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PHYLOGENETIC RELATIONSHIPS WITHIN ARAUCARIACEAE BASED ON *RBCL* GENE SEQUENCES[1]

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Phylogenetic relationships were determined in the Araucariaceae, which are now found mainly in the Southern Hemisphere. This conifer family was well diversified and widely distributed in both hemispheres during the Mesozoic era. The sequence of 1322 bases of the *rbcL* gene of cpDNA was determined from 29 species of Araucariaceae, representing almost all the species of the family. Phylogenetic trees determined by the parsimony method indicate that Araucariaceae are well defined by *rbcL* sequences and also that the monophyly of *Agathis* or *Araucaria* is well supported by high bootstrap values. The topology of these trees revealed that *Wollemia* had derived prior to *Agathis* and *Araucaria*. The *rbcL* phylogeny agrees well with the present recognition of four sections within *Araucaria*: *Araucaria, Bunya, Eutacta*, and *Intermedia*. Morphological characteristics of the number of cotyledons, position of male cone, and cuticular micromorphologies were evaluated as being phylogenetically informative. Section *Bunya* was found to be derived rather than to be the oldest taxon. Infrageneric relationships of *Agathis* could not be well elucidated because there are few informative site changes in the *rbcL* gene, suggesting the more recent differentiation of the species as their fossil records indicate. The New Caledonian *Araucaria* and *Agathis* species each formed a monophyletic group with very low differentiation in *rbcL* sequences among them, indicating rapid adaptive radiation to new edaphic conditions, i.e., ultramafic soils, in the post-Eocene era.

Key words: *Agathis*; *Araucaria*; Araucariaceae; Gondwana; *rbcL*; *Wollemia*.

From the biogeographical point of view, the Araucariaceae are one of the most interesting families with a primarily Southern Hemisphere distribution. They occur in South America, Australia, New Zealand, New Guinea, New Caledonia, and other South Pacific islands. The family consists of three well-defined genera, *Araucaria* de Jussieu (19 extant species sensu de Laubenfels [1972, 1988], *Agathis* Salisbury (13 species: Mabberley, 1987) and the monotypic genus *Wollemia* W. G. Jones, K. D. Hill and J. M. Allen. The first two genera have been recognized for more than a century; *Wollemia* was recently found in New South Wales, Australia, and described in 1995. All species of *Araucaria* and most of *Agathis* species are restricted to the Southern Hemisphere. Some species of *Agathis* occur north of the equator in Malaysia, but this is regarded as a result of migration from the Southern Hemisphere to the Northwest during the Plio-Pleistocene (Florin, 1963). Thus, the extant species of the family are assumed to be of southern origin.

The genera *Araucaria* and *Agathis* each have distinctive morphological characteristics of leaves and cone elements (bract scale, ovuliferous scale, and seed), described before *Wollemia* was known. *Wollemia* shows intermediate characteristics between *Araucaria* and *Agathis* (Jones, Hill, and Allen, 1995), and similar characteristics are known only in fossil taxa such as *Podozamites* from the Jurassic to Tertiary Periods.

Araucaria is the most diversified genus in the family, being disjunctively distributed throughout the Southern Hemisphere (Chile, Argentina, southern Brazil, New Caledonia, Norfolk Island, Australia, and New Guinea). Although this distribution from a southern Pacific-Antarctic link to South America is generally taken as the result of a vicarious event and/or long-distance dispersal (Pole, 1994; Macphail, 1997), araucarian fossils have been widely excavated not only from the Southern but also the Northern Hemisphere. Further, they had been a major component of the Mesozoic forests (Miller, 1977; Stockey, 1982; Stocky, Nishida, and Nishida, 1992; Hill, 1995). Therefore, *Araucaria*'s present distribution might be considered as the relic type, although its extant species show a distribution pattern very similar to that of *Nothofagus* and other Gondwanan groups.

Fossils of *Araucaria* are among the oldest fossils of extant coniferous genera that have been found since the

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TABLE 1. The geological appearance, distribution, and extant species of five sections of *Araucaria*.

			Section		
	Bunya	*Yezonia*	*Intermedia*	*Araucaria*	*Eutacta*
Earliest fossil record	Jurassic[a]	Cretaceous	late Cretaceous	Tertiary (or late Cretaceous)	Cretaceous (or Jurassic?)
Distribution of fossils	Europe Argentina	Northern Japan	New Zealand	Australia Argentina	Australia (and England?)
Extant species	*A. bidwillii* (Australia)	extinct	*A. hunsteinii* (New Guinea)	*A. araucana* *A. angustifolia* (South America)	*A. heterophylla* (Norfolk Island) *A. cunninghamii* (New Guinea) *A. bernieri* *A. biramulata* *A. columnaris* *A. humboldtensis* *A. laubenfelsii* *A. luxurians* *A. montana* *A. muelleri* *A. nemorosa* *A. rulei* *A. scopulorum* *A. schmidii* *A. subulata* (New Caledonia)

[a] See Discussion.

Triassic or Jurassic eras (Miller, 1977, 1988; Stockey, 1982). Before 1995, *Araucaria* had been infragenerically classified into four extant Sections: *Araucaria* (= *Columbea*), *Bunya, Eutacta,* and *Intermedia* (Wilde and Eames, 1952). In 1995, Ohsawa, Nishida, and Nishida (1995) added the new Section *Yezonia* to include the extinct species. This sectional classification was based on morphology: leaves, attachment of pollen cones and ovulate cones, cone-scale, vascular system cone-scale complex, type of seedling germination, and seedling. Fossil records and extant species within these sections are compared in Table 1. The oldest records of *Araucaria* fossils are those of the Sections *Bunya* and *Eutacta*; they were widespread across both hemispheres during the Jurassic (we are cautious in regard to the treatment of Triassic fossils as Hill [1995] recommended). In the other two extant sections, *Intermedia* and *Araucaria*, the distribution of both extant and extinct species is limited to the Southern Hemisphere (Australia, New Zealand, Tasmania, and Argentina), and their fossil records are relatively recent, starting with the late Cretaceous. Therefore, it is expected that Sections *Bunya* or *Eutacta* will be revealed to be the oldest in the genus *Araucaria* and will locate at the base of the phylogenetic tree of the extant species.

In contrast to that of the much-studied *Araucaria*, the classification of the *Agathis* remains somewhat controversial. In his revision of the entire genus, Whitmore (1980) recognized 13 species based mainly on characteristics of the male cones; *Agathis vitiensis* (from Fiji) and *A. obtusa* (from Vanuatu) were reduced to synonymy with *A. macrophylla* (cf. Whitmore, 1977). However, the species *A. vitiensis* is still recognized in local flora as being distinctive from others (e.g., Smith, 1981). de Laubenfels (1988) recognized 21 species, but his treatment has not gained acceptance. Although infrageneric classification has been proposed by both authors, the morphological differences among groups or sections are very minute compared to those in the infrageneric classification of *Araucaria*.

The highest concentration of specific diversity of Araucariaceae is in New Caledonia. In spite of its small area (19 000 km^2), New Caledonia possesses a very rich and distinctive flora (Jaffré, 1995). This is especially true in the case of the Araucariaceae: 13 of the 19 species of *Araucaria* and five of the 13 species of *Agathis* are endemic to this island and are well diversified in their morphological characteristics (e.g., de Laubenfels, 1972; Veillon, 1978, 1980). Thus in the phylogenetic study of the Araucariaceae, it is indispensable to include all or many New Caledonian species.

