

7 Fossil plant studies from late Early Miocene of the Santa Cruz Formation: paleoecology and paleoclimatology at the passive margin of Patagonia, Argentina

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Abstract

This chapter analyses the plant fossils including phytoliths, carbonized wood, and leaf compressions, along with microcharcoal, chrysophycean stomatocyst, sponge spicules, and diatoms, recovered from the Estancia La Costa Member, Santa Cruz Formation (late Early Miocene), in the Atlantic margin of Patagonia, Argentina. The floristic composition and paleoclimatic inferences based on this fossil plants assemblage from the late Early Miocene are presented. The fossil flora is characterized by the presence of herbaceous components including chloridoid, panicoid, danthonioid, pooid, and festucoid grasses. The arboreal elements include members of the Araucariaceae, Lauraceae, Arecaceae, Nothofagaceae, Myrtaceae, Cunoniaceae, Fabaceae (Faboideae), and ?Proteaceae. The vegetation was a mixture of open temperate semi-arid forests and humid warm-temperate forests. The integrated analysis of multiple sets of proxy data suggests that southeastern Patagonia, during late Early Miocene, was composed by a temperate to warm-temperate and semi-arid to humid climate, where seasonal low levels of precipitation served as a limiting factor for plant growth.

Resumen

Este capítulo analiza el registro paleobotánico preservado como fitolitos, leños fósiles y compresiones foliares, junto con microcarbónes, estomatocistos de crisostomatáceas, espículas de esponjas y diatomeas, hallados en el Miembro Estancia La Costa de la Formación Santa Cruz (Mioceno Temprano tardío), en el margen atlántico de Patagonia, Argentina. Se discute la composición florística y las interpretaciones paleoclimáticas en base a la asociación de plantas fósiles restringidas al Mioceno Temprano tardío. La flora estaba caracterizada por la presencia de componentes herbáceos tales como gramíneas cloridoideas, panicoides, dantoneas, pooides y festucoideas. Los elementos

arbóreos estaban integrados por Araucariaceae, Lauraceae, Arecaceae, Nothofagaceae, Myrtaceae, Cunoniaceae, Fabaceae (Faboideae) y Proteaceae? La vegetación representa un ambiente heterogéneo integrado por bosques abiertos templados semiáridos y bosques templado-cálidos y húmedos. El análisis integral de datos múltiples sugiere que en la región sudeste de Patagonia, durante el Mioceno Temprano tardío, el clima era templado a templado-cálido y semiárido a húmedo, con bajas precipitaciones estacionales que actuaron como uno de los factores limitantes para el crecimiento vegetal.

7.1 Introduction

Late Early Miocene continental outcrops from the Santa Cruz Formation are found along the Atlantic coast of southernmost Patagonia, Argentina, between the Río Coyle and Río Gallegos (c. S 51° 00' S, W 69° 10'; see Vizcaíno *et al.*, Chapter 1, Figs. 1.1 and 1.2). The Santa Cruz Formation, known by an exceptionally rich mammal fossil fauna, is composed of two members: the lower Estancia La Costa Member, with a predominance of pyroclastic deposits, and the upper Estancia La Angelina Member, mainly composed of claystones, mudstones, and sandstones (Tauber, 1997, 1999; Matheos and Raigemborn, Chapter 4).

The Santa Cruz Formation has been dated by $^{40}\text{Ar}/^{39}\text{Ar}$ between 16.56 Ma and 16.18 Ma, at Monte Observación and Monte León localities (Fleagle *et al.*, 1995). Integrating results of the tephra correlations and radiometric ages indicates that the Santa Cruz Formation spans the interval ~18 to 16 Ma in the Atlantic coastal plain, indicating an Early Miocene age (see Perkins *et al.*, Chapter 2).

Fossil wood and silica microfossil records from the Miocene in Patagonia are scarce (Schönfeld, 1954; Hünicken, 1995; Schöning and Bandel, 2004; Zucol *et al.*, 2007). However, palynological information documents a flora characterized by the occurrence of xerophytic and halophytic shrubby-herbaceous plants belonging to the extant families Asteraceae, Chenopodiaceae, Ephedraceae,

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Convolvulaceae, Fabaceae, and Poaceae. Podocarpaceae, Araucariaceae, and Nothofagaceae dominated forest communities, with a few tropical elements including Arecaceae, Symplocaceae, and Lauraceae (Romero, 1970; Barreda, 1993, 1996; Barreda and Palazzessi, 2007; Palazzessi and Barreda, 2007). During the Middle to Late Miocene, palynological records show an increase in diversity, with increasingly abundant xerophytic taxa (including members of the Asteraceae, Chenopodiaceae, Anacardiaceae, and Convolvulaceae) and sclerophyll trees (Casuarinaceae, Fabaceae, and Proteaceae), but forest and riparian forest communities as well (Barreda and Palazzessi, 2007; Palazzessi and Barreda, 2007; Barreda *et al.*, 2007). The development of xerophytic plant communities is probably linked with a water deficit in open forest areas or along marginal coastlines (Barreda and Palazzessi, 2007, 2010, and references therein).

The possible causes for the expansion of xerophytic elements with a pronounced ecological change in the late Miocene include both global and local factors. On the one hand there was the uplift of Patagonian Andes in the west, which presumably established a pronounced rain shadow by the Middle Miocene (Blisniuk *et al.*, 2005); on the other hand the global cooling since ~14.5 Ma, which was associated with rapid growth of the Antarctic ice sheet and with major biogeographic changes on all southern continents (Zachos *et al.*, 2001).

Analysis of microscopic silica from continental sediments can be valuable for clarifying paleoenvironmental conditions. Phytolith studies in particular can contribute to understanding factors related to ecosystem diversity, climate, and paleoecology (Kondo *et al.*, 1988).

Fossil dicotyledonous woods can be used to establish paleoecological and paleoclimate conditions (Carlquist, 1977; Wiemann *et al.* 1998, 1999, 2001; Wheeler and Bass, 1991, 1993; Poole and van Bergen, 2006). The approach proposed by Wiemann *et al.* (1998, 1999) has demonstrated that temperature-related climate variables, particularly mean annual temperature (MAT), can be estimated from anatomical features of wood. Also, calculations of Vulnerability Index (V) and Mesomorphy Ratio (M) show strong reliability because they are strongly correlated with rainfall and temperature (Carlquist, 1977). The Vulnerability Index is used as an indicator of hydric conductivity. A low value indicates greater capacity for withstanding water stress or freezing. High values of M denote mesomorphic wood structure (Carlquist, 1977).

In this chapter we present the first study of the Estancia La Costa Member of the Santa Cruz Formation based on the paleobotanical record from the Atlantic coast of Patagonia, analyzing phytoliths, carbonized wood, and leaf compressions, as well as records of microcharcoals, chrysophycean stomatocysts, sponge spicules, and diatom remains. These data are used to reconstruct the plant communities and

paleoclimatic conditions. The records fall within the temporal interval called the Mid-Miocene Climatic Optimum (MMCO) (Zachos *et al.*, 2001; Blisniuk *et al.*, 2005), a period of time when the world was much warmer than today and plant communities experienced marked changes in floristic composition.

7.2 Institutional abbreviations

BAPb ex CIRGEO PALEOB: Colección de Paleobotánica del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina.

TK: Laboratory of Phylogenetic Botany, Faculty of Science, Chiba University, Japan.

MPM-PB: Colección Paleobotánica del Museo Regional Provincial Padre Manuel Jesús Molina, Río Gallegos, Argentina.

CIDPalbo: Colección Laboratorio de Paleobotánica, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción, Diamante, Argentina.

MNHN: Collection des végétaux fossiles du Muséum National d’histoire naturelle de Paris.

DJ: British Antarctic Survey Paleontological Collections, Cambridge, UK.

LPPB: Colección Paleobotánica, Museo de La Plata, La Plata, Argentina.

S: Swedish Museum of Natural History, Stockholm, Sweden.

A-PF: Colección Paleoxilológica Torres, Instituto Antártico Chileno, Santiago, Chile.

P: British Antarctic Survey, Cambridge, UK.

7.3 Material and methods

Four localities were examined for silica microremains at Punta Sur (PS, sample 1970), Campo Barranca (CB, samples 1971–1973), Anfiteatro (ANF, samples 1974–1975), and Estancia La Costa (ELC, samples 1976–1982), all from the lower levels of the Estancia La Costa Member (see Table 7.1). This represents the lower unit of the Santa Cruz Formation, late Early Miocene, which is present as outcrops along the Atlantic coast of southernmost continental Patagonia in Argentina (see Vizcaíno *et al.*, Chapter 1, Figs. 1.1 and 1.2, and Matheos and Raigemborn, Chapter 4, Figs. 4.3, and 4.4). A total of 13 sedimentary samples contained silica microremains.

The silica microremains were extracted using standard wet oxidation and heavy-liquid flotation techniques following the protocol described in Zucol *et al.* (2010a, 2010b). Silica microremains were mounted for viewing on microscope slides in both liquid (oil immersion) and solid (Canada balsam) media, and examined using a Nikon Eclipse E200 light microscope. Photomicrographs were taken with a Nikon Coolpix 990 digital camera.

Table 7.1. *Microremains abundance, and isolated phytolith morphotypes in each sample*

Locality	ELC							ANF		CB			PS	Botanical
Sample	1982	1981	1980	1979	1978	1977	1976	1975	1974	1973	1972	1971	1970	affinities
<i>Microcharcoal</i>	NO	R	R	NO	F	S	F	S	NO	F	NO	VF	S	
<i>Stomatocyst</i>	NO	NO	NO	S	S	S	NO	NO	S	NO	NO	NO	NO	
<i>Sponge spicule</i>	F	R	R	S	NO	S	R	NO	NO	S	NO	S	R	
<i>Diatom</i>	NO	NO	R	S	NO	S	S	S	S	NO	NO	NO	R	
<i>Articulated phytolith</i>	R	R	VF	NO	S	NO	NO	NO	S	NO	NO	NO	S	
<i>Isolated phytolith</i>	VF	VF	F	VF	VF	VF	VF	VF	VF	VF	NO	VF	VF	
Isolated phytolith types														
<i>Point-shaped</i>	NO	X	NO	X	X	X	NO	NO	NO	X	NO	X	X	(1) ^{a,b}
<i>Saddle</i>	NO	NO	NO	NO	NO	X	NO	NO	NO	NO	NO	NO	X	(2) ^{a,b}
<i>Cylindrical vascular element</i>	NO	NO	NO	X	NO	NO	NO	NO	NO	NO	NO	NO	X	(1) ^{a,b}
<i>Dumbbell and Cross</i>	NO	NO	NO	X	NO	X	NO	NO	X	X	NO	X	X	(3) ^{a,b}
<i>Bilobate stipa-type</i>	NO	NO	NO	X	NO	NO	NO	NO	NO	NO	NO	NO	NO	(4) ^c
<i>Fan-shaped</i>	NO	NO	NO	NO	NO	X	X	NO	NO	NO	NO	X	X	(1) ^{a,b}
<i>Globular</i>	NO	NO	X	X	NO	X	NO	X	NO	NO	NO	NO	X	(5) ^{a,d,e}
<i>Lobular</i>	NO	NO	NO	X	NO	NO	NO	NO	NO	NO	NO	NO	X	(6) ^a
<i>Elongate</i>	X	X	X	X	X	X	X	X	X	X	NO	X	X	(1) ^{a,b}
<i>Truncated cone</i>	NO	NO	NO	X	X	X	NO	X	X	X	NO	X	X	(7) ^a
<i>Conical</i>	NO	NO	NO	X	NO	NO	NO	NO	NO	X	NO	NO	NO	(8) ^{a,d}
<i>Polyedrical</i>	NO	X	NO	X	X	X	NO	X	NO	NO	NO	X	X	(1) ^{a,b}
<i>Festucoid boat</i>	NO	NO	NO	NO	X	X	X	NO	NO	NO	NO	NO	X	(9) ^a
<i>Oblong/Circular/Square</i>	NO	NO	NO	X	NO	X	NO	NO	NO	NO	NO	NO	X	(10) ^{a,b}
<i>With modified surface</i>	NO	X	NO	X	NO	NO	NO	X	NO	X	NO	NO	X	--
<i>Other</i>	X	NO	NO	X	X	X	X	X	X	X	NO	X	X	--

VF, very frequent; F: frequent; R, rare; S: scarce; NO: not observed; X: presence; PS: Punta Sur locality; CB: Campo Barranca locality; ANF: Anfiteatro locality; ELC: Estancia La Costa locality.

Botanical affinities of isolated phytolith types: 1. Non diagnostic types; 2. Chloroidoideae phytoliths; 3. Panicoideae phytoliths; 4. Stipeae phytoliths; 5. Echinete globular: Arecaceae phytoliths (I and IV), Smooth globular: Nothofagaceae phytolith (I and V), Cunoniaceae, Lauraceae and Myrtaceae phytolith (I); 6. Dicot phytoliths; 7. Danthoneae phytoliths; 8. Cyperaceae phytoliths; 9. Festuceae (Pooideae) phytoliths; 10. Pooideae phytoliths.

^a Kondo *et al.* (1994), ^b Twiss (1992), ^c Fredlund and Tieszen (1994), ^d Bertoldi de Pomar (1971), ^e Whang and Hill (1995).

