On the persistence of Tropical Paleofloras in central Chile during the Early Eocene

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Abstract

Mixed paleofloras first appeared during the Early Eocene of southern South America. These floras were a blend of cold and warm taxa with Austral-Antarctic and Neotropical affinities. Despite the onset of mixed floras, Neotropical floras persisted in central Chile during the Early Eocene. In this study, we analyze the reasons for this persistence and also show that a relationship exists between this persistence and regional paleoclimate. We established the taxonomical composition, associated paleoclimate and phytogeographic affinities of an Early Eocene flora at Caleta Cocholgüe, coastal central Chile. Our results indicate that tropical and subtropical taxa prevailed at Caleta Cocholgüe. These were chiefly Lauraceae, today associated with a humid-warm climate. Physiognomic analyses indicate Mean Annual Temperature and Mean Annual Precipitation above 19 °C and 260 cm, respectively. Moreover, a phytogeographic analysis demonstrates that the Caleta Cocholgüe is closely related to other tropical floras, and poorly linked to contemporary mixed floras. These results strongly suggest that tropical floras persisted in central Chile during the Early Eocene and formed a belt across current subtropical latitudes from southern South America, between 25°S and 37°S. This persistence might be related to the Early Eocene Climatic Optimum and to a shrinking tropical belt, compared to its former Paleocene/Eocene extension.

Keywords: Paleogene of Arauco; Early Eocene; leaf physiognomy; paleoclimate; central Chile

1. Introduction

Several models of past vegetation distribution spanning the Paleogene and Neogene of southern South America indicate a spatial and temporal succession of four Paleofloras: Neotropical, Antarctic, Mixed and Subtropical (Romero, 1978, 1986; Hinojosa and Villagrán, 1997; Troncoso and Romero, 1998).

Neotropical Paleofloras are found throughout in South America during the Paleocene, reaching at to least 46°S during the Paleocene/Eocene transition (Ligorio Marquez taphoflora—46° 36′S, Suárez et al., 2000; Troncoso et al., 2002). The ample dominance of Neotropical Paleofloras during this period has been explained by an expanded tropical belt reaching even 40°S, and by the existence of warm longitudinal marine currents (Hinojosa and Villagrán, 1997; Villagrán and Hinojosa, 1997), associated with a very warm global climate (Zachos et al., 1993, 2001; Malumián and Caramés, 1997; Bains et al., 2000; Pearson and Palmer, 2000; Wilf, 2000; Francis and Poole, 2002; Hinojosa, 2003, 2005a; Svensen et al., 2004).

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During the Early Eocene, however, these tropical floras were replaced throughout southern South America by the Mixed Paleofloras. Defined by Romero (1978, 1986) as a forest formation composed by taxa with different ecological requirements and biogeographic origins, they contain both Neotropical (e.g. *Myrceugenia* and *Escallonia*) and Austral-Antarctic (*Laurelia* and *Eucryphia*) floristic regions (Hinojosa and Villagrán, 2005). Mixed paleofloras have been found during the Paleogene at Quinamávida, central Chile (35° 47′S; Troncoso, 1992), and at Laguna del Hunco (42° 27′ S, Berry, 1925; Wilf et al., 2002) and at Río Pichileufú (41° 01′S, Berry, 1938) from the Argentinean Patagonia. This biogeographic turnover in vegetation formations is probably linked to the Early Eocene Climatic Optimum (Wolfe, 1971; Romero, 1986; Christophel and Greenwood, 1989; Wing and Greenwood, 1993; Zachos et al., 1993; Greenwood and Wing, 1995; Dingle et al., 1998; Rull, 1999; Pearson and Palmer, 2000; Wilf, 2000; Zachos et al., 2001; Hinojosa, 2003; Svensen et al., 2004).

Neotropical floras persisted, however, at several localities during the Early Eocene, including the tropical floras known from Arauco, Caleta Cocholgüe and Lota-Coronel. These floras are floristically divergent when compared to other Early Eocene floras, such as Quinamavida, Río Pichileufú and Laguna del Hunco. With the above in mind, we ask: why do Early Eocene floras from the Paleogene of Arauco exhibit a Neotropical character, whereas throughout most of South America mixed floras occurred? One possible answer may lie in a contraction of the tropical belt during the Early Eocene Climatic Optimum from its Paleocene/Eocene extension. In fact, the presence of a tropical fauna at Arauco during the Early Eocene led Tavera (1942) to suggest that the tropical belt of South America may have been extended to these latitudes.

In this present paper we assess the persistence of Neotropical floras using taxonomic, palaeoclimatic and phytogeographic analyses. We test the hypothesis that during the Early Eocene Climatic Optimum the tropical belt shifted northward allowing tropical floras to persist in central Chile, a phytogeographic remnant of the Paleocene/Eocene transition floras, whereas the rest of southern South America was overrun by Mixed Paleofloras.

The study is based on a fossil flora from Caleta Cocholgüe, located in Mediterranean climatic zone along coastal central Chile (Fig. 1, 36° 35′ S). Previous works carried out at Caleta Cocholgüe (Moreno-Chacón et al., 2000, 2001; Moreno-Chacón, 2000; Gayó, 2001) revealed preponderance of tropical lineages, suggesting a Neotropical character. According to Gayó (2001), Caleta Cocholgüe exhibits a strong floristic

