Araucariaceae macrofossil record from South America and Antarctica

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Araucariaceae fossils are abundant in Patagonia and on Seymour (Marambio) and King George (25 de Mayo) islands, Antarctica. Araucariacean macrofossil suites are represented by records of 121 woods, leaves, ovuliferous scales, cones, one seed and seedlings, many of them placed in 50 formalized morphospecies. Although Araucariaceae fossil pollen is known since the Triassic, the oldest reliable macrofossil records in South America and Antarctica are from the Early Jurassic. In the Early Cretaceous, the family reached its widest distribution, with records from northern South America (cones and leaves from Colombia and Brazil). In the Late Cretaceous, the abundance of Araucariaceae began to decline. In the Cenozoic, all the fossils are derived from Patagonia and Antarctica, and this probably reflects a genuine contraction in the family's distribution.

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ARAUCARIACEAE is an ancient family of conifers that, in the modern flora, is restricted mostly to the Southern Hemisphere, with some species that pass the Equator in Malaysia (Whitmore 1980). Most modern Araucariaceae occur in rainforest under subtropical–temperate (mesothermal) climates (Dutra & Stranz 2003) and in some temperate to cool temperate (microthermal) forests in South America (Page 1990, Enright *et al*. 1995). The family has three living genera incorporating 41 species and one variety (Kunzmann 2007). *Wollemia* Jones, Hill & Allen, 1995 is a monotypic genus with a modern distribution restricted to southeastern Australia. *Agathis* Salisbury, 1807 has *ca* 21 extant species mostly distributed in Indomalaya, Australasia and some southwest Pacific islands. *Araucaria* Jussieu, 1789 is the most geographically widespread with 19 extant species in Australia, Norfolk Island, New Caledonia, New Guinea and South America (Kunzmann 2007). In South America, *Araucaria* is represented by two species that belong to the section *Araucaria*: *Araucaria angustifolia* (Bertol.) Kuntze, 1898 and *Araucaria araucana* K. Koch, 1873. The former occurs in southeastern Brazil and northeastern Argentina where it is dominant in subtropical to temperate rainforests (Dutra & Stranz 2003). Its occurrence in Paraguay is not confirmed (Dutra & Stranz 2003). *Araucaria araucana*, native to Argentina and Chile, has a relatively restricted natural distribution between 37°20′ and 40°20′S. It occurs in temperate to cool temperate mixed conifer–angiosperm forests up to the timber line in the Andes of South America (Enright *et al*. 1995; Fig. 1).

Araucariaceae was more widespread in the Mesozoic, being distributed across both hemispheres (Kunzmann 2007). Araucariaceae fossils are relatively common in Oceania, but are considered rare in other regions of the world (Kershaw & Wagstaff 2001, Kunzmann 2007). The oldest araucariacean macrofossil is an ovuliferous scale from the Triassic of India (Lele 1956). *Araucarioxylon arizonicum* Knowlton (1889) is a well-known fossil wood from the Late Triassic of North America (for its recent taxonomic appraisal see Savidge 2007) but its affiliation with the Araucariaceae is uncertain (Ash & Creber 2000).

Several pollen types have been found in araucariacean microsporangiate cones. They are: *Araucariacites*, *Cyclusphaera* and *Balmeiopsis* (Archangelsky & Del Fueyo 2010). A range of other dispersed pollen grains have also been assigned to Araucariaceae based on morphological similarities to extant pollen (Balme 1995). *Araucariacites australis* Cookson, 1947 is the most widely distributed pollen morphospecies

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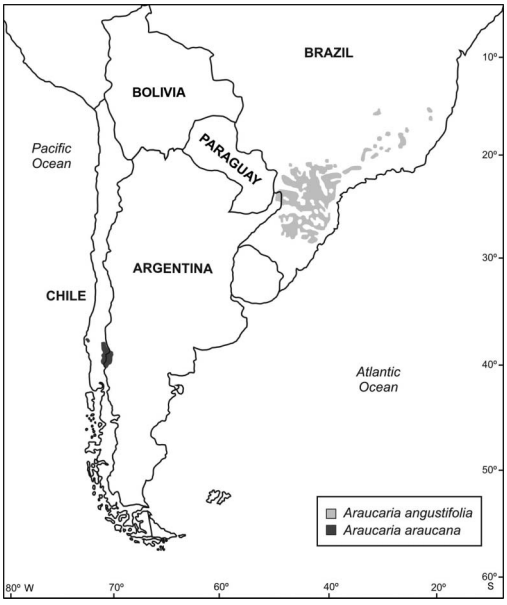

Fig. 1. Map showing the distribution of extant Araucariaceae in South America.

and has a continuous record in southern South America that starts in the Middle to Late Triassic of west central Argentina (Zavattieri 1991).

Araucariaceae macrofossil records from Australia and New Zealand have been previously surveyed by Hill & Brodribb (1999), Kershaw & Wagstaff (2001), Pole (2008) and Pole & Philippe (2010). Stockey (1994) published a revision of Mesozoic Araucariaceae analyzing each organ separately. Although there have been some overviews of the Araucariaceae macrofossil record from South America and Antarctica (Dutra & Stranz 2003, 2008, Dutra *et al.* 2007), these are of limited accessibility and only mention the major araucariacean fossils. The current contribution complements those studies by presenting an updated and comprehensive survey of the macrofossil record of Araucariaceae from South America and Antarctica, to complete our knowledge of the past distribution of the family in southern latitudes and to help resolve the biogeographical and evolutionary history of Araucariaceae.

Macrofossil record of South America and Antarctica

Araucariaceae is represented by 121 macrofossil records from Antarctica and South America (Table 1; Figs 2–5). Each record is mentioned in the text and briefly evaluated.

According to de Laubenfels (1953) araucariacean leaves are coriaceous, broad, ovate to lanceolate, flat, with multiple parallel veins. The attachment to the stem is narrow in *Agathis* and broad in *Araucaria*. *Wollemia* has considerable variability, especially between the adult and juvenile foliage. The adult leaves are twisted near their base, have rounded apices, multiple parallel veins, and are attached by the full width of the leaf base (Chambers *et al.* 1998). A large number of fossil leaves have been referred to the Araucariaceae, but many are from genera doubtfully attributed to the family based on impressions (Stockey 1982). Taxon diversity is also difficult to judge in fossil assemblages owing to the foliar dimorphism expressed between juvenile and adult specimens of modern taxa (Stockey 1994). Consequently, without the attachment of cones to branches bearing imbricate helically arranged leaves, cuticular remains are essential to determine an araucariacean affinity of leafy twigs. Broad-leafed araucarians have discontinuous rows of stomata that are oriented mostly parallel to the long axis of the leaf, whereas araucarians with imbricate, rhombic leaves usually have oblique orientations. Four or five subsidiary cells are common and epidermal cell outlines are usually elongate and rectangular (Stockey & Ko 1986). *Araucaria* lacks Florin rings, and polar extensions are common but do not show the bilobed structure evident in *Agathis* (Stockey 1994). Cuticular features of adult and juvenile leaves of *Wollemia* are markedly different with respect to stomatal distribution, orientation and density. Like *Araucaria*, adult *Wollemia* leaves lack Florin rings, have stomata sunken to the level of the hypodermis and have a smooth exterior cuticular surface (Chambers *et al.* 1998). *Brachyphyllum* and *Pagiophyllum* are leaf morphogenera not considered here, since their affinity to the Araucariaceae can not be unambiguously established.

The typical araucarian cone is spherical to ovoid and sheds its cone–scale complexes at maturity. Cones of *Agathis* have fully fused bract and ovuliferous scales, unlike those of *Araucaria*, which usually have a free ovuliferous scale tip (Stockey 1994). In *Wollemia*, cone scales have a woody spine projected distally and, like *Agathis*, ovuliferous and bract scales are intimately fused (Chambers *et al.* 1998).

Araucarioxylon was created by Kraus (1870) to group fossil woods exclusively represented by secondary xylem with araucarioid type pitting similar to extant Araucariaceae. However, this morphogenus does not imply a direct affiliation to the Araucariaceae, because woods with that kind of tracheid pitting were common since the Palaeozoic and some

	Age	Formation	Location	Taxon	Organ	References
1	Early Jurassic	Roca Blanca	Estancia Los Pirineos, Santa Cruz, Argentina	*Agathoxylon protoaraucana* (Brea) Gnaedinger & Herbst	Wood	Brea 1997, **Gnaedinger & Herbst 2009**
2	Early Jurassic	Piedra Pintada	Piedra Pintada, Neuquén, Argentina	*Araucarites* sp.	Leaf	Herbst 1966
3	Early Jurassic	Piedra del Águila	Piedra del Águila, Neuquén, Argentina	*Araucarites* sp.	Ovuliferous scale	Ferello 1947
4	Early Jurassic	Piedra Pintada	Cerro Mesa, Neuquén, Argentina	*Araucarioxylon termieri* Gnaedinger	Wood	**Gnaedinger 2006**
5	Early Jurassic	Nestares	Alicurá, Neuquén, Argentina	*Araucarites philipsi* Carruthers	Ovuliferous scale	Arrondo & Petriella 1980
6	Early Jurassic	Quebrada Pobre	La Ligua, V Región, Chile	*Agathoxylon liguaensis* Torres & Philippe	Wood	**Torres & Philippe 2002**
7	Middle Jurassic	Taquetrén	Cañadón del Zaino, Chubut, Argentina	*Araucarites* sp.	Ovuliferous scale	Herbst & Anzótegui 1968, Hunter *et al.* 2005, Escapa *et al.* 2008
8	Middle Jurassic	Lotena	Mina La Perla, Neuquén, Argentina	*Araucarites* sp.	Ovuliferous scale	Baldoni 1980
9	Middle Jurassic	Mount Flora	Hope Bay, Antarctic Peninsula, Antarctica	*Araucarites antarcticus* (Gee) Birkenmajer & Ociepa (= *Araucarites cutchensis* Feistmantel, = *Araucaria antarctica* Gee, = *Araucarites* cf. *cutchensis* Rees & Cleal)	Ovuliferous scale	Nathorst 1904, Andersson 1907, Nathorst 1907, Halle 1913, Gee 1989, Rees & Cleal 2004, Hunter *et al.* 2005, **Birkenmajer & Ociepa 2008**
10	Middle Jurassic	Mount Flora	Hope Bay, Antarctic Peninsula, Antarctica	*Araucarioxylon arayaii* Torres, Valenzuela & Gonzales	Wood	Torres *et al.* 2000, Hunter *et al.* 2005
11	Middle–Late Jurassic	Chon Aike	Laguna Flecha Negra, Santa Cruz, Argentina	*Araucarites* sp.	Ovuliferous scale	Chaning *et al.* 2007
12	Middle–Late Jurassic	La Matilde	Cerro Madre e Hija, Santa Cruz, Argentina	*Agathoxylon matildense* Zamuner & Falaschi	Wood	**Zamuner & Falaschi 2005**
13	Middle–Late Jurassic	La Matilde	Cerro Alto, Santa Cruz, Argentina	*Dadoxylon (Araucarioxylon)* sp.	Wood	Gothan 1925
14	Middle–Late Jurassic	La Matilde	Cerro Alto, Santa Cruz, Argentina	*Pararaucaria patagonica* Wieland (= *Pararaucaria elongata* Wieland)	Ovuliferous cone	**Wieland 1929**, Wieland 1935, Calder 1953
15	Middle–Late Jurassic	La Matilde	Cerro Alto, Santa Cruz, Argentina	*Araucaria mirabilis* (Spegazzini) Windhausen (= *Araucarites miriabilis* Spegazzini, = *Araucaria windhauseni* Gothan, = *Proaraucaria mirabilis* Wieland, = *Proaraucaria elongata* Wieland)	Ovuliferous cone	Spegazzini 1924, Gothan 1925, Wieland 1929, 1935, **Windhausen 1931**, Darrow 1936, Calder 1953, Stockey 1975, 1978

(*continued*)

Table 1. (*Continued*).