The various phytolith morphotypes present in each sample were recorded, and counts were made of the number of phytoliths belonging to each. Phytolith morphotypes were classified according to existing classifications (Zucol *et al.* 2010c and references therein) considering their botanical affinities (see Table 7.1) and described using the morphotype descriptors proposed by the IPCNWG (2005). Chrysophycean stomatocysts were described following the terminology used in Rull and Vegas-Vilarrúbia (2000) and Coradeghini and Vigna (2001).

To quantify the relative abundances of analyzed microremains, a scale was used which references the comparative abundance of each morphotype, where elements with relative frequency values greater than 30% in the sample are categorized as very frequent (VF); 20–29.9% as frequent

(F); 10–19.9% as rare (R); and less than 9.9% as scarce (S) (Zucol *et al.*, 2010b).

Processed sediment samples and microscope slides have been deposited in the Laboratorio de Paleobotánica of the CICYTTP, Diamante (Argentina), with the label heading CIDPalbo.

Leaf compressions were collected from the lowermost levels of the Estancia La Costa Member that crop out in the intertidal shore platform at Rincón del Buque, north of the Río Coyle (see Vizcaíno *et al.*, Chapter 1, Fig. 1.2 and Matheos and Raigemborn, Chapter 4, Fig. 4.4). The leaves are preserved in poorly consolidated medium to fine sands and muddy sediments right above an oyster bed. Whole leaves are preserved with petiole and apex but no good detail in vein architecture. Because of the fragmentary

Table 7.2. Fossil wood species from Punta Sur locality (PS) used in the multivariate anatomical analyses

Taxa	Wood anatomical character											
	(1) mult	(2) spir	(3) <100 µm	(4) sept	(5) >10 ser	(6) heter4+	(7) stor	(8) abs	(9) marg	(10) RP	(11) para	(12) homo
<i>Laurinoxylon atlanticum</i> (Lauraceae)	0	0	1	0	0	0	0	0.5	0	0	1	0
<i>Nothofagoxylon triseriatum</i> (Nothofagaceae)	0.5	0	1	0	0	0	0	1	0	0.5	0	0
<i>Myrceugenia chubutense</i> (Myrtales)	0	0	1	0	0	0	0	0	0	0.5	0	0
<i>Eucryphiaceoxylon eucryphioides</i> (Cunoniaceae)	0.5	0	1	0	0	0	0	0	0	0.5	0	0
<i>Doroteoxylon vicenti-perezii</i> (Proteaceae?)	0	0	1	0	0.5	0	0	0	0	1	1	0
aff. <i>Xilotype 3</i> Pujana, 2008 (Fabaceae)	0	1	1	0	0	0	0	0.5	0	0.5	1	1

Abbreviations: (1) Vessels with multiple perforations (mult). (2) Spiral thickenings present in the vessels (spir). (3) Vessel mean tangential diameter less than 100 µm (<100 µm). (4) Fibers septate (sept). (5) Rays commonly more than 10 cells wide (>10 ser). (6) Rays heterocellular with four or more rows of upright cells (het4+). (7) Rays storied (stor). (8) Axial parenchyma absent or rare (abs). (9) Marginal parenchyma present (marg). (10) Wood ring-porous (RP). (11) Paratracheal parenchyma (para). (12) Homocellular rays (homo).

character of the matrix, large blocks of rock were taken from the bed and carried to the laboratory wrapped in film to conserve humidity and retard drying. The best leaf samples were mechanically cleaned using needles under a stereoscope, and photographed at the Museo de La Plata.

The wood materials consist of 20 carbonized wood specimens from the Punta Sur locality, which were recovered at 20 m below the tuff levels that appear in the Estancia La Costa Member (see Chapter 1, Fig. 1.2 and Chapter 4, Fig. 4.4). Only 13 specimens have well-preserved anatomical features. Thin-sections were made using petrographic techniques for the three characteristic wood sections: transverse (TS), tangential longitudinal (TLS) and radial longitudinal section (RLS). The terminology used for the wood descriptions follows the IAWA Lists of Features Suitable for Hardwood Identification (IAWA Committee, 1989, 2004), with some terms also taken from Carlquist (2001). The number of vessels per square millimeter was counted individually following Wheeler (1986). The fossil woods were identified using the wood atlases and descriptions of Wagemann (1948), Tortorelli (1956), Rancusi *et al.* (1987), and Pujana (2008, 2009a, 2009b), as well as the InsideWood database (2004 onwards, accessed on March 2011).

One of the main functions of wood is water conduction, so climatic differences that affect water availability may be reflected in wood structure. Studies of ecological adaptations reflected in the anatomical characteristics of wood, from various vegetation communities and geographical areas, have demonstrated that wood anatomy can be used to estimate environmental parameters (Baas, 1976; Van der Graaff and Baas, 1974; Wheeler and Baas, 1991, 1993; Baas and Wheeler, 1996).

The relation between wood anatomy and climatic factors was proposed by pioneer plant anatomists (Bailey and Tupper, 1918; Frost 1930a, b, 1931) and then confirmed by various authors (see Baas, 1986; Wheeler and Baas, 1991; Lindorf, 1994; Baas *et al.*, 2004 and references therein). Furthermore, Wiemann *et al.* (1998, 1999) proposed equations for estimating some paleoclimate factors using simple and multiple regressions. The climate variables calculated by wood features (Table 7.2) in the present work were: mean annual temperature (MAT), mean annual range in temperature (MART), cold month mean temperature (CMMT), mean annual precipitation (MAP), and length of dry season (DRY). Two tested equations (Eq. (12) and (15) of Wiemann *et al.*, 1999 and Poole *et al.*,

Table 7.3. Summary of the quantitative palaeoclimate data from Punta Sur locality (PS)

Wood physiognomy (WP)	Punta Sur locality
Temperature	
MAT (°C ± 1.7 °C)	
(Eq. 12)	19.31
24.78 + 36.57(stor) – 15.61(marg) – 16.41(abs)	
(Eq. 15)	9.35
17.07 + 25.23(stor) – 23.17(abs) + 13.79(sept)	
MART (°C ± 2.4 °C)	4.26
4.16 + 0.319(spir) + 0.135(<100 µm) – 0.373(> 10ser) – 0.154(het4+)	
CMMT (°C ± 2.6 °C)	9.80
9.91 – 0.355(spir) – 0.098(< 100 µm) + 0.845(> 10ser) + 0.368(het4+) + 0.528(stor) – 0.210(abs)	
DRY (months ± 1.4 months)	6.80
6.81 – 0.186(mult) – 0.122(sept)	
Precipitation	
MAP (mm, ± 940 mm)	
–6.06 +6.332(sept) + 7.901(abs)	869

MAT, mean annual temperature; **MART**, mean annual range in temperature; **CMMT**, cold month mean temperature; **DRY**, length of dry season; **MAP**, mean annual precipitation. Eq. 12 and 15 are equations in Wiemann *et al.* (1999) and Poole *et al.* (2005). For codification of wood anatomical characters see Table 7.2.

2005; see Table 7.3) were considered best for estimating MAT based on how well they worked as MAT predictors in present-day sites (Wiemann *et al.*, 1999). The standard errors for MAT, MART, CMMT, MAP, and DRY are 1.7 °C, 2.4 °C, 2.6 °C, 940 mm, and 1.4 months, respectively. These wood physiognomy methods are appropriate for using fossil wood assemblages to determine terrestrial paleotemperatures, but they do not possess the same level of accuracy in determining precipitation levels. Nevertheless, the results of all of the analyses proposed by Wiemann *et al.* (1998), including precipitation, are included here. The sample size recommended by Wiemann *et al.* (1998) is 20–25 woods of different types from each locality. Unfortunately, with these Miocene fossil woods this prerequisite could not be satisfied. However, an interpretation based upon diverse bioproxies, such as that proposed in this chapter, would reduce the potential error.

The Vulnerability Index (V = mean vessel diameter divided by mean vessel frequency) and Mesomorphy Ratio (M = Vulnerability Index multiplied by mean vessel member length) were calculated using the equations of Carlquist (1977). Vulnerability Index is indicative of the sensitivity to the risks of embolisms. Low Vs indicate woods with numerous, narrow vessels and high safety in conduction, whilst high Vs are typical of efficient water conductors with wide, infrequent vessels. Mesomorphy is used as a measure of the water availability of the species, with high values being typical for species with a mesic

ecology. Mesic habits have a moderate or a well-balanced supply of moisture (Baas, 1986).

A diverse range of wood anatomical characteristics were also analyzed in terms of their ability to serve as paleoecological indicators, including vessel diameter, number of vessels per square millimeter, degree of vessel grouping, vessel arrangement, length of vessel elements, perforation plate type, porosity, presence of vasicentric and vascular tracheids, axial parenchyma, and growth rings (Carlquist and Hoekman, 1985; Wheeler and Baas, 1991, 1993; Lindorf, 1994; Woodcock, 1994).

The terms tropical, subtropical, and temperate are used to indicate broad geographic/macroclimatic zones. “Tropical” implies non-seasonal, equable warm and wet climates, while “temperate” implies markedly seasonal climates, with seasonality in temperature and/or water availability following Wheeler and Baas (1993). For temperature inferences based on grass phytoliths, the terms megathermal (>24 °C MAT), meso-megathermal (20–24 °C), mesothermal (14–20 °C), and microthermal (<14 °C) are used following Greenwood (1994) and Burkart (1975).

The quantitative values provided in the wood anatomical description are averages of 25 measurements. The average is cited first, followed by the minimum and maximum values, which are given in brackets.

The photomicrographs of the fossil wood sections were taken with a Nikon Coolpix S4 digital camera. The wood fossil materials, including thin-section slides and leaf

compressions, were deposited at the Museo Regional Provincial Padre Manuel Jesús Molina, Río Gallegos, Santa Cruz Province, Argentina, labeled as MPM-PB 4381–4393 (wood fossils) and MPM-PB 4928–4931 (leaf compressions). Thin-section slides bear the specimen numbers followed by a lower-case letter indicating the particular section: a, transverse section; b, radial longitudinal section; and c, tangential longitudinal section.

7.4 Results

7.4.1 Microfossil records

For the analysis of microremains from the Estancia La Costa Member, 13 sedimentary samples from four localities were selected (PS, CB, ANF, and ELC) (Chapter 4; Fig. 4.4). This lower part of the Member also contained carbonized wood and plant remains that permit comparative analysis. All but one of the 13 samples (1972 – a clay from CB locality) contained microremains that possess heterogeneous assemblages classified as: microcharcoals, chrysophycean stomatocysts, sponge spicules, diatoms, and phytoliths (which occur in both articulated and isolated forms). A low abundance of microremains was observed in the other samples from the CB locality (1971 and 1973), as well as in the upper samples from the ELC locality (1980–1982). The samples with the highest phytolith abundance and variability, on the other hand, were from PS (1970), ANF (1975), and ELC (1977 and 1979) localities.

The microcharcoal remains (Table 7.1) are considered for the purpose of contextualizing the presence of the carbonized wood macroremains, because in some samples only these small carbonized fragments were present. In some cases these had indeterminate forms, whereas in others individual cells and tissue fragments could be recognized. Microcharcoal is abundant in the lower samples of the analyzed sequence (especially in PS and CB samples) and in the basal samples of the ELC section (1976 and 1978). Correspondingly, similar high abundances and variability of phytolith assemblages were observed in the PS and CB samples while the ELC basal samples showed less phytolith variability.

Chrysophycean stomatocysts (Table 7.1) were mainly present in the ELC basal samples (1976–1979), with a variety of types (Fig. 7.1o). These stomatocysts had either smooth or scrobiculate surfaces, simple or ornamented operculi, and spherical to ovoid shapes.

Sponges (Table 7.1) were represented mainly by whole or fragmented macroscleres (Fig. 7.2g), with either smooth or, rarely, lightly echinate surfaces. These were present in great abundance, mainly as whole elements, in the PS sample (1970), and in the lowest ELC samples (1977 and 1979). In the CB samples (1971 and 1973) as well as in the upper ELC samples (1976 and 1980–1982) the sponge remains were scarce, occurring either whole or fragmented.

Diatom remains (Table 7.1) were present in the form of either whole or fragmented frustules (Fig. 7.2f). These were most abundant in the PS sample, and were found in very low proportions in samples from the ANF (1974 and 1975) and ELC (1976, 1977, 1979 and 1980) localities. The frustules that remained whole were small or medium types, while large diatoms were observed in fragmented forms.

Articulated phytoliths (Fig. 7.2e) formed by multiple cells were abundant in the PS sample and in the upper samples from the ELC locality, but in some samples (as in ANF 1974) phytoliths consisting of sections of articulated silicified epidermal tissue were found. The great majority of these articulated phytoliths are graminoid in origin, and are made up of epidermal and subepidermal elements such as long and short cells, hair and prickle cell elements, and bulbiform cells (fan-shaped and polyhedral types).

Isolated phytoliths were abundant and variable, some well preserved, some heavily eroded (especially in the 1975 sample and to a lesser degree 1979) (Fig. 7.1n). The greatest variability of isolated phytoliths is seen at the PS and CB localities.

The most abundant phytolith morphotypes are non-diagnostic elongated forms, including small elongated prismatic (Fig. 7.1j) and elongated prismatic with diverse contours (Fig. 7.2a). On the other hand, point-shaped phytoliths (Fig. 7.1k) along with their variants are present in samples from the PS, CB, and ELC localities; while fan-shaped (Fig. 7.2d) and polyedral (Fig. 7.2b) phytoliths are mainly present in samples from PS and lower samples from ELC.

