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palevol
2021 • 20 • 3

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art. 20 (3) — Published on 25 January 2021
www.cr-palevol.fr

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Fossil leaf of *Nothofagus simplicidens* Dusén, 1899 from the Rio Turbio Formation, Argentina. Photo: Bárbara Vento.

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ISSN (imprimé / *print*): 1631-0683/ ISSN (électronique / *electronic*): 1777-571X

Paleoclimate estimates for the Paleogene-Neogene in southern South America using fossil leaves as proxies

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Submitted on 30 August 2019 | Accepted on 23 December 2019 | Published on 25 January 2021

urn:lsid:zoobank.org:pub:F731FA4B-CDE8-434C-8104-9040CD4B4DCB

Vento B., Puebla G. G, Pinzón D. & Prámparo M. 2021. — Paleoclimate estimates for the Paleogene-Neogene in southern South America using fossil leaves as proxies. *Comptes Rendus Palevol* 20 (3): 29-48. https://doi.org/10.5852/cr-palevol2021v20a3

ABSTRACT

It is widely recognized that fossil leaves are good proxies for paleoclimate estimates, and leaf physiognomy analysis is a traditional technique used to make climate estimates. There are only a few paleoclimate reconstructions for the southern part of South America based on this technique. Here we report climate parameters using fossil leaves from the Río Turbio (Eocene-Oligocene) and Río Guillermo (Oligocene-early Miocene?) formations in southern South America, Cuenca Austral, Argentina. We used univariate (leaf margin and leaf foliar area analysis) and multivariate methods (CLAMP, DiLP) on two datasets from South America, in the Southern Hemisphere. Lower and upper members of the Río Turbio Formation show a mixed paleoflora represented by paratropical as well as cool-temperate taxa such as *Nothofagus*, with a similar percentage of untoothed fossil leaves. Climate estimates indicate warm and humid conditions for both Río Turbio Formation members. The Río Guillermo Formation is represented by mostly cool-temperate elements, mainly *Nothofagus,* and most with toothed margins. The paleoclimate analysis indicates a decrease in temperature and precipitation when comparing the two studied formations. Today, temperate forests in southern Argentina have a plant composition and climate more similar to the estimates made for the Río Guillermo Formation.

KEY WORDS
Paleoclimate,
leaf physiognomy,
temperature,
precipitation.

RÉSUMÉ

Estimations du paléoclimat pour le Paléogène-Néogène dans le sud de l'Amérique du Sud en utilisant des feuilles fossiles comme indicateurs.

Il est largement reconnu que les feuilles fossiles sont de bons indicateurs pour les estimations paléoclimatiques, de même que l'analyse de la physionomie des feuilles est une technique traditionnelle utilisée pour faire des estimations climatiques. Il n'existe que quelques reconstitutions paléoclimatiques pour la partie sud de l'Amérique du Sud basées sur cette technique. Nous présentons ici les paramètres climatiques en utilisant des feuilles fossiles des formations du Río Turbio (Eocène-Oligocène) et du Río Guillermo (Oligocène-Début du Miocène ?) dans le sud de l'Amérique du Sud, à Cuenca Austral, en Argentine. Nous avons utilisé des méthodes univariées (analyse de la marge foliaire et de la surface foliaire des feuilles) et multivariées (CLAMP, DiLP) sur deux ensembles de données provenant d'Amérique du Sud, dans l'hémisphère sud. Les membres inférieurs et supérieurs de la formation du Río Turbio montrent une paléoflore mixte représentée par des taxons paratropicaux et tempérés comme *Nothofagus*, avec un pourcentage similaire de feuilles fossiles dentées. Les estimations climatiques indiquent des conditions chaudes et humides pour les deux membres de la formation du Río Turbio. La formation du Río Guillermo est représentée par des éléments tempérés et froids, principalement des *Nothofagus*, et la plupart avec des marges dentelées. L'analyse paléoclimatique indiquent une diminution de la température et des précipitations lors de la comparaison des deux formations étudiées. Aujourd'hui, les forêts tempérées du sud de l'Argentine ont une composition végétale et un climat plus proches des estimations réalisées pour la formation du Río Guillermo.

MOTS CLÉS
Paléoclimat,
physionomie des feuilles,
température,
précipitations.

INTRODUCTION

Relationships between leaf physiognomy and environmental variables can be used to predict climate conditions from floral assemblages of extant or fossil leaves (Wolfe 1990, 1993, 1995; Wiemann *et al.* 1998). Woody dicots such as trees and shrubs are most trustworthy for climate predictions because they have longer life cycles than herbs (Bailey & Sinnott 1916). It is widely recognized that leaf traits such as size and shape are important features to estimate temperature and precipitation (Wolfe 1978, 1979; Wilf 1997; Huff *et al.* 2003; Wilf *et al.* 2003; Greenwood *et al.* 2005; Royer *et al.* 2005 among others) and leaves are potential proxies for reconstructing paleoenvironments and paleoclimates (Traiser *et al.* 2018). Paleobotanists have used fossil plants as proxies for estimating past climate variables at different geological times (Hinojosa *et al.* 2006a; Arens & Harris 2015; Caviglia 2018; Lowe *et al.* 2018; Gutiérrez *et al.* 2019). Estimates of the past climate conditions are derived from present-day calibration data set as close as possible to the climate response of the studied fossil leaves (Wolfe 1993; Jordan 1997; Gregory-Wodzicki 2000; Jacobs 2002; Greenwood *et al.* 2004 among others). A positive relationship between temperature and the percentage of woody dicot species with entire margins has been observed and used to estimate paleotemperatures (Bailey & Sinnott 1915, 1916; Wolfe 1978; Greenwood *et al.* 2004; Arens & Harris 2015).

The Paleogene-Neogene was characterized by global climate changes with several episodes of warming and cooling conditions (Zachos *et al.* 2001a, b; Bohaty & Zachos 2003). Diverse geological evidence indicates major physical events that influenced the paleofloral composition. At high latitudes in the South Hemisphere, Australia was rafted farther north, away from Antarctica, the Drake Passage between Antarctica and southern South America opened and massive ice sheets covered Antarctica during the first major glaciation of the Cenozoic (Axelrod *et al.* 1991). These events contributed to a reorganization of the cold current ocean circulation and together with the uplift of the Andes caused climate changes with a cooling trend in southern South America (Zachos *et al.* 2001a; Nullo & Combina 2011). The early-middle Eocene was characterized by warm and humid conditions with a high diversity of fossil plants (Wilf *et al.* 2005). During the middle-late Eocene a mixed paleoflora evolved in Patagonia under warmer conditions (Romero 1978, 1986; Hinojosa & Villagrán 1997) composed of paratropical and cold temperate fossil species (Romero 1986; Hinojosa & Villagrán 1997; Iglesias *et al.* 2011; Vento *et al.* 2017; Vento & Prámparo 2018; Gutiérrez *et al.* 2019).

A global climate deterioration with temperate cool conditions in the early Oligocene is reflected by changes in floral composition (Wilf *et al.* 2003; Hinojosa 2005; Bowen 2007; Gutiérrez *et al.* 2019). The vegetation changed from paratropical to a colder temperate biome with temperate-cool representatives (Hinojosa 2005; Vento *et al.* 2017; Gutiérrez *et al.* 2019).

On the other hand, mean annual precipitation decreased throughout the Cenozoic with a maximum in the early-middle Eocene, and from the middle Eocene to the lower Miocene it dropped drastically (Hinojosa & Villagrán 2005).

Despite an exhaustive study of paleontological plant collections in southern South America, studies that quantify climatic trends are limited (Gregory-Wodzicki 2000; Hinojosa 2005; Hinojosa *et al.* 2006a) and most paleoclimate studies have been developed in southern Chile (Hinojosa 2005; Hinojosa & Villagrán 2005; Gayó *et al.* 2005; Hinojosa *et al.* 2006a; Gutiérrez *et al.* 2019). Paleoclimate reconstructions in Argentina using different techniques have increased in recent years and temperature and precipitation were estimated for Laguna del

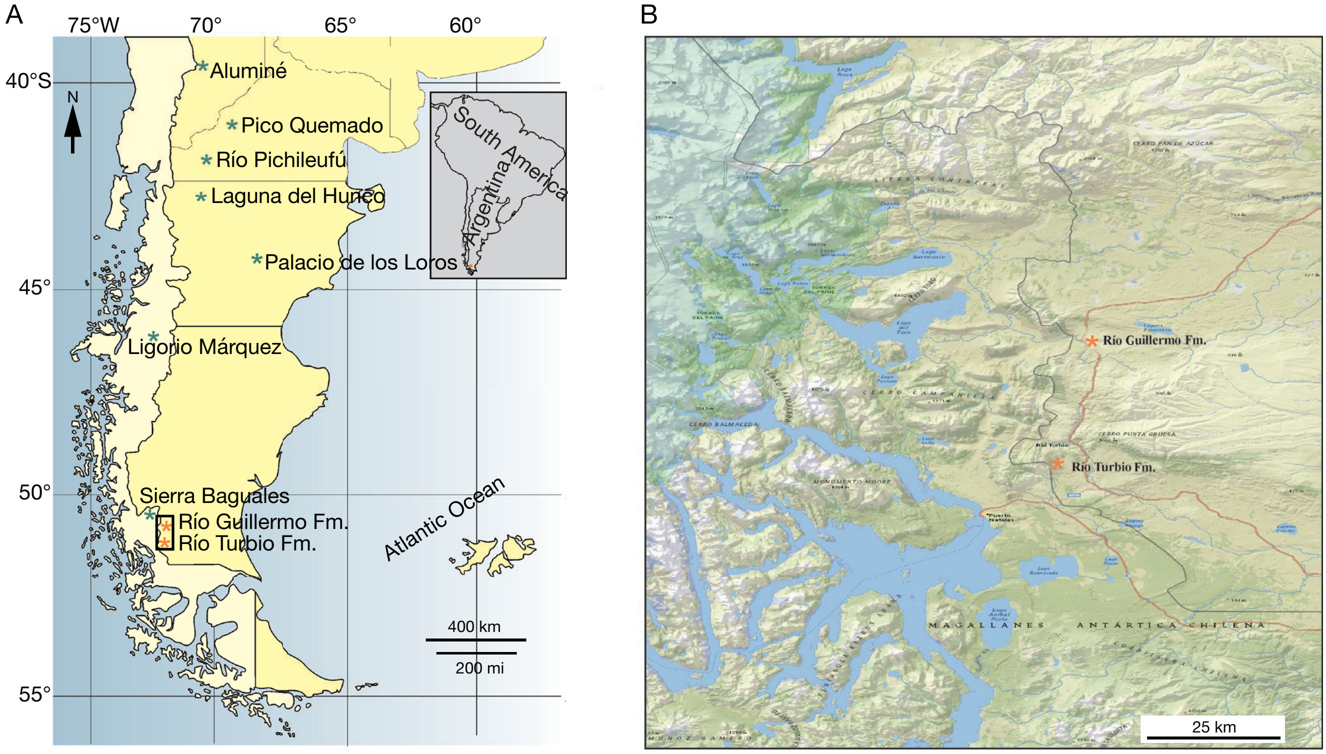

FIG. 1. — **A**, Map of southernmost South America with the location of the studied formations: Río Turbio and Río Guillermo and other sites from southernmost Chile and Argentina, which were used for the discussion; **B**, detailed of the location of the two studied areas in southern Argentina where the fossil leaves come from.

Hunco (early Eocene) and Palacios de los Loros (Salamanca Formation, early Paleocene) localities in Argentina (Peppe *et al.* 2011; Iglesias *et al.* 2007). More recently, paleoclimate estimates were calculated for the Ñirihuau Formation (middle Miocene) in southern Argentina (Caviglia 2018).

Different methods have been developed for estimating climate parameters (Wolfe 1979; Wilf 1997; Greenwood *et al.* 2004; Royer *et al.* 2005). These include both univariate and multivariate analysis such as Leaf Margin Analysis (LMA), Leaf Area Analysis (LAA), Climate Multivariate Program (CLAMP) and Digital Leaf Physiognomy (DiLP) (Wolfe 1993; Huff *et al.* 2003; Hinojosa 2005; Royer *et al.* 2005; Peppe *et al.* 2011).

Fossil leaves as climate proxies lead to better understanding of how and why climate changes occurred over time (Fricke & Wing 2004). Quantitative estimates employing this kind of proxy to know past climate conditions are necessary, and past climate reconstructions are still scarce in Argentina and South America.

In this work, we have estimated climate parameters using physiognomic characters of fossil leaves from the Río Turbio (Eocene-Oligocene) and Río Guillermo (Oligocene-early Miocene?) formations in southern South America, Cuenca Austral, Argentina. To constrain the age of the formations we followed the detrital zircon dating by Fosdick *et al.* (2011, 2015a, b). We use both univariate and multivariate analysis as well as different datasets to predict climate conditions. We performed an analysis of our data with the most recent Digital Leaf Physiognomy (DiLP) in order to test the ability of this technique to make climate predictions and compare the results to other climate models.

GEOLOGICAL SETTING

The Río Turbio Formation (RTF) (Malumián *et al.* 2000) is located in the Austral Basin between 72°10'W and the border between Argentina and Chile (72°31'W), and 51°15'S (Cancha Carrera) and 51°35'S (Sierra Dorotea) (Fig. 1). The formation is informally divided into two members: lower and upper (Malumián & Caramés 1997). The lower member unconformably overlies the Maastrichtian-Paleocene Cerro Dorotea Formation. It is composed of a thin basal conglomerate, overlain by sandstone and silty sandstone facies with marine invertebrates, plant remains and silicified trunks. Coal seams are present at both the lower and the upper members and a highly glauconitic horizon overlies the lower member (Fig. 2). It is interpreted as the base of a conspicuous transgressive episode and it is used to separate the lower from the upper member (Malumián & Caramés 1997).

An unconformity separates the strata of the Río Turbio Formation from the overlying continental Río Guillermo Formation (RGF) (Hünicken 1955; García 1988). The age of the formation using paleofloristic elements, invertebrates and dinoflagellate cysts was estimated as middle-upper Eocene (Hünicken 1955; Malumián *et al.* 2000; González Estebenet *et al.* 2014; Guerstein *et al.* 2014). Fosdick *et al.* (2015a, b) revised the age of the Río Turbio Formation using detrital zircon U/Pb geochronology. Their results constrained the lower member of the Río Turbio Formation to the middle-upper Eocene (46-47 Ma) and determined that the sedimentation of the upper member occurred during the Eocene-Oligocene transition (33-34 Ma) and continued until *c.* 26 Ma (Fig. 2).

