On the distribution of gymnosperm genera, their areas of endemism and cladistic biogeography

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Abstract. A distributional analysis of 81 gymnosperm genera was undertaken. On the basis of the congruence in the distribution of these genera, nine areas of endemism were recognised. Many of these areas also represent areas of endemism for other plant and animal taxa. South-western China and New Caledonia are particularly interesting from the viewpoint of gymnosperm diversity and endemism. The suggested areas of endemism agree in part with some floristic regions previously proposed. The congruence between the areas of endemism suggested and postulated Pleistocene refuges and panbiogeographic nodes is discussed. A cladistic biogeographic analysis was carried out and a general area cladogram obtained by strict consensus shows two major components, one Gondwanic and the other almost Laurasian. This cladogram was compared with previous studies and the similarities and differences among relationship areas are discussed.

Introduction

Gymnosperms are seed plants that primarily inhabit the temperate zones of both hemispheres. They have been important elements in fossil and extant plant communities and are represented in the fossil record from the end of the Paleozoic era. Due to their antiquity, events such as continental drift and processes of climatic change have been important in influencing the current distributional patterns of gymnosperms.

Wegener (1929) drew attention to gymnosperm distribution, especially in the Southern Hemisphere, where related genera and even congeneric species were separated by vast oceans, representing the living evidence of continental drift. This distributional pattern has two different, and sometimes complementary, historical explanations, which are dispersal and vicariance. The former process involves a common ancestor that originally ocurred in one area and later dispersed into another, where its descendants survived until the present day. The latter process involves an ancestor that was originally widespread in a bigger area that became fragmented, leaving descendants that survived in the fragments until now (Morrone and Crisci 1995). Cladistic biogeography gives more importance to the process of vicariance than to dispersal events, because vicariance affects different groups of organisms and not

isolated cases usually invoked in dispersal explanations (Nelson and Platnick 1981). Many studies of the distribution of the gymnosperms have been published from a dispersalist viewpoint (Li 1953; Silba 1984, 1990; Farjon 1990). Recent studies of their systematics and biogeography can help explain the distributions of many of the genera as the result of vicariance. Cladistic biogeography represents a combination of phylogenetic systematics and panbiogeography and searches for patterns of relationship among areas of endemism (Espinosa and Llorente 1993; Humphries and Parenti 1999).

Innovative ideas on the classification of gymnosperms have been proposed from a cladistic point of view. For example, inclusion of the genus *Sciadopitys* in a monotypic family has been suggested in cladistic analyses with molecular and morphological data (Price and Lowenstein 1989; Brunsfeld *et al.* 1994). De Laubenfels (1985) suggested that *Podocarpus* comprises two subgenera, *Podocarpus* and *Foliolatus*. However, in a recent cladistic analysis of Podocarpaceae (Kelch 1997), *Podocarpus* seems to be paraphyletic; in this work *Foliolatus* is treated as a distinct genus. Other authors (Eckenwalder 1976; Hart 1987; Brunsfeld *et al.* 1994) have suggested that Taxodiaceae is paraphyletic and is located in a basal position in relation to Cupressaceae. From morphological and molecular studies

both families constitute a monophyletic group. Hart (1987) and Chaw *et al.* (1993) suggest that the families Taxaceae and Cephalotaxaceae must be included in the order Coniferales, on the basis of recent cladistic analyses of morphological and molecular data.

The relictual nature of the distribution of some gymnosperm genera deserves special attention in historical biogeography because of the congruent distributional areas of two or more monophyletic taxa in the same geographic region, allowing us to identify areas of endemism (Harold and Mooi 1994). These areas represent the basis for studies in cladistic biogeography and can be recognised by congruence of the geographic distributions of two or more endemic taxa (Espinosa and Llorente 1993). Endemism too has been used to quantify the biological uniqueness of an area (Peterson and Watson 1998).

The aim of this work is to analyse the distribution of gymnosperm genera, in order to identify their areas of endemism. In addition, we accomplish a cladistic biogeographic analysis of gymnosperms on the basis of previous phylogenetic studies, of these areas of endemism and others previously recognised in other works.

Material and methods

Distributional data of gymnosperm genera were obtained from revisionary studies of Cycadales (Stevenson *et al.* 1990; Jones 1993; Osborne *et al.* 1999), Coniferales (Silba 1984, 1990; Jaffré *et al.* 1987; Page 1988; Farjon 1989, 1990) and Ginkgoales (Silba 1984; Liguo *et al.* 1999) and collections from the following herbaria: National Herbarium at the Instituto de Biología, Universidad Nacional Autónoma de México (MEXU), herbarium of the Instituto Politécnico Nacional (ENCB), herbarium of the Instituto de Ecología in Xalapa City (XAL), herbarium of the Missouri Botanical Garden (MO) and herbarium of the Universidad Autónoma Chapingo (CHAP). Recent publications of new genera were considered, e.g. *Afrocarpus*, *Halocarpus*, *Lagarostrobos*, *Nageia*, *Retrophyllum* and *Sundacarpus* of Podocarpaceae (Quinn 1982; Page 1988), *Nothotsuga* of Pinaceae (Page 1988), *Chigua* of Zamiaceae (Stevenson 1990) and *Wollemia* of Araucariaceae (Jones *et al.* 1995).