Among the diagnostic phytolith morphotypes, saddles (Fig. 7.1c) are present in the sample 1970 and 1977; dumbbells (Fig. 7.1a), crosses (Fig. 7.1b) and polylobate dumbbells (Fig. 7.1e) are present in samples 1977 and 1979 from ELC; while sample 1979 (not shown) is the only one that contains stipa-type bilobate phytoliths. Truncated cones (Fig. 7.1l) are distributed throughout most of the sequence (1970–1979) with greatest abundance in samples 1973–1977. Other phytolith types that are more abundant in the lower section from ELC (samples 1976–1979) and scarce in sample 1970 are the festucoid boats (Fig. 7.1f), circular to oblong (Fig. 7.1h), square (Fig. 7.1d), and small conical (Fig. 7.1g) phytoliths.

Cylindrical vascular element (Fig. 7.2c) and lobular (Fig. 7.1i) phytoliths were found in samples 1970 and 1979; while globular phytoliths (Fig. 7.1m) are abundant in samples from PS and ANF, and in the lower ELC samples. These phytoliths are spherical to slightly elliptical in contour and differentiated by their surface texture, which can be either smooth (Fig. 7.1m, upper row) or echinate (Fig. 7.1m, lower row). The globular echinate phytoliths are more abundant in the majority of the cases, whereas smooth surfaced types are relatively abundant in samples 1970, 1977, and 1979.

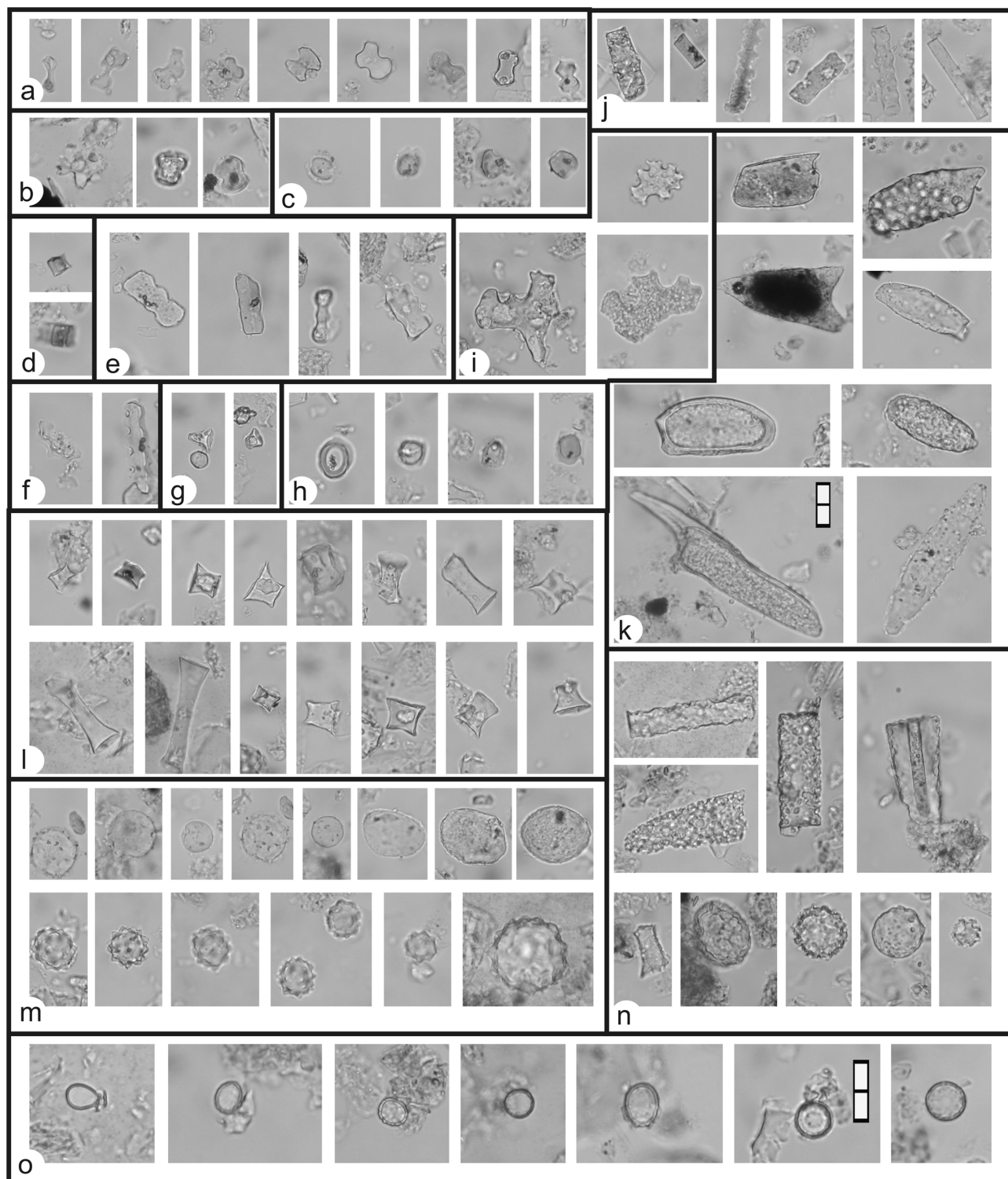


Fig. 7.1. Silica microremains. **Phytoliths:** a, Dumbbell. b, Cross. c, Saddle. d, Square. e, Polylobate dumbbell. f, Festucoid boat. g, Small conical. h, Rondel and oblong. i, Lobate. j, Small elongate. k, Point-shaped. l, Truncated cones. m, Smooth and echinate globular. n, Microremains with modified surface. **Chrysophycean stomatocysts:** o, Different stomatocyst types. Scale bar in k = 20 μm (applies to a–n); scale bar in o = 20 μm .

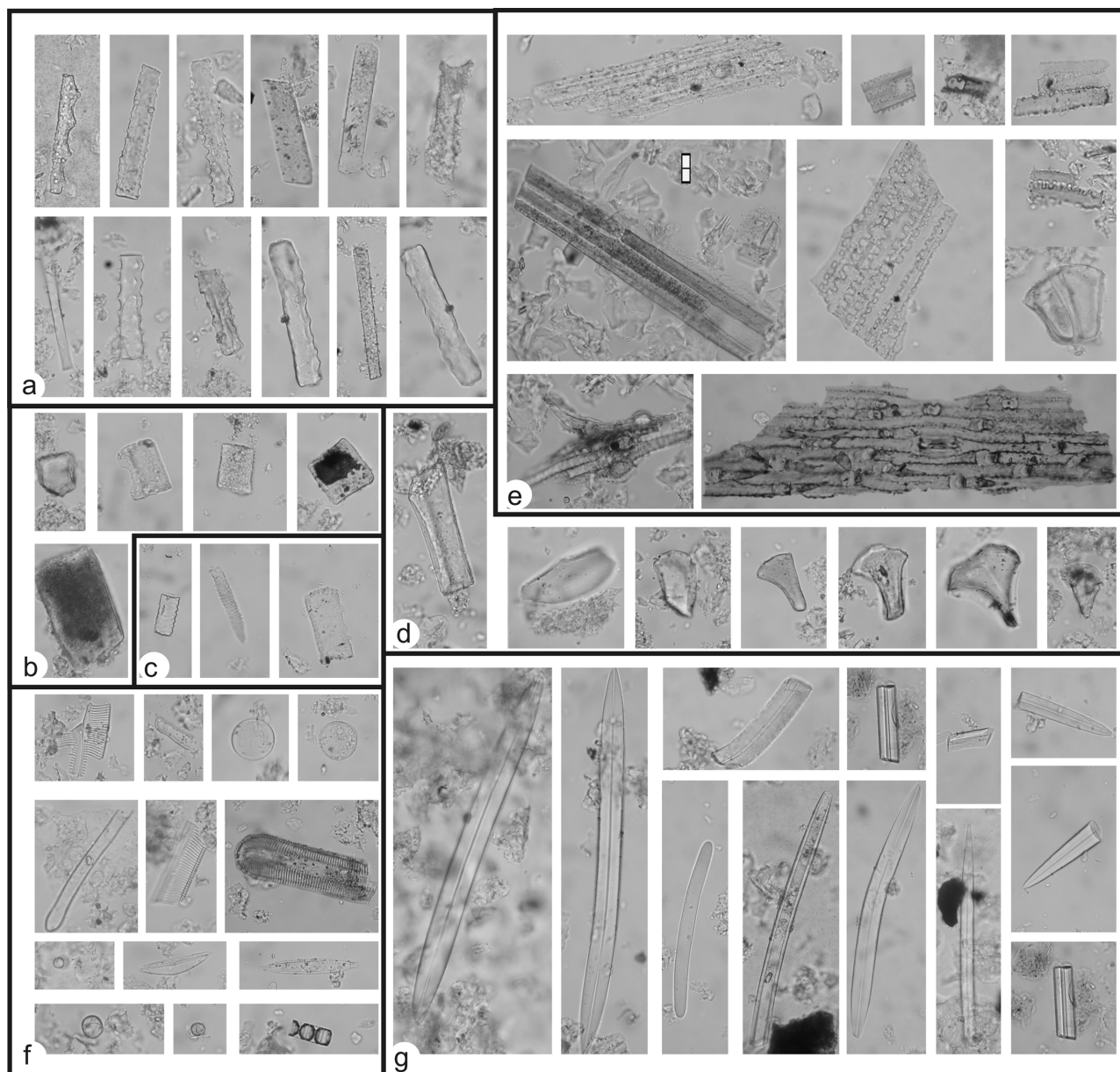


Fig. 7.2. Silica microremains. **Isolated phytoliths:** a, Elongate. b, Polyedral. c, Cylindrical vascular elements. d, Fan-shaped. **Articulated phytoliths:** e, Different phytoliths originated in epidermal and bulliform cells. **Diatoms:** f, Fragmented and entire diatoms. **Sponge spicules:** g, Sponge macroscleres. Scale bar = 20 μ m.

Several of the phytolith morphotypes, such as panicoid (dumbbells, crosses and polylobate dumbbells), chloridoid (saddles), danthonioid (truncated cones), stipoid (stipa-type bilobate), pooid and festuroid (circular to oblong, square, small conical and festuroid boat) elements, indicate the presence of graminoid vegetation (Table 7.1). Other types are associated with dicotyledonous vegetation elements (lobular), while still others have arecoid affinity, such as globular echinate phytoliths. The globular smooth types are linked by some authors with the Nothofagaceae (Kondo *et al.*, 1994; Whang and Hill,

1995), with some size and surface variations also assigned to Cunoniaceae, Lauraceae, and Myrtaceae (Kondo *et al.*, 1994). The distribution of this particular smooth globular type jointly with the globular echinate phytoliths in the middle–lower section of the Estancia La Costa Member sequence indicates the presence of arecoid/nothofagoid components.

Danthonioids grass elements characterize the ANF locality. Phytoliths representing the megathermal grass groups are abundant in the samples from ELC sequence, with a predominance of chloridoid grass elements found in the

basal sample (1970) and panicoid elements in the middle samples (1974, 1977, and 1979). On the other hand, microthermal elements (such stipoid, pooid, and festucoid) are most abundant in lower samples from the ELC locality (1977 and 1978), with similar relative abundances of the previously mentioned megathermal elements.

7.4.2 Leaf compression records

Leaf compressions were collected from the lowermost levels of the Estancia La Costa Member at Rincón del Buque locality. This is the first record of fossil leaves for the Santa Cruz Formation, being the only fossil record for leaf compressions in east Patagonia. Although lacking detail of vein architecture, all leaves can be unequivocally assigned to the Nothofagaceae family based on leaf shape and size, tooth type and venation, primary and secondary venation pattern, and leaf surface plication (Romero, 1980; Romero and Dibern, 1985). Three leaf types were recognized (Fig. 7.3), although more intensive studies are required to determine whether they correspond to more than one species, and possible relationships with other fossil and modern species.

While microfossil and wood remains could represent allochthonous floras, the leaf record is a good evidence of the autochthony (Gastaldo *et al.*, 1987). Although leaves can be transported over long distances, the quality of preservation for this record, with complete blades, attached petioles, well-preserved apices, no macerated tissue (coarse texture, plicate relief preserved), and no mechanical damage to the blade, allows us to infer that transportation could only have been over a short distance from the source, up to a few kilometers

(Gastaldo *et al.*, 1987). The leaf size selection and the low presence of leaf debris suggest wind dispersion for these specimens. The low quality of the vein architecture is related to the coarse rock matrix, not to long-distance transport. The leaves preserved in muddy lenses are best preserved, and sometimes show whole-leaf architecture (Fig. 7.3).

Leaf records of indubitable Nothofagaceae affinity are present from the Paleocene in Patagonia and Antarctica (Iglesias *et al.*, 2007). After the opening of the Drake Passage in the Upper Eocene and Oligocene, they are more frequent in the Patagonian fossil record but always associated to outcrops in the Andean region (Dusén, 1907; Romero and Dibern, 1985; Romero, 1986). The new fossils establish a parautochthonous character for the record of the Nothofagaceae trees in eastern Patagonia.