This study aims to construct a sequence database for the chloroplast encoded *rbcL* gene in order to reconstruct a molecular phylogeny for the family and to use this phylogeny to address the following questions: (1) Are the three genera of Araucariaceae supported? (2) What is the relationship among *Wollemia, Araucaria,* and *Agathis*? (3) Is the infrageneric classification of *Araucaria* supported? (4) Which section is located in the basal cluster within *Araucaria*? (5) What phylogenetic relationships are observed among species of *Araucaria* and *Agathis* in New Caledonia?

MATERIALS AND METHODS

Material—Plant material was collected from natural habitats or cultivated plantings, dried and preserved in silica gel. In total, 29 species were selected representing all species of *Araucaria* (19 species) sensu de Laubenfels (1972, 1988), and ten species of *Agathis*. The *rbcL* sequence of *Wollemia nobilis* was referenced from GenBank. Materials and collection/source data are listed in Table 2.

Total DNA extraction—Dry samples were frozen using liquid nitrogen and pulverized to a fine powder. Before the DNA extraction, leaf powder was suspended in HEPES buffer (pH 8.0) and centrifuged at 10 000 rpm and 20°C for 5 min to remove the sticky polysaccharide

TABLE 2. Taxa compared for *rbcL* sequence variation and collection/source data.

Species	Collection data/source [cultivation no.]	GenBank accession number
Genus *Araucaria*		
A. angustifolia (Bertol.) Kuntze	Cultivated in Botanical Garden, Universidad Austral de Chile, Chile: Nakazawa and Ono s.n.	GBANU96470
A. araucana (Molina) K.Koch	Cultivated in Botanical Garden, Universidad Austral de Chile, Chile: Nakazawa and Ono s.n.	GBANU96467
A. bernieri Buchholz	New Caledonia: Setoguchi NC95060 (MAK)	GBANU96460
A. bidwillii Hook.	New South Wales, Australia: Setoguchi AUS023 (MAK)	GBANU96472
A. biramulata Buchholz	New Caledonia: Setoguchi NC95019 (MAK)	GBANU96475
A. columnaris (G.Forst.) Hook.	New Caledonia: Setoguchi NC95016 (MAK)	GBANU96461
A. cunninghamii Aiton ex D.Don	Cultivated in Singapore Botanic Garden [no cultivated number]: Setoguchi s.n.	GBANU96469
A. heterophylla (Salisb.) Franco	Norfolk Island: J.-C. Pintaud 381 (MAK)	GBANU96462
A. humboldtensis Buchholz	New Caledonia: Setoguchi NC95077 (MAK)	GBANU96471
A. hunsteinii K. Schum.	Cultivated in Singapore Botanic Garden [B-26]: Setoguchi s.n.	GBANU96468
A. laubenfelsii Corbasson	New Caledonia: Setoguchi NC95014 (MAK)	GBANU96463
A. luxurians (Brongn. et Gris) de Laub.	New Caledonia: Setoguchi NC95058 (MAK)	GBANU96464
A. montana Brongn. et Gris	New Caledonia: Setoguchi NC95090 (MAK)	GBANU96457
A. muelleri (Carriere) Bongn. et Gris	New Caledonia: J.-C. Pintaud no number (MAK)	GBANU96465
A. nemorosa de Laub.	New Caledonia: J.-C. Pintaud 471 (MAK)	GBANU96458
A. rulei F. Muell.	New Caledonia: T. Jaffré 3265 (NOU)	GBANU96466
A. schmidii de Laub.	New Caledonia: J.-C. Pintaud 466 (MAK)	GBANU96473
A. scopulorum de Laub.	New Caledonia: Setoguchi NC95086 (MAK)	GBANU96459
A. subulata Vieill.	New Caledonia: Setoguchi NC97009 (MAK)	GBANU96474
Genus *Agathis*		
A. borneensis Warb.	Cultivated in Singapore Botanic Garden [XG-17]: Setoguchi s.n.	GBANU96476
A. dammara (Lamb.) Rich.	Cultivated in Bogor Botanical Garden [V.F.8-A]: *Setoguchi s.n.*	GBANU96477
A. lanceolata Lindl. ex Warb.	New Caledonia: Setoguchi NC93082 (MAK)	GBANU96481
A. montana de Laub.	New Caledonia: J.-C. Pintaud 467 (MAK)	GBANU96478
A. moorei (Lindl.) Mast.	New Caledonia: Setoguchi NC95059 (MAK)	GBANU96480
A. obtusa Mast.	Cultivated in Bogor Botanical Garden [V.F.7]: Setoguchi s.n.	GBANU96482
A. ovata (Moore) Warb.	New Caledonia: Setoguchi NC95061 (MAK)	GBANU96483
A. palmerstoni F. Muell.	Cultivated in Bogor Botanical Garden [V.F.58]: Setoguchi s.n.	GBANU96479
A. robusta (C.Moore ex F.Muell.) F.M.Bailey	Cultivated in Pamplemouses Botanical Garden, Mauritius, Ohsawa no number (MAK)	GBANU96484
A. vitiensis Benth. et Hook. f. ex Drake	Fiji Islands: Setoguchi F95027 (MAK)	GBANU96485
Genus *Wollemia*		
W. nobilis E.G.Jones, K.D.Hill and J.M.Allen	(referenced GenBank)	GBANU87757

(Setoguchi and Ohba, 1995). Total DNA was isolated from the collected pellet using the CTAB method of Hasebe and Iwatsuki (1990).

Amplification and sequencing of the rbcL gene of cpDNA—The double-stranded DNA of most of the *rbcL* gene of cpDNA, $\sim$1350 bp, was amplified by 30 cycles of symmetric polymerase chain reaction (PCR) as shown by use of primers aF and cR of Hasebe et al. (1994) for *rbcL*. PCR cycle conditions in the first cycle consisted of 2 min at 94°C for denaturation, 1 min at 45°C for primer annealing, and 1 min at 72°C for primer extension. Denaturation time at 94°C was reduced to 1 min during the next 28 cycles. The time at 72°C was increased to 5 min in the last cycle. PCR products were purified by electrophoresis in 1.0% agarose gel using 1 × TAE buffer. The gel was stained with ethidium bromide and the DNA was eluted using Geneclean II (Bio 101, Vista, California, USA). Purified DNAs were sequenced in both directions by the standard methods of the Taq dye deoxy terminator cycle sequencing kit (Perkin Elmer, Foster City, California, USA) on an Applied Biosystems Model 373A automated sequencer (Applied Biosystems, Foster City, California, USA). Primers for this sequence determination were aF, cF, cR, bR, and cR of Hasebe et al. (1994) and originally designed primers ARGbF, ARGsF, and ARGsR. The sequences of these original primers are as follows: ARGbF, 5′-TACCCCTTAGACCTTTTTGAAGAAGGTTC; ARGsF, 5′-ACTGTAGTAGGTAAACTTGAAGGTGAACG; ARGsR, 5′-GAACCTTCCTCAAAAAGGTCTAAGGGGTA. Sequence data were aligned manually with the GENETYX program (The Software Development Co., Tokyo, Japan).

