

The Pennsylvania State University

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**PLANT EXTINCTION AND RECOVERY DYNAMICS ACROSS THE CRETACEOUS-
PALEOGENE TRANSITION IN SOUTHERN SOUTH AMERICA**

A Thesis in

Geosciences

by

Elena Stiles

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The thesis of Elena Stiles was reviewed and approved* by the following:

Peter Wilf
Professor of Geosciences
Thesis Advisor

Timothy Bralower
Professor of Geosciences

Mark Patzkowsky
Professor of Geosciences
Associate Head for Graduate Programs and Research

*Signatures are on file in the Graduate School

ABSTRACT

The 66 Ma Cretaceous-Paleogene (K-Pg) mass extinction appears to have been globally heterogeneous for some marine and terrestrial organismal groups. Previous studies on limited Southern Hemisphere K-Pg microfloras show lower extinction percentages and faster-paced recoveries than their Northern Hemisphere counterparts, but no Southern Hemisphere macrofloral turnover studies comparable with the well-constrained analyses of North American (NAM) macrofloras had been possible until now. Through the analysis of over 4,000 dicot leaves from the latest Cretaceous (Maastrichtian) strata of the Lefipán Formation and the early Paleocene (Danian) Salamanca and Peñas Coloradas formations of Argentine Patagonia, this study addresses macrofloral extinction and recovery with a large sample size for the first time in the Southern Hemisphere. Based on a morphotype classification, macrofloral extinction is >90%, and rarefaction analysis showed a ca. 45% drop in diversity across the K-Pg where compositionally homogeneous, low diversity Paleocene floras superseded rich Maastrichtian assemblages. Comparison with rarefied NAM macrofloras shows much higher Patagonian species richness not only in Danian but also Maastrichtian macrofloras, suggesting a deep history of exceptional South American floral diversity before the Paleocene and into the terminal Cretaceous at least. Morphospace analysis of Maastrichtian and Danian leaf assemblages indicates continuity and expansion of leaf types and their underlying ecological and phylogenetic diversity across the boundary despite the lower Danian morphotype richness. Comparison of published palynomorph and taxonomic macrofossil records provides evidence for a low family-level turnover both across the K-Pg and despite the ca. 400 km separating the studied areas of the Lefipán and Salamanca formations. The increase of lobed and toothed morphotypes in the Patagonian Paleocene contrasts with the loss of lobed leaves across the K-Pg in NAM. Further contrasting with Patagonian results, NAM rarefaction analysis shows a ca. 75% drop in diversity across the boundary. Interestingly, leaves with affinity to Lauraceae are a dominant component of Danian macrofloras in Patagonia, a pattern also observed in some NAM

floras. The significant macrofloral extinction percentage, drop in rarefied diversity across the K-Pg, and low diversity homogeneous Danian floras are consistent with substantial species-level extinction in Argentine Patagonia broadly following similar patterns to NAM. However, the contrasts arising between Patagonian and NAM macrofloral records in Maastrichtian and Danian standing species richness, and morphological turnover appear to reflect a geographically heterogeneous Northern vs. Southern Hemisphere extinction and recovery pattern as observed in other marine and paleontological records.

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PREFACE

This thesis is written in the style of the journal *Paleobiology*, where it will be submitted for publication. The coauthors of this manuscript are Peter Wilf of the Pennsylvania State University, Ari Iglesias of the Universidad Nacional del Comahue, CONICET, Argentina, María Alejandra Gandolfo of Cornell University, and Néstor Rubén Cúneo of the Museo Paleontológico Egidio Feruglio (MEF), Trelew, and CONICET, Argentina. P. W. contributed to the design and development of the project, discussion of results, and reviews of the written content. A. I. contributed materials and the classification of specimens of the Salamanca and Peñas Coloradas formations. M. A. G. contributed a preliminary classification of specimens of the Lefipán Formation and discussion. N. R. C. led the collection of Lefipán Fm. specimens and the initial morphotype classification and granted me permission for their collaborative use in this study.

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I dedicate this thesis to my grandmother, Helena Sanmartín, who refused to believe Penn State is not in New York City. I aspire to have her quick sense of humor and incredible strength in the most difficult times. Forever loved, forever with me.

To my mother and father, Loreta Rosselli and F. Gary Stiles. Invariably supportive of my endeavors from aspiring rockstar, to designer, to scientist. I suspect they are pleased I chose the latter.

1. Introduction

Sixty-six million years ago (Clyde et al. 2016), a bolide impacted the Earth at the Mexican Yucatán Peninsula (Alvarez et al. 1980; Hildebrand et al. 1991; Schulte et al. 2010) with devastating environmental consequences for global biotas (Wolbach et al. 1990; McGhee et al. 2004; Kring 2007; Schulte et al. 2010; Vellekoop et al. 2014; Tyrrell et al. 2015; Artemieva and Morgan 2017; Brugger et al. 2017). Initial heat released from the impact itself is hypothesized to have caused a wave of global wildfires (Wolbach et al. 1988, 1990; Toon et al. 1997; Harvey 2008). Soot, dust, and impact-derived climatically active sulfur compound gases released into the atmosphere led to global darkness, climatic cooling, and acid rain during a period of impact winter that lowered global temperatures for decades and blocked photosynthesis for months or years, providing a diversity of kill mechanisms (Alvarez et al. 1980; Prinn and Fegley 1987; Robertson et al. 2013; Vellekoop et al. 2014; Tyrrell et al. 2015; Artemieva and Morgan 2017; Brugger et al. 2017). Approximately 70% of Cretaceous living species became extinct in the wake of the bolide impact, marking the Cretaceous-Paleogene boundary (K-Pg) as the most recent of the big five mass extinctions in geologic history (Raup and Sepkoski 1982; Jablonski 1991; Alroy 2008; Schulte et al. 2010).

The K-Pg affected biotas globally, yet the severity of the extinction and the pacing of the recovery was geographically heterogeneous for some organisms; Southern Hemisphere records of some groups indicate lower extinction percentages and faster recovery times than Northern Hemisphere counterparts (Vajda et al. 2001; Iglesias et al. 2007; McLoughlin et al. 2008; Jiang et al. 2010; Schulte et al. 2010; Barreda et al. 2012; Goin et al. 2012; Wilf et al. 2013; Schueth et al. 2015; Donovan et al. 2016). Proposed hypotheses have included

decreasing influence from impact ejecta and heat in Southern Hemisphere sites far the Mexican impact site (Schulte et al. 2010), oceanic buffering of impact winter temperatures in the Southern Hemisphere (Bardeen et al. 2017), and a bolide impact angle that would have directed most ejecta and debris towards the Northern Hemisphere atmosphere (Schultz and D Hondt 1996).

Heterogeneous Northern vs. Southern Hemisphere extinction patterns are observed in both marine calcareous nannoplankton and terrestrial paleontological records. Southern Hemisphere calcareous nannoplankton extinction percentages were lower and recovery was almost immediate relative to Northern Hemisphere counterparts (Jiang et al. 2010; Schueth et al. 2015). However, Southern Hemisphere shallow marine macroinvertebrates experienced similar extinction percentages globally, while offshore species showed no sign of disruption (Aberhan and Kiessling 2014; Witts et al. 2016). Despite the sudden extinction observed in shallow benthic communities of Antarctica, there was little ecological turnover compared to some Northern Hemisphere sites, providing evidence for geographic heterogeneity in post-extinction recovery patterns (Whittle et al. 2019).

On land, monotreme and gondwanathere mammals of nominally Mesozoic vertebrate groups, and the first records of boundary-spanning chelonid turtles are reported in the early Paleogene records of Patagonia (Pascual et al. 1992; Bonaparte et al. 1993; Goin et al. 2006; Gelfo et al. 2009; Sterli and de la Fuente 2019). Australian seed fern macrofossils of Paleogene *Corystospermales* (McLoughlin et al. 2008) and Oligocene *Bennettittales* (McLoughlin et al. 2011) provide the only Cenozoic records of these otherwise Mesozoic plant groups. Palynological records in New Zealand indicate lower species extinction and faster-paced recoveries than in the Western Interior of North America (WINA) (Vajda et al.

2001; Vajda and Raine 2003; Pole and Vajda 2009), and there is little evidence for any extinction in Antarctic spore and pollen records (Askin 1988). Previously studied Cretaceous-Paleogene macrofloras from New Zealand revealed a paleoclimatic cooling trend across the K-Pg consistent with global records, but they did not provide a macrofloral extinction estimate due to their uncertain stratigraphic placement relative to the boundary (Kennedy et al. 2002).

Consistent with a globally heterogeneous K-Pg extinction, recent studies of the latest Cretaceous (Maastrichtian) and early Paleocene (Danian) paleofloras of the Lefipán, Salamanca, and Peñas Coloradas formations of Chubut, Argentine Patagonia, show lower palynological extinction, faster insect-feeding damage diversity recovery, and remarkably diverse Danian macrofloras relative to WINA sections of the same ages (Iglesias et al. 2007; Barreda et al. 2012; Donovan et al. 2016, 2018). Lefipán Fm. boundary-spanning spore and pollen records show <10% extinction across the K-Pg compared to the 30-40% extinction in WINA palynofloras (Nichols and Fleming 1990; Sweet and Braman 2001; Hotton 2002; Nichols 2002; Barreda et al. 2012). Notably, Patagonian palynological records also include the youngest global report of the otherwise Mesozoic conifer family Cheirolepidiaceae (Archangelsky 1973; Barreda et al. 2012; Clyde et al. 2014). Insect feeding- damage diversity recovered to pre-K-Pg diversity levels within 4 My, compared to the estimated 9 My in WINA counterparts (Donovan et al. 2016, 2018). Danian macrofloras of the Salamanca and Peñas Coloradas formations are much more diverse than WINA counterparts of the same age, suggesting a faster-paced recovery compared to WINA (Iglesias et al. 2007). However, although the macrofloras of the Maastrichtian strata of the Lefipán and Danian Salamanca and Peñas Coloradas formations have been the subject of detailed

taxonomic studies (Table 1) and insect-feeding damage observations (Donovan et al. 2016, 2018; Martínez et al. 2018), they had not been compared to estimate a K-Pg macrofloral species extinction in Patagonia.

For the first time in the Southern Hemisphere, extensive dicot leaf collections from the Maastrichtian Lefipán Fm. and the Danian Salamanca and Peñas Coloradas formations of Patagonia offer insight into macrofloral K-Pg extinction and recovery dynamics with exceptionally preserved and stratigraphically and age constrained collections (Iglesias et al. 2007; Scasso et al. 2012; Clyde et al. 2014; Donovan et al. 2016, 2018). Macrofloras offer a high taxonomic resolution, which coupled with the high stratigraphic but low taxonomic resolution of the existing palynological records from the same areas advance our understanding of species and family level floral turnover.

This study addresses the K-Pg macrofloral turnover of the Lefipán, Salamanca and Peñas Coloradas formations through morphotype comparisons, morphospace analysis, and correlation of published pollen records to test species-level turnover and its underlying ecological and environmental significance. The macrofloras of these formations provide insight into Cretaceous-Paleogene diversity and turnover in southern South America and potential differences with North American floral extinction and recovery dynamics. Results presented here indicate that South American turnover across the K-Pg is consistent with an extinction event broadly following patterns observed in the well-studied WINA macrofloras (Wolfe and Upchurch 1986, 1987; Johnson et al. 1989; Johnson and Hickey 1990; Johnson 2002) and support a globally disruptive event. However, contrasts arising between Patagonian and WINA macrofloras may reflect geographically complex climatic,

phylogenetic, and ecological mechanisms impacting floral extinction and recovery dynamics.

2. Geological and paleoenvironmental setting

2.1. Lefipán Formation

The siliciclastic Lefipán Formation represents the latest Cretaceous (Maastrichtian) to earliest Paleocene (Danian) infilling of the Jurassic-early Paleocene Cañadón Asfalto Basin in Chubut province of Argentine Patagonia (Spalletti 1996; Scasso et al. 2012; Figari et al. 2015). The formation crops out along the middle Chubut River valley in northwestern Chubut, conformably overlying the Campanian-Maastrichtian Paso del Sapo Fm., and unconformably overlain by the Eocene Barda Colorada Ignimbrite (Spalletti 1996; Aragón and Mazzoni 1997; Scasso et al. 2012). The Lefipán Fm. was deposited at the foothills of the NNW-SSE trending paleocordillera in the shallow Atlantic Paso del Sapo Embayment near the northern margin of the Cañadón Asfalto Basin (Scasso et al. 2012), which in the Danian was connected to the San Jorge Basin immediately to the south (Fig. 1) (Scasso et al. 2012; Figari et al. 2015).

The Lefipán Fm. encompasses a suite of marginal to fully marine sediments within a tidally dominated deltaic setting, spanning the Cretaceous-Paleogene transition from the Maastrichtian (possibly even late Campanian) to the early Danian (Barreda et al. 2012; Scasso et al. 2012; Vellekoop et al. 2017). The lithologies of the Lefipán Fm. consist predominantly of sandstones and mudstones interbedded with sparse coquina and conglomerate beds (Scasso et al. 2012). Maastrichtian strata range from fully marine distal delta front deposits to marginal tidal flat, sharply transitioning back to a distal delta front in the Paleocene following a regional Maastrichtian-Paleocene regression-transgression cycle (Legarreta and Uliana 1994; Spalletti 1996; Scasso et al. 2012; Comer et al. 2015; Vellekoop et al. 2017).

The Lefipán Fm. was deposited within the seasonal, warm-temperate paleoclimatic belt (Scasso et al. 2012), where several sources of evidence indicate very warm local temperatures in the Maastrichtian (Vellekoop et al. 2017; Woelders et al. 2017). Leaf-cuticular $p\text{CO}_2$ estimates from Maastrichtian Lefipán Fm. dicot leaf *Lefipania padillae* indicate values of approximately 464 ppm (Martínez et al. 2018). Sea surface temperature estimates based on the TEX_{86} proxy from Lefipán Fm. samples (Scasso et al. 2012; Vellekoop et al. 2017) and the northern Patagonian Neuquén basin (Woelders et al. 2017) ranged between 25–27° C. Pollen assemblages and macrofloras, including thermophilic Malvaceae, Arecaceae, and Aquifoliaceae, and drought-sensitive gymnosperms of the Podocarpaceae (Baldoni 1992; Baldoni et al. 1993; Barreda et al. 2012; Wilf et al. 2017) also indicate frost-free environments.

The strata of interest in this study are found in Scasso et al.'s (2012) 380 m thick San Ramón section (SRS), located south of the Chubut River in northwestern Chubut (Fig 1A, 1B, 1D). The SRS is the most complete of the Lefipán Formation, comprising sediments ranging from the Campanian/Maastrichtian to the Danian (Barreda et al. 2012; Vellekoop et al. 2017). Although the SRS spans the Cretaceous-Paleogene transition, the impact layer recognized at other sites around the world (e.g., Alvarez et al., 1980, 1990; Orth et al., 1981; Brooks et al., 1986; Lerbekmo and St. Louis, 1986; Schulte et al., 2010) is not preserved, probably due to bioturbation or erosion (Scasso et al. 2012). However, the K-Pg in the Lefipán Fm. is constrained to about 4 m of section based on significant changes in invertebrate faunas (Scasso et al. 2012; Aberhan and Kiessling 2014), including a marker *Turritella malaspina* lag bed determined as the first Danian deposits (Fig. 1D) (Medina and Camacho 1990; Scasso et al. 2012), the presence of latest Maastrichtian and earliest Danian

dinoflagellate index taxa (Barreda et al. 2012; Vellekoop et al. 2017), and age-diagnostic continental palynomorphs (Barreda et al. 2012). Dinoflagellate assemblages indicate a dynamic environment in the SRS, with fluctuating salinities and pulses of terrestrial runoff (Vellekoop et al. 2017).