7.4.3 The fossil wood record

Systematic paleontology

Family ARAUCARIACEAE

Araucaria de Jussieu, 1789

Type species: *Araucaria araucana* (Molina) K. Koch, 1873

Araucaria marensii Cantrill and Poole, 2005

Fig. 7.4a–l

Holotype: DJ 1057.53.

Type locality: Seymour (Marambio) Island (Antarctica).

Type formation: La Meseta Formation (late Early Eocene to latest Eocene).

Material studied: MPM-PB-4388.

Locality: Punta Sur, Santa Cruz Province, Argentina.

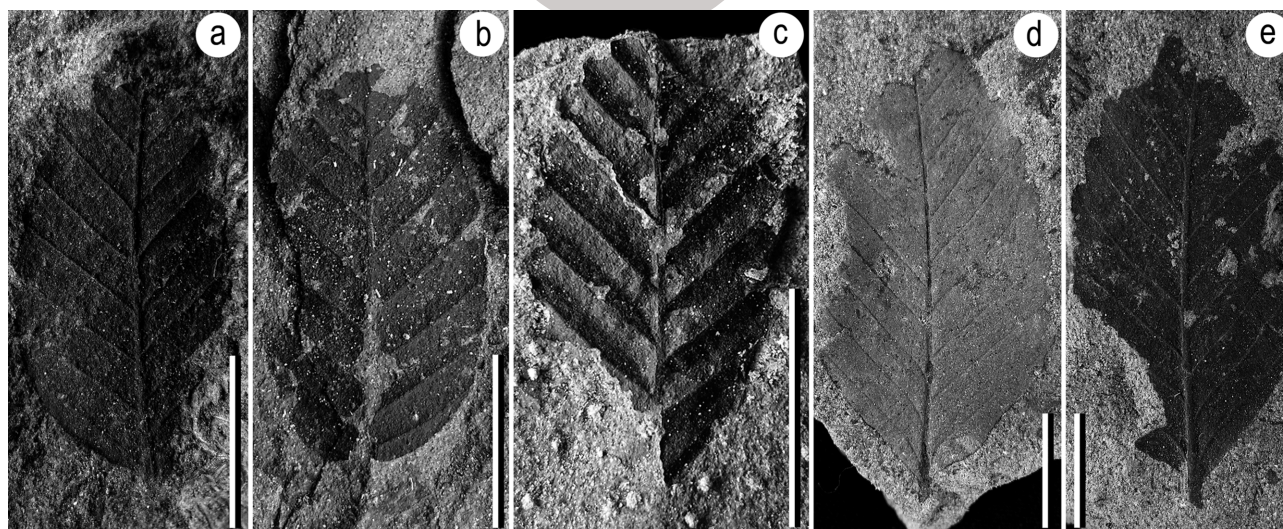


Fig. 7.3. Three leaf types of Nothofagaceae. a and b, Leaf type 1 (a = MPM-PB 4928, b = MPM-PB 4929); note rounded base, eight pairs of secondary veins, and percurrent tertiary veins with tertiary angles decreasing exmedially from the axis of symmetry. c, Leaf type 2 (MPM-PB 4930); note small size, plicate blade surface, and uniform angles in tertiary veins. d and e, Leaf type 3, part and counterpart (MPM-PB 4931); note asymmetric cuneate base, and nine or more secondary veins. Scale bars = 1 cm.

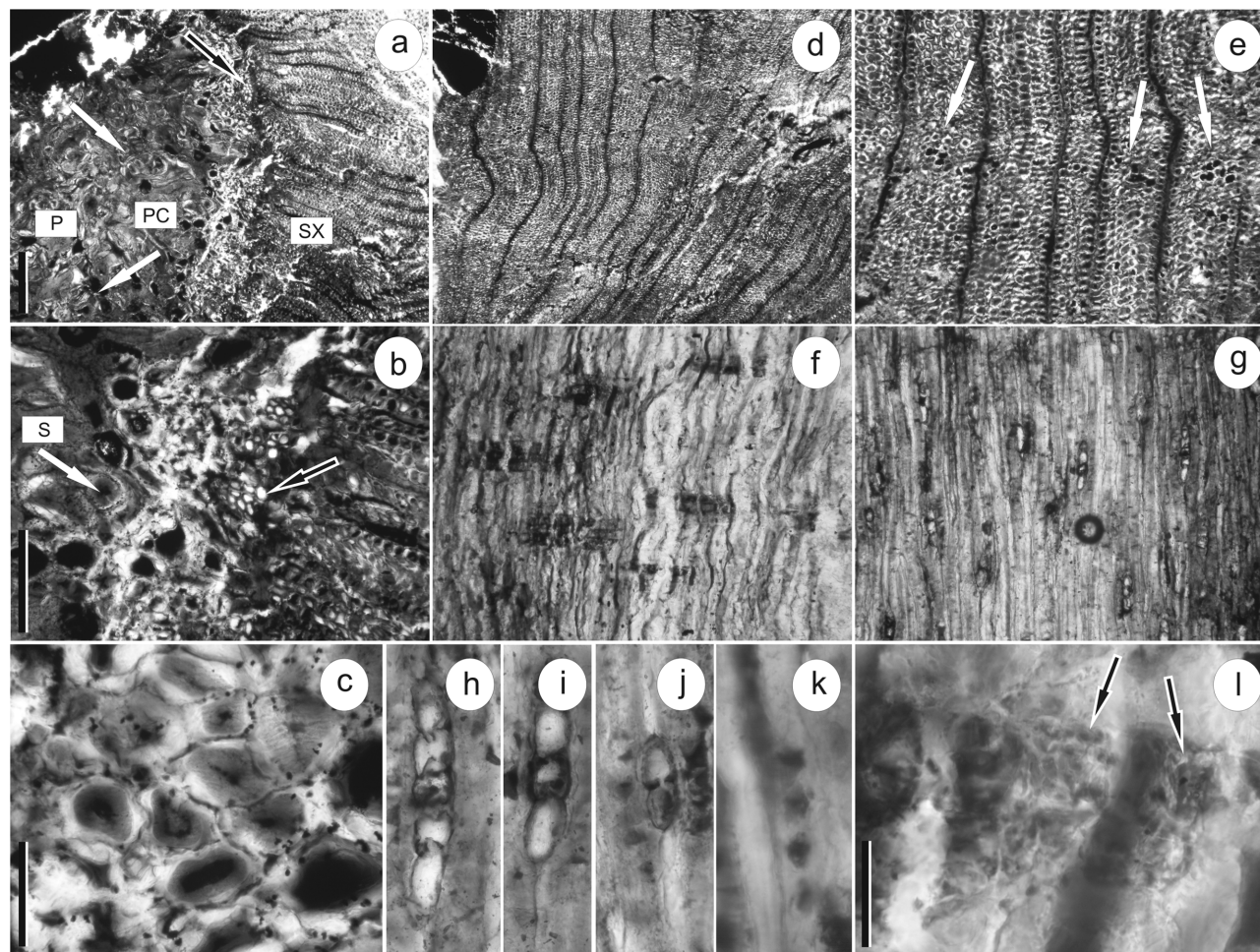


Fig. 7.4. *Araucaria marenzii*. a, TS in general view, showing heterogeneous pith (P), sclereids in cluster (white arrows), parenchyma cells (PC), primary xylem (black arrow) and secondary xylem (SX). b, TS, details of sclereid cell (S, white arrow), tracheids in radial files of the primary xylem (black arrow). c, TS, details of thick-walled sclereid from pith. d, TS in general view, showing growth rings slightly demarcated and the gradual transition from earlywood to latewood. e, TS, showing axial parenchyma (white arrows). f, RLS in general view, illustrating the distribution of pitting and homogeneous rays. g, TLS in general view, showing the uniseriate rays distribution. h, TLS showing uniseriate ray composed of five cells. i, TLS showing uniseriate ray composed of three cells. j, TLS showing uniseriate ray composed of two cells. k, TLS showing the tracheid radial walls with uniseriate bordered pitting. l, RLS, cross-field regions with three to seven crowded araucarioid pits (black arrows). Scale bars: a, d = 300 µm; b, e-g = 200 µm; c, h-j = 50 µm; k, l = 30 µm.

Formation: Santa Cruz Formation, Estancia La Costa Member.

Age: late Early Miocene.

Description: this specimen is a single piece of gymnosperm twig wood. Transverse section: the preserved twig is eccentric (54.23 mm × 36.61 mm in diameter) and 8 cm in length. Pith, primary xylem, and secondary xylem were preserved in this specimen. The heterogeneous pith is sub-circular with a diameter of 4.89 mm × 4.27 mm, composed of parenchyma and sclerenchyma tissues. Parenchyma consists of thin-walled individual cells ranging from 59–108 µm in diameter (Fig. 7.4a). Sclereid clusters range from 274 to 470 µm in diameter with thick walls and are hexagonal in

cross-section (Fig. 7.4a–c). In transverse section, the primary xylem is dispersed in wedge-shaped bundles at the periphery of the pith, and is composed of endarch protoxylem and centrifugal metaxylem, with tracheids in radial files showing a gradual transition from primary xylem to first-formed secondary xylem (Fig. 7.4a, b). The cells of the primary tracheids are thin-walled and range from 15 to 28 µm in diameter (Fig. 7.4b). Secondary xylem is centrifugal and radially arranged (Fig. 7.4a,d,e). Growth rings are characterized by distinct ring boundaries; each ring has a gradual transition from earlywood to latewood, and the latewood has a few layers of thick-walled, radially narrower tracheids.

Tracheids are quadrate to rectangular in cross-section. In earlywood, the mean tangential diameter of tracheids is 29 (23–38) μm and the mean radial diameter is 30 (23–35) μm . In latewood, the mean tangential diameter of tracheids is 22 (15–28) μm and the mean radial diameter is 19 (13–30) μm . Tracheids arranged in regular radial rows are separated by rays (Fig. 7.4d, e). The rays are separated from each other by 1–11 rows of tracheids; with an average of 5 rows. The mean number of rays per linear millimeter is 7 (4–9 per linear mm) (Fig. 7.4d, e). Axial parenchyma rarely observed (Fig. 7.4e).

Radial longitudinal section: the radial system is homogeneous, comprising procumbent parenchyma cells (Fig. 7.4f). Radial walls have uniseriate-bordered pits (Fig. 7.4k), occasionally biseriate. The bordered pits are circular and have a separate arrangement. Where biseriate, pits are alternate. Cross-field regions with 3–7, usually crowded araucarioid pits (Fig. 7.4l).

Tangential longitudinal section: rays are uniseriate, short and squat, ranging from one to seven cells in height (Fig. 7.4h–j). Rays are 21 (15–30) μm wide by 79 (30–135) μm high.

Comments The material studied here is closely related to *Araucaria marensii* by the presence of pith heterogeneous with sclerenchyma and parenchyma, wood pycnoxylic with uniseriate or alternate biseriate pits, cross-field pitting araucarioid with four to six pits per cross-field, and rays short and squat (one to ten cells tall). Cantrill and Poole (2005) described this species at Seymour (Marambio) Island, Antarctica, from the late Early Eocene to latest Eocene La Meseta Formation. The holotype (DJ 1057.53) is a preserved trunk 28.5 cm long by 15.2 cm in diameter with its outer surface covered by a layer of bark. The specimen described here (MPM-PB 4388) possessed well-preserved features of the primary xylem.

Family LAURACEAE

Laurinoxylon Felix, 1883 *emend* Dupéron, Dupéron-Laudoueneix, Sakala and De Franceschi 2008

Type species: *Laurinoxylon diluviale* (Unger) Felix, 1883 *emend* Dupéron, Dupéron-Laudoueneix, Sakala and De Franceschi, 2008

Holotype: MNHN No. 8652 to 8655.

Type locality: Jáchymov Mine, Bohemia.

Type formation: unknown? (Oligocene).

Synonyms

Ulminium diluviale Unger, 1842.

Betulinium diluviale (Unger) Felix, 1882.

Perseoxylon diluviale (Unger) Felix, 1887.

Betuloxylon diluviale (Unger) Lakowitz, 1890.

Laurinium diluviale (Unger) Edwards, 1931.

Laurinoxylon atlanticum (Romero)

Dupéron-Laudoueneix and Dupéron, 2005

Fig. 7.5a–l

Holotype: LPPB 7812 a-m; pm LPPB 774–797.

Type locality: Bahía Solano, Chubut, Argentina.

Type formation: unknown (Eocene).

Synonyms

Ulminium atlanticum Romero, 1970

Material studied: MPM-PB 4384–4386, and MPM-PB 4393.

Locality: Punta Sur, Santa Cruz Province, Argentina.

Formation: Santa Cruz Formation, Estancia La Costa Member.

Age: late Early Miocene.

Affinity: Angiospermae, Laurales, Lauraceae, more closely with *Persea* Mill, and less closely with *Beilschmiedia* Ness, *Nectandra* Rottb. and *Ocotea* Aubl.

