, then its history dates to the Early Cretaceous (Albian). Contraction of the genus to northeastern Queensland, where five species survive today, occurred in latest Tertiary-Quaternary times (Kershaw & Wagstaff 2001). Fossil occurrences of *Agathis* in New Zealand have yet to be confirmed, but Stöckler *et al.* (2002) accept a record for undescribed mid-Cretaceous foliage. Today there is one species in New Zealand, and the remainder of non-Australian taxa occur in New Caledonia, Vanuata, Fiji, and Malesia with the most northern occurrence in the Philippines.

The known fossil distribution of *Wollemia* is based on fossil pollen, which resolves first appearances of the genus in the Late Cretaceous (Turonian) and a Late Cretaceous-Early Tertiary distribution in Antarctica, New Zealand and Australia. By the latest Tertiary, *Wollemia* was confined to Australia and New Zealand, and today is relict at one locality in New South Wales. Older (Early Jurassic, Early Cretaceous) macrofossil taxa nominated as potentially representing *Wollemia* are all preserved as impressions lacking cuticular and anatomical detail, and should not be accepted as unambiguous evidence of the genus.

The Araucariaceae has a long and complex history, some understanding of which is revealed by the fossil record. This underscores the antiquity of *Araucaria*, and expresses the higher diversity levels and more widespread geographical distribution of the genus in the past than at present. It also emphasises earlier appearances of *Araucaria* (Early Jurassic) than either *Agathis* (late Early Cretaceous) or *Wollemia* (early Late Cretaceous). In this context the fossil record lends more support to phylogenies that resolve *Araucaria* occupying a more basal position in the family than *Agathis* and *Wollemia*.

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