	Age	Formation	Location	Taxon	Organ	References
16	Middle–Late Jurassic	La Matilde	Cerro Alto, Santa Cruz, Argentina	"woods"	Wood (with primary structures)	Calder 1953
17	Middle–Late Jurassic	La Matilde	Cerro Alto, Santa Cruz, Argentina	"seedlings" cf. *Araucaria mirabilis* (Spegazzini) Windhausen	Seedling	Calder 1953
18	Middle–Late Jurassic	La Matilde	Cerro Alto, Santa Cruz, Argentina	*Araucarites sanctaecrucis* Calder (= *Proaraucaria mirabilis* (Spegazzini) Wieland)	Leaf	Spegazzini 1924, Wieland 1935, **Calder 1953**
19	Middle–Late Jurassic	La Matilde	Gran Bajo de San Julián, Santa Cruz, Argentina	*Araucaria* sp.	Ovuliferous scale	Berry 1924
20	Middle–Late Jurassic	La Matilde ?	Laguna del Molino, Santa Cruz, Argentina	'Squame seminifere di *Araucaria*'	Ovuliferous scale	Feruglio 1951
21	Middle–Late Jurassic	Cañadón Asfalto	Estancia La Vistosa, Chubut, Argentina	*Araucarites* sp.	Ovuliferous scale	Cortés & Baldoni 1984
22	Middle–Late Jurassic	Cañadón Asfalto	Cañadón Asfalto, Chubut, Argentina	*Araucarites cutchensis* Feistmantel	Ovuliferous scale	Frenguelli 1949
23	Early Cretaceous	?	Villa de Leyva, Boyacá, Colombia	*Araucariostrobus creutzbergii* Huertas	Ovuliferous cone	**Huertas 1970**, Van Waveren *et al.* 2002
24	Early Cretaceous	?	Villa de Leyva, Boyacá, Colombia	*Araucariostrobus camargoi* Huertas	Microsporangiate cone	**Huertas 1970**
25	Early Cretaceous	?	Villa de Leyva, Boyacá, Colombia	*Araucariostrobus archangelskii* Huertas	ovuliferous cone	**Huertas 1976**
26	Early Cretaceous	?	Villa de Leyva, Boyacá, Colombia	*Araucariostrobus* sp. cf. *A. archangelskii*	Ovuliferous cone	van Waveren *et al.* 2002
27	Early Cretaceous	Crato	Nova Olinda, Ceará, Brazil	cf. *Wollemia* sp.	Leaf	Martill *et al.* 2005
28	Early Cretaceous	Crato	Nova Olinda, Ceará, Brazil	cf. *Agathis* sp.	Leaf	Martill *et al.* 2005
29	Early Cretaceous	Crato	Santana do Cariri, Ceará, Brazil	cf. *Araucaria* sp.	Cone	Kunzmann *et al.* 2004
30	Early Cretaceous	Crato	Santana do Cariri, Ceará, Brazil	*Araucariostrobus* sp.	Cone	Kunzmann *et al.* 2004
31	Early Cretaceous	Santana	Crato, Ceará, Brazil	*Araucarites vulcanoi* Duarte	Ovuliferous scale	**Duarte 1989**, Duarte 1993
32	Early Cretaceous	Santana	Crato, Ceará, Brazil	*Araucaria cartellei* Duarte	Leaf	**Duarte 1993**
33	Early Cretaceous	Punta del Barco	Estancia El Verano, Santa Cruz, Argentina	*Araucaria grandifolia* Feruglio	Leaf	**Feruglio 1951**, Del Fueyo & Archangelsky 2002
34	Early Cretaceous	Punta del Barco	Estancia El Verano and Cerro Cuadrado, Santa Cruz, Argentina	*Araucarites baqueroensis* Archangelsky (= *Araucaria* section *Colymbea*)	Ovuliferous scale	Feruglio 1951, Archangelsky 1966

(*continued*)

Table 1. (*Continued*).

	Age	Formation	Location	Taxon	Organ	References
35	Early Cretaceous	Anfiteatro de Ticó	Anfiteatro de Ticó, Santa Cruz, Argentina	*Alkastrobus peltatus* Del Fueyo & Archangelsky	Microsporangiate cone	**Del Fueyo & Archangelsky 2005**
36	Early Cretaceous	Anfiteatro de Ticó	Bajo Grande, Santa Cruz, Argentina	*Araucarites minimus* Archangelsky	Ovuliferous scale	**Archangelsky 1966**
37	Early Cretaceous	Anfiteatro de Ticó	Cerro Testigo, Anfiteatro de Ticó and Bajo Grande, Santa Cruz, Argentina	*Araucarites baqueroensis* Archangelsky	Ovuliferous scale	**Archangelsky 1966**
38	Early Cretaceous	Anfiteatro de Ticó	Bajo Grande, Santa Cruz, Argentina	*Notopehuen brevis* Del Fueyo	Microsporangiate cone (with branch)	**Del Fueyo 1991**
39	Early Cretaceous	Springhill	El Cóndor, Santa Cruz, Argentina	*Araucarites chilensis* Baldoni	Ovuliferous scale	**Baldoni 1979**
40	Early Cretaceous	Springhill	Pozo El Dorado, XI Región, Chile	*Araucarites* sp.	Ovuliferous scale	Archangelsky 1976
41	Early Cretaceous	Apeleg	Arroyo lechoso, XI Region, Chile	*Agathoxylon* sp.	Wood	Philippe *et al.* 2000
42	Early Cretaceous	Cumberland Bay	South Georgia Island, Antarctica	*Dadoxylon (Araucarioxylon)* sp.	Wood	Gordon 1930, Jefferson & MacDonald 1981
43	Early Cretaceous	Neptune Glacier	Coal Nunatak, Alexander Island, Antarctica	*Araucarites wollemiaformis* Cantrill & Falcon–Lang	Ovuliferous scale	**Cantrill & Falcon Lang 2001**
44	Early Cretaceous	Neptune Glacier	Citadel Bastion, Alexander Island, Antarctica	*Araucarites citadelbastionensis* Cantrill & Falcon–Lang	Ovuliferous scale	**Cantrill & Falcon Lang 2001**
45	Early Cretaceous	Neptune Glacier	Coal Nunatak, Alexander Island, Antarctica	*Araucaria alexandrensis* Cantrill & Falcon–Lang	Leaf	**Cantrill & Falcon Lang 2001**
46	Early Cretaceous	Neptune Glacier	Titan Nunatak, Alexander Island, Antarctica	*Araucaria chambersi* Cantrill & Falcon–Lang	Leaf	**Cantrill & Falcon Lang 2001**
47	Early Cretaceous	Neptune Glacier	Triton Point, Alexander Island, Antarctica	*Araucariopitys* sp.	Wood	Falcon Lang & Cantrill 2000
48	Early Cretaceous	Neptune Glacier	Triton Point, Alexander Island, Antarctica	*Araucarioxylon* sp.	Wood	Falcon Lang & Cantrill 2000
49	Early Cretaceous	Cerro Negro	Byers Peninsula, Livingston Island, Antarctica	*Araucarioxylon* sp. 1	Wood	Falcon Lang & Cantrill 2001
50	Early Cretaceous	Cerro Negro	Byers Peninsula, Livingston Island, Antarctica	*Araucarioxylon* sp. 2	Wood	Falcon Lang & Cantrill 2001
51	Early Cretaceous	Cerro Negro	Byers Peninsula, Livingston Island, Antarctica	*Araucarites* sp.	Ovuliferous scale	Parica *et al.* 2007

(*continued*)

Table 1. (*Continued*).

	Age	Formation	Location	Taxon	Organ	References
52	Early Cretaceous	Cerro Negro	Byers Peninsula, Livingston Island, Antarctica	*Araucarites* sp. cf. *A. baqueroensis*	Leaf	Hernández & Azcarate 1971
53	Early Cretaceous	Cerro Negro	Byers Peninsula, Livingston Island, Antarctica	*Araucarioxylon arayaii* Torres, Valenzuela & Gonzales	Wood	**Torres *et al.* 1982**
54	Early Cretaceous ?	?	Shirreff Cape, Livingston Island, Antarctica	*Araucarioxylon* sp.	Wood	Torres 1993
55	Early Cretaceous	?	President Head, Snow Island, Antarctica	*Araucarioxylon arayaii* Torres, Valenzuela & Gonzales	Wood	Torres *et al.* 1995
56	Early Cretaceous	?	President Head and Hall Peninsula, Snow Island, Antarctica	*Araucarioxylon* sp. A	Wood	Torres *et al.* 1997
57	Early Cretaceous	Kotick Point	Lost Valley, James Ross Island, Antarctica	*Agathoxylon* sp.	Wood	Ottone & Medina 1998
58	Late Cretaceous	Cerro Cazador	Cerro Guido, XII Región, Chile	*Araucarites patagonica* Kurtz	Ovuliferous scale	**Kurtz 1902**, Hünicken 1971, 1995
59	Late Cretaceous	Cerro Cazador	Cerro Guido, XII Región, Chile	*Pseudoaraucaria valentini* (Kurtz) Menéndez (= *Abietites valentini* Kurtz)	Ovuliferous scale	Kurtz 1902, Hünicken 1971, 1995, **Menendez 1972**
60	Late Cretaceous	Divisadero	Meseta Correntoso, XI Región, Chile	*Araucarioxylon* sp.	Wood	Nishida *et al.* 1990
61	Late Cretaceous	Divisadero	Meseta Correntoso, XI Región, Chile	*Araucarioxylon ohzanum* Nishida, Ohsawa, H. Nishida & Rancusi	Wood	Nishida *et al.* 1992
62	Late Cretaceous	Divisadero	Meseta Correntoso, XI Región, Chile	*Araucarioxylon pichasquense* Torres & Rallo	Wood	Nishida *et al.* 1990, 1992
63	Late Cretaceous	Chile Chico	Río de las Nieves, XI Región, Chile	*Araucarioxylon kellerense* (Lucas & Lacey) (= *Dadoxylon kellerense* Lucas & Lacey)	Wood	**Nishida *et al.* 1990**, 1992
64	Late Cretaceous	Chile Chico	Río de las Nieves, XI Región, Chile	*Araucarioxylon pichasquense* Torres & Rallo	Wood	Nishida *et al.* 1990, 1992
65	Late Cretaceous	Quiriquina	Quiriquina Island, VIII Región, Chile	*Araucarioxylon parachoshiense* Nishida & Nnishida	Wood	**Nsihida & Nishida 1987**
66	Late Cretaceous	Quiriquina	Quiriquina Island, VIII Región, Chile	*Araucarioxylon pluriresinosum* Torres & Biro–Bagoczky	Wood	**Torres & Biro Bagoczky 1986**

(*continued*)

Table 1. (*Continued*).

	Age	Formation	Location	Taxon	Organ	References
67	Late Cretaceous	Quiriquina	Quiriquina Island, VIII Región, Chile	*Araucarioxylon resinosum* Torres & Biro–Bagoczky	Wood	**Torres & Biro Bagoczky 1986**
68	Late Cretaceous	?	Pichasca, IV Región, Chile	*Araucarioxylon pichasquense* Torres & Rallo	Wood	**Torres & Rallo 1981**
69	Late Cretaceous	Bajo Barreal	Puesto Confluencia, Chubut, Argentina	*Agathoxylon* sp.	Wood	Pujana *et al*. 2007
70	Late Cretaceous	?	Williams Point, Livingston Island, Antarctica	*Araucarioxylon floresii* Torres & Lemoigne	Wood	**Torres & Lemoigne 1989**, Phillippe *et al*. 1993
71	Late Cretaceous	?	Williams Point, Livingston Island, Antarctica	*Araucarioxylon chapmanae* Poole & Cantrill	Wood	Chapman & Smellie 1992, **Poole & Cantrill 2001**
72	Late Cretaceous	?	Williams Point, Livingston Island, Antarctica	*Araucariopitys antarcticus* Poole & Cantrill	Wood	Chapman & Smellie 1992, **Poole & Cantrill 2001**
73	Late Cretaceous	López de Bertodano	Cape Lamb, Vega Island, Antarctica	*Araucaria fibrosa* (= *Araucaria antarctica* César, Marenssi & Santillana)	Ovuliferous cone (with leaves)	**César *et al.*** 2001, **2009**
74	Late Cretaceous	Zamek	Zamek Hill, King George Island, Antarctica	*Araucaria* sp.	Leaf	Dutra & Batten 2000
75	Late Cretaceous	Table Nunatak	Kenyon Peninsula, Antarctica	bract–scale complex	Ovuliferous scale	Eklund *et al*. 2004
76	Early Cenozoic ?	?	Keller Peninsula, King George Island, Antarctica	*Dadoxylon* sp.	Wood	Lucas & Lacey 1981
77	Early Cenozoic ?	?	Keller Peninsula, King George Island, Antarctica	*Dadoxylon pseudoparenchymatosum* Gothan	Wood	Lucas & Lacey 1981
78	Early Cenozoic ?	?	Keller Peninsula, King George Island, Antarctica	*Dadoxylon kellerense* Lucas & Lacey	Wood	**Lucas & Lacey 1981**
79	Cenozoic	?	Lago Fontana, Chubut, Argentina	*Dadoxylon pseudoparenchymatosum* Gothan	Wood	Kräusel 1924
80	Cenozoic	?	Río Collón Curá (Katapuliche), Neuquén, Argentina	*Araucarioxylon doeringii* Conwentz	Wood	**Conwentz 1885**
81	Cenozoic	?	Río de las Minas, XII Región, Chile	*Dadoxylon pseudoparenchymatosum* Gothan	Wood	Kräusel 1924

(*continued*)

Table 1. (*Continued*).