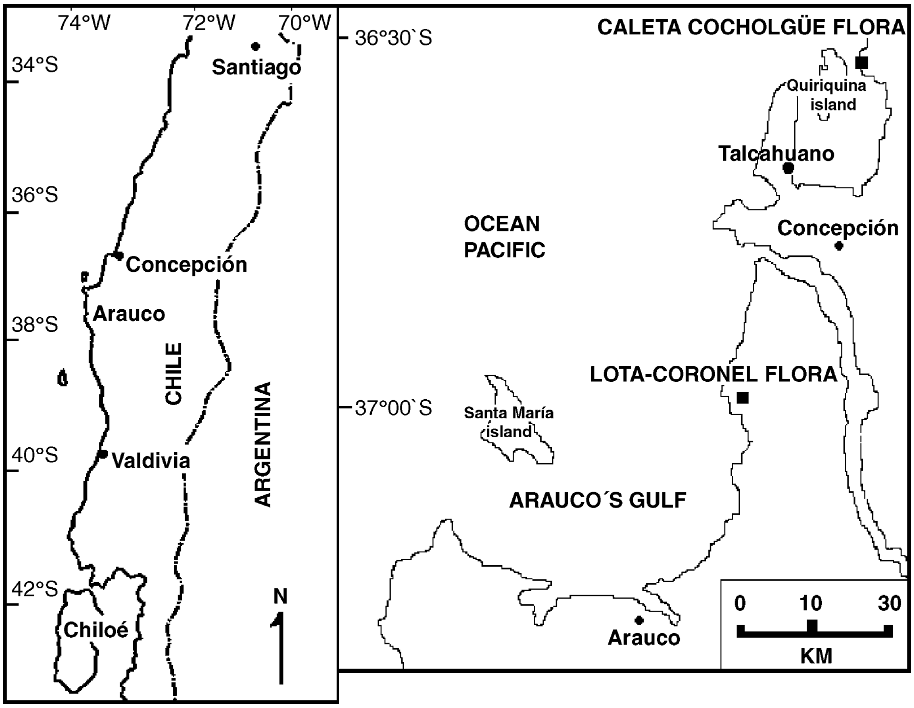

Fig. 1. Locality map indicating the Paleogene of Arauco outcrops: Lota-Coronel and Caleta Cocholgüe.

link with the Lota-Coronel flora (37°S, Lota Member of the Curanilahue Formation) from the Paleogene of Arauco complex, one of the most important Neotropical taphofloras from southern South America. Indeed, geological studies carried out at Caleta Cocholgüe and Lota-Coronel (Fig. 1, Biró-Bagóczky, 1982; Frutos et al., 1982; Tanai, 1986), indicate that the Paleogene sandstones of Caleta Cocholgüe are coeval with the Lota Member of the Curanilahue Formation (Early Eocene, Brüggen, 1915; Tavera, 1942; Muñoz Cristi, 1956; Pineda, 1983).

2. Methods

2.1. Taxonomic composition

Fossil leaf imprints from Caleta Cocholgüe belong to two different collections, identified by the following letters: **Ch** and **Co**: collected by the authors, and **Q** and **Ter-C**: collection from the Museo de Paleontología Departamento Ciencias de la Tierra, Universidad de Concepción. Using morphological affinities we separated into 40 different morphotypes. Their taxonomic identification was determined by an exhaustive leaf architecture analysis, following the nomenclature proposed by Hickey (1974). To assign a morphotype to a particular taxon, we compared our descriptions with fossil taxa recorded in Tropical and Mixed floras from southern South America. In some cases we also compared the imprints with taxa from the present day southern South American forests (Barrera, 1992).

2.2. Paleoclimate estimates

Associated climate was established by using leaf physiognomic models. These are based on the existence of a relationship between climate and different leaf morphology characters. We employed both Univariate and Multivariate predictive models. Within the Multivariate analysis we used Multiple Linear Regressions (MLR) and Climate–Leaf Analysis Multivariate Program (CLAMP, Wolfe, 1993, 1995). MLR models are an extension of Simple Linear Regression Models (SLR), in which a climatic variable can be predicted by more than one leaf physiognomic character (Wing and Greenwood, 1993; Gregory, 1994; Gregory and McIntosh, 1996; Wiemann et al., 1998; Jacobs, 1999). CLAMP, on the other hand uses Canonical Correspondence Analysis (CCA) to estimate climatic parameters based on 31 woody Angiosperms leaf physiognomy characters (Wolfe, 1993, 1995; Herman et al., 1996; Wiemann et al., 1998; Gregory-Wodzicki, 2000). Here, we used the CLAMP 3B SA data set (Hinojosa, 2003, 2005a; Hinojosa and Villagrán, 2005), derived from modern vegetation in Asia, the Northern Hemisphere (Wolfe, 1995), Bolivia (Gregory-Wodzicki, 2000) and central Chile (Hinojosa, 2003, 2005a,b; Hinojosa and Villagrán, 2005).

The physiognomic array of Caleta Cocholgüe taphoflora exhibits high proportions of leaves with entire margin leaf (77%), large leaves (59%) and ovate (57%) and elliptic (43%) leaves. Poor preservation of some characters such as apex and base is a problem, however. For that reason we computed Pearson's correlation coefficients among climatic variables considered in CLAMP 3B SA, and other well represented characters (see background data set).

The characters strongly correlated with climatic parameters were further selected to develop SLR and MLR models. We employed the "Forward selection" function for model establishment.

Table 1
Linear (SLR) and Multiple (MLR) Regression models used for temperature (°C) and precipitation (cm) estimations. MAT: Mean Annual Temperature; CMMT: Cold Month Mean Temperatures; WMMT: Warm Month Mean Temperatures; GSL: Growing Season Length (months); LnMAP: natural logarithm of Mean Annual Precipitation (SLR's equation established by Hinojosa, 2003, 2005a and Hinojosa and Villagrán, 2005); GSP: Growing Season Precipitation; 3DRY: precipitation during the three driest months; SE = standard error; r^2 = coefficient of determination

Parameter	Equation	SE	r^2
TMA	=1.8116+(0.2400*% no teeth)+(.06795*L:W 2–3:1)	2.1	0.88
CMMT	=−12.1013+(0.3182*% no teeth)+(0.1433*L:W 2–3:1)	3.8	0.81
WMMT	=16.9076+(0.1218*% no teeth)+(0.1406*nanophylla)	3.2	0.54
GSL	=2.5238+(0.09765*% no teeth)+(0.08584*L:W 3–4:1)+(0.02334*L:W 2–3:1)	1.2	0.83
LnMAP	=1.6355+0.492*MlnA	Ln 0.5	0.60
GSP	=−180.5805+(4.2098*% L:W 2–3:1)+(2.8854*% elliptic)	58.2	0.56
3DRY	=−47.5145+(1.0320*% elliptic)+(.9776*% Microphylla3)	15.6	0.59

Abbreviations of leaf characters: No teeth: margin type category (entire margin), L:W (2–3:1 and L:W 3–4:1): Length/width ratio categories; Nanophylla and Microphylla3: leaf size categories; Elliptic: elliptic leaf shape; MlnA: natural logarithm of leaf area.