Because the Lefipán Fm. comprises both fully marine and marginal sediments that span the K-Pg, it has provided significant insight into late Maastrichtian diversity and patterns of Southern Hemisphere biotic turnover across the boundary for both marine and terrestrial organisms within a paleoclimatic context. Marine invertebrates in offshore facies show little turnover, whereas shallow species reveal fast turnover across the K-Pg and the notable disappearance of dominant taxa replaced by previously rare species (Scasso et al. 2012; Aberhan and Kiessling 2014). The Lefipán Fm. also holds the oldest record of therian mammals in South America. The Danian-aged marsupial *Cocatherium lefipanum*, belonging to the derived bunodont marsupials first known from the North American Cretaceous, provides evidence for a Late Cretaceous evolutionary radiation for this group and its persistence across the boundary in South America when coupled with Paleocene records in Bolivia and northern Argentina (Goin et al. 2006).

Paleofloras of the Lefipán Fm. have provided evidence for floral diversity and turnover across the K-Pg boundary in the region (Barreda et al. 2012; Wilf et al. 2017; Andruchow-Colombo et al. 2018). The Maastrichtian fern and angiosperm-dominated microfloras of the Lefipán Fm. are interpreted to belong to a shore-line assemblage of shrubby vegetation with dispersed wooded areas and mangroves (Baldoni 1992; Baldoni et al. 1993; Barreda et al. 2012). The Lefipán Fm. palynoflora is diverse, comprised of several gymnosperms of the Araucariaceae and Podocarpaceae, ferns of the Blechnaceae and

Gleicheniaceae, and abundant angiosperms including palms (Arecaceae), Proteaceae, Liliaceae, and others (Baldoni 1992; Baldoni et al. 1993; Barreda et al. 2012). In the San Ramón Section, spore and pollen records span the K-Pg (Fig. 1) and reveal a sudden and significant floral turnover across the boundary followed by a gradual restoration of nearly all the Cretaceous palynotaxa, consistent with a widespread and short-lived environmental disturbance (Barreda et al. 2012).

Spores and pollen have fewer taxonomically informative morphological characters than macrofossils, and at their finest taxonomic resolution are interpreted to generally represent botanical families or genera at best (Johnson and Hickey 1990; Nichols and Johnson 2008). Palynological records indicate a low overall extinction of higher taxa across the K-Pg in the SRS, where <10% palynomorphs disappear definitively in the Danian. However, angiosperms suffered the highest extinction rates of the vascular plants, with approximately 50% of palynomorph species disappearing across the boundary (Barreda et al. 2012). Maastrichtian angiosperm and fern dominated palynofloras shifted to low-diversity Danian gymnosperm and fern dominated floras as Maastrichtian pollen species temporarily vanished, before the resurgence of most Maastrichtian angiosperm palynotaxa (Barreda et al. 2012). Conifer pollen of the extinct family Cheirolepidiaceae, *Classopollis* sp., dominates early Danian assemblages. Cheirolepidiaceae, is otherwise known from Mesozoic sediments worldwide and disappears in most regions across the K-Pg, but its last records are reported at this time in Patagonia (Barreda et al. 2012; Clyde et al. 2014).

Macrofloras are only preserved in the Late Cretaceous strata of the Lefipán, and have been subject to several detailed systematic studies (Table 1) (Wilf et al. 2017; Andruchow-Colombo et al. 2018; Escapa et al. 2018; Martínez et al. 2018), along with the examination

of insect-plant ecology in fossil leaves (Donovan et al. 2016, 2018; Martínez et al. 2018). From the lower Lefipán Fm. Cañadón del Loro locality, north of the Chubut River, Andruchow-Colombo et al. (2018) described a new member of Araucariaceae, *Araucaria lefipanensis*, belonging to a living Southern Hemisphere genus (Escapa and Catalano 2013). Martínez et al. (2018) described six dicot leaf morphotypes from that locality, including the widespread Cretaceous cuticle form *Lefipania padillae* from which $p\text{CO}_2$ levels were estimated from preserved cuticle.

South of the Chubut River in the terminal Maastrichtian strata of the San Ramón Section studied here, leafy branches and leaves, respectively, of the conifers *Retrophyllum superstes* (Podocarpaceae; Wilf et al., 2017) and a likely *Agathis* (Araucariaceae; Escapa et al., 2018), indicate the early presence of genera that persisted in other Cenozoic floral assemblages of Patagonia (Wilf et al. 2014, 2017; Andruchow-Colombo et al. 2019). However, most of the floral diversity in this section remains undescribed in the extensive and diverse angiosperm leaf collections (see Materials), the systematic affinities of which remain largely unknown. Donovan et al. (2016, 2018) coupled observations of insect-feeding damage on these dicot leaf assemblages from the SRS with collections of the Danian Salamanca and Peñas Coloradas formations to reconstruct a K-Pg insect damage record. Their results revealed complete leaf mining herbivore turnover across the boundary and recovery in mining, although with different mine types, and other feeding diversity within ca. 4my.

2.2. Salamanca and Peñas Coloradas formations

The early Paleocene (Danian) Salamanca and Peñas Coloradas formations are the first Cenozoic sedimentary units in the north-central San Jorge Basin of southern Chubut

and northern Santa Cruz provinces, Argentine Patagonia (Fig. 1) (Sylwan 2001; Clyde et al. 2014; Comer et al. 2015). The N-S trending San Bernardo fold belt, a Miocene compressional structure that deforms older strata and divides the basin into eastern and western areas (Sylwan, 2001 and references therein), structurally separates the Jurassic-Miocene San Jorge Basin. The Salamanca and Peñas Coloradas outcrops of interest in this study are located along the eastern flank of the San Bernardo fold belt, south and east of the city of Sarmiento (Fig. 1) (Iglesias 2007; Comer et al. 2015). In that area, the primarily marine early Danian Salamanca Fm. unconformably overlies fluvial and pyroclastic deposits of the Late Cretaceous (Campanian) Bajo Barreal Formation of the Chubut Group or the La Angostura Basalt (Iglesias 2007; Clyde et al. 2014; Comer et al. 2015) and is unconformably overlain by the fluvial and pyroclastic deposits of the late Danian Peñas Coloradas Formation of the Rio Chico Group (Iglesias 2007; Clyde et al. 2014; Comer et al. 2015).

The early Danian Salamanca Formation records a transition from fully marine to marginal environments within a tidally influenced estuarine setting, capped unconformably by the continental fluvial deposits of the Peñas Coloradas Fm. of late Danian age (Legarreta and Uliana 1994; Iglesias 2007; Comer et al. 2015). In the study area, Comer et al. (2015) recognized three of the original four Salamanca Fm. members described by Feruglio (1949); the Glauconítico, Fragmentosa and Banco Verde, and included within and at the top of the Salamanca Fm. the Banco Negro Inferior, a regional marker bed for which the stratigraphic placement had been disputed in the past (Andreis et al. 1975; Legarreta and Uliana 1994; Iglesias 2007; Comer et al. 2015).

The basal Glauconítico-Fragmentosa sandstone and mudstone-dominated marine sediments represent the initial transgressional deposition stages in the earliest Paleocene

(Legarreta and Uliana 1994; Comer et al. 2015). The overlying Banco Verde interbedded sandstones and mudstones and the dark Banco Negro Inferior mudstones reflect decreasing marine influence in a tidally-influenced estuarine environment (Legarreta and Uliana 1994; Comer et al. 2015). The fluvio-volcanic Peñas Coloradas Fm. conformably overlies the Banco Negro Inferior, marking the onset of continental sedimentation of the Rio Chico Group (Raigemborn et al. 2010; Comer et al. 2015). Comer et al. (2015) further divided these facies in the fossil-collection areas based on fossil preservation, sedimentological features, and paleoenvironmental interpretations, providing a detailed stratigraphic and depositional context for the floral collections from these formations.

Macro and microfloral records, leaf margin analysis, and faunal records in the Salamanca and Peñas Coloradas formations are consistent with humid, warm-temperate, frost-free climates in the Danian San Jorge Basin (Bonaparte et al. 1993; Brea et al. 2005; Iglesias et al. 2007; Palazzesi and Barreda 2007; Futey et al. 2012; Clyde et al. 2014; Ruiz et al. 2017). Foraminifera, dinoflagellates, and calcareous nannoplankton biostratigraphy indicate an early Danian age for the Salamanca Fm., with a maximum absolute age of 66.95 ± 0.37 Ma from $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the La Angostura Basalt flow underlying the Salamanca Fm. in the easternmost exposures of the study area (Clyde et al. 2014). U-Pb dates from a tuff layer in the Peñas Coloradas Fm. yielded an age of 61.984 ± 0.041 Ma, placing it in the late Danian (Clyde et al. 2014). Magnetostratigraphic correlations of the sections have further constrained the fossil localities of interest, assigning each locality to a geomagnetic polarity chron providing age ranges for the macrofloras (see Materials section for details) spanning C29n (65.58 - 64.88 Ma) and C28n (64.67 – 63.49 Ma) for the Salamanca Fm. and

C27n (62.52-62.22 Ma) for the Peñas Coloradas Fm. (Fig. 1D) (Iglesias et al. 2007; Clyde et al. 2014; Comer et al. 2015).

The Salamanca Formation has been the source of significant contributions in the study of early Paleocene South American faunal and floral diversity and post-K-Pg terrestrial recovery dynamics in the Southern Hemisphere (e.g. Pascual et al., 1992; Bonaparte et al., 1993; Krause and Bonaparte, 1993; Gelfo et al., 2007; Iglesias et al., 2007; Clyde et al., 2014; Donovan et al., 2016; Jud et al., 2017, 2018a, 2018b; Andruchow-Colombo et al., 2018; Escapa et al., 2018; Sterli and de la Fuente, 2019). The Banco Negro Inferior strata that crop out along the coast have produced the Peligran Local Fauna, one of the oldest Paleocene vertebrate assemblages in South America, which includes several K-Pg survivor lineages (Pascual et al. 1992; Bonaparte et al. 1993; Krause and Bonaparte 1993; Goin et al. 2006; Sterli and de la Fuente 2019). Monotreme (Pascual et al. 1992) and gondwanathere (Goin et al. 2012) mammals, crocodylians of the Alligatoridae and ?Crocodylidae superfamilies (Bonaparte et al. 1993), meiolaniform turtles (Sterli and de la Fuente 2019), and pipoid and anuran frogs (Bonaparte et al. 1993) are representatives of K-Pg survivor lineages from the Peligran Fauna reported thus far.

Microfloras of the Salamanca Fm. and related strata show a range of environments, which include mangrove swamps, lowland, and upland forests representing a warm, subtropical climate (Petriella and Archangelsky 1975; Zamaloa and Andreis 1995; Volkheimer et al. 2007). Local pollen records in the Salamanca Fm. study area are indicative of warm-temperate climates with a diverse angiosperm-dominated flora, including taxa of the Liliaceae, Arecaceae, Proteaceae, Malvaceae, and others, and notably include the same

gymnosperm *Classopollis* sp. pollen observed in the Danian strata of the Lefipán Fm. to the north (Petriella and Archangelsky 1975; Clyde et al. 2014).

Macrofloras from the Salamanca have revealed the presence of Podocarpaceae leafy branches (Quiroga et al. 2015; Andruchow-Colombo et al. 2019), Araucariaceae leaves, wood and reproductive structures (Brea et al. 2005; Ruiz et al. 2017; Escapa et al. 2018), possibly Cupressaceae wood (Ruiz et al. 2017), fruits and wood of Arecaceae (palms) (Romero 1968; Futey et al. 2012), wood of the Fabaceae and Myrtaceae families (Ragonese 1980; Brea et al. 2008) and flowers and leaves of the Rhamnaceae family (Jud et al. 2017) (Table 1). In the Palacio de los Loros sampling area, plant macrofossils include beautifully preserved flowers, fruits, seeds, cones and extensive leaf collections that have allowed the detailed systematic description of some of the oldest records for some gymnosperm and angiosperm families and genera that represent K-Pg survivor lineages. The podocarp *Kirketapel salamanquensis* and araucarian conifer *Agathis immortalis* represent the earliest global records of the scale-leaved clade of the Podocarpaceae and the genus *Agathis*, respectively, pushing back the evolutionary origins of these groups to millions of years older than previously thought (Escapa et al. 2018; Andruchow-Colombo et al. 2019). Flowers of the Cunoniaceae species *Lacinipetalum spectabilum* of the tribe Schizomerieae indicate the presence of derived groups within the Cunoniaceae in the early Paleocene of Argentina, which coupled with Upper Cretaceous pollen records of the family in Argentina and Antarctica suggest the lineage survived the K-Pg in western Gondwana (Jud et al. 2018a). Endocarps and leaves of the Menispermaceae family with affinity to the Cissampelidae tribe, *Stephania psittaca*, and *Wilkinsoniophyllum menispermoides*, respectively, are the

oldest unequivocal evidence of the family worldwide and signal that its diversification was underway by the early Paleocene (Jud et al. 2018c).

3. Materials

For this work, I examined dicot leaf collections from the terminal Maastrichtian strata of the Lefipán Fm. San Ramón section, and early and late Danian dicot leaf collections from the Salamanca Fm. Palacio de los Loros and the Peñas Coloradas Fm. Las Flores localities, respectively. Dicot leaves are the most common and diverse type of plant macrofossil in the Lefipán, Salamanca, and Peñas Coloradas formations, and thus they have the potential to provide insight into floral turnover across the K-Pg transition. The dicot leaf specimens analyzed in this study are primarily the same collections analyzed by Donovan et al. (2016, 2018) and Iglesias et al. (2007), with additional specimens from material previously not catalogued (Appendix A). In their studies, Iglesias et al. (2007) documented the diversity of the Danian collections by morphotyping and assigning systematic affinities when possible (Table 1) (Iglesias 2007; Iglesias et al. 2007). Donovan et al. (2016, 2018) documented the insect-feeding damage diversity on the leaves from Maastrichtian and Danian collections but did not focus on the leaf taxa and their variations across the boundary. Subsequent systematic papers including leaves from these localities (e.g., Jud et al. 2018c) have been published in recent years, but there have been no comparable analyses of the Lefipán Fm. dicot-leaf floras other than the preliminary morphotypes published by Donovan et al., (2016). All these leaf collections were compiled over a series of field trips involving the four junior authors and others since 2005 based from the Museo Paleontológico Egidio Feruglio (MEF, repository acronym MPEF-Pb), Trelew, Argentina. All specimens analyzed in this study are curated in the Paleobotanical Collection of the MEF.

The Maastrichtian dicot leaf specimens analyzed here come from the latest Maastrichtian portion of Scasso's (2012) San Ramón Section (SRS). The SRS macrofloral localities LefW, LefE and LefL, as in Donovan et al. (2016, 2018) and Wilf et al. (2017), yielded a total of 1062 dicot leaf specimens from unbiased collections constrained to the 67-66 Ma range based on dinoflagellate and palynomorph index fossils (Fig. 1D) (Barreda et al. 2012; Scasso et al. 2012; Vellekoop et al. 2017). The LefW macrofloral site corresponds to the same plant-bearing beds discussed in Scasso et al. (2012) and Vellekoop et al. (2017). The collection includes 278 dicot leaf specimens spanning about 25 m of stratigraphic section from seven collecting horizons, the youngest of which is located 8.3 m below the Danian *Turritella* marker bed (Donovan et al. 2016). Approximately 1000 m map distance to the east of LefW is the single fossiliferous horizon yielding the macrofloras of the LefE and LefL collection sites. LefE, 21.5 m below the *Turritella* marker bed, is closest to LefW. It extends about 40 m along the fossiliferous horizon (Wilf et al. 2017), from where 614 dicot leaf fossils were collected. LefL is located approximately 500 m east of LefE at 24 m below the *Turritella* bed (Donovan et al. 2016) and yielded 170 dicot leaf specimens. The LefE + LefL fossiliferous horizon cannot be correlated directly to the horizons in LefW due to cover and erosion.