Outgroup—Before the phylogenetic analysis of the Araucariaceae, we examined the phylogenetic position of Araucariaceae among conifers in order to select the outgroup to Araucariaceae. Following Chase et al. (1993), we used the *rbcL* sequences of 20 coniferous taxa and *Ginkgo* (as an outgroup), which were registered in GenBank, along with several species of Araucariaceae. As a result, a cluster of Cupressaceae, Podocarpaceae, and Taxodiaceae formed the sister group to Araucariaceae, and we used the *rbcL* sequences of *Juniperus conferta* (GBANL12573: Cupressaceae), *Taxodium distichum* (GBANS75127: Taxodiaceae), and *Podocarpus gracilior* (GBANX58135: Podocarpaceae) to root phylogenetic trees of Araucariaceae.

Phylogenetic analysis—A database of 1322 bp of the *rbcL* gene was used for the phylogenetic analyses. For the present study, *rbcL* gene sequence (positions 28–1350) were phylogenetically analyzed using PAUP (Phylogenetic Analysis Using Parsimony) version 3.1.1 (Swofford, 1993). We performed the heuristic search under the equal weighting criteria using Tree Bisection Reconnection (TBR) branch-swapping algorithm with MULPARS on, Steepest Descent on, and 100 replicates of random taxon addition. Accelerated transformation (ACCTRAN) was used for optimization in the analyses. We used the bootstrap analysis

TABLE 3. Pairwise distances between species of Araucariaceae and three outgroups. Below diagonal shows absolute distances, and above diagonal shows mean distances.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 *Agathis borneensis*		0.005	0.005	0.005	0.006	0.007	0.007	0.007	0.007	0.008	0.028	0.028	0.028	0.029
2 *Agathis dammara*	7	—	0.005	0.005	0.004	0.003	0.002	0.003	0.002	0.003	0.026	0.026	0.026	0.026
3 *Agathis montana*	7	6	—	0.004	0.001	0.002	0.005	0.002	0.005	0.005	0.024	0.024	0.024	0.025
4 *Agathis palmerstoni*	6	7	5	—	0.005	0.005	0.005	0.005	0.005	0.006	0.026	0.026	0.026	0.027
5 *Agathis moorei*	8	5	1	6	—	0.001	0.004	0.001	0.004	0.005	0.025	0.025	0.025	0.026
6 *Agathis lanceolata*	9	4	2	7	1	—	0.003	0.000	0.003	0.004	0.024	0.024	0.024	0.025
7 *Agathis obtusa*	9	3	6	7	5	4	—	0.003	0.000	0.001	0.026	0.026	0.026	0.026
8 *Agathis ovata*	9	4	2	7	1	0	4	—	0.003	0.004	0.024	0.024	0.024	0.025
9 *Agathis robusta*	9	3	6	7	5	4	0	4	—	0.001	0.026	0.026	0.026	0.026
10 *Agathis vitiensis*	10	4	7	8	6	5	1	5	1	—	0.026	0.026	0.026	0.027
11 *Araucaria montana*	37	34	32	35	33	32	34	32	34	35	—	0.000	0.000	0.001
12 *Araucaria nemorosa*	7	34	32	35	33	32	34	32	34	35	0	—	0.000	0.001
13 *Araucaria scopulorum*	37	34	32	35	33	32	34	32	34	35	0	0	—	0.001
14 *Araucaria bernieri*	38	35	33	36	34	33	35	33	35	36	1	1	1	—
15 *Araucaria columnaris*	37	34	32	35	33	32	34	32	34	35	0	0	0	1
16 *Araucaria heterophylla*	36	33	33	36	32	33	35	33	35	36	7	7	7	8
17 *Araucaria laubenfelsii*	37	34	32	35	33	32	34	32	34	35	0	0	0	1
18 *Araucaria luxurians*	37	34	32	35	33	32	34	32	34	35	0	0	0	1
19 *Araucaria muelleri*	40	37	35	38	36	35	37	35	37	38	3	3	3	4
20 *Araucaria rulei*	42	39	37	40	38	37	39	37	39	40	5	5	5	6
21 *Araucaria araucana*	33	32	29	31	30	31	32	31	32	33	17	17	17	18
22 *Araucaria hunsteinii*	34	29	30	30	29	28	29	28	29	30	16	16	16	17
23 *Araucaria cunninghamii*	40	35	38	40	37	36	37	36	37	38	14	14	14	15
24 *Araucaria angustifolia*	32	29	28	30	29	28	29	28	29	30	16	16	16	17
25 *Araucaria humboldtensis*	37	34	32	35	33	32	34	32	34	35	0	0	0	1
26 *Araucaria bidwillii*	36	31	32	32	31	30	31	30	31	32	16	16	16	17
27 *Araucaria schmidii*	37	34	32	35	33	32	34	32	34	35	0	0	0	1
28 *Araucaria subulata*	37	34	32	35	33	32	34	32	34	35	0	0	0	1
29 *Araucaria biramulata*	37	34	32	35	33	32	34	32	34	35	0	0	0	1
30 *Wollemia nobilis*	27	24	22	23	21	22	24	22	24	25	21	21	21	22
31 *Podocarpus*	119	116	116	115	115	116	116	116	116	117	113	113	113	114
32 *Juniperus*	115	113	113	112	112	113	113	113	113	114	111	111	111	112
33 *Taxodium*	113	112	110	111	111	112	112	112	112	113	107	107	107	108

(Felsenstein, 1985; Felsenstein and Kishino, 1993) of 1000 replicates by the heuristic search under unweighted criteria to assess the internal support for clades. Character state reconstructions were performed using MacClade, version 3.05 (Maddison and Maddison, 1992). All character changes were treated as unrooted, equally weighted, and were resolved using two ways of optimization: accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN).

RESULTS

Sequences for 29 species were obtained and deposited in GenBank (Table 2). Pairwise distances between taxa are listed in Table 3. Values of pairwise percentage sequence divergence ranged from 0 to 1.7% among *Araucaria* species, from 0 to 0.8% among *Agathis* species, from 2.1 to 3.2% between *Araucaria* and *Agathis* species, from 1.3 to 2.0% between *Wollemia* and *Araucaria* species, from 1.6 to 2.0% between *Wollemia* and *Agathis* species, and from 7.4 to 9.0% between Araucariaceae and outgroup taxa. In particular, the values were very low among New Caledonian *Araucaria* and *Agathis* species, between 0 and 0.5% and between 0.1 and 0.2%, respectively (Table 3).

Parsimony analysis resulted in 20 most-parsimonious trees of 281 steps with a Consistency Index of 0.766 (excluding uninformative characters) and a Retention Index of 0.925 under the equal weighting criterion. The strict consensus tree is shown in Fig. 1 with bootstrap values. Furthermore, the topology supported by 50% majority consensus is shown by dotted lines. The topology of the 20 trees was unaltered when Albert's weightings (Albert, Chase, and Mishler, 1993) were substituted.

Relationships between Araucaria, Agathis and Wollemia—The Araucariaceae are well defined by the *rbcL* sequence, and its monophyly is supported to 100% in bootstrap value. The topology of these trees reveals that *Wollemia* derived first and then *Agathis* and *Araucaria*. The monophyly of *Agathis* or *Araucaria* is well supported by high bootstrap values in each search (100 and 89%, respectively).