The paleoenvironment of the RTF was interpreted as littoral marine or coastal deposits with fluctuating sea levels (García 1988; Azcuy & Amigo 1991). During the middle Eocene, a regressive stage developed, probably associated the uplift of an Andean sector. From that time, the paleoenvironments changed from coastal marine (Río Turbio Formation) to purely continental (Río Guillermo and Río Leona formations) (Nullo & Combina 2002).

The Río Guillermo Formation (RGF) (Leanza 1972; Malumián & Caramés 1997) is exposed between 51°15'S and 72°12'W in the Austral Basin (Fig. 1). The stratigraphic sequence begins in the area as an erosive disconformity on the top of the Río Turbio Formation, indicated by the presence of a basal conglomerate several meters thick. The Río Guillermo Formation is unconformably covered by the Cerro Mirador conglomerate (Hünicken 1955; Malumián *et al.* 2000). It is a clastic sequence composed of varied sized conglomerates interbedded with medium to thick-grain sandstones, siltstones and scarce claystones (Nullo & Combina 2002) indicating a high-energy fluvial paleoenvironment (Malumián *et al.* 2000) (Fig. 2). The age of the formation was established as Oligocene-Miocene by Hünicken (1955), based on the floral assemblage. Malumián *et al.* (2000) suggested a late Eocene-early Oligocene age for the unit based on foraminifera biostratigraphy. Nullo & Combina (2002) refined the age and confirmed a middle-upper Oligocene age for the formation based on its stratigraphic relationships with the Río Turbio and Río Leona formations. Bostelman *et al.* (2013) indicated that the Río Leona and Río Guillermo formations probably represent the same depositional interval. Barreda *et al.* (2009), based on palynological studies carried out at the Río Leona Formation, and a plant macrofossil assemblage studied by Césari *et al.* (2015), refined the age of this unit to the early-late Oligocene. Gutiérrez *et al.* (2017) analyzed the stratigraphic succession exposed at Sierra Baguales, Magallanes region, southern Chile based on two new detrital zircon U/Pb and they proposed a Rupelian age for the base of Río Leona Formation. Fosdick *et al.* (2011, 2015b), using U/Pb detrital zircon geochronology, indicated the onset of the fluvial sedimentation in the basin after 23.5 Ma together with a volcanic ash dating carried out at the top of the Río Guillermo Formation, which constrain the top of this unit to 21.7 Ma.

Here we considered the U/Pb detrital zircon geochronology proposed by Fosdick *et al.* (2011, 2015a, b) for the Río Turbio and Río Guillermo formations, which was based on data from the Cenozoic Magallanes foreland basin (near 51°S) in both Argentina and Chile. However, the ages of the different lithostratigraphic units and the stratigraphic correlation with the Río Turbio and Río Guillermo formations should be reviewed following the results published by Fosdick *et al.* (2015a, b).

ABBREVIATIONS

3-DRY	Three Driest Months Precipitation;
3-WET	Three Wettest Months Precipitation;
CCA	Canonical Correspondence Analysis;
CLAMP	Climate Leaf Analysis Multivariate Program;
CLAMP3B SA	Climate Leaf Analysis Multivariate Program 3B South America dataset;
CM(M)T	Cold Month Mean Temperature;
GLS	Growing Season Length;
GSP	Growing Season Precipitation;
DiLP	Digital Leaf Physiognomy;
LAA	Leaf Area Analysis;
LMA	Leaf Margin Analysis;
MAP	Mean Annual Precipitation;
MAT	Mean Annual Temperature;
MlnA	Natural log of the Mean Leaf Area;
SH90	South Hemisphere dataset;
RGF	Río Guillermo Formation;
RTF	Río Turbio Formation;
WM(M)T	Warm Month Mean Temperature.

MATERIAL AND METHODS

FOSSIL LEAVES AND PRESERVATION

Preservation of the fossil leaves is poor and most of them are fragmentary, suggesting transportation and mechanical damage before burial. Although fossil leaves from the Río Turbio and Río Guillermo formations are fragmentary, they are a valuable source of information about Eocene-Oligocene-Miocene climate in South America. Over 52 leaf taxa of woody dicot angiosperms were included in our study. Most of the plant macrofossils were previously collected and described by Hünicken (1955, 1967). Recently, Vento *et al.* (2017) and Vento & Prámparo (2018) revised this fossil material updating the taxonomic descriptions, incorporating undescribed material and photographs of each specimen from the collection. Additionally, a few taxa from the Río Turbio and Río Guillermo formations were incorporated from Panti (2011, 2018) (Appendix 1).

The Río Turbio Formation yielded a mixed paleoflora with the record of families such as Anacardiaceae, Lauraceae, Myricaceae, Myrtaceae, Nothofagaceae, Rhamnaceae, Salicaceae, Sapindaceae, Vitaceae and Vochysiaceae (Vento & Prámparo 2018). On the other hand, the Río Guillermo Formation is composed of a predominantly temperate-cool paleoflora mainly represented by Nothofagaceae (Vento *et al.* 2017). Detailed taxonomic descriptions, using the methodology outlined by Ellis *et al.* (2009) and photographs of each fossil specimen as well as some line drawings (morphotypes) can be found in Vento *et al.* (2017) and Vento & Prámparo (2018).

Fossil specimens were assigned to 38 and 16 morphotypes for the lower and upper members of the Río Turbio Formation respectively, and 12 morphotypes for the Río Guillermo Formation (Appendix 1).

PALEOCLIMATE RECONSTRUCTION: CLIMATE PROXIES

We estimated climate variables using several methods of leaf physiognomy analysis, which consider only woody dicot leaves specimens. We employed both univariate and multivariate analysis to reconstruct climate conditions for

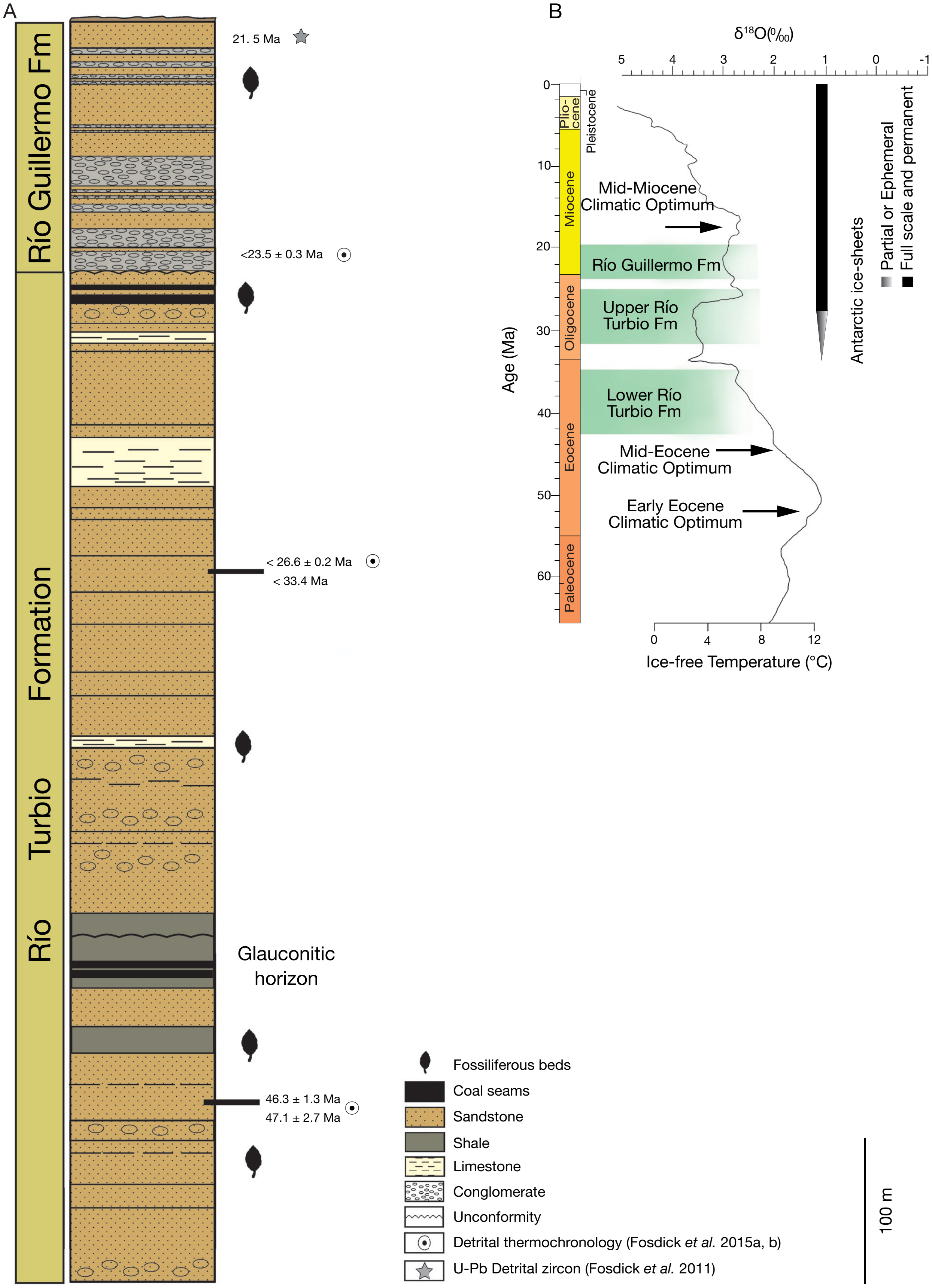

FIG. 2. — **A**, Stratigraphic composite profile from Río Turbio and Río Guillermo formations (modified from Hünicken 1967) with U/Pb detrital zircon age calibration based on Fosdick *et al.* (2011, 2015a, b); **B**, global climate fluctuations from stable isotopes (Zachos *et al.* 2008).

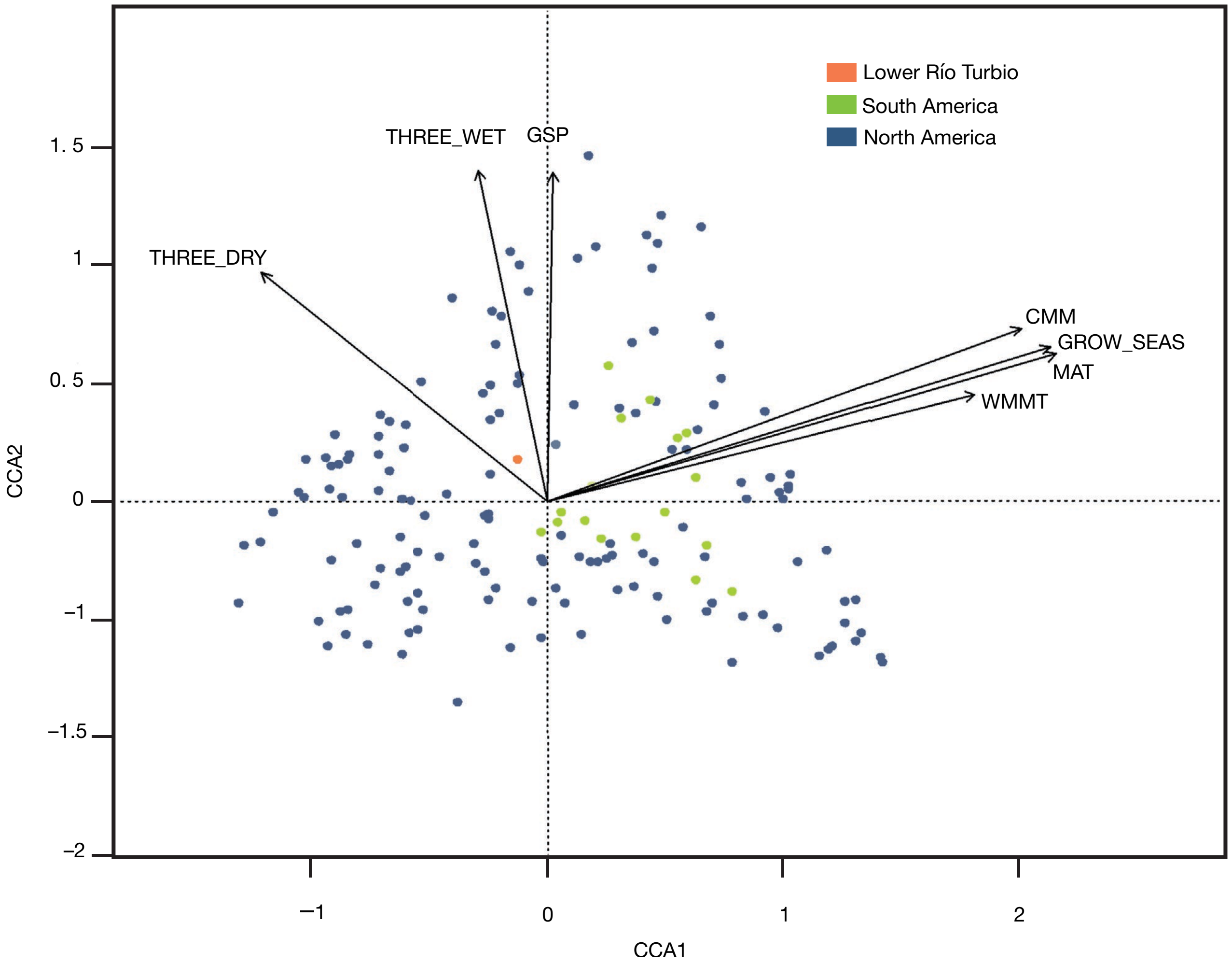

FIG. 3. — Canonical Correspondence Analysis using CLAMP3B SA dataset. The axes **CCA1** and **CC2** accumulate a total of 0.64% of the variance.

the lower member of the Río Turbio Formation. Due to the scarce available material and the extremely fragmented fossil leaves, we only used univariate methods for the climate reconstruction in the upper member of the Río Turbio and the Río Guillermo formations. We used univariate correlations to estimate Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP), considering the prevalence of untoothed margins and leaf size, respectively. We estimated Mean Annual Precipitation (MAP) using Leaf Area Analysis (LAA) from the natural log of the site mean leaf area (MlnA). We calculated leaf area digitally from our own photographs using the software ImageJ (Schneider *et al.* 2012). Simple linear regression models are based on Leaf Margin Analysis as one of the oldest and reliable methods that introduces observations of the percentage of untoothed woody dicot species as a predictor for mean annual temperature (Wolfe 1979; Wilf 1997; Hunt & Poole 2003; Greenwood *et al.* 2004). It is recognized that leaf size is useful for estimating mean annual precipitation because leaf size decreases with decreasing rainfall (Dilcher 1973; Givnish 1984; Wilf *et al.* 1998).