The unbiased, field-censused early Paleocene leaf collections analyzed in this study were collected from two early Danian Salamanca Fm. localities in the Palacio de los Loros sampling area (PL1, PL2), and one unbiased collection in the late Danian Peñas Coloradas Fm. Las Flores section (LF) (Fig. 1D) (Iglesias 2007; Iglesias et al. 2007; Clyde et al. 2014). Combined analysis of magnetostratigraphic constraints, biostratigraphy, U-Pb and Ar-Ar dates discussed earlier, place PL1, PL2 and LF within chrons C29n (65.58-64.88Ma), C28n

(64.67-63.49Ma), and C27n (62.52-62.22 Ma), respectively (Clyde et al. 2014; Comer et al. 2015), based on the 2012 Geologic Time Scale (Gradstein and Kerp 2012).

Macrofloral localities PL1, PL2, and LF were deposited in different paleoenvironments, documented in Comer et al., 2015 and summarized here. Locality PL1, the oldest of the Danian macrofloral localities in the Salamanca Fm. addressed in this study, yielded a total of 1089 leaf specimens. Macrofloras from the PL1 site are preserved in sand-siltstone sediments interpreted as lateral accretion beds of abandoned tidal channel fill (facies *S_{ab}* in Comer et al., 2015). Locality PL2 yielded 1132 dicot leaf specimens, deposited in silty claystones interpreted as the transitional facies of tidal flats prograding over a coastal plain (facies *SC_r* in Comer et al., 2015). Sediments in locality LF are the coarsest-grained of the Danian macrofossil yielding sites, from where 564 dicot leaf specimens were recovered from poorly sorted litharenites interpreted as channel fills (facies *LF1* in Comer et al., 2015). Based on sedimentology and preservational quality of the Salamanca Fm. macrofloras, PL1 was deposited in a high energy environment where combined water and wind transport is possible, while the outstanding preservation of PL2 macrofloras and the facies interpretation is evidence of little transport and was thus likely to represent a parautochthonous assemblage (Comer et al. 2015). Floras from the LF Peñas Coloradas locality are fragmented and poorly preserved in the highest energy facies of the Danian sites, suggesting the order of potential transport distances from the highest to lowest is LF, PL1, PL2. Donovan et al. (2018) noted that preservation quality in Salamanca Fm. locality PL1 is similar to that of the Lefipán Fm., indicating minimal preservation bias between the oldest Paleogene locality and the Maastrichtian collections of the Lefipán Formation.

4. Methods

Macrofloral turnover between the Maastrichtian Lefipán and Danian Salamanca and Peñas Coloradas formations was evaluated through a three-step analysis addressing (1) species level turnover, (2) whole flora-level morphological change across the K-Pg in the region, and (3) the potential effect of the ≈ 400 km separation of the Cretaceous from the Paleogene samples in the floral composition and differences between sites. The morphotype classification of the specimens was the basis for the first two steps of the analysis. The extensive dicot leaf collections, curated at the Museo Paleontológico Egidio Feruglio (MEF) in Trelew, Chubut, Argentina were revised over multiple visits to ensure a consistent classification of Maastrichtian and Danian morphotypes. Dicot leaf fossils from the Lefipán Fm. San Ramón section (LefW, LefL, and LefE), Salamanca Fm. PL1 and PL2 localities, and Peñas Coloradas Fm. Las Flores (LF) were observed. Danian morphotypes of the Salamanca and Peñas Coloradas formations are based on the initial published set of Danian morphotypes of the PL1, PL2 and LF macrofloral localities (Iglesias 2007; Iglesias et al. 2007), and an additional collection of new morphotypes published in the supplementary information of Donovan et al., (2016) (Appendix A. A). In some cases, Danian morphotypes exhibiting extensive variation between end members were subdivided in this study (see 4.2.).

Preliminary Lefipán Fm. Maastrichtian San Ramón morphotypes (Donovan et al. 2016) were significantly revised and updated based on leaf architectural characters described in the Manual of Leaf Architecture (Ellis et al. 2009) (Appendix A. B.). Danian morphotypes of the Salamanca and Peñas Coloradas formations were based on the published initial set of Danian morphotypes of the PL1, PL2 and LF macrofloral localities (Iglesias

2007; Iglesias et al. 2007), and new preliminary morphotypes published in the supplementary information of Donovan et al., (2016) (Appendix A. A.). An updated morphotype inventory of all previously established Danian Salamanca and Peñas Coloradas formations morphotypes and new Maastrichtian Lefipán Fm. morphotypes established here are found with corresponding specimen numbers in Appendix E.

4.1. Macrofloral extinction

Johnson et al.'s (1989) method for estimating a macrofloral extinction based on a morphotype classification was applied to the Patagonian macrofloras. After establishing defined morphotypes, the presence of Maastrichtian morphotypes in Danian collections is documented (Johnson et al. 1989; Ash et al. 1999). Exemplar specimens (Appendix A) for each of the Maastrichtian Lefipán and Danian Salamanca and Peñas Coloradas formations leaf morphotypes were selected. Guided by the Manual of Leaf Architecture (Ellis et al. 2009), I compared each Maastrichtian morphotype to all Danian morphotypes. Specimens that preserved over half of the length of the blade and margin, an apex, base, and both second and third order venation patterns were considered the best preserved. This process resulted in 58 Maastrichtian morphotypes and 43 Danian morphotypes (Appendix A), which are considered a proxy for the number of dicot species present in the assemblages. Each morphotype is interpreted as having been produced by a single species with morphologically distinct leaves. From here on, each morphotype is considered for convenience as a species and will be referred to as such.

Danian assemblages from the Salamanca Fm. PL1 and PL2 localities were grouped for several analyses with leaves of the Peñas Coloradas Fm. LF locality into a single Danian assemblage due to their homogeneous floral composition (see Fig. 6). I compared each of

the Maastrichtian morphotypes to all the Danian morphotypes in search of survivor pairs based on a detailed comparison of their leaf architecture. Danian morphotypes that shared all morphological characters of Maastrichtian morphotypes, or fell within the continuous morphological variation among specimens of the same Maastrichtian morphotype, were considered survivor pairs and carefully documented. One of the benefits of this method is its independence from taxonomy, but if available in previous descriptions (Iglesias 2007; Iglesias et al. 2007), the systematic affinity of the survivor pairs was noted.

For rarefied (Tipper 1979) species diversity across the K-Pg, the Maastrichtian Lefipán Fm. LefE and LefL sites were considered a single locality (LefE+ LefL) because they were collected along the same fossiliferous horizon. Locality LefW was not included in this analysis because it includes specimens collected from multiple collection horizons with uncertain stratigraphic relationships to horizon LefE+LefL. In this analysis, the unbiased Salamanca (PL1, PL2) and Peñas Coloradas (LF) formations localities (Iglesias 2007; Iglesias et al. 2007) were considered separately for rarefaction. Magnetostratigraphic constraints of these macrofloral collections show they span three time intervals in the early Danian (see Materials; Clyde et al. 2014), offering an opportunity to track changes in diversity through time in the post-K-Pg Patagonian landscapes. Each rarefied species diversity curve was plotted with a 95% confidence interval using R package iNext (Hsieh et al. 2019).

For comparison of rarefied species diversity between Patagonian and representative North American K-Pg assemblages, dicot leaf counts from three selected meter-binned collections of the Hell Creek and Fort Union formations spanning the boundary in North Dakota were extracted after Wilf & Johnson (2004). A first filter applied to all meter bins

selected collections with total dicot specimen counts of over 350 specimens each following Burnham (1993). Within remaining bins, the most species-rich assemblage, found 15m below the K-Pg boundary (Dean Street level), was selected as representative of the latest Maastrichtian HCIII zone Hell Creek localities. Four Fort Union Fm. bins remained after initial filtering; 0m, 7m, 18m and 38m above the boundary layer. Horizons 0 m, 7m and 18m above the boundary plotted approximately along the same rarefaction curve, and because the 7m horizon had the highest specimen count of the three, it was selected as an early Danian representative. The stratigraphically highest binned collection above the boundary with over 350 specimens, 38m, was included in the analysis as a temporal analog to the oldest Danian PL1 locality because they both correspond to deposition during geomagnetic polarity chron C29N (Hicks et al. 2002; Johnson 2002; Clyde et al. 2014).

The replacement of dominant taxa by previously rare taxa is a common pattern across extinction events observed in the fossil record (Raup 1994). A similar pattern is observed in the Cretaceous-Paleogene palynological record of the Lefipán Fm., where gymnosperms became the dominant components of the flora in the early Paleocene as the previously dominant ferns and angiosperms were reduced in richness and abundance (Barreda et al. 2012). To test this pattern using the dicot macrofloral survivor pairs, the relative abundances of each pair were calculated as a percentage of the dicot leaf assemblage in which they are found. Following Johnson and Hickey (1990), dominant components are morphotypes representing over 5% of the overall composition in their respective assemblages.

4.2. Whole-flora morphological change

Species richness and morphological diversity are not always coupled, and this disconnect may be driven by underlying ecological pressures and evolutionary mechanisms (Foote 1993; Roy and Foote 1997). Morphospace analysis is a quantitative tool to measure morphological diversity and phenotypic relationships between organisms, by summarizing morphological characters in a mathematical space where dissimilarities in morphology are observed as graphical distances (Mitteroecker and Huttegger 2009). Leaf architecture is related not only to systematic affinities but to underlying environmental parameters (e.g., Wolfe 1995; Wilf 1997; Little et al. 2010; Givnish and Kriebel 2017), making leaves ideal candidates to simultaneously test species and morphological turnover across the K-Pg. Through morphospace analysis, the relationships between morphological characters and their combinations can shed light on selective morphological extinction patterns if present, and how morphological disparity is related to species richness.

Morphospace analysis requires the ordination of a matrix containing a set of either discrete or continuous characters describing each of the species or morphotypes analyzed. In this study, based on the Manual of Leaf Architecture (Ellis et al. 2009) forty-six discrete shape, size, margin, and venation characters were scored for each one of the Maastrichtian and Danian morphotypes (Appendix B). Features that were not preserved in over one-fourth of the specimens were excluded to reduce noise in the dataset. These included fourth and higher order venation. Character states for each morphotype were based on one or two of the exemplar specimens in the case that a single specimen did not preserve all morphological characters. If a morphotype showed variation in one or more characters based on the observation of all available examples, end members were designated by the letters A, B or

C, following the morphotype name (e.g., SA009A, SA009B) to represent morphological diversity within comparatively variable morphotypes. (Appendix C). When a character was not preserved in any of the specimens for a given morphotype, it was coded as “NA.”

In the analysis of morphospace occupation across the K-Pg in Patagonia, macrofloral assemblages in each of the Lefipán Fm. localities (LefW, LefE, and LefL) and Salamanca and Peñas Coloradas fms (PL1, PL2 and LF) were grouped into two general assemblages, Maastrichtian and Danian, based on their similar floral composition (Fig. 6) and equivalent morphospace occupation observed in graphical analysis (Appendix F) and calculated measures of disparity (Appendix G).

The morphological matrix was ordinated using Principal Coordinates Analysis (PCoA) with the R Package Ape (Paradis and Schliep 2018). PCoA compares each morphotype on a character-by-character basis, omitting characters with missing data in each comparison. In contrast, Principal Components Analysis (PCA) can only ordinate morphotypes with no missing data, resulting in a loss of valuable morphological information and morphotype comparisons because most morphotypes do not preserve all coded characters. For this reason, PCoA is better suited for ordinations of fossil taxa with uneven preservation and missing characters (Foote 1994, 1995; Roy and Foote 1997). The effect of missing character data on the calculation of distance matrices and ordinations is not yet understood, but following Gerber (2019), the percentage of missing data for each character and each morphotype is reported in Appendix H.

To quantify morphological diversity, four disparity measures were calculated separately for each Maastrichtian (LefW, LefE and LefL) and Danian (PL1, PL2, LF) leaf assemblage and for grouped Maastrichtian (LefW+LefE+LefL) and Danian (PL1+PL2+LF)

assemblages. Based on the first four axes of the PCoA because they record the highest variances of all axes, a (1) hypercuboid volume and (2) a sum of ranges were estimated. Based on the Euclidean pairwise distance matrix, the (3) average pairwise distance and (4) maximum pairwise distance were both extracted. The hypercuboid volume was estimated by multiplying the ranges of the first four axes (Wills et al. 1994). (2) The sum of ranges was obtained by adding the ranges of the axes, which as a measure of disparity is thought to perform better than (1) when datasets include a large number of axes (Foote 1994; Wills et al. 1994). Following Gerber's (2019) proposed measures of disparity for discrete character spaces, the (3) average and (4) maximum pairwise distances of the Euclidean distance matrix are reported here for each assemblage and the grouped Maastrichtian and Danian assemblages.

4.3. Pollen and regional floral heterogeneity

There is a 360-400 km distance separating the Lefipán, Salamanca, and Peñas Coloradas macrofloral localities along the paleo-Atlantic coastline (Fig. 1). To benefit from the regional signal of floral composition yielded by microfloras (Behrensmeyer et al. 2000), previously published spore and pollen lists from the same areas as the macrofloral collections (Barreda et al. 2012; Clyde et al. 2014) were compared to test the effect of geographic separation in floral composition as a possible spatial bias influencing the macrofloral extinction estimates. There are no Danian macrofloras in the Lefipán Fm., but the palynological records span the boundary (Fig. 1D) (Barreda et al. 2012), and Danian Lefipán Fm. palynofloras are comparable to those of the Salamanca Fm. (Clyde et al. 2014). However, the fine temporal correlations between the Danian strata of the Lefipán and Salamanca formations are not yet established.

The palynological records of the Lefipán and Salamanca formations include a combination of samples from the same macrofloral collection quarries and additional samples from nearby sections localities (Fig. 1) (Barreda et al. 2012; Clyde et al. 2014). Barreda et al. (2012) compiled a taxonomic list for Maastrichtian and Danian samples collected from the Lefipán Fm. San Ramón section. M.C. Zamaloa (in Clyde et al., 2014) reported Salamanca Fm. palynofloras from samples collected in the Palacio de los Loros area and from the nearby Bosque Ormachea (Fig. 1). In this study, the taxonomic lists for the Maastrichtian-Danian Lefipán Fm. (Barreda et al. 2012; Scasso et al. 2012) and the Danian Salamanca Fm. (Clyde et al. 2014) were compared to the early Danian sites in the Salamanca Fm. (Fig. 1D) (from M. C. Zamaloa in Clyde et al., 2014). Comparisons were made on a taxon-by-taxon basis and sample-level composition. Dr. Viviana Barreda (Museo Argentino de Ciencias Naturales) kindly reviewed the photos and listed species in Clyde et al. (2014) to establish equivalences between palynomorph morphotypes (e.g., “Proteaceae sp. A” and “Proteaceae sp. B”) among the Lefipán and Salamanca formations taxonomic lists. Only species-level identifications and equivalences established by Dr. Barreda were included in subsequent analyses (Table 2).

Palynological records offer the closest possible point of comparison to macrofloras, and in the absence of macrofloras provide information about changes in regional composition. The initial comparison between Danian Salamanca and Maastrichtian Lefipán Fm. samples served as a palynological analog to the sediments containing the macrofloral collections analyzed in this study, testing compositional differences between the strata of the two macrofloral collection areas in terms of botanical families present.

The taxonomic comparison included all reported vascular and non-vascular spore and pollen taxa of the Lefipán and Salamanca Fm. samples mentioned above. The comparison of sample-level composition was divided into three analyses: (1) all palynomorph taxa, (2) angiosperm and gymnosperm pollen taxa (representing the dominant macrofloral fossil-producing components in these floras), and (3) only angiosperm taxa (the focus of macrofloral turnover in this study). A presence-absence matrix of palynomorph species and equivalent pollen morphotypes was compiled (based on Table 2), and processed in R Vegan package (Oksanen et al. 2017).