Table 2
Equations used for temperature (°C) and precipitation (cm) estimations under Canonical Correspondence Analysis (Hinojosa, 2003, 2005a; Hinojosa and Villagrán, 2005)

Parameter	Equation	SE	r^2
MAT	$= -8.1231 + \mathrm{EXP}[3.0962 + (0.2407 * \mathrm{vMAT})]$	2.1	0.88
WMMT	$= 23.634 + (3.4172 * \mathrm{v\ WMMT}) + (-0.4028 * \mathrm{vWMMT})^2$	3.3	0.52
CMMT	$= -35.1955 + \mathrm{EXP}[3.7147 + (0.181 * \mathrm{vCMMT})]$	3.8	0.81
GSL	$= -14.2108 + \mathrm{EXP}[3.1147 + (0.1098 * \mathrm{vGSL})]$	1.1	0.84
GSP	$= 75.4875 * \mathrm{EXP}(0.528 * \mathrm{vGSP})$	42.6	0.77
3DRY	$= 17.4628 * \mathrm{EXP}(0.6729 * \mathrm{v3DRY})$	15.3	0.61

SE = standard error, r^2 = coefficient of determination. vMAT: MAT's vector, vWMMT: WMMT's vector, vCMMT: CMMT's vector, vGSL: GSL's vector, vGSP: GSP's vector, v3DRY: 3DRY's vector.

The SLR model for prediction of Mean Annual Temperature (MAT) has had ample use (Bailey and Sinnott, 1915; Wolfe, 1979; Greenwood, 1992; Wing and Greenwood, 1993; Wilf, 1997, 2000; Greenwood and Wing, 1995; Wilf et al., 1998; Greenwood et al., 2004). Nevertheless, the "Forward selection" procedure suggests that all climatic parameters are explained by numerous characters, thus we established MLR models for MAT and other temperature and precipitation parameters (Table 1), except for Mean Annual Precipitation (MAP). Thus, we employed an SLR model for MAP prediction proposed by Hinojosa (2003, 2005a) and Hinojosa and Villagrán (2005, Table 1) based on the relationship between the natural logarithm of leaf area (MlnA) and MAP identified by Wilf et al. (1998).

We ran the CCA model using the complete CLAMP3B SA data set in the software CANOCO for Windows version 4 (Ter Braak and Smilauer, 1998). Estimates of each climatic parameter were obtained replacing the value of the pertinent climatic vector into equations proposed by Hinojosa (2003, 2005a) and Hinojosa and Villagrán (2005, Table 2).

Table 3
Paleocene and Early Eocene floras from southern South America considered in phytogeographic affinity analysis

Flora	Latitude (°S)	Longitude (°W)	Paleoflora	Age
Ligorio Márquez	46° 45′	71°50′	N	Paleocene–Eocene transition
Lota-Coronel	37° 01′	73° 08′	N	Early Eocene
C. Cocholgüe	36° 35′	72° 58′	N	Early Eocene
Quinamávida	35° 47′	71° 24′	M	Early Eocene
Pichileufú	41° 70′	70° 00′	M	Early Eocene
L. del Hunco	42° 27′	70° 00′	M	Early Eocene

Paleoflora characters are according to paleophytogeographic models of Romero (1978, 1986) and Hinojosa and Villagrán (1997). N: Neotropical Paleoflora, M: Mixed Paleoflora.

2.3. Phytogeographic affinities

Phytogeographic relations among Caleta Cocholgüe and Paleogene tropical and mixed floras from southern South America (Table 3), we assessed using cluster analysis. We aimed at establishing phytogeographic comparisons between Caleta Cocholgüe and the selected floras by estimating the percentage of phytogeographic elements (defined by the modern distributions of the genera, Villagrán and Hinojosa, 1997) present in each. The classification of the species into phytogeographic elements was done according to Villagrán and Hinojosa (1997) and Gayó (2004). We ran the cluster analysis employing UPGMA clustering method and the Gower general similarity coefficient (Gower, 1971). Statistical significance was established by bootstrap (95% confidence, 100 random).

3. Results

3.1. Taxonomic composition

We recognized 40 different morphotypes. Among these, only 20 have been cataloged as known taxa. Taxonomical analysis (Table 4) suggests that Caleta Cocholgüe is dominated by members of the Lauraceae family, with 11 taxa. Notable among these are *Nectandra* (*N. prolifica* and *N. patagonica*) and *Cinnamomum* (sp. 1 and sp. 2) and *Persea* (*P. microphylla*, *P. macrophylloides* and *Persea* sp.).

Also present are two important taxa of Myrtaceae family, represented by two species, *Myrcia reticulovenosa* and *Myrceugenia* sp. Seven other families, each one represented by a single species are also present in this flora. Examples include *Cupania patagonica* (Sapindaceae), and *Schinus* sp. (Anacardiaceae).

One noteworthy aspect is the current relation of the Caleta Cocholgüe flora to current species of modern day Chilean forests, chiefly distributed in the Mediterranean climatic region of central Chile. A few examples

Table 4
A list of identified taxa from Caleta Cocholgüe including the number of species per genus

Family	Genus	Number of species
Lauraceae	*Goeppertia*	1
Lauraceae	*Notaphoebe*	1
Lauraceae	*Ocotea*	1
Lauraceae	*Phoebe*	1
Lauraceae	*Cinnamomum*	2
Lauraceae	*Nectandra*	2
Lauraceae	*Persea*	3
Myrtaceae	*Myrceugenia*	1
Myrtaceae	*Myrcia*	1
Anacardiaceae	*Schinus*	1
Anonnaceae	*Annona*	1
Bignoniaceae	*Adenocalymma*	1
Cochlospermaceae	*Choclospermum*	1
Flacourtiaceae	*Casearia*	1
Sapindaceae	*Cupania*	1
Sterculiaceae	*Sterculia*	1

include: *Persea* sp. which is related to *P. lingue*, an endemic Chilean species; *Myrceugenia* sp. related to *M. obtusa*, and *Schinus* sp. with *S. polygamus* and *S. molle*.

