



Early Miocene climate estimations in Patagonia: The case of Pico Quemado, Ñirihuau Formation (Lower-Middle Miocene)



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ABSTRACT

The climate during the early Neogene in Patagonia is characterized by the increase of the average temperatures until the mid-Miocene Climatic Optimum. However, the terrestrial paleoclimate of southern South America during this period is unclear. Therefore, a physiognomic analysis on the Pico Quemado (Ñirihuau Formation, lower-middle Miocene) megaflora was realized. Three types of analyses were performed: 1) Leaf Margin Analysis (LMA); 2) Leaf Area Analysis (LAA); and 3) a CLAMP analysis (Climate Leaf Analysis Multivariate Program) with two different dataset. The LMA and CLAMP predicted an estimated a Mean Annual Temperature of 10.4 ± 2.1 °C, 8.5 ± 2.1 °C and 7.2 ± 1.4 respectively. The estimations of Mean Annual Precipitation were of 123.7 ± 21.2 cm. Through the CCA, other parameters were estimated, i. e. Cold Mean Month Temperature (-3.3 ± 3.8 °C, 1.6 ± 1.6 °C); Warm Mean Month Temperature (17.4 ± 3.3 °C; 14.1 ± 1.2 °C); Mean Growing Season Precipitation (121.9 ± 42.6 cm; 78.1 ± 42.6 cm); Precipitation of the Three Consecutive Wettest Months (116.2 ± 15.3 cm; 88.5 ± 15.3 cm); and Precipitation of the Three Consecutive Driest Months (40.2 ± 19.8 cm; 54.1 ± 19.8 cm). From these results, the Pico Quemado megaflora can be characterized as having a cool temperate climate, with moderate precipitations and the development of bi-seasonality. The obtained estimations are concordant with previous morphological studies in Pico Quemado, which had proposed the same climate conditions. However, these results are inconsistent compared to other studies of early Neogene Southern Hemisphere that suggest that the climate could be warmer. This difference might be due to the few studies of climatic estimations during the early Neogene in Patagonia, precluding detailed comparisons. In conclusion, Pico Quemado paleoflora exhibits unique climatic conditions, and also floral compositions, as suggested in previous works and here corroborated. The study realized constitutes the first climatic estimations for an Argentinean megaflora developed during the Neogene.

1. Introduction

The study of the climate at the past allows understanding present climate and the evolution of the floral communities, due to the interconnection between the vegetal physiognomy with continent and planet events. Paleobotanical studies in southern South America area led to the proposition of the development of four types of paleofloras during the Paleogene and Neogene periods, under different climatic and geological settings from those of present day (Volkheimer, 1971; Romero, 1978, 1986; Hinojosa and Villagrán, 1997; Troncoso and Romero, 1998; Hinojosa, 2005). These paleofloras suggests that in the late Paleocene and early Eocene, the Neotropical paleoflora developed, with tropical-humid forests covering up to mid-latitudes of the area (Hinojosa and Villagrán, 1997; Troncoso and Romero, 1998; Hinojosa, 2003, 2005). In the same area, a floristic replacement occurred during the Eocene with the development of the Mixed paleofloras, under more

temperate and dry conditions (Romero, 1978, 1986; Troncoso and Romero, 1998). The climate continued to become cooler and drier between late Eocene and Oligocene/Miocene boundary, and the Subantarctic paleofloras were developed, characterized by cold-temperate dry forest (Villagrán and Hinojosa, 1997; Troncoso and Romero, 1998). Finally, the climate then warmed and became wetter, culminating in the middle Miocene climatic optimum, and the Subtropical floras were developed (Hinojosa, 2005; Hinojosa and Villagrán, 1997).

Physiognomic analyses are used to quantitatively estimate terrestrial paleoclimate, for example employing the correlation between the occurrence rate of entire margins in a flora and temperature. The methodology implemented is based in the pioneer works of Bailey and Sinnott (1915, 1916), who observed this robust positive relationship suggesting that could be used as a paleothermometer. Some reasons that explain this phenomenon are: the activity of the physiologic margin, which is higher during the growing season, and in serrated leaf

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margin might be more advantageous in cooler climates (Royer and Wilf, 2006); and the increasing of the activity in the respiration and photosynthesis in leaf species with dentate or lobate margin (Baker-Brosch and Pet, 1997).

The different methodologies more commonly used to estimate climatic parameters in the past are: the Leaf Margin Analysis that estimates the Mean Annual Temperature of a flora (Wolfe, 1979; Wing and Greenwood, 1993; Wilf, 1997); the Leaf Area Analysis, that estimates the Mean Annual Precipitation (Wilf et al., 1998); Climate Leaf Analysis Multivariate Program (CLAMP), more recently proposed by Wolfe (1993), that estimates eight different climatic variables of a particular flora; and the Digital Leaf Phisiognomy, which is similar to the Leaf Margin and Area Analysis, but incorporating more variables (e.g.: number of teeth, size of teeth, foliar perimeter), theoretically resulting in a more informative analysis (Huff et al., 2003; Royer et al., 2005; Peppe et al., 2011).

However, there are few quantitative data on the Cenozoic terrestrial paleoclimate of southern South America. Such data are critical yet, because they can be used to better understanding the evolution of the flora and fauna in the region. Particularly in Argentina the physiognomic studies are scarce. Furthermore, there are no psysiognomical analyses on any Neogene paleoflora, being all the climatic parameters estimated so far belong to ones developed during the Paleogene, such as Salamanca and Río Turbio Formations, and the localities of Laguna del Hunco and Pichileufú River (Hinojosa, 2005; Hinojosa and Villagrán, 1997; Gayó et al., 2005; Peppe et al., 2011). Moreover, Neogene gondwanic paleofloras were physiognomically analyzed in other areas, including Chile or New Zealand (Hinojosa, 2005; Gayó et al., 2005; Reichgelt et al., 2013; Reichgelt et al., 2016).

Under this context, a psysiognomical analysis was made in an Argentinean Neogene paleoflora, located at the Pico Quemado locality, Ñirihuau Formation. The main objective is to characterize the climate of the paleoflora. In second place, compare the result with previously published information and incorporate them in the early Neogene paleoclimatic context.

2. Geological framework

The Pico Quemado locality is sited at both banks of the Arroyo Montoso, next to the mine with homonym name (Fig. 1), and is stratigraphically placed at the base of Ñirihuau Formation (Aragón and Romero, 1984). The Ñirihuau basin is located in the eastern border of the North Patagonian Andes between 41° and 43°S (Cazau, 1972; Cazau et al., 1989, 2005). Its infill is represented by the Nahuel Huapi Group, constituted, from base to top, by the Ventana, Ñirihuau and Collón Curá Formations (González Bonorino and González Bonorino, 1978; Cazau et al., 1989; Asensio et al., 2010; Bechis et al., 2014a). The Ñirihuau Formation comprises clastic and pyroclastic deposits and subordinated carbonates interpreted as deposited in alluvial, lacustrine, deltaic and fluvial environments (Cazau, 1972, 1980; Spalletti, 1981; Cazau et al., 1989; Mancini and Serna, 1989; Bechis, 2004; Giacosa et al., 2005; Paredes et al., 2009). The lower and middle members have been interpreted as deposited mainly in alluvial and lacustrine environments, while from the top of the middle member upwards, deltaic and fluvial deposits prograded over the lacustrine beds (Aragón and Romero, 1984; Spalletti, 1981, 1983; Asensio et al., 2004).