First, the presence-absence matrix was transformed using Beal's smoothing (McCune 1994; McCune and Grace 2002; Münzbergová and Herben 2004), a method designed to account for unevenness in ecological sampling by replacing each species' occurrence record with a probability of occurrence calculated independently of a species' presence or absence in a sample but instead on occurrences and co-occurrences in the sample pool. This method is not commonly applied to the fossil record (Allen and Dodson 2011; Birks 2014), but in the comparison of Lefipán and Salamanca formations palynofloras, it is a promising tool to reduce the underlying compositional heterogeneity caused by the inherent sampling bias of the fossil record due to taphonomic and paleoenvironmental processes. The samples were then clustered based on the Bray-Curtis dissimilarity indices calculated from the Beals-smoothed dataset and linked using Ward's Method algorithm (McCune and Grace 2002; Oksanen et al. 2017).

5. Results

5.1. Macrofloral extinction

The detailed architectural comparison of Maastrichtian-Danian leaf morphotypes of the Lefipán, Salamanca and Peñas Coloradas formations yielded 5 Maastrichtian morphotypes considered to have a corresponding survivor in the Danian assemblages (Figs. 2 and 3, detailed descriptions in Appendix D). Survivorship of five of the 58 Maastrichtian morphotypes indicates a dicot macrofloral extinction of 92.2 % across the Cretaceous-Paleogene boundary in Argentine Patagonia (Figs. 2 and 3). Excluding singletons (species represented by a single specimen), the extinction is slightly reduced to 90.6%. The Danian morphotypes considered K-Pg survivors are Salamanca Fm. morphotypes SA8, SA19, SA20, SA35, and SA78 (Iglesias 2007; Iglesias et al. 2007; Donovan et al. 2016).

Following Iglesias et al. (2007), the closest botanical affinity to morphotype SA8 is the Rosaceae family, SA19 is equivalent to some specimens designated "*Sterculia*" *acuminalobata* Berry 1937 of the Malvaceae family, and the affinities of morphotypes SA35 and SA78 remain unknown. Morphotype SA20 is interpreted to have a botanical affinity to the family Cunoniaceae based on its architectural characters (Appendix D), and supported by the well-documented presence (and earliest global occurrence) of this family from abundant co-occurring *Lacinipetalum spectabilis* flowers with in-situ pollen from the macrofloral locality PL2 and other Salamanca Fm. localities (Jud et al. 2018a). These results indicate the survivorship of members of the family Rosaceae, previously unreported, along with macrofloral evidence to support the persistence of the Malvaceae and Cunoniaceae (Barreda et al. 2012; Jud et al. 2018a) in Argentine Patagonia.

When estimating relative abundances of each survivor pair within assemblages (Fig. 4), an interesting pattern emerged. Survivor pairs LF6-SA19 (Malvaceae) and LF18-SA8 (Rosaceae) were relatively minor components of Maastrichtian floras but became major components in the earliest Danian assemblage before dropping in abundance in the later Danian. Conversely, survivor pair LF57-SA20 (Cunoniaceae) and to a lesser degree pair LF55-SA78 (unknown affinity) significantly dropped in abundance between the Maastrichtian and early Danian, partially recovering in the later Danian. These trends may resemble the replacement of incumbent taxa by less abundant species, a pattern commonly observed across mass extinction intervals (e.g., Jablonski 2001, 2005; Erwin 2002).

Rarefied morphotype diversity curves for Maastrichtian LefL+LefE and Danian PL1, PL2 and LF localities showed that dicot leaf diversity adjusted for sample size dropped by almost half across the K-Pg and remained comparatively low from early to late Danian (Fig. 5). A drop in rarefied species diversity is also observed in the North American Cretaceous-Paleogene floras of the Hell Creek-Fort Union formations as in Johnson (2002) and Wilf and Johnson (2004). However, rarefaction also shows that Patagonian floras are significantly more diverse than North American Hell Creek-Fort Union formations macrofloras not only in the early Paleocene (Iglesias et al. 2007) but also in the Maastrichtian (Fig. 5).

Several morphotypes in both the Maastrichtian and Danian leaf assemblages have a strong affinity to the Lauraceae family based on their architectural characters, increasing the list of survivor families across the K-Pg in Patagonia. Based on a conservative “lumping” approach when morphotyping laurophylls in the Lefipán Fm., four morphotypes with a lauraceous affinity were established. Morphotypes LF8, LF24, LF26, and LF32 have entire margins and looping secondary venation (brochidodromous) with the basal-most pair of

secondaries departing from the primary vein at a lower angle than the rest (acute basal secondary syndrome), typical features of leaves within the Lauraceae (Hickey and Wolfe 1975). Nonetheless, cuticular preservation is needed to confirm a lauraceous leaf beyond a doubt (e.g., Carpenter et al. 2018) and is not available in the Lefipán Fm. macrofloral assemblages studied here.

In the Danian Salamanca and Peñas Coloradas formations' assemblages, the lauraceous *Laurophyllum piatnitzkyi* Berry and *Laurophyllum chubutensis* Berry share the entire margins and brochidodromous venation observed in Lefipán Fm. morphotypes, with additional preserved surface characters (Berry 1937; Iglesias et al. 2007). Abundant idioblasts and a thick cuticular layer are preserved in *Laurophyllum piatnitzkyi* specimens, both characters of lauraceous leaves (Iglesias 2007). *Laurophyllum chubutensis* lacks the acute basal secondary syndrome but maintains a strong marginal vein and thick cuticular layer consistent with a Lauraceous affinity. *Laurophyllum piatnitzkyi* Berry is notable for its predominance in the PL1, PL2 and LF macrofloral assemblages; averaging 17% of total floral composition where the mean compositional percentage per morphotype oscillates around 2.3%. It is only rivaled in abundance by morphotype SA9 ("*Cissites*" *patagonicum*) of unknown botanical affinity, which averages 15% of the total floral composition in the same assemblages.

Lauraceae is not represented in either the Lefipán or Salamanca formations' palynological records, probably due to the low preservation potential of lauraceous pollen (e.g., Herendeen et al. 1994; Upchurch 1995; Vajda and Bercovici 2014). However, the presence of lauraceous morphotypes reported here for the first time in Maastrichtian assemblages of Patagonia, coupled with previous reports of Lauraceae leaves in the Danian

Salamanca and Peñas Coloradas formations' assemblages (Berry 1937; Iglesias et al. 2007) suggests that Lauraceae was among the plant families surviving across the K-Pg in Patagonia and was a dominant component of Danian floras.

5.2. Whole-flora morphological change

Morphospace analysis of Maastrichtian and Danian leaf assemblages shows significant overlap in the morphospaces occupied by pre- and post-K-Pg morphotypes, with higher morphological disparity in the Danian despite lower morphotype richness as indicated by all four measures of disparity estimated for the first four axes of the Principal Coordinates Analysis (Fig. 7). The graphical analysis of morphospaces occupied by Maastrichtian and Danian morphotypes indicates that morphospace expansion in the Danian is due to an increase in lobed and toothed margined leaves, or a combination of both characters (Fig. 8). In the extended space occupied by Danian morphotypes, two groups of morphotype outliers stood out and could be divided based on a comparison of their morphologies. Outlier groups I and II are both comprised of characteristically lobed leaves, uncommon in Maastrichtian assemblages (Fig. 8). Leaves with toothed margins and secondary venation that terminates at the margin (craspedodromous) characterize Group I. Morphotypes in Group II are entire margined, but secondary venation is a mix of craspedodromous venation in Danian morphotypes, and looping secondaries (brochidodromous) in the included Maastrichtian morphotype.

End members representing the morphological variation along axis 1 (Fig. 8A) reflect extremes not only in leaf lobation and margin characters but also in secondary venation patterns. Both end members of the morphological diversity along axis 1 (Fig. 8A) are notably Danian morphotypes, and each has a distinctive margin, lobation, and secondary

venation. End member 1 is lobed, has craspedodromous secondary venation, and toothed margins, whereas end member 2 is unlobed, entire-margined and has looping brochidodromous venation. Intermediate morphotypes display combinations of these characters and additional, less common venation types. Maastrichtian morphotypes are mostly clustered towards the entire margined, unlobed, brochidodromous venation end of the axis (Fig. 8B), while Danian morphotypes not only occupy the same space but expand through combinations of lobation and toothed margined characters previously absent in the Maastrichtian (e.g., lobed leaves with toothed margins) (Fig. 8B).

Danian morphotypes in groups I and II of the initial graphical analysis are generally larger than Maastrichtian morphotypes. To further explore possible size-related patterns in morphospace occupation across the K-Pg, Maastrichtian, and Danian character scores were then plotted and colored by size class classification (Fig. 9) (Raunkiaer 1934; Webb 1959; Ellis et al. 2009). The smallest leaves in the assemblages, belonging to the microphyll size class, show complete overlap in morphospace occupation, indicating similar character combinations in both the Maastrichtian and Danian collections (Fig. 9A). Although there is significant morphospace occupation overlap in notophyll-sized leaf morphotypes, Danian morphotypes tend to have toothed margins and craspedodromous venation, while Maastrichtian notophyll morphotypes are more commonly entire margined or have large teeth along their margin (Fig. 9B). The most notable change in morphospace occupation is observed in the larger mesophyll size class (Fig. 9C), wherein Danian species occupy a morphospace 35.5% larger than the Maastrichtian species based on the sum of ranges for the first four axes. Mesophyll Danian morphotypes span a wide range of morphological diversity including lobed, unlobed entire margined, and toothed margin morphotypes.

Mesophyll Maastrichtian morphotypes are generally entire margined, but some margins appear to have wide undulations (“wavy, lettuce-like margins”) (Fig. 9C). Greater Danian morphospace occupation may also occur in the larger macrophyll and megaphyll size classes, but there are too few morphotypes of these sizes in either assemblage to explore this pattern further.

Morphospace occupation of lobed vs. unlobed species varies both within Maastrichtian and Danian floras and between Maastrichtian-only and Danian-only assemblages (Fig. 10A). Maastrichtian lobed and unlobed morphotypes occupied largely overlapping morphospaces of equivalent sizes, although there are seven lobed morphotypes and 50 unlobed morphotypes (Fig. 10B), indicating diverse character combinations in lobed leaves. Danian morphotypes also show higher morphospace occupation of lobed morphotypes relative to the unlobed morphotypes, although the proportion of lobed vs. unlobed morphotypes is much higher than observed in the Maastrichtian (Fig. 10C.). This result indicates that there is a higher morphological diversity in the Danian assemblage overall compared to the Maastrichtian, driven by higher variation among shape, size, venation, and character combinations.

Toothed and entire-margined morphotypes occupy distinctive areas of morphospace that are similar in size but overlap little in graphical analyses, including all Maastrichtian vs. Danian morphotypes and within Maastrichtian- and Danian-only subsets (Fig. 11). In Maastrichtian assemblages, although toothed and entire margined morphotypes occupy distinct areas of space, there is a spatial overlap characterized by the presence of leaf types with wavy margins or margins with small rounded teeth (crenate) (Fig. 11B). The distinct areas of morphospace occupied by Danian toothed and entire margined morphotypes show

no overlap at all and are well separated (Fig. 11C). The distinct spatial separation of Danian morphotypes based on tooth characters suggests that there are combinations of traits occurring predominantly in either leaves with toothed or entire margins.

In summary, the significant overlap in Maastrichtian-Danian morphospace occupation coupled with the expansion of morphospace in Danian assemblages shows preservation and expansion of the range of leaf forms with no loss of characters across the boundary. Graphical analyses of morphospace occupation by overlaying specific morphological characters as different colors on the ordination plots (Figs. 8-11) revealed that lobation and margin characters are the most important drivers in occupation patterns both including all Maastrichtian and Danian morphotypes and within Maastrichtian and Danian assemblages. In each case, the separation between toothed and entire margined and between lobed and unlobed morphotypes was stronger in Danian morphotypes compared to the Maastrichtian, suggesting distinct character combinations in the Danian previously not occurring in Maastrichtian leaves.

5.3. Pollen and regional floral heterogeneity

Comparison of species-level spore and pollen reports, including all plant groups showed that approximately 60% of species in the Danian Salamanca Fm. were shared with the Maastrichtian Lefipán Formation. Results provide evidence for the presence of most of the same higher plant taxa in microfloras of both formations and across the K-Pg.

Approximately 75% of species were shared between the Salamanca Fm. and Danian strata of the Lefipán Fm. including all taxa shared with the Maastrichtian Lefipán Fm. and several exclusively Danian taxa like the marker *Nothofagidites dorotensis* (Barreda et al. 2012) (Table 2). The high percentage of shared species between Danian microfloras of both

formations suggests low spatial heterogeneity in composition of higher taxa represented by palynomorph species, not only across the K-Pg but also the 400 km separating the two collection areas.

Within the shared Danian taxa of the two formations, 80% are Cretaceous-Paleogene survivors, demonstrating the persistence of the gymnosperm family Podocarpaceae, a morphotype of *Classopollis* sp., and the angiosperm families Arecaceae, Liliaceae, Proteaceae, Symplocaceae, and Gunneraceae, as well as various bryophyte and fern families across the boundary (Table 2). The high proportion of shared palynomorph species between the Danian Salamanca and Lefipán formations indicates the persistence of higher taxa not only across the Cretaceous-Paleogene transition but also despite the distance between the sampling areas.

Despite the 300-400 km separation between localities in the Lefipán and Salamanca formations, the percentage of shared species between them is comparable to that among Maastrichtian and Danian Lefipán Fm. samples within the SRS. This result suggests that although geographic separation of the Lefipán and Salamanca formations drives some of the observed geographical heterogeneity in the microfloras, it does not influence composition of higher taxa between the two localities any more than sampling or temporal biases affecting sample composition within the same section. Therefore, the parallel comparison of macrofloras from the Lefipán, Salamanca, and Peñas Coloradas formations is likely to reflect real underlying species turnover.

Cluster analysis of a Beal's smoothed compositional matrix tested the heterogeneity of the species associations between the Lefipán and Salamanca formations. The results show that despite a high percentage of palynomorph species shared between the two formations,

consistently different floral associations responding to age and formation cluster in each of the three analyses shown in Figure 12. Based on the height of the cluster dividing the Lefipán and Salamanca formations samples in each analysis, the highest heterogeneity in floral associations was observed between formations, not across the K-Pg.

The most significant difference between the compositions of the Lefipán and Salamanca formations palynofloras measured by the height of the first cluster is seen when including all taxa (Fig. 12A). The smallest difference is observed when considering angiosperm pollen taxa only (Fig. 12C). This suggests that angiosperm composition is not the most significant source of heterogeneity between the Lefipán and Salamanca formations, even though angiosperms are the most affected vascular plant group across the K-Pg in the Lefipán Fm. San Ramón section (Barreda et al. 2012). Compared to the 65 % pteridophytes and the 85.7 % survivor species of gymnosperms in the San Ramón section, angiosperms suffer a 50% palynofloral extinction. The proportionally higher angiosperm extinction observed in palynofloras would translate into a significant species-level turnover documented in macrofloras, such as the dicot leaf assemblages addressed in this study.

6. Discussion

6.1. Macrofloral extinction

Coupling the high angiosperm macrofloral extinction percentage estimated in this study with the observed drop in rarefied morphotype diversity across the K-Pg, Patagonian macrofloras and supporting palynological data from the same sections provides evidence of a floral extinction event as seen in the North American Williston Basin and Ratón Basin (Fig. 5) (Wolfe and Upchurch 1986; Johnson and Hickey 1990; Johnson 2002; Wilf and Johnson 2004). Compositionally, diverse pre-K-Pg Maastrichtian macrofloras of the Lefipán Fm. are replaced by much lower diversity post-K-Pg Salamanca and Peñas Coloradas formations assemblages that remain homogeneous in the 3my interval spanned by the PL1, PL2, and LF sites (Fig.6), despite the range of estuarine floodplain to entirely continental facies the floras are preserved in (Iglesias et al. 2007; Comer et al. 2015). Low diversity, homogeneous early Paleocene assemblages are characteristic of recovery floras observed in North American sections (Wolfe and Upchurch 1986; Johnson and Hickey 1990; Johnson 1992; Barclay et al. 2003; Wilf et al. 2003a; Wilf and Johnson 2004), suggesting Patagonian Danian floras agree with the North American pattern of floral recovery following the mass extinction event.