A multivariate approach is the Climate Leaf Analysis Multivariate Program (CLAMP). The procedure for this method involves the codification of leaf character variables and uses ordination techniques such as correspondence analysis to estimate a set of climate variables (Wolfe 1993, 1995). Multivariate analysis is a combination of leaf features rather than just one. We used CLAMP to estimate a set of climatic variables (Wolfe 1990, 1993, 1995; Yang *et al.* 2011, 2015) as a technique that includes two related data sets for calibration. The first dataset corresponds to the physiognomy of woody dicot angiosperms and the other one corresponds to the meteorological characteristics of the site where these plants grow. We examined the leaves in the fossil assemblage for the codification of 31 morphological characters (Wolfe 1990, 1993; Herman Spicer 1996) (Appendix 1). We coded leaf characters for 38 morphotypes from the lower Río Turbio Formation and we analyzed the resulting data with the online CLAMP analysis tool (accessed December 2018). We used the CLAMP3B SA dataset for calibration (Hinojosa & Villagrán 2005), which included 161 modern vegetation samples (Wing & Greenwood 1993; Wilf 1997). The dataset is based on Physg3brcAZ but the coldest sites were removed and 17 South American localities (12 sites from Bolivia and 5 sites from Chile) with living

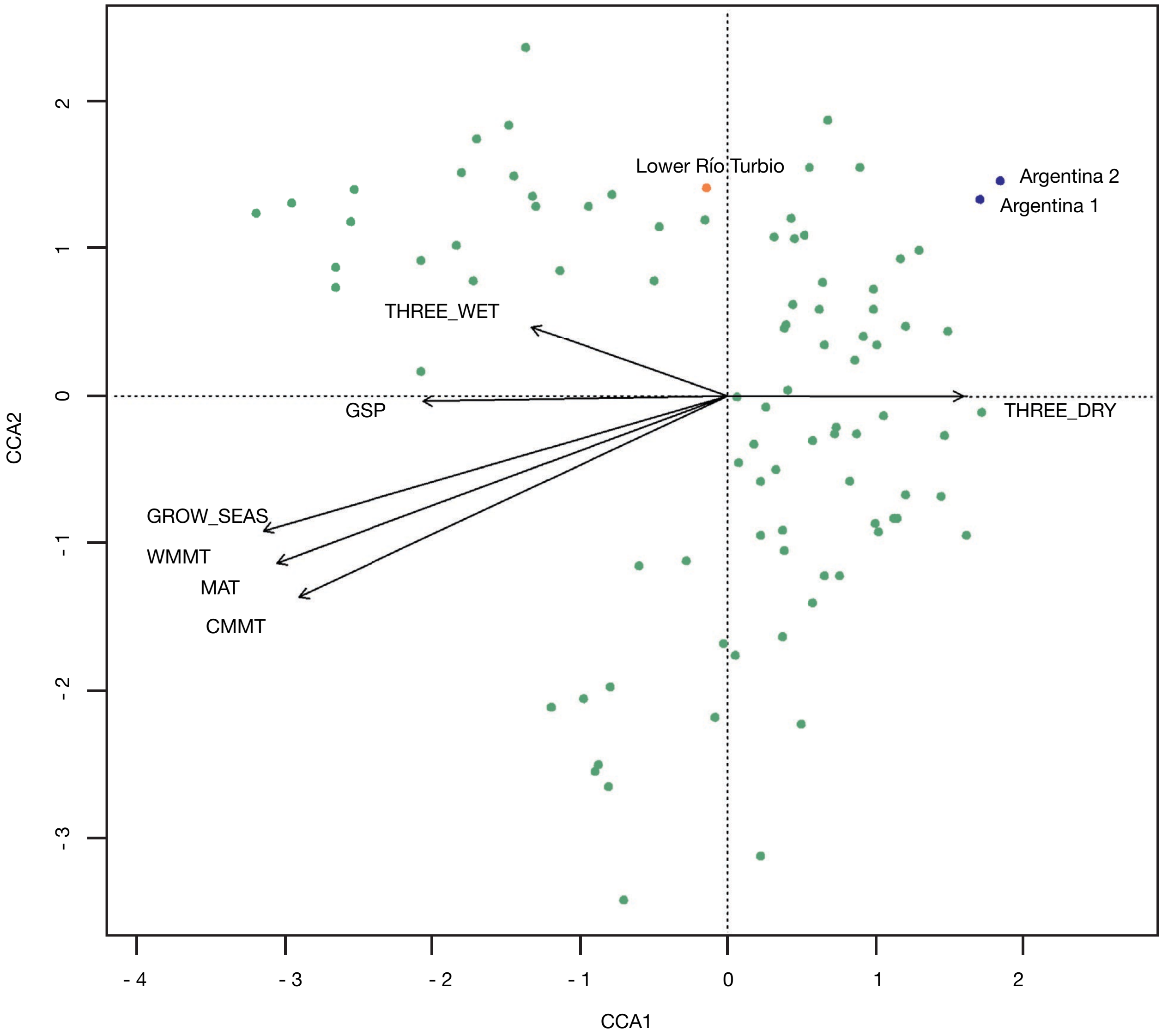

FIG. 4. — Canonical Correspondence Analysis using CLAMP SH90 dataset. The axes **CCA1** and **CC2** accumulate a total of 0.32% of the variance.

TABLE 1 — Estimated values of temperature and precipitation for the lower Río Turbio Formation member.

Lower RTF		**Equation**	**Dataset**	**R²**	**Error**	**Source**
Temperature (°C)	16.5	MAT = 3.25 + 0.24*% non-tooth	CLAMP 3B SA	0.9	2.1°C	Hinojosa 2005; Hinojosa & Villagrán 2005
Temperature (°C)	15.7	MAT = 26.03pE + 1.31	SA	0.82	2.8°C	Hinojosa *et al.* 2011
Temperature (°C)	15.6	MAT = 0.204E + 4.6	LMA	0.58	4.8°C	Peppe *et al.* 2011
Temperature (°C)	16.9	See manuscript (1)	DiLP	0.7	4°C	Peppe *et al.* 2011
Precipitation (mm)	1764	Ln(MAP) = 1.63 + 0.49*MLnA	CLAMP 3B SA	0.6	Ln(0.5) cm	Hinojosa 2005; Hinojosa & Villagrán 2005
Precipitation (mm)	1435	lnMAP = 0.283(MlnA) + 2.92	LAA	0.23	0.61 cm	Peppe *et al.* 2011
Precipitation (mm)	1303	See manuscript (2)	DiLP	0.27	0.6 cm	Peppe *et al.* 2011

vegetation were added (Gregory-Wodzicki 2000; Hinojosa & Villagrán 2005). Equations for the leaf margin analysis are summarized in tables 1-3. Moreover, we used the database for the South Hemisphere (Kennedy *et al.* 2014) with up to 90 sites (SH90) from Australia, New Zealand, Pacific Islands, southern Africa, Bolivia and two sites from Argentina. We performed a Canonical Correspondence Analysis (CCA) using the R program version 3.5.2 (R Core Team 2018).

We performed a data analysis using Digital Leaf Physiognomy (DiLP). This recent method has been proposed as an alternative multivariate model that uses continuous characters and a set of leaf features that differ from those

TABLE 2 — Estimated values of temperature and precipitation for the upper Río Turbio Formation member. *Scarce fossil material.

Upper RTF		Equation	Dataset	R^2	Error	Source
Temperature (°C)	15.3	MAT = 3.25 + 0.24*% non-tooth	CLAMP 3B SA	0.9	2.1°C	Hinojosa 2005; Hinojosa & Villagrán 2005
Temperature (°C)	14.3	MAT = 26.03pE + 1.31	SA	0.82	2.8°C	Hinojosa *et al.* 2011
Temperature (°C)	14.8	MAT = 0.204*E + 4.6	LMA	0.58	4.8°C	Peppe *et al.* 2011
Precipitation (mm)	*	Ln(MAP) = 1.63 + 0.49*MLnA	CLAMP 3B SA	0.6	Ln(0.5) cm	Hinojosa 2005; Hinojosa & Villagrán 2005
Precipitation (mm)	*	lnMAP = 0.283(MlnA) + 2.92	LAA	0.23	0.61	Peppe *et al.* 2011

TABLE 3 — Estimated values of temperature and precipitation for the Río Guillermo Formation.

RGF		Equation	Dataset	R^2	Error	Source
Temperature (°C)	5.3	MAT = 3.25 + 0.24*% non-tooth	CLAMP 3B SA	0.9	2.1°C	Hinojosa 2005; Hinojosa & Villagrán 2005
Temperature (°C)	3.5	MAT = 26.03pE + 1.31	SA	0.82	2.8°C	Hinojosa *et al.* 2011
Temperature (°C)	6.3	MAT = 0.204E + 4.6	LMA	0.58	4.8°C	Peppe *et al.* 2011
Precipitation (mm)	682	Ln(MAP) = 1.63 + 0.49*MLnA	CLAMP 3B SA	0.6	Ln(0.5) cm	Hinojosa 2005; Hinojosa & Villagrán 2005
Precipitation (mm)	829	lnMAP = 0.283(MlnA) + 2.92	LAA	0.23	0.61	Peppe *et al.* 2011

used by CLAMP (Huff *et al.* 2003; Royer *et al.* 2005; Peppe *et al.* 2011). We coded a set of characters for the DiLP and prepared the leaves to separate the petiole and teeth from the leaf blade. We measured leaves using ImageJ (Schneider *et al.* 2012), following the protocol established by Peppe *et al.* (2011) and Royer *et al.* (2005). Equations for estimating paleoclimate parameters using DiLP (Peppe *et al.* 2011) were:

(1) $\text{MAT} = (\text{LMP} \times 0.21) + (\text{FDR} \times 42.296) + (\#\text{teeth: internal perimeter} \times -2.609) - 16.004$

(2) $\ln(\text{MAP}) = (\text{MlnA} \times 0.298)\ (\ln[\#\text{teeth:internal perimeter}] \times -0.279) + (\ln[\text{perimeter ratio}] \times 2.717) + 3.033$

Climate variables estimated in the analysis were: Mean Annual Temperature (MAT), Warm Month Mean Temperature (WMMT), Cold Month Mean Temperature (CMMT), Precipitation during the Growing Season (GSP), Precipitation of Three Wettest Months (3-WET), Precipitation of Three Driest Months (3-DRY) and Growing Season Length (GSL) (Wolfe 1993).

RESULTS

Untoothed fossil leaf percentage was a little higher in the lower RTF member compared to the upper member of this formation. The Río Guillermo Formation had a notoriously higher percentage in toothed fossil leaves compared to both members of the Río Turbio Formation. Approximately 90% of the fossil leaves recorded in this formation were toothed (Fig. 3).

Tables 1-4 summarize the estimated values obtained for the three studied members. Paleotemperature estimates for the lower RTF member using the univariate regression method indicate values that range from 15.7°C to 16.5°C (Table 1). The estimated values for precipitation were 1435 mm and 1764 mm. The upper RTF member has values of temperature that ranged from 14.3°C to 15.3°C. Precipitation could not be estimated because of the scarce available material and the poor preservation that made it difficult to calculate the foliar area of the fossil leaves (Table 2). Temperature and precipitation values notoriously decreased in the Río Guillermo Formation. The predicted values of temperature for this formation ranged from 3.5°C to 6.3°C and precipitation estimates ranged from 682 to 829 mm (Table 3).

On the other hand, CLAMP analysis results are shown in table 4. Scoring completeness for the lower RFT member was 97% (Appendix 1). We used two different datasets: CLAMP3B SA with 161 localities and CLAMP SH with 90 localities. The results using CLAMP3B SA estimates a MAT of 12.7°C, WMMT of 23.2°C, CMMT of 3.4°C, MGSP 1741 mm, 3-WET 784 mm, 3-DRY 334 mm, and GSL 7.7 months.

The results using CLAMP SH90 estimates a MAT of 12.2°C, WMMT of 21.5°C, CMMT of 4°C, MGSP 1394 mm, 3-WET 460 mm, 3-DRY 160 mm, and GSL 7.4 months.

The outcomes using DiLP predicted a temperature value of 16.9°C, a precipitation of 1303 mm and GSL 7.4 months (Table 4).

The Canonical Correspondence Analysis showed the lower RTF member within the leaf physiognomy space created by the modern data used by CLAMP3B SA and SH 90 (Figs 3-4). The CCA for CLAMP 3B SA indicates that the CCA 1 axis accumulates a variance of 0.49% and the CCA 2 accumulates a variance of 0.15%, and the cumulative variance for both CCA 1 and CCA 2 is 0.64% (Fig. 3). On the other hand, The CCA for SH 90 indicates that the CCA 1 axis accumulates a variance of 0.24% and the CCA 2 accumulates a variance of 0.08%, and the cumulative variance for both CCA 1 and CCA 2 is 0.32% (Fig. 4).

The temperature gradient using the LMA for the studied formations indicates that the lower RTF member had the highest temperature value and the Río Guillermo Formation had the lowest (Fig. 5).

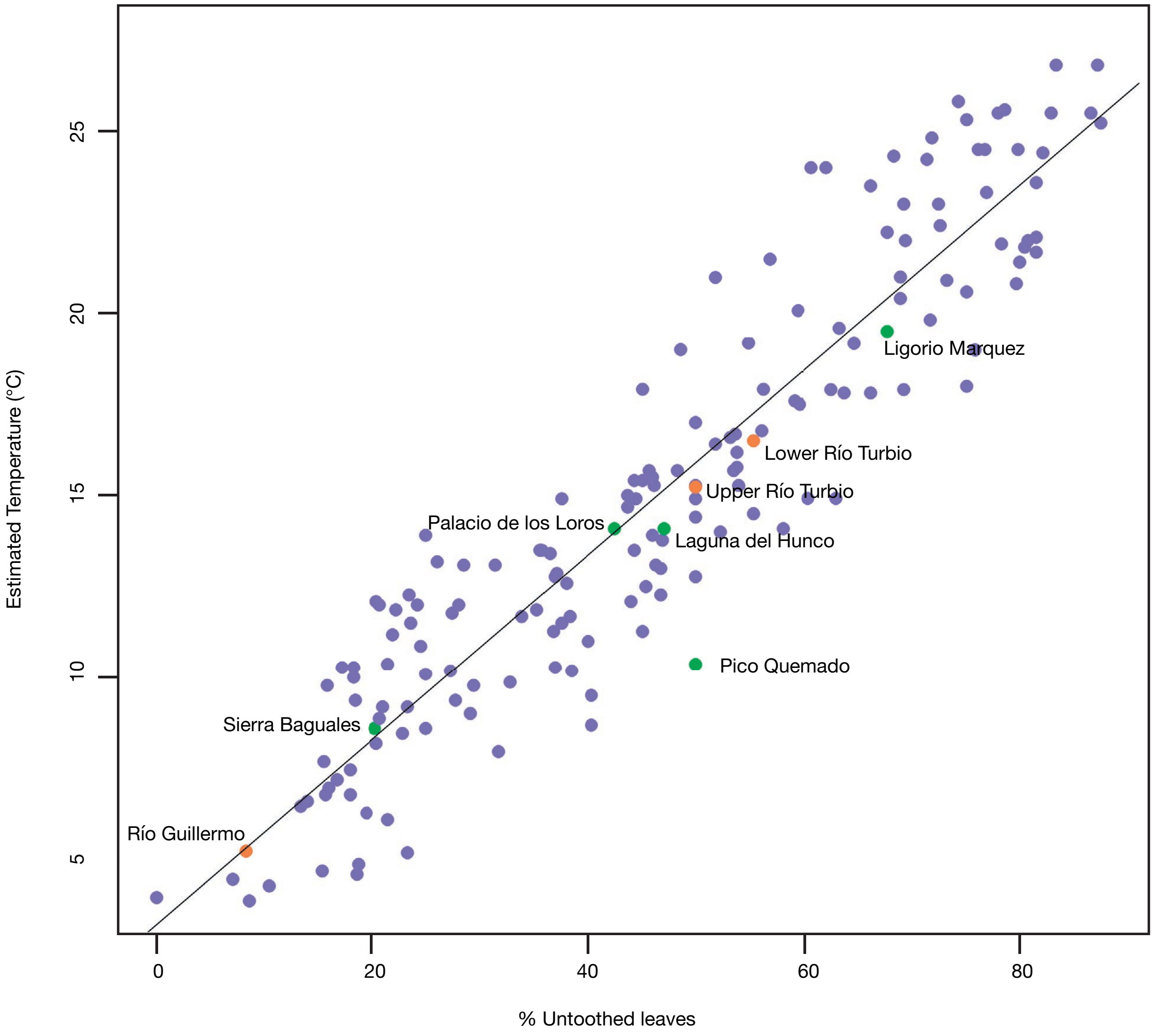

Fig. 5. — Correlation between mean annual temperature and leaf margin from the Río Turbio and Río Guillermo formations and published fossil sites in South America during the Eocene-Oligocene-Miocene.