Phylogeny within Araucaria—The phylogeny of *Araucaria* is relatively well resolved in the present phylogenetic analysis. The phylogenetic trees divided into two clades at first: one clade consists of all 15 species of Section *Eutacta* and another consists of the remaining sections, *Araucaria, Bunya*, and *Intermedia*. In the former clade, *Araucaria cunninghamii* (distributed in Australia and New Guinea) was derived first, and after that, *A. heterophylla* (from Norfolk Island). The 13 endemics of New Caledonia formed a monophyletic group. The homology of *rbcL* sequences among New Caledonian species is very high, between 99.5 and 100% (Table 3). The sequence in ten of the 13 endemics (*Araucaria biramulata, A. columnaris, A. humboldtensis, A. lauben-*

TABLE 3. Extended.

15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
0.028	0.027	0.028	0.028	0.030	0.032	0.025	0.026	0.030	0.024	0.028	0.027	0.028	0.028	0.028	0.020	0.090	0.087	0.085
0.026	0.025	0.026	0.026	0.028	0.030	0.024	0.022	0.026	0.022	0.026	0.023	0.026	0.026	0.026	0.018	0.088	0.085	0.085
0.024	0.025	0.024	0.024	0.026	0.028	0.022	0.023	0.029	0.021	0.024	0.024	0.024	0.024	0.024	0.017	0.088	0.085	0.083
0.026	0.027	0.026	0.026	0.029	0.030	0.023	0.023	0.030	0.023	0.026	0.024	0.026	0.026	0.026	0.017	0.087	0.085	0.084
0.025	0.024	0.025	0.025	0.027	0.029	0.023	0.022	0.028	0.022	0.025	0.023	0.025	0.025	0.025	0.016	0.087	0.085	0.084
0.024	0.025	0.024	0.024	0.026	0.028	0.023	0.021	0.027	0.021	0.024	0.023	0.024	0.024	0.024	0.017	0.088	0.085	0.085
0.026	0.026	0.026	0.026	0.028	0.030	0.024	0.022	0.028	0.022	0.026	0.023	0.026	0.026	0.026	0.018	0.088	0.085	0.085
0.024	0.025	0.024	0.024	0.026	0.028	0.023	0.021	0.027	0.021	0.024	0.023	0.024	0.024	0.024	0.017	0.088	0.085	0.085
0.026	0.026	0.026	0.026	0.028	0.030	0.024	0.022	0.028	0.022	0.026	0.023	0.026	0.026	0.026	0.018	0.088	0.085	0.085
0.026	0.027	0.026	0.026	0.029	0.030	0.025	0.023	0.029	0.023	0.026	0.024	0.026	0.026	0.026	0.019	0.089	0.086	0.085
0.000	0.005	0.000	0.000	0.002	0.004	0.013	0.012	0.011	0.012	0.000	0.012	0.000	0.000	0.000	0.016	0.085	0.084	0.081
0.000	0.005	0.000	0.000	0.002	0.004	0.013	0.012	0.011	0.012	0.000	0.012	0.000	0.000	0.000	0.016	0.085	0.084	0.081
0.000	0.005	0.000	0.000	0.002	0.004	0.013	0.012	0.011	0.012	0.000	0.012	0.000	0.000	0.000	0.016	0.085	0.084	0.081
0.001	0.006	0.001	0.001	0.003	0.005	0.014	0.013	0.011	0.013	0.001	0.013	0.001	0.001	0.001	0.017	0.086	0.085	0.082
—	0.005	0.000	0.000	0.002	0.004	0.013	0.012	0.011	0.012	0.000	0.012	0.000	0.000	0.000	0.016	0.085	0.084	0.081
7	—	0.005	0.005	0.008	0.009	0.014	0.013	0.010	0.014	0.005	0.013	0.005	0.005	0.005	0.015	0.085	0.083	0.082
0	7	—	0.000	0.002	0.004	0.013	0.012	0.011	0.012	0.000	0.012	0.000	0.000	0.000	0.016	0.085	0.084	0.081
0	7	0	—	0.002	0.004	0.013	0.012	0.011	0.012	0.000	0.012	0.000	0.000	0.000	0.016	0.085	0.084	0.081
3	10	3	3	—	0.003	0.015	0.014	0.013	0.014	0.002	0.014	0.002	0.002	0.002	0.018	0.088	0.085	0.082
5	12	5	5	4	—	0.017	0.016	0.014	0.016	0.004	0.016	0.004	0.004	0.004	0.020	0.089	0.087	0.084
17	18	17	17	20	22	—	0.008	0.016	0.002	0.013	0.010	0.013	0.013	0.013	0.015	0.079	0.078	0.075
16	17	16	16	19	21	11	—	0.015	0.008	0.012	0.002	0.012	0.012	0.012	0.013	0.081	0.082	0.082
14	13	14	14	17	19	21	20	—	0.015	0.011	0.015	0.011	0.011	0.011	0.019	0.088	0.086	0.085
16	19	16	16	19	21	3	10	20	—	0.012	0.009	0.012	0.012	0.012	0.014	0.081	0.079	0.076
0	7	0	0	3	5	17	6	14	16	—	0.012	0.000	0.000	0.000	0.016	0.085	0.084	0.081
16	17	16	16	19	21	13	2	20	12	16	—	0.012	0.012	0.012	0.014	0.082	0.082	0.082
0	7	0	0	3	5	17	16	14	16	0	16	—	0.000	0.000	0.016	0.085	0.084	0.081
0	7	0	0	3	5	17	16	14	16	0	16	0	—	0.000	0.016	0.085	0.084	0.081
0	7	0	0	3	5	17	16	14	16	0	16	0	0	—	0.016	0.085	0.084	0.081
21	20	21	21	24	26	20	17	25	19	21	19	21	21	21	—	0.078	0.074	0.076
113	112	113	113	116	118	105	107	116	107	113	109	113	113	113	103	—	0.084	0.093
111	110	111	111	113	115	103	108	114	104	111	109	111	111	111	98	111	—	0.039
107	108	107	107	109	111	99	108	112	100	107	109	107	107	107	100	123	51	—

felsii, A. luxurians, A. montana, A. nemorosa, A. schmidii, A. scopulorum, and *A. subulata*) was identical.

The second major clade in *Araucaria* further divided into two clades, one cluster consists of two South American species of Section *Araucaria* (*A. araucana* and *A. angustifolia*), and of New Guinean species of Section *Intermedia* (*A. hunsteinii*) and Australian species of Section *Bunya* (*A. bidwilli*).

Phylogeny within Agathis—Unlike *Araucaria*, the *rbcL* sequences resolved the relationships in *Agathis* poorly. In the strict consensus tree (Fig. 1), only two monophyletic groups were present: one of *Agathis borneensis* and *A. palmerstonii* (distributed in South East Asia) and another of *A. obtusa* (Vanuatu), *A. robusta* (Australia), and *A. vitiensis* (the Fiji Islands). The 50% majority rule consensus suggested a closer relationship between all four endemics to New Caledonia, and also a relationship between *A. dammara* (distributed in Malaysian region), *A. obtusa, A. robusta*, and *A. vitiensis*, but there is no support for these clusters in the data (bootstrap value <50%).

DISCUSSION

In this study, the *rbcL* sequence data set indicates that the Araucariaceae are a highly coherent taxon and that the monophyly of the genera *Araucaria* and *Agathis* is well supported.