The outcrops of Pico Quemado locality form part of the lower member of Ñirihuau Formation (Aragón and Romero, 1984; Cazau et al., 1989). It is composed by brown gray siltstones and claystones, and represented a fluvial-lacustrine environment (Aragón and Romero, 1984). Its flora was recently studied revealing a dominance of the genus *Nothofagus*, and the presence of Rosaceae, Myrtaceae, Myricaceae, Fabaceae, Malvaceae, Araucariaceae and Podocarpaceae elements (Falaschi et al., 2012; Caviglia and Zamalao, 2014). The most important elements of its angiospermic flora are illustrated in Fig. 2.

The first data of the Ñirihuau Formation indicated a Lower Miocene

age for the unit (22–16 ma.), according to Cazau et al. (1989). But recently, in the works of Bechis et al. (2014a) and Ramos et al. (2015), new data restricted the Ñirihuau Formation unit to the Middle Miocene age (15–11 ma.). Moreover, the upper section of the subyacent Ventana Formation has been indicated with a Lower Miocene age (19–22 ma.), according to Bechis et al. (2014b). Considering that in Pico Quemado locality there are outcrops that belong to the basal section of the Ñirihuau Formation, its age can be considered early Middle Miocene. However, it should be considered that there is no precise age information from the base of Ñirihuau Formation outcrops, including Pico Quemado locality, and it could be possible that its age would be older regarding the complexity of Ñirihuau basin (Cazau et al., 1989; Asensio et al., 2010).

3. Material and methods

3.1. Material

The fossil material is deposited in the Paleobotanical collection, of the Geology Department of the Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires (FCENCBBP), the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (BAPB), and the Museo de la Asociación Paleontológica de Bariloche (MAPBAR). They comprise a total of 600 specimens, preserved as imprints or compressions. There were described 30 morphotypes, finding dominance of Nothofagaceae and Podocarpaceae families (Falaschi et al., 2012; Caviglia and Zamalao, 2014). In addition, less represented, were identified the Araucariaceae, Rosaceae, Malvaceae, Fabaceae and Myricaceae families. The most important angiosperm taxa are represented in Fig. 2.

3.2. Methods

3.2.1. Univariate methods

These types of analyses are based on simple linear regressions. They were realized a *Leaf Margin Analysis* (LMA) for the estimation of the mean annual temperature (MAT), and a *Leaf Area Analysis* (LAA) for the estimation of the mean annual precipitation (MAP). As it was explained before, the LMA were proposed from the positive relationship between climatic warmth and the percentage of dicotyledonous species in a flora that have leaves with entire margins (Bailey and Sinnott, 1915, 1916; Wolfe, 1979; Wilf, 1997). In the present work, the equation used for LMA was developed by Hinojosa et al. (2010), and it's exclusively for South American floras (Table 1).

The *Leaf Area Analysis* relates the mean of the natural logarithm of the leaf area as a function of MAP (Bailey and Sinnott, 1915, 1916; Wilf et al., 1998). The latest proposed equation, published by Peppe et al. (2011), is used in the present work (Table 1). The area measures were realized using SigmaScan Pro 5 (Appendix A). For the reconstruction of incomplete fossil leaves and inferred foliar area of them, the methodology described in Peppe et al. (2011) was followed.

3.2.2. Multivariate methods

A *Climate Leaf Analysis Multivariate Program* (CLAMP) was realized. This is based in a Canonical Correspondence Analyses (CCA) of modern leaf traits with their respective climates (Wolfe, 1993, 1995). CLAMP uses CCA to estimate climate parameters based on 31 woody angiosperm leaf characters. The original data set of CLAMP was developed by Wolfe (1993), based on systematic collection of plant and climate data from North America and Asia. Later, an extended dataset was developed, from South American and Australian flora values (Hinojosa, 2005; Hinojosa et al., 2006a; Hinojosa and Villagrán, 1997; Kennedy et al., 2014). In the present work two different data set were used: the CLAMP 3B SA (Hinojosa et al., 2006b), which excluded data from the coldest and driest localities, values not registered for South American climates; and the data set elaborated by Kennedy et al. (2014) which

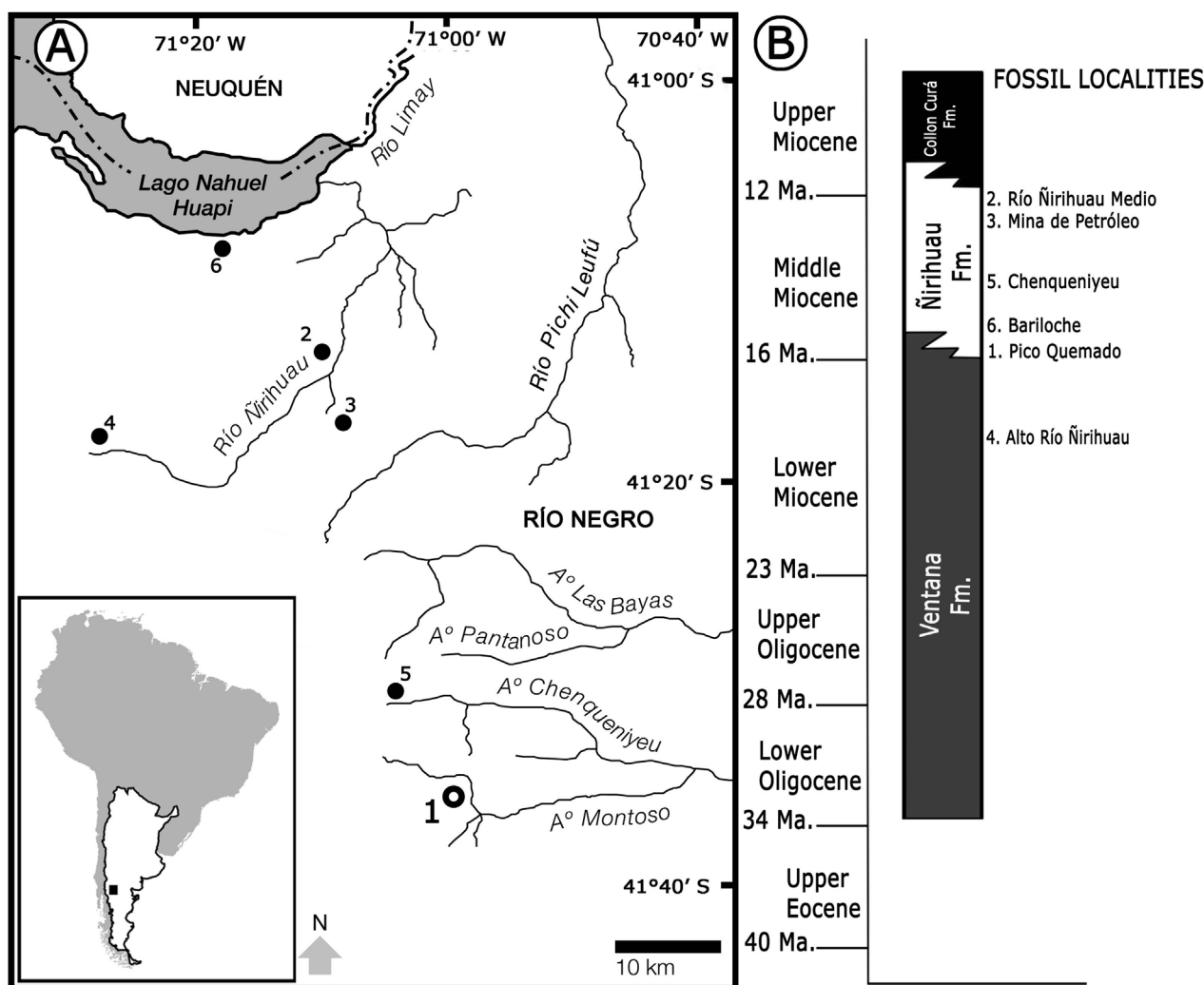


Fig. 1. A, geographical location of the fossiliferous localities of Ñirihuau and Ventana Formations: 1, Pico Quemado (present work); 2, Nahuel Huapi; 3, Río Ñirihuau Medio; 4, Mina de Petróleo; 5, Alto Río Ñirihuau; 6, Chenqueniyeu; 7, Bariloche. B, age of Ñirihuau basin Formations, and stratigraphic position of their macrofloral localities (based on Aragón and Romero, 1984; Cazau et al., 1989; Bechis, 2004; Falaschi et al., 2012; Ramos et al., 2015).