DISCUSSION

Comparison to other Paleogene-Neogene paleofloras from South America

The physiognomy analysis for the Río Turbio and Río Guillermo formations allowed us to estimate paleoclimate conditions for the middle-upper Eocene-Oligocene-early Miocene in southern South America (Tables 1-4). The middle-late Eocene-Oligocene was characterized by warm and humid conditions and the Oligocene-early Miocene was a period of cool-temperate conditions (Zachos *et al.* 2001b; Hinojosa 2005; Gutiérrez *et al.* 2019).

Higher values of MAT and MAP were recorded for the lower RTF member and cooler and drier conditions for the RGF (Tables 1-4). The paleofloristic association for both geological formations presented different percentages of untoothed margins. The lower and upper RTF members present at least 50% untoothed leaves but the RGF only has 8% untoothed fossil leaves (Fig. 5). Wolfe (1971, 1979) found a linear relationship between mean annual temperature and the percentage of untoothed margin for the Northern Hemisphere. This relationship was also significant in the Southern Hemisphere (Greenwood *et al.* 2004). Fig. 5 shows a temperature gradient when the margin of fossil leaves was analyzed: the regression model indicated higher temperature values for the RTF and lower ones for the RGF. Leaves in cold climates typically have larger, more numerous teeth and are more highly dissected (Peppe *et al.* 2011) that leaves in warmer climates which are associated with fewer and smaller teeth (Huff *et al.* 2003).

A mixed paleoflora, composed of paratropical together with cool-temperate representatives, evolved during the Eocene-Oligocene in southern South America (Romero 1978, 1986; Hinojosa & Villagrán 1997; Hinojosa 2005). Our results clearly indicate climate differences between the Río Turbio and Río Guillermo formations (Tables 1-4) and distinctiveness in the paleoflora composition (Vento *et al.* 2017; Vento & Prámparo 2018). The paleoflora from both the lower and upper member of the Río Turbio Formation is composed of paratropical representatives together with cool-temperate fossil species of the genera *Nothofagus* Blume 1851 and *Drymis* Jussieu 1789 (Romero 1978, 1986; Vento & Prámparo 2018). The lower RTF member has the majority of studied fossil leaves (38 morphotypes) and for this reason a complete paleofloristic and paleoclimatic analysis, using univariate and multivariate methods, was performed. Families present in this member were: Anacardiaceae, Annonaceae, Dilleniaceae, Lauraceae, Malvaceae, Myricaceae, Myrtaceae, Nothofagaceae, Rhamnaceae, Salicaceae, Sapindaceae, Sapotaceae, Styracaceae, Urticaceae, Vitaceae, Vochysiaceae and Winteraceae (Hünicken 1955, 1967; Vento & Prámparo 2018). On the other hand, the upper RTF member was represented by the paratropical families Bignoniaceae, Ulmaceae, Lauraceae, Vitaceae, Sapindaceae and the cool-temperate family Nothofagaceae (Hünicken 1955, 1967; Vento & Prámparo 2018).

Paleofloras from the Paleocene-early Eocene in southern Argentina were dominated by a rainforest composed of many angiosperms with warm-temperate affinities (Barreda & Palazzesi 2007 and references therein). Mixed fossil floras during the Cenozoic in South America occupied a large temporal and spatial range due to thermal equability (Axelrod *et al.* 1991; Hinojosa & Villagrán 2005), this means that they occurred under relatively homogeneous mean annual temperatures (Hinojosa & Villagrán 2005). Two mixed paleofloras without *Nothofagus* were recorded in Argentina: Laguna del Hunco (early Eocene) and Río Pichileufú (early-middle Eocene) with more than one hundred recognized leaf species (Wilf *et al.* 2003; Wilf *et al.* 2005). These sites (Table 5) represent a frost-free humid biome in South American middle latitude of warm Eocene (Wilf *et al.* 2005). Similar conditions to tropical-paratropical rainforest were suggested for Laguna del Hunco and Río Pichileufú based on the leaf fossil analysis (Wilf *et al.* 2009).

A mixed paleoflora evolved at the end of the Eocene until the early Miocene in southern Argentina and Chile, under cooler and less humid conditions than the flora at the early-middle Eocene (Romero 1978; Hinojosa & Villagrán 1997; Troncoso & Romero 1998; Hinojosa 2005). In Argentina, a mixed paleoflora with the presence of *Nothofagus* was identified and described in the early-middle Miocene Pico Quemado, Ñirihuau Formation (Berry 1928; Fiori 1931, 1939; Romero 1978, 1986; Troncoso & Romero 1998; Caviglia & Zamaloa 2014). The analyzed fossil assemblage from Pico Quemado indicated a cold-temperate climate with high levels of humidity and seasonality. This paleoflora was characterized as "transitional mixed to sub-antarctic" (Caviglia 2018) due to the lack of thermal equability (Hinojosa & Villagrán 2005). The coexistence of elements, which today occupy different climatic zones with different ecophysiological requirements, could be a consequence of relict Cretaceous lineages enriched by cold-temperate elements from Antarctica, warm elements from the Neotropics and a strictly endemic element that originated in southern South America (Hinojosa & Villagrán 2005). A fossil flora from Sierra Baguales, Río Leona Formation (early Oligocene) in southern Chile (Table 5) was characterized by a mixed paleoflora association, dominated by the family Nothofagaceae with micro-thermal requirements (Gutiérrez *et al.* 2019). Fossil woods in life position from Aluminé locality, Neuquén province, Rancahué Formation (late Oligocene 27-26 Ma) indicated *Nothofagoxylon* as dominant with almost 40% in terms of diversity and abundance, and conifers are absent (Brea *et al.* 2015).

We observed a decrease in the diversity of recorded families in the Río Guillermo Formation, where most of its representatives had toothed margins (Fig. 5). In this formation, the paleoflora was mostly represented by six fossil species of *Nothofagus* and the families Anacardiaceae, Lauraceae, Myrtaceae and Rosaceae (Panti 2011; Vento *et al.* 2017). The fossil flora of RGF suggests cool-temperate climate conditions (Hünicken 1995; Barreda & Palazzesi 2007; Panti 2011; Vento *et al.* 2017) and the record of *Nothofagus* and *Myrcia bagualensis* indicated an affinity to the sub-antarctic forest (Romero 1978; Hünicken 1995; Hinojosa & Villagrán 1997). This paleoflora evolved under cooler and drier conditions, following the global cooling trend as a consequence of the Antarctic glaciation (Hinojosa 2005; Gutiérrez *et al.* 2019). A wood physiognomy method allowed to infer a MAT between 19.31 ± 1.7°C and 9.35 ± 1.7°C for the Santa Cruz Formation, southernmost Argentina (early Miocene, *c.* 18-16 Ma). Estimates indicated that some species would live in humid areas or greater soil humidity and other ones presented xeromorphic features which could indicate seasonal arid conditions (Brea *et al.* 2012; Brea *et al.* 2017).

Nowadays, a flora blend of central Chile (33°57'-41°15') resembles the mixed paleofloras because of the endemic and Austral-Antarctic representatives (Hinojosa *et al.* 2006b). In Sierra Baguales, the proportion of dicot fossil species with toothed margins increased due to the global temperature drop, and the decrease in rainfall resulted in smaller leaves (Gutiérrez *et al.* 2019). Our results indicate a similar result; when temperatures decreased the proportion of toothed species significantly increased (Fig. 5). Cenozoic Mixed Paleofloras of southern South America evolved as a response to a climate regime characterized by warm temperatures and rainfall throughout the year. These climate conditions could only have existed with a much lower Andes Cordillera (Hinojosa & Villagrán 2005).

Palynological associations are an additional source of information in the analysis of a paleofloristic association and contribute to better understand paleoclimate conditions. There are several studies from the RTF continental palynomorphs, mainly from core samples from different wells but also from surface sections (Archangelsky 1972; Romero & Zamaloa 1985; Romero & Castro 1986; Romero 1978), but unfortunately without any differentiation among the palynofloras from the lower or upper member of the formation. The RTF palynoflora is composed mainly of Pteridophytes, gymnosperms of the genera *Araucariacites, Podocarpidites, Phyllocladidites, Microcachryidites*, *Dacrydiumites* and among angiosperms abundant *Nothofagidites* and representatives of different families such as

TABLE 4 — Estimated values for the climate variables in the lower Río Turbio Formation member from CLAMP analysis using the CLAMP3B SA and CLAMPSH90 data set.

CLAMP Climate parameters	Estimates	Error	Dataset	Estimates	Error	Data set
Mean annual temperature (°C)	12.7	2.1	CLAMP3BSA	12.2	4.83	CLAMPSH90
Warm month mean temperature (°C)	23.2	3.3	CLAMP3BSA	21.5	7.5	CLAMPSH90
Cold month mean temperature (°C)	3.4	3.8	CLAMP3BSA	4	4.6	CLAMPSH90
Mean Growing Season Precipitation (mm)	1741	42.6	CLAMP3BSA	1394	68	CLAMPSH90
3-Wettest Months Precipitation (mm)	784	19.8	CLAMP3BSA	460	35	CLAMPSH90
3-Driest Months Precipitation (mm)	334	15.3	CLAMP3BSA	160	22.8	CLAMPSH90
Length Growing Season	7.7	1.2	CLAMP3BSA	7.4	0.8	CLAMPSH90

TABLE 5 — Fossil locations from Southern South America and age in million of years. Studied geological formations and sites used for comparison in the discussion.

Fossil Site	Geological Formation	Age (Ma)	Source
Pico Quemado	Ñirihuau	middle Miocene?	Caviglia 2018
Cancha Carreras, Estancia Tres Marías	Río Guillermo	≤21.7 ± 0.3 to ≤23.5 ± 0.3	Fosdick *et al.* 2011; 2015a, b
Aluminé Basin	Rancahué	25.0 ± 1.4 to 26.0 ± 1.5	Brea *et al.* 2015; Franzese *et al.* 2011
Sierra Baguales	Río Leona	33.0 ± 2.8	Gutiérrez *et al.* 2017, 2019
Upper Río Turbio	Río Turbio	≤26.6 ± 0.2 to ≤33.4 to	Fosdick *et al.* 2015a
Lower Río Turbio	Río Turbio	≤46.3 ± 1.3 to ≤47.1 ± 2.7	Fosdick *et al.* 2015a
Río Pichileufú	Ventana	47.46 ± 0.05	Wilf *et al.* 2005
Laguna del Hunco	La Huitrera	51.91 ± 0.22	Wilf *et al.* 2005
Ligorio Márquez	Ligorio Márquez	<57	Suárez *et al.* 2000; Hinojosa 2005
Palacio de los Loros	Salamanca	61.7	Iglesias *et al.* 2007

Proteaceae and Myrtaceae. The angiosperm taxa distribution is uniform in the formation (Romero & Castro 1986). Currently members of paratropical and tropical floras of South America were mentioned in the RTF palynological assemblages such as Aquifoliaceae (*Ilex*) (Romero & Castro 1986; Quattrocchio *et al.* 2013) and Malphigiaceae (Fernández *et al.* 2012). Quattrocchio *et al.* (2013) did a quantitative analysis of Cenozoic palynofloras from Patagonia based on published data and concluded that the middle Eocene and Oligocene was characterized by the "Mixed Paleoflora" developed under a less humid climate due to the onset of the Antarctic glaciation. Palynological studies of the end of the Cenozoic (Pleistocene) in the southern part of Argentina indicate that species such as *Nothofagus* and *Drymis* were dominant trees together with *Empetrum rubrum* (Heusser, 1993).

Currently, a cold-humid forest (Andino Complex) is the characteristic bioma that evolved in the western part of Santa Cruz province (Burgos 1985; Roig *et al.* 1985), where the Río Turbio and Río Guillermo formations are located. Extant vegetation is mainly represented by *Nothofagus antarctica* (G.Forst.) Oerst., *N. pumilio* (Poepp. & Endl.) Krasser, *N. betuloides* (Mirb.) Oerst., *Drimys winteri* J.R.Forst. & G.Forst., *Embothrium coccineum* (L.f.) Hook. & Arn., *Escallonia rubra* (Ruiz & Pav.) Pers., *Gaultheria mucronata* J.R.Forst. & G.Forst. and *Fuchsia magellanica* Lam. among other herbs and grasses (Roig *et al.* 1985).

COMPARISON OF METHODS

Although leaf margin analysis is widely used and recognized, it is based on one character state, the presence or absence of teeth (Royer *et al.* 2005). Percentages of untoothed woody dicot leaves have been strongly correlated to mean annual temperatures and most of the methods and datasets were developed for the Northern Hemisphere (Wolfe 1979; 1993; Wilf 1997; Greenwood *et al.* 2004), but this relationship is not globally uniform (Kennedy *et al.* 2014). Recently, equations and climate estimate models have been developed for South America (Gregory-Wodzicki 2000; Hinojosa 2005; Gayó *et al.* 2005; Hinojosa *et al.* 2006a) and the Southern Hemisphere (Kennedy *et al.* 2014). Our estimates were mainly based on equations and datasets for South America or even the Southern Hemisphere (Hinojosa 2005; Kennedy *et al.* 2014).