3.2. Paleoclimate

Our paleoclimate estimates indicate that humid-warm conditions with MAT above 19 °C and a MAP of ~260 cm distributed evenly throughout the year prevailed at Caleta Cocholgüe. Hence, the SLR gave MAP of 265 cm (SE +104.3, SE −171.9, Table 5). Likewise, MLR and CLAMP analysis gave a Growing Season Precipitation (GSP) of 190 cm (SE ±58.2) and 268 cm (SE ±42.6), respectively. These GSP's values agree with the estimates of Growing Season Length (GSL), because it was extended throughout the year (over 11 months, Table 5). Thus, precipitation during the three driest months (3DRY) was equivalent to a quarter of the annual precipitation values (Table 5).

Table 5
Caleta Cocholgüe's temperature (°C) and precipitation (cm) estimates based on Simple Linear Regression (SLR), Multiple Linear Regression (MLR) and Canonical Correspondence Analysis (CCA)

Parameter	SLR 263	MLR	CCA
MAP	(+104.3, −171.9)		
GSP		190 (±58.2)	268 (±42.6)
3DRY		30 (±59)	58 (±15.3)
MAT		25.5 (±2.1)	19.3 (±2.1)
WMMT		27.0 (±3.2)	22.6 (±3.3)
CMMT		22.4 (±3.8)	13.2 (±3.8)
GSL		13 (±1.2)	11 (±1.1)

Values in parentheses represent model standard error.

The MLR gave a MAT estimation of 26 °C (SE ±2.1), whereas the corresponding value using CLAMP was 19 °C (SE ±2.1), and indicate a warm climate for Caleta Cocholgüe. The MLR estimates of extreme annual temperature, Warm Month and Cold Month Mean Temperatures (WMMT and CMMT), were 27 °C (SE ±3.2) and 22 °C (SE ±3.8), respectively. CLAMP estimates are 23 °C (SE ±3.3) and 13 °C (SE ±3.8). These results suggest overall thermal homogeneity throughout the year (annual thermal oscillation between 5–10 °C), which agrees with a prolonged growing season.

3.3. Phytogeographic affinities

Our results show the dominance of Neotropical, Pantropical and Australasian affinity (Table 6) in all taphofloras considered. The tropical floras of Ligorio Márquez, Lota-Coronel, Caleta Cocholgüe and Quinamávida also exhibit relatively equal proportions of warm elements. Australasian elements decline at Lota-Coronel and Quinamávida, however, and Neotropical elements increase. Austral-Antarctic and Endemic elements become prominent in mixed floras of Río Pichileufú and Laguna del Hunco.

The cluster analysis revealed two main groups (Fig. 2), separated by a similarity coefficient of 0.40. The first node integrates all tropical floras and the mixed flora of Quinamávida from central Chile, and the second node includes the Early Eocene mixed floras from Argentine Patagonia. Within the tropical group, Caleta Cocholgüe is closely related to Ligorio Márquez (Paleocene/Eocene transition), with a similarity coefficient of 0.84. Both floras are related to Lota-Coronel (Early Eocene, similarity coefficient of 0.69), and less related to the mixed flora of Quinamávida (similarity coefficient of 0.61). The cluster integrated by Early Eocene mixed floras shows strong relationship among Río

Table 6
Percentages of phytogeographic elements for each flora considered in the phytogeographic affinities analysis

FLORA	Proportion of phytogeographic elements				
	P	AU	N	AA	E
Río Pichileufú	28.3	20.4	45.1	2.7	3.5
Laguna del Hunco	26.6	23.3	43.3	3.3	3.3
Quinamávida	27.3	13.6	59.0	0	0
Lota-Coronel	35.5	18.4	46.0	0	0
Caleta Cocholgüe	30.0	30.0	40.0	0	0
Ligorio Márquez	31.8	36.4	31.8	0	0

P: Pantropical, AU: Australasian, N: Neotropical, AA: Austral-Antarctic, and E: Endemic.

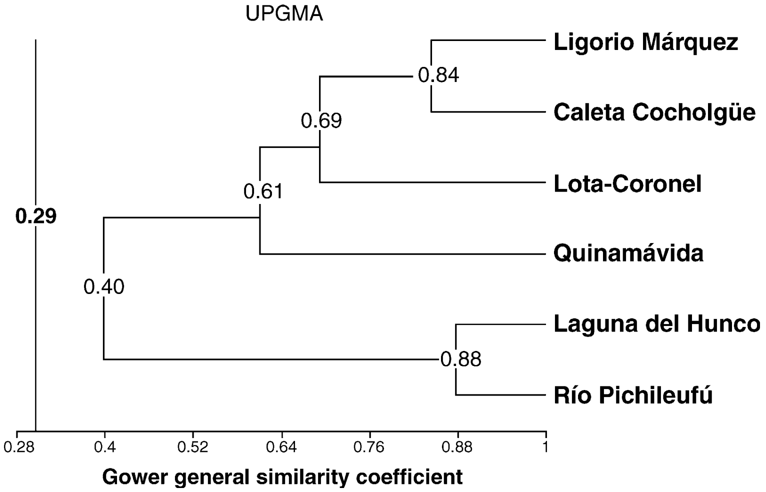

Fig. 2. A phytogeographic affinity analysis between Caleta Cocholgüe and five tropical and mixed floras from southern South America. Tropical floras: Ligorio Márquez and Lota-Coronel; Mixed floras: Río Pichileufú, Quinamávida and Laguna del Hunco. Bootstrap significance >0.29.

Pichileufú and Laguna del Hunco, with the highest similarity coefficient of the analysis (0.88).

4. Discussion

4.1. Taxonomical composition and phytogeographic affinities

The taxonomical composition reveals that tropical and subtropical taxa prevailed at Caleta Cocholgüe. This includes ~60% of the flora, such as *Persea*, *Ocotea*, *Notaphoebe*, *Phoebe*, *Myrcia*, *Adenocalymma*, *Nectandra*, *Sterculia* and *Anonna*. The abundance of taxa with humid warm climatic requirements, such as the Lauraceae family, together with the dominance of warm phytogeographic elements (Pantropical, Australasian, and mainly Neotropical), suggest that the Early Eocene flora of Caleta Cocholgüe should be considered as a Neotropical Paleoflora.