comprises data from Argentina, Bolivia, South Africa, Australia and New Zealand floras. The CCA was performed using R (Core Development Team, 2008). The environmental variables considered were: mean annual temperature (MAT); cold-month mean temperature (CMMT); warm-month mean temperature (WMMT); mean growing season precipitation (MGSP); precipitation of the three consecutive wettest months (MPW); and precipitation of the three consecutive driest months (MPD). Appendix B contains the morphological scores, utilized for CLAMP study, obtained for 22 morphotypes. The equations used for the estimations based on CLAMP 3B SA are in Table 2. The estimations made with Kennedy et al. (2014) dataset were obtained with the CLAMP online website (<http://clamp.ibcas.ac.cn/>).

Finally, the present climatic data of Pico Quemado locality was obtained with the DIVA-GIS program, and the latest updated dataset of <http://www.worldclim.org>.

4. Results

Table 3 exhibits the results for MAT and MAP obtained with both univariate and multivariate methods. According to univariate method, the estimate for MAT was $10.4 (\pm 2.8) ^\circ\text{C}$, meanwhile, the estimate for MAP was a value of $123.7 (\pm 38)$ cm. The climatic variables analyzed with the multivariate model and the CLAMP 3B SA show a predicted MAT of $8.5 (\pm 2.1) ^\circ\text{C}$. For warm-month mean temperature and cold-

month mean temperature, CLAMP estimates values of a $17.4 (\pm 3.7) ^\circ\text{C}$ and $-3.3 (\pm 3.2) ^\circ\text{C}$, respectively. Mean growing season precipitation estimate by CCA model were 121.9.

(± 42.6) cm. Finally, mean precipitation of wet and dry season values are a $116.6 (\pm 19.8)$ cm of and $40.4 (\pm 15.3)$ cm. (Table 3). With the SH dataset, the predicted MAT was $7.2 (\pm 1.4) ^\circ\text{C}$. For warm-month mean temperature and cold-month mean temperature, CLAMP estimates values of a $14.1 (\pm 1.2) ^\circ\text{C}$ and $1.6 (\pm 1.6) ^\circ\text{C}$, respectively. Mean growing season precipitation estimate were $78.1 (\pm 42.6)$ cm. Finally, mean precipitation of wet and dry season values are $88.5 (\pm 15.3)$ cm of and $54.1 (\pm 19.8)$ cm. (Table 3).

5. Discussion

5.1. Characterization of the flora

The MAT and MAP realized estimations suggest that the Pico Quemado paleoflora presented conditions of cold temperate climate (MAT = $8.5 \pm 2.1 ^\circ\text{C}$ and $7.2 \pm 1.4 ^\circ\text{C}$ according to CLAMP) with well-developed levels of humidity (MAP = 123.7 ± 21.2 cm according to LAA). Also, the estimations of CMMT ($-3.3 \pm 3.8 ^\circ\text{C}$ with 3B SA dataset, and $1.6 \pm 1.6 ^\circ\text{C}$ with SH dataset) and WMMT ($17.4 \pm 3.3 ^\circ\text{C}$ with 3B SA dataset, and $14.1 \pm 1.2 ^\circ\text{C}$ with SH dataset), with the 3-WMP ($116.2 \pm 15.3 ^\circ\text{C}$ with the 3B SA dataset, and $88.5 \pm 15.3 ^\circ\text{C}$