The parallels between the North American and the new Patagonian Cretaceous-Paleogene macrofloral records show they are both consistent with significant floral extinction and recovery across the K-Pg boundary, supporting a floral disruption of global extent in the aftermath of the bolide impact (Vajda et al. 2001; Nichols and Johnson 2008; Barreda et al. 2012; Vajda and Bercovici 2014). However, the contrast in macrofloral diversity between the K-Pg assemblages of Patagonia and North American is striking.

Rarefied species diversity in this study shows that not only the Danian floras, including the approximately coeval Paleocene (Iglesias et al. 2007) Salamanca Fm. PL1 and Fort Union 38m bin, both constrained to chron C29n (Hicks et al. 2002; Johnson 2002; Clyde et al. 2014), but also Maastrichtian assemblages in Patagonia are significantly more diverse than North American macrofloras. Macrofloras of the Lefipán Fm. LefE+LefL fossil horizon are approximately 40% richer than comparable Maastrichtian Hell Creek Fm. assemblages of the diverse 15 m bin below the boundary (Fig. 5).

Previous studies of the Patagonian Danian Salamanca Fm. macrofloras (Iglesias 2007; Iglesias et al. 2007) and Eocene Laguna del Hunco and Río Pichileufú macrofloras (Wilf et al. 2003*b*, 2005) provided evidence for an ancient history of exceptional South American Cenozoic floral diversity. The results presented in this study suggest that the history of higher South American floral diversity precedes the K-Pg, extending into the Late Cretaceous. Furthermore, rarefied species diversity across the K-Pg in WINA and Patagonia signals a significantly more severe species-level extinction in WINA. The high diversity of Salamanca Fm., Laguna del Hunco and Río Pichileufú assemblages compared to WINA equivalents has been hypothesized in part to be the legacy of low floral extinction as observed in the palynological record (Barreda et al. 2012). The diverse Lefipán Fm. floras show that early Danian floral richness in Patagonia could be a legacy not only of a lower extinction rate, but also richer Maastrichtian floras.

In the North American Williston Basin, macrofloral diversity drops $\approx 75\%$ between the terminal Maastrichtian Hell Creek Fm. -15 m bin below the boundary, the richest of the Hell Creek Fm. macrofloral assemblages, and the Danian Fort Union Fm. +38 m bin above the K-Pg. Comparatively, in Patagonia, diversity drops by $\approx 45\%$ between the terminal

Maastrichtian Lefipán Fm. LefE+LefL stratigraphic horizon and the Danian Salamanca Fm. PL1 locality, which is approximately coeval to the Fort Union Fm. 38 m bin (Fig. 5). The significantly higher drop in rarefied diversity across the transition between the Hell Creek-Fort Union formations indicates a much more severe macrofloral extinction across the K-Pg in North America compared to Patagonia based on rarefaction, which led to the lower diversity Danian WINA paleofloras.

Coupling the K-Pg macrofloral extinction estimate calculated in this study with the previously estimated microfloral extinction percentages of the Lefipán Fm. (Barreda et al., 2012), underpins high species-level but low family-level turnover across the K-Pg in Argentine Patagonia. Continuity of higher taxa is supported by taxonomic studies of Maastrichtian Lefipán Fm. and Danian Salamanca Fm. macrofossils revealing shared gymnosperm families Araucariaceae and Podocarpaceae, and the persistence of the angiosperm families Cunoniaceae, Arecaceae, and others in the Salamanca Fm. (Table 1), and based on this study, Lauraceae, Rosaceae, and Malvaceae. Most macrofloras of the Lefipán, Salamanca and Peñas Coloradas remain undescribed, and future studies could increase the list of K-Pg survivor families in the region's macrofloral record.

In Patagonian microfloras, angiosperms suffered the highest extinction percentage ($\approx 50\%$) of all vascular plants (Barreda et al. 2012) across the K-Pg, in agreement with the high dicot species-level turnover observed in the macrofloras of this study. Similar observations have been made in the palynological records of western North America and New Zealand (Nichols et al. 1986; Sweet et al. 1990; Vajda and Raine 2003), and have been hypothesized to be related to the severe insect extinction (Labandeira et al. 2002*a, b*; Donovan et al. 2014) across the K-Pg (Sweet et al. 1990, 1999; Sweet and Braman 2001).

By analogy to insect herbivory studies across the K-Pg in Patagonia (Donovan et al. 2016, 2018), insect pollinators surviving the primary effects of the impact would have been severely affected by the permanent or temporary loss of their associated plants (Labandeira et al. 2002a). Disrupted pollinator vectors would have negatively impacted zoophilous (animal pollinated) angiosperm reproduction in the early Paleocene, and could provide a mechanism behind the relatively high angiosperm pollen extinction in Patagonia (Barreda et al. 2012).

Laurophyll leaves are present in both Maastrichtian and Danian macrofloras of Patagonia. Notably, however, the Lauraceae leaf *Laurophyllum piatnitzkyi* Berry represent approximately 20% abundance in the macrofloral assemblages from early to late Danian in PL1, PL2, and LF, while leaves with lauraceous affinity are a minor component, less than 5% abundance, in the Maastrichtian Lefipán Formation assemblages. The dominance of laurophyll leaves in Danian floras was also observed by Upchurch (1995) and Berry (2019) in the North American Ratón Fm., where despite a drop in Lauraceae diversity across the boundary, the family was a dominant component of the Ratón Fm. angiosperm floras in both Maastrichtian and Danian assemblages (Upchurch 1995).

Lauraceae has most recently been proposed as the principal component of K-Pg recovery macrofloras alongside the classic fern spike in the North American Ratón Basin, a pattern that has until now gone unnoticed due to the low preservation potential of lauraceous pollen (Berry 2019). In Patagonia, the notable predominance of *Laurophyllum piatnitzkyi* Berry in early Paleocene assemblages parallels the patterns observed in the Ratón Formation and would be consistent with a Lauraceae-dominated K-Pg recovery flora in both areas.

Although the macrofloral turnover observed in this study is reflective of an underlying pattern of high turnover of lower taxonomic levels, the estimated extinction percentage may be too high. Macrofloral extinction in North American localities of the Ratón Basin and Hell Creek-Fort Union formations, where overall microfloral extinction ranges from 30-40% (Nichols and Fleming 1990; Sweet et al. 1990; Sweet and Braman 2001; Nichols 2002), varies from 57% to 66%, and 78% when only the upper 5m, the upper 15m or all Cretaceous Hell Creek strata are considered in the estimate respectively, excluding singletons (Wilf and Johnson 2004). In Patagonia, angiosperm palynological extinction is approximately 50% (Barreda et al. 2012), and the angiosperm macrofloral extinction is $\approx 92\%$ when including singletons, and $\approx 90\%$ when excluding them. However, the macrofloral turnover observed in Patagonia may then be driven not only by an extinction event, but also the caveats of the stratigraphic, geographic, and climatic biases of these collections, as well as their much coarser temporal sampling (see next paragraph).

Coarse temporal sampling in both Maastrichtian and Danian Patagonian macrofloras imparts a bias in extinction percentage estimates. The uncertain placement of the Lefipán Fm. macrofloras within the last ca. million years before the K-Pg boundary (Barreda et al. 2012; Vellekoop et al. 2017), and the lack of earliest Danian sediments preserved in the Salamanca Fm. provide a source of temporal and possibly climatic biases against finding a higher number of survivor pairs. A first temporal bias is imparted in the Salamanca Fm., which unlike the Fort Union Fm. (Hicks et al. 2002; Johnson 2002), is missing critical post recovery floras encompassed by chron C29r (66.398 – 65.688 Ma) because the earliest sediments correspond to chron C29n (Clyde et al. 2014).

In the extensive stratigraphic sampling of the Hell Creek-Fort Union macrofloras in North Dakota (Johnson et al. 1989 Johnson, 2002; Wilf and Johnson, 2004), there is a general trend of lower percentages of survivor species as the distance below the boundary layer increases (Fig. 13). Furthermore, extinction may exceed 90% when some intervals are considered on their own despite their position relatively close to the boundary, as can be seen in the 20-30 m and 40-50 m intervals of the Hell Creek Formation (Fig. 13). The limited stratigraphic horizons spanned by macrofloras in the upper Lefipán Fm. are an analogous situation to considering a small interval of the Hell Creek Formation. Although there are macrofloral collections from lower Lefipán Fm. strata (Andruchow-Colombo et al. 2018; Martínez et al. 2018), their precise age is not known and the preservation of dicot leaves is not nearly so extensive as in the upper Lefipán studied here. Therefore, it is not possible to observe the variability of extinction rates within a wide stratigraphic range in the Lefipán Fm. at this time.

Marine and terrestrial paleontological and proxy records show a relatively short-lived climatic warming within the last 500ky of the Maastrichtian, followed by cooling during the final 100 ky of the Maastrichtian persisting into the early Paleocene (Stott et al. 1990; Huber and Watkins 1992; Wilf et al. 2003a; Bowman et al. 2014; Vellekoop et al. 2017; Woelders et al. 2017; Barnet et al. 2018; Huber et al. 2018). The uncertain age of the Maastrichtian Lefipán Fm. macrofloras also introduces an important potential climatic bias. In the Hell Creek Formation, peak richness of floral diversity (HCIII flora) is correlated to the highest temperature estimates during the late Maastrichtian global warming event, followed by a decline in species richness during the rapid cooling in the terminal Maastrichtian (Wilf et al. 2003a). A comparison only between peak diversity Maastrichtian

floras and the relatively depauperate Danian floras would result in an overestimation of extinction percentages (Wilf et al. 2003a; Wilf and Johnson 2004). The high species richness and related proxy temperatures observed in the Maastrichtian Lefipán Fm. assemblage could indicate it corresponds to this warming event, which could translate into an overestimation of macrofloral extinction in this study.

6.2. Whole-flora morphological change

Despite the estimate of almost complete species-level macrofloral turnover, morphospace analysis of Maastrichtian and Danian leaf assemblages showed not only continuity but expansion of leaf morphologies and their underlying ecological and phylogenetic diversity across the K-Pg. Overlap of morphospaces occupied by Maastrichtian and Danian floras shows that extinction was not character selective. However, areas of morphospace occupied by Danian toothed and entire margined morphotypes show much stronger separation than toothed and entire-margined morphospaces occupied by Maastrichtian assemblages. This pattern could be driven by character combinations absent in Maastrichtian floras that resulted in a morphologically and perhaps phylogenetically rich, albeit species poor Danian recovery flora.

Low diversity, homogeneous Danian floral assemblages occupy a larger area of morphospace than the richer Maastrichtian floras, and are characterized by an approximate 20% increase in leaves with toothed margins, doubling of the proportion of lobed leaf morphotypes, and an increase in the frequency of craspedodromous secondary venation (Figs. 7-10). In studies of modern assemblages, lobation and margin type are correlated to climatic parameters. Floras with relatively high proportions of toothed and dissected blades

are more likely to characterize cooler and possibly seasonal temperatures (e.g. Bailey and Sinnott 1915; Wolfe 1971, 1993, 1995; Baker-Brosh and Peet 1997; Royer et al. 2005)

The proportion of toothed margined species in a floral assemblage has been consistently shown to have the strongest correlation to mean annual temperature out of any environmental parameter (Wolfe 1995; Wilf 1997; Greenwood et al. 2004), resulting in its widespread use for paleotemperature estimation. Phylogenetic history may present a source of error, as it is expressed as a non-random signal that significantly limits the accurate estimation of paleotemperatures based on this metric (Little et al. 2010). However, margin-based paleotemperature estimates may be best applied to approximations of relative temperature change between assemblages from similar regions and similar underlying composition (Little et al. 2010). The Maastrichtian Lefipán and Danian Salamanca and Peñas Coloradas formations leaf assemblages fulfill these criteria. Using the correlations of Wilf (1997) based on the proportion of toothed vs. entire-margined leaves, a relative cooling of ca. 5°C was estimated between the Maastrichtian and Danian floral assemblages. Cooler temperatures persisted in the three-million-year period spanned by the Danian localities.

Morphological extinction and recovery patterns across the K-Pg in North American macrofloras show interesting contrasts with macrofloral turnover in Patagonia. Latest Cretaceous Ratón Basin and Hell Creek Fm. leaves are generally small (Wolfe and Upchurch 1987; Johnson and Hickey 1990; Johnson 2002), suggestive of a drier environment than that of the Lefipán Fm. floras where there is a variety of sizes ranging up to macrophyll-sized leaves. Maastrichtian assemblages of North America are characterized by the abundance of leaves with a “Cretaceous look” or unusual lobation (Johnson 2002), a character that is drastically reduced in the early Paleocene depauperate assemblages

(Johnson and Hickey 1990; Johnson 2002). The predominance of lobed Cretaceous morphotypes was also observed by Wolfe and Upchurch in the Ratón Basin, replaced in a post-boundary floral succession by unlobed leaves (Wolfe and Upchurch 1986, 1987). In contrast, lobation and “Cretaceous look” increases in the early Paleocene of Patagonia (Fig. 8; Iglesias et al. 2007).

6.3. Pollen and regional floral heterogeneity

Cluster analysis of Beals-smoothed Maastrichtian-Danian microfloral assemblages of the Lefipán Fm. supports the floral turnover and successive stages of recovery across the K-Pg observed by Barreda et al. (2012), in which angiosperms regain dominance in the later Danian samples D10-D12 (Figs 1D and 12). Because angiosperm species dominate all Salamanca Fm. microfloras (Clyde et al. 2014), they either correspond to the later Danian recovery stages observed in the Lefipán Fm., or they are younger. If younger, the palynological records of the Lefipán and Salamanca formations would not represent coeval but rather successive assemblages in the Danian, providing a stratigraphic mechanism for the heterogeneity observed in the cluster analysis (Fig. 12). However, if Danian Lefipán and Salamanca microfloral assemblages were coeval, cluster analysis is sensitive to differences in microfloral composition between the two areas despite a high percentage of shared species between them.

The differences between the Lefipán and Salamanca formations microfloras provides evidence for geographical heterogeneity of family-level associations, which would accentuate species-level contrasts observed in the macrofloras between the two areas due to the low spatial resolution of macrofloral deposits (Behrensmeyer et al. 2000; Nichols and Johnson 2008). Different underlying species associations suggests that the 400km spatial

separation of Maastrichtian and Danian assemblages plays a role in the overestimation of Patagonian macrofloral extinction by imparting a geographical bias. Spatially-driven compositional changes could also explain the contrast between the >90% macrofloral extinction, despite rarefied species diversity dropping $\approx 45\%$ between Maastrichtian and Danian assemblages (Fig. 5).

7. Summary

Comparison of the Maastrichtian Lefipán and Danian Salamanca and Peñas Coloradas formations' dicot leaf collections provided the first K-Pg macrofloral extinction investigation in the Southern Hemisphere based on large, stratigraphically and age constrained collections. A comparison of Maastrichtian-Danian macrofloras of Patagonia yielded a 92% K-Pg macrofloral turnover. However, this extinction percentage is likely an overestimation due to the geographic, stratigraphic, and paleoenvironmental caveats associated with the collections. Nonetheless, analysis of the Maastrichtian and Danian macrofloras of Patagonia through rarefied species diversity, observation of their architectural characters, and morphospace analysis, revealed patterns broadly resembling extinction and recovery observed in North American K-Pg macrofloras supporting a global floral extinction, and interesting differences that suggest complex underlying mechanisms driving differences in floral turnover between North America and Patagonia.