The simple and multiple linear regression models allowed estimates of temperature and precipitation values for the two studied geological formations. For the lower RTF, the temperature values using LMA, and equations from Hinojosa (2005), Hinojosa & Villagrán (2005) and Hinojosa *et al.* (2011) were similar. The DiLP analysis resulted in the highest temperature value of all applied univariate methods and equations.

The precipitation values were similar for the LAA and the DiLP analysis and the highest value was obtained for the equations from Hinojosa (2005) and Hinojosa & Villagrán (2005) (Table 1). The lower RTF member presents similar values for the different methods. However, DiLP and precipitation estimates were made due to the scarce fossil material (Table 2). The RGF temperature values were similar when the equations of Hinojosa (2005), Hinojosa and Villagrán (2005) and Peppe *et al.* (2011) were applied. The value drops of at least 50% compared to the temperature values that were obtained for the derived equation from Hinojosa *et al.* (2011) (Table 3).

The MAT, WMT, CMT and GLS estimates from CLAMP3B SA and SH90 dataset were similar for the lower RTF. Moreover, MAP values present some differences among datasets with higher values of MAP, 3-DRY, 3-WET for the CLAMP3B SA dataset (Table 4). The canonical analysis resulted in a more cumulative variance for this data set compared with the cumulative variance of SH90 dataset (Figs 3-4). Estimates of mean annual temperature based on Leaf Margin Analysis are at least as precise as those derived from the CLAMP dataset (Wilf 1997). However, multivariate approaches may help to compensate for regional differences in univariate leaf climate relationships (Greenwood *et al.* 2004). In most cases, the performance of the applied method depends on the predictor dataset (Gregory-Wodzicki 2000). We detected that temperature estimates were lower when analyzed using multivariate methods (Tables 1; 4).

Multivariate methods are more appropriate than linear univariate methods because plants respond complexly to environmental variables (Gregory-Wodzicki 2000) and might be expected to improve the predictive ability of models (Wiemann *et al.* 1998). Studies made in extant floras of Australia and New Zealand have shown a different relationship to climates than Northern Hemisphere floras. Considering this fact, a new calibration dataset for the Southern Hemisphere comprising data from two sites in southern Argentina, Bolivia, South Africa, Australia, New Zealand and other Pacific Islands with a precision similar to those of North Hemisphere was developed (Kennedy *et al.* 2014).

Multiple regression analysis tends to produce the most accurate estimates for small datasets with a narrow range of environmental variation that have similar relationships to the flora, and linear regression or canonical correspondence analysis for the larger and more varied CLAMP dataset (Gregory-Wodzicki 2000). This climate analysis was criticized because the character states are not defined with sufficient precision, and variations in scoring similar leaves by different researchers can be made (Wilf 1997; Wiemann *et al.* 1998; Wilf *et al.* 1998). To improve the leaf-margin analysis without the scoring imprecision of CLAMP, a new leaf physiognomy analysis was introduced (Huff *et al.* 2003; Royer *et al.* 2005). Digital Leaf Analysis (DiLP) is a technique that has major advantages over the traditional univariate and multivariate methods as most of the measurements uses continuous variables, such as number of teeth and tooth area, in contrast to binary characters used in leaf-margin analysis and CLAMP (Huff *et al.* 2003). It is more precise than univariate approaching and closer to independent climate evidence than other leaf-climate approaches (Peppe *et al.* 2011). Our results, using DiLP for the lower RTF member, suggested MAT and MAP values consistent with LAA and LMA. Nevertheless, more calibration sites from Europe, Africa, southern South America, Oceania, and the tropics are needed (Peppe *et al.* 2011).

On the other hand, mean temperature estimates using DiLP are higher compared to both CLAMP3B SA and SH90 dataset, but the opposite situation is for MAP estimates (Table 1). Even though the SH90 dataset is mainly from Southern Hemisphere, only two sites in southern South America (Kennedy *et al.* 2014) were used for the calibration.

PALEOCLIMATE CONSIDERATIONS

During the past 65 million years and beyond, the climate of the Earth experienced continuous changes, drifting from extreme warmth to extreme cold with continental ice sheets (Zachos *et al.* 2001b). The paleofloristic record indicates that the climate of the southern part of South America showed a trend to higher temperatures during the Paleocene and early Eocene and a deterioration through the middle and late Eocene (Romero 1978, 1986) with strong temperate-cool conditions for the Eocene-Oligocene boundary in accordance with the global climate trend (Zachos *et al.* 2001a). Climate changes in southern South America and the Antarctic Peninsula during the Cenozoic show a strong correlation with ocean warming and cooling events, related to tectonic processes (Le Roux 2012).

The Paleocene and early Eocene was warm with tropical conditions (Wilf *et al.* 1998; Zachos *et al.* 2001a, b). Some fossil sites in South America have been studied for this geological time (Table 5) and paleoclimate parameters have been estimated. In southern Argentina, paleoclimate reconstructions for the early Paleocene Palacio de los Loros resulted in MAT estimates from 12.9°C to 14.1°C and MAP estimates ranged from 1150-1440 mm, suggesting warm and wet conditions (Iglesias *et al.* 2007; Peppe *et al.* 2011). In southern Chile, the physiognomy leaf analysis for Ligorio Márquez Formation (late Paleocene) indicated high values of temperature and precipitation, with an estimated range of MAT from 16.9°C to 19.5°C and MAP of 1570 mm (Hinojosa 2005; Hinojosa *et al.* 2006a).

Foliar analysis indicates that during the early-middle Eocene a warm and wet paleoclimate still dominated in southern South America (Wilf *et al.* 2005; Wilf *et al.* 2009; Gutiérrez *et al.* 2019). The early Eocene Laguna del Hunco, La Huitrera Formation was characterized with a MAT estimates of 15.6°C and a MAP of 1000-1200 mm (Wilf *et al.* 2003, 2005). More recent estimates for the same area made by Peppe *et al.* (2011) indicates similar paleoclimate conditions with a temperature of 10.9-16.9°C and a rainfall of 1270-1420 mm. The warm and wet climate at Laguna del Hunco favored an expansion of the vegetation and it reached high diversity indices during the Eocene (Wilf *et al.* 2005; Gutiérrez *et al.* 2019). In North America, a paleoclimate reconstruction for the early Eocene McAbee fossil beds, Tranquille Formation, Canada, indicated an estimated MAT ranging from 10°C to 12°C and MAP estimates of approximately 1000 mm. The diversity of dicots of this site despite lower MAT is comparable with Laguna del Hunco (Lowe *et al.* 2018). Temperature estimates for the lower RTF member (middle-upper Eocene) ranged from 12.7°C to 16.8°C, the precipitation ranged from 1390 to760 mm and seasonality is inferred (Tables 1; 4). A temperate-warm paleoclimate could be interpreted based on the estimated values and paleoclimate reconstruction. On the other hand, temperature estimates, the unique climate parameter calculated for the upper RTF member (Upper Eocene-Oligocene), shows a slight decrease compared with the lower RTF member (Table 2). In Australia, paleoclimate reconstructions, using fossil leaves and different methods, were made for some sites. The middle Eocene Anglesea and Golden Grove MAT estimates ranged from 15.5°C to 23.1°C; the middle Eocene-Oligocene, West Dale ranged from 14.2°C to 19.6°C and the early Oligocene Cethan site resulted a MAT estimates of 4.2°C to 8.3°C (Greenwood *et al.* 2004).

Global climate trends, using marine isotopes, indicate that the late Eocene-Oligocene was clearly marked by a decline of temperature and a deterioration of the climate from warm to cooler conditions (Zachos *et al.* 2001a). This decline is difficult to observe in our analysis not only due to the scarce fossil leaves from the upper RTF member but also for the unconformity at the top of the Río Turbio Formation. The scarce number of fossil leaves may produce distortion in the results and more fossil material is necessary for a better reconstruction and discussion of data. The number of species per sample has a major effect on the precision of MAT estimates, both in predictor data sets and in fossil samples for which a MAT estimate is desired (Wilf 1997). The profile made by Hünicken (1967) showed that Río Guillermo Formation unconformably overlies the RTF (Hünicken 1967; Vento *et al.* 2017). Moreover, an erosive unconformity between Río Turbio and Río Guillermo formations is showed by Fosdick *et al.* (2015a, Fig. 1B). Under the estimated paleoclimate conditions, both RTF members can be characterized by warm and humid conditions (Romero 1986; Vento & Prámparo 2018). Hinojosa & Villagrán (2005) and Hinojosa (2005) made estimates for the RTF, with a MAT of 17.7°C and a MAP of 2510 mm. These values are a little higher than our estimates probably because the authors do not make any distinction among fossil leaves from the lower and the upper member of this formation.

More recently, a paleoclimate reconstruction for the Oligocene Sierra Baguales, Río Leona Formation, estimated a microthermal climate with evidenced seasonality and temperate conditions with a MAT between 6.7-8.9°C and a MAP of 931 mm (Gutiérrez *et al.* 2019). Using fossil wood as proxies indicated temperate and humid conditions during the late Oligocene (27-26 Ma) in Rancahué Formation, supported by values of MAT between 10-14°C and a MAP between 1800-2000 mm (Brea *et al.* 2015). Paleoclimate estimates for the RGF indicated a significant decrease of MAT ranging from 3.5°C to 6.3°C and MAP from 680 to 830 mm, which will indicate a temperate-cool climate for this formation with drier conditions compared with the RTF (Table 3; Fig. 5). However, estimates from two early Miocene sites in Australia: Yallourn Clays and Kiandra, resulted in higher temperatures from 17.1°C to 23.5°C, probably due to regional conditions (Greenwood *et al.* 2004). A paleoclimate reconstruction was recently published for the early-middle Miocene Pico Quemado locality with an estimated MAT value of 7.2°C and MAP of 1237 mm, suggesting a temperate-cold climate with seasonality. A fossil flora analysis recorded a warmer and more humid event in the middle Miocene compared to the previous Eocene-Oligocene period, probably related to the middle Miocene Climatic Optimum (Hinojosa 2005). The results from Pico Quemado are not in accordance with the global trend that indicates warmer conditions for this age, probably due to local conditions (Caviglia & Zamaloa 2014; Caviglia 2018). However, Caviglia (2018) remarked that there is no precise age information from the base of the Ñirihuau Formation outcrops, including the Pico Quemado locality, and that it could be possible that its age would be older regarding the complexity of Ñirihuau Basin (Asensio *et al.* 2010; Cazau *et al.* 1989). According to our analysis, a decrease of temperature is detected from the Eocene to early Miocene, with higher values recorded for the Río Turbio Formation and the lowest values for the Río Guillermo Formation. A slight cooling is observed from the middle to upper Eocene when compared to temperature values for fossil sites in South America and a strong decline for the Eocene-Oligocene (Fig. 5). This climate trend was followed by a redistribution of the vegetation with a reduction of tropical forests and subantarctic paleoflora extended in southern South America (Romero 1986; Hinojosa & Villagrán 1997; Hinojosa 2005). The response of the paleoflora from Sierra Baguales to the global decrease of temperature caused an increase in the proportion of dicot morphospecies with toothed margins, whereas the decrease in precipitation resulted in smaller leaves (Gutiérrez *et al.* 2019). Glade-Vargas *et al.* (2018) suggested that some traits, in the evolution of the margin type, are constrained by phylogenetic relationships in the family Nothofagaceae, and traits such as size and shape suggested adaptations to environment conditions.

The Eocene-Oligocene transition is nearly coincident with an unconformity (Malumián *et al.* 2013) and the climate transition coincides with the first permanent ice sheets of the Cenozoic (Zachos *et al.* 2001a; De Conto & Pollard 2003a, b). Our results indicate a slight deterioration in climate conditions from the upper Eocene to the early Oligocene (RTF lower and upper member) and a significant decrease of MAT and MAP toward the early Miocene (RGF) (Fig. 5).

Continental climate changes seem to be driven by plate tectonics, with mid-ocean activity leading to higher sea levels and warmer ocean water, together with an increase in atmospheric CO_2 and CH_4 as a result of volcanic activity during the Cenozoic. These events expanded the vegetation and had an effect in plant productivity (Le Roux 2012). Climate deterioration from warmer to cooler conditions was documented not only in South America but also as a global climate trend (Zachos *et al.* 2001a, b; Bohaty & Zachos 2003; De Conto & Pollard 2003a, b; Hinojosa 2005; Gutiérrez *et al.* 2019). In South America, the Drake passage opening was an event that began in the Oligocene and was coincident with the global marine cooling and glaciation in Antarctica with the record of lower temperatures (Zachos *et al.* 2001b; De Conto & Pollard 2003a; Gutiérrez *et al.* 2019).

It is recognized that there is a coupling between climate and the carbon cycle (Pearson & Palmer 2000; Zachos *et al.* 2001a; Zachos *et al.* 2008) and changes in temperature could affect the response of the paleofloral composition (Wilf *et al.* 2005; Gutiérrez *et al.* 2019). Climate models using paleofloras from Antarctica suggested that vegetation-climate feedback during the Eocene-Oligocene transition played a significant role in the rapid glaciation of the continent (Thorn & De Conto 2006).

Current ocean circulation and tectonic events produced changes in the CO_2 levels (Zachos *et al.* 2001a, b). A reduction in atmospheric CO_2 levels may cause climatic deterioration with lower temperatures for the late Oligocene-early Miocene (Zachos *et al.* 2001b; Zachos *et al.* 2008). Inferences made by Nullo & Combina (2011) confirmed that the decrease in temperatures during the Cenozoic were caused by restriction in the ocean circulation. Paleogeographic changes occurred in the western part of southern Argentina, where the Andes began to rise and it clearly divided the Pacific from the Atlantic domain.

Zachos *et al.* (2001a) postulated a cooling and rapid expansion of Antarctic continental ice sheets in the earliest Oligocene. These ice sheets persisted until the latter part of the Oligocene (26 to 27 Ma), when a warming trend reduced the extent of Antarctic ice. From this point until the middle Miocene (*c.* 15 Ma), global ice volume remained low with the exception of several brief periods of glaciation. One of these events, referred to as Mi-1, occurred at -23 Ma, which was followed by a series of intermittent but smaller glaciations. A simulation climate model implied that declining Cenozoic CO_2 first led to the formation of small, highly dynamic ice caps on the Antarctic, reinforcing the importance of CO_2 as a fundamental condition for Cenozoic climate change (De Conto & Pollard 2003b; Thorn & De Conto 2006). The opening of Southern Ocean gateways which produced changes in ocean currents may have also contributed to the glaciation of Antarctica (Sijp & England 2004).