Phylogenetic position of Wollemia—In the phylogenetic tree, the genus *Wollemia* is derived before the divergence of *Araucaria* and *Agathis*. Based on the topology, *Wollemia* can be interpreted as the earliest diverged genus in Araucariaceae. *Wollemia* shares morphologies among *Araucaria* and *Agathis* (Jones, Hill, and Allen, 1995). Morphological characteristics shared by both *Wollemia* and *Araucaria* (i.e., closely crowned sessile and amphistomatic leaves, aristate bract scales) or *Wollemia* and *Agathis* (i.e., fully fused bract and ovuliferous scale, winged seed) are interpreted as plesiomorphic characters in the family. To examine this theory, further knowledge is needed, especially on the comparative morphology of *Wollemia* and related fossil taxa, for understanding the relationships among *Wollemia, Araucaria* and *Agathis*.

Infrageneric relationships of Araucaria—The *rbcL* phylogeny agrees well with the present infrageneric classification system, which recognizes four sections of extant species: *Araucaria, Bunya, Eutacta*, and *Intermedia*. The classification is based on the combination of morphological characteristics, such as leaf shape, stomatal distribution and orientation, polar extension, position of male cone, number of vascular supplies to cone scale and their arrangement, dehiscence of cone scale, number of cotyledons, and germination manner (Wilde and Eames, 1952; Stockey, 1982; Stockey and Ko, 1986). Therefore, most of these morphological characteristics well reflect

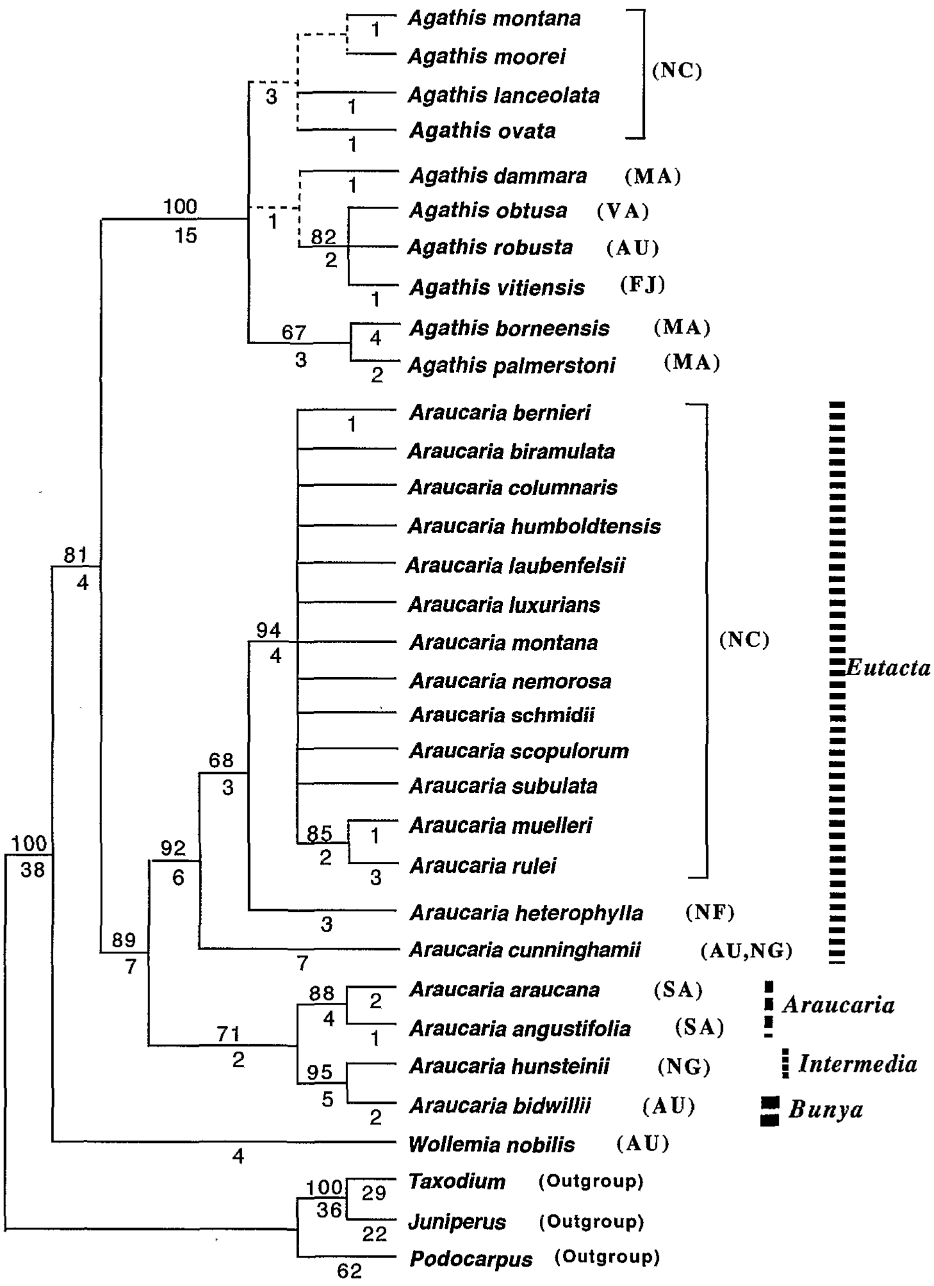

Fig. 1. Consensus tree of the 20 equally parsimonious ones for Araucariaceae based on cpDNA *rbcL* sequences, showing the clades that are supported in the strict consensus by solid lines and the clades that collapse by dotted ones. Length = 281 steps, CI = 0.766 (excluding uninformative data), RI = 0.925. A percentage of the 1000 bootstrap values (>50%) is given for each node. Distribution area for each species is indicated within parentheses. Sectional attribute for each species is indicated by a dashed line. Figure abbreviations: AU = Australia, FJ = Fiji, MA = Malaysian region, NC = New Caledonia, NF = Norfolk Island, NG = New Guinea, NZ = New Zealand, SA = South America, VA = Vanuatu.

the phylogenetic relationships of the genus. In particular, the major branching of the *rbcL* phylogeny in *Araucaria*, which splits Section *Eutacta* from the other sections, corresponded to the number of cotyledons (four in Section *Eutacta* and two in other sections), position of male cone (terminal in Section *Eutacta* and axillary in other sections), stomatal orientation to long axis of leaf (mostly oblique or perpendicular in Section *Eutacta* and mostly parallel in other sections), and stomatal distribution (mostly two bands or groups in Section *Eutacta* and discontinuous rows in other sections). These morphological characteristics should be evaluated as being phylogenetically informative and will be pertinent to estimating the phylogenetic position of extinct species of *Araucaria*.