	Age	Formation	Location	Taxon	Organ	References
82	Cenozoic	?	Quiriquina Island, VIII Región, Chile	*Araucarioxylon pseudoparenchymatosum* (Gothan) (= *Dadoxylon pseudoparenchymatosum* Gothan)	Wood	**Nishida 1984**
83	Cenozoic	?	Quiriquina Island, VIII Región, Chile	*Araucarioxylon doeringii* Conwentz	Wood	Nishida 1981, 1984
84	Cenozoic	?	Quiriquina Island, VIII Región, Chile	*Araucarioxylon quiriquinaense* Nishida	Wood	**Nishida 1984**
85	Cenozoic	?	Barton Peninsula, King George Island	*Dadoxylon*	Wood	Hee & Soon 1991
86	Paleocene	Chorrillo Chico	Riesco Island, XII Región, Chile	*Araucarioxylon* sp.	Wood	Nishida *et al.* 2006
87	Paleocene	Lota y Coronel	Curanilahue y Lota, VIII Región, Chile	*Araucaria araucoensis* Berry	Leaf	**Berry 1922**
88	Paleocene	Cross Valley	Seymour (Marambio) Island, Antarctica	*Araucaria imponens* Dusen	Leaf	**Dusen 1908**, Cantrill *et al.* 2011
89	Late Paleocene–early Eocene	'Fossil Hill member'	Fildes Peninsula, King George Island, Antarctica	cf. *Araucaria nathorsti* Dusen	Leaf	Troncoso 1986, Birkenmajer 2001
90	Late Paleocene–early Eocene	'Fossil Hill member'	Fossil Hill, King George Island, Antarctica	*Araucaria* sp.	Leaf	Liu 1990, Zhou & Li 1994, Birkenmajer 2001
91	Late Paleocene–early Eocene	'Fossil Hill member'	Fossil Hill, King George Island, Antarctica	Isolated leaf	Leaf	Zhou & Li 1994, Birkenmajer 2001
92	Eocene	?	Arroyo Cardenio, XI Región, Chile	*Araucarioxylon* sp. cf. *A. kellerense*	Wood	Terada *et al.* 2006a
93	Eocene	?	Arroyo Cardenio, XI Región, Chile	*Araucarioxylon pichasquense* Torres & Rallo	Wood	Terada *et al.* 2006a
94	Eocene	Río Turbio	Río Turbio, Santa Cruz, Argentina	*Araucarites* sp. (= *Araucaria* ? sp. Hünicken 1967)	Seed	Hünicken 1955, 1967
95	Eocene	Huitrera	Laguna del Hunco, Chubut, Argentina	*Araucaria* sp.	Ovuliferous scale	Wilf *et al.* 2003
96	Eocene	Huitrera	Pampa de Jones, Río Negro, Argentina	cf. *Araucaria pichileufulensis* Berry	Ovuliferous scale	Wilf *et al.* 2010
97	Eocene	Ventana	Río Pichileufú, Río Negro, Argentina	*Araucaria pichileufulensis* Berry	Ovuliferous scale	**Berry 1938**, Wilf *et al.* 2005

(*continued*)

Table 1. (*Continued*).

	Age	Formation	Location	Taxon	Organ	References
98	Eocene	La Meseta	Seymour (Marambio) Island, Antarctica	*Dadoxylon pseudoparenchymatosum* Gothan	Wood	**Gothan 1908**, Torres *et al.* 1994
99	Eocene	La Meseta	Seymour (Marambio) Island, Antarctica	*Araucarioxylon novae–zeelandiae* Stopes	Wood	Torres *et al.* 1994
100	Eocene	La Meseta	Seymour (Marambio) Island, Antarctica	*Araucarioxylon seymourense* Torres, Marenssi & Santillana	Wood	**Torres *et al.* 1994**
101	Eocene	La Meseta	Seymour (Marambio) Island, Antarctica	'Specimen D'	Leaf	Case 1988
102	Eocene	La Meseta	Seymour (Marambio) Island, Antarctica	*Araucaria marensii* Cantrill & Poole	Wood (with bark)	**Cantrill & Poole 2005**
103	Eocene	La Meseta	Seymour (Marambio) Island, Antarctica	*Araucaria nathorsti* Dusen	Leaf	Doktor *et al.* 1996
104	Eocene	?	Mount Discovery, McMurdo Sound, Antarctica	*Araucaria* sp.	Leaf	Pole *et al.* 2000
105	Eocene	?	Mina Bluff, McMurdo Sound, Antarctica	Type A	Wood	Francis 2000
106	Late Eocene–early Oligocene	Sloggett	Bahía Slogget, Tierra del Fuego, Argentina	*Araucaria pararaucana* Panti, César, Marenssii & Olivero	Leaf	**Panti *et al.* 2007**
107	Late Eocene–early Oligocene	Arctowski Cove	Petrified Forest Creek, King George Island, Antarctica	*Araucarioxylon* sp. 1	Wood	Torres & Lemoigne 1988
108	Late Eocene–early Oligocene	Arctowski Cove	Petrified Forest Creek, King George Island, Antarctica	*Araucarioxylon* sp. 2	Wood	Torres & Lemoigne 1988
109	Oligocene	Río Guillermo	Estancia Cancha Carrera, Santa Cruz, Argentina	*Araucaria nathorsti* Dusen	Leaf	Hünicken 1995
110	Late Oligocene–middle Miocene	Ñirihuau	Pico Quemado, Río Negro, Argentina	*Araucaria nathorsti* Dusen	Leaf	Menendez & Caccavari 1966
111	Late Oligocene–Middle Miocene	Ñirihuau	Locality 176, Río Negro, Argentina	*Araucaria nathorsti* Dusen	Leaf	Berry 1928
112	Late Oligocene–middle Miocene	Ñirihuau	Mina de Petróleo, Río Negro, Argentina	*Araucaria nathorsti* Dusen	Leaf	Fiori 1939

(*continued*)

Table 1. (*Continued*).

	Age	Formation	Location	Taxon	Organ	References
113	Late Oligocene–early Miocene	Mina Chilena	Cerro Dorotea, XII Región, Chile	*Araucarioxylon kellerense* (Lucas & Lacey) (= *Dadoxylon kellerense* Lucas & Lacey)	Wood	Terada *et al.* 2006b
114	Late Oligocene–early Miocene	Mina Chilena	Cerro Dorotea, XII Región, Chile	*Araucarioxylon pichasquense* Torres & Rallo	Wood	Terada *et al.* 2006b
115	Late Oligocene–early Miocene	Loreto	Río de las Minas, XII Región, Chile	*Araucaria nathorsti* Dusen	Leaf	**Dusen 1899**
116	Late Oligocene–early Miocene	Loreto	Río de Las Minas, XII Región, Chile	*Araucarioxylon pichasquense* Torres & Rallo	Wood	Terada *et al.* 2006c
117	Middle Eocene–early Oligocene	'Arctowski Interglacial'	Admiralty Bay, King George Island, Antarctica	'lotto (sample) no. 2'	Wood	Cortemiglia *et al.* 1981, Birkenmajer 1988
118	Miocene	Navidad	Navidad, VI Región, Chile	*Araucarioxylon chilense* Nishida	Wood	**Nishida 1970**, Nishida 1984
119	Miocene	Navidad	Matanzas, VI Región, Chile	*Araucaria* sp.	Leaf	Troncoso 1991, Troncoso & Romero 1993
120	Miocene	Navidad	Matanzas, VI Región, Chile	*Araucaria* sp. 2	Leaf	Troncoso & Romero 1993
121	Late Miocene–early Pliocene	Navidad	Cerro Centinela, VI Región, Chile	*Araucaria* sp.	Leaf	Troncoso & Encinas 2006

Table 1. Records of Araucariaceae macrofossils from South America and Antarctica. Each record represents a morphotype from a locality (except closely asociated localities of the same stratigraphic position, which are grouped as single records), ordered by age. Bold text indicates the morphospecies' original citation. Records from theses and conference abstracts are not included.

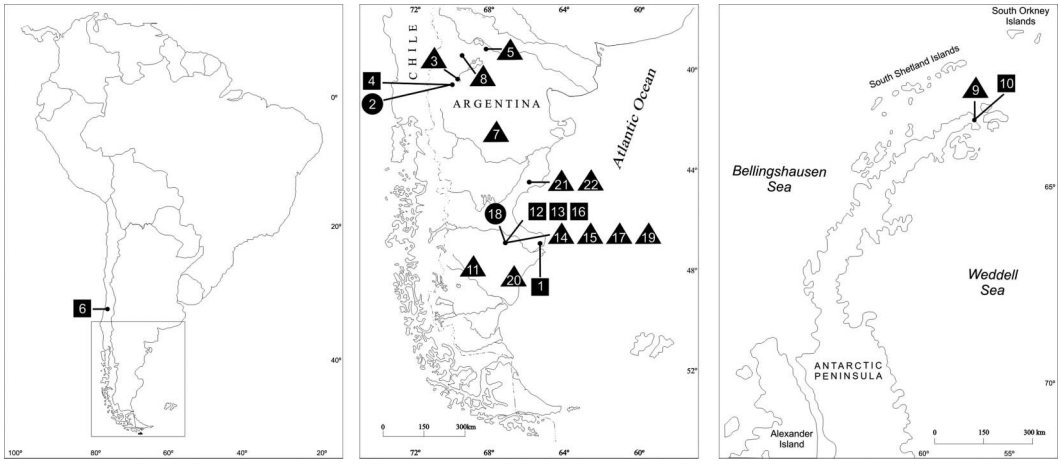

Fig. 2. Maps showing the Jurassic fossil localities. Numbers follow the table numeration. Localities are marked with circles for leaves, squares for woods and triangles for a seedling, cones and isolated ovuliferous scales.

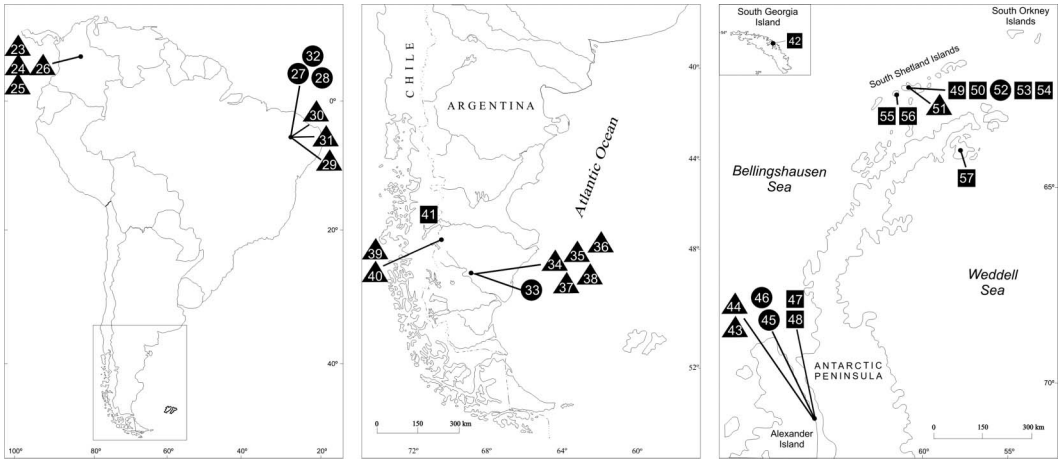

Fig. 3. Maps showing the Early Cretaceous fossil localities. Numbers follow the table numeration. Localities are marked with circles for leaves, squares for woods and triangles for cones and isolated ovuliferous scales.

species of *Araucarioxylon* have been linked to other plant groups, particularly in the Palaeozoic and Triassic (i.e. Zamuner 1996). Moreover, *Araucarioxylon* was considered nomenclaturally superfluous by Philippe (1993) and has been replaced in recent publications (i.e. Pujana *et al.* 2007, Crisafulli & Herbst 2008) by the morphogenus *Agathoxylon* Hartig, 1848. *Dadoxylon* Endlicher, 1847 has also been frequently used to describe araucariacean woods (i.e. Lucas & Lacey 1981), but this genus was considered an illegitimate synonym of *Pinites* Witham, 1833 (see Philippe 1993). *Araucariopitys* Jeffrey, 1907 has also been used for araucariacean woods (i.e. Poole & Cantrill 2001). In addition, Araucariaceae fossil woods from South America and Antarctica have been assigned to numerous morphospecies on the basis of subtle anatomical differences with limited evaluation of intraspecific variation. A substantial revision of these fossils is needed. Consequently, synonyms proposed in some articles for fossil woods (i.e. Nishida *et al.* 1990) are not considered here, although they are mentioned in some parts of the text.

Brea (1997) described *Araucarioxylon protoaraucana*, a Triassic wood that anatomically resembles extant Araucariaceae because of the alternate biseriate pitting and cross-field pit type (Brea *et al.* 2008). However, the direct affiliation of the Triassic woods to the family can not be assured due to the absence of other araucariacean fossils in the same strata. Menéndez (1951) briefly described a putative *Araucarioxylon* wood from the Triassic of Argentina and Minello (1994) described *Araucarioxylon* sp. from the Triassic of Brazil that also has typically araucariacean anatomy but these are not considered indubitable araucariaceans for the same reasons.

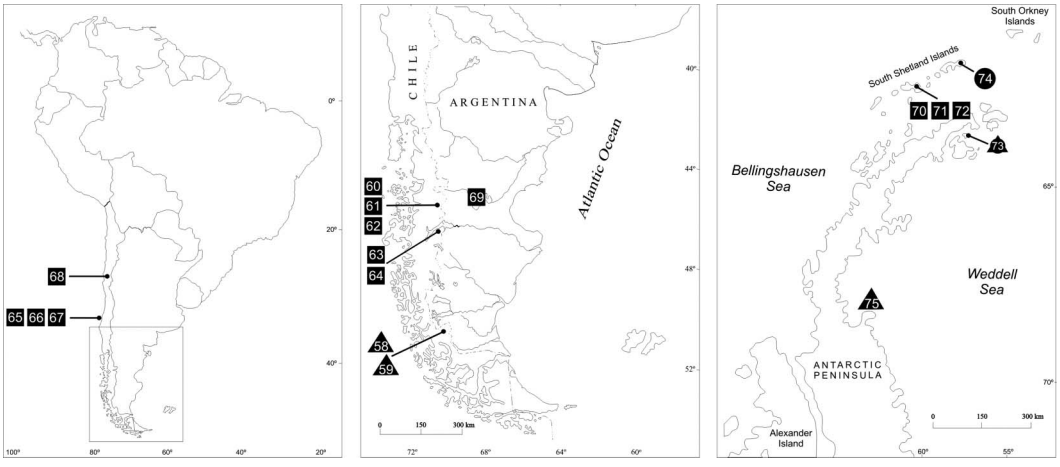

Fig. 4. Maps showing the Late Cretaceous fossil localities. Numbers follow the table numeration. Localities are marked with circles for leaves, squares for woods and triangles for cones and isolated ovuliferous scales.