On the other hand, MAP estimates showed considerable variations when comparing the lower RTF member and the RGF. A decrease of precipitation is recorded in our analysis in RGF (Table 3). Abundant moisture may have been an important factor in maintaining warm, frost-free conditions in the Eocene because of the major role of water vapor in retaining and transporting atmospheric heat (Wilf *et al.* 1998). However, the decrease in precipitation can be regionally correlated with an important pulse of uplift of the Andes and changes in paleocurrent directions during the early Oligocene and the developed of the South America arid diagonal (Gutiérrez *et al.* 2019). Estimates of MAP indicate a decrease during the Cenozoic (Hinojosa & Villagrán 2005) which is coincident with our results. A maximum MAP of 1663 mm and 1937 mm occurs for the Pichileufú and Laguna del Hunco mixed paleofloras without *Nothofagus* and it drastically dropped from the middle Eocene to early Miocene with a recorded value of 1520 mm for the Río Turbio, without member distinction (Hinojosa & Villagrán 2005).

Nowadays, the areas where the Río Turbio and Río Guillermo formations are located exhibit a mean annual temperature oscillating between 6°C and 8°C, and a mean annual precipitation of 200-300 mm with a strong east-west gradient from 200 mm to more than 1000 mm (Servicio Meteorológico Nacional 1981-2010). The paleoclimatic estimates obtained for RTF, suggested a MAT difference of more than 8°C compared to the current temperature and a precipitation difference of approximately 200-300 mm to more than 1000-1400 mm. Paleotemperatures for RGF ranged from 6°C to 8°C and the precipitation difference is approximately more than 300-400 mm. It presented similar values compared to the temperature today. The Andes uprising produced an intense rainshadow on the major circulation systems of the southern cone of South America (Hinojosa & Villagrán 2005).

CONCLUSIONS

There are only a few paleoclimate reconstructions using quantitative estimates for southern South America. Here we attempt to estimate paleoclimate conditions using physiognomic characters of fossil leaves from the Río Turbio and Río Guillermo formations, following the results of detrital zircon U/Pb thermochronology by Fosdick *et al.* (2011, 2015a, b) to constrain the age of the geologic units.

The outcomes obtained by different techniques for the lower Río Turbio Formation member resulted in similar estimates when univariate methods and the recent Digital Leaf Physiognomy (DiLP) analysis were used. Climate Leaf Analysis Multivariate Program (CLAMP) produced higher values of temperature and precipitation compared to the above methodologies. We found slight differences when we used the CLAMP3B SA and SH90 datasets. However, the CLAMP3B dataset includes several sites from southern South America and it is probably more trustworthy than the dataset from the Southern Hemisphere until new calibrations incorporating more sites have been made. Both members of the Río Turbio Formation showed a mixed paleoflora with paratropical representatives together with cool-temperate taxa as *Nothofagus*, with similar percentages of untoothed fossil leaves. The estimates indicate warm and humid conditions for both the lower and upper Río Turbio Formation members and seasonality for the lower Río Turbio member, when we used univariate and multivariate models. Conversely, the Río Guillermo Formation was represented by cool temperate representatives, mainly *Nothofagus* and most of them with toothed margins. The composition of the fossil flora of this formation is more similar to modern temperate forests developed in southern Argentina.

Comparing the two studied palofloras (Río Turbio and Río Guillermo formations) a decrease in mean annual temperature and precipitation is inferred. These values are in accordance with the global trend of warming and humid conditions for the Eocene with a cooling trend to the late Eocene-early Oligocene and again a warming trend with brief periods of cold conditions after the Oligocene-Miocene boundary postulated by Quattrocchio *et al.* (2013) and Zachos *et al.* (2001a).

Events such as the Drake passage opening, the ice-sheet in Antarctica and the uplift of the Andes influenced local climate conditions and contribute to the cooling conditions evidenced in the paleoflora of southern South America at the Eocene-Oligocene. The decline in CO2 levels probably affected the paleoflora composition during the Eocene-Oligocene-Miocene in southern South America. This decline caused a transition from a paratropical to a cool-temperate forest. New collections and studies of fossil plants will provide a more robust continental paleoclimate reconstruction in the future.

Acknowledgements

A special thanks to Dr M. Ontivero for helping us on the map of the study area. We are grateful to one anonymous reviewer and Dr Kvaček for the comments and suggestions made on the manuscript. This work was supported by the National Scientific and Technical Research Council (CONICET-Argentina).

REFERENCES

Archangelsky S. 1972. — Esporas de la Formación Río Turbio Eoceno, Provincia de Santa Cruz. *Revista Museo de La Plata* 6: 65-100.

Arens N. C. & Harris E. B. 2015. — Paleoclimatic reconstruction for the Albian-Cenomanian transition based on a dominantly angiosperm flora from the Cedar Mountain Formation, Utah, USA. *Cretaceous Research* 53: 140-152. https://doi.org/10.1016/j.cretres.2014.11.004

Asensio M. A., Cornou M. E., Malumián N., Martínez M. A. & Quattrocchio M. E. 2010. — Formación Río Foyel, Oligoceno de la Cuenca de Ñirihuau: la transgresión pacífica en la Cordillera Norpatagónica. *Revista de la Asociación Geológica Argentina* 66 (3): 399-405. https://revista.geologica.org.ar/raga/article/view/769

Axelrod D., Kalin-Arroyo M. T. & Raven P. 1991. — Historical development of temperate vegetation in the Americas. *Revista Chilena de Historia Natural* 64: 413-446. http://rchn.biologiachile.cl/pdfs/1991/3/Axelrod_et_al_1991.pdf

Azcuy C. & Amigo A. 1991. — Geología y paleoambiente de la Formación Río Turbio (Eoceno), en la sierra Dorotea, provincia de Santa Cruz. *Revista de la Asociación Geológica Argentina* 46: 201-210. http://ppct.caicyt.gov.ar/index.php/raga/article/view/17921

Bailey I. W. & Sinnott E. W. 1915. — A botanical index of Cretaceous and Tertiary climates. *Science* 41: 831-834. https://doi.org/10.1126/science.41.1066.831

Bailey I. W. & Sinnott E. W. 1916. — The climatic distribution of certain types of angiosperm leaves. *America Journal of Botany* 3: 24-39. https://doi.org/10.1002/j.1537-2197.1916.tb05397.x

Barreda V. & Palazzesi L. 2007. — Patagonian vegetation turnovers during the Paleogene-early Neogene: origin of arid-adapted floras. *The Botanical Review* 73: 31-50. https://doi.org/b9vzhk

Barreda V., Palazzesi L. & Marenssi S. 2009. — Palynological record of the Paleogene Río Leona Formation (southernmost South America): Stratigraphical and paleoenvironmental implications. *Review of Palaeobotany and Palynology* 154: 22-33. https://doi.org/10.1016/j.revpalbo.2008.11.005

Berry E. W. 1928. — Tertiary fossil plants from the Argentine republic. *Proceedings of the United States National Museum* 73: 1-27. https://doi.org/10.5479/si.00963801.73-2743.1

Blume C. L. 1851. — *Museum Botanicum Lugduno-Batavum, sive, stirpium exoticarum novarum vel minus cognitarum ex vivis aut siccis brevis expositio et descriptio*. E.J. Brill, Leiden, 396 p.

Bohaty S. M. & Zachos J. C. 2003. — Significant Southern Ocean warming event in the late middle Eocene. *Geology* 31: 1017-1020. https://doi.org/10.1130/G19800.1

Bostelmann J. E., Le Roux J. P., Vásquez A., Gutiérrez N. M., Oyarzún J. L., Carreño C., Torres T., Otero R., Llanos A., Fanning C. M. & Hervé F. 2013. — Burdigalian deposits of the Santa Cruz Formation in the Sierra Baguales, Austral (Magallanes) Basin: Age, depositional environment and vertebrate fossils. *Andean Geology* 40 (3): 458-489. https://doi.org/10.5027/andgeoV40n3-a04

Bowen G. J. 2007. — When the world turned cold. *Nature* 445: 607-608. https://doi.org/10.1038/445607a

Brea M., Zucol A. F. & Iglesias A. 2012. — Fossil plant studies from late early Miocene of the Santa Cruz Formation: paleoecology and paleoclimatology at the passive margin of Patagonia, Argentina, *in* Vizcaíno S. F., Kay R. F. & Bargo M. S. (eds), *Early Miocene paleobiology in Patagonia. Height-latitude paleocommunities of the Santa Cruz Formation*. Cambridge University Press, Cambridge: 104-128. https://doi.org/10.1017/CBO9780511667381.008

Brea M., Artabe A. E., Franzese J. R., Zucol A. F., Spalletti L. A., Morel E. M., Veiga G. & Ganuza D. G. 2015. — Reconstruction of a fossil forest reveals details of the palaeoecology, palaeoenvironments and climatic conditions in the late Oligocene of South America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 418: 19-42. https://doi.org/10.1016/j.palaeo.2014.11.013

Brea M., Zucol A. F., Bargo MS., Fernicola J. C. & Vizcaíno S. F. 2017. — First Miocene record of Akaniaceae in Patagonia (Argentina): a fossil wood from the Early Miocene Santa Cruz Formation and its palaeobiogeographical implications. *Botanical Journal of the Linnean Society* 183: 334-347. https://doi.org/10.1093/botlinnean/bow014

Burgos J. J. 1985. — Clima del extremo sur de Sudamerica, *in* Boelcke O., Moore D. M. & Roig F. A. (eds), *Transecta botánica de la Patagonia austral*. CONICET (Argentina), Instituto de la Patagonia (Chile) & Royal Society (UK), Buenos Aires: 10-40.

Caviglia N. 2018. — Early Miocene climate estimations in Patagonia: The case of Pico Quemado, Ñirihuau Formation (lower-middle Miocene). *Journal of South American Earth Sciences* 88: 64-71. https://doi.org/10.1016/j.jsames.2018.08.002

Caviglia N. & Zamaloa M. C. 2014. — Angiosperm flora of Pico Quemado, Ñirihuau Formation (late Oligocene), Río Negro province. *Ameghiniana* 51: 209-225. https://doi.org/10.5710/AMGH.24.02.2014.800

Cazau L., Mancini D., Cangini J. & Spalletti L. 1989. — Cuenca de Ñirihuau, *in* Chebli G. A., Spalletti L. (eds), *Cuencas sedimentarias argentinas*. Serie Correlación Geológica, Universidad Nacional de Tucumán, San Miguel de Tucumán: 299-318.

Césari S., Panti C., Pujana R., Francis J. & Marenssi S. 2015. — The late Oligocene flora from Río Leona Formation, Argentinean Patagonia. *Review of Paleobotany and Palynology* 216: 143-158. https://doi.org/10.1016/j.revpalbo.2015.01.002

De Conto R. M. & Pollard D. 2003a. — Rapid Cenozoic glaciation of Antarctica induced by declining atmospheric CO2. *Nature* 421: 245-249. https://doi.org/10.1038/nature01290

De Conto R. M & Pollard D. 2003b. — A coupled climate-ice sheet modeling approach to the Early Cenozoic history of the Antarctic ice sheet. *Palaeogeography, Palaeoclimatology, Palaeoecology* 198: 39-52. https://doi.org/10.1016/S0031-0182(03)00393-6

Dilcher D. L. 1973. — A paleoclimatic interpretation of the Eocene floras of southeastern North America, *in* Graham A (ed.), *Vegetation and vegetational history of northern Latin America*. Elsevier, Amsterdam: 39-53.

Ellis B., Daly D. C., Hickey L. J., Johnson K. R., Mitchell J. D., Wilf P. & Wing S. L. 2009. — *Manual of Leaf Architecture*. Cornell University Press, Ithaca, New York, 190 p.

Fernández D. A., Panti C., Palazzesi L. & Barreda V. D. 2012. — The presence of a neotropical family (malpighiaceae) in the far south of South America during the Eocene. *Revista brasileira de paleontologia* 15 (3): 386-391. https://doi.org/10.4072/rbp.2012.3.13

Fiori A. 1931. — Fillite terziarie della Patagonia. I. Fillite dela riva meridionalle del Lago Nahuel Huapí. *Giornale di Geologia* 4: 101-116.

Fiori A. 1939. — Fillite terziarie della Patagonia. II. Fillite del Río Ñirihuau. *Giornale di Geologia* 13: 1-27.

Fosdick J. C., Romans B. W., Fildani A., Bernhardt A., Calderón M. & Graham S. A. 2011. — Kinematic Evolution of the Patagonian Retroarc Fold-and-Thrust Belt and Magallanes Foreland Basin, Chile and Argentina, 51°30'S. *Geological Society of America Bulletin* 123: 1679-98. https://doi.org/10.1130/B30242.1

Fosdick J. C., Grove M., Graham S. A., Hourigan J. K., Lovera O. & Romans B. W. 2015a. — Detrital thermochronologic record of foreland burial heating, sedimentary provenance, and orogenesis in Patagonia. *Basin Research* 27: 546-572. https://doi.org/10.1111/bre.12088

Fosdick J. C., Bostelmann J. E., Leonard J., Ugalde R., Oyarzún J. L. & Griffin M. 2015b. — Timing and rates of foreland sedimentation: New detrital zircon U/ Pb geochronology of the Cerro Dorotea, Río Turbio, and Río Guillermo formations, Magallanes basin. *XIV Congreso Geológico Chileno*, La Serena: 763-766.

Franzese J. R., D'Elia L., Bilmes A., Muravchik M. & Hernández M. 2011 — Superposición de cuencas extensionales y contraccionales oligo-miocenas en el retroarco andino norpatagónico: la

Cuenca de Aluminé, Neuquén, Argentina. *Andean geology* 38 (2): 319-334. http://www.andeangeology.cl/index.php/revista1/article/view/V38n2-a04/1507

Fricke H. C. & Wing S. L. 2004. — Oxygen isotope and paleobotanical estimates of temperature and d18O-latitude gradients over North America during the Early Eocene. *American Journal of Science* 304: 612-635. https://doi.org/10.2475/ajs.304.7.612

García J. A. S. 1988. — Caracterización sedimentológica del área de Río Turbio, Cuenca Austral, Provincia de Santa Cruz, República Argentina. *Estudios Geológicos* 44: 199-210. https://doi.org/10.3989/egeol.88443-4538

Gayó E., Hinojosa L. F. & Villagrán C. 2005. — On the persistence of tropical paleofloras in central Chile during the early Eocene. *Review of Paleobotany and Palynology* 137 (1-2): 41-50. https://doi.org/10.1016/j.revpalbo.2005.09.001

Givnish T. 1984. — Leaf and canopy adaptations in tropical forests, *in* Medina E., Mooney H. A. & Vázquez-Yanes C. (eds), *Physiological ecology of plants of the wet tropics. Proceedings of an international symposium held in Oxatepec and Los Tuxtlas, Mexico.* Dr. W. Junk Publishers, The Hague: 51-84.