We further polarized the morphological characteristics discussed above (Figs. 2–6). Figure 2 shows the evolutionary trend in the number of cotyledons. Cotyledons of *Araucaria* vary in number as discussed above, but all species of *Agathis* and *Wollemia* have two (de Laubenfels, 1972, 1988; Whitmore, 1980; Jones, Hill, and Allen, 1995). ACCTRAN and DELTRAN without outgroups showed the same distribution and evolutionary trends of

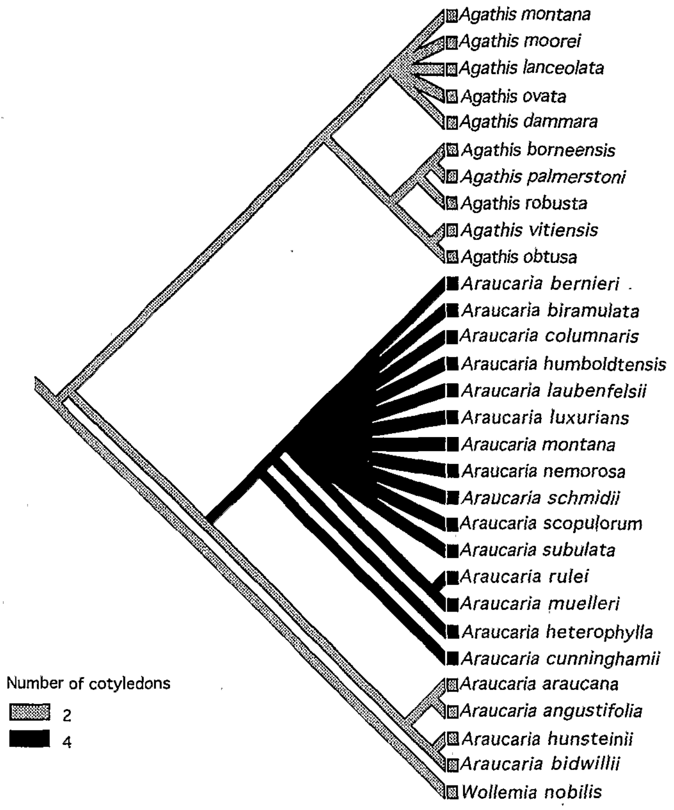

Fig. 2. Parsimonious replacement of characters of the number of cotyledons with ACCTRAN and DELTRAN optimization on the most parsimonious phylogenetic tree based on the *rbcL* gene sequences (Fig. 1). There is no difference in the character distribution between ACCTRAN and DELTRAN optimization.

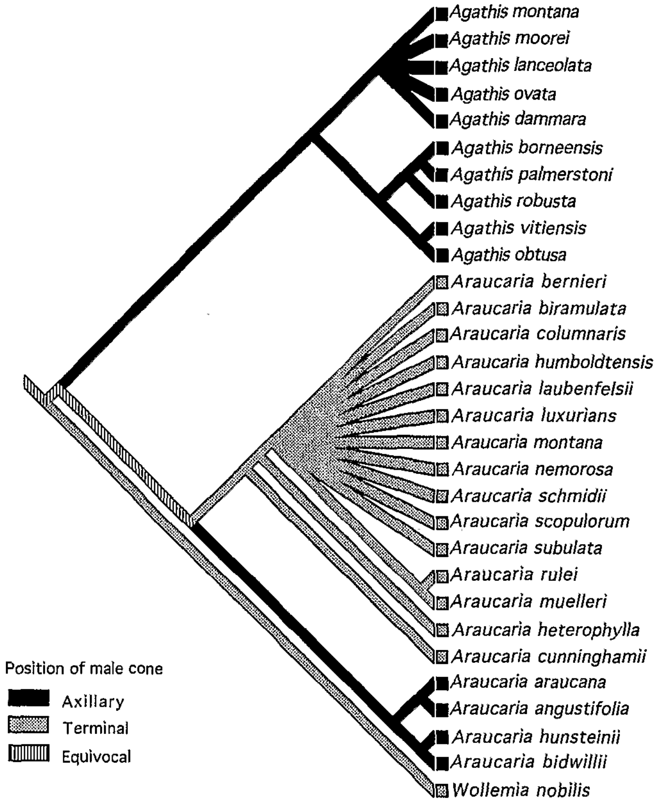

Fig. 3. Parsimonious replacement of the position of the male cone with ACCTRAN and DELTRAN optimization on the most parsimonious phylogenetic tree based on the *rbcL* gene sequences (Fig. 1). There is no difference in the character distribution between ACCTRAN and DELTRAN optimization.

these characters. Parsimony evaluated the plesiomorphy as two both in *Araucaria* and Araucariaceae. This fact agrees well with palaeobotanical data since all araucarian fossil species from the Mesozoic have dicotyledonous embryos (Stockey, 1975, 1978, 1980a, b; Stockey, Nishida, and Nishida, 1992). An increase from two to four cotyledons occurred once at the level of the common ancestor of section *Eutacta*.

Figure 3 shows the evolutionary trend in position of male cone, which is terminated in *Wollemia* (Jones, Hill, and Allen, 1995) and axillary in *Agathis* (Whitmore, 1980). Parsimonious replacement of the character indicates that the plesiomorphic state cannot be determined in either *Araucaria* or the Araucariaceae. A shift from terminal to axillary or from axillary to terminal occurred more than once in the family. The position of the male cone in the fossil record is needed to interpret more about the evolutionary trend.

Figure 4 shows the evolutionary trend in stomatal orientation. Stomata of *Agathis* are obliquely and/or perpendicularly oriented to the long axis of the leaf (Stockey and Atkinson, 1993) and those of *Wollemia* have not been observed. ACCTRAN and DELTRAN evaluated the plesiomorphy as being oblique and/or perpendicular in *Araucaria*. Parallel orientation arose in the ancestor of sections *Araucaria, Bunya,* and *Intermedia.* It has been difficult to assess the placement of the leaves in any extant section because of bad preservation of leaf cuticles in Mesozoic fossil leaves (Stockey, 1994). Therefore, further details of micromorphology of fossil *Araucaria* and cuticle micromorphology in *Wollemia* are needed to determine the evolutionary trends in this character in the family.

Figure 5 shows the evolutionary trend of stomatal distribution. Stomata of *Agathis* occur in discontinuous rows (Stockey and Atkinson, 1993), and those of *Wollemia* are unknown. ACCTRAN and DELTRAN evaluated the plesiomorphy of the stomatal distribution as occurring in discontinuous rows in *Araucaria.* A shift from discontinuous rows to two bands appears to have occurred once in the ancestor of section *Eutacta*, with reversal among New Caledonian *Araucaria.*

Phylogenetic position of the Section Bunya in the genus Araucaria—Before we obtained the *rbcL* phylogeny of Araucariaceae, we expected that *Araucaria bidwillii* of Section *Bunya* would be placed at the bottom of the phylogenetic tree of *Araucaria* since Section *Bunya* is one of the oldest recorded sections from the Jurassic (Wieland, 1935; Calder, 1953; Stockey, 1975, 1978). However, the molecular data do not support the early divergence of Section *Bunya,* because *A. bidwillii* was found to be located in the terminal cluster together with *A. hunsteinii.*

Several palaeobotanical works have already pointed out the differences between *Araucaria bidwillii* and the

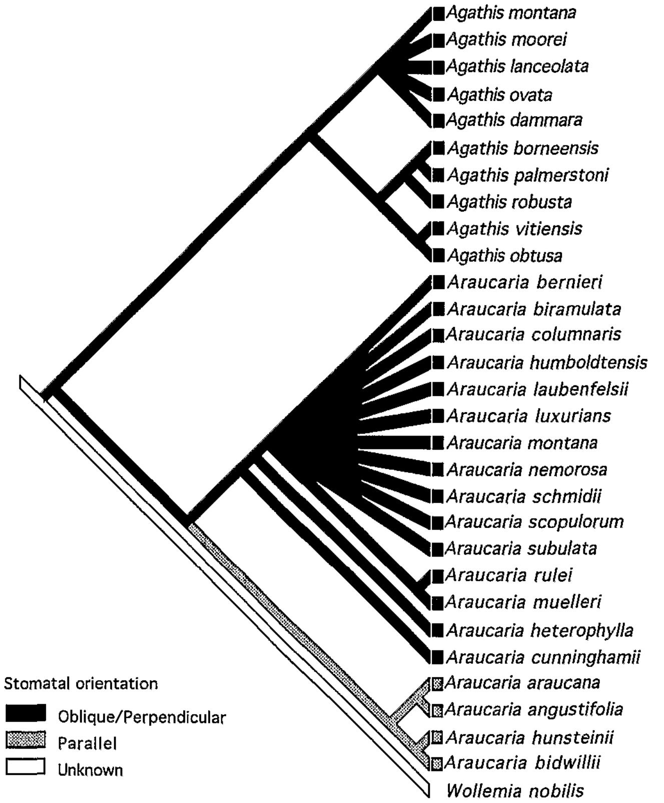

Fig. 4. Parsimonious replacement of stomatal orientation with ACCTRAN and DELTRAN optimization on the most parsimonious phylogenetic tree based on the *rbcL* gene sequences (Fig. 1). There is no difference in the character distribution between ACCTRAN and DELTRAN optimization.