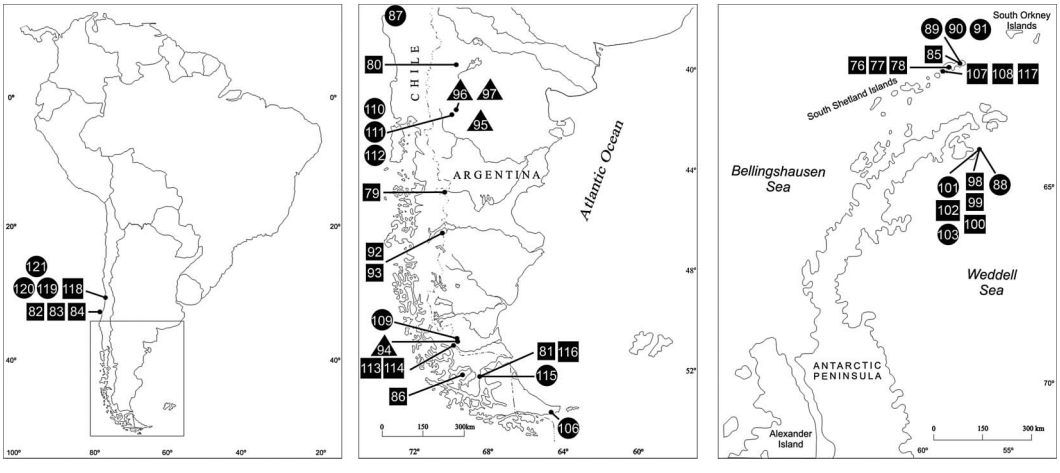

Fig. 5. Maps showing the Cenozoic fossil localities. Numbers follow the table numeration. Localities are marked with circles for leaves, squares for woods and triangles for a seed, cones and isolated ovuliferous scales. Records 104 and 105 are not included.

Jurassic

Gnaedinger & Herbst (2009) documented the occurrence of '*Araucarioxylon*' *protoaraucana* in the Early Jurassic of Argentinean Patagonia and reassigned it to the morphogenus *Agathoxylon* Hartig, (1848). Although the type material of *Agathoxylon protoaraucana* (Brea) Gnaedinger & Herbst, 2009 is from a wood not considered araucariacean with certainty (Brea 1997), this younger fossil wood is considered more confidently araucariacean according to Gnaedinger & Herbst (2009), although the affiliation is equivocal because there is no evidence of other araucariacean fossils in the same strata. *Agathoxylon termieri* Gnaedinger, 2006, a fossil wood with typically Araucariaceae characters (alternate pitting and numerous cross-field pits) was described from the Lower Jurassic Piedra Pintada Formation and Herbst (1966) described a fossil leaf from the same formation that corroborates the presence of the family. Ferello (1947) referred (with doubts) an ovuliferous scale to *Araucarites* from Piedra del Águila in Argentina. Despite the characteristic rhombic shape and multiple parallel veins, the poor description and illustration do not allow confident affiliation of the scale to Araucariaceae. *Araucarioxylon liguaensis* Torres & Philippe, 2002 from Chile has uni-biseriate alternate pitting and cupressoid cross-field pits that suggest a close affinity to the Araucariaceae, but, again, the affiliation is equivocal in the absence of other araucariacean fossils that assure the presence of the family. *Araucarites philipsi* Arrondo & Petriella, 1980 was described from the Early Jurassic of Patagonia. It is a cuneiform ovuliferous scale with an elongated seed that can be referred to Araucariaceae with reasonable confidence. Similar dispersed ovuliferous scales, commonly assigned to *Araucarites*, have been

reported from throughout the Jurassic of Patagonia by Berry (1924), Frenguelli (1949), Feruglio (1951), Herbst & Anzótegui (1968), Baldoni (1980), Cortés & Baldoni (1984) and Channing *et al*. (2007)—see Table 1. The Cerro Cuadrado Petrified Forest in Santa Cruz province, Argentina and the nearby localities Cerro Alto and Cerro Madre e Hija have yielded numerous macrofossils including reproductive cones, woods and leaves. *Araucaria mirabilis* (Spegazzini) Windhausen (1931) is an ovuliferous cone (Fig. 6A–C) varying in shape from spherical to ellipsoid, with single-seeded ovuliferous scales bearing thick woody wings and deciduous laminar tips arranged in a close spiral (Calder 1953). *Pararaucaria patagonica* Wieland, 1929 is another ovuliferous cone from the same localities, but is ovoid with thick bracts that are free from each corresponding scale for the majority of their length (Calder 1953). *Araucarites sanctaecrucis* Calder, 1953 is represented by imbricate rhombic leaves, each with an incurved apex. Calder (1953) also described some seedlings, probably of *Araucaria mirabilis* and some fossil woods with affinity to Araucariaceae. A fossil wood very similar to extant *Araucaria araucana* was also described as *Agathoxylon matildense* Zamuner & Falaschi, 2005 from the same deposits. Gothan (1925) also mentioned fossil woods (assigned to *Dadoxylon* sp.) from a nearby locality but these can probably be placed in *A. matildense* according to his description. A microsporangiate cone from the same petrified forests was described by Menéndez (1960) that might also be related to Araucariaceae.

Antarctic Araucariaceae of Jurassic age include uniovulate cone–scale complexes such as *Araucarites antarcticus* (Gee) Birkenmajer & Ociepa, 2008. This material from the Mount Flora Formation was first assigned to *Araucaria* because of the winged ovuliferous scale, partially fused to the woody bract, which is very similar to those present in extant species of this genus. However, with the recent discovery of *Wollemia*, both the fossil bract and ovuliferous scales might represent either *Araucaria* or *Wollemia* (*sensu* Chambers *et al*. 1998, Cantrill & Falcon Lang 2001). This was the reason for the reassignment to *Araucarites antarcticus* by Birkenmajer & Ociepa (2008). Torres *et al*. (2000) described an araucariacean wood from the same stratigraphic unit.

Early Cretaceous

In addition to the increase in the number of araucariacean fossil records in the Early Cretaceous, a wider distribution in South America is evident with the northernmost examples (ovuliferous and microsporangiate cones) recorded from Colombia. *Araucariostrobus creutzbergii* Huertas, 1970 is a female subspherical cone from Colombia, with imbricate, striate and spirally arranged bracts that have a distinct keel and end in an acute apex (van Waveren *et al*. 2002). *Araucariostrobus camargoi* Huertas, 1970 is a microsporangiate elliptical cone with acute apex and with bracts and pollen sacs preserved. Later, that author described from the same area *Araucariostrobus archangelskii* Huertas, 1976, a female cone with subrounded apex, concave and truncate base with mamillate bracts lacking seeds. Van Waveren *et al*. (2002) described a similar ovuliferous cone from this region but, as it is smaller than the holotype, they assigned it tentatively to *Araucariostrobus* sp. cf. *A. archangelskii*. *Araucaria cartellei* Duarte, 1993 is the only formally named fossil leaf known for this period from South America outside Patagonia; it was collected in northeastern Brazil. It is an asymmetrical leaf, ovate–lanceolate, with an obtuse–decurrent base and attenuate apex. Duarte (1989) described *Araucarites vulcanoi* from the same formation as megasporophylls (ovuliferous scales) with a cuneiform base and curved margins (Duarte 1993). From the Crato Formation, Kunzmann *et al*. (2004) and Martill *et al*. (2005) informally assigned four cones, including male and female forms, and associated leaves, to the Araucariaceae. The narrowly lanceolate foliage and parallel-veined leaves spirally attached to the distal portion of a smooth stem, resemble the foliage of extant *Agathis*. Shoemaker (1982) briefly mentioned the presence of two morphospecies of fossil wood (*Araucarioxylon*) from the Early Cretaceous of Ecuador, but in the absence of anatomical studies, these records can not be confirmed. In Patagonia, the Baqueró Group, was revised by Cladera *et al*. (2002) and includes the Punta del Barco, Bajo Tigre and Anfiteatro de Ticó formations. *Araucaria grandifolia* Feruglio, 1951 leaves (Fig. 6D), with preserved cuticle, have been recorded from the Punta del Barco Formation by Feruglio (1951). This morphospecies has large, amphistomatic, triangular–lanceolate, imbricate, spirally arranged leaves, each with an acute apex, decurrent base and a strong keel on the abaxial surface (Del Fueyo & Archangelsky 2002). *Notopehuen brevis* Del Fueyo (1991), from Anfiteatro de Ticó Formation, is a microsporangiate cone containing *Araucariacites* Cookson, 1947 pollen grains that are organically attached to branches with leaves of the *Brachyphyllum* type. Archangelsky (1966) described two cone scales, *Araucarites baqueroensis* and *Araucarites minimus*, from the same Formation. *Araucarites baqueroensis* is a cuneiform ovuliferous scale with lateral wings, acuminate apex and a single seed

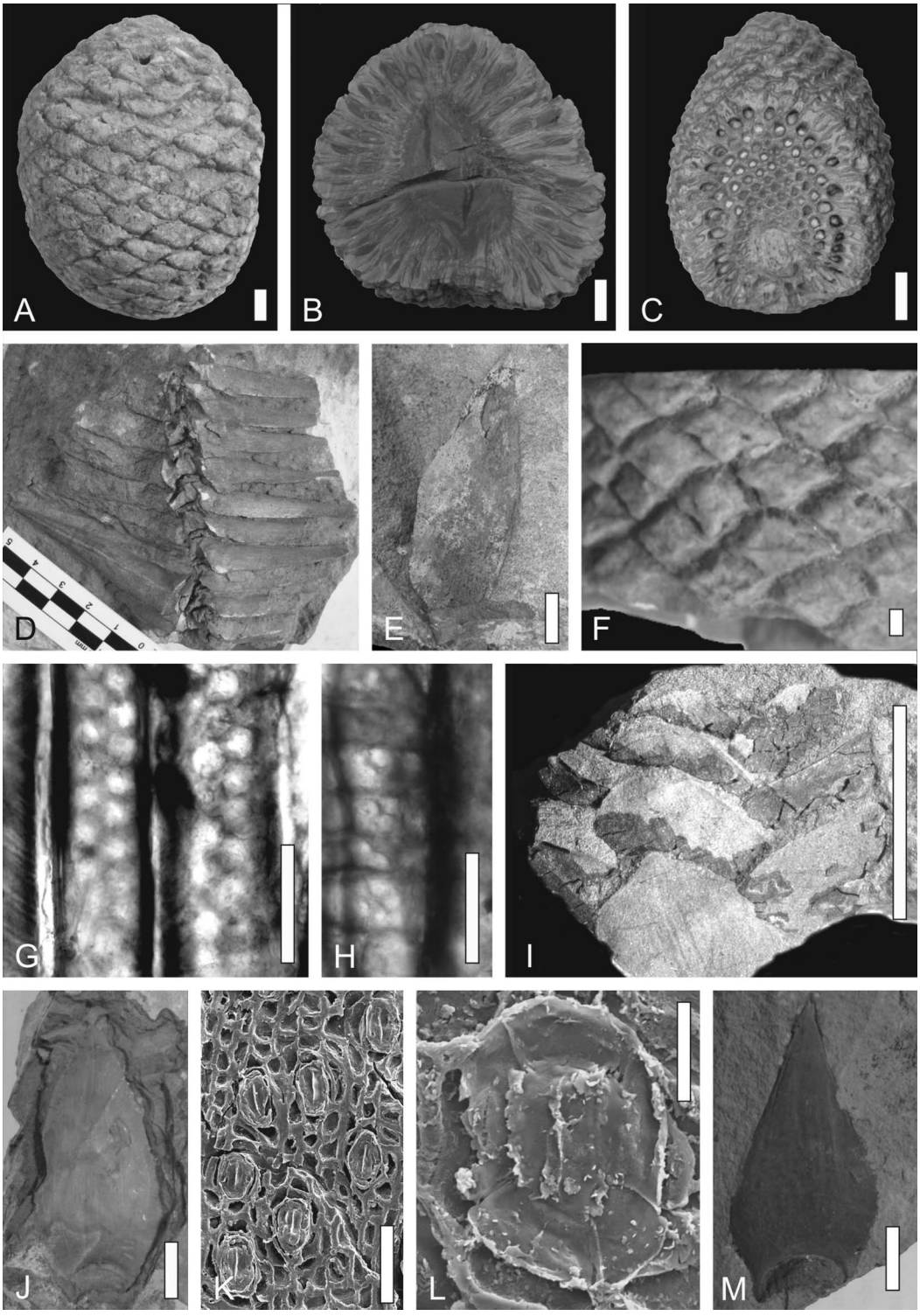

Fig. 6. Selected Araucariaceae fossils from South America and Antarctica. **A–C**, *Araucaria mirabilis* (Spegazzini) Windhausen, 1931; **A**, BAPb 41; **B**, LPPb 8079; **C**, LPPb 181; **D**, *Araucaria grandifolia* Feruglio (BAPb 1455); **E–F**, *Araucaria fibrosa* (Césari, Marenssi & Santillana) Césari, Marenssi & Santillana, 2009; **E**, BAFCPB 16330a; **F**, BAFCPB 16331; **G–H**, *Araucarioxylon seymourense* Torres *et al.*, 1994 (BAPb 12234); **G**, Alternate pitting on tracheid radial walls; **H**, Cross-field pitting; **I–L**, *Araucaria pararaucana* Panti *et al.*, 2007; **I**, BAPb 13541; **J**, BAPb 13542; **K**, general view of discontinuous stomatal rows (interior of abaxial surface cuticle); **L**, subrounded stomata; **M**, *Araucaria nathorsti* Dusén, 1899. Scale bars: **A–E**, **I–J**, **M** = 10 mm, **F** = 2 mm, **K** = 10 μm, **G–H**, **L** = 50 μm.

embedded in the scale; similar material was described by Feruglio (1951) as *Araucaria* (sect. *Colymbea*). *Araucarites minimus* is a broad scale with irregularly lobed margins and bears a single seed. Del Fueyo & Archangelsky (2005) described *Alkastrobus peltatus*, an anatomically preserved male cone with peltate microsporangia bearing pollen of *Cyclusphaera* Elsik, 1966 type from the same unit. The sediments of the Springhill Formation, exposed in Argentina and Chile, have yielded a cuneiform uniovulate scale with an acuminate protuberance (*Araucarites chilensis* Baldoni, 1979). Archangelsky (1976) had previously reported a similar ovuliferous scale and assigned it to *Araucarites* sp. Fossil wood from the Apeleg Formation in Chilean Patagonia was described by Philippe *et al.* (2000) as *Agathoxylon* sp.