Areas of endemism are recognised from the overlap of the areas of distribution of two or more endemic taxa. In this work, the following two types of overlap were used (Espinosa and Llorente 1993): (1) homopatric, which consist in a total overlap of two areas; and (2) endopatric, where one area is included in a second and bigger area. We followed these two criteria and recognised areas of endemism of gymnosperm genera from congruence in the distributions of two or more taxa. Currently, areas of endemism represent the basic unit in cladistic biogeographic research (Morrone 1994).

Another 14 areas of endemism were incorporated, on the basis of other animal and plant taxa (Cabrera and Willink 1973; Takhtajan 1985; Cracraft 1991; Crisci *et al.* 1991; Amorim and Tozoni 1994; Enghoff 1995; Linder and Crisp 1995; Wang *et al.* 1996; Tan and Pócs 2000), because many gymnosperm genera are widespread.

The areas of endemism obtained from distributional analysis of gymnosperm genera and from other plant and animal taxa were utilised for the cladistic biogeography analysis. The software used for this latter analysis was COMPONENT 2.0 (Page 1993), which requires resolved cladograms for its input. In the case of polytomies, the program resolves them randomly; this was the case for Araucariaceae, Cupressaceae and Podocarpaceae. In this analysis assumption 0 was applied with the

option 'map widespread associates', because there may be numerous possible combinations of areas to be deleted with the option 'map widespread associates' turned off (Enghoff 1998).

In the current literature only phylogenetic analyses at generic level are available for gymnosperms, except for Araucariaceae, which has been analysed at the species level. Gilmore and Hill (1997) included 10 species and Setoguchi *et al.* (1998) 30 species in their analyses. These works offer different phylogenies, possibly because the authors selected different outgroups. For Cupressaceae, a similar anomaly occurs as the phylogenetic analyses of Hart (1987) included all the genera of the family, while the work of Brunsfeld *et al.* (1994) excluded seven genera.

The phylogenies of genera of Cycadales (Crane 1988), Araucariaceae (Setoguchi *et al.* 1998), Cupressaceae (Hart 1987), Pinaceae (Farjon 1990), Podocarpaceae (Kelch 1997) and Taxales (Hart 1987) were used to construct a general area cladogram. Since taxonomic cladograms are essential building blocks for analysis in cladistic biogeography, we based our study in this available information. New Guinea and Tasmania were considered as separate areas, despite the fact that they are part of the same continental block as Australia (Linder and Crisp 1995). The same situation occurs with North America, which was divided into three areas. The general area cladogram obtained was compared with previously published works in cladistic biogeography at a continental scale (Crisci *et al.* 1991; Amorim and Tozoni 1994; Enghoff 1995; Linder and Crisp 1995; Morrone 1996).

Results

The 81 gymnosperm genera included in this work are listed in Appendix 1; 40 genera are distributed exclusively or primarily in the Northern Hemisphere, 29 are restricted to the Southern Hemisphere and 12 are present in both hemispheres. Exceptionally, some species of few genera almost restricted to one of the two hemispheres can cross the Equator, e.g. *Podocarpus* with a distribution primarily in the Southern Hemisphere, exceptionally crosses the Equator and reaches north-eastern Mexico and south-eastern Asia; the same situation occurs with *Prumnopitys*, with one species reaching Costa Rica (Silba 1984; Kappelle *et al.* 2000). Among the northern genera, some species of *Juniperus*, *Pinus* and *Taxus* inhabit tropical regions and extend southwards.

These generic distributional patterns are also found at the familial level: for example, Cephalotaxaceae, Ginkgoaceae, Pinaceae and Taxaceae exhibit a primarily northern distribution, with the only exception being the genus *Austrotaxus* (Taxaceae), which is restricted to New Caledonia in the Southern Hemisphere; Araucariacae, Podocarpaceae and Stangeriaceae have a mainly southern distribution; Cupressaceae, Cycadaceae and Zamiaceae are present in both hemispheres. However, in the gymnosperm genera other types of distribution can also be recognised, namely, disjunct, endemic and widespread in one hemisphere. *Abies*, *Cupressus*, *Juniperus*, *Larix*, *Picea* and *Pinus* are widespread in the Northern Hemisphere; in the Southern Hemisphere only *Podocarpus* presents a wide distribution. *Araucaria* and *Lepidothamnus* each have a disjunct distribution in the Southern Hemisphere and *Pseudotsuga* and *Thuja* in the north. Some of these

Table 1. Diversity of gymnosperm genera in the areas of endemism recognised from gymnosperm distribution
Column 1 represents the total number of genera recorded in an area, including widespread genera; column 2 represents the percentage of the total (81) genera of gymnosperms; column 3 contains the names of genera restricted to each area; column 4 is the percentage of endemic genera in each area

Area of endemism	No. of genera	Proportion of total genera (%)	List of endemic genera	Endemism (%)
South-western China	31	38.27	*Cathaya, Fokienia, Ginkgo, Glyptostrobus, Metasequoia, Nothotsuga, Pseudolarix, Pseudotaxus*	25.80
Japan	19	23.45	*Sciadopitys, Thujopsis*	10.52
New Caledonia	17	20.98	*Austrotaxus, Neocallitropsis, Parasitaxus*	17.64
Western North America	14	17.28	*Sequoia, Sequoiadendron*	14.28
Mesoamerica	11	13.58	*Ceratozamia, Dioon*	18.18
Southern South America	8	9.87	*Austrocedrus, Fitzroya, Pilgerodendron, Saxegothaea*	50.00
Eastern Australia	10	12.34	*Bowenia, Lepidozamia, Wollemia*	30.00
Tasmania	8	9.87	*Athrotaxis, Diselma, Microcachrys*	37.50
Southern Africa	5	6.17	*Stangeria, Widdringtonia*	40.00