Description: indistinct growth rings (Fig. 7.5a). Diffuse porous. Vessels frequently solitary (47%), rarely in radial multiples of two to three elements (6%), some in radial multiples of four to five elements (4% and 2% respectively), and rarely in clusters (Fig. 7.5a, b, f–h). The vessels are circular in outline and are thick-walled (Fig. 7.5f–h). The mean vessel tangential diameter is 62 (25–115) μm and mean vessel radial diameter is 57 (20–110) μm . Mean vessel element length is 155 (60–290) μm . Many vessels have tyloses (Fig. 7.5a, b, d, f, g). The mean vessel density is 21 (17–18)/ mm^2 . Perforation plates are simple (Fig. 7.5i), with oblique or straight end walls (Fig. 7.5c–e). Intervessel pits are bordered, alternate and polygonal with a mean diameter of 1.70 (1.34–2.31) μm (Fig. 7.5j). The axial parenchyma is scanty paratracheal (Fig. 7.5a, b). The rays are multiseriate, two to three cells wide (73% and 7% respectively), or uniseriate (20%) (Fig. 7.5c). The mean number of rays per linear millimeter is 16 (12–22 per linear mm). Rays are heterocellular, body composed of procumbent cells, with one row of upright cells (Fig. 7.5d, e). Mean ray width is 22 (13–30) μm for multiseriate rays and 19 (15–25) μm for uniseriate rays. Mean ray height is 265 (85–510) μm for multiseriate rays and 125 (70–200) μm for uniseriate rays. Vessel-ray pits, poorly preserved, with reduced borders, similar to intervessel pits in size and shape, with a mean diameter of 2.37 (3.17–1.84) μm (Fig. 7.5k). Some rays appear to contain idioblastic secretory cells (“oil cells”), most common in the ray margins (Fig. 7.5e,l). Fibers are non-septate, quadrangular to rectangular in outline, and have a mean diameter of 26 (20–36) μm . They are thick-walled, with a mean wall thickness of 8 (6–10) μm . Pits were not observed.

Comments The combination of solitary vessels, multiple radial vessels, simple perforation plates, alternate intervessel pits, vessel-ray pits similar to intervessel pits in size and

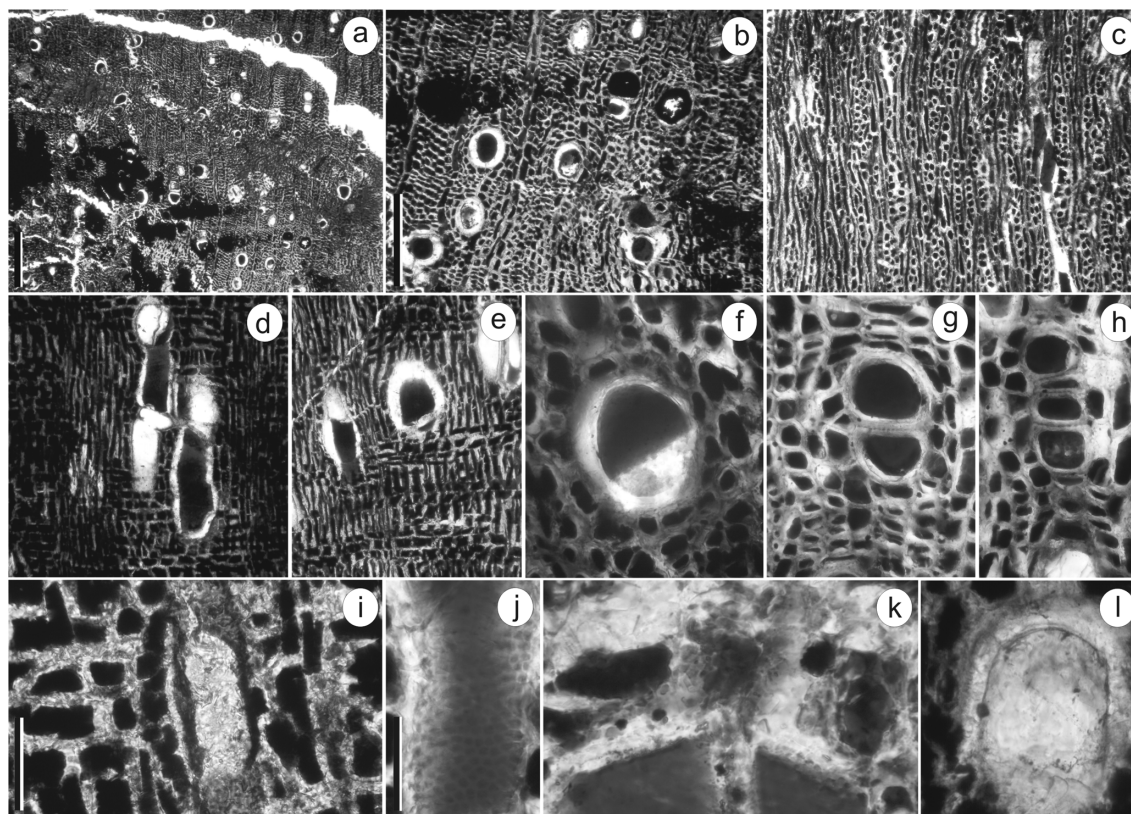


Fig. 7.5. *Laurinoxylon atlanticum*. a, TS, general view. b, TS, showing solitary and radial multiple vessels. c, TLS, detail of multiseriate and uniseriate rays. d, RLS, detail of heterocellular rays and vessel elements with oblique end walls and simple perforation plate. e, RLS, details of vessel element, heterocellular rays and idioblasts in ray margins. f, TS, detail showing circular outline and thick-walled vessels. g, TS, detail of radial multiple of two elements. h, TS, detail of radial multiple of four elements. i, TLS, showing a simple perforation plate. j, TLS, showing intervessel pits pattern. k, RLS, vessel-ray parenchyma pits with reduced borders. l, RLS, detail showing idioblastic secretory cells (“oil cells”). Scale bars: a = 300 μ m; b–e = 200 μ m; f–i, l = 50 μ m; j–k = 30 μ m.

shape, and idioblastic secretory cells (probable “oil cells”) assigned this fossil to *Laurinoxylon* which is related to the Lauraceae family (Dupéron-Laudoueneix and Dupéron, 2005; Dupéron *et al.*, 2008).

Family NOTHOFAGACEAE

Nothofagoxylon Gothan, 1908 *emend* Poole, Hunt and Cantrill, 2001

Type species: *Nothofagoxylon scalariforme* Gothan, 1908 *emend* Poole, 2002.

Lectotype: Specimen no. 14 (S004067).

Syntypes: Specimen no. 13 (S004067) and no. 18 (S004068).

Type locality: Marambio (Seymour) Island, Antarctica.

Other materials and synonyms: see Poole (2002) and Pujana (2009b).

Nothofagoxylon triseriatum

Torres and Lemoigne, 1988 *emend* Poole, 2002

Fig. 7.6a–e

Holotype: A-PF-51.

Paratype: A-PF-53.

Type locality: Rey Jorge Island, Antarctica.

Type formation: Arctowski Cove Formation (Middle Eocene).

Other materials: MPM-PB 1966 and 1967 (Pujana, 2009b).

Synonyms

Nothofagoxylon paleoglauca Torres and Lemoigne (1988)

Material studied: MPM-PB 4392.

Locality: Punta Sur, Santa Cruz Province, Argentina.

Formation: Santa Cruz Formation, Estancia La Costa Member.

Age: late Early Miocene.

Affinity: Angiospermae, Fagales, Nothofagaceae, *Nothofagus* Blume.

Description: Growth rings distinct, marked by a reduction of vessel radial diameter of the last latewood fibers (Fig. 7.6a). Semi-ring porous to diffuse. Vessels roughly circular to slightly oval in transverse section, solitary, in radial files up to six vessels and in clusters (Fig. 7.6a).

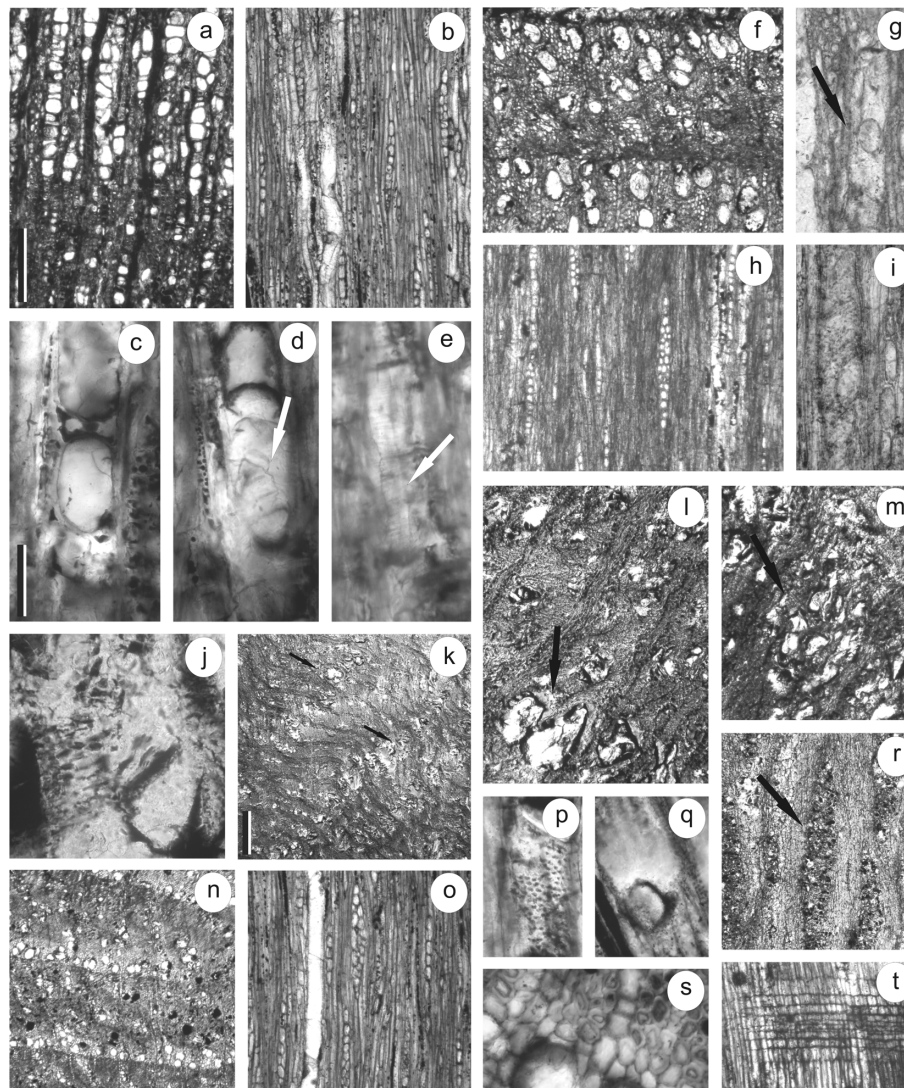


Fig. 7.6. *Nothofagoxylon triseriatum* (a–e): a, TS, showing growth ring, solitary vessels, in radial files up to six vessels and in clusters. b, TLS, general view shows uniseriate and biseriate rays. c, RLS, detail of a simple perforation plate. d, RLS, showing a scalariform perforation plate (white arrow). e, TLS, showing short vessel elements and intervessel pits (white arrow). *Myrceugenia chubutense* (f–i): f, TS, showing growth ring and vessel elements. g, TLS, showing a simple perforation plate (black arrow). h, TLS, showing uniseriate and triseriate rays. i, TLS, showing vessels elements with intervessel pits and simple perforation plate. *Doroteoxylon vicenti-perezii* (j–m, r): j–r) TLS, detail showing intervessel pits. k, TS, general view, of growth rings and large solitary vessels (black arrows). l, TS, detail of large solitary vessels (black arrows) in the earlywood. m, TS, detail of small vessels in clusters (black arrow) in the latewood. r, TLS, detail showing multiseriate rays. *Eucryphiaceoxylon eucryphioides* (n–q, s, t): n, TS, general view showing growth ring and vessel mainly solitary. o, TLS, general view showing ray types. p, TLS, detail showing intervessel pitting. q, RLS, detail of simple perforation plate. s, TS, detail showing vessel elements and fibers. t, RLS, detail showing heterocellular rays. Scale bars: k, n = 300 μm ; a–b, f, h, l, m, o, r, t = 200 μm ; c–e, g, i, j, p–q, s = 50 μm .

The mean tangential vessel diameter is 41 (25–55) μm and mean radial vessel diameter is 42 (25–70) μm . Mean vessel element length is 99 (50–205) μm . Mean vessel density is 58 (47–72)/ mm^2 . Tyloses are present in many vessels. Perforation plates are simple and horizontal (Fig. 7.6c), rarely scalariform with few bars (Fig. 7.6d), and oblique perforation plates are present in the latewood vessels. Intervessel pits are circular to polygonal with an alternate to opposite arrangement with a mean diameter of 16 (11–19) μm (Fig. 7.6e). Axial parenchyma is mainly apotracheal, rare, and diffuse (Fig. 7.6a). Rays are triseriate, biseriate, and uniseriate (Fig. 7.6b), heterocellular, and composed of procumbent body cells with one or two rows of square to upright marginal cells. Mean ray width is 24 (15–35) μm and mean ray height is 243 (145–400) μm . The mean number of rays per linear millimeter is 11 (6–17 per linear

mm). Fibers form a ground mass and are quadrangular or roughly circular in cross-section. They are non-septate and thick-walled, with a mean diameter of 17 (10–25) μm . Fiber pitting was not observed.