Fossil woods, leaves, cones and isolated ovuliferous scales are widely distributed in Antarctic Lower Cretaceous strata. Jefferson & MacDonald (1981) described *Dadoxylon* sp. from South Georgia, a fossil wood previously mentioned by Gordon (1930). The sediments of the Neptune Glacier Formation on Alexander Island have yielded several morphospecies of araucariacean leaves and scales (Cantrill & Falcon Lang 2001). *Araucaria alexandrensis* Cantrill & Falcon Lang, 2001 are branches with strongly imbricate, spirally inserted, lanceolate to ovate spreading leaves with broad and decurrent bases. *Araucaria chambersi* Cantrill & Falcon Lang, 2001 in contrast, is represented by plagiotropic shoots bearing linear–lanceolate, slightly concave and spreading leaves that have a slightly contracted and twisted base. These two species have the typical coriaceous, imbricate foliage with numerous parallel veins of the Araucariaceae. *Araucarites wollemiaformis* Cantrill & Falcon Lang, 2001 are large, woody, cuneate cone scales with a prominent apical spine. The distal portion of the scale has a distinct, broad, triangular scar on the adaxial surface. *Araucarites citadelbastionensis* Cantrill & Falcon Lang, 2001 are cone scales comprising a cuneate to wedge-shaped woody bract and attached ovuliferous scale. From the same unit, Falcon Lang & Cantrill (2000) described two types of fossil wood assigning them to *Araucariopitys* sp. and *Araucarioxylon* sp. Torres *et al.* (1982) described *Araucarioxylon arayaii* with biseriate and locally triseriate pitting, from the Cerro Negro Formation on Livingstone Island. The same taxon was reported from Snow Island (Torres *et al.* 1995). Later, Torres *et al.* (1997) described a fossil wood from the same locality on Snow Island and assigned it to *Araucarioxylon* sp. A. The Cerro Negro Formation has also yielded two forms of *Araucarioxylon* not assigned to formal species (Falcon Lang & Cantrill 2001), a fossil leaf similar to *Araucarites baqueroensis* (Hernández & Azcarate 1971) and an ovuliferous scale assigned to *Araucarites* sp. (Parica *et al.* 2007). Torres (1993) described a wood with affinity to *Araucarioxylon* from sediments of Cape Shirreff on Livingston Island, of probable Early Cretaceous age. Ottone & Medina (1998) described another fossil wood with purported affinity to extant *Araucaria araucana* from the Kotick Point Formation on James Ross Island.

Late Cretaceous

The South American record for this interval consists mostly of fossil woods. However, one scale, *Araucarites patagonica* Kurtz, 1902 was described from the Cerro Cazador Formation, Chile. The brief description makes reference to the lower portion of the cone scale but it was not illustrated. The morphospecies was considered a *nomen nudum* by Hünicken (1971, 1995) due to its poor preservation and incomplete description. *Pseudoaraucaria valentini* (Kurtz) Menéndez, 1972, was also described from Chilean Patagonia. It is an ovuliferous scale that bears two seeds, a unique character of *Pseudoaraucaria*, and is placed in the Araucariaceae because it shares with *Agathis* the fused bract and ovuliferous scale. Torres & Rallo (1981) described *Araucarioxylon pichasquense* from central Chile, a fossil wood with high rays and numerous cupressoid cross-field pits. Later, Nishida *et al.* (1990, 1992) found the same morphospecies at two localities in southern Chile. Nishida *et al.* (1990, 1992) also mentioned the occurrence of other Araucariaceae fossil woods, *Araucarioxylon* sp., *Araucarioxylon ohzanum* Nishida, Ohsawa, H. Nishida & Rancusi, 1992 and the new combination *Araucarioxylon kellerense* (Lucas & Lacey) Nishida, Ohsawa & Rancusi, 1990 in southern Chile. Three fossil wood morphospecies were described from Quiriquina Island: *Araucarioxylon parachoshiense* Nishida & Nishida 1987, with very low rays, *Araucarioxylon resinosum* Torres & Biro Bagoczky, 1986 and *Araucarioxylon pluriresinosum* Torres & Biro Bagoczky, 1986, these last two are very similar and share abundant resiniferous content. A fossil wood described by Pujana *et al.* (2007) as being very similar to extant *Araucaria araucana* is the only Late Cretaceous macrofossil of Araucariaceae found in Argentina.

From Vega Island near the Antarctic Peninsula, a female cone with attached leaves, *Araucaria fibrosa* (Césari, Marenssi & Santillana) Césari, Marenssi & Santillana, 2009 was described. It has large, spreading and widely separated, lanceolate to ovate leaves with acute tips and decurrent bases (Fig. 6E). The

numerous rhombic cone scales (Fig. 6F) have a median ridge and marked lateral wings and are arranged in a close spiral (César *et al*. 2001). Eklund *et al*. (2004) described a putative Araucariaceae scale–bract complex, similar to, but smaller than, other Aracucariaceae fossils, from the Late Cretaceous of the Antarctic Peninsula. Dutra & Batten (2000) mentioned a leaf, *Araucaria* sp., from sediments of the Zamek Formation at King George (25 de Mayo) Island but no description or illustration was provided, preventing any possible discussion of its assignment.

Araucarioxylon floresii Torres & Lemoigne, 1989, a fossil wood with indistinct growth rings and axial parenchyma, *Araucarioxylon chapmanae* Poole & Cantrill, 2001, a fossil wood with bi–triseriate alternate pitting and *Araucariopitys antarcticus* Poole & Cantrill, 2001, another fossil wood with commonly uniseriate pitting were described from Livingston Island (Torres & Lemoigne 1989, Chapman & Smellie 1992, Philippe *et al*. 1993, Poole & Cantrill 2001).

Cenozoic

All Cenozoic records of the Araucariaceae derive from Patagonia and Antarctica, which probably reflects a genuine contraction in the family's distribution in America. Dramatic decline in Araucariaceae abundance has been reported from both palynological and macrofossil assemblages across the Cretaceous–Paleogene boundary in New Zealand (Vajda & Raine 2003, Pole & Vajda 2009) but high-resolution studies across this boundary in South America are not yet available to test whether this was a pattern common to the entire Southern Hemisphere. *Araucarioxylon doeringii* Conwentz, 1885 from northern Patagonia was the first South American macrofossil assigned to the family. This wood has alternate pitting and locally biseriate high rays and, although not precisely dated, it is presumed to derive from Cenozoic strata. Later, Nishida (1981, 1984) described the same morphospecies from Quiriquina Island in Chile. Kräusel (1924) mentioned two records of *Dadoxylon pseudoparenchymatosum* Gothan, 1908 in Patagonia and later Nishida (1984) cited the same morphospecies from Quiriquina Island as *Araucarioxylon pseudoparenchymatosum* (Gothan) Nishida, 1984. He also described *Araucarioxylon quiriquinaense* Nishida, 1984 from that island, a fossil wood with normally biseriate pitting and low rays, very similar to the wood of extant *Araucaria araucana*. There are only three records from the Paleocene: *Araucarioxylon* sp., a fossil wood from Riesco Island (Nishida *et al*. 2006), *Araucaria araucoensis* Berry, 1922 from the Lota y Coronel Formation, an ovate to lanceolate unkeeled and asymmetrical fossil leaf, differing from modern *A. araucana* in the smaller size and less crowded arrangement of the leaves, and *Araucaria imponens* Dusén, 1908, from the Cross Valley Formation on Seymour Island. The last is a linear leaf that was apparently shed independently of the parent branch (Cantrill *et al*. 2011). Eocene sediments have yielded a range of fossils in South America, including two woods, *Araucarioxylon pichasquense* and *Araucarioxylon* sp. cf. *A. kellerense* (Terada *et al*. 2006a), both from southern Chile. *Araucaria pichileufulensis* Berry, 1938 was described from the lower Eocene of Río Negro, Argentina. It is represented by cone scales that consist of a kite-shaped central portion, which is thick and armed with a stout central point and contains a large obovate central seed, and leaves arranged in a close spiral that are pointed, triangular, falcate and thick. Later, Wilf *et al*. (2010) mentioned the probable presence of this morphospecies at a nearby locality. Wilf *et al*. (2003) assigned another ovuliferous scale to *Araucaria* sp. from Patagonia. These last three Patagonian scales represent the only fossil reproductive structures of the family found in South America and Antarctica from the Cenozoic. Hünicken (1955, 1967) mentioned a seed from the Río Turbio Formation and suggested its affinity to Araucariaceae based only on external morphological features. *Araucariacites* pollen is well represented in the Río Turbio Formation (Romero 1977) and thus supports the presence of Araucariaceae in the Formation. From the upper Eocene–early Oligocene strata of Tierra del Fuego, Panti *et al*. (2007) described *Araucaria pararaucana*, based on gross morphological and cuticular features. The leaves are acutely pointed, ovate–lanceolate and imbricate (Fig. 6I–J). The stomata are arranged in parallel and discontinuous rows and are elliptical to sub-rounded (Fig. 6K–L). The only other undoubted araucariacean macrofossil from the Oligocene is a fossil leaf from the Río Guillermo Formation (Hünicken 1995). *Araucaria nathorsti* Dusén, 1899 was originally described from the late Oligocene–Miocene Loreto Formation in Chile and later Terada *et al*. (2006c) mentioned the presence of the fossil wood *Araucarioxylon pichasquense* in the same unit. *Araucaria nathorsti* was also recorded from the Oligocene–Miocene Ñirihuau Formation (see Paredes *et al*. 2009) at three localities in Argentinean Patagonia and consists of leaves (Fig. 6M) with preserved cuticle (Berry 1928, Fiori 1939, Menéndez & Caccavari 1966). A detailed revision of the stratigraphy of these fossiliferous localities is needed, hence they are considered as separate records.

The wood taxa *Araucarioxylon kellerense*, *Araucarioxylon pichasquense* (Terada *et al*. 2006b) and *Araucarioxylon chilense* Nishida, 1970 (Nishida 1984) together with *Araucaria* sp. leaves, described as rhombic imbricate and spirally arranged (Troncoso 1991, Troncoso & Romero 1993, Troncoso & Encinas 2006), have been reported elsewhere from the late Oligocene–Miocene of Chile (Table 1).

Many araucariacean fossils that have been reported from Antarctica are from the Eocene La Meseta Formation on Seymour (Marambio) Island. These include indeterminate araucariacean leaves recorded by Case (1988) as 'Specimen D' (undescribed) and *Araucaria nathorsti* (Doktor *et al*. 1996). Woods include *Dadoxylon pseudoparenchymatosum* that was apparently first described from La Meseta Formation (Gothan 1908) with alternate biseriate pitting and septate tracheids that resemble axial parenchyma. Torres *et al*. (1994) described a new morphospecies of fossil wood, *Araucarioxylon seymourense* (Fig. 6G–H) with alternate pitting and rays up to 40 cells high, and also mentioned the occurrence of *Araucarioxylon novae-zeelandiae* (Stopes) Torres *et al*., 1994 and Cantrill & Poole (2005) described a specimen, probably a branch, retaining bark, and assigned it to a new species, *Araucaria marenssii*. Eocene sediments of McMurdo Sound have yielded the only two records of araucariacean macrofossils from East Antarctica: leaves of *Araucaria* (Pole *et al*. 2000) and several woods with *Araucarioxylon* affinity (Francis 2000). King George (25 de Mayo) Island is the other Antarctic island that also hosts Cenozoic fossils with Araucariacean affinity. Lucas & Lacey (1981) briefly described *Dadoxylon kellerense* from Keller Peninsula having common triseriate alternate pitting; they also recorded woods assignable to *Dadoxylon* sp. and *Dadoxylon pseudoparenchymatosum*. From the Barton Peninsula, Hee & Soon (1991) also recorded a fossil with *Dadoxylon* affinity. From the late Eocene–early Oligocene strata of the Petrified Forest Creek, Torres & Lemoigne (1988) described two fossil woods of *Araucarioxylon* without assignment to morphospecies. From the 'Fossil Hill Member' (see Birkenmajer 2001) a fossil leaf resembling *Araucaria nathorstii* was described by Troncoso 1986. Later, Liu (1990) and Zhou & Li (1994) described araucariacean leaves from the same strata that, despite their poor preservation, closely resemble some species of the section *Eutacta*. Apparently, the youngest araucariacean macrofossil from Antarctica is a fossil wood described by Cortemiglia *et al*. (1981) from Admiralty Bay and with a supposed middle Eocene–early Oligocene age.