Glade N. S., Hinojosa L. F. & Leppe M. 2018. — Evolution of climatic related leaf traits in the family Nothofagaceae. *Frontiers in Plant Science* 9: 1-10. https://doi.org/10.3389/fpls.2018.01073

González Estebenet M. S., Guerstein G. R. & Rodríguez Raising M. E. 2014. — Middle Eocene dinoflagellate cysts from Santa Cruz Providence, Argentina: Biostratigraphy and paleoenvironment. *Review of Palaeobotany and Palynology* 211: 55-65. https://doi.org/10.1016/j.revpalbo.2014.09.002

Greenwood D. R., Wilf P., Wing S. L. & Christophel D. C. 2004. — Paleotemperature estimation using leaf-margin analysis: is Australia different? *Palaios* 19: 129-142. https://doi.org/drwf87

Greenwood D. R., Archibald B. S., Mathewes R. W. & Moss P. T. 2005. — Fossil biotas from the Okanagan Highlands, southern British Columbia and northeastern Washington State: climates and ecosystems across an Eocene landscape. *Canadian Journal of Earth Science* 42: 167-185. https://doi.org/10.1139/e04-100

Gregory-Wodzicki K. 2000. — Relations between leaf morphology and climate, Bolivia: implications for estimating paleoclimate from fossil floras. *Paleobiology* 26 (4): 668-688. https://doi.org/b6fjqz

Guerstein G. R., González Estebenet M. S., Alperín M. I., Casadío S. A. & Archangelsky S. 2014. — Correlation and paleoenvironments of middle Paleogene marine beds based on dinoflagellate cysts in southwestern Patagonia. Argentina. *Journal of South American Earth Sciences* 52: 166-178. https://doi.org/10.1016/j.jsames.2014.02.011

Gutiérrez N. M., Le Roux J. P., Vásquez A., Carreño C. & Pedroza V. 2017. — Tectonic events reflected by palaeocurrents, zircon geochronology, and palaeobotany in the Sierra Baguales of Chilean Patagonia. *Tectonophysics* 695: 76-99. https://doi.org/10.1016/j.tecto.2016.12.014

Gutiérrez N. M., Pino J. P., Le Roux J. P., Pedroza V., Oyarzun J. L. & Hinojosa L. F. 2019. — An Oligocene microthermal forest dominated by *Nothofagus* in Sierra Baguales, Chilean Patagonia: Response to global cooling and tectonic events. *Palaeogeography, Palaeoclimatology, Palaeoecology* 528: 1-13. https://doi.org/10.1016/j.palaeo.2019.04.006

Herman A. B. R. A. & Spicer R. A. 1996. — Palaeobotanical evidence for a warm Cretaceous Arctic Ocean. *Nature* 380: 330-333. https://doi.org/10.1038/380330a0

Hinojosa L. F. 2005. — Cambios climáticos y vegetacionales inferidos a partir de Paleofloras Cenozoicas del sur de Sudamérica. *Revista Geológica de Chile* 32: 95-115. https://doi.org/10.4067/S0716-02082005000100006

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. *Revista Chilena de Historia Natural* 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? *Palaeogeography, Palaeoclimatology, Palaeoecology* 217: 1-23. https://doi.org/10.1016/j.palaeo.2004.11.013

Hinojosa F. L., Pesce O., Yabe A., Uemura K. & Nishida H. 2006a. — Physiognomical analysis and paleoclimate of the Ligorio Márquez fossil flora, Ligorio Márquez Formation, 46º45'S, Chile, *in* Nishida H. (ed.), *Chile. Post Cretaceous floristic changes in southern Patagonia*. Chile, Chuo University, Tokyo: 45-55.

Hinojosa L. F., Armesto J. J. & Villagrán C. 2006b. — Are Chilean coastal forests pre-Pleistocene relicts? Evidence from foliar physiognomy, palaeoclimate, and phytogeography. *Journal of Biogeography* 33(2): 331-341. https://www.jstor.org/stable/3554890

Hinojosa L. F., Pérez F., Gaxiola A. & Sandoval I. 2011. — Historical and phylogenetic constraints on the incidence of entire leaf margins: insights from a new South American model. *Global Ecology and Biogeography* 20: 380-390. https://doi.org/10.1111/j.1466-8238.2010.00595.x

Huff P. M., Wilf P. & Azumah E. J. 2003. — Digital future for paleoclimate estimation from fossil leaves? Preliminary results. *Palaios* 18: 266-274. https://doi.org/dvm8t9

Hünicken M. 1955. — Depósitos neocretácicos y terciarios del extremo S. S.W. de Santa Cruz: Cuenca Carbonífera de Río Turbio (Vol. 4, no. 1), *in* Neocretaceous and tertiary deposits from the austral S. S.W. of Santa Cruz: Río Turbio Carboniferous basin. *Instituto Nacional de Investigación de las Ciencias Naturales:* 11-164.

Hünicken M. 1967. — Flora terciaria de los estratos de Río Turbio, Santa Cruz (Niveles plantíferos del Arroyo Santa Flavia). Revista de la Facultad de Ciencias Exactas, Físicas y Naturales de la Universidad de Córdoba [Tertiary flora from Río Turbio strata, Santa Cruz (Arroyo Santa Flavia plant levels)]. *Serie Ciencias Naturales* 56: 139-262.

Hünicken M. 1995. — Floras Cretácicas y Terciarias, *in* Stipanicic P. N. & Hünicken M. A. (eds), *Revisión y actualización de la obra paleobotánica de Kurtz en la República Argentina*. Actas de la Academia Nacional de Ciencias 11, Córdoba: 199-219.

Hunt R. J. & Poole I. 2003. — Paleogene West Antarctic climate and vegetation history in light of new data from King George island, *in* Wing S. L., Schmitz B., Thomas E. (eds), Causes and Consequences of Globally Warm Climates in the Early Paleogene. *Geological Society of America Special Papers* 369: 395-412. https://doi.org/10.1130/0-8137-2369-8.395

Iglesias A., Wilf P., Johnson K. R., Zamuner A. B., Cúneo N. R., Matheos S. D. & Singer B. S. 2007. — A Paleocene lowland macroflora from Patagonia reveals significantly greater richness than North American analogs. *Geology* 35 (10): 947-950. https://doi.org/10.1130/G23889A.1

Iglesias A. R., Artabe A. E. & Morel E. M. 2011. — The evolution of Patagonian climate and vegetation from the Mesozoic to the present. *Biological Journal of Linnean Society* 103 (2): 409-422. https://doi.org/10.1111/j.1095-8312.2011.01657.x

Jacobs B. F. 2002. — Estimation of low-latitude paleoclimates using fossil angiosperm leaves: examples from the Miocene Tugen Hills, Kenya. *Paleobiology* 28: 399-421. https://doi.org/bc5s2q

Jordan G. J. 1997. — Uncertainty in paleoclimatic reconstructions based on leaf physiognomy. *Australian Journal of Botany* 45: 527-547. https://doi.org/10.1071/BT96035

Jussieu A. L. 1789. — *Genera Plantarum Secundum Ordines Naturales disposita, juxta methodum in horto regio parisiensi Exaratum.* Viduam Hérissant & Theophilum Barrois, Paris, 498 p.

Kennedy E. M., Arens N. C., Reichgelt T., Spicer R. A., Spicer T. E., Stranks L. & Yang J. 2014. — Deriving temperature estimates from Southern Hemisphere leaves. *Palaeogeography, Palaeoclimatology, Palaeoecology* 412: 80-90. https://doi.org/10.1016/j.palaeo.2014.07.015

Leanza A. F. 1972. — Andes Patagónicos Australes, *in* Leanza A. F. (ed.), Geología regional Argentina, Córdoba. *Academia Nacional de Ciencias*: 689-706.

Le Roux J. P. 2012. — A review of Tertiary climate changes in southern South America and the Antarctic Peninsula. Part 1: Oceanic conditions. *Sedimentary Geology* 247: 1-20. https://doi.org/10.1016/j.sedgeo.2011.12.014

Lowe A. J., Greenwood D. R., West C. K., Galloway J. M., Sudermann M. & Reichgelt T. 2018. — Plant community ecology and climate on an upland volcanic landscape during the Early Eocene Climatic Optimum: Mc Abee Fossil Beds, British Columbia, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology* 511: 433-448. https://doi.org/10.1016/j.palaeo.2018.09.010

Malumián N. & Caramés A. 1997. — Upper Campanian-Paleogene from the Río Turbio coal measures in southern Argentina: micropaleontology and the Paleocene/Eocene boundary. *Journal of South America Earth Sciences* 10: 189-201. https://doi.org/10.1016/S0895-9811(97)00015-1

Malumián N., Panza J., Parici C., Nañez C., Caramés A. & Torre E. 2000. — Hoja Geológica 5172- III, Yacimiento Río Turbio, provincia Santa Cruz, 1:250.000. *Boletín del Servicio Geológico Minero Argentino* 247, 108 p. http://repositorio.segemar.gov.ar/308849217/1801

Malumián N., Hromic T. & Náñez C. 2013. — El Paleógeno de la cuenca de Magallanes: bioestratigrafía y discontinuidades. *Anales del Instituto de la Patagonia* 41: 29-52. https://doi.org/10.4067/S0718-686X2013000100003

Nullo F. E. & Combina A. M. 2002. — Sedimentitas Terciarias continentales, *in* Haller M. J. (ed.), Relatorio XV. Congreso Geológico Argentino. *Geología y Recursos Naturales de Santa Cruz.* El Calafate: 245-258.

Nullo F. & Combina A. 2011. — Patagonian continental deposits (Cretaceous-Tertiary). *Biological Journal of the Linnean Society* 103 (2): 289-304. https://doi.org/10.1111/j.1095-8312.2011.01654.x

Panti C. 2011. — Palaeofloristic analysis of the Río Guillermo Formation (late Eocene-early Oligocene?), Santa Cruz, Argentina. *Ameghiniana* 48: 320-335. https://doi.org/10.5710/AMGH.v48i3(349)

Panti C. 2018. — Fossil leaves of subtropical lineages in the Eocene-? Oligocene of southern Patagonia. *Historical Biology* 32: 1-15. https://doi.org/10.1080/08912963.2018.1487421

Peppe D. J., Royer D. L., Cariglino B., Oliver S. Y., Newman S., Leight E., Grisha E., Fernández M., Herreras F., Adams J., Correa E., Curranos E., Erickson M., Hinojosa L., Hoganson J., Iglesias A., Jaramillo C., Johnson K., Jordan G., Kraft N., Lovelock E., Lusk C., Niinemets U., Peñuelas J., Rapson G., Wing S. & Wright I. 2011. — Sensitivity of leaf size and shape to climate: global patterns and paleoclimatic applications. *New Phytologist* 190: 724-739. https://doi.org/10.1111/j.1469-8137.2010.03615.x

Pearson P. & Palmer M. 2000. — Atmospheric carbon dioxide concentrations over the past 60 million years. *Nature* 406: 695-699. https://doi.org/10.1038/35021000

Quattrocchio M. E., Martínez M. A., Hinojosa L. F. & Jaramillo C. 2013. — Quantitative analysis of Cenozoic palynofloras from Patagonia, southern South America. *Palynology* 37: 246-258. https://doi.org/10.1080/01916122.2013.787126

R Core Team 2018. — R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna. http://www.R-project.org/

Roig F. A., Anchorena J., Dollenz O., Faggi A. M. & Méndez E. 1985. — Las comunidades vegetales de la transecta botánica de la Patagonia Austral. *Transecta botánica de la Patagonia Austral*: 350-456. https://issuu.com/jpintoz/docs/1985_roig_et_com-vegtbpa1-vegarcont_

Romero E. J. 1978. — Paleocología y paleofitogeografía de las tafofloras 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: 449-461. https://doi.org/10.2307/2399123

Romero J. E. & Zamaloa M. C. 1985. — Polen de Angiospermas de la Formación Río Turbio (Eoceno), Provincia de Santa Cruz, República Argentina. *Ameghiniana* 22: 43-51. https://ameghiniana.org.ar/index.php/ameghiniana/article/view/1739

Romero E. J. & Castro M. T. 1986. — Material fúngico y granos de polen de angiospermas de la Formación Río Turbio (Eoceno), provincia de Santa Cruz, República Argentina. *Ameghiniana* 23 (1-2): 101-118. https://www.ameghiniana.org.ar/index.php/ameghiniana/article/view/1815

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. *American Journal of Botany* 92: 1141-1151. https://doi.org/10.3732/ajb.92.7.1141

Servicio Meteorológico Nacional 1981-2010. — Estadisticas. http://www.smn.gov.ar/estadisticas

Schneider C. A., Rasband W. S. & Eliceiri K. W. 2012. — NIH Image to ImageJ: 25 years of image analysis. *Nature methods* 9 (7): 671-675. https://doi.org/10.1038/nmeth.2089

Sijp W. P. & England M. H. 2004. — Effect of the Drake Passage Throughflow on Global Climate. *Journal of Physical Oceanography* 34: 1254-1266. https://doi.org/b28xwr

Suárez M., De la Cruz R. & Troncoso A. 2000. — Tropical/subtropical upper Paleocene-lower Eocene fluvial deposits in eastern central Patagonia, Chile (46°45'S). *Journal of South American Earth Sciences* 13 (6): 527-536.

Traiser C., Roth-Nebelsick A., Grein M., Kovar-Eder J., Kunzmann L., Moraweck K., Lange J., Kvaček J., Neinhuis C., Folie A., De Franceschi D., Kroh A., Prestianni C., Poschmann M. & Wuttke M. 2018. — MORPHYLL: A database of fossil leaves and their morphological traits. *Palaeontologia Electronica* 21 (1): 1-17. https://doi.org/10.26879/773

Thorn V. C. & De Conto R. 2006. — Antarctic climate at the Eocene/Oligocene bou ndary climate model sensitivity to high latitude vegetation type and comparisons with the palaeobotanical record. *Palaeogeography, Palaeoclimatology, Palaeoecology* 231 (1-2): 134-157. https://doi.org/10.1016/j.palaeo.2005.07.032

Troncoso A. 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), *Monographs in Systematic Botany*. Missouri Botanical Garden Press 6th Proceedings of Congreso Latinoamericano de Botánica, Mar del Plata, Argentina: 149-172.