As previously noted, the Caleta Cocholgue includes species related to modern tree species of central Chile. This suggests an early Paleogene origin for the central Chilean flora, in agreement with previous hypotheses (Schmithüsen, 1956; Raven, 1971; Solbrig et al., 1977; Landrum, 1981; Arroyo et al., 1995; Villagrán and Hinojosa, 1997; Hinojosa, 2003). According to these authors, the modern day flora of central Chile is the outcome of the blending of lineages that arrived at the southern cone during the Paleogene and Neogene, when the geographical configuration of South America was different. Nevertheless, as noted by Hinojosa and Villagrán (1997) Hinojosa (2003, 2005a,b), the relationship between ancient tropical floras and the modern flora of central Chile is relatively poor, mostly due to in situ evolution of these Paleofloras under a very unique climatic and geological setting.

The cluster analysis also indicates the that Caleta Cocholgüe is closely related to tropical floras, particularly to Ligorio Márquez, and less related to mixed floras of Laguna del Hunco and Río Pichileufú. The close relationship between Ligorio Márquez and Caleta Cocholgüe might be related to the equal distribution of warm elements in both these floras (Neotropical, Pantropical, Australasian). In contrast, the reduction of Australasian elements at Lota-Coronel might explain the lower degree of affinity observed between this flora and the Ligorio Márquez–Caleta Cocholgüe group. The association of these tropical floras agrees with correlations previously established between the Paleocene/Eocene transition flora and the Paleogene of Arauco (Suárez et al., 2000; Troncoso et al., 2002), and between Lota-Coronel and Caleta Cocholgüe (Biró-Bagóczky, 1982; Frutos et al., 1982; Tanai, 1986; Gayó, 2001). The incorporation of the Quinamávida taphoflora within the tropical cluster is an unexpected result. Based on phytogeographic affinities, Troncoso (1992) assigned the Quinamávida flora to a mixed flora. We thus expected a closer affinity with the mixed floras of Río Pichileufú and Laguna del Hunco. Yet warm elements, principally Neotropical, abound in the Quinamávida flora and furthermore, Austral-Antarctic elements are absent (Table 6). This phytogeographic array differs from the mixed flora concept (sensu Romero, 1978, 1986) because it lacks a mixture of warm and cold-temperate elements (Romero, 1978, 1986; Hinojosa and Villagrán, 1997; Troncoso and Romero, 1998; Hinojosa, 2003).

Despite its overall tropical character, however, the Quinamávida flora was considered a mixed flora based on the high proportion (22.3%) of Anacardiaceae and Sapindaceae families, which are considered proper of mixed floras (Romero, 1986; Troncoso and Romero, 1998). This proportion is comparable to those found at Río Pichileufú (16.8%) and Laguna del Hunco (26.7%).

Overall, the phytogeographic affinity analysis of Caleta Cocholgüe suggests a tropical character. Thus, these Early Eocene floras from central Chile are in disagreement with the distribution of mixed floras proposed in current Paleogene and Neogene phytogeographic models.

The poor phytogeographic relationship between Early Eocene mixed floras and the Paleogene of Arauco floras seen in this study agrees with previous relationships evaluated by Romero (1978) and Fuenzalida (1980). These authors suggested that the Lota-Coronel and Argentinean Patagonia mixed floras exhibit a low floristic similarity coefficient chiefly because cold-temperate and Endemic elements are lacking in Paleogene of Arauco floras.

4.2. Associated paleoclimate

Paleoclimate reconstructions derived from leaf physiognomic analyses indicate a humid-warm for Caleta Cocholgüe, with MAT >19 °C (19–26 °C) and MAP ~260 cm (190–268 cm) distributed evenly throughout the year.

Temperature estimates based on MLR models suggest a MAT of 26 °C (SE ± 2.1) and an annual thermal oscillation of 5 °C. This result, taken together with the percentage of entire margin leaves (77%) suggests a tropical rainforest according to Wolfe's (1971) classification. Estimates using the CLAMP model give a MAT of 19 °C (SE ± 2.1) and an annual thermal oscillation of 9 °C, and suggest a Montane rainforest (Wolfe, 1971). When the proportion of entire margin leaves and physiognomic index (large leaves/small leaves) proposed by Dilcher (1973) are considered, however, Caleta Cocholgüe was associated with an overall warm climate and low annual thermal amplitude.

Our results agree with the humid-warm conditions obtained by Hinojosa (2003, 2005a) for the tropical floras present at Ligorio Márquez and Lota-Coronel. MAP at Ligorio Márquez was estimated at 297 cm, MAT at 25 °C and the annual thermal oscillation of 6 °C. For Lota-Coronel, the corresponding values are 365 cm, 22 °C, and 9 °C. This contrasts with the bi-seasonal subtropical climate inferred for Early Eocene mixed floras (Hinojosa, 2003, 2005a; Hinojosa and Villagrán, 2005). Estimates for Río Pichileufú gave a MAP of 167 cm, MAT of 18 °C and an annual thermal oscillation of 11 °C. Whereas, for Quinamávida and Laguna del Hunco, MAP was estimated at 89 and 223 cm, respectively, MAT ~18 °C, and a thermal oscillation ~11 °C.

By adding the Caleta Cocholgüe values to reconstructions of the South American Paleogene and Neogene (Hinojosa, 2003, 2005a), we note that the Arauco floras display intermediate climate conditions between the tropical flora of Ligorio Márquez (Paleocene/Eocene transition) and the mixed floras (Laguna del Hunco, Río Pichileufú and Quinamáivida). On one hand, the Arauco floras exhibit a higher thermal oscillation and were relatively colder than Paleocene/Eocene counterparts. On the other hand, the mixed floras from Argentine Patagonia and Quinamávida were associated with a bi-seasonal precipitation regime, lower temperatures and higher thermal amplitude when compared to the Arauco floras. Furthermore, it is probably the very same subtropical conditions associated with the Argentine Patagonia floras that could be responsible for the mixture of elements with different ecological requirements (Hinojosa, 2003, 2005a; Hinojosa and Villagrán, 2005). The tropical nature of the Early Eocene Quinamávida flora together with its phytogeographic relationship with the Arauco floras, suggests that it was adapted to increased continentality. Hence, its greater thermal amplitude and values similar to those of Laguna del Hunco, might explain the phytogeographic array dominated by warm elements together with the prevalence of the Sapindaceae–Anacardiaceae component.