Diverse Maastrichtian floras were superseded by lower diversity, compositionally homogeneous Danian assemblages for the 3 my following the K-Pg in Patagonia. Coupled with the observed sharp decrease in rarefied species richness across the K-Pg, impoverished homogeneous Paleocene floras are consistent with the extinction and recovery pattern observed in North American sites. However, North American macrofloras suffered a much more severe drop in species richness across the boundary suggesting higher species-level extinction than in Patagonia, and are much less diverse not only in Danian (Iglesias et al. 2007) but also Maastrichtian floras. This study reports rich Maastrichtian macrofloras in Patagonia for the first time, extending the history of exceptional floral diversity in South America before the Paleocene and into the terminal Cretaceous. Leaves with strong

lauraceous affinity are characteristically dominant in the Patagonian macrofloral assemblages, supporting the hypothesis of Lauraceae as significant component of K-Pg recovery floras in a pattern that may be geographically extensive with further evidence.

Morphospace analysis of Maastrichtian-Danian Patagonian macrofloras shows that not only was there no character loss across the K-Pg extinction but that Danian macrofloras are morphologically more diverse than Maastrichtian assemblages. Morphologically disparate Danian floras, rich in lobed and toothed morphotypes, appear to be a notable Patagonian characteristic that contrasts with North American macrofloras, where lobed forms largely disappear across the K-Pg. Increased toothed morphotypes in Danian Patagonian assemblages is a pattern that may be related to a climatic cooling across the K-Pg, aligning with global records if the Maastrichtian Lefipán assemblages correspond to the terminal Cretaceous warming event.

Comparison of published Cretaceous-Paleogene palynological and macrofloral taxonomic records of the Lefipán and Salamanca formations shows that angiosperms experienced the highest extinction of the vascular plants, supporting the high species-level turnover observed in the dicot leaf assemblages of this study. However, palynological records and taxonomically studied macrofloras show there is persistence of higher taxonomic levels across the K-Pg along the paleo-Atlantic coastline between the Maastrichtian and Danian macrofloras.

Extinction and recovery in Patagonian macrofloras parallel that of North American assemblages in the drop of rarefied species diversity and low diversity, homogeneous Paleocene floras, indicating floras in both areas were disrupted by the K-Pg bolide impact and its environmental consequences. Contrasts between Patagonian and North American

macrofloras emerge in macrofloral extinction severity, floral diversity, and morphological turnover across the K-Pg. The subtle differences between Patagonian and North American K-Pg macrofloras may be a product of local palenvironmental conditions and floral composition, but possibly reflect a geographically heterogeneous Southern vs. Northern Hemisphere extinction and recovery pattern as observed in other marine and paleontological records.

8. References

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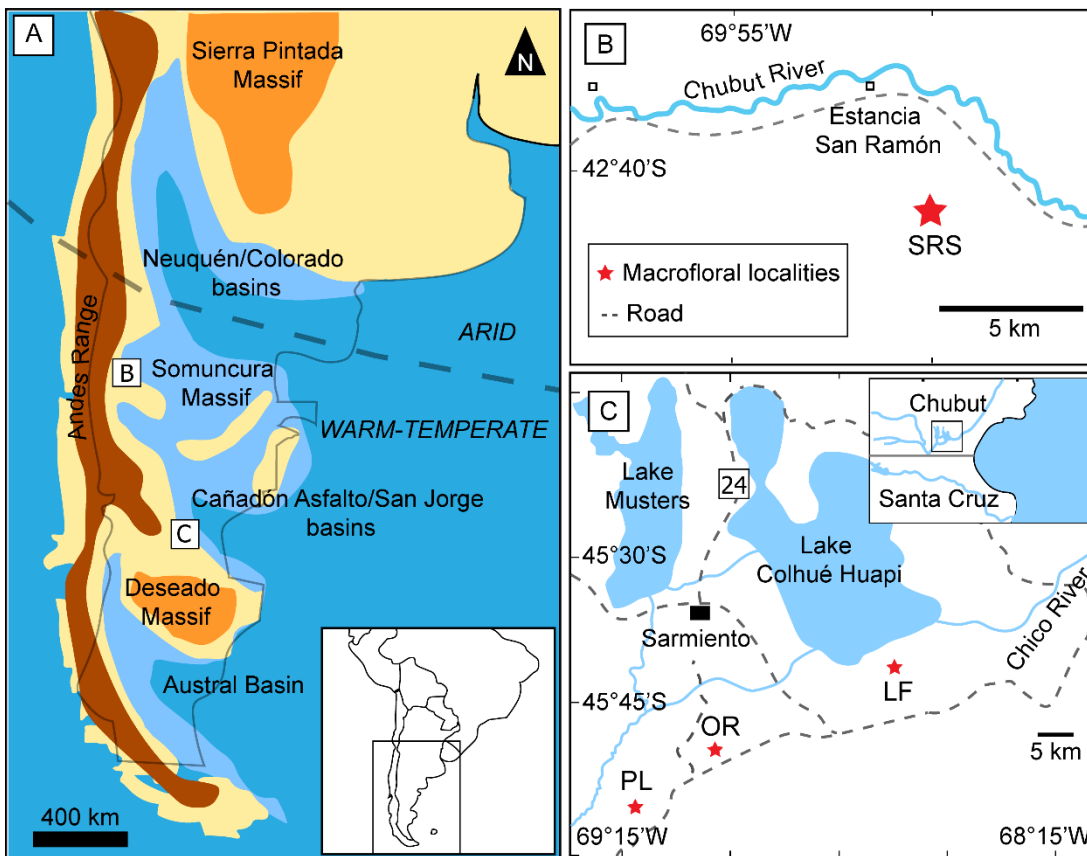
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Figure 1. **A.** Paleogeographic reconstruction of Patagonia during the Cretaceous-Paleogene transition. Dark blue: deep water, light blue: shallow platform, yellow: coastal lowlands. Dashed line represents the approximate boundary between the arid and warm-temperate paleoclimatic belts inferred by Scasso et al 2012. Redrawn from Scasso et al. (2012). **B.** Location of Scasso et al.'s (2012) Lefipán Fm. San Ramón Section, modified after Barreda et al. (2012). **C.** Location of Salamanca Fm. Palacio de los Loros macrofloral sampling localities (PL), Peñas Coloradas Fm. Las Flores (LF) and microfloral (also macrofloral, though macrofloras not used here) locality Ormachea (OR). Modified after B. Clyde et al. (2014) and C. Comer et al. (2015) **D.** Summarized stratigraphic chart showing placement of palynological samples and macrofloral collection sites in the Lefipán, Salamanca and Peñas Coloradas formations addressed in this study (Iglesias, 2007; Barreda et al., 2012; Clyde et al., 2014; Comer et al., 2015; Donovan et al. 2016:2018). Palynological samples designated by tick marks along the column, macroflora collection sites labeled by gray stars. Refer to the Materials section for information about the macrofloral collection sites and their stratigraphic relationships. Absolute dates and magnetostratigraphy in the Salamanca Fm. after Clyde et al. (2014).



D Northern Chubut

Southern Chubut

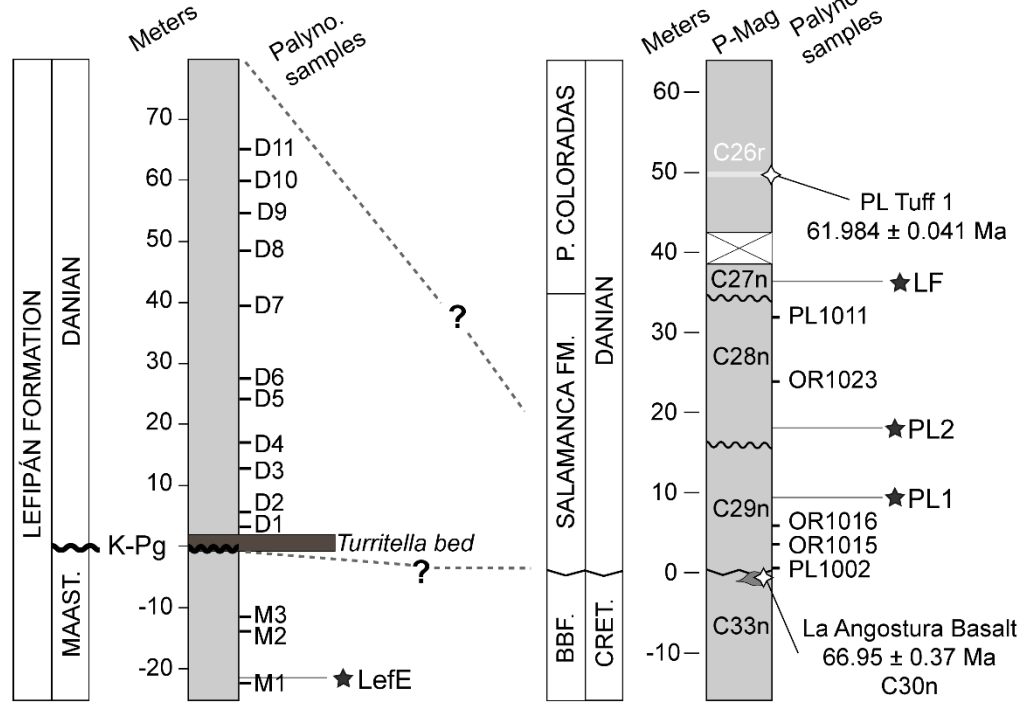


Figure 2. Maastrichtian-Danian survivor pair example specimens from Lefipán, Salamanca and Peñas Coloradas formations localities (K=Maastrichtian, D=Danian). Maastrichtian morphotypes marked with a blue circle. **A-F.** LEF57-SA020. Note ovate shape, asymmetrical base, curved primary, long rounded sinuses and semicraspedodromous venation. **G-J.** LEF64-SA035. Note lobed leaf base, straight opposite secondaries and alternate percurrent tertiary venation. **K-M.** LEF55-SA078. Note ovate leaf shape, thick primary vein, and opposite to subopposite secondaries with brochidodromous venation. **A.** MPEF-Pb-4416 from K locality LefE. **B.** MPEF-Pb-4334 from D locality LefL. **C.** MPEF-Pb-4349 from K locality LefE. **D.** PL1-912 from D locality PL1. **E.** MPEF-Pb-4023 from D locality PL2. **F.** PL1-1031 from K locality LefE. **G.** LL5a from K locality LefL. **H.** MPEF-Pb-2031 from D locality PL1. **I.** LL5b detail of alternate percurrent tertiary venation **J.** MPEF-Pb-2031 detail of alternate percurrent tertiary venation **K.** MPEF-Pb-4870 from K locality LefL. **L.** MPEF-Pb-4835 from K locality LefE. **M.** MPEF-Pb-3019 from D locality LF.

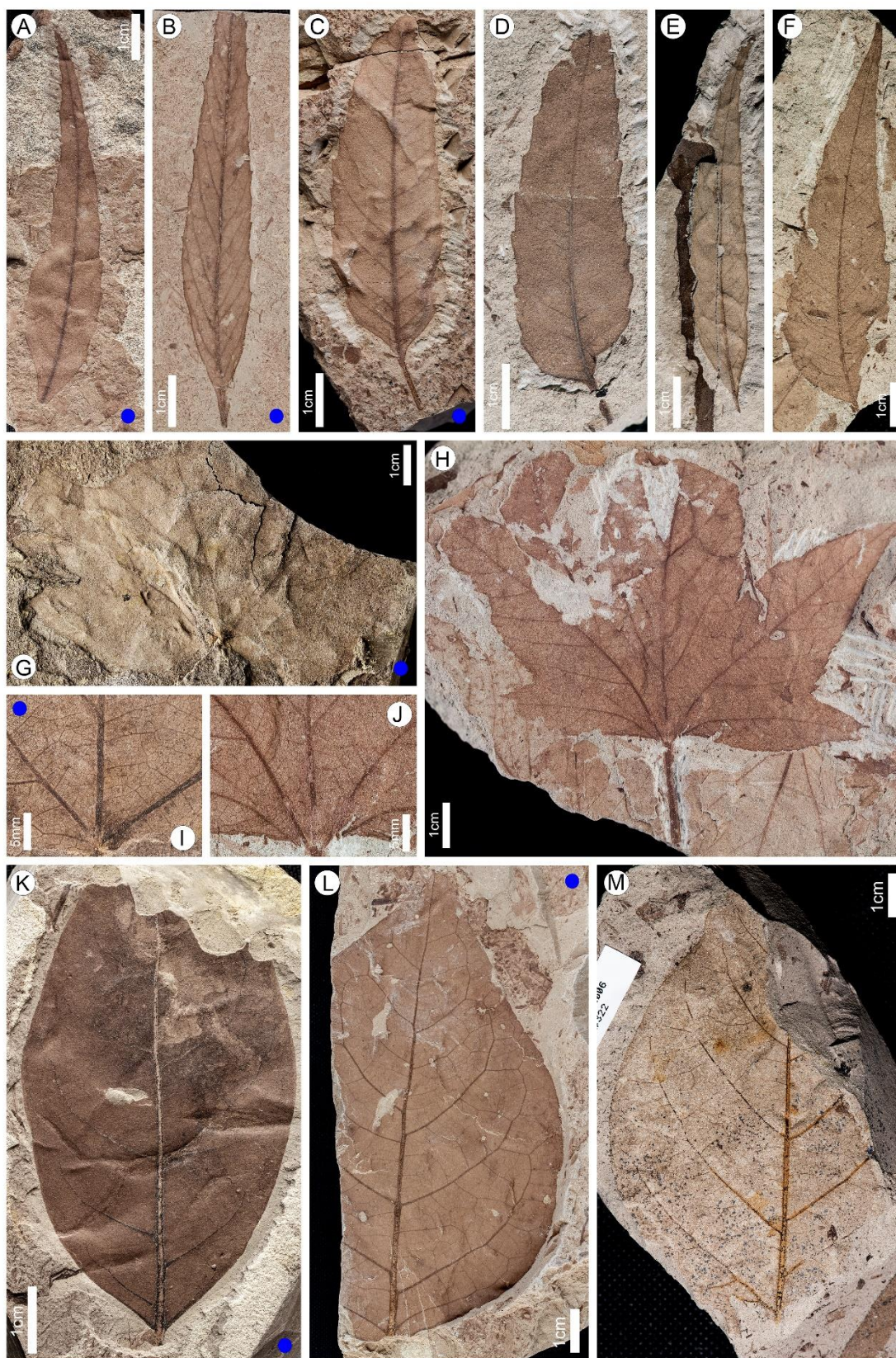


Figure 3. Maastrichtian-Danian survivor pair example specimens from Lefipán, Salamanca and Peñas Coloradas formations localities (K=Maastrichtian, D=Danian). Maastrichtian morphotypes marked with a blue circle. **A-C.** LEF6-SA019. Note the three-lobed form, three primary veins, central primary deflected by basalmost pair of secondaries, brochidodromous secondary spacing decreasing apically and tertiaries nearly perpendicular to primary. **C-F.** LEF18-SA08. Note ovate shape, pinnately lobed, lobes compound with rounded tips, opposite to subopposite secondaries. **A.** MPEF-Pb-4662a from K locality LefW. **B.** PL1-527 from D locality PL1. **C.** Example of 5-lobed morphotype occurring in Danian assemblages, PL2-1245 from D locality PL2. **D.** MPEF-Pb-4487 from K locality LefE. **E.** MPEF-Pb-4882 from locality K LefE. **F.** PL1-589 from D locality PL1.