Comments The presence of predominantly triseriate and not vertically fused rays, simple occasionally scalariform perforation plates, axial parenchyma diffuse and opposite, alternate and scalariform intervessel pits justify assignment to *Nothofagoxylon triseriatum* from an Antarctic Eocene flora. *Nothofagoxylon palaeoglaucum*, which has been found in Rey Jorge Island, Antarctica, in the Arctowski Cove Formation (Middle Eocene), (Torres and Lemoigne, 1988) has been synonymized with *N. triseriatum* based upon the fact that the only major distinguishing features between these two species are the presence of septate fibers and

helical thickenings in the vessels, as well as differences in the predominance of biseriate rays. This synonymization is supported by the hierarchical cluster analysis performed by Poole (2002).

Family MYRTACEAE

Myrceugenia O. Berg, 1855

Type species: *Myrceugenia myrtoides* O. Berg, 1857.

Holotype: BAPb ex CIRGEO PALEOB. No. 139, 140, 141-PB No. 408.

Type locality: Puesto Álvarez, Chubut Province, Argentina.

Type formation: Salamanca Formation, Bustamante Member (Paleocene).

Myrceugenia chubutense Ragonese, 1980

Fig. 7.6f–i

Material studied: MPM-PB 4387.

Locality: Punta Sur, Santa Cruz Province, Argentina.

Formation: Santa Cruz Formation, Estancia La Costa Member.

Age: late Early Miocene.

Affinity: Angiospermae, Myrtales, Myrtaceae, *Myrceugenia* O. Berg.

Description: this specimen is based on one stem or trunk piece of wood of unknown diameter. Growth rings are demarcated by reduction of the radial diameter of the last two or four rows of latewood fibers (Fig. 7.6f). Diffuse porous with a tendency to semi-ring-porosity. Vessels are mainly solitary (70%), rarely in radial pairs (18%) and in tangential pairs (12%). Vessels are radially elliptic to circular in cross-section (Fig. 7.6f). Vessels are thin-walled. Mean tangential vessel diameter is 53 (30–80) μm and mean radial vessel diameter is 84 (50–120) μm . Mean vessel element length is 239 (160–330) μm with oblique or straight end walls (Fig. 7.6i). Some vessels have tyloses. Vessels are numerous, with a mean vessel density is 62 (57–67)/ mm^2 . Perforation plates are exclusively simple (Fig. 7.6g). Intervessel pits are circular to horizontally elliptic and have an alternate arrangement. Ray-vessel pits appear to be small and circular. Axial parenchyma is diffuse and diffuse-in-aggregate. Rays are heterocellular composed of procumbent body cells with one to two upright marginal cells. Rays are short, with a mean height of 301 (110–480) μm , and are 12 (4–21) cells high. Mean ray width is 31 (13–53) μm . The mean number of rays per linear millimeter is 9 (6–11 per linear mm). Rays are mainly biseriate with uniseriate portions (57%), with some uniseriate (22%) and triseriate (23%) rays also present (Fig. 7.6h). The cells in the biseriate portions are smaller than those in the uniseriate portions. Fibers are non-septate and circular in outline, and fiber pitting was not observed. Mean fiber diameter is 20 (10–38) μm and fiber walls have a mean thickness of 4 (4–11) μm .

Comments Five fossil species of Myrtaceae are known from southern Argentina, Chile, and Antarctica: *Myrceugenellites maytenoides* (Nishida *et al.*, 1988); *Myrceugenellites antarcticum* (Poole *et al.*, 2001; Pujana, 2009a); *Myrceugenellites oligocenicum* (Pujana, 2009a); *Myrceugenelloxylon pseudoapiculatum* (Nishida, 1984a, b) and *Myrceugenia chubutense* (Ragonese, 1980). The anatomy of this new fossil wood allows the material to be assigned to the Patagonian species *Myrceugenia chubutense*. This species is recognized by having almost exclusively solitary vessels that also occur in tangential and radial pairs, exclusively simple perforation plates, numerous and narrow vessels, rays mainly biseriate, and axial parenchyma diffuse and diffuse-in-aggregate.

Family CUNONIACEAE

Eucryphiaceoxylon Poole, Mennega and Cantril, 2003

Type species: *Eucryphiaceoxylon eucryphioides* (Poole *et al.*, 2001) *comb. nov.* Poole, Mennega and Cantrill, 2003.

Basionym: *Weinmannioxylon eucryphioides* Poole, Hunt and Cantrill, 2001.

Holotype: P.3023.11.

Type locality: Fildes, Peninsula, King George (25 de Mayo) Island, Antarctic Peninsula.

Type formation: Middle unit of the Fildes Formation (Middle Eocene).

Additional material: DJ.1057.62, DJ.1057.57, DJ.1057.63A, DJ.1055.32 (group 1); DJ.1054.1, DJ.1056.56, DJ.1056.14, DJ.1056.22 (group 2); DJ.1057.38 (group 3).

Eucryphiaceoxylon eucryphioides

(Poole *et al.*, 2001) *comb. nov.*

Poole, Mennega and Cantrill, 2003

Fig. 7.6n–q, s, t

Material studied: MPM-PB 4391.

Locality: Punta Sur, Santa Cruz Province, Argentina.

Formation: Santa Cruz Formation, Estancia La Costa Member.

Age: late Early Miocene.

Affinity: Angiospermae, Rosales, Cunoniaceae, *Eucryphia* Cav.

Description: Growth rings are distinct and demarcated by a narrow zone of radially flattened fibers and a decrease in vessel diameter and abundance (Fig. 7.6n). Diffuse porous or occasionally semi-ring-porous. Vessels are roughly circular to radially elliptical in cross-section. Vessels are mainly solitary or paired, but also occur in radial group of three elements (Fig. 7.6n). Mean tangential vessel diameter is 49 (25–70) μm and mean radial vessel diameter is 44 (20–65) μm . Mean vessel element length is 230 (130–385) μm with oblique or straight end walls. Some vessels have tyloses. Mean vessel density is 45 (35–55)/ mm^2 . Perforation plates are simple (Fig. 7.6q) or rarely scalariform with five to

nine fine bars, which are sometimes branched. Intervessel pits are circular and opposite (Fig. 7.6p) to transitional and scalariform. Axial parenchyma is diffuse and diffuse-aggregated (Fig. 7.6n). Rays are heterocellular composed of procumbent body cells with one to three rows of square and upright marginal cells (Fig. 7.6t). Mean ray height is 269 (80–385) μm and mean ray width is 36 (15–60) μm . The mean number of rays per linear millimeter is 7 (6–9 per linear mm). Rays are mainly uniseriate and biseriate, or may also be triseriate (Fig. 7.6o). Fibers are non-septate and circular in outline, and fiber pitting was not observed. Fibers are thick walled and have a mean diameter of 13 (10–15) μm (Fig. 7.6s).

Comments: The combination of characters – predominantly uniseriate rays; scalariform and simple perforation plates; circular, opposite, transitional and scalariform intervessel pitting; and transitional to scalariform vessel ray pitting – is characteristic of *Eucryphia* Cav. of the Cunoniaceae (or Eucryphiaceae). The King George (25 de Mayo) Island specimens previously assigned to *Weinmannioxylon eucryphioides* by Poole *et al.* (2001) were transferred to *Eucryphia-ceoxylon eucryphioides* by Poole *et al.* (2003). The reason was that these specimens differ from other members of *Weinmannioxylon* described from South America and Antarctica by their ray characteristics and the presence of entirely scalariform perforation plates (Poole *et al.*, 2000). The specimen studied here shows the greatest anatomical similarity with Group 2, especially with DJ. 1054.1 described by Poole *et al.* (2003). These divisions are predominantly on the basis of ray width and difference in relative abundance of scalariform vs. simple perforation plates.

Family **FABACEAE**
Subfamily **FABOIDEAE**
Xilotype 3 Pujana, 2008

Type species: Xilotype 3 Pujana, 2008

Holotype: MPM-PB 2112.

Paratypes: MPM-PB 2110, 2115, 2117, 2120, and 2122.

Other specimen: MPM-PB 2102.

Type locality: Cerro Calafate, Santa Cruz Province, Argentina.

Type formation: upper section of the Río Leona Formation (Oligocene).

aff. Xilotype 3 Pujana, 2008
Fig. 7.7a–l

Material studied: MP-MPB 4390.

Locality: Punta Sur, Santa Cruz Province, Argentina.

Formation: Santa Cruz Formation, Estancia La Costa Member.

Age: late Early Miocene.

Affinity: Angiospermae, Fabales, Fabaceae, Faboidea, *Sophora* section *Edwardsia*.

Description: growth rings distinct. Diffuse porous to semi-ring-porous (Fig. 7.7a, b). Vessels are mainly solitary (50%), in radial and tangential series of two to three elements (13%), or in clusters (17%) (Fig. 7.7a–c). Tangential bands of vessels, and diagonal and irregular dendritic patterning of vessels are also present (Fig. 7.7a–c). Vessels are circular to oval in cross-section. Mean tangential vessel diameter is 58 (30–90) μm and mean radial vessel diameter is 57 (30–90) μm . Mean vessel element length is 214 (160–285) μm . Mean vessel density is 137 (114–181)/ mm^2 . Perforation plates are mainly simple (Fig. 7.7d, g, l) or rarely reticulate (Fig. 7.7f). Intervessel pits are bordered round to irregular in outline with alternate arrangement with a mean diameter of 6 (3–9) μm (Fig. 7.7i, j). Vascular tracheids are present around the vessels, irregular in shape. The mean tracheid length is 112 (89–141) μm . The vascular tracheids have bordered pits with a mean diameter of 7 (4–10) μm (Fig. 7.7l). Axial parenchyma is vasicentric scarce and apotracheal diffuse (Fig. 7.7a–c). Vessel-ray parenchyma pits are similar in size and shape to intervessel pits (Fig. 7.7g). Helicoidal thickenings present throughout the length of the vessel elements (Fig. 7.7k). Rays are homocellular composed of procumbent cells (Fig. 7.7d). The rays are uniseriate (Fig. 7.7e), biseriate (Fig. 7.7e), and multiseriate, four to six cells wide (Fig. 7.7e). The mean height of uniseriate ray is 133 (55–165) μm and 5 (3–7) cells high, and the mean width of uniseriate rays is 22 (20–25) μm . The mean height of biseriate ray is 205 (160–260) μm and 8 (6–11) cells high, and the mean width of biseriate rays is 39 (37–40) μm . The mean height of multiseriate rays is 474 (195–725) μm and 18 (9–28) cells high, and the mean width of multiseriate rays is 71 (55–90) μm and 5 (4–6) cells wide. Mean number of rays per linear millimeter is 8 (6–11 per linear mm). Fibers are non-septate, and hexagonal in cross-section (Fig. 7.7h). They are thick-to very thick-walled, with a mean thickness of 2 (2.5–5) μm and a mean diameter of 13 (9–20) μm .

Comments The following combination of characters of vessels in tangential bands to irregular dendritic patterns, narrow vessels, simple perforation plates, presence of vascular tracheids, uni-biseriate rays and presence of multiseriate rays, and vasicentric axial parenchyma, also occur in Pujana's *Xilotype 3* Fabaceae-Faboideae specimen (Pujana, 2008 and R. Pujana, personal communication, 2010). This was represented by material collected from the Cerro Calafate locality, Santa Cruz Province, Argentina, from the Oligocene Río Leona Formation. However, *Xilotype 3* differs from the specimen described here by the presence of diffuse axial apotracheal parenchyma, occasionally reticulate perforation plates, helical thickenings in vessel elements and bordered, alternated, and round to irregular in outline intervessel pits.