Conclusions

The Araucariaceae macrofossil record is substantial in South America and Antarctica, especially in Patagonia and the Antarctic Peninsula and adjacent islands (Figs 2–5). For East Antarctica there are only two records (Francis 2000, Pole *et al*. 2000). In South America and Antarctica there are 121 macrofossil records and 50 morphospecies from different localities. Most of the records correspond to fossil woods (47%), followed by isolated ovuliferous scales and cones (29%), and leaves (23%); only one seed and one record of seedlings are known. Fossil woods of Araucariaceae are abundant and readily distinguishable on the basis of their alternate crowded pitting ('araucarioid' type). Unfortunately, fossil woods permit limited infrafamilial discrimination since the sections of *Araucaria* and even the genera *Agathis* and *Araucaria* can not always be distinguished on wood anatomy.

In South America and Antarctica, the Araucariaceae were present at least since the Jurassic, after which they expanded and diversified until the Early Cretaceous. Kunzmann (2007) argued that Araucariaceae, were comparatively more abundant and diverse worldwide during the Early Cretaceous and this hypothesis is consistent with the abundance of fossils in South America and Antarctica from that time (Fig. 3). After the Early Cretaceous, the diversity decreased both in South America and globally (Kershaw & Wagstaff 2001). The family's continued distributional contraction and decline in abundance through the Cenozoic is more likely a result of climatic deterioration rather than competition with other plants (Kershaw & Wagstaff 2001).

Slow rates of evolutionary change apparently characterize Araucariaceae (Page 1990). Since the Jurassic, evolutionary morphological and anatomical changes are evident principally in leaves and microsporangiate cones (Del Fueyo 1991). The wood anatomy, with typical alternate pitting arrangement, uniseriate rays and bordered cross-field pits is highly conservative (Pujana *et al*. 2007). This is confirmed by the strong similarity between some Jurassic woods (i.e. *Agathoxylon matildense*) and extant *Araucaria araucana*. With this work and the macrofossil revisions of Kershaw & Wagstaff (2001), Hill & Brodribb (1999) and Pole (2008) a complete survey of austral Araucariaceae macrofossils is now complete. Only two macrofossil morphospecies are purportedly common to Antarctica and New Zealand: a fossil wood, *Araucarioxylon novae-zeelandiae* (Stopes 1914), and an ovuliferous scale, *Araucarites cutchensis* (Arber 1917), although a more detailed reappraisal of these

fossils will be needed to confirm their identities. No macrofossil morphospecies of Araucariaceae are common to Antarctica–South America and Australia. Further comprehensive biogeographical analysis of these Southern Hemisphere macrofossil revisions suites may help to understand the evolutionary history of the family.

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References

Andersson, R.D., 1907. Geological fragments of Tierra del Fuego. *Bulletin of the Geological Institution of the University of Uppsala 8*, 169–183.

Arber, E.A.N., 1917. The earlier Mesozoic floras of New Zealand. *New Zealand Geological Survey Bulletin 6*, 1–80.

Archangelsky, S., 1966. New gymnosperms from the Tico flora, Santa Cruz province, Argentina. *Bulletin of the British Museum (Natural History), Geology 13*, 201–295.

Archangelsky, S., 1976. Vegetales fósiles de la Formación Springhill, Cretácico en el subsuelo de la Cuenca Magallánica, Chile. *Ameghiniana 13*, 141–158.

Archangelsky, S. & Del Fueyo, G.M., 2010. Endemism of Early Cretaceous conifers in Western Gondwana. In *Plants in Mesozoic Time: Innovations, Phylogeny, Ecosystems*, C.T. Gee, ed., Indiana University Press, Bloomington, 247–268.

Arrondo, O.G. & Petriella, B., 1980. Alicurá, nueva localidad plantífera liásica de la provincia de Neuquén, Argentina. *Ameghiniana 17*, 200–215.

Ash, S.R. & Creber, G.T., 2000. The Late Triassic *Araucarioxylon arizonicum* trees of the petrified forest National Park, Arizona, USA. *Palaeontology 43*, 15–28.

Baldoni, A.M., 1979. Nuevos elementos paleoflorísticos de la tafoflora de la Formación Springhill. Límite Jurásico–Cretácico, subsuelo de Argentina y Chile Austral. *Ameghiniana 16*, 103–119.

Baldoni, A.M., 1980. Plantas fósiles jurásicas de una nueva localidad en la Provincia del Neuquén. *Ameghiniana 17*, 255–272.

Balme, B.E., 1995. Fossil *in situ* spores and pollen grains: an annotated catalogue. *Review of Palaeobotany and Palynology 87*, 81–323.

Berry, E.W., 1922. The flora of the Concepción–Arauco Coal Measures of Chile. *John Hopkins University Studies in Geology 4*, 73–142.

Berry, E.W., 1924. Mesozoic plants from Patagonia. *American Journal of Science 7*, 473–482.

Berry, E.W., 1928. Tertiary fossil plants from the Argentine Republic. *Proceedings of the United States National Museum 73*, 1–27.

Berry, E.W., 1938. Tertiary flora from the Río Pichileufú, Argentina. *John Hopkins University Studies in Geology 12*, 1–149.

Birkenmajer, K., 1988. Tertiary glacial and interglacial deposits, South Shetland Islands, Antarctica: geochronology versus biostratigrahpy (A progress report). *Bulletin of the Polish Academy of Sciences: Earth Science 36*, 133–145.

Birkenmajer, K., 2001. Mesozoic and Cenozoic stratigraphic units in parts of the South Shetland Islands and northern Antarctic Peninsula (as used by the polish Antarctic programmes). *Studia Geologica Polonica 118*, 1–188.

Birkenmajer, K. & Ociepa, A.M., 2008. Plant-bearing Jurassic strata at Hope Bay, Antarctic Peninsula (West Antarctica): geology and fossil-plant descriptions. *Studia Geologica Polonica 128*, 5–96.

Brea, M., 1997. Una nueva especie del género *Araucarioxylon* Kraus 1870, emend. Maheshwari 1972 del Triásico de Agua de la Zorra, Uspallata, Mendoza, Argentina. *Ameghiniana 34*, 485–496.

Brea, M., Artabe, A.E. & Spalleti, L.A., 2008. Ecological reconstruction of a mixed Middle Triassic forest from Argentina. *Alcheringa 32*, 365–393.

Calder, M.G., 1953. A coniferous petrified forest in Patagonia. *Bulletin of the British Museum, Geological Series 2*, 97–138.

Cantrill, D.J. & Falcon Lang, H., 2001. Cretaceous (Late Albian) coniferales of Alexander Island, Antarctica. 2. Leaves, reproductive structures and roots. *Review of Palaeobotany and Palynology 115*, 119–145.

Cantrill, D.J. & Poole, I., 2005. A new Eocene *Araucaria* from Seymour Island, Antarctica: evidence from growth form and bark morphology. *Alcheringa 29*, 341–350.

Cantrill, D.J., Tosolini, A-M.P. & Francis, J.E., 2011. Paleocene flora from Seymour Island, Antarctica: revision of Dusén's (1908) pteridophyte and conifer taxa. *Alcheringa 35*, 309–328.

Case, J.A., 1988. Paleogene floras from Seymour Island, Antarctic Peninsula. In *Geology and Paleontology of Seymour Island, Antarctic Peninsula*, R.M. Feldmann & M.O. Woodburne, eds, The Geological Society of America Memoir 169, Geological Society of America, Boulder, 523–530.

Césari, S.N., Marenssi, S.A. & Santillana, S.N., 2001. Conifers from the Late Cretaceous of Cape Lamb, Vega Island, Antarctica. *Cretaceous Research 22*, 309–319.

Césari, S.N., Marenssi, S.A. & Santillana, S.N., 2009. *Araucaria fibrosa*, a new name to replace the illegitimate name *Araucaria antarctica* Césari, Marenssi and Santillana, 2001. *Cretaceous Research 30*, 1169.

Chambers, T.C., Drinnan, A.N. & McLoughlin, S., 1998. Some morphological features of Wollemi pine (*Wollemia nobilis*: Araucariaceae) and their comparison to Cretaceous plant fossils. *International Journal of Plant Sciences 159*, 160–171.

Channing, A., Zamuner, A.B. & Zúñiga, A., 2007. A new Middle–Late Jurassic flora and hot spring chert deposit from the Deseado Massif, Santa Cruz province, Argentina. *Geological Magazine 144*, 401–411.

Chapman, J.L. & Smellie, J.L., 1992. Cretaceous fossil wood and palynomorphs from Williams Point, Livingston Island, Antarctic Peninsula. *Review of Palaeobotany and Palynology 74*, 163–192.

Cladera, G., Andreis, R., Archangelsky, S. & Cúneo, R., 2002. Estratigrafía del Grupo Baquero, Patagonia (provincia de Santa Cruz, Argentina). *Ameghiniana 39*, 3–20.

Conwentz, H., 1885. Árboles fósiles del Río Negro. *Boletín de la Academia Nacional de Ciencias (Córdoba) 7*, 435–456.

Cookson, I.C., 1947. Plant microfossils from the lignites of the Kerguelen Archipelago. *British and New Zealand Antarctic Research Expedition, 1929–1931, Reports Series 2A*, 129–142.

Cortemiglia, G.C., Gastaldo, P. & Terranova, R., 1981. Studio di piante fossili tróvate nella King George Island délle isole Shetland del Sur (Antartide). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano 122*, 37–61.

Cortés, J.M. & Baldoni, A.M., 1984. Plantas fósiles jurásicas al sur del Río Chubut medio. *Actas del 9° Congreso Geológico Argentina, Bariloche, Argentina 4*, 432–443.

Crisafulli, A. & Herbst, R., 2008. Maderas gimnospérmicas de la Formación Solca (Pérmico Inferior), provincia de La Rioja, Argentina. *Ameghiniana 45*, 737–751.

Darrow, B.S., 1936. A fossil araucarian embryo from the Cerro Cuadrado of Patagonia. *Botanical Gazette 98*, 328–337.

De Laubenfels, D.J., 1953. The external morphology of coniferous leaves. *Phytomorphology 3*, 1–20.

Del Fueyo, G.M., 1991. Una nueva Araucariaceae cretácica de Patagonia, Argentina. *Ameghiniana 28*, 149–161.

Del Fueyo, G.M. & Archangelsky, A., 2002. *Araucaria grandifolia* Feruglio from the Early Cretaceous of Patagonia, Argentina. *Cretaceous Research 23*, 265–277.

Del Fueyo, G.M. & Archangelsky, S., 2005. A new araucarian pollen cone with *in situ Cyclusphaera* Elsik from the Aptian of Patagonia, Argentina. *Cretaceous Research 26*, 757–768.

Doktor, M., Gazdzicki, A., Jerzmanska, A., Porebski, S. & Zastawniak, E.A., 1996. A plant-and-fish assemblage from the Eocene La Meseta Formation of Seymour Island (Antarctic Peninsula) and its environmental implications. *Palaeontologia Polonica 55*, 127–146.

Duarte, L., 1989. Remains of the Lower Cretaceous plants from northeast of Brazil. *11 Congresso Brasileiro de Paleontologia, Curitiba, Brasil 1*, 219–233.

Duarte, L., 1993. Araucariaceae remains in the Santana Formation, Crato Member (Aptian); northeastern Brazil. *Anais da Academia Brasileira de Ciencias 65*, 357–362.

Dúsen, P., 1899. Über die tertiäre Flora der Magallans-Lander. In *Wissenschaftliche Ergebnisse der Schwdischen Expedition nach den Magallans-Länder 1895–97 vol. 1*, O. Nordenskjöld, ed., Lithographisches Institut des Generalstabs, Stockholm, 87–108.

Dúsen, P., 1908. Über die Tertiäre Flora der Seymour Insel. In *Wissenschaftliche Ergebnisse der Schwedischen Südpolar Expedition 1901–1903 vol. 3 (3)*, O. Nordenskjöld, ed., Lithographisches Institut des Generalstabs, Stockholm, 1–27.

Dutra, T.L. & Batten, D.J., 2000. Late Cretaceous floras of King George Island, West Antarctica, and their palaeoenvironmental and phytogeographic implications. *Cretaceous Research 21*, 181–209.

Dutra, T.L. & Stranz, A., 2003. História das Araucariaceae: a contribuição dos fósseis para o entendimento das adaptações modernas da família no Hemisfério Sul, com vistas a seu manejo e conservação. In *Tecnologia diagnóstico e planejamento ambiental*, L.R. Ronchi & O.G.W. Coehlo, eds, UNISINOS, São Leopoldo, 293–351.