4.3. Early Eocene biogeographic patterns

Why did the Early Eocene floras from the Paleogene of Arauco exhibit a Neotropical character while the region was dominated by mixed floras? We hypothesised that this might be related to the northward displacement of the tropical belt of South America from its Paleocene/Eocene position further south, This event, together with the Eocene Climatic Optimum, might have permitted the persistence of tropical floras in central Chile, at least in Quinamávida (35° to 37° S). This event, together with the occurrence of the Early Climatic Optimum, might have permitted the persistence of tropical floras in central Chile, at least along what is today the Arauco coast and at Quinamávida (35° to 37°S). Our climatic estimates support this idea. The Arauco floras grew under a relatively colder and drier climate than did those from Ligorio Márquez

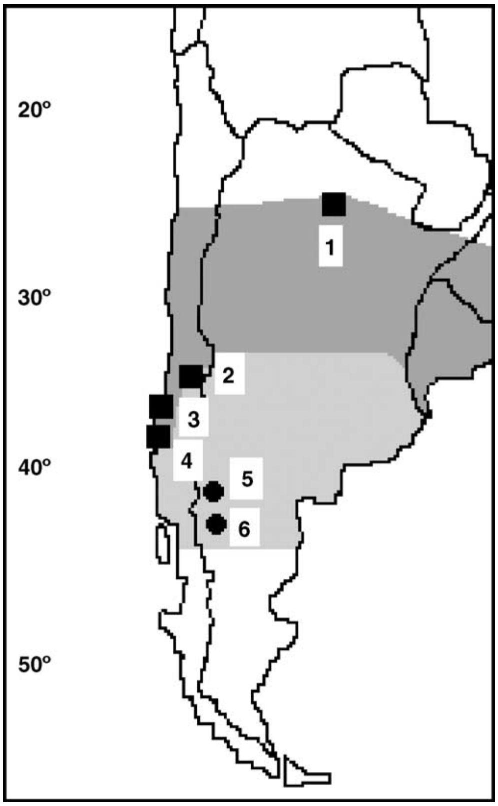

Fig. 3. The Early Eocene distribution of tropical and mixed floras in southern South America. Dark grey and squares symbols: distribution of tropical floras (1—Lumbrera Formation, 2—Quinamávida, 3—Caleta Cocholgüe and 4—Lota-Coronel). Bright grey and round symbols: mixed floras distribution (5—Río Pichileufú and 6—Laguna del Hunco).

(46°S, Paleocene/Eocene transition), which suggests that these floras were associated with the Early Eocene Climatic Optimum (Hinojosa, 2003, 2005a; Hinojosa and Villagrán, 2005). Likewise, the subtropical conditions of Early Eocene mixed floras such as those from Río Pichileufú (41°S) and Laguna del Hunco (42°S), imply that the tropical belt was situated north of 40°S during the Early Eocene (Tavera, 1942; Hinojosa and Villagrán, 1997; Villagrán and Hinojosa, 1997). The presence of coeval of tropical and mixed floras in southern South America during the Early Eocene, especially the existence of tropical floras in central Chile, has mostly been omitted from current phytogeographic models and knowledge of their spatial distribution is an important issue. Unfortunately, additional paleobotanical records from the Early Eocene of central Chile, except for the floras of Arauco and Quinamávida, are unknown. In this respect, key data could be obtained from an Early Eocene flora of the Lumbrera Formation in NW Argentina (25°S 64°W, Fig. 3) which indicates a tropical affinity (Quatrocchio, 1978; Quatrocchio and Volkheimer, 1990).

These preliminary data, when taken together with the evidence presented here, suggests that tropical floras and associated climate possibly formed a belt across current subtropical latitudes of southern South America, between 25°S and 37°S (Fig. 3). The presence of mixed floras, south of these localities (such as those found at Laguna del Hunco and Río Pichileufú) would imply that subtropical conditions occurred south of this tropical belt.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at 10.1016/j.revpalbo.2005.09.001.

References

Arroyo, M.T.K., Caviares, L., Marticorena, C., Muñoz-Schick, M., 1995. Convergence in the Mediterranean Floras in Central Chile and California: insights from comparative biogeography. In: Arroyo, M.T.K., Zedler, P., Fox, M. (Eds.), Ecology and Biogeography of Mediterranean Ecosystem in Chile, California and Australia, Ecological Studies, vol. 108. Springer-Verlag, NY, pp. 43–88.

Bailey, I.W., Sinnott, E.W., 1915. A botanical index of Cretaceous and Tertiary climates. Science 41, 831–834.

Bains, S., Norris, R., Cordfield, R., Faul, K., 2000. Termination of global warmth at the Palaeocene–Eocene boundary through productivity feedback. Nature 407, 171–173.

Barrera, E., 1992. Arquitectura foliar de árboles chilenos I. Subclase Magnoliidae. Bol. Mus. Nac. Hist. Nat. Chile 43, 41–54.

Berry, E., 1925. A Miocene flora from Patagonia. Johns Hopkins Univ., Stud. Geol. 47, 121–132.

Berry, E., 1938. Tertiary flora from Río Pichileufú, Argentina. Spec. pap. - Geol. Soc. Am. 12, 1–149.

Biró-Bagóczky, L., 1982. Revisión y redefinición de los "estratos de Quiriquina," Campaniano–Maastrichtiano, en su localidad tipo, en la Isla Quiriquina, 36°37′ Lat. Sur, Chile, Sudamérica, con un perfil complementario de Cocholgüe. Contrib. Dep. Geocienc., Univ. Concepción 5, 29–64.