Table 2. Diversity of gymnosperm genera in the areas of endemism recognised from different animal and plant taxa
Column 1 represents the total number of genera recorded in an area, including widespread genera. Column 2 represents the percentage of the total (81) genera of gymnosperms. Column 3 includes the taxa and references that support the areas of endemism

Areas of endemism	No. of genera	Proportion of total genera (%)	Areas of endemism based on the following taxa
Central Africa	4	4.93	Diptera (Amorim and Tozoni 1994); flowering plants (Linder and Crisp 1995)
Madagascar	2	2.46	Bryophytes (Tan and Pócs 2000); diptera (Amorim and Tozoni 1994); vascular plants (Takhtajan 1985; Linder and Crisp 1995)
Eastern North America	9	11.11	Diptera (Amorim and Tozoni 1994); vascular plants (Takhtajan 1985); vertebrate and invertebrates (Enghoff 1995)
Northern North America	9	11.11	Diptera (Amorim and Tozoni 1994); vascular plants (Takhtajan 1985)
Antilles	5	6.17	Animal and plant taxa (Cabrera and Willink 1973)
Brazilian	2	2.46	Animal and plant taxa (Cabrera and Willink 1973; Morrone 1999); diptera (Amorim and Tozoni 1994)
Northern South America	5	6.17	Animal and plant taxa (Cabrera and Willink 1973; Crisci *et al.* 1991); bryophytes (Tan and Pócs 2000)
New Zealand	10	12.34	Vascular plants (Takhtajan 1985; Linder and Crisp 1995); animal and plant taxa (Crisci *et al.* 1991; Amorim and Tozoni 1994)
Fiji	8	9.87	Diptera (Amorim and Tozoni 1994); vascular plants (Takhtajan 1985)
Western Australia	4	4.93	Beetles (Wang *et al.* 1996); vascular plants (Takhtajan 1985); vertebrates (Cracraft 1991)
New Guinea	12	14.81	Animal and plant taxa (Crisci *et al.* 1991); beetles (Wang *et al.* 1996); bryophytes (Tan and Pócs 2000); vascular plants (Takhtajan 1985; Linder and Crisp 1995)
Malay Archipelago	12	14.81	Diptera (Amorim and Tozoni 1994)
Eurasia	7	8.64	Diptera (Amorim and Tozoni 1994); vertebrate and invertebrates (Enghoff 1995)
Southern India	2	2.46	Bryophytes (Tan and Pócs 2000); vascular plants (Takhtajan 1985)

discontinuous distributions show a similar pattern, encompassing different areas along the margins of the Pacific Ocean. This distributional pattern agrees with the existence of a Pacifica paleocontinent (Nur and Ben-Avraham 1981); however, there is no consensus in the scientific community about the existence of the paleocontinent (see Humphries and Parenti 1999). The breakup of Pacifica and the subsequent migration and collision of its fragments to the marginal areas of the continents around the Pacific Ocean would help explain the current distributional pattern of these gymnosperm taxa from a vicariant viewpoint.