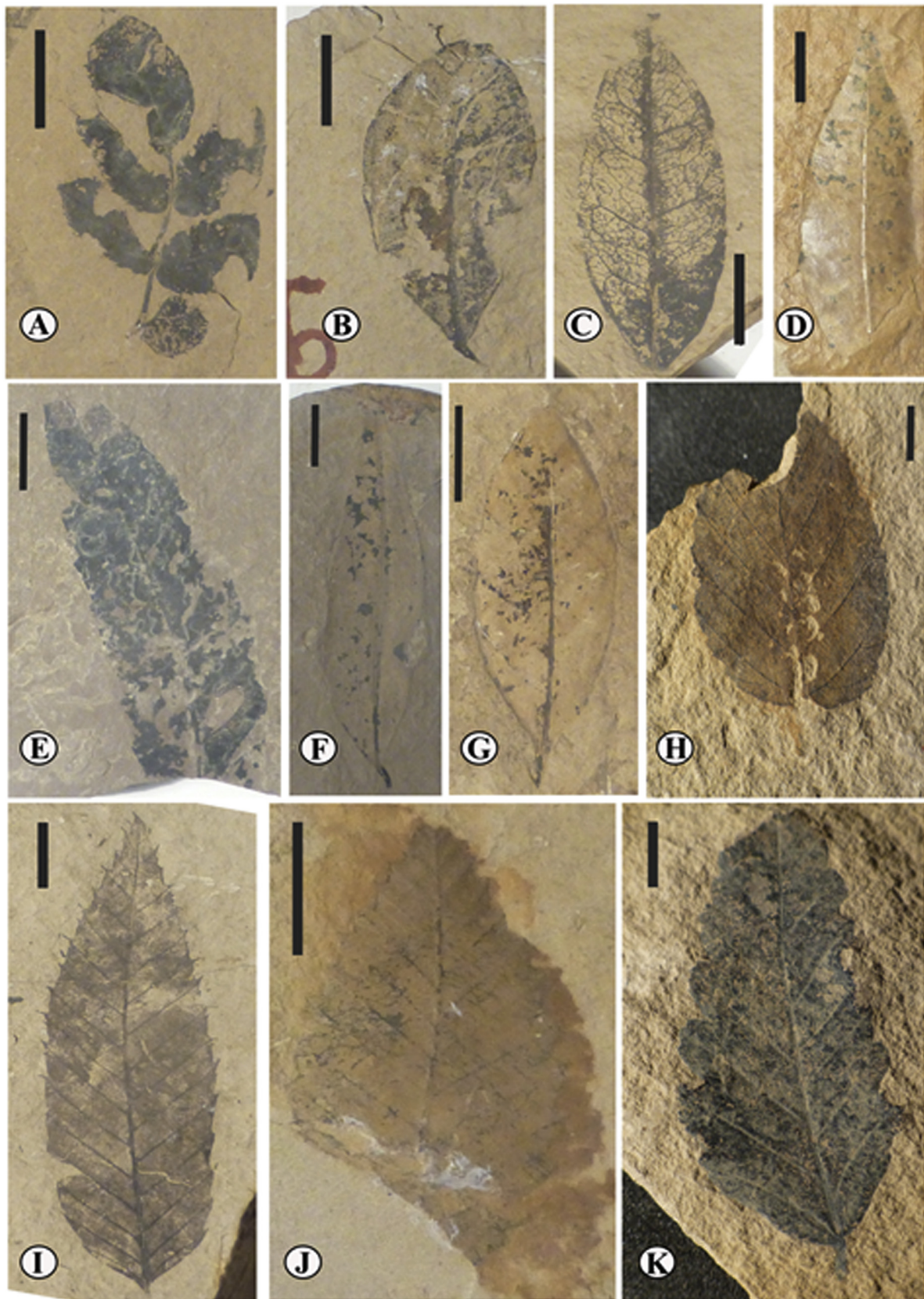


Fig. 2. Angiospermic flora from Pico Quemado locality (Ñirihuau Formation, lower-middle Miocene). **A.** *Acaena* sp., FCENCBPB 357. **B.** *Cassia* cf. *obtusatafolia* Fiori, FCENCBPB 374. **C.** *Eugenia comparabilis* Hollick, FCENCBPB 365. **D.** *Myrciaria acuminata* Engelhardt, FCENCBPB 376. **E.** *Myrica premira* Berry, FCENCBPB 345. **F.** *Myrcia chubutensis* Berry, FCENCBPB 389. **G.** *Myrcia* sp., FCENCBPB 397. **H.** *Nothofagus magelhaenica* Dusén, FCENCBPB 360. **I.** *Nothofagus serrulata* Dusén, FCENCBPB 335. **J.** *Nothofagus simplicidens* Dusén, FCENCBPB 317. **K.** *Nothofagus variabilis* Dusén, FCENCBPB 359. Scale Bar = 1 cm.

Table 1

Linear simple regressions models used for temperature (°C) and precipitation (cm.) estimations, based on the equations of Hinojosa et al. (2010) and Peppe et al. (2011).

Parameter	Variables	Coefficient	r2	SE
MAP	Leaf area average (ln)	0.283	0.23	0.61 (log)
	Constant	2.92		
MAT	Entire proportion	18.85	0.82	2.8
	Constant	3.83		

Abbreviations. MAP: Mean annual precipitation. MAT: Mean annual temperature. SE = standard error. r2 = coefficient of determination.

with the SH dataset) and 3-DMP ($40.2 \pm 19.8^\circ\text{C}$ with the 3B SA dataset, and $54.1 \pm 19.8^\circ\text{C}$ with the SH dataset), suggest bi-seasonality: a cold and a warm season, and a dry and rainy season during the year. These results are similar to the characteristics proposed for the *Humid Continental* type of climate (Koppen, 1923; Belda et al., 2014). This type of climate is characterized by large seasonal temperature differences, with warm summers and cold winters, and precipitations during all year. Finally, the results of the SH dataset are lower than 3B SA dataset. Kennedy et al. (2014) showed that the relationship between leaf margin and temperature is variable, both between Southern and Northern Hemispheres and regionally; and proposed the SH dataset, with a precision similar to those dataset that included Northern Hemisphere floras.

Recent morphological studies of Pico Quemado flora diversity agree with the paleoclimatic estimations made here (Falaschi et al., 2012; Caviglia and Zamaloa, 2014). At first, the locality of Pico Quemado was characterized with a warm and wet environment, according to its geology, woods and presence of some carbon deposits (Aragón and Romero, 1984; Cazau et al., 1989). Recently, Falaschi et al. (2012) studied the gymnospermic and palynoflora of Pico Quemado. According to the found association, the authors infer that the locality had characteristics of high level of humidity, in concordance with the results of this work. In particular, the presences of the genus *Dacrycarpus*, along with fungal evidence, support the hypothesis of high level of humidity requirements. Later, Caviglia and Zamaloa (2014) characterized the angiosperm flora of Pico Quemado, and they found a dominance of the genus *Nothofagus* and important presence of Myrtaceae elements. In addition, important presence of *Nothofagus* pollen was also found (Falaschi et al., 2012). The rest of the families identified (Rosaceae, Malvaceae, Fabaceae and Myricaceae) are cosmopolitan ones (Cronquist, 1981).

The results presented here support previous studies that suggested physiognomical differences between the lower section of Ñirihuau Formation, where Pico Quemado materials were deposited, and the upper section, which could be indicative of higher humidity conditions at the beginning of the deposition (Romero and Dibbern, 1984; Aragón and Romero, 1984; Passalía and Bechis, 2012). For example, it was mentioned that the progressive disappearance of coal levels and the presence of eolianite in the middle section deposits could be evidence of an aridization process (Spalleti, 1981). Falaschi et al. (2012) proposed

Table 2

Equation used for temperature (°C) and precipitation (cm.) estimations under Canonical Correspondance Analyses based on Hinojosa (2005)

Parameter	Equation	r2	SE
Mean annual temperature	$\text{MAT} = -8.1 + \exp(3.1 + (0.24 \cdot \text{MATv}))$	0.88	2.1
Warm month mean temperature	$\text{WMMT} = 23.6 + (4.42 \cdot \text{WMMTv}) - (0.4 \cdot \text{WMMTv}^2)$	0.52	3.3
Cold month mean temperature	$\text{CMMT} = -35.2 + \exp(3.7 + (0.2 \cdot \text{CMMTv}))$	0.81	3.8
Mean growing season precipitation	$\text{MGSP} = 75.5 \cdot \exp(0.53 \cdot \text{MGSPv})$	0.77	42.6
Mean precipitation wet season	$\text{MPW} = -32.6 + \text{EXP}(4.3 + 0.3 \cdot \text{MPWv})$	0.7	19.8
Mean precipitation dry season	$\text{MPD} = 17.5 \cdot \exp(0.7 \cdot \text{MPDv})$	0.61	15.3

Abbreviations. MAT: Mean annual temperature. WMMT: Warm Month Mean Temperatures. CMMT: Cold Month Mean Temperatures. MGSP: Mean Growing Season Precipitation. MPW: Mean Precipitation Wet Season. MPD: Mean Precipitation Dry Season. SE = standard error. r2 = coefficient of determination.

Table 3

Result from both univariate and multivariate methods on Pico Quemado paleoflora with standard deviation.

Parameter	Method	Results
MAP (cm.)	LAA	123.7 ± 21.2
MAT (°C)	CLAMP (3B SA dataset)	8.5 ± 2.1
	CLAMP (SH dataset)	7.2 ± 1.4
WMMT (°C)	LMA	10.4 ± 2.1
	CLAMP (3B SA dataset)	17.4 ± 3.3
CMMT (°C)	CLAMP (SH dataset)	14.1 ± 1.2
	CLAMP (3B SA dataset)	$(-3.3) \pm 3.8$
GSP (cm.)	CLAMP (SH dataset)	1.6 ± 1.6
	CLAMP (3B SA dataset)	121.9 ± 42.6
3-WMP (cm.)	CLAMP (SH dataset)	78.1 ± 42.6
	CLAMP (3B SA dataset)	116.2 ± 15.3
3-DMP (cm.)	CLAMP (SH dataset)	88.5 ± 15.3
	CLAMP (3B SA dataset)	40.2 ± 19.8
	CLAMP (SH dataset)	54.1 ± 19.8

Abbreviations. MAP: Mean annual precipitation. MAT: Mean annual temperature. WMMT: Warm Month Mean Temperatures. CMMT: Cold Month Mean Temperatures. MGSP: Mean Growing Season Precipitation. MPW: Mean Precipitation Wet Season. MPD: Mean Precipitation Dry Season. LAA: Leaf Area Analysis. LMA: Leaf Margin Analysis. CLAMP 3B SA dataset from Hinojosa et al. (2006b). CLAMP SH dataset from Kennedy et al. (2014).

that, on one hand, the presence of orthonconglomerate and diamictite could be recording a regressive episode linked with a sudden drop of the sea level, tied with the Antarctic glaciation; however, it could be also evidence of the Andean uplifting beginning, as well proposed by Spalleti (1981). The results of this work record a high level humidity at the beginning of the deposition. Unfortunately, no complete macrofloras have been identified from the upper section in order to test the hypothesis of aridization.