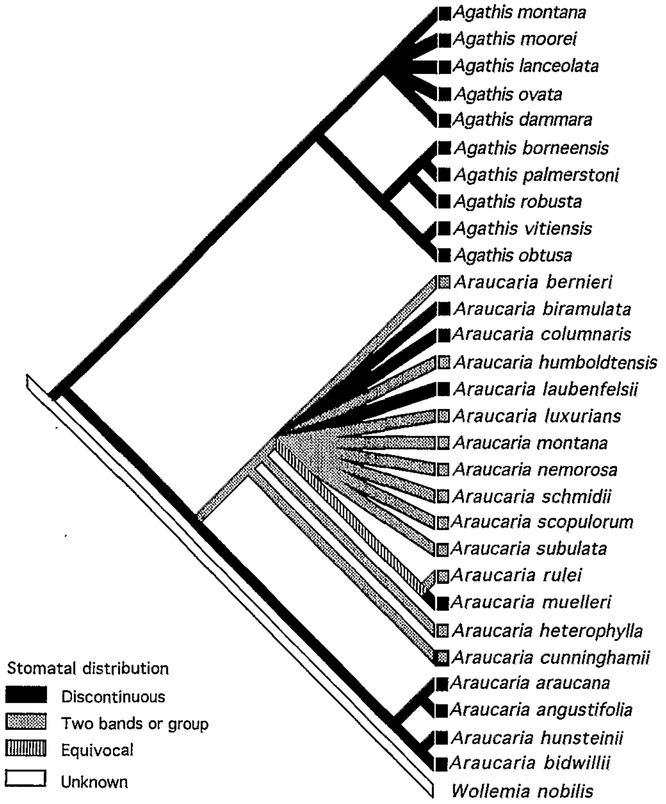

Fig. 5. Parsimonious replacement of stomatal distribution with ACCTRAN and DELTRAN optimization on the most parsimonious phylogenetic tree based on the *rbcL* gene sequences (Fig. 1). There is no difference in the character distribution between ACCTRAN and DELTRAN optimization.

fossil species assigned to Section *Bunya* in seed size and seedling anatomy. The seed size of *A. bidwillii* is large, 5–6 cm in length and 2.5–3.5 cm in width (Burrows, Boag, and Stockey, 1992) compared with 0.8–1.3 cm in length and 0.2–0.6 cm in width in *A. mirabilis* from Argentina (Stockey, 1975, 1978), 0.8 cm in length and 0.3 cm in width in *A. brownii* from the UK (Stockey, 1980a), 1.6 cm in length and 0.7 cm in width in *A. sphaerocarpa* from the UK (Stockey, 1980b). Seed size is also small in all other fossil species, such as *A. nihongii* (Stockey, Nishida, and Nishida, 1992) or *A. nipponensis* (Stockey, Nishida, and Nishida, 1994). Burrows, Boag, and Stockey (1992) indicated that seeds of extinct species were too small for cryptogeal (hypogeal) germination, and Stockey (1994) even suggested that hypogeal germination was a relatively recent phenomenon in the Araucariaceae. Thus it is suggested that epigeal germination is the general condition (plesiomorphy) within Section *Bunya*.

Stockey, Nishida, and Nishida (1990), Burrows, Boag, and Stockey (1992), and Burrows and Stockey (1994) showed that seedlings of *Araucaria bidwillii* develop concentric rings of vascular tissue between shoot apex and hypocotyl, but such a structure is not present in the fossil seedlings.

The present finding on the phylogenetic position of *Araucaria bidwillii* is consistent with these paleobotanical data. We conclude that the Mesozoic araucarians assigned to Section *Bunya*, which were distributed in both hemispheres, should be separately treated from the extant *Bunya* species. Hypogeal germination can be evaluated as an autapomorphy for *A. bidwillii* in the section. We should add further molecular data to enhance the statistical probability concerning the present position of *A. bidwillii* in the phylogenetic tree.

Evolution of Araucaria—The *rbcL* tree indicates that the genus *Araucaria* is divided into two clades. In the cluster of Sections *Araucaria, Bunya*, and *Intermedia*, extant species attributed to these sections are distributed in South America, Australia, or New Guinea. This distribution pattern linking South America and Australasia is often considered to be the result of the Mesozoic break up of Gondwanaland followed by continental drift (see Raven and Axelrod, 1972, 1974). Fossils of Sections *Araucaria* and *Intermedia* have also been found only from the Southern Hemisphere (Argentina + Australia and New Zealand, respectively; see Table 1), and fossils assigned to Section *Bunya* should be separately treated from the extant *Bunya* species as discussed above. Therefore, common ancestral taxa of Sections *Araucaria* and *Intermedia*, and possibly Section *Bunya*, were distributed in Gondwanaland during the Mesozoic and the early Tertiary, and their evolution into Sections *Araucaria* and *Intermedia* (and possibly Section *Bunya*) were completed before South America separated from Antarctica, during the Eocene at the latest. The oldest fossil records in these sections are late Cretaceous (Bose, 1975) and agree well with the fact that there was a continuous landmass from South America to Antarctica, Australia, New Zealand, and New Guinea 70–80 million years ago, in the late Cretaceous (Wilford and Brown, 1994). Therefore, the present finding indicating the monophyly of Sections *Araucaria, Intermedia*, and *Bunya* agrees with these fossil and geological facts.

The monophyly of Section *Eutacta* was strongly supported. Section *Eutacta* has been regarded as the oldest taxon together with Section *Bunya* based on their Jurassic to Cretaceous fossil records. In the present study, *rbcL* phylogeny suggests that Section *Eutacta* is older than the other sections. However, recent paleobotanical findings have indicated that some Mesozoic Northern Hemisphere species may have been inappropriately assigned to Section *Eutacta*.

Fossils of *Araucaria* are usually fragmentary, i.e., found as a part of the whole plant and have been discussed in their sectional attributes on the basis of partial fossils such as cones or leaves. Ohsawa, Nishida, and Nishida (1995) found a new specimen of *Araucaria* whose cone was attached to the vegetative organs that had been described as *Yezonia vulgaris*. They reconstructed the whole plant and proposed a new section, *Yezonia*, based on the combination of features quite different from other extant sections. The cone anatomy of this fossil coincided with that of *Araucaria nihongii* (Stockey, Nishida, and Nishida, 1992), which has cones externally similar to those of Section *Eutacta*. External and anatomical features of shoots of *Yezonia* closely resemble *Brachyphyllum*, which is sometimes associated with araucarian cone fossils assigned to Section *Eutacta*. Thus, the taxonomic positions of Mesozoic araucarian fossils that have been included in Section *Eutacta* are now doubtful after the finding of *Yezonia*. Reexamination of Mesozoic fossils assigned to Section *Eutacta* is needed.