Thirty-four genera have restricted distributions, 29 of these genera occur in the same areas (Table 1). On the basis of both criteria of overlap mentioned previously, nine areas of endemism were recognised exclusively on the basis of distributions of gymnosperm genera. As many gymnosperm genera are distributed in more areas than the nine proposed
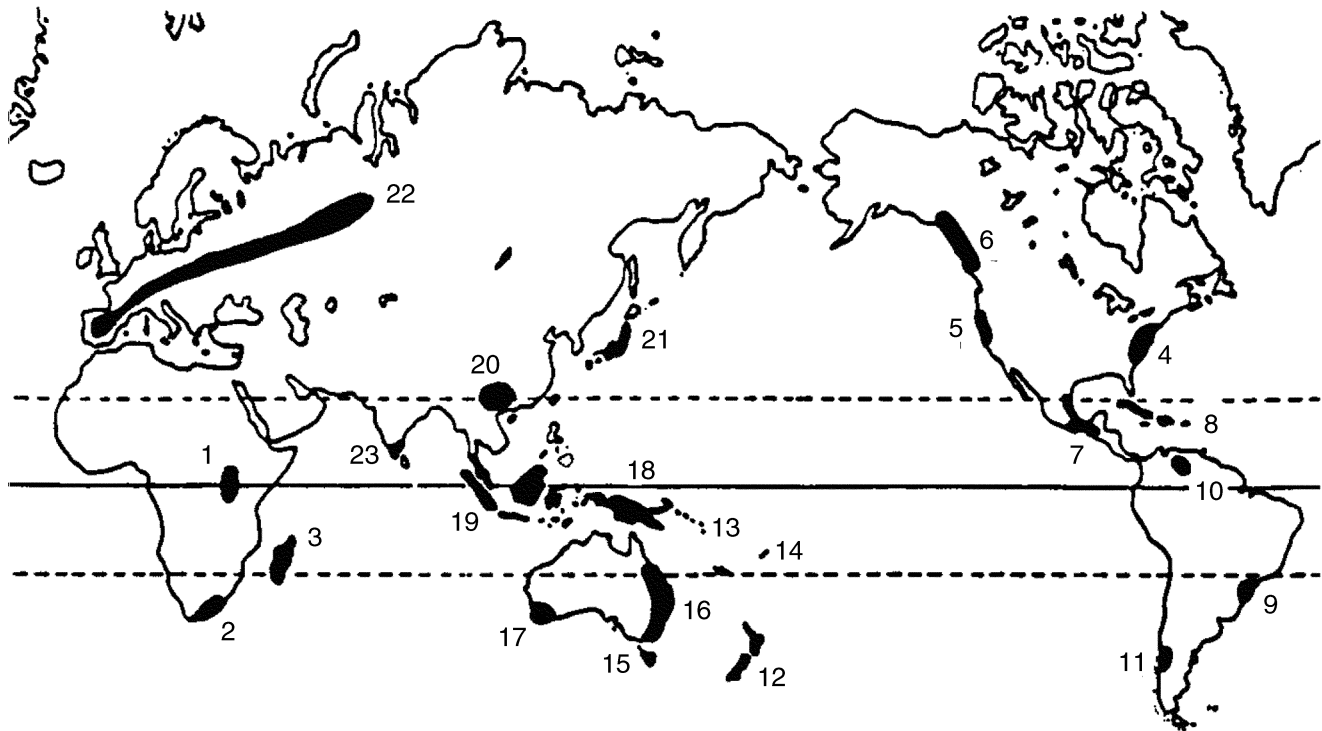
Fig. 1. Areas of endemism used in the analysis of cladistic biogeography of gymnosperm genera: central Africa (CAF, 1), southern Africa (SAF, 2), Madagascar (MAD, 3), eastern North America (ENA, 4), western North America (WNA, 5), northern North America (NNA; 6), Mesoamerica (MESO, 7), Antilles (ANT, 8), south-eastern Brazil (BRAS, 9), northern South America (NSA, 10), southern South America (SSA, 11), New Zealand (NZ, 12), New Caledonia (NC, 13), Fiji (FIJI, 14), Tasmania (TAS, 15), eastern Australia (EAUS, 16), western Australia (WAUS, 17), New Guinea (NG, 18), Malay Archipelago (ARMA, 19), south-western China (CHI, 20), Japan (JAP, 21), Eurasia (EAA, 22) and southern India (IND, 23).

here and these areas are required for the cladistic biogeographic analysis, we decided to incorporate other areas of endemism on the basis of the distributions of other plant and animal taxa (Table 2). The areas used in the cladistic analysis were the following: central Africa (CAF), southern Africa (SAF), Madagascar (MAD), eastern North America (ENA), western North America (WNA), northern North America (NNA), Mesoamerica (MESO), Antilles (ANTI), Brazilian (BRAS), northern South America (NSA), southern South America (SSA), New Zealand (NZ), New Caledonia (NC), Fiji (FIJI), Tasmania (TAS), eastern Australia (EAUS), western Australia (WAUS), New Guinea (NG), Malay Archipelago (ARMA), south-western China (CHI), Japan (JAP), Eurasia (EAA) and southern India (IN) (Fig. 1).

From our data file of gymnosperm distributions and phylogenies (Appendix 2), 81 cladograms resulted. From these trees, a strict consensus cladogram was obtained (Fig. 2). The general area cladogram obtained from the cladistic biogeographic analysis showed two major components, one Gondwanic and the other almost Laurasian, with the exception of continental Africa.

Discussion

We recognise nine areas of endemism on the basis of only the distribution of gymnosperm genera. The area of south-western China includes eight endemic genera, more taxa than any of the other areas of endemism proposed.

The following two areas are very interesting from a viewpoint of gymnosperm diversity: south-western China and New Caledonia. South-western China includes the highest diversity of gymnosperms in the world, with 31 genera present. This area also represents the centre of diversity of many other taxa of vascular plants, e.g. the genus *Camellia* (Luna 1997; Luna and Contreras-Medina 2000). New Caledonia is a smaller, but exceptional, region, harbouring a high species diversity of gymnosperms (Jaffré *et al.* 1987) and comprising 17 genera, three of them endemic to this island. The highest concentration of specific diversity of the Araucariaceae is in New Caledonia (Setoguchi *et al.* 1998). This diverse gymnosperm flora contrasts with the low diversity of gymnosperms, especially for Coniferales, in Madagascar, a much larger island (Li 1953). In the same way, the diversity of cycad genera in
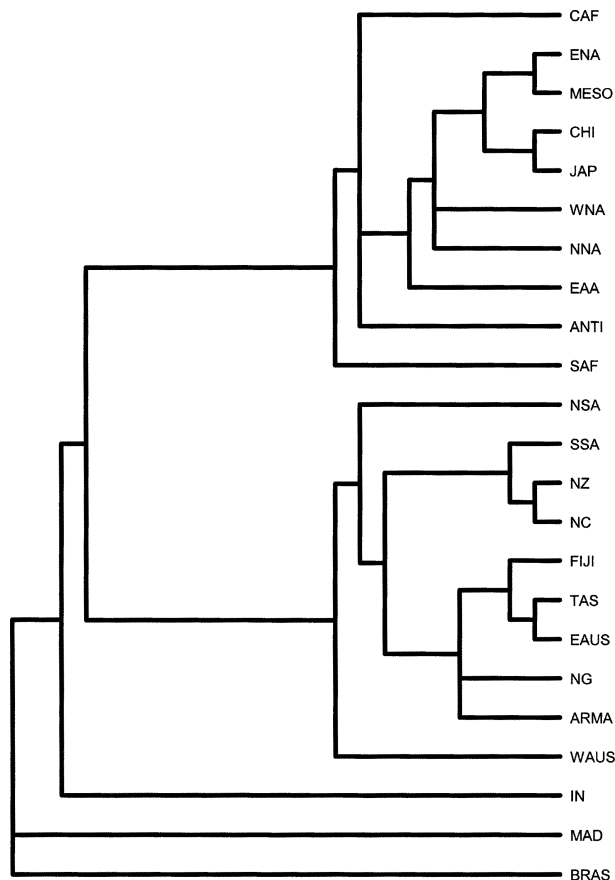
Fig. 2. General area cladogram for areas of endemism where gymnosperm genera are distributed. This tree represents a strict consensus cladogram from 81 trees resulted from the analysis by COMPONENT 2.0.