Vento B., Gandolfo M. A., Nixon K. C. & Prámparo M. 2017. — Paleofloristic assemblage from the Paleogene Río Guillermo Formation, Argentina: preliminary results of phylogenetic relationships of *Nothofagus* in South America. *Historical Biology* 29: 93-107. https://doi.org/10.1080/08912963.2015.1136930

Vento B. & Prámparo M. 2018. — Angiosperm association from the Río Turbio Formation (Eocene-? Oligocene) Santa Cruz, Argentina: Revision of Hünicken's (1955) fossil leaves collection. *Alcheringa: An Australasian Journal of Palaeontology* 42: 125-153. https://doi.org/10.1080/03115518.2017.1408854

Wiemann M. C., Manchester S. R., Dilcher D. L., Hinojosa L. F. & Wheeler E. 1998. — Estimation of temperature and precipitation from morphological characters of dicotyledonous leaves. *American Journal of Botany* 85: 1796-1802 https://doi.org/10.2307/2446514

Wilf P. 1997. — When are leaves good thermometers? A new case for Leaf Margin Analysis. *Paleobiology* 23: 373-390. https://doi.org/10.1017/S0094837300019746

Wilf P., Wing S. L., Greenwood D. R. & Greenwood C. L. 1998. — Using fossil leaves as paleoprecipitation indicators: an Eocene example. *Geology* 26(3): 203-206. https://doi.org/10.1130/0091-7613(1998)026<0203:UFLAPI>2.3.CO;2

Wilf P., Cúneo N. R., Johnson K. R., Hicks J. F., Wing S. L. & Obradovich J. D. 2003. — High plant diversity in Eocene South America: evidence from Patagonia. *Science* 300: 122-125. https://doi.org/10.1126/science.1080475

Wilf P., Johnson K. R., Cúneo N. R., Smith M. E., Singer B. S. & Gandolfo M. A. 2005. — Eocene plant diversity at Laguna del Hunco and Río Pichileufú, Patagonia, Argentina. *American Naturalist* 165: 634-650. https://doi.org/10.1086/430055

Wilf P., Little S. A., Iglesias A., del Carmen Zamaloa M., Gandolfo M. A., Cúneo N. R. & Johnson K. R. 2009. — Papuacedrus (Cupressaceae) in Eocene Patagonia: a new fossil link to Australasian rainforests. *American Journal of Botany* 96 (11): 2031-2047. https://doi.org/10.3732/ajb.0900085

Wing S. L. & Greenwood D. R 1993. — Fossils and fossil climate: the case for equable continental interiors in the Eocene. *Philosophical Transactions of the Royal Society B* 341: 243-252. https://doi.org/10.1098/rstb.1993.0109

Wolfe J. A. 1971. — Tertiary climatic fluctuations and methods of analysis of Tertiary floras. *Palaeogeography, Palaeoclimatology, Palaeoecology* 9: 27-57. https://doi.org/10.1016/0031-0182(71)90016-2

Wolfe J. A. 1978. — A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere: Data from fossil plants make it possible to reconstruct Tertiary climatic changes, which may be correlated with changes in the inclination of the earth's rotational axis. *American Scientist* 66: 694-703. https://www.jstor.org/stable/27848958

Wolfe J. A. 1979. — Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions in the Northern Hemisphere and Australasia. *U. S. Geological Survey Professional Paper* 1106: 1-37. https://doi.org/10.3133/pp1106

Wolfe J. A. 1990. — Palaeobotanical evidence for a marked temperature increase following the Cretaceous-Tertiary boundary. *Nature* 343: 153-156. https://doi.org/10.1038/343153a0

Wolfe J. A. 1993. — A method of obtaining climatic parameters from leaf assemblages. *U. S. Geological Survey Bulletin* 2040: 1-71. https://doi.org/10.3133/b2040

Wolfe J. A. 1995. — Paleoclimatic estimates from Tertiary leaf assemblages. *Annual Review of Earth Planetary Sciences* 23: 119-142. https://doi.org/10.1146/annurev.ea.23.050195.001003

Yang J., Spicer R. A., Spicer T. E. & Li C. S. 2011. — 'CL AMP Online': a new web-based palaeoclimate tool and its application to the terrestrial Paleogene and Neogene of North America. *Palaeobiodiversity and Palaeoenvironments* 91: 163-183. https://doi.org/10.1007/s12549-011-0056-2

Yang J., Spicer R. A., Spicer T. E., Arens N. C., Frederic J. M. B., Tao S., Kennedy E. M., Herman A. B., Steart D. C., Gaurav S., Mehrotra R. C., Valdes P. J., Mehrotra N. C., Zhou Z.-K. & Lai J.-S. 2015. — Leaf form-climate relationships on the global stage:an ensemble of characters. *Global Ecology and Biogeography* 24: 1113-1125. https://doi.org/10.1111/geb.12334

Zachos J. C., Shackleton N. J., Revenaugh J. S., Pälike H. & Flower B. P. 2001a. — Climate response to orbital forcing across the Oligocene-Miocene boundary. Science 292 (5515): 274-278. https://doi.org/10.1126/science.1058288

Zachos J., Pagani H., Sloan L., Thomas E. & Billups K. 2001b. — Trends, rhythms, and aberrations in |global climate: 65 Ma to present. *Science* 292: 686-693. https://doi.org/10.1126/science.1059412

Zachos J. C., Dickens G. R. & Zeebe R. E. 2008. — An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* 451 (7176): 279. https://doi.org/10.1038/nature06588

Submitted on 30 August 2019;
accepted on 23 December 2019;
published on 25 January 2021.

APPENDICES — SUPPLEMENTARY MATERIAL

APPENDIX 1.— Supplementary material including the fossil specimens from the studied sites and the morphological character scores for CLAMP analysis

Lower Río Turbio Fm	**LMA**	**LAA**	**Source**
Acrodiclidium flavianum	*	*	Hünicken 1967; Vento & Prámparo 2018
Allophylus graciliformis	*	*	Hünicken 1967; Vento & Prámparo 2018
Anacardites pichileufensis	*	*	Hünicken 1967; Vento & Prámparo 2018
Annona sp.	*	*	Hünicken 1967; Vento & Prámparo 2018
Casearia sp.	*	*	Hünicken 1967; Vento & Prámparo 2018
Cissus pichileufensis	*	*	Hünicken 1967; Vento & Prámparo 2018
Cinnamomum neogaea	*	*	Hünicken 1967; Vento & Prámparo 2018
Cupania grosse-serrata	*	-	Hünicken 1967; Vento & Prámparo 2018
Cupania latifolioides	*	*	Hünicken 1967; Vento & Prámparo 2018
Cupania patagonica	*	*	Hünicken 1967; Vento & Prámparo 2018
Cupania santacrucensis	*	*	Hünicken 1967; Vento & Prámparo 2018
Drimys patagonica	*	*	Hünicken 1967; Vento & Prámparo 2018
Drimys sp.	*	*	Hünicken 1967; Vento & Prámparo 2018
Eucalyptus sp.	*	*	Hünicken 1967; Vento & Prámparo 2018
Escallonia sp.	*	–	Hünicken 1967; Vento & Prámparo 2018
Myrcia sp.	*	*	Hünicken 1967; Vento & Prámparo 2018
Myricaceae	*	*	Hünicken 1967; Vento & Prámparo 2018
Myrica hunzikerii	*	*	Hünicken 1967; Vento & Prámparo 2018
Nectandra prolifica	*	*	Hünicken 1967; Vento & Prámparo 2018
Nothofagus subferruginea	*	*	Hünicken 1967; Vento & Prámparo 2018
Nothofagus variabilis	*	*	Hünicken 1967; Vento & Prámparo 2018
Nothofagus serrulata	*	*	Hünicken 1967; Vento & Prámparo 2018
Nothofagus elongata	*	–	Hünicken 1967
Ocotea menendezi	*	*	Hünicken 1967; Vento & Prámparo 2018
Ocotea sp.	*	*	Hünicken 1967; Vento & Prámparo 2018
Persea sp.	*	*	Hünicken 1967; Vento & Prámparo 2018
Psidium liociardensis	*	*	Hünicken 1967; Vento & Prámparo 2018
Qualea patagonica	*	*	Hünicken 1967; Vento & Prámparo 2018
Schinopsis patagonica	*	*	Hünicken 1967; Vento & Prámparo 2018
Styrax sp.	*	*	Hünicken 1967; Vento & Prámparo 2018
Styrax glandulifera	*	*	Hünicken 1967; Vento & Prámparo 2018
Tetracera cf. *patagonica*	*	*	Hünicken 1967; Vento & Prámparo 2018
Zyziphus chubutensis	*	*	Hünicken 1967; Vento & Prámparo 2018
Malvaceae	*	*	Hünicken 1967; Vento & Prámparo 2018
Urticaceae	*	–	Hünicken 1967; Vento & Prámparo 2018
cf. *Pouterlabatia clark*	*	*	Hünicken 1967; Vento & Prámparo 2018
Paullinia sp.	*	–	Panti 2018
Banisteriophyllum	*	–	Panti 2018

Upper Río Turbio Fm	**LMA**	**Source**
Celtis sp.	*	Hünicken 1967; Vento & Prámparo 2018
Cinnamomum sp.	*	Panti 2018; Vento & Prámparo 2018
Cupania grosse-serrata	*	Panti 2018
Nothofagus dicksonii	*	Hünicken 1967; Vento & Prámparo 2018
Nothofagus elongata	*	Hünicken 1967; Vento & Prámparo 2018
Nothofagus serrulata	*	Hünicken 1967; Vento & Prámparo 2018
Nothofagus simplicidens	*	Hünicken 1967; Vento & Prámparo 2018
Nothofagus subferruginea	*	Hünicken 1967; Vento & Prámparo 2018
Nothofagus variabilis	*	Hünicken 1967; Vento & Prámparo 2018
cf. *Tabebuia ipiformis*	*	Hünicken 1967; Vento & Prámparo 2018
Angiosperm indet.	*	Hünicken 1967; Vento & Prámparo 2018
Nectandra aff. *N. prolifica*	*	Panti 2018
Ocotea aff. *O. menendezii*	*	Panti 2018
Persea aff. *P. borelloi*	*	Panti 2018
Cissus sp.	*	Panti 2018
Allophyllus gracilis	*	Panti 2018

Río Guillermo Fm	**LMA**	**LAA**	**Source**
Acaena brandmayri	*	*	Panti 2011; Vento *et al.* 2017
Myrcia bagualense	*	*	Panti 2011; Vento *et al.* 2017
Rhoophyllum serratum	*	–	Vento *et al.* 2017
Nothofagus subferruginea	*	–	Panti 2011; Vento *et al.* 2017
Nothofagus crenulata	*	*	Vento *et al.* 2017
Nothofagus elongata	*	*	Panti 2011; Vento *et al.* 2017
Nothofagus serrulata	*	*	Panti 2011; Vento *et al.* 2017
Nothofagus simplicidens	*	*	Panti 2011
Nothofagus variabilis	*	*	Panti 2011; Vento *et al.* 2017
Rubus sp.	*	–	Panti 2011
Anacardiaceae	*	–	Panti 2011
Lauraceae	*	–	Panti 2011

Species/Mophotypes	Margin Character States (CS)										Size Character States									Apex CS				Base CS			Length to Width CS					Shape CS		
	No Teeth	**Teeth**	**Teeth Regular**	**Teeth Irregular**	**Teeth Close**	**Teeth Distant**	**Teeth Round**	**Teeth Acute**	**Teeth Compound**	**Compound<50%**	**Nanophyll**	**Leptophyll I**	**Leptophyll II**	**Microphyll I**	**Microphyll II**	**Microphyll III**	**Mesophyll I**	**Mesophyll II**	**Mesophyll III**	**Emarginate**	**Round**	**Acute**	**Attenuate**	**Cordate**	**Round**	**Acute**	**L:W <1:1**	**L:W 1-2:1**	**L:W 2-3:1**	**L:W 3-4:1**	**L:W >4:1**	**Obovate**	**Elliptic**	**Ovate**
Acrodiclidium flavianum	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	1	–	–	–	1	–	–	–	1
Allophylus graciliformis	–	1	1	–	1	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	1	–	–	–	1	–	–	–	–	1
Anacardites pichileufensis	–	1	1	–	1	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	1	–	1	–	–	–	–	–	1
Annona sp.	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	1	–	–	–	1	–	–	–	–	1
Casearia sp. cf. *C. spinuloso serrata*	–	1	1	–	1	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	1	–	–	1	–	–	1	–	–
Cinnamomum neogaea	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	1	–	1	–	–	–	–	–	1
Cissus pichileufensis	–	1	–	1	–	1	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	1	–	–	1	–	–	–	1	–	–
Cupania latifolioides	–	1	1	–	1	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	1	–	–	–	–	–	1	–	–	1
Cupania grosse-serrata	–	1	–	1	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	1	–	1	–	–	–	–	–	1
Cupania patagonica	–	1	1	–	1	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	1	–	–	–	1	–	–	–	–	1
Cupania santacrucensis	–	1	1	–	1	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	1	–	–	–	1	–	–	–	–	1
Drimys patagonica	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	1	–	–	1	–	–	1	–	–
Drimys sp.	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	1	–	–	1	–	–	–	–	1
Escallonia sp.	–	1	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Eucaliptus sp.	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	1	–	–	–	1	–	–	1	–
Malvaceae	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Myrcia cf. *M reticulo venosa*	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	1	–	–	–	1	–	–	–	1
Myrica hunzikeri	–	1	1	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	1	–	–	1	–	–	–	–	1
Myricaceae	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	1
Nectandra prolifica	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	1	–	–	1	–	–	–	–	1
Nothofagus serrulata	–	1	–	1	1	–	–	1	1	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	1	–	1	–	–	–	–	–	1
Nothofagus elongata	–	1	–	1	1	–	–	1	–	1	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	1	–	–	–	1	–	–	–	1
Nothofagus subferruginea	–	1	1	–	1	–	–	1	1	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	1	–	–	–	–	1	–	–	–	1
Nothofagus variabilis	–	1	–	1	1	–	1	–	1	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	1	–	–	1	–	–	–	–	–	1
Ocotea menendezii	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	1	–	–	1	–	–	–	–	–	1
Ocotea sp.	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	1
cf. *Pouterlabatia lanceolata*	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	1	–	–	1
Persea sp.	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	1	–	–	–	1	–	–	–	–	1
Psidium araciformis	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Qualea patagonica	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	1	–	–	–	1	–	–	–	1
Schinopsis patagonica	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	1	–	–	–	1
Styrax glanfulifera	–	1	1	–	1	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	1	–	–	–	–	1	–	–	–	1
Styrax sp.	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	1	–	–	1	–	–	–	–	1
Tetracera cf. *T. patagonica*	–	1	1	–	1	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	1	–	1	–	–	–	–	–	1
Urticaceae	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1
Ziziphus chubutensis	–	1	1	–	–	1	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	1	–	–	–	1	–	–	–	1	–