Nowadays, Pico Quemado locality exhibits a MAT of 7.7°C and a MAP of 62.7 cm. During the winter, shows a mean temperature of 0.1°C , meanwhile the mean temperature of the summer is 11.5°C . The estimated paleoclimate obtained for Pico Quemado suggest similar MAT values, with univariate (a little higher) and multivariate methods, higher values of MAP, and higher thermic amplitude, according CMMT and WMMT values. The similar MAT values are in agreement with the hypothesis that the climate cooling of the area took place at the beginning of the Miocene (Aragón et al., 2011). It has to be considered that, at this time, important geological changes affected the climate in Patagonia: opening of Drake's passage and establishment of the Antarctic Circumpolar Current, the initiation of the Antarctic Glaciation, and the Andean uplift (Lyle et al., 2007; Le Roux, 2012; Charrier et al., 2015). These events produced a decrease in the temperatures and precipitations in Patagonia since the late Eocene (Hinojosa, 2005; Hinojosa and Villagrán, 2005). It was suggested that the deposits of the lower section of the Ñirihuau Formation are related to an extensional stage of the basin, and the deposit of the upper section are related to the North Patagonian Andes uplift (Mancini and Serna, 1989; Bechis, 2004; Bechis et al., 2014a; Orts et al., 2012; Ramos et al., 2015). But recently, other authors proposed that the Ñirihuau Formation is developed in a

Table 4

Comparison of Pico Quemado with other Miocene floras. Estimated values taken from Hinojosa (2005); Hinojosa et al., 2006a; Hinojosa et al., 2010; Reichgelt et al., 2015; and Reichgelt et al., 2016. References: *estimated values from Lake Manuherikia are averaged. MAP values from Pupuya are not specified in Hinojosa (2005). MAP values of Lake Manuherikia and Dunedin Volcano were estimated with a different methodology (Reichgelt et al., 2015; Reichgelt et al., 2016).

Floras	MAT (°C)	MAP (cm.)	Age	Location	Latitude
Pico Quemado	7.2 ± 1.4	123.7 ± 21.2	middle Miocene	Patagonia, Argentina	41° 34'
Goterones	16.9 ± 2.4	112.0 (+72.7; -44.1)	early Miocene	Patagonia, Chile	33°57'
Pupuya	21.7 ± 2.1	-	middle Miocene	Patagonia, Chile	33°57'
Jakokkota	21.4 ± 2.1	43.6 (+28.3; -17.2)	late Miocene	Bolivia	17°17'
Lake Manuherikia*	18.2* ± 2.8	-	early Miocene	New Zealand	48°17'
Dunedin Volcano	11.7 ± 1.4	-	mid/late Miocene	New Zealand	45°55'

foreland basin as a consequence of the last orogenic stage of the North Patagonian Andes (Orts et al., 2015). Considering both theories, and the humidity levels estimated for the studied area, Pico Quemado paleoflora could be evidence of the last Patagonian humid forest, as it was suggested by Falaschi et al. (2012).

5.2. The development of Pico Quemado paleoflora during the Miocene of Patagonia

Pico Quemado estimations do not appear to be consistent with the general climate trend recognized during the early Neogene in Patagonia. The late Paleogene was characterized by the deterioration of the climate conditions, with both temperature and precipitation tending to decrease; but in the Paleogene/Neogene limit, the temperature increased (Zachos et al., 2001; Hinojosa, 2005). One of the most important physiognomic changes in the late Oligocene-early Miocene was the replacement of the humid forest communities, that were developed in some portions of extra-andean Patagonia during early Miocene, by the xerophytic forests, lower and open, with Fabaceae, Anacardiaceae and Ulmaceae, towards the late Miocene (Troncoso and Romero, 1998; Barreda and Palazzesi, 2007; Palazzesi and Barreda, 2007). During the Miocene, the central Chile forests incorporated warm elements, whereas the austral Antarctic elements decreased (Hinojosa, 2005; Hinojosa et al., 2006a; Quattrocchio et al., 2013). On the contrary, Pico Quemado estimations do not indicate warm conditions at the same time, and its composition (both micro and megaflores), reveal a dominance of austral elements, as it was mentioned earlier (Falaschi et al., 2012; Caviglia and Zamalao, 2014).

Pico Quemado paleoflora exhibits unique characteristics, as it was suggested before; this could be due to its characteristics were not found in others paleofloras from Patagonia yet (Falaschi et al., 2012; Caviglia and Zamalao, 2014). The study of the floral composition led to categorize it as “transitional between Mixed with *Nothofagus* and Subantarctic”. The estimations obtained in this work are in agreement with this affirmation. It cannot be considered a Mixed paleoflora because they are characterized by thermal equability (thermal amplitude equal to 0 °C), and MAT values around 14 °C (Hinojosa, 2005; Hinojosa and Villagrán, 2005), whereas in the Pico Quemado flora they range between 8 °C and 10 °C. Unfortunately, no Subantarctic paleoflora was physiognomically analysed yet, but Troncoso and Romero (1998) affirmed that they should have been dry forests. On the other hand the existence of Subantarctic paleofloras in the past has not very much consensus nowadays. Historically, it was considered that the late Paleogene cooling and drying of the climatic conditions allowed the replacement of the Mixed paleofloras with the Subantarctic paleofloras (Romero, 1978, 1986; Hinojosa and Villagrán, 1997; Troncoso and Romero, 1998; Pearson and Palmer, 2000; Zachos et al., 2001). However, it was recently suggested that the Mixed paleofloras were replaced by Subtropical Gondwanic ones, where tropical elements continues being important in relative abundance (Gayó et al., 2003; Hinojosa, 2005; Hinojosa and Villagrán, 2005; Quattrocchio et al., 2013). However, this characterization is not suitable for several paleofloras of the Oligocene-Miocene limit, including Pico Quemado. For example, the

Río Leona, Río Guillermo and Barrancas Carmen Silva paleofloras have important presence of Nothofagaceae elements and few representatives of tropical families (Dusén, 1899; Panti, 2011; Césari et al., 2015).