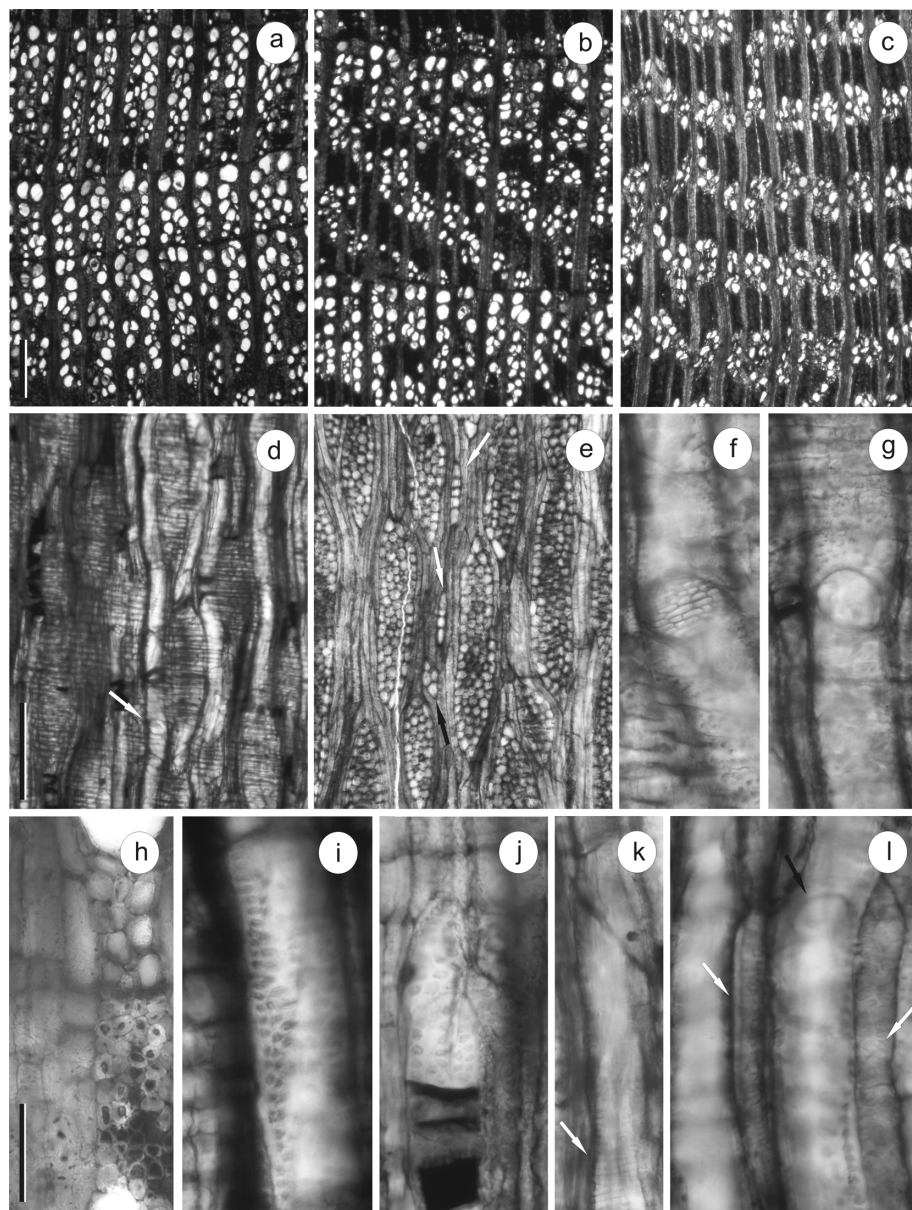


Fig. 7.7. a–l, aff. *Xilotype* 3. a, TS, showing growth ring boundary and vessels in irregular dendritic pattern. b, TS, showing vessels in diagonal patterning. c, TS, showing tangential bands patterning of vessels. d, RLS, showing homocellular rays and simple perforation plate (white arrow). e, TLS, detail of uniseriate (white arrows), biseriate (black arrow) and multiseriate rays. f, RLS, showing detail of reticulate perforation plate. g, RLS, detail of simple perforation plate and vessel-ray parenchyma pitting. h, TS, detail of axial parenchyma cells, ray cells, and fibers. i, j, RLS, showing bordered, round to irregular in outline, intervessel pits with alternate arrangement. k, RLS, showing vessel elements with helicoidal thickenings (white arrow). l, RLS, showing vascular tracheids (white arrows) and simple perforation plate (black arrow). Scale bars: a–c = 300 μ m; d, e = 200 μ m; f–l = 50 μ m.

Family **PROTEACEAE?**

Doroteoxylon Nishida, Nishida and Ohsawa, 1989

Type species: *Doroteoxylon vicenti-perezii* Nishida, Nishida and Ohsawa, 1989

Holotype: TK No. 797848.

Type locality: Cerro Dorotea, Última Esperanza, Chile.

Type formation: Mina Chilena Formation (Late Oligocene–Early Miocene).

Other materials: MP-MPB 1955 (Pujana, 2009a).

Doroteoxylon vicenti-perezii Nishida,
Nishida and Ohsawa, 1989

Fig. 7.6j–m, r

Material studied: MPM-PB 4381–4384.

Locality: Punta Sur, Santa Cruz Province, Argentina.

Formation: Santa Cruz Formation, Estancia La Costa Member.

Age: late Early Miocene.

Affinity: Angiospermae, Fabales, Fabaceae, Caesalpinoideae.

Description: this description is based upon three pieces of stem or trunk wood of unknown diameter. The material is not well preserved. Growth rings are demarcated by reduction of the radial diameter of the last two to four rows of latewood fibers, reduction in vessel size, and the presence of vessel clusters in the latewood (Fig. 7.6m). Ring porous. Vessels occur in two distinct sizes. Larger vessels

are solitary or in tangential pairs in the earlywood (Fig. 7.6k, l), and have a mean tangential diameter of 140 (50–245) μm . Narrower vessels are arranged in clusters, and have a mean tangential diameter of 56 (40–100) μm . Mean vessel element length is 225 (59–323) μm with oblique or straight end walls. Mean vessel density is 12 (9–16)/ mm^2 . Vessel elements are short. Narrow vessels have helical thickenings, and large vessels commonly have abundant tyloses. Perforation plates are exclusively simple. Intervessel pits are hexagonal and have an alternate arrangement with a mean diameter of 10 (9–13) μm . Ray-vessel pits are similar to the intervessel pits. Axial parenchyma is vasicentric. Rays are heterocellular composed of procumbent cells forming the body with two to four upright marginal cells. Rays are moderately long, and their mean height is 771 (392–1078) μm . Mean ray width is 131 (88–196) μm . Rays are multiseriate, 5 to 13 cells wide (Fig. 7.6r). Fibers are non-septate, and circular in outline.

Comments The holotype of *Doroteoxylon vicenti-perezii* comes from the Cerro Dorotea, Chilean Patagonia (Nishida *et al.*, 1989), from sediments of the Mina Chilena Formation (late Oligocene–early Miocene). Terada *et al.* (2006) described additional specimens from the same locality. These authors consider that the most probable affinity is to the Proteaceae, because of the presence of multiseriate rays and the tendency to form tangential bands of earlywood vessels. Pujana (2009a) describes an exceptionally well-preserved new specimen from Argentina that gives more anatomical details. The storied and pitted fibers, extent of vessel density, and vessel element length values suggest to Pujana (2009a) that this fossil species shares greater affinity with members of the subfamily Caesalpinoideae, in particular with *Gleditsia* L. and *Robinia* L., both genera native to the Northern Hemisphere.

7.4.4 Physiognomic and paleoclimatic inferences obtained from the dicotyledonous wood structure

The modern climate at the Atlantic coast of Santa Cruz Province between the Coyle and Gallegos rivers is characterized as a cold semi-desert area, with windy and cold winters, and dry and warm summers. Climatic values for Río Gallegos locality are: mean annual temperature (MAT) 7.6 °C, mean annual range in temperature (MART) 12.5 °C, cold month mean temperature (CMMT) 0.9 °C, annual precipitation (MAP) 242 mm, and length of the dry season (DRY) c. 3 months during winter and spring. The modern dominant vegetation is medium height (20–80 cm), low density (1 plant every 6 m^2), in an arid shrubby-herbaceous steppe. An intensive W–E gradient in the floristic composition is a consequence of the rain-shadow effects of the modern Cordillera interacting with the Antarctic

anticyclone weather system. Grasses replace the low bushes as precipitation decreases (León *et al.*, 1998; Coronato *et al.*, 2008). However, in the Mid-Miocene Climatic Optimum, between 17 and 15 Ma (Zachos *et al.*, 2001), climatic conditions were very different from those of today. The added effect of the Andean rain shadow on changing climate during the Miocene (Blisniuk *et al.*, 2005), discussed by Kay *et al.* in Chapter 17, is seen in the changing taxonomical composition of the paleoflora studied here.

Twelve anatomical characteristics were used to estimate climate variables (Tables 7.2, 7.3). The MAT estimates for PS locality were 19.31 ± 1.7 °C and 9.35 ± 1.7 °C from equations (12) and (15) respectively (Table 7.3). CMMT and MART values were 9.8 ± 2.6 °C and 4.26 ± 2.4 °C respectively (Table 7.3). However, CMMT and MART estimates are considered less precise than those for other climate variables. The DRY value was 6.8 ± 1.4 months, and MAP was estimated at 869 ± 940 mm. The MAP value obtained from the multivariable anatomical analyses must be considered as potentially less accurate than the MAT estimate (Wiemann *et al.*, 1998). These data will be discussed further below.

The Vulnerability Index (V) and Mesomorphy Ratio (M) values range from 0.43 to 8.17 and from 70 to 1837 respectively. *Nothofagoxylon triseriatum*, *Eucryphiaceoxylon eucryphioides*, *Myrceugenia chubutense* and aff. *Xilotype* 3 have V values less than 2.5, and M values less than 1500 (Table 7.4). These values suggest that these woods possess well-developed xeromorphic features. However, *Laurinoxylon atlanticum* and *Doroteoxylon vicenti-perezii* have mesomorphic features (Table 7.4), indicating that these taxa would have lived in more humid areas and/or areas with greater soil humidity.

Vessel diameter is one of the most significant indicators of hydraulic efficiency in angiosperm wood, because of the relationship that exists between conductive capacity and the fourth power of the diameter of the conduit (Zimmermann, 1983). All the fossil specimens from the PS locality have mean tangential vessel diameters less than 100 μm (Table 7.4). In extant woods, values such as these are common in cool temperate or high montane tropical species (Wheeler and Baas, 1991). Based upon these modern ecological patterns, this would indicate that these Miocene fossil woods developed in cool and/or xeric climate (Lindorf, 1994).

High vessel densities (40/ mm^2 or more) are typical of cool temperate to arctic species, tropical high montane species, and xerophytes. High vessel density is seen in 67% of the Miocene woods studied here (Table 7.4). In addition, many of these woods from the PS locality have simple perforation plates, which are considered an adaption to more efficient water transport (Baas, 1976; Carlquist, 1977; Wheeler and Baas, 1993; Lindorf, 1994). *Xilotype* 3 (Pujana, 2008) shows tangential bands of vessels and

Table 7.4. Anatomical wood data used for determinate paleoclimate signals, and to calculate Vulnerability Index and Mesomorphy Ratio

Taxa	Growth rings	Vessel tangential diameter (µm)	Vessels per mm ²	Vessel element length (µm)	Perforation plates	Porosity	Axial parenchyma	Fiber type	Vulnerability Index (V)	Mesomorphy Ratio (M)
<i>Laurinoxylon atlanticum</i>	P	62 (25–115)	21 (17–28)	155 (60–290)	SI	D	Vs	n-sp	2.95	458
<i>Nothofagoxylon triseriatum</i>	P	41 (25–55)	58 (47–72)	99 (50–205)	SI, SC	D	D	n-sp	0.71	70
<i>Myrceugenia chubutense</i>	P	53 (30–80)	62 (57–67)	239 (160–330)	SI	D to S	D to D-DA	n-sp	0.85	287
<i>Eucryphiaceoxylon eucryphioides</i>	P	49 (25–70)	45 (35–55)	230 (130–385)	SI, SC	S to D	D to D-DA	n-sp	1.09	251
<i>Doroteoxylon vicenti-perezii</i>	P	98 (42–172)	12 (9–16)	225 (59–323)	SI	R	Vs	n-sp	8.17	1837
aff. <i>Xilotype 3</i> Pujana, 2008	P	58 (30–90)	135 (114–181)	214 (160–285)	SI	S	Vs	n-sp	0.43	92

Growth rings: P, present. **Perforation plates:** SI, simple perforation plate, SC, scalariform plate. **Porosity:** D, wood diffuse-porous; S, wood semi-ring-porous; R, wood ring-porous. **Axial parenchyma:** D, diffuse; D-DA, diffuse-in-aggregates; Vs, vasicentric scarce. **Fiber type:** n-sp, non-septate. **Vulnerability Index (V)** = mean vessel diameter/number of vessels per mm²; **Mesomorphy Ratio (M)** = (mean vessel diameter/number of vessels per mm²) × vessel element length.

diagonal and irregular dendritic vessel patterns, a feature largely restricted to woods from temperate to subtropical regions (Wheeler and Baas, 1991, 1993). The occurrence of vessels in clusters is more common in subtropical to temperate floras than in tropical floras. More than 50% of the woods from the fossil assemblages studied here have grouped vessels, whether in radial multiples or clusters.

The presence of helical thickenings in narrow vessels in *Doroteoxylon vicenti-perezii* is associated with regions that experience water stress created by drought or freezing. It might diminish the danger of cavitation, aid in refilling of vessels, or increase vessel wall strength (Carlquist, 2001; Wheeler *et al.*, 2007).

The relation between porosity type and the evergreen habit in angiosperm trees has also been used for climatic interpretation (Studhalter, 1955; Boura and De Franceschi, 2007; Wheeler *et al.*, 2007). The presence of semi-ring to ring-porosity, as seen in *Eucryphiaceoxylon eucryphiodes*, *Myrceugenia chubutense*, *Doroteoxylon vicenti-perezii*, and aff. *Xilotype 3*, could be related to existence of semi-arid and arid climatic conditions (Woodcock, 1994; Moglia and Giménez, 1998). Furthermore, these two characteristics (semi-ring porosity and ring porosity) are usually, but not always, associated with temperate climates and/or deciduousness (Chowdhury, 1964; Wheeler and Baas, 1993; Boura and De Franceschi, 2007). Therefore, deciduousness could be correlated to seasonality in precipitation, temperature, or day length (Wheeler and Manchester, 2002; Poole and van Bregen, 2006). The presence of ring-porosity in fossil specimens can be used to infer seasonality of the paleoclimate (Boura and De Franceschi, 2007). Ring-porous wood appears to be more narrowly adapted to strongly seasonal environments where growing conditions are suitable for only part of the year (Baas *et al.*, 2004). All Miocene woods studied here show distinct growth rings (Table 7.4), which indicates growth in a seasonal environment (Wheeler and Baas, 1991).

Seasonality in temperature or in rainfall is also correlated with significant reductions in vessel element length (Baas *et al.*, 1983). The vessel element lengths measured in these Miocene woods are short (99–239 μm ; see Table 7.4), suggesting xeric conditions, at least seasonally (Baas *et al.*, 1983; Lindorf, 1994).