Brüggen, J., 1915. El Cretáceo del Algarrobo y las supuestas relaciones entre las formaciones cretácea y Terciaria de Chile. Sociedad Imprenta-Litografía Barcelona, Santiago-Valparaíso. 15 pp.

Christophel, D.C., Greenwood, D.R., 1989. Changes in climate and vegetation in Australia during the Tertiary. Rev. Palaeobot. Palynol. 58, 95–109.

Dilcher, D., 1973. The Eocene floras of southeastern North America. In: En Graham A, D. (Ed.), Vegetation and Vegetational History of Northern Latin America. Elsevier, Amsterdam, pp. 39–59.

Dingle, R.V., Marenssib, S.A., Lavellea, M., 1998. High latitude Eocene climate deterioration: evidence from the northern Antarctic Peninsula. J. South Am. Earth Sci. 11 (6), 571–579.

Francis, J.E., Poole, I., 2002. Cretaceous and Tertiary climates of Antarctica: evidence from fossil wood. Palaeogeogr. Palaeoclimatol. Palaeoecol. 182, 47–64.

Frutos, J., Mencarini, P., Pincheira, M., Bourret, Y., Alfaro, G., 1982. Geología de la Isla Quiriquina. III Congreso Geológico Chileno. Actas III, Concepción-Chile, pp. F307–F338.

Fuenzalida, H., 1980. Historia vegetacional de Chile. Estudios geográficos: homenaje a Dr. Humberto Fuenzalida. Notas Mens. Mus. Hist. Nat. 15 (287), 21–39.

Gayó, E., 2001. Estudio de improntas terciarias y estimaciones paleoclimáticas en la zona de Concepción, VIII región del Bío-Bío, Chile. Thesis, Facultad de Ciencias Naturales y Oceanográficas. Universidad de Concepción., Chile.

Gayó, E., Estudio taxonómico y fisionómico-climático de la tafoflora Caleta Cocholgüe (36° 35′ s y 72° 58′ w), Eoceno inferior, Chile Central. MSc. thesis, Facultad de Ciencias, Universidad de Chile, Chile.

Gower, J.C., 1971. A general coefficient of similarity and some of its properties. Biometric 27 (4), 857–871.

Greenwood, D., 1992. Taphonimic constraints on foliar physiognomic interpretations of Late Cretaceous and Tertiary paleoclimates. Rev. Palaeobot. Palynol. 71, 149–190.

Greenwood, D., Wing, S., 1995. Eocene continental climates and latitudinal temperature gradients. Geology 23 (11), 1044–1048.

Greenwood, D., Wilf, P., Wing, S., Christophel, D.C., 2004. Paleotemperature estimation using Leaf-Margin analysis: is Australia different? Palaios 19, 129–142.

Gregory, K.M., 1994. Palaeoclimate and palaeoelevation of the 35 ma Florissant flora, Front Range, Colorado. Palaeoclimates 1, 23–57.

Gregory, K.M., McIntosh, W.C., 1996. Paleoclimate and paleoelevation of the Oligocene Pitch–Pinnacle flora, Sawatch Range, Colorado. Geol. Soc. Am. Bull. 108, 545–561.

Gregory-Wodzicki, K., 2000. Relations between leaf morphology and climate, Bolivia: implications for estimating paleoclimate from fossil floras. Paleobiology 26 (4), 668–688.

Herman, A., Spicer, R., Wolfe, J.A., Collinson, M.E., 1996. Guide to obtaining a CLAMP analysis. Unpublished manuscript.

Hickey, L., 1974. Clasificación de la arquitectura de las hojas de Dicotiledóneas. Bol. Soc. Argent. Bot. XVI (1–2), 1–25.

Hinojosa, L.F., 2003. Fisonomía foliar y clima de las Paleofloras Mixtas del Terciario de Sudamérica. Ph.D. thesis, Facultad de Ciencias, Universidad de Chile, Chile.

Hinojosa, L.F., 2005a. Cambios climáticos y vegetacionales inferidos a partir de paleofloras cenozoicas del sur de Sudamérica. Rev. Geol. Chile 32 (1), 95–115.

Hinojosa, L.F., 2005b. Historia Terciaria de la Cordillera de la Costa: relaciones fisionómicas y fitogeográficas de la vegetación de la Cordillera de la Costa y las Paleofloras Terciarias del sur de Sudamérica. In: Smith, C., Armesto, J.J., Valdovinos, C. (Eds.), Biodiversidad y Ecología de los Bosques de la Cordillera de la Costa de Chile. Editoral Universitaria, Santiago, pp. 90–104.

Hinojosa, L.F., Villagrán, C., 1997. Historia de los bosques del sur de Sudamérica I: antecedentes paleobotánicos, geológicos y climáticos del Terciario del cono sur de América. Rev. Chil. Hist. Nat. 70, 225–239.

Hinojosa, L.F., Villagrán, C., 2005. Did South American Mixed Paleofloras evolve under thermal equability or in the absence of an effective Andean barrier during the Cenozoic? Palaeogeogr. Palaeoclimatol. Palaeoecol. 217, 1–23.

Jacobs, B.F., 1999. Estimation of rainfall variables from leaf characters in tropical Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol. 145, 231–250.

Landrum, L., 1981. The phylogeny and geography of *Myrceugenia* (Myrtaceae). Brittonia 33 (1), 105–129.

Malumián, N., Caramés, A., 1997. Upper Campanian–Paleogene from the Río Turbio coal measures in southern Argentina: micropaleontology and the Paleocene/Eocene boundary. J. South Am. Earth Sci. 10 (2), 189–201.

Moreno-Chacón, M., 2000. Estudio de la arquitectura foliar de Angiospermas fósiles del Paleógeno de Cocholgüe, VIII región (Chile). Thesis, Facultad de Ciencias Naturales y Oceanográficas. Universidad de Concepción. Chile.

Moreno-Chacón, M., Palma-Heldt, S., Leppe, M., 2000. Estudio de la arquitectura foliar de Angiospermas fósiles del Paleógeno de Cocholgüe, VIII región (Chile). XII Reunión Anual de la Sociedad Botánica de Chile-XXVII Jornadas Argentinas de Botánica. Concepción. Gayana, Bot. 57, 54.