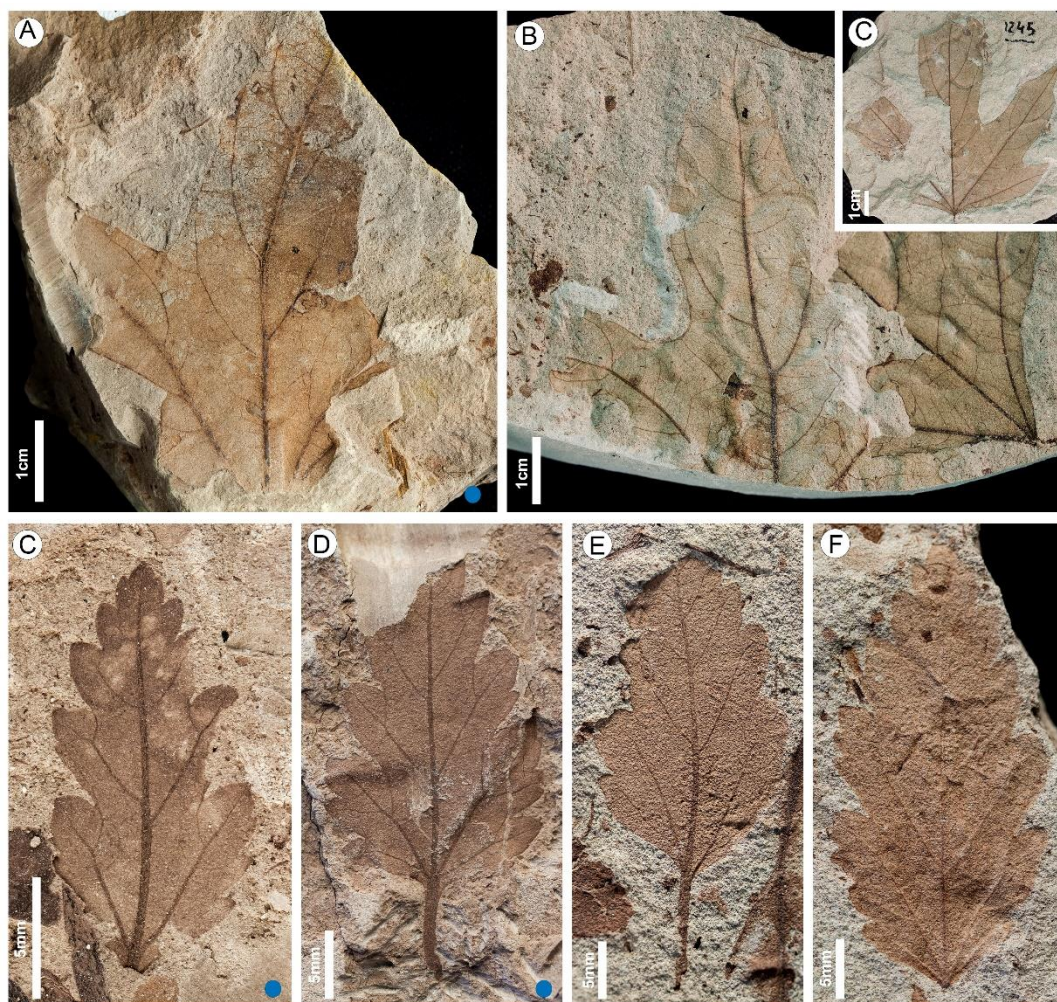


Figure 4. Proportions of survivor pairs through time in overall Maastrichtian and Danian floral assemblages. Major components represent 5% or more of total assemblage.

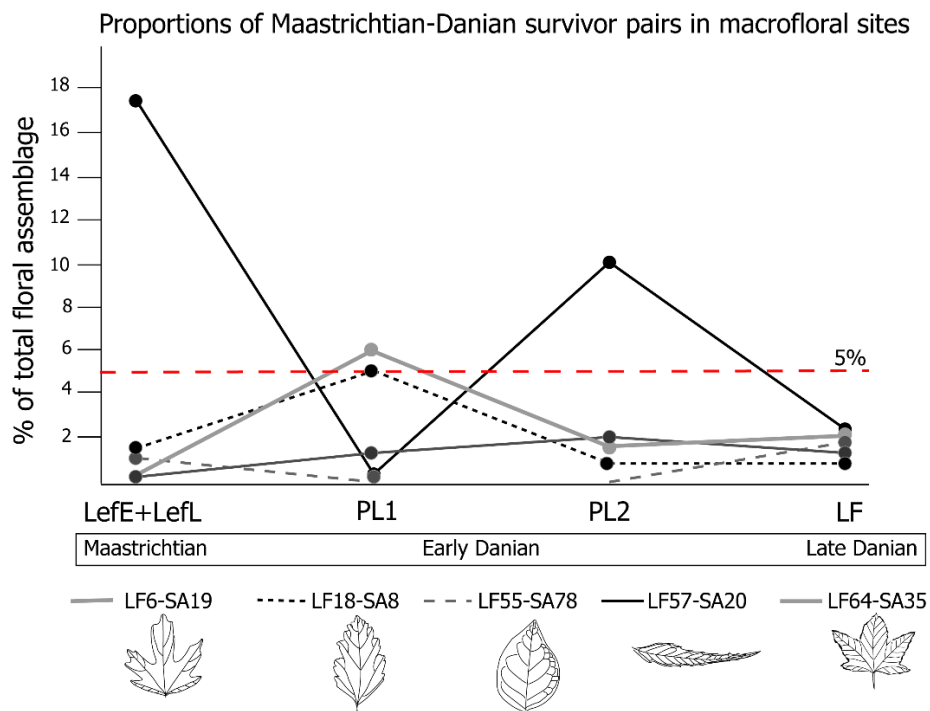


Figure 5. Estimated rarefied species richness with 95% confidence intervals for Maastrichtian (black) LefE+LefL Lefipán Fm. macrofloral localities, early Danian (gray) PL1 and PL2 Salamanca Fm. macrofloras, and late Danian Peñas Coloradas Fm. LF macrofloras. Established K-Pg extinction and recovery North American Maastrichtian Hell Creek and Danian Fort Union dicot leaf assemblage richness after Wilf & Johnson (2004) plotted for comparison.

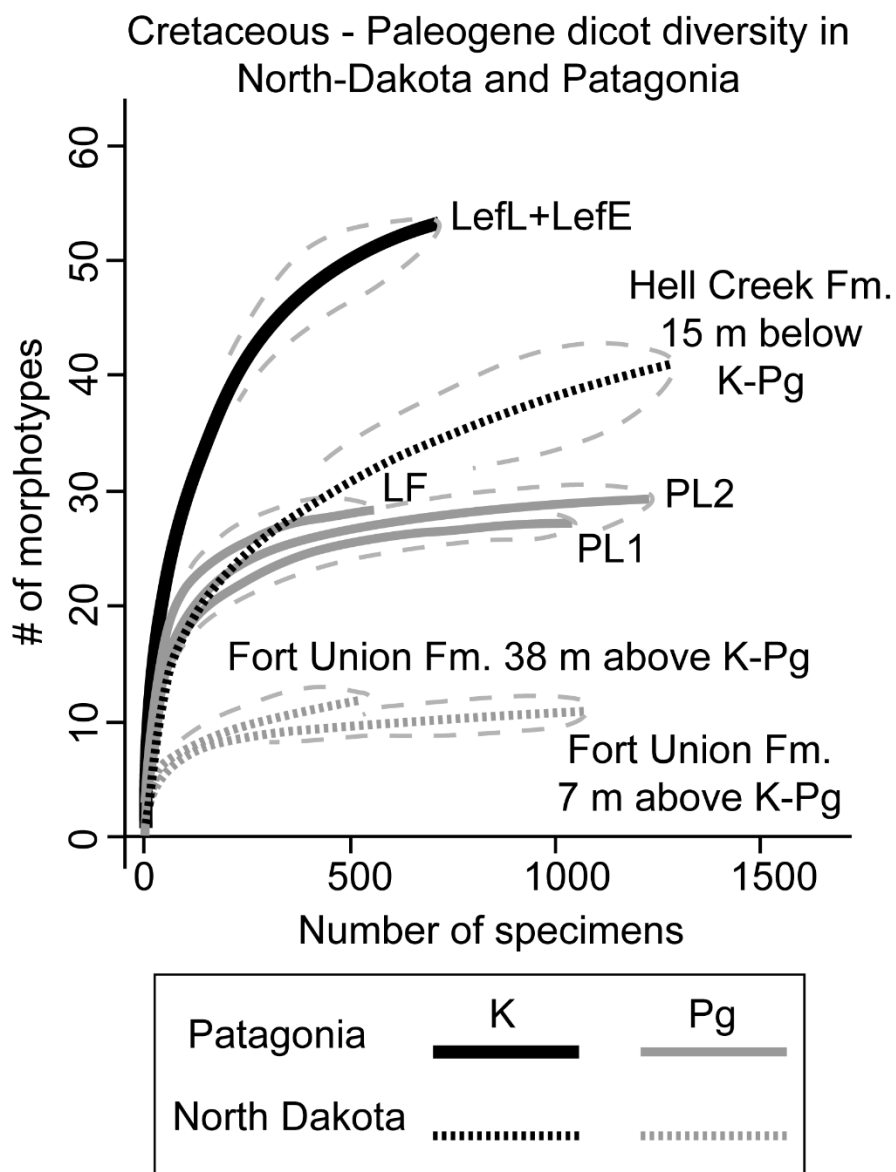


Figure 6. Sample-based Principal Coordinates Analysis (PCA) highlighting the similar floral compositions of Maastrichtian Lefipán Fm. LefW collection with horizon LefE+LefL as they cluster on the left side of the plot along PCA1, and the homogeneous floral composition of Salamanca and Peñas Coloradas Fms. PL1, PL2 and LF collections clustered towards the right side of the plot along PCA1.

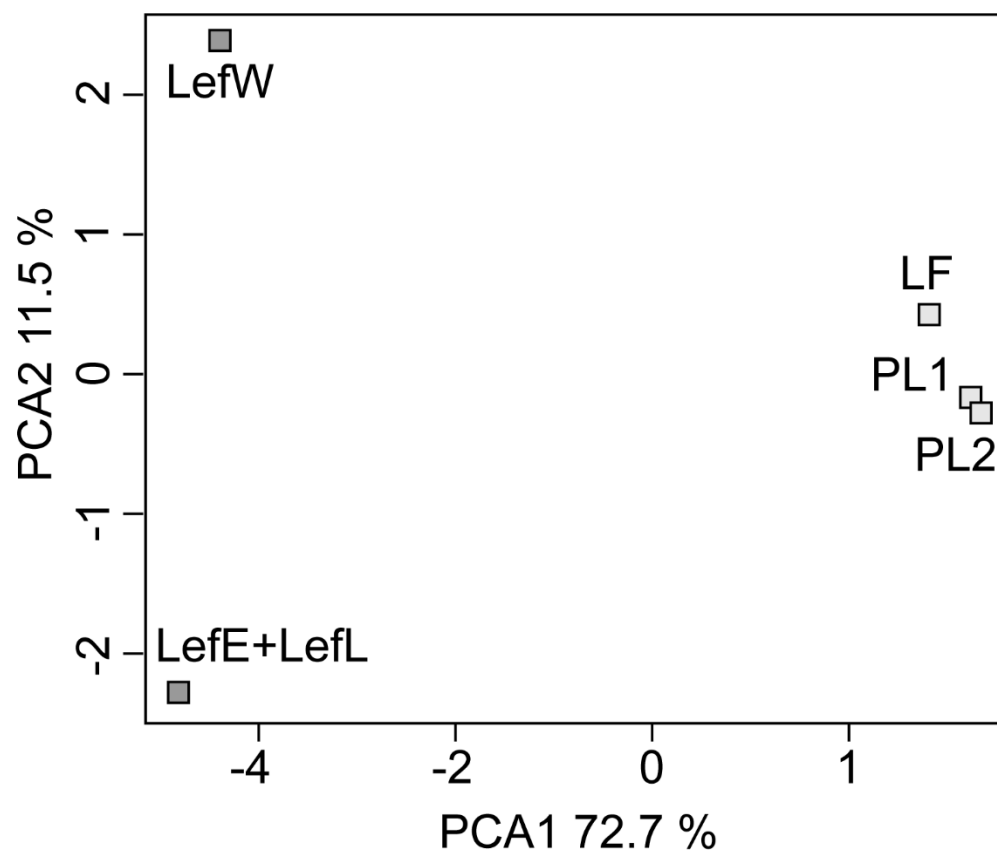


Figure 7. Increase of macrofloral morphospace occupation across the K-Pg transition based on four calculated measures of disparity: (1) sum of ranges, (2) hypercuboid volume, (3) Average pairwise distance, and (4) Maximum pairwise distance.

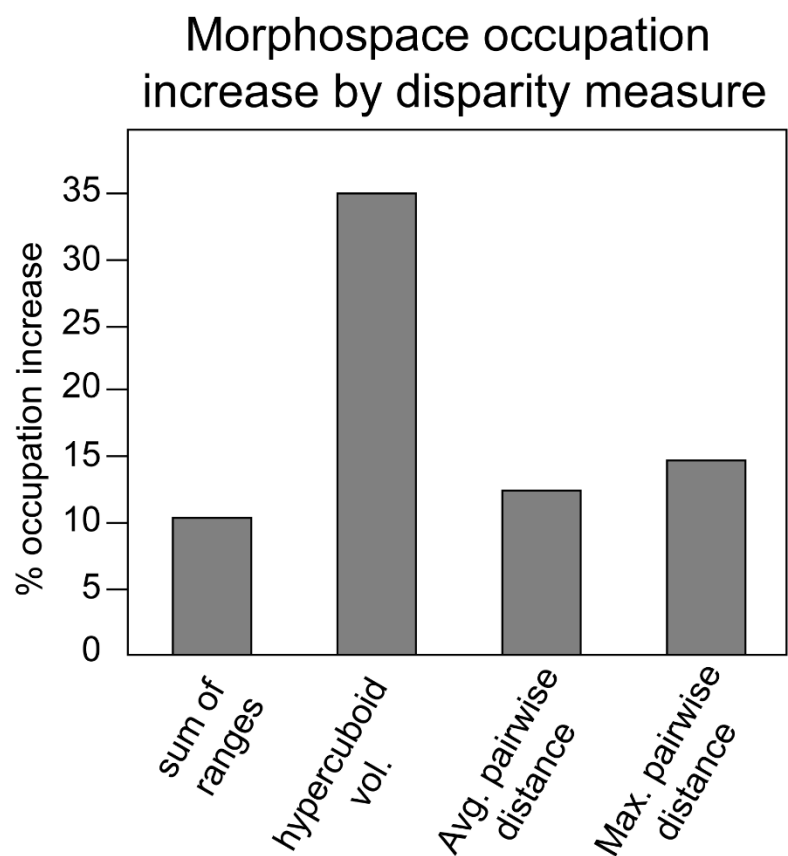


Figure 8. Morphospace occupation of Maastrichtian and Danian leaf assemblages shows significant overlap in pre- and post-K-Pg leaf assemblages in Axes 1 and 2, and higher morphological diversity in Danian assemblages in Axes 1, 2, and 3. **A.** Outliers are classified into groups I and II. Group I is characteristically lobed with toothed margins, Group II is lobed with entire margins. Morphotypes listed as part of each group are 1. SA35 2. LF64, 3. LF5, 4. SA55, 5. SA39, 6. SA19A, 7. SA19B. **B.** End members 1 and 2: 1. SA35, 2. SA50.

