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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.
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 temperatures and precipitations. It is widely recognized that leaf traits such as size and shape are important features to estimate temperatures and precipitations.

INTRODUCTION

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.
Paleoclimate for the Paleogene-Neogene in South America

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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 with 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; Malumíán & 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; Malumíán 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 (Malumíán et al. 2000) (Fig. 2). The age of the formation was established as Oligocene-Miocene by Hünicken (1955), based on the floral assemblage. Malumíán et al. (2000) suggested a late Eocene-early Oligocene age for the unit based on foraminifera biostratigraphy. Nullo & Combina (2002) indicated a late Eocene-early Oligocene age for the unit based on 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), decided 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).

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 PROXYs

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).
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. 3.—Canonical Correspondence Analysis using CLAMP3B SA dataset. The axes CCA1 and CCA2 accumulate a total of 0.64% of the variance.](image-url)
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 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   InMAP = 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               |
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:

\[
\text{MAT} = (LMP \times 0.21) + (FDR \times 42.296) + \#\text{teeth} \times (-2.609) - 16.004
\]

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

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

Unoothed 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 theCCA 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).
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 Drynias 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 paleoecological 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, Styra- caceae, 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).

Paleoflores 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 paleoflores 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 Que- mado, Nürihuau Formation (Berry 1928; Fiori 1931, 1939; Romero 1978, 1986; Troncoso & Romero 1998; Caviglia & Zamaloa 2014). The analyzed fossil assemblage from Pico Que-mado 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 occupant different climatic zones with different ecophysiological requirements, could be a consequence of relic 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 & Villa- grán 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 Alumíné locality, Neuquén province, Rancabahu 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 Myricagaulanesis 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 paleoflores 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 spe- cies significantly increased (Fig. 5). Cenozoic Mixed Paleoflores from 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 palynoflores from the lower or upper member of the formation. The RTF palynoflora is composed mainly of Pteridophytes, gymnosperms of the genera Araucariaceae, Podocarpaceae, Phyllocadidae, Microcachrydites, Dacyridiites and among angiosperms abundant Nothofagidites and representatives of different families such as
Protoceae 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 Malphigiacaeae (*Fernández et al.* 2012). Quattrocchio et al. (2013) did a quantitative analysis of Cenozoic palyno floras 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 glacia tion. Palynological studies of the end of the Cenozoic (Eocene) 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 the Río Turbio and Río Guillermo formations are located. Extant vegetation is mainly represented by *Nothofagus* and *Drymis* were dominant trees together with *Empetrum rubrum* (Heusser, 1993).

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**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 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 (Wie mann 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 Huítrea 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 Angleslea 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 isotope stages, 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 CO2 and CH4 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 CO2 levels (Zachos et al. 2001a, b). A reduction in atmospheric CO2 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 CO₂ first led to the formation of small, highly dynamic ice caps on the Antarctic, reinforcing the importance of CO₂ 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 (Siip & Englund 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 formations, respectively. A simulation climate model implied that declining Cenozoic CO₂ first led to the formation of small, highly dynamic ice caps on the Antarctic, reinforcing the importance of CO₂ 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 (Siip & Englund 2004).

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 untoothing 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 lower 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 pallofloras (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 leaves will provide a more robust continental paleoclimate reconstruction in the future.

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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 |
| Myrcia Hunzikerii |   |   | 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 menendezii |   |   | 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 |
| Zygiphus chubutensis |   |   | Hünicken 1967; Vento & Prámparo 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 |
| Persia aff. P. boreloi | * | Panti 2018 |
| Cissus sp. | * | Panti 2018 |
| Allophylus 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/Morphotypes   | Margin Character States (CS) | Size Character States | Apex CS | Base CS | Length to Width CS | Shape CS |
|-----------------------|-----------------------------|-----------------------|---------|--------|--------------------|----------|
|                       | No Teeth | Teeth Regular | Teeth Irregular | 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 | Enlarged | Round | Acute | 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 flavum  |          |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Allephylus graciliformis |       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Anacardites pichileum  |          |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Alnus sp.              | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Cinnamomum neogaea     | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Cissus pichileum       | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Cupania latifoliae     | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Cupania gross-serrata  | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Cupania patagonica     | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Cupania spinuloso serrata |       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Drimys patagonica      | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Escallonia sp.         | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Eucalyptus sp.         | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Malvaceae              | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Myrica cf. M reticulo varosa |       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Myrica hundelvi       | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Myrtaceae              | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Neocarpa prochica      | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Nothofagus serrulata   | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Nothofagus elongata    | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Nothofagus subfertuginea |       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Nothofagus variabilis  | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Ocotea menendeli       | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Ocotea sp.             | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| cf. T. ruta (arida)    | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Parsea sp.             | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Pseudium acranformis   | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Qualea patagonica      | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Schinopsis patagonica  | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Styra gianulifera      | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Styra sp.              | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Tetracera cf. T. patagonica |       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Unhassia sp.           | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |
| Ziziphus chubutensis   | 1       |              |                |               |            |            |               |           |             |           |               |           |             |             |             |           |             |               |           |       |      |       |        |       |       |       |       |       |       |         |        |       |