Moreno-Chacón, M., Leppe, M., Palma-Heldt, S., 2001. Arquitectura foliar y aproximaciones paleoclimáticas de improntas del paleógeno de Cocholgüe, VIII Región, Chile. XIII Reunión Anual de la Sociedad de Botánica de Chile, La Serena — Chile. Gayana, Bot. 58 (1), 71.

Muñoz Cristi, J., 1956. Chile. In: Yenks, W.F. (Ed.), Handbook of South American Geology, Geol. Soc. Am. Men., vol. 65, pp. 187–214.

Pearson, P., Palmer, M., 2000. Atmospheric carbon dioxide concentrations over the past 60 million years. Nature 406, 695–699.

Pineda, V., 1983. Evolución Paleogeográfica de la Península de Arauco durante el Cretácico Superior–Terciario. Thesis, Departamento de Geología y Geofísica. Facultad de Ciencias Físicas y Matemáticas. Universidad de Chile. Chile.

Quatrocchio, M., 1978. Estudio palinológico preliminar de la Formación Lumbrera (Grupo Salta), localidad Pampa Grande, Provincia de Salta, República de Argentina. II Congreso Argentino de Paleontología y Biostratigrafía, I Congreso Latinoamericano de Paleontología. Actas II, 31–149.

Quatrocchio, M., Volkheimer, W., 1990. Paleogene paleoenvironmental trends as reflected by palynological assemblage types, Salta Basin, NW Argentina. N.J. B Geol. Pläont. Abh 181 (1–3), 337–396.

Raven, P.H., 1971. The relationship between “Mediterranean” floras. In: Davis, P.A., Harper, P.C., Hedge, I.C. (Eds.), Plant Life of South-West Asia. Bot. Soc. Edinburgh, Edinburgh, pp. 119–134.

Romero, E., 1978. Paleoecología y Paleofitogeografía de las Tafofloras del Cenofítico de Argentina y áreas vecinas. Ameghiniana 15, 209–227.

Romero, E., 1986. Paleogene phytogeography and climatology of South America. Ann. Missouri. Bot. Gard. 73, 449–461.

Rull, V., 1999. Palaeofloristic and palaeovegetational changes across the Paleocene/Eocene boundary in northern South America. Rev. Palaeobot. Palynol. 107 (1–2), 83–95.

Schmithüsen, J., 1956. Die räumliche Ordnung der chilenischen Vegetation. Bonn. Geogr. Abh. 17, 1–86.

Solbrig, O., Cody, M.L., Fuentes, E.R., Glanz, W., Hunt, J.H., Moldenke, A.R., 1977. The origin of the Biota. In: Mooney, H.A. (Ed.), Convergent Evolution in Chile and California: Mediterranean Climate Ecosystems. Dowden, Hutchinson and Ross, Stroudsburg, PA, pp. 13–26.

<ontribución al estudio de la estratigrafía y Paleontología del Terciario de Arauco. An. I. Cong. Panam. Ing. Min. Geol.. Santiago. Tomo II, pp. 580–632.

Ter Braak, C.J.F., Smilauer, P., 1998. Canoco Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4). Microcomputer Power, Ithaca, New York, USA.

Troncoso, A., 1992. La tafoflora terciaria de Quinamávida (VII región). Bol. Mus. Nac. Hist. Nat. Chile 43, 155–178.

Troncoso, A., Romero, E., 1998. Evolución de las comunidades florísticas en el extremo sur de Sudamérica durante el Cenofítico. In: Fortunato, R., Bacigalupo, N. (Eds.), Proceedings of the VI Congreso Latinoamericano de Botánica, Monographs in Systematic Botany from the Missouri Botanical Garden, vol. 68, pp. 1–30.

Troncoso, A., Suárez, M., De la Cruz, R., Palma-Heldt, S., 2002. Paleoflora de la Formación Ligorio Márquez (XI Región, Chile) en su localidad tipo: sistemática, edad e implicancias paleoclimáticas. Rev. Geol. Chile 29, 113–135.

Villagrán, C., Hinojosa, L.F., 1997. Historia de los bosques del sur de Sudamérica II: análisis fitogeográfico. Rev. Chil. Hist. Nat. 70, 241–267.

Wiemann, M., Manchester, S., Dilcher, D., Hinojosa, L.F., Wheeler, E., 1998. Estimation of temperature and precipitation from morphological characters of dicotyledonous leaves. Am. J. Bot. 85 (12), 1796–1802.

Wilf, P., 1997. When are leaves good thermometers? Paleobiology 23, 373–390.

Wilf, P., 2000. Late Paleocene–Early Eocene climate change in southwestern Wyoming: paleobotanical analysis. G. S. A. Bulletin 112 (2), 292–307.

Wilf, P., Wing, S., Greenwood, D., Greenwood, C., 1998. Using fossil leaves as paleoprecipitation indicators: an Eocene example. Geology 26 (3), 203–206.

Wilf, P., Cuneo, R., Johnson, K.R., Hicks, J., Wing, S., Obradovich, J.D., 2002. High plant diversity in Eocene South America: evidence from Patagonia. Science 300, 122–125.

Wing, S.L., Greenwood, D.R., 1993. Fossils and fossil climate: the case for equable continental interiors in the Eocene. Philos. Trans. R. Soc. Lond., Ser. B 341, 243–252.

Wolfe, J., 1971. Tertiary climatic fluctuations and methods of analysis of Tertiary floras. Paleogeogr. Paleoclimatol. Paleoecol. 9, 27–57.

Wolfe, J.A., 1979. Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the northern hemisphere and Australasia. U.S. G.S. Professional Paper 1106, 1–37.

Wolfe, J., 1993. A method of obtaining climatic parameters from leaf assemblages. U.S. Geol. Surv. Bull. 2040.

Wolfe, J., 1995. Paleoclimatic estimates from Tertiary leaf assemblages. Annu. Rev. Earth Planet. Sci. 23, 119–142.

Zachos, J.C., Lohmann, K.C., Walker, J.C.G., Wise, S.W., 1993. Abrupt climate change and transient climates during the Paleogene: a marine perspective. J. Geol. 101, 191–213.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292, 686–693.