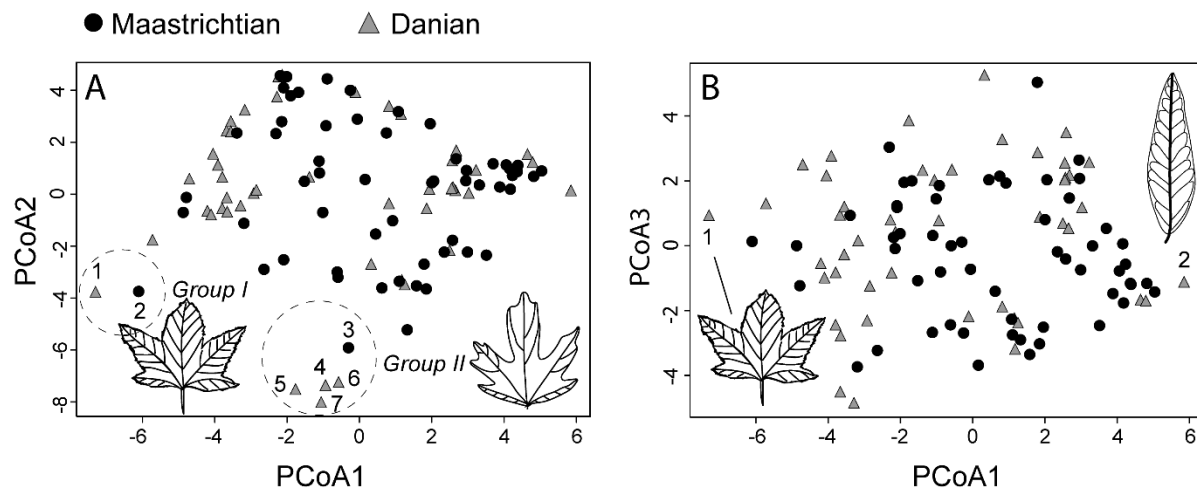


Figure 9. Morphospace occupation of Maastrichtian-Danian leaf assemblages extracted from the same assemblage-wide ordination (Fig. 8), subdivided by leaf size classes. Microphyll is the smallest size class, mesophyll is the largest. **A.** Microphyll selected end member morphotypes are 1. LEF16, 2. LEF20, 3. SA50, 4. LEF34. **B.** Notophyll examples are 1. LEF57, 2. LEF1, 3. SA63, 4. LEF5. **C.** Mesophyll selected examples are 1. SA35, 2. SA74, 3. LEF13, 4. SA73, 5. LEF7, 6. LEF26, 7. SA55.

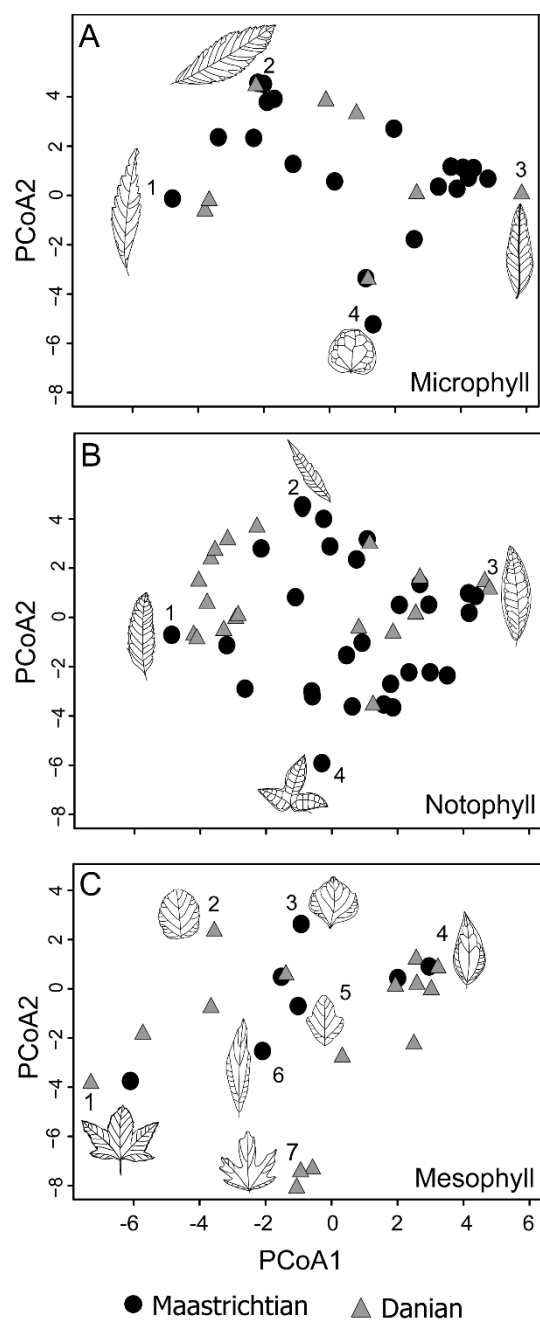


Figure 10. Scores extracted from the same assemblage-wide ordination (Fig. 8). **A.** Morphospace occupation of lobed vs. unlobed leaf morphotypes, including all Maastrichtian-Danian morphotypes. **B.** Morphospace occupation of lobed vs. unlobed leaves in Maastrichtian assemblages. Morphological endmembers are 1. LF64, 2. LF66, 3. LF46, 4. LF5. **C.** Morphospace occupation of Danian lobed vs. unlobed leaf morphotypes. Chosen examples of morphological diversity are 1. SA35, 2. SA48, 3. SA50, 4. SA39.

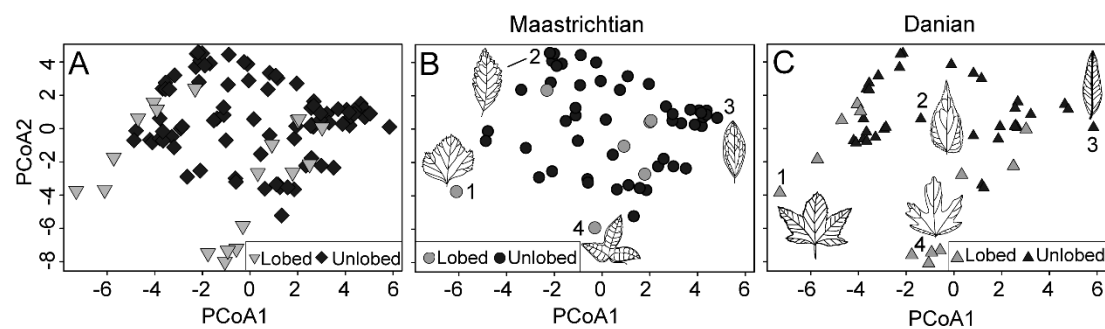


Figure 11. Scores extracted from the same assemblage-wide ordination (Fig. 8). **A.** Morphospace occupation of morphotypes with entire and toothed margins, including all Maastrichtian and Danian assemblages. **B.** Maastrichtian morphospace occupation of morphotypes with toothed and entire margins. Selected graphical examples of end members and morphotypes within the morphospace overlap are 1. LF64, 2. LF53, 3. LF7 and 4. LF46. **C.** Danian morphospace occupation of morphotypes with entire and toothed margins. Selected graphical examples of end member variations are 1. SA35 and 2. SA50.

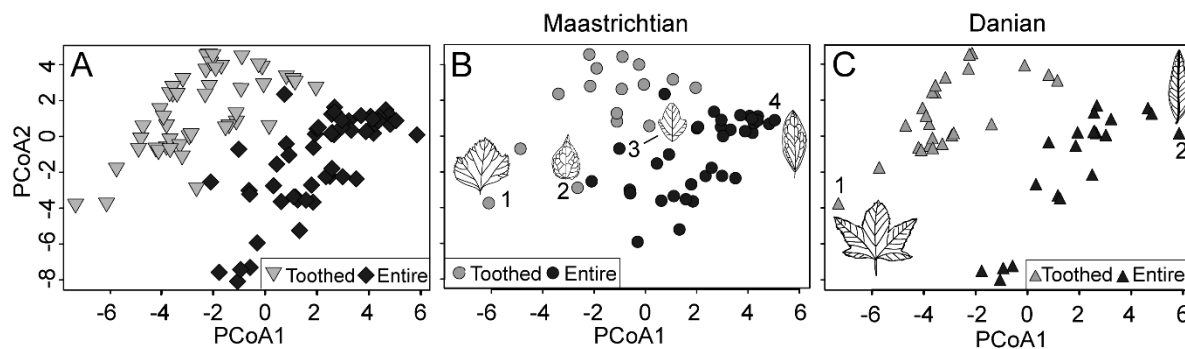


Figure 12. Cluster analysis of species-level Beals-smoothed palynological community data from the Maastrichtian-Danian Lefipán Fm (Barreda et al., 2012) and Danian Salamanca Fm. (Clyde et al., 2014). Lefipán Fm. Maastrichtian samples M1-3, Danian Samples D1-11. Salamanca Fm. samples with prefix PL or OR **A.** All species level palynomorph identifications. **B.** Gymnosperm and angiosperm pollen only. **C.** Angiosperm pollen only.

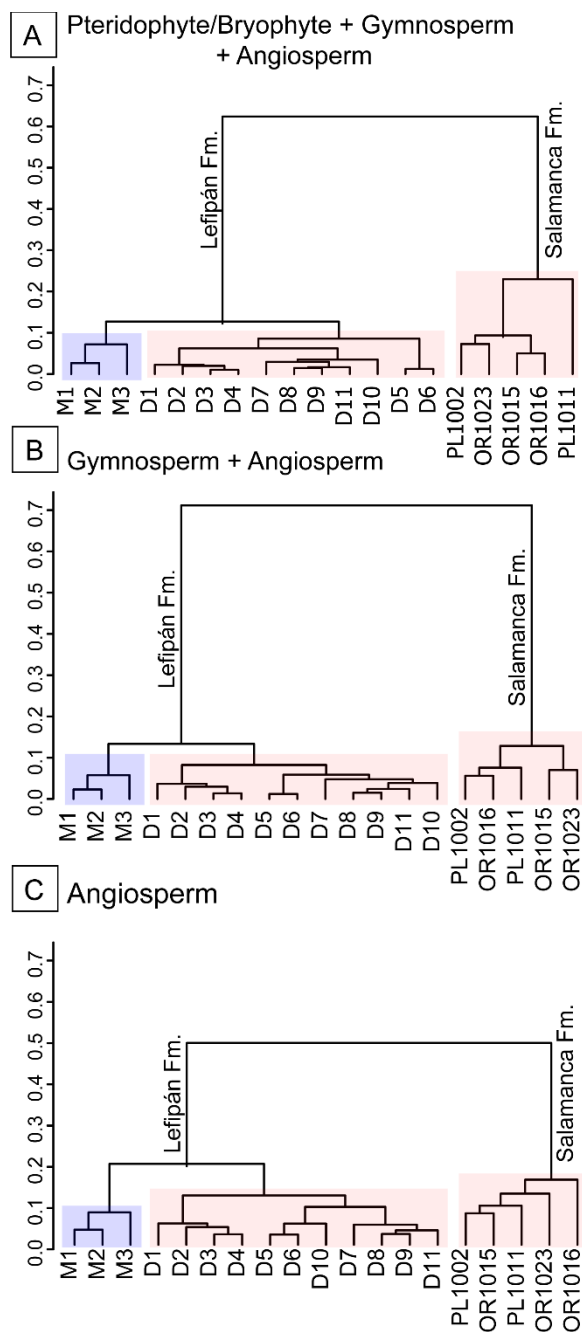


Figure 13. Percentage of boundary-spanning taxa observed in the North Dakota Hell Creek-Fort Union macrofloral localities vs. stratigraphic distance from the boundary layer based on dicot leaf morphotype counts in 10 m bins including singletons, for comparability with the present work, from Wilf and Johnson (2004). Graph shows a general trend of decreasing percentage or survivor species as the distance from boundary layer increases.

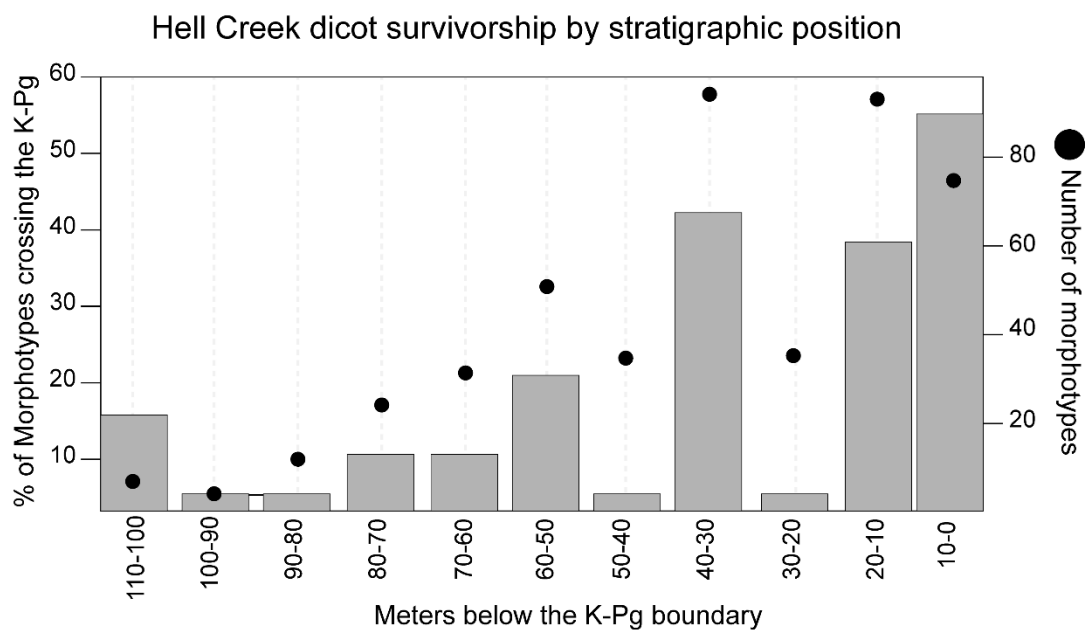


Table 1. Maastrichtian-Danian macrofloral records with recent systematics work from the Lefipán, Salamanca and Peñas Coloradas formations.

| | | Family | Species | Organs | References | |
|--|---------------|--|----------------|--|--|--|
| <i>Records from the same macrofloral localities analyzed in this study</i> | | | | | | |
| DANIAN | Salamanca Fm. | Ferns | Salviniaceae | <i>Azolla keuja</i> De Benedetti & Zamalao, <i>emend</i> Hermsen, Jud & Gandolfo | Sporophyte leaves, root fascicles, micro and megasporangia | Hermsen et al., <i>in press</i> |
| | | Gymnosperms | Araucariaceae | <i>Agathis immortalis</i> Escapa, Iglesias, Wilf, Catalano, Caraballo & Cúneo | Leaves, pollen cones, ovuliferous complexes, seeds | Escapa et al., 2018 |
| | | | Podocarpaceae | <i>Kirketapel salamanquensis</i> Andruchow-Colombo | Leafy branches | Andruchow-Colombo et al., 2019 |
| | | | | <i>Dacrycarpus</i> sp. | Leafy branches | Quiroga et al. 2015 |
| | | Angiosperms | Akaniaceae | <i>Akania</i> sp. | Leaves | Iglesias et al., 2007 |
| | | | Cunoniaceae | <i>Lacinipectalum spectabilum</i> Jud, Gandolfo, Iglesias & Wilf | Flower | Jud et al., 2018 |
| | | | Fabaceae | Morphotype SA045 | Leaves | Iglesias et al., 2007 |
| | | | Lauraceae | <i>Paracacioxylon frenguellii</i> Brea | Wood | Brea et al. 2008 |
| | | | | <i>Laurophyllum piatnitzkyi</i> Berry, <i>Laurophyllum chubutensis</i> Berry | Leaves | Iglesias et al., 2007 |
| | | | Malvaceae | “ <i>Sterculia</i> ” <i>acuminalobata</i> Berry, Morphotype SA058 | Leaves | Iglesias et al., 2007 |
| | | | Menispermaceae | <i>Stephania psittaca</i> Jud & Gandolfo | Endocarp | Iglesias et al. 2007; Jud et al., 2018 |
| | | | | <i>Wilkinsoniophyllum