The Ñirihuau Formation was physiognomically analysed and characterized in previous works (Hinojosa, 2005; Hinojosa and Villagrán, 2005; Hinojosa et al., 2006a), based on the materials described by Berry (1928) and Fiori (1931, 1939; 1940). These descriptive contributions presented materials recollected in several localities closely to Pico Quemado: Río Ñirihuau and Nahuel Huapí (Berry, 1928); Nahuel Huapí (Fiori, 1931); Río Ñirihuau Medio and Alto Río Ñirihuau (Fiori, 1939); and Mina de Petróleo and Chenqueniyeu (Fiori, 1940). However, not all of them belong to Ñirihuau Formation (Aragón and Romero, 1984; Romero and Dibbern, 1984; Cazau et al., 1989). For example, Nahuel Huapí is included in Huitrera Formation (Eocene; Aragón and Romero, 1984), and Alto Río Ñirihuau belongs to Ventana Formation (Lower-Upper Oligocene; Aragón and Romero, 1984). The rest of the localities are included in Ñirihuau Formation, and are located geographically and stratigraphically in Fig. 1. The physiognomic estimations made on the contributions early mentioned included all the localities studied by Berry (1928) and Fiori (1931, 1939; 1940), therefore, these estimations were made with some localities that don't are included in Ñirihuau Formation. For example, predicted MAT for Ñirihuau Formation was between 17.2 ± 2.1 and 18.4 ± 2.2 °C (Hinojosa, 2005; Hinojosa and Villagrán, 2005), values much higher in comparison with Pico Quemado. Considering that these estimations included data from older localities, it seems logic that the predicted values are not similar with the realized in the present work.

In the Southern Hemisphere few Miocene paleofloras were analysed. Specifically in South America Pupuya, Goterones and Jakokkota Formations were used for comparisons (Hinojosa, 2005; Hinojosa et al., 2006a; Hinojosa et al., 2010). However, they appear to be very different from the Pico Quemado paleoflora (Table 4): Goterones was characterized as Mixed and both the others as Neotropical, all of them have MAT and MAP values twice higher than Pico Quemado (Hinojosa, 2005; Hinojosa et al., 2006a). It has to be considered several differences between these paleofloras and Pico Quemado: 1) the taxonomic compositions of Goterones, Pupuya and Jakokkota paleofloras present important relevance of tropical elements (Troncoso, 1991; Gregory-Wodzicki, 2000); 2) these paleofloras were developed in lower latitudes (Tables 4 and 3) the development of the paleofloras during the Miocene was not similar in Chile and Argentina (Barreda et al., 2007; Palazzesi and Barreda, 2007; Quattrocchio et al., 2013), principally due the geological changes that occurred at this time and that were mentioned earlier.

Several CLAMP estimations were made in Miocene age New Zealand localities also (Table 4). Reichgelt et al. (2015) analysed localities from Lake Manuherikia area, and Reichgelt et al. (2016) did the same for Dunedin Volcano area. Both contributions obtained estimations higher than Pico Quemado, characterizing the areas with warm temperature and high precipitations. These estimations are between normal parameters, if it is considered that New Zealand paleoclimate is characteristically subtropical during late Oligocene-middle Miocene, and a sea level fall with a cooler climate is observed just in the late Miocene

(Onheiser et al., 2015; Prebble et al., 2017). In contrast, in Argentina the cooling would began earlier, the early-middle Miocene floras were dominated by elements of the austral forests, like Nothofagaceae, Araucariaceae, Podocarpaceae, among others (Barreda et al., 2007).

The analysis performed on the material of Pico Quemado shows concordance with the studies of the locality (Aragón and Romero, 1984; Falaschi et al., 2012; Caviglia and Zamalao, 2014), but it does not agree with the general understanding of the early Neogene of Patagonia or other Southern Hemispheres paleofloras. This could be for two reasons: first, the climate understanding of Patagonia in Argentina during the early.

Neogene is not well known yet. In fact, Pico Quemado's estimations represent the first in an Argentinean paleoflora developed during the Miocene. Floras of similar age in Argentina, such as Barrancas Carmen Silva and Cullen Formation (Troncoso and Romero, 1998) should be analysed in order to provide more information for comparisons and discussion. Otherwise, the discrepancies found in the estimations made could be due local effects on Pico Quemado locality, as it was suggested in previous works (Falaschi et al., 2012; Caviglia and Zamalao, 2014). Ñirihuau Formation represents an important paleoflora in Patagonia, and its composition is not studied in detail yet. Further work is need in order to better categorize it and contribute to the general understanding of early Neogene in Patagonia.

6. Conclusions

The Pico Quemado paleoflora was found as a cold-temperate one, with well-developed levels of humidity and seasonality, similar to the actual Humid Continental climate type. These results are concordant with the previous studies at the locality. There were found differences between the results and the general climate trends in Patagonia during the early Neogene based in other localities. It is suggested that the Pico Quemado paleoflora constitutes an assemblage with unique characteristics, and no other one with similar features were described yet.

Pico Quemado brings new information about the development of the early Neogene in Patagonia, and it's the first paleoflora studied using physiognomic analyses for the Miocene of Argentina. No other Neogene Argentinean paleoflora was physiognomically studied yet. Furthermore, other megaflores of similar age were described several years ago, and its morphological information is quite doubtful and needs to be revised. Further climatic estimations made in other coeval units may increase the available information, resulting in a more complete perspective of the climatic trends established during the Miocene in Patagonia, allowing to understand the particular conditions recorded in the Pico Quemado paleoflora.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.jsames.2018.08.002>.

References

Aragón, E., Romero, E.J., 1984. Geología, paleoambientes y paleobotánica de yacimientos terciarios del occidente de Río Negro, Neuquén y Chubut. 9º Congreso Geológico Argentino (San Carlos de Bariloche). Acta 4, 475–507.

Aragón, E., Goin, F.J., Aguilera, Y.E., Woodburne, M.O., Carlini, A.A., Roggerio, M.F.,

2011. Palaeogeography and palaeoenvironments of northern Patagonia from the late cretaceous to the Miocene: the palaeogeographic and the rise of the North Patagonian high plateau. *Biol. J. Linn. Soc.* 103, 305–315.

Asensio, M., Zavala, C., Arcuri, M., 2004. Evidencias de la acción de mareas en la Cuenca de Ñirihuau. In: 10th Reunión Argentina de Sedimentología, Resúmenes, pp. 19–21.

Asensio, M.A., Cornou, M.E., Malumán, N., Martínez, M.A., Quattrocchio, M.E., 2010. Formación Río Foyel, Oligoceno de la Cuenca de Ñirihuau: la transgresión pacífica en la Cordillera Norpatagónica. *Rev. Asoc. Geol. Argent.* 66 (3), 399–405.

Bailey, I.W., Sinnott, E.W., 1916. The climatic distribution of certain types of angiosperm leaves. *Am. J. Bot.* 3, 24–39.

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

Baker Brosh, K.F., Pet, R.K., 1997. The Ecological Significance of Lobed and Toothed Leaves in Temperate forest Trees: *Ecology* 78, pp. 1250–1255.

Barreda, V., Palazzesi, L., 2007. Patagonian vegetation turnovers during the Paleogene–Early Neogene: origin of arid-adapted floras. *Bot. Rev.* 73, 31–50.

Barreda, V., Anzotegui, L.M., Prieto, A., et al., 2007. Diversificación y cambios de las angiospermas durante el Neógeno en Argentina. *Ameghiniana, Publicación Especial* 11, 173–191.

Bechis, F., 2004. Geología y estructura del sector medio de los ríos Ñirihuau y Pichileufú, provincia de Río Negro. Trabajo Final de Licenciatura, Universidad de Buenos Aires, pp. 121.

Bechis, F., Encinas, A., Concheyro, A., Litvak, V.D., Aguirre-Urreta, B., Ramos, V.A., 2014a. New age constraints for the Cenozoic marine transgressions of northwestern Patagonia, Argentina (41°–43° S): paleogeographic and tectonic implications. *J. S. Am. Earth Sci.* 52, 72–93.