Mesoamerica (with three genera) and Australia (with four genera) contrasts with their absence in Europe, New Zealand and southern South America.

The congruence among the areas of endemism suggested in this work, and the restricted distributions of other biological groups of animals and plants, support the existence of these areas of endemism (e.g. Takhtajan 1985; Amorim and Tozoni 1994; Tan and Pócs 2000).

The existence of these areas of endemism agrees partially with the Pleistocene refuge model of Haffer (1982); many of the postulated forest refuges of the world are congruent with several of the areas of endemism suggested in this work. These areas have had suitable climatic conditions that have allowed the survival of certain forest taxa since the Mesozoic era (Li 1953).

Also, some of these areas of endemism agree with previously suggested nodes achieved from a panbiogeographic analysis of gymnosperm genera (Contreras-Medina *et al.* 1999). The congruence between these areas of endemism and the nodes agrees with the following definition of 'node' proposed by Craw (1989): 'an

area of endemism where two or more standard tracks overlap'. The nodes that coincide with the areas of endemism obtained are south-western China, Japan, New Caledonia, Tasmania and western North America. Although other areas of endemism (e.g. southern South America, Mesoamerica, eastern North America, western Australia, Fiji, southern India and southern Africa) do not coincide with nodes, they represent the distal parts of some generalised tracks in the panbiogeographic analysis (Contreras-Medina *et al.* 1999).

Thirty-four genera of gymnosperms have restricted distributions (41.9%), 29 of them are localised in nine areas of endemism. The areas inhabited by a single endemic genus are the following: Cuba (*Microcycas*), Colombia (*Chigua*), New Zealand (*Halocarpus*), south-western Australia (*Actinostrobus*) and south-eastern Siberia (*Microbiota*). The patterns of endemism suggested in this work were compared with the floristic regions and subregions proposed previously by Good (1974) and Takhtajan (1985), some of which corresponded exactly. For example, New Caledonia was proposed by Takhtajan (1985) as the Neocaledonian Region and by Good (1974) as the New Caledonia floristic region; western North America was recognised by Takhtajan (1985) as the Rocky Mountain Region and by Good (1974) as the Pacific North American floristic region. Both areas also represent areas of endemism and diversity for bryophytes (Tan and Pócs 2000).

In the general area cladogram, the position of the most basal areas (BRAS, MAD and IN) may be explained by the low diversity of gymnosperms in these areas, only two genera being present in each. Similarly, continental Africa (CAF, SAF) is included in the Laurasian component. The position of continental Africa in this component is inconsistent with geological knowledge (see Linder and Crisp 1995) and previous studies (Crisci *et al.* 1991; Amorim and Tozoni 1994; Linder and Crisp 1995; Morrone 1996). The low number of genera in continental Africa may have obscured its resolution in the general area cladogram.

The component that includes all the areas located in the Northern Hemisphere comprises the 'Tertiary boreotropical flora' named by Tiffney (1985). Eastern North America represents the sister area of Mesoamerica in this study, an idea also suggested by Rosen (1978) on the basis of different biological groups and Wen and Shi (1999) on the biogeography and phylogeny of *Hamamelis*. However, eastern North America has been proposed as more closely related to Europe (Amorim and Tozoni 1994; Enghoff 1995), western North America (Xiang *et al.* 2000) and eastern Asia (Zhengyi 1983). Possibly, this area had a complex history, closely related at different times to Mesoamerica, western North America, Europe and eastern Asia.

The close relationship between eastern Asia (China–Japan) with eastern North America is not new; the discontinuity in plant and animal ranges has been recognised since the 19th century (e.g. Gray 1859; Hemsley 1888).

Recently, this fact has been reconsidered by Li (1952, 1972), Graham (1972), Wood (1972), Good (1974) and De-yuan (1993), among others. Zhengyi (1983) found about 120 genera of vascular plants with this range, which reflects the well-known disjunction pattern displayed by many moist-temperate forest plants that inhabit both regions (Latham and Ricklefs 1993). Good (1974) proposed that many of these genera could be survivors of an ancient flora now extinct in Europe and western Asia and regarded them as 'circumboreal' in distribution. Instead, Zhengyi (1983) assumed that these genera might be relicts of a warm temperate–subtropical montane flora derived from a Tertiary paleotropical flora. Furthermore, the isolation of most disjunct taxa in eastern Asia and eastern North America is proposed to have occurred during the global climatic cooling period that took place throughout the late Tertiary and Quaternary (Xiang *et al.* 2000). This relationship was corroborated by phylogenetic analysis of *Suillus* species, a genus of pored mushrooms, by using molecular data (Wu *et al.* 2000).