Evolution of Agathis—Fossils of *Agathis* have been excavated from Tertiary sediments restricted to Australia and New Zealand (Cookson and Duigan, 1951; Florin, 1963; Hill and Bigwood, 1987). The oldest known fossil is a collection of leaves from the middle Cretaceous (Albian) in Australia (Cantrill, 1992), but no cones are known from the Mesozoic. Stockey (1994) stated that *Agathis* is known from the Cretaceous, and Hill (1995) gave its time of appearance as the beginning of the Tertiary. Despite the molecular evidence for the sister-group relationship between *Agathis* and *Araucaria*, our current knowledge of the fossil record only traces *Agathis* back to the Cretaceous/Tertiary boundary and suggests that the genus may always have been more restricted to the southern hemisphere.

Infrageneric relationships of *Agathis* were poorly resolved by the data, and the low sequence divergence suggests the recent diversification of extant agathian species. The bootstrap values are very low in each node of the tree, and we will not discuss the evolution of *Agathis* based on the present trees. We are now examining *matK* sequence data for the Araucariaceae in order to derive a better understanding of the evolution of *Agathis* as well as to solve some other problems uncovered in the present study.

New Caledonian species—New Caledonia possesses 13 endemics of *Araucaria* and five of *Agathis*, and their morphological characteristics and preferred habitats are well diversified (see de Laubenfels, 1972; CTFT, 1975; Veillon, 1978, 1980; Jaffré, 1995). Nevertheless, the very high or identical homology of their *rbcL* gene sequences was observed among the species in each genus (Table 3). High morphological diversity with the low sequence divergence, the low restriction site divergence, or low genetic differentiation is usually observed in endemics to the oceanic islands, by means of rapid adaptive radiation and speciation to new niches (e.g., Carr and Kyhos, 1986; Crawford, Stuessy, and Silva, 1987; Ito and Ono, 1990; Ito et al., 1990; Crawford et al., 1992, 1993; Soejima et al., 1994).

New Caledonia, one of the continental islands, originated from a part of Gondwanaland and was separated from the continent between the Triassic and the end of the Jurassic (Raven and Axelord, 1974; Paris, 1981). However, a large area of New Caledonia is covered with ultramafic soil derived from peridotite, and it is suggested that this area was formed at the end of the Eocene. Most of the species of Araucariaceae are distributed in this soil (12 of the 13 species in *Araucaria* and four of the five species in *Agathis*). Jaffré (1995) suggested that there was differentiation of new species of *Araucaria* in the post-Eocene, after the emplacement of peridotite. His discussion agrees with the findings of very low sequence divergence in the *rbcL* gene among endemics of *Araucaria* and *Agathis*. It is suggested that the adaptive radiation to new edaphic conditions, i.e., ultramafic soils, caused their rapid differentiation after the Eocene.

As a result, although New Caledonia is an old continental island that had been a part of Gondwanaland, the evolutionary trend of the Araucariaceae is rather like that of oceanic islands. Setoguchi et al. (1997) found a similar pattern in New Caledonian *Nothofagus* using an *atpB-rbcL* intergenic spacer sequence. Further case studies will be needed to examine the origin and speciation of Gondwanan floristic elements in New Caledonia.

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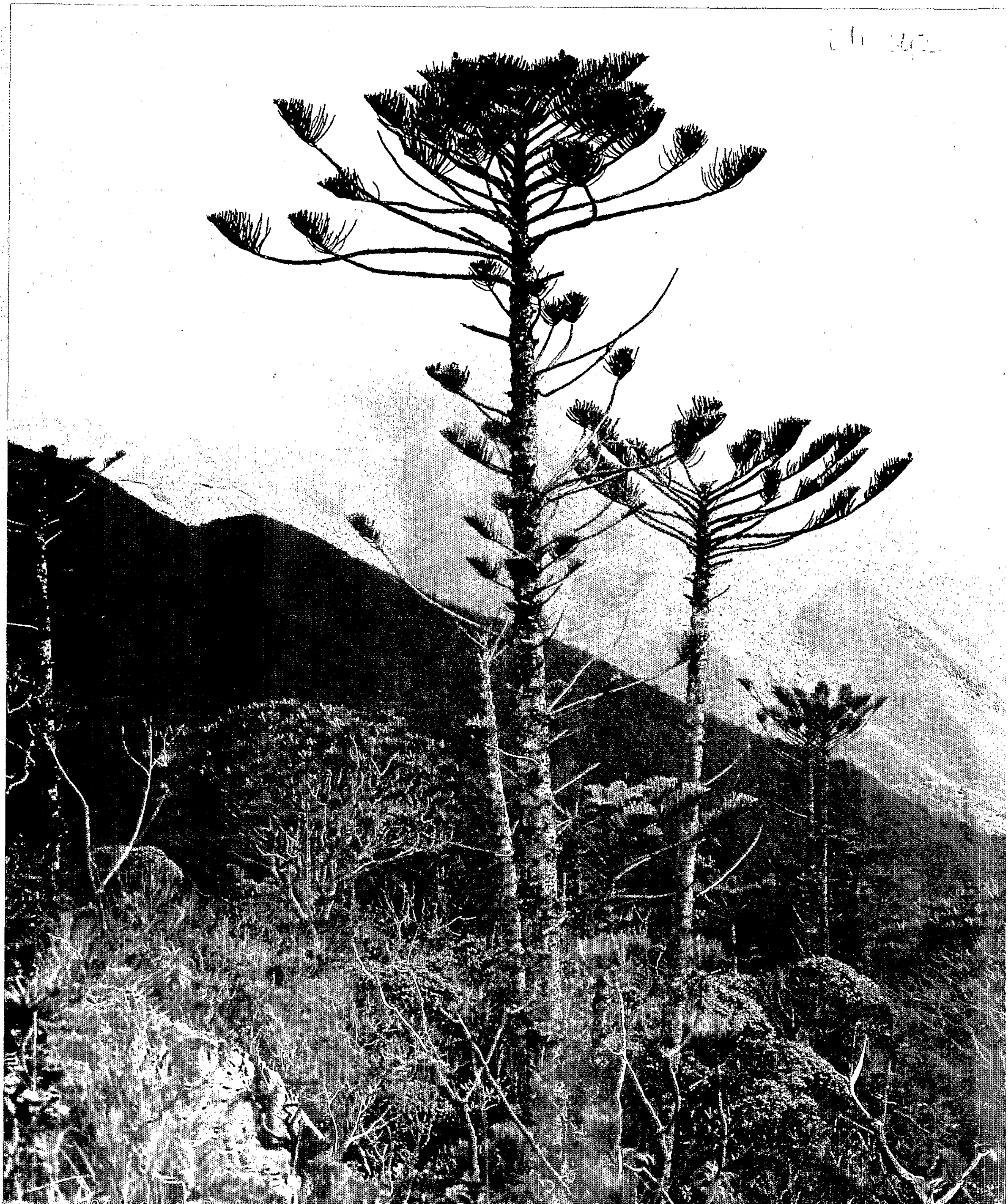

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