Dutra, T.L. & Stranz, A., 2008. Biogeografia, evolução e ecologia da família Araucariaceae: o que mostra a paleontologia. In *Floresta com Araucária; ecologia, conservação e desenvolvimento sustentável*, C. Fonseca, A.F. Souza, A.M. Leal Zanchet, T.L. Dutra, A. Backes & G. Ganade, eds, Holos Editora, São Paulo, 15–34.

Dutra, T.L., Stranz, A. & Wilberger, T.P., 2007. Araucariaceae: a phytohistory of a family. In *A Brief History of the Gymnosperms*, J. Anderson, H.M. Anderson & C. Cleal, eds, National Biodiversity Institute, Pretoria, 56–61.

Eklund, H., Cantrill, D.J. & Francis, J.E., 2004. Late Cretaceous plant mesofossils from Table Nunatak, Antarctica. *Cretaceous Research 25*, 211–228.

Elsik, W.C., 1966. New sporomorph genera from the Upper Cretaceous of Perú. *Pollen et Spores 8*, 553–564.

Endlicher, S., 1847. Conspectus coniferarum fossilium. In *Synopsis Coniferarum 52*, S. Endlicher, ed., Scheitlin & Zolikofer, St.- Gall, 52.

Enright, N.J., Hill, R.S. & Veblen, T.T., 1995. The southern conifers—an introduction. In *Ecology of the Southern Conifers*, N.J. Enright & R.S. Hill, eds, Melbourne University Press, Melbourne, 1–9.

Escapa, I., Cúneo, R. & Cladera, G., 2008. New evidence for the age of the Jurassic Flora from Cañadón del Zaino, Sierra de Taquetrén, Chubut. *Ameghiniana 45*, 633–637.

Falcon Lang, H. & Cantrill, D.J., 2000. Cretaceous (Late Albian) coniferales of Alexander Island, Antarctica. 1: Wood taxonomy: a quantitative approach. *Review of Palaeobotany and Palynology 111*, 1–17.

Falcon Lang, H. & Cantrill, D.J., 2001. Gymnosperm woods from the Cretaceous (mid-Aptian) Cerro Negro Formation, Byers Peninsula, Livingston Island, Antarctica: the arborescent vegetation of a volcanic arc. *Cretaceous Research 22*, 277–293.

Ferello, R., 1947. Los depósitos plantíferos de Piedra del Águila (Neuquén) y sus relaciones. *Boletín de Informaciones Petroleras 278*, 3–16.

Feruglio, E., 1951. Piante del Mesozoico della Patagonia. *Publicazione dell Istituto Geologico della Universitá di Torino 1*, 35–80.

Fiori, A., 1939. Filliti terziarie della Patagonia. II. Filliti del Río Ñirihuau. *Giornale di Geologia 13*, 41–67.

Francis, J.E., 2000. Fossil wood from Eocene high latitude forests, McMurdo Sound, Antarctica. *Antarctic Research Series 76*, 253–260.

Frenguelli, J., 1949. Los estratos con '*Estheria*' en el Chubut (Patagonia). *Revista de la Asociación Geológica Argentina 4*, 11–24.

Gee, C.T., 1989. Revision of the Late Jurassic/Early Cretaceous flora from Hope Bay, Antarctica. *Palaeontographica 213B*, 149–214.

Gnaedinger, S., 2006. Maderas jurásicas de Piedra Pintada, Neuquén. *Revista del Museo Argentino de Ciencias Naturales 8*, 171–177.

Gnaedinger, S. & Herbst, R., 2009. Primer registro de maderas gimnospérmicas de la Formación Roca Blanca (Jurásico inferior), provincia de Santa Cruz, Argentina. *Ameghiniana 46*, 59–72.

Gordon, W.T., 1930. A note on *Dadoxylon (Araucarioxylon)* from the Bay of Isles. In *Report on the Collections made during the voyage of the 'Quest' on the Shackleton-Rowett Expedition to the Atlantic and Weddell Sea in 1921–22*, Trustees of the British Museum, London, 24–27.

Gothan, W., 1908. Die fossilen Hölzer von der Seymour und Snow Hill Insel. In *Wissenschaftliche Ergebnisse der Schwedischen Südpolar Expedition 1901–1903 vol. 3 (8)*, O. Nordenskjöld, ed., Lithographisches Institut des Generalstabs, Stockholm, 1–33.

Gothan, W., 1925. Sobre restos de plantas fósiles procedentes de la Patagonia. *Boletín de la Academia Nacional de Ciencias 28*, 197–212.

Halle, T.G., 1913. The Mesozoic flora of Graham Land. *Wissenchaftliche Ergebnisse der Schwedischen Südpolar Expedition 1901–1903*, *3*, 1–123.

Hartig, T., 1848. Beiträge zur Geschichte der Pflanzen und zur Kenntniss der norddeutschen Braunkohlen-Flora. *Botanik Zeitung 6*, 185–190.

Hee, Y.C. & Soon, K.C., 1991. Study on the gymnospermous fossil woods from King George Island. *Korean Journal of Polar Research 2*, 179–185.

Herbst, R., 1966. Revisión de la flora Liásica de Piedra Pintada, provincia de Neuquén, Argentina. *Revista del Museo de La Plata (nueva serie), Sección Paleontología 5*, 27–53.

Herbst, R. & Anzótegui, L.M., 1968. Nuevas plantas de la flora del Jurásico Medio (Matildense) de Taquetrén, Prov. de Chubut. *Ameghiniana 5*, 183–190.

Hernández, P.J. & Azcarate, V., 1971. Estudio paleobotánico preliminar sobre restos de una tafoflora de la Península Byers (Cerro Negro), isla Livingston, islas Shetland del Sur, Antártica. *Serie Científica INACH 2*, 15–50.

Hill, R.S. & Brodribb, T.J., 1999. Southern conifers in time and space. *Australian Journal of Botany 47*, 639–696.

Huertas, G., 1970. Sertum florulae fossilis Villae de Leyva II. *Caldasia 46*, 595–602.

Huertas, G., 1976. Sertum Florulae Fossilis Villae de Leiva III. *Caldasia 54*, 18–23.

Hünicken, M.A., 1955. Depósitos neocretácicos y terciarios del extremo SSW de Santa Cruz. Cuenca carbonífera de Río Turbio. *Revista del Museo Argentino de Ciencias Naturales, Ciencias Geológicas 4*, 1–164.

Hünicken, M.A., 1967. Flora terciaria de los estratos de Río Turbio, Santa Cruz (niveles plantíferos del arroyo Santa Flavia). *Revista de la Facultad de Ciencias Exactas Físicas y Naturales, Universidad Nacional de Córdoba, Serie Ciencias Naturales 27*, 139–227.

Hünicken, M.A., 1971. Atlas de la flora fósil de Cerro Guido (Cretácico Superior), Última Esperanza, Chile (especímenes examinados por F. Kurtz). *Ameghiniana 8*, 231–250.

Hünicken, M.A., 1995. Floras cretácicas y terciarias. *Actas de la Academia Nacional de Ciencias 11*, 199–226.

Hunter, M.A., Cantrill, D.J., Flowerdew, M.J. & Millar, I.L., 2005. Mid-Jurassic age for the Botany Bay Group: Implications for Weddell Sea basin creation and Southern Hemisphere biostratigraphy. *Journal of the Geological Society London 162*, 745–748.

Jefferson, T.H. & MacDonald, D.M., 1981. Fossil wood from South Georgia. *Bulletin of the British Antarctic Survey 54*, 57–64.

Jeffrey, E.C., 1907. *Araucariopitys*, a new genus of araucarians. *Botanical Gazette 44*, 435–444.

Jones, W.G., Hill, K.D. & Allen, J.M., 1995. *Wollemia nobilis*, a new living Australian genus and species in the Araucariaceae. *Telopea 6*, 173–176.

Jussieu, A.L. de, 1789. *Genera plantarum secundum ordines naturales disposita, juxta methodum in horto regio parisiensi exaratam, anno M.DCC.LXXIV*. Paris, 498 pp.

Kershaw, P. & Wagstaff, B., 2001. The southern conifer family Araucariaceae: history, status, and value for paleoenvironmental reconstruction. *Annual Review of Ecology and Systematics 32*, 397–414.

Knowlton, F.H., 1889. New species of fossil wood (*Araucarioxylon arizonicum*) from Arizona and New Mexico. *Proceedings of the United States National Museum 11*, 1–4.

Koch, K., 1873. *Dendrologie; Bäume, Sträucher und Halbsträucher, welche in Mittel- und Nord-Europa im Freien kultivirt werden, vol. 2, Die cupuliferen, coniferen und monocotylen*. Verlag von Ferdinand Enke, Erlangen, 472 pp.

Kraus, G., 1870. *Araucarioxylon*. In *Traité de paléontologie végétale ou la flore du monde primitif dans ses rapports avec les formations géologiques et la flore du monde actuel, vol. 2*, W. Schimper, J.B. Baillière et Fils, Paris, 380–385.

Kräusel, R., 1924. Beiträge zur Kenntnis der fossilen Flora Südamerikas 1. Fossile Hölzer aus Patagonien und benachbarten Gebieten. *Arkiv för Botanik 19*, 1–36.

Kuntze, C.E.O., 1898. *Revisio Generum Plantarum 3*. Leipzig, 576 pp.

Kunzmann, L., 2007. Araucariaceae (Pinopsida): Aspects in palaeobiogeography and palaeobiodiversity in the Mesozoic. *Zoologischer Anzeiger 246*, 257–277.

Kunzmann, L., Mohr, B.A.R. & Bernardes de Oliveira, M.E.C., 2004. Gymnosperms from the Lower Cretaceous Crato Formation (Brazil). *Mitteilungen aus dern Museum für Naturkunde, Berlin, Geowissenschaftliche Reihe 7*, 155–174.

Kurtz, F., 1902. Sobre la existencia de una Dakota–Flora en la Patagonia Austro-Occidental (Cerro Guido, Gobernación de Santa Cruz). Contribuciones a la Palaeophytologia Argentina III. *Revista del Museo de La Plata 10*, 43–60.

Lele, K.M., 1956. Plant fossils from Parsora in the South Rewa Gondwana Basin, India. *The Palaeobotanist 4*, 23–34.

Liu, Q., 1990. Tertiary flora on Fildes Peninsula of King George Island, Antarctica and its environmental significance. *Antarctic Research 2*, 39–45.

Lucas, R.C. & Lacey, W.S., 1981. A permineralized wood flora of probable early Tertiary age from King George Island, South Shetland Islands. *British Antarctic Survey Bulletin 53*, 147–151.

Martill, D.M., Liveridge, R.F., Ferreira Gomes de Andrade, J.A. & Herzog Cardoso, A., 2005. An unusual occurrence of amber in laminated limestones: The Crato Formation Lagerstätte (Early Cretaceous) of Brazil. *Palaeontology 48*, 1399–1408.

Menéndez, C.A., 1951. La flora mesozoica de la Formación Llantenes (provincia de Mendoza). *Revista del Instituto Nacional de Investigación de las Ciencias Naturales, Ciencias Botánicas 2*, 147–261.

Menéndez, C.A., 1960. Cono masculino de una conifera fósil del bosque petrificado de Santa Cruz. *Ameghiniana 2*, 11–17.

Menéndez, C.A., 1972. Paleofloras de la Patagonia. In *La región de los bosques andino-patagónicos*, M.J.L. Dimitri, ed., Colección Científica INTA, Buenos Aires, 129–165.

Menéndez, C.A. & Caccavari, M.A., 1966. Estructura epidérmica de *Araucaria nathorsti* Dus., del Terciario de Pico Quemado. Río Negro. *Ameghiniana 4*, 195–199.

Minello, L.F., 1994. As 'florestas petrificadas' da região de São Pedro do Sul et Mata. *Acta Geologica Leopoldensia 17*, 75–91.

Nathorst, A.G., 1904. Die oberdevonische Flora des Ellesmerelandes. In *Report of the Second Norwegian Arctic Expedition in the Fram, 1898–1902 Vol. 1*, Videnskabs-selskabet i Kristiania, Oslo, 1–22.

Nathorst, A.G., 1907. Über Trias- und Jurapflanzen von der Insel Kotelny. *Memoirs of the Academy of Imperial Science Saint Petersburg 21*, 1–13.

Nishida, H., Kazuhiko, U., Terada, K., Yamada, T., Rancusi, M.H. & Hinojosa, L.F., 2006. Preliminary report on permineralized plant remains possibly from the Paleocene Chorrillo Chico Formation, Magallanes Region, Chile. In *Post-Cretaceous Floristic Changes in Southern Patagonia, Chile*, H. Nishida, ed., Faculty of Science and Engineering, Chuo University, Tokyo, 11–28.

Nishida, M., 1981. Petrified woods from the Tertiary of Quiriquina Island (a preliminary report). In *A Report of the Paleobotanical Survey to Southern Chile*, M. Nishida, ed., Faculty of Science, Chiba University, Chiba, 38–40.

Nishida, M., 1984. The anatomy and affinities of the petrified plants from the Tertiary of Chile II. *Araucarioxylon* from Quiriquina Island, near Concepción. In *Contributions to the Botany in the Andes I*, M. Nishida, ed., Academia Scientific Book, Tokyo, 86–90.

Nishida, M. & Nishida, H., 1987. Petrified woods from the Late Cretaceous of the Quirquina Island, near Concepción, Chile. In *Contributions to the Botany in the Andes II*, M. Nishida, ed., Academia Scientific Book, Tokyo, 5–11.