The relationship between North America and eastern Asia was considered by Xiang *et al.* (1998), in relation to molecular phylogenetic analyses of seven genera of plants and by Wen *et al.* (1998) on the basis of the phylogeny and biogeography of *Aralia*, where eastern North America and western North America show a close relationship and eastern Asia is the sister area of these last two areas. Despite the proximity of eastern North America and western North America, the temperate forests of these two areas share few genera, in relation to those shared between eastern Asia and eastern North America (Latham and Ricklefs 1993). The relationship between eastern Asia and western North America has also been proposed, with the consideration of a paleoregion named Asiamerica (see Cox 1974; Enghoff 1995).

An austral component is evident in the general area cladogram, including the following areas: southern South America, New Zealand, New Caledonia, Fiji, Tasmania, eastern Australia, New Guinea and the Malay Archipelago. This pattern is similar to others cited in previous studies (Crisci *et al.* 1991; Amorim and Tozoni 1994; Linder and Crisp 1995; Morrone 1996), but differs in the relationships of some areas.

The results of this work support a hybrid origin of the South American biota, which was proposed previously by Crisci *et al.* (1991) and Morrone (1996); the same happens for the North American and Australian biotas. The following three patterns are reported that show the relation of some areas of the southern Pacific: (1) southern South America (New Zealand, Australia), on the basis of plant data (Linder and Crisp 1995); (2) Australia (southern South America, New Zealand), supported by insect and geological data (Linder and Crisp 1995); and (3) New Zealand (southern South America, Australia), on the basis of animal and plant data (Amorim and Tozoni 1994). In this study, a different pattern emerges that links southern South America as a sister area to New Zealand and New Caledonia; these three areas constitute a sister-area relationship to the southern Pacific areas. The relationship between New Caledonia and New Zealand is supported by geological (Linder and Crisp 1995) and biological evidence (Craw 1982).

In the analysis carried out by Linder and Crisp (1995), New Guinea was the sister area of eastern Australia and Tasmania. In contrast, in our study Fiji was the sister area of eastern Australia and Tasmania. In this work, a trichotomy resulted among New Guinea, Malay Archipelago and [Fiji, (Tasmania, eastern Australia)].

Differences between the results of this study and previous studies can be explained resulting from the fact that the areas of endemism have more than one history of area relationships, as well as from the different methods employed in each biogeographic analysis. Morrone and Carpenter (1994) suggested that the different methods in cladistic biogeography give basically the same results only if data are very 'clean', with few widespread taxa, redundant distributions, or missing areas. In addition, in the gymnosperms the patterns are probably obscured by many other factors, i.e. the existence of relictual groups (extinction), insufficient sampling of taxa, a problem that affects most studies of this kind, and that the phylogeny of the group until now is not completely resolved, so the cladograms can have some errors, especially those based only on morphological evidence.

Acknowledgments

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Appendix 1. List of gymnosperms genera of the world and their taxonomic placement

This scheme of classification is based on recent cladistic studies (Hart 1987; Crane 1988; Price and Lowenstein 1989; Chaw *et al.* 1993; Gadek and Quinn 1993; Brunsfeld *et al.* 1994; De Luca *et al.* 1995; Hill 1996, 1998; Kelch 1997). The following list offers, in alphabetic sequence, a brief summary of the distribution and the number of species of each genus (Silba 1984, 1990; Page 1988; Farjon 1990; Jones 1993; Rodríguez and Quezada 1995; De Laubenfels 1996; Hill 1996, 1998; Osborne *et al.* 1999)

Order Cycadales
  Cycadaceae
    Cycas (65 spp.). Africa, Australia, New Caledonia, Fiji, southern and eastern Asia.
  Stangeriaceae
    Bowenia (3 spp.). Restricted to north-eastern Australia.
    Stangeria (1 sp.). Restricted to southern Africa.
  Zamiaceae
    Ceratozamia (12 spp.). Mexico and Central America.
    Chigua (2 spp.). Restricted to Colombia.
    Dioon (10 spp.). Mexico and Central America.
    Encephalartos (61 spp.). Central and Southern Africa.
    Macrozamia (39 spp.). Restricted to Australia.
    Microcycas (1 sp.). Restricted to Cuba.
    Lepidozamia (2 spp.). Restricted to eastern Australia.
    Zamia (49 spp.). Tropical America, from Florida to middle South America.
Order Ginkgoales
  Ginkgoaceae
    Ginkgo (1 sp.). Restricted to south-western China.
Order Pinales
  Araucariaceae
    Agathis (21 spp.). Australia, New Zealand, New Caledonia, Fiji and Malaysia.
    Araucaria (19 spp.). Australasia and southern South America.
    Wollemia (1 sp.). Restricted to south-eastern Australia.
  Cephalotaxaceae
    Cephalotaxus (8 spp.). Eastern Asia.
  Cupressaceae
    Actinostrobus (3 spp.). Restricted to south-western Australia.
    Athrotaxis (2 spp.). Restricted to Tasmania.
    Austrocedrus (1 sp.). Restricted to southern South America.
    Callitris (19 spp.). Australia and New Caledonia.
    Calocedrus (3 spp.). Eastern Asia and western North America.
    Chamaecyparis (6 spp.). Eastern Asia and North America.
    Cryptomeria (1 sp.). Eastern Asia.
    Cunninghamia (1 sp.). Eastern Asia.
    Cupressus (13 spp.). Widely distributed in Northern Hemisphere.
    Diselma (1 sp.). Restricted to Tasmania.
    Fitzroya (1 sp.). Restricted to southern South America.
    Fokienia (1 sp.). Southern China and northern Vietnam.
    Glyptostrobus (1 sp.). South-western China.
    Juniperus (50 spp.). Widely distributed in the Northern Hemisphere.
    Libocedrus (8 spp.). New Caledonia and New Zealand.
    Metasequoia (2 spp.). South-western China.
    Microbiota (1 sp.). Restricted to south-eastern Siberia.
    Neocallitropsis (1 sp.). Restricted to New Caledonia.
    Papuacedrus (1 sp.). Restricted to New Guinea.
    Pilgerodendron (1 sp.). Southern South America.
    Platycladus (1 sp.). Eastern Asia.
    Sequoia (1 sp.). Restricted to western North America.
    Sequoiadendron (1 sp.). Restricted to western North America.