Bechis, F., Encinas, A., Litvak, V., Valencia, V., Ramos, V.A., 2014b. Nuevas edades U-Pb del relleno de la cuenca de Ñirihuau, Andes Norpatagónicos. 19º Congreso Geológico Argentino, Córdoba, Simposio Tectónica Andina, Actas, pp. S22 12.

Belda, M., Holtanová, E., Halenka, T., Kalvová, J., 2014. Climate classification revisited: from Köppen to Trewartha. *Clim. Res.* 59, 1–13.

Berry, E.W., 1928. Tertiary fossil plants from the Argentine republic. *Proceedings US National Museum* 73, 1–27.

Caviglia, N., Zamalao, M.C., 2014. Flora angiospérmica de Pico Quemado, Formación Ñirihuau (Oligoceno tardío), Provincia de Río Negro. Argentina. *Ameghiniana* 51 (3), 209–225.

Cazau, L., 1972. Cuenca del Ñirihuau–Ñorquinco–Cushamen. In: *Geología Regional Argentina. Academia Nacional de Ciencias, Córdoba*, pp. 299–318.

Cazau, L.B., 1980. Cuenca de Ñirihuau e Ñorquinco e Cushamen. In: Turner, J.C. (Ed.), *Geología Regional Argentina. Academia Nacional de Ciencias de Córdoba*, pp. 1149–1171.

Cazau, L., Mancini, D., Cangini, J., Spalletti, L., 1989. Cuenca de Ñirihuau. In: Chebli, G.A., Spalletti, I. (Eds.), *Cuencas Sedimentarias Argentinas. Serie Correlación Geológica* 6. Universidad Nacional de Tucumán, pp. 299–318.

Cazau, L., Cortiñas, J., Reinante, S., Asensio, M., Bechis, F., Aprea, D., 2005. Cuenca de Ñirihuau. In: En: G., Chebli, J.S., Cortiñas, L., Spalletti, L., Legarreta, E.L. Vallejo (Eds.), *Frontera Exploratoria de la Argentina. 6º Congreso de Exploración y Desarrollo de Hidrocarburos (Mar del Plata)*, Actas, pp. 251–273.

Césari, S.N., Panti, C., Pujana, R.R., Francis, J.E., Marensi, S., 2015. The late Oligocene flora from the Río Leona formation, argentinian patagonian. *Rev. Palaeobot. Palynol.* 216, 143–158.

Charrier, R., Ramos, V.A., Tapia, F., Sagripanti, L., 2015. Tectono-stratigraphic evolution of the andean orogen between 31 and 37°S (Chile and Western Argentina). In: *Geodynamic Processes in the Andes of Central Chile and Argentina*.

Cronquist, A., 1981. An Integrated System of Classification of Flowering Plants. The New York Botanical Garden. Columbia University Press, Nueva York, pp. 1262.

Dusén, P., 1899. Über die tertiäre Flora der Magellansländer. *Wissenschaftliche Ergebnisse der Schwedischen Expedition nach der Magellansländern*, pp. 84–107 1895–1897, band 1.

Falaschi, P., Zamalao, M.C., Caviglia, N., Romero, E.J., 2012. Flora gimnospérmica de la Formación Ñirihuau (Oligoceno tardío–Mioceno temprano), Provincia de Río Negro. *Ameghiniana* 49 (4), 525–551.

Fiori, A., 1931. Fillite terziare della Patagonia. I. Fillite della riva meridionale del Lago Nahuel Huapi. *Giorn. Geol.* 6, 101–116.

Fiori, A., 1939. Fillite terziare della Patagonia. II. Fillite del Río Ñirihuau. *Giorn. Geol.* 13, 1–27.

Fiori, A., 1940. Fillite terziare della Patagonia. III. Fillite del Río Chenqueniyeu. *Giorn. Geol.* 14, 93–133.

Gayó, E., Hinojosa, L.F., Villagrán, C., 2003. On the persistence of tropical paleofloras in Central Chile during the early Eocene. *Rev. Palaeobot. Palynol.* 137, 41–50.

Giacosa, R., Alfonso, J., Heredia, N., Paredes, J.M., 2005. Tertiary tectonics of the sub-andean region of the North Patagonian Andes, southern central Andes of Argentina (41–42 30' S). *J. S. Am. Earth Sci.* 20, 157–170.

González Bonorino, F., y González Bonorino, G., 1978. Geología de la región de San Carlos de Bariloche: un estudio de las formaciones terciarias del Grupo Nahuel Huapi. *Revista Asociación Geológica Argentina* 33, 175–210.

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

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

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 equality or in the absence of an effective andean barrier during the