Nishida, M., Ohsawa, T. & Rancusi, M.H., 1990. Miscellaneous notes on the petrified coniferous woods from central Chilean Patagonia, XI Region, Chile. In *A Report of the Paleobotanical Survey to Patagonia, Chile*, M. Nishida, ed., Faculty of Science, Chiba University, Chiba, 21–29.

Nishida, M., Ohsawa, T., Nishida, H. & Rancusi, M.H., 1992. Permineralized coniferous woods from the XI Region of Chile, central Patagonia. *Research Institute of Evolutionary Biology 7*, 47–59.

Nishida, M., 1970. On some fossil plants from Chile, South America. *Annual Report of the Foreign Students' College of Chiba University 5*, 13–18.

Ottone, E.G. & Medina, F.A., 1998. A wood from the Early Cretaceous of James Ross Island, Antarctica. *Ameghiniana 35*, 291–298.

Page, C.N., 1990. Araucariaceae. In *The Families and Genera of Vascular Plants, Volume I, Pteridophytes and Gymnosperms*, K. Kubitzky, K.U. Kramer & P.S. Green, eds, Springer, Berlin, 294–299.

Panti, C., Césari, S.N., Marenssi, S.A. & Olivero, E.B., 2007. A new araucarian fossil species from the Paleogene of southern Argentina. *Ameghiniana 44*, 215–222.

Paredes, J.M., Giacosa, R.E. & Heredia, N., 2009. Sedimentary evolution of Neogene continental deposits (Ñirihuau Formation) along the Ñirihuau River, North Patagonian Andes, Argentina. *Journal of South American Earth Sciences 28*, 74–88.

Parica, C.A., Salani, F.M., Vera, E., Remesal, M. & Césari, S.N., 2007. Geología de la Formación Cerro Negro (Cretácico) en Isla Livingston: aportes a su geocronología y contenido paleontológico. *Revista de la Asociación Geológica Argentina 62*, 553–567.

Philippe, M., 1993. Nomenclature générique des trachéidoxyles fossiles mésozoïques à champs araucarioïdes. *Taxon 42*, 74–80.

Philippe, M., Barale, G., Covacevich, V. & Torres, T., 1993. First study of *in situ* fossil woods from the Upper Cretaceous of Livingston Island. South Shetland Islands, Antarctica: palaeoecological investigations. *Comptes Rendus de l'Académic des Sciences, Paris 317*, 103–108.

Philippe, M., Quiroz, D. & Torres, T., 2000. Early Cretaceous fossil wood from Aysen area (Patagonia, Chile) and their bearings on the role of the Araucariaceae in the Andean forest at this time. *IX Congreso Geológico Chileno, Puerto Varas, Chile 2*, 235–239.

Pole, M., 2008. The record of Araucariaceae macrofossils in New Zealand. *Alcheringa 32*, 405–426.

Pole, M. & Philippe, M., 2010. Cretaceous plant fossils of Pitt Island, the Chatham group, New Zealand. *Alcheringa 3*, 231–263.

Pole, M. & Vajda, V., 2009. A new terrestrial Cretaceous–Paleogene site in New Zealand—turnover in macroflora confirmed by palynology. *Cretaceous Research 30*, 917–938.

Pole, M., Hill, B. & Harwood, D., 2000. Eocene plant macrofossils from erratics, McMurdo Sound, Antarctica. *Antarctic Research Series 76*, 243–251.

Poole, I. & Cantrill, D., 2001. Fossil woods from Williams Point Beds, Livingston Island, Antarctica: A Late Cretaceous southern high latitude flora. *Palaeontology 44*, 1081–1112.

Pujana, R.R., Umazano, A.M. & Bellosi, E.S., 2007. Maderas fósiles afines a Araucariaceae de la Formación Bajo Barreal, Cretácico Tardío de Patagonia central (Argentina). *Revista del Museo Argentino de Ciencias Naturales, nueva serie 9*, 161–167.

Rees, P.M. & Cleal, C.J., 2004. Lower Jurassic floras from Hope Bay and Botany Bay, Antarctica. *Special Papers in Palaeontology 72*, 5–89.

Romero, E.J., 1977. *Polen de gimnospermas y fagáceas de la Formación Río Turbio (Eoceno), Santa Cruz, Argentina*. CIRGEO, Buenos Aires, 224 pp.

Salisbury, R.A., 1807. The characters of several genera in the natural order Coniferae. *Transactions of the Linnean Society of London 8*, 308–318.

Savidge, R.A., 2007. Wood anatomy of Late Triassic trees in Petrified Forest National Park, Arizona, USA, in relation to *Araucarioxylon arizonicum* Knowlton, 1899. *Bulletin of Geosciences 82*, 301–328.

Shoemaker, R.E., 1982. Fossil leaves from the Lower Cretaceous Ciano Formation, southwestern Ecuador. *Palaeontographica 180B*, 120–132.

Spegazzini, C., 1924. Coniferales fósiles patagónicas. *Anales de la Sociedad Científica Argentina 98*, 125–139.

Stockey, R.A., 1975. Seeds and embryos of *Araucaria mirabilis*. *American Journal of Botany 62*, 856–868.

Stockey, R.A., 1978. Reproductive biology of Cerro Cuadrado fossil conifers: Ontogeny and reproductive strategies in *Araucaria mirabilis* (Spegazzini) Windhausen. *Palaeontographica 166B*, 1–15.

Stockey, R.A., 1982. The Araucariaceae: an evolutionary perspective. *Review of Palaeobotany and Palynology 37*, 133–154.

Stockey, R.A., 1994. Mesozoic Araucariaceae: Morphology and systematic relationships. *Journal of Plant Research 107*, 493–502.

Stockey, R.A. & Ko, H., 1986. Cuticle micromorphology of *Araucaria* de Jussieu. *Botanical Gazette 147*, 508–548.

Stopes, M.C., 1914. A new *Araucarioxylon* from New Zealand. *Annals of Botany 28*, 341–350.

Terada, K., Asakawa, T.O. & Nishida, H., 2006a. Fossil woods from Arroyo Cardenio, Chile Chico Province, Aisen (XI) Region, Chile. In *Post-Cretaceous floristic changes in Southern Patagonia, Chile*, H. Nishida, ed., Faculty of Science and Engineering, Chuo University, 57–65.

Terada, K., Asakawa, T.O. & Nishida, H., 2006b. Fossil wood assemblage from Cerro Dorotea, Última Esperanza, Magallanes (XII) Region, Chile. In *Post-Cretaceous Floristic Changes in Southern Patagonia, Chile*, H. Nishida, ed., Faculty of Science and Engineering, Chuo University, 67–90.

Terada, K., Asakawa, T.O. & Nishida, H., 2006c. Fossil woods from the Loreto Formation of Las Minas, Magallanes (XII) Region, Chile. In *Post-Cretaceous Floristic Changes in Southern Patagonia, Chile*, H. Nishida, ed., Faculty of Science and Engineering, Chuo University, 91–101.

Torres, T., 1993. Primer hallazgo de madera fósil en Cabo Shirreff, isla Livingston, Antártica. *Serie Científica INACH 43*, 31–39.

Torres, T. & Biro Bagoczky, L., 1986. Xilotomía de coníferas fósiles de la isla Quiriquina, Chile. *Universidad de Chile, Comunicaciones 37*, 65–80.

Torres, T. & Lemoigne, Y., 1988. Maderas fósiles terciarias de la Formación Caleta Arctowski, Isla Rey Jorge, Antártica. *Serie Científica INACH 37*, 69–107.

Torres, T. & Lemoigne, Y., 1989. Hallazgos de maderas fósiles de Angiospermas y Gimnospermas del Cretácico Superio en punta Williams, Isla Livingston, Islas Shetland del Sur, Antártica. *Serie Científica INACH 39*, 9–29.

Torres, T. & Philippe, M., 2002. Nuevas especies de *Agathoxylon* y *Baieroxylon* del Lías de La Ligua (Chile) con una evaluación del registro paleoxilológico en el Jurásico de Sudamérica. *Revista Geológica de Chile 29*, 151–165.

Torres, T. & Rallo, M., 1981. Anatomía de troncos fósiles del Cretácico Superior de Pichasca, en el norte de Chile. *Anais II Congreso Latinoamericano de Paleontología, Porto Alegre, Brasil 2*, 385–398.

Torres, T., Valenzuela, E. & Gonzales, I., 1982. Paleoxilología de Península Byers, Isla Livingston, Antártica. *III Congreso Geológico Chileno, Concepción, Chile 1*, 321–341.

Torres, T., Marenssi, S.A. & Santillana, S., 1994. Maderas fósiles de la isla Seymour, Formación La Meseta, Antártica. *Serie Científica INACH 44*, 17–38.

Torres, T., Philippe, M., Galleguillos, H. & Hauck, F., 1995. Nuevos descubrimientos de restos vegetales en la Isla Snow. *Boletín Antártico Chileno 14*, 25–28.

Torres, T., Barale, G., Meon, H., Philippe, M. & Thevenard, F., 1997. Cretaceous floras from Snow Island (South Shetland Islands Antarctica) and their biostratigraphic significance. In *The Antarctic Region: Geological Evolution and Processes*, C.A. Ricci, ed., Terra Antarctica Publication, Siena, 1023–1028.

Torres, T., Galleguillos, H. & Philippe, M., 2000. Maderas fósiles en el Monte Flora, Bahía Esperanza, Península Antártica. *IX Congreso Geológico Chileno, Puerto Varas, Chile*, 386–390.

Troncoso, A., 1986. Nuevas órgano-especies en la tafoflora terciaria inferior de península Fildes, Isla Rey Jorge, Antártica. *Serie Científica INACH 34*, 23–46.

Troncoso, A., 1991. Paleomegaflora de la Formación Navidad, Miembro Navidad (Mioceno), en el área de Matanzas, Chile central occidental. *Boletín del Museo de Historia Natural de Chile 42*, 131–168.

Troncoso, A. & Encinas, O., 2006. La tafoflora de Cerro Centinela (Chile, VI Región): vegetación y clima de Chile central a fines del Mioceno-comienzos del Plioceno. *Ameghiniana 43*, 171–180.

Troncoso, A. & Romero, E.J., 1993. Consideraciones acerca de las Coníferas del Mioceno de Chile central occidental. *Boletín del Museo Nacional de Historia Natural de Chile 44*, 47–71.

Vajda, V. & Raine, J.I., 2003. Pollen and spores in marine Cretaceous/Tertiary boundary sediments at mid-Waipara River, North Canterbury, New Zealand. *New Zealand Journal of Geology and Geophysics 46*, 255–273.

van Waveren, I.M., van Konijnenburg-van Cittert, J.H.A., van der Burgh, J. & Dilcher, D.L., 2002. Macrofloral remains from the Lower Cretaceous of the Leiva region (Colombia). *Scripta Geologica 123*, 1–39.

Whitmore, T.C., 1980. A monograph of *Agathis*. *Plant Systematics and Evolution 135*, 41–63.

Wieland, G.R., 1929. The world's two greatest petrified forests. *Science 69*, 60–63.

Wieland, G.R., 1935. *The Cerro Cuadrado Petrified Forest*. Publications of the Carnegie Institution of Washington Vol. 449, Washington, 180 pp.

Wilf, P., Cúneo, R., Johnson, K.R, Hicks, J.F, Wing, S.L. & Obradovich, J.D., 2003. High plant diversity in Eocene South America: evidence from Patagonia. *Science 300*, 122–125.

Wilf, P., Johnson, K.R., Cúneo, N.R., Smith, M.E., Singer, B.S. & Gandolfo, M.A., 2005. Eocene plant diversity at Laguna del Hunco and Río Pichileufú, Patagonia, Argentina. *American Naturalist 165*, 634–650.

Wilf, P., Singer, B.S., Zamaloa, M.C., Johnson, K.R. & Cúneo, R., 2010. Early Eocene $^{40}Ar/^{39}Ar$ age for the Pampa de Jones plant, frog, and insect biota (Huitrera Formation, Neuquén Province, Patagonia, Argentina). *Ameghiniana 42*, 207–216.

Windhausen, A., 1931. Geología Argentina. In *Geología Histórica y Regional del Territorio Argentino (Segunda Parte)*, Peuser, Buenos Aires, 1–40.

Witham, H., 1833. *The internal structure of fossil vegetables accompanied by representations of their internal structure, as seen through the microscope*. Blackwood, Edinburgh, 72 pp.

Zamuner, A.B., 1996. *Araucarioxylon petriellae* n. sp., una posible Glossopteridal de la Formación Melo (Pérmico Inferior), Uruguay. *Ameghiniana 1*, 77–82.

Zamuner, A.B. & Falaschi, P., 2005. *Agathoxylon matildense* n. sp., leño araucariaceo del Bosque Petrificado del cerro Madre e Hija, Formación La Matilde (Jurásico Medio), provincia de Santa Cruz, Argentina. *Ameghiniana 42*, 339–346.

Zavattieri, A.M., 1991. Granos de polen de la Formación Las Cabras (Triásico), en su localidad tipo, provincia de Mendoza, Argentina. Parte 1. *Ameghiniana 28*, 3–29.

Zhou, Z. & Li, H., 1994. Early Tertiary Fossil Hill flora from Fildes Peninsula of King George Island, Antarctica. In *Stratigraphy and Palaeontology of Fildes Peninsula, King George Island, Antarctica*, Y.B. Shen, ed., Science Press, Beijing, 208–221.