Taiwania (1 sp.). Eastern Asia.
Taxodium (2 spp.). Eastern North America, Mexico and Guatemala.
Tetraclinis (1 sp.). Northern Africa and Spain.
Thuja (5 spp.). Eastern Asia and North America.
Thujopsis (1 sp.). Restricted to Japan.
Widdringtonia (3 spp.). Restricted to southern Africa.
Pinaceae
  Abies (41 spp.). Widely distributed in the Northern Hemisphere.
  Cathaya (1 sp.). Restricted to China.
  Cedrus (4 spp.). Central Asia and northern Africa.
  Keteleeria (5 spp.). China, Laos and Vietnam.
  Larix (15 spp.). Widely distributed in the Northern Hemisphere.
  Nothotsuga (1 sp.). Restricted to China.
  Picea (34 spp.). Widely distributed in the Northern Hemisphere.
  Pinus (93 spp.). Widely distributed in the Northern Hemisphere.
  Pseudolarix (1 sp.). Restricted to China.
  Pseudotsuga (6 spp.). Eastern Asia and North America, including Mexico.
  Tsuga (10 spp.). Eastern Asia and North America.
Podocarpaceae
  Acmopyle (2 spp.). New Caledonia and Fiji.
  Afrocarpus (6 spp.). Central and Southern Africa.
  Dacrycarpus (9 spp.). Malaysia and eastern Asia.
  Dacrydium (21 spp.). Malaysia and islands around Australia.
  Falcatifolium (5 spp.). Islands around Australia.
  Foliolatus (53 spp.). Eastern Asia and Australasia.
  Halocarpus (3 spp.). Restricted to New Zealand.
  Lagarostrobos (2 spp.). Tasmania and New Zealand.
  Lepidothamnus (3 spp.). Southern Chile and New Zealand.
  Microcachrys (1 sp.). Restricted to Tasmania.
  Microstrobos (2 spp.). South-eastern Australia, including Tasmania.
  Nageia (6 spp.). Eastern Asia, Malaysia, India, New Guinea and New Caledonia.
  Parasitaxus (1 sp.). Restricted to New Caledonia.
  Phyllocladus (7 spp.). Islands around Australia and eastern Asia.
  Podocarpus (41 spp.). Widely distributed in the Southern Hemisphere.
  Prumnopitys (9 spp.). Central and South America and Australasia.
  Retrophyllum (5 spp.). New Caledonia, New Guinea, Fiji and South America.
  Saxegothaea (1 sp.). Restricted to southern South America.
  Sundacarpus (1 sp.). Malaysia, New Guinea, Philippines and Australia.
Sciadopityaceae
  Sciadopitys (1 sp.). Restricted to Japan.
Taxaceae
  Amentotaxus (5 spp.). Eastern Asia.
  Austrotaxus (1 sp.). Restricted to New Caledonia.
  Pseudotaxus (1 sp.). Restricted to China.
  Taxus (7 spp.). Widely distributed in the Northern Hemisphere.
  Torreya (6 spp.). Eastern Asia and North America.

Appendix 2. Data file for COMPONENT 2.0

#nexus
[AUS. SYST. BOT.]
begin taxa;
dimensions ntax = 23;
taxlabels CAF SAF MAD ENA WNA NNA MESO ANTI BRAS NSA
SSA NZ NC FIJI TAS EAUS WAUS NG ARMA CHI JAP EAA IN;
endblock;

begin distribution;
title = 'Cycadales';
ntax = 10;
range
Cycas: CAF MAD ARMA NG NC FIJI CHI JAP EAUS IN,
Bowenia: EAUS,
Stangeria: SAF,
Dioon: MESO,
Macrozamia: WAUS EAUS,
Lepidozamia: EAUS,
Encephalartos: CAF SAF,
Ceratozamia: MESO,
Zamia: ENA MESO ANTI NSA,
Microcycas: ANTI;
tree set1 = (1,((2,3),(4,((7,(5,6)),(8,(9,10))))));
endblock;