- cenozoic? Paleogeography. *Paleoclimatology and Paleoecology* 217 (1–2), 1–23.
- Hinojosa, L.F., Armesto, J.J., Villagrán, C., 2006a. Are Chilean coastal forests pre-Plesitocene relicts? Evidence from foliar physiology, palaeoclimate and phytoecology. *J. Biogeogr.* 33, 331–341.
- Hinojosa, L.F., Pesce, O., Yabe, A., Uemura, K., Nishida, H., 2006b. In: Nishida, H. (Ed.), *Physiological Analysis and Paleoclimate of the Ligorio Márquez Fossil flora, Ligorio Márquez Formation, 46°45'S, Chile. Post Cretaceous Floristic Changes in Southern Patagonia, Chile*. Chuo University, Tokyo, pp. 45–55.
- Hinojosa, L.F., Pérez, F., Gaxiola, A., Sandoval, I., 2010. Historical and phylogenetic constraints on the incidence of entire leaf margins: insights from a new South American model. *Global Ecol. Biogeogr.* 1–11.
- Huff, P.M., Wilf, P., y Azumah, E.J., 2003. Digital future for paleoclimate estimation from fossil leaves? Preliminary results. *Palaios* 18, 266–274.
- Kennedy, E.A., Arens, N.A., Reichgelt, T., Spicer, R.A., Spicer, T.V.E., Stranks, L., Yang, J., 2014. Deriving temperature estimates from Southern Hemisphere leaves. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 412, 80–90.
- Köppen, W., 1923. *Die Klimate der Erde. Grundriss der Klimakunde*. Walter de Gruyter, Berlin, pp. 223.
- Le Roux, J.P., 2012. A review of Tertiary climate changes in southern South America and the Antarctic Peninsula. Part 1: oceanic conditions. *Sediment. Geol.* 247 (248), 1–20.
- Lyle, M., Gibbs, S., Moore, T.C., Rea, D.K., 2007. Late Oligocene initiation of the antarctic circumpolar current: evidence from the South Pacific. *Geology* 35 (8), 691–694.
- Mancini, D., Serna, M., 1989. Evaluación petrolera de la Cuenca de Ñirihuaú. *Sudoste de Argentina. 1º Congreso Nacional de Exploración de Hidrocarburos (Buenos Aires)*. Acta 2, 739–762.
- Ohneiser, C., Florindo, F., Stocchi, P., Roberts, A.P., Deconto, R.M., Pollard, D., 2015. Antarctic glacio-eustatic contributions to late Miocene Mediterranean desiccation and reflooding. *Nat. Commun.* 6, 8765.
- Orts, D.L., Folguera, A., Encinas, A., Ramos, M., Tobal, J., Ramos, V., 2012. Tectonic development of the North Patagonian Andes and their related Miocene foreland basin (41°30'–43°S). *Tectonics* 31, 1–24.
- Orts, D.L., Folguera, A., Gimenez, M.E., Ruiz, F., Encinas, A., Rojas Vera, E.A., Klinger, F.L., 2015. Cenozoic deformational processes in the North Patagonian Andes. *J. Geodyn.* 86, 26–41.
- Palazzesi, L., Barreda, V., 2007. Major vegetation trends in the Tertiary of Patagonia (Argentina): a qualitative paleoclimatic approach based on palynological evidence. *Flora* 202, 328–337.
- Panti, C., 2011. Análisis paleoflorístico de la Formación Río Guillermo (Eoceno tardío–Oligoceno temprano?), Santa Cruz, Argentina. *Ameghiniana* 48, 320–335.
- Paredes, J.M., Giacosa, R.E., Heredia, N., 2009. Sedimentary evolution of Neogene continental deposits (Ñirihuaú Formation) along the Ñirihuaú river, North Patagonian Andes of Argentina. *J. S. Am. Earth Sci.* 28, 74–88.
- Passalia, M.G., Bechis, F., 2012. Megafloras de la sección basal de la Formación Ñirihuaú (Oligoceno Superior–Mioceno Inferior) en las localidades Pico Quemado y Cordón de las Bayas, provincia de Río Negro, Argentina. In: 15th Simposio Argentino de Paleobotánica y Palinología, Corrientes, Proceedings in CDROM.
- Pearson, P.N., Palmer, M.R., 2000. Atmospheric carbon dioxide concentrations over the past 60 million years. *Nature* 406, 695–699.
- Peppe, D.J., Royer, D., Cariglino, B., Oliver, S.Y., Newman, S., Leight, E., Enikolopov, G., Fernandez-Burgos, M., Herrera, F., Adams, J.M., Correa, E., Currano, E., Erickson, J.M., Hinojosa, L.F., Hoganson, J.W., Iglesias, A., Jaramillo, C.A., Johnson, K.R., Jordan, G.J., Kraft, N.J., Lovelock, E.C., Lusk, C.H., Niinemets, U., Peñuelas, J., Rapson, G., Wing, S.L., Wright, I.J., 2011. Sensitivity on leaf size and shape to climate: global patterns and paleoclimate applications. *New Phytol.* 190, 724–739.
- Prebble, J.A., Reichgelt, T., Mildenhalla, D.C., Greenwood, D.G., Raine, J.I., Kennedy, E.A., Seebeck, H.C., 2017. Terrestrial climate evolution in the Southwest Pacific over the past 30 million years. *Earth Planet Sci. Lett.* 459, 136–144.
- Quattrocchio, M.E., Martínez, M.A., Hinojosa, L.F., Jaramillo, C., 2013. Quantitative analysis of cenozoic palynofloras from Patagonia, southern South America. *Palynology* 37 (2), 246–258.
- R Development Core Team, 2008. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria ISBN 3-900051-07-0. <http://www.R-project.org>.
- Ramos, M.E., Tobal, J., Sagripanti, L., Folguera, A., Orts, D.L., Giménez, M., Ramos, V.A., 2015. The North Patagonian orogenic front and related foreland evolution during the Miocene, analyzed from synorogenic sedimentation and U/Pb dating (~42°S). *J. S. Am. Earth Sci.* 64, 467–485.
- Reichgelt, T., Kennedy, E.M., Mildenhall, D.C., Conran, J.G., Greenwood, D.R., y Lee, D.E., 2013. Quantitative paleoclimates estimates for early Miocene southern New Zealand: evidence from foulden maar. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 378, 36–44.
- Reichgelt, T., Kennedy, E.M., Conran, J.G., Mildenhall, D.C., Lee, D.E., 2015. The early Miocene paleolake Manuherikia: vegetation heterogeneity and warm-temperate to subtropical climate in southern New Zealand. *Journal of Paleolimnology* 53, 349–365.
- Reichgelt, T., Kennedy, E.M., Jones, W.A., Jones, D.T., Lee, D.E., 2016. Contrasting palaeoenvironments of the mid/late Miocene Dunedin Volcano, southern New Zealand: climate or topography? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 441, 696–703.
- Romero, E.J., 1978. Paleogeología y Paleofitogeografía de las taofloras del Cenofítico de Argentina y áreas vecinas. *Ameghiniana* 15, 209–227.
- Romero, E.J., 1986. Paleogene Phytogeography and Climatology of South America: *Annals of the Missouri Botanical Garden* 73, pp. 449–461.
- Romero, E.J., Dibern, M.C., 1984. Floras fósiles cenozoicas. En: *geología y recursos naturales de la provincia de Río Negro*. Relatorio IX Congreso Geológico Argentino 373, 382.
- Royer, D.L., Wilf, P., 2006. Why do toothed leaves correlate with cold climates? Gas exchange at leaf margins provides new insights into a classic paleotemperature proxy. *Int. J. Plant Sci.* 167, 11–18.
- Royer, D.L., Wilf, P., Janesko, D.A., Kowalski, E.A., Dilcher, D.L., 2005. Correlations of climate and plant ecology to leaf size and shape: potential proxies for the fossil record. *Am. J. Bot.* 92, 1141–1151.
- Spalletti, L.A., 1981. Facies sedimentarias de la Formación Ñirihuaú en la región de San Carlos de Bariloche, provincia de Río Negro. *Rev. Asoc. Geol. Argent.* 36, 286–311.
- Spalletti, L.A., 1983. Paleogeografía de la Formación Ñirihuaú y sus equivalentes en la región Occidental de Neuquén, Río Negro y Chubut. *Rev. Asoc. Geol. Argent.* 38, 454–468.
- Troncoso, A.A., 1991. Paleomegaflores de la Formación Navidad, Miembro Navidad (Mioceno), en el área de Matanzas, Chile central Occidental. *Boletín Museo Nacional Historia Natural Chile* 42, 131–168.
- Troncoso, A., Romero, E.J., 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*, pp. 149–172.
- Villagrán, C., Hinojosa, L.F., 1997. Historia de los bosques del sur de Sudamérica, II: análisis fitogeográfico. *Rev. Chil. Hist. Nat.* 70, 241–267.
- Volkheimer, W., 1971. Aspectos paleoclimatológicos del terciario Argentino. *Rev. Mus. Argent. Cienc. Nat. Bernardino Rivadavia* 8, 241–264.
- Wilf, P., 1997. When are leaves good thermometers? A new case for Leaf Margin Analysis. *Paleobiology* 23, 373–390.
- Wilf, P., Wing, S.L., Greenwood, D.R., Greenwood, C.L., 1998. Using Fossil Leaves as Paleoprecipitation Indicators, an Eocene Example. *Geology* 26, pp. 203–206.
- Wing, S., Greenwood, D.R., 1993. Fossils and fossil climate: the case for equable continental interiors in the Eocene. *Phil. Trans. Roy. Soc. Lond. B* 341, 243–252.
- Wolfe, J.A., 1979. Temperature Parameters of Humid to Mesic Forests of Eastern Asia and Relation to Forests of Other Regions of Northern Hemisphere and Australasia. 1106. US Geological Survey Professional Paper, pp. 37.
- Wolfe, J., 1993. A method of obtaining climatic parameters from leaf assemblages. *US Geol. Surv. Bull.* 2040, 71.
- Wolfe, J., 1995. Paleoclimatic estimates from tertiary leaf assemblages. *Annu. Rev. Earth Planet Sci.* 23, 119–142.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., y Billups, K., 2001. Trends, rhythms and aberrations in global climate 65 Ma to present. *Science* 292, 686–693.