Vasicentric or vascular tracheids are present in aff. *Xilotype 3*. This feature provides additional safety in water transport and is especially common in taxa subject to seasonally arid conditions (Wheeler and Baas, 1991).

Diffuse, diffuse-in-aggregates, or vasicentric scarce axial parenchyma are more common in temperate floras than in the tropical ones. On the other hand, septate fibers and abundant parenchyma are more frequently found in tropical floras and not in temperate ones. Extrapolating this pattern to the PS flora would indicate a seasonal temperate climate,

an inference that is also supported by the presence of growth rings in all of the fossil specimens.

7.5 Discussion

Microremain assemblages show the presence of a variety of components. In the majority of cases these are dominated by phytoliths, but some samples also include microcharcoal, sponge spicules, diatoms, and chrysophycean stomatocysts. The phytolith assemblages are characterized by the presence of articulated grass phytoliths, which are particularly abundant in the PS samples and upper samples from the ELC locality, as well as isolated phytoliths with the presence of graminoid (poooid, festucoid, stipoid, danthonioid, chloridoid, and panicoid), arecoid, nothofagoid, and general dicotyledonous elements.

Microremain assemblages representing this particular type of floristic composition have also been reported in some present-day soils from New Zealand's North Island (Kondo *et al.*, 1994). This comparison is based not only on the coexistence of megathermic and microthermic grasses, but also on the pronounced abundance of arecoid (palm), nothofagoid, and dicotyledonous elements, floristic assemblages absent in present-day South America.

The coexistence of microthermal and megathermic elements is better represented in the PS locality than at ELC. Although the percentage of microthermic grass components (poooid, festucoid, and stipoid) is lower, in most cases, than the percentage of megathermic elements, the occurrence of panicoid and chloridoid elements in association with the arecoid phytoliths suggests warm but somewhat arid climatic conditions. The profusion of whole freshwater sponge spicules and diatoms also suggests the presence of water courses in the local environment of the PS and ELC localities. The PS and CB samples contain the greatest abundance of microcharcoal. The elements that would indicate the presence of freshwater streams—sponge spicules, diatoms, and stomatocysts—are absent at the CB locality. At the CB and ANF localities, danthonioid grass phytoliths dominate the assemblages. The 1975 sample yielded a high abundance of silica microremains with superficial damage and only scarce amounts of aquatic elements, which when considered in conjunction with the sample's granulometric characteristics (see Matheos and Raigemborn, Chapter 4) seems to indicate an aeolian source for the sediments, which may have occurred in a semi-arid temperate climate.

In the basal and middle samples from the ELC locality, high relative abundances of poooid, stipoid, and festucoid linked phytoliths are observed, with an increase in the 1977–1979 samples of the sponge spicules and diatoms, together with the presence of chrysophycean stomatocysts. This type of assemblage suggests humid cold-temperate climatic conditions, with seasonality in water availability.

In this locality's middle levels, an increase of panicoid elements is seen along with a decrease in pooid/festucoid elements, indicating increase in temperature. Also, a pronounced presence of palm and nothofagoid elements is observed in the samples 1977 and 1979 from the ELC locality (Matheos and Raigemborn, Chapter 4, Fig. 4.4). The upper section of the ELC locality has relatively few phytoliths, but those that are present tend to be large, well preserved, and articulated.

The megafossil record found in the PS locality includes several pieces of wood and leaf compressions. Although the fossil woods were transported, the complete leaf preservation containing tips, margins, and petioles, and the articulated grass phytoliths suggest that the fossil plants were living close to the final deposition area, or only transported short distances from the growth site. This is the first macrofossil documentation of a floristically diverse forest with components of Araucariaceae, Lauraceae, Nothofagaceae, Cunoniaceae, Myrtaceae, Fabaceae, and ?Proteaceae, so far from its modern Andean distribution, demonstrating that forests of the *Nothofagidites* Province covered southern Patagonia, as hitherto noted in palynological records (Barreda and Palazzesi 2007; Barreda *et al.*, 2007; Iglesias *et al.*, 2011).

Fossil wood assemblages similar to those described here have also been reported from Late Cretaceous and early Cenozoic context in Antarctica (Poole and Cantrill, 2006 and references therein; Poole *et al.*, 2005). Growth rings and angiosperm anatomical analyses from the Paleocene/Eocene interval in Antarctica have demonstrated the existence of seasonally warm humid rainforests with estimated MAT of 7 to 15 °C, but these data also indicate that conditions deteriorated through the Late Eocene, when cold seasonal climates were emplaced (Francis and Poole, 2002). Paleogene floras from the Antarctic Peninsula are very similar to the extant cool temperate rainforests of the Valdivia region in Chile, where characteristic elements such as Nothofagaceae, Myrtaceae, Cunoniaceae, Lauraceae, Monimiaceae, Cupressaceae, and Podocarpaceae have been described (Poole *et al.*, 2001, 2003).

The Early Miocene macroflora from Bacchus Marsh in Victoria, Australia, is poorly known in general, but leaves of Nothofagus, Myrtaceae, Araucariaceae, and Podocarpaceae dominate fossil assemblages. The same vegetation is still found in the Victoria region today, suggesting that similar climatic conditions prevailed in the Miocene. Similarly the Miocene flora from Latrobe Valley, Australia, contains elements including Araucariaceae, Podocarpaceae, Nothofagaceae, Lauraceae, Cunoniaceae, and Proteaceae (Greenwood, 1994). Also, Pole (1989) found an Early Miocene plant macrofossil assemblages from the Manuherikia Group, Central Otago, New Zealand with Nothofagaceae, Myrtaceae, Casuarinaceae, Fabaceae, and Arecaceae.

Closer to the Andean region from Patagonia, similar vegetation assemblages to the paleoflora present at the PS are recorded from the Oligocene Río Leona Formation (Pujana, 2007, 2008, 2009a, 2009b; Barreda *et al.*, 2009), with fossil woods being assigned to the families Nothofagaceae, Cunoniaceae, Leguminosae, Proteaceae, Anacardiaceae, Myrtaceae, Araucariaceae, and Podocarpaceae. Palynological assemblages indicate an abundance of freshwater algae, rushes, and sedges. Rainforests composed of Nothofagaceae, Podocarpaceae, Araucariaceae, Myrtaceae, Fabaceae, Proteaceae, and Casuarinaceae have also been reconstructed, with other elements including Gunneraceae, Onagraceae, Poaceae, and Asteraceae. Presence of pteridophytes and bryophytes suggest coastal streams or lowland regions with swampy areas (Barreda *et al.*, 2009).

Seasonal *Nothofagus* forests composed of taxa with varying ecological requirements and phytogeographic origins occur in the Middle and Late Miocene on the Pacific coast of central Chile (Hinojosa and Villagrán, 1997, 2005). The Climate Leaf Analysis Multivariate Program (CLAMP) analyses from their studies produced MATs between 15.9 (± 2.4) °C and 21.4 (± 2.1) °C for the Navidad-Goretone and Navidad-Boca Pupuya fossil localities, respectively. Mean annual precipitation (MAP) was estimate at 93.1 cm and the estimates of Miocene mean dry season precipitation (MPD) for two members of the Navidad Formation were 17.2 (± 15.3) and 20.0 (± 15.3) cm.

On the Arauco Peninsula in central Chile, a diverse Miocene has been reconstructed, containing Anacardiaceae, Boraginaceae, Euphorbiaceae, Fagaceae, Lauraceae, Fabaceae, Monimiaceae, Myristicaceae, Myrtaceae, and Proteaceae. These Arauco paleoforests are thought to have possessed a rich flora with mostly dicotyledonous plants, with apparent regression of gymnosperms occurring during the Miocene. Moreover, the occurrence of predominantly tropical angiosperms in fossil assemblages suggests a stronger influence of Amazonian paleofloras on those of the southern Andean coastal range during the Miocene (Schöning and Bandel, 2004). In the present study, Miocene paleoforests located in high latitudes at the Atlantic coast of Patagonia are inferred to be growing in a climate with estimated MATs of 19.31 ± 1.7 °C and 9.35 ± 1.7 °C, with a low thermal amplitude (< 10 °C). This pattern is typically associated with coastal marine climates, such as present-day vegetation communities in central Chile, southeastern Australia, and New Zealand's North Island (Hueck, 1978; San Martín *et al.*, 1984; Donoso Zegers, 1993; Hill, 1994; Kondo *et al.*, 1994; Armesto *et al.*, 1995).

In particular, the Mediterranean area of central Chile is characterized by the presence of mesophite vegetation, with precipitation of 200–1000 mm/year and average temperatures between 15 and 20 °C. The heterogeneous floristic composition of this area is characterized by the presence of

the most austral distributed palm, *Jubaea chilensis* (Molina) Baill., which coexists at the same latitude with xerophytic forests composed of Rosaceae, Lauraceae, Cunoniaceae, Winteraceae, Myrtaceae, and Nothofagaceae (Hueck, 1978; San Martín *et al.*, 1984; Donoso Zegers, 1993; Armesto *et al.*, 1995). *Jubaea chilensis* reaches a southern limit of around 37° S, although palms present at the PS locality indicate that during the late Early Miocene this region was much warmer than today.

The V and M Index values suggest that the climate at the PS locality was characterized by a season with low water availability, and according to the results obtained in this study this is consistent with other palynological inferences (Barreda and Palazzesi, 2010), which suggest that throughout the Early and early Middle Miocene, angiosperms with megathermal affinities persisted. Many of these have been reported from both southern and northern Patagonia. During the Early Miocene, xerophytic taxa were dominant, as Casuarinaceae, Ephedraceae, Chenopodiaceae, Anacardiaceae, and Fabaceae. Members of the Poaceae and Asteraceae were also present. The development of these floras was probably linked with a restricted water supply in open forests or coastal regions (Palazzesi and Barreda, 2007, and references therein).

7.6 Conclusions

Based upon fossil floral assemblages, including fossil wood and leaf compressions, phytoliths, microcharcoal, chrysophycean stomatocysts, sponge spicules, and diatoms, we have obtained the first detailed evidence of the floristic composition and paleoclimatic conditions of the continental sequences of the Santa Cruz Formation that crop out along the Atlantic coast of Patagonia. These bioproxies have enabled us to reconstruct paleovegetation patterns and climate variables at several localities by means of comparative analysis using nearest living relative (NLR) and physiognomy-based methodologies. This latter approach estimates paleoclimatic parameters by assuming that the relationship between wood anatomical characteristics and climatic factors were the same in the past as they are in the present day (Poole and van Bergen, 2006).

The Punta Sur locality yielded the most complete information for the analyzed bioproxies. The plant terrestrial community at PS had a herbaceous component dominated by chloridoid and panicoid grasses, but also contained less common danthonioid, pooid, and festucoid grasses, and an arboreal component that included members of the Araucariaceae, Arecaceae, Nothofagaceae, Myrtaceae, Cunoniaceae, and Fabaceae (Faboideae). A second plant community at PS is characterized by marked fluvial influences, with characteristic elements including members of the Lauraceae and Proteaceae?, and indication of fluvial

processes based upon the presence of microremains including sponge spicules and diatoms. The forests at PS had evergreen and deciduous elements with growth rings in their woods. For this particular late Early Miocene locality, a mean annual temperature (MAT) is variously estimated to have been 19.31 ± 1.7 °C and 9.35 ± 1.7 °C. The V and M Index values, and many of the anatomical characters observed in the fossil woods, are likely to have contributed to hydraulic safety, reflecting dry temperate and temperate-warm climatic conditions. The results based on wood physiognomy methods are provisional, and more data and fieldwork are needed to confirm the inferences proposed here.

Floras similar in composition and anatomical characteristics with the coexistence of micro- and megathermal floristic elements identified at PS are found today in several regions of the Southern Hemisphere including central Chile, southeastern Australian, and New Zealand, three regions with pronounced marine influence on their climates, especially the moderation of seasonal extremes. Floral microremains at Anfiteatro suggest multiple contributing sources for these deposits, with an abundance of allochthonous elements that in some cases show considerable superficial damage.

At the Estancia La Costa locality, the basal and mid-level samples (1976–1979) have similar microremain assemblages to those from the Punta Sur locality, but with some variation in composition, such as a greater abundance of temperate grasses in the basal samples, which give way in mid-level samples to more tropical panicoid grasses. This may reflect changes from colder, humid conditions to warmer humid conditions during a short depositional lapse of this sedimentary sequence. Also, the presence of chrysophycean stomatocysts (Bertoldi de Pomar, 1973) suggests that moisture conditions were not constant, with the presence of periods of low water availability, possibly with seasonal occurrence.

The new records of leaf compressions at Rincón del Buque locality establish a parautochthonous character for the fossil record described here, being the first record of fossil leaves for the Santa Cruz Formation and for the eastern side of Patagonia.

This is the first record of diverse forest with components of Araucariaceae, Lauraceae, Nothofagaceae, Cunoniaceae, Myrtaceae, Fabaceae, and ?Proteaceae in the Atlantic margin, so far from the Andean modern distribution, corroborating a previous hypothesis (Barreda and Palazzesi, 2007; Barreda *et al.*, 2007) about forests covering Patagonia in the Oligocene–Miocene (today a steppe) from the Pacific up to the Atlantic coast.

The record of palms in Punta Sur locality provides concrete evidence of warmer conditions during this period of time. This record is 15° of latitude further south than the southernmost record of a palm in South America today.

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