begin distribution;
title = 'Pinaceae';
ntax = 11;
range
Abies: NNA ENA WNA EAA MESO JAP CHI,
Cedrus: EAA,
Keteleeria: CHI,
Nothotsuga: CHI,
Pseudolarix: CHI,
Tsuga: CHI JAP NNA ENA WNA,
Pseudotsuga: CHI JAP WNA MESO,
Larix: NNA ENA CHI JAP EAA,
Cathaya: CHI,
Picea: NNA ENA WNA CHI JAP EAA,
Pinus: NNA ENA WNA MESO ANTI CHI JAP ARMA EAA;
tree set2 = (((1,2),(6,(5,(3,4)))),(11,(10,(9,(7,8)))));
endblock;

begin distribution;
title = 'Taxales';
ntax = 6;
range
Amentotaxus: CHI,
Torreya: CHI JAP WNA ENA,
Pseudotaxus: CHI,
Taxus: ENA WNA MESO CHI JAP ARMA EAA,
Austrotaxus: NC,
Cephalotaxus: CHI JAP;
tree set3 = (6,(5,((1,2),(3,4))));
endblock;

begin distribution;
title = 'Podocarpaceae';
ntax = 19;
range
Saxegothaea: SSA,
Phyllocladus: ARMA TAS NC NG NZ,

Microcachrys: TAS,
Microstrobos: TAS EAUS,
Lagarostrobos: TAS NZ,
Lepidothamnus: SSA NZ,
Halocarpus: NZ,
Parasitaxus: NC,
Sundacarpus: EAUS NG ARMA,
Prumnopitys: NSA SSA EAUS NC NZ,
Acmopyle: NC FIJI,
Dacrycarpus: CHI ARMA NC NG FIJI NZ,
Dacrydium: ARMA NG NC FIJI NZ,
Falcatifolium: ARMA NG NC,
Foliolatus: CHI JAP ARMA NG EAUS NC FIJI,
Podocarpus: CAF SAF MAD MESO ANTI NSA BRAS SSA NZ NC
EAUS TAS WAUS,
Retrophyllum: NSA ARMA NG NC FIJI,
Afrocarpus: CAF SAF,
Nageia: CHI JAP ARMA NC FIJI NG IN;
tree set4 = (1,(10,(9,(8,(7,(6,(5,(2,(3,4))))))))),
((16,(15,((11,12),(13,14)))),(19,(17,18))));
endblock;

begin distribution;
title = 'Cupressaceae';
ntax = 30;
range
Sciadopitys: JAP,
Athrotaxis: TAS,
Sequoia: WNA,
Sequoiadendron: WNA,
Glyptostrobus: CHI,
Metasequoia: CHI JAP,
Taxodium: MESO ENA,
Taiwania: CHI,
Cryptomeria: CHI JAP,
Cunninghamia: CHI,
Microbiota: EAA,
Platycladus: CHI JAP,
Thuja: WNA ENA NNA CHI JAP EAA,
Thujopsis: JAP,
Fokienia: CHI,
Calocedrus: WNA CHI,
Juniperus: CAF MESO ANTI WNA ENA NNA CHI JAP EAA,
Chamaecyparis: WNA ENA CHI JAP,
Cupressus: MESO WNA CHI EAA,
Tetraclinis: EAA,
Diselma: TAS,
Fitzroya: SSA,
Pilgerodendron: SSA,
Austrocedrus: SSA,
Libocedrus: NC NZ,
Papuacedrus: NG,
Neocallitropsis: NC,
Widdringtonia: SAF,
Callitris: NC TAS EAUS WAUS,
Actinostrobus: WAUS;
tree set5 = (1,(2,((3,4),((5,(6,7)),(8,(9,10)),((11,12),((13,14),
(15,(16,(17,18,19)),(20,((21,22),23),(24,25,26),27,(28,(29,30)))))))))));
endblock;

begin distribution;
title = 'Araucariaceae';

ntax = 30;
range
Agathis_montana: NC,
Agathis_moorei: NC,
Agathis_lanceolata: NC,
Agathis_ovata: NC,
Agathis_dammara: ARMA,
Agathis_obtusa: FIJI,
Agathis_robusta: EAUS,
Agathis_vitiensis: FIJI,
Agathis_borneensis: ARMA,
Agathis_palmerstoni: ARMA,
Araucaria_bernieri: NC,
Araucaria_biramulata: NC,
Araucaria_columnaris: NC,
Araucaria_humboldtensis: NC,
Araucaria_laubenfelsii: NC,
Araucaria_luxurians: NC,

Araucaria_montana: NC,
Araucaria_nemorosa: NC,
Araucaria_schmidii: NC,
Araucaria_scopulorum: NC,
Araucaria_subulata: NC,
Araucaria_muelleri: NC,
Araucaria_rulei: NC,
Araucaria_heterophylla: NC,
Araucaria_cunninghamii: EAUS NG,
Araucaria_araucana: SSA,
Araucaria_angustifolia: BRAS,
Araucaria_hunsteinii: NG,
Araucaria_bidwillii: EAUS,
Wollemia_nobilis: EAUS;
tree set6 = (30,(((3,4,(1,2)),(5,(6,7,8)),(9,10)),(((26,27),(28,29)),
(25,(24,(11,12,13,14,15,16,17,18,19,20,21,(22,23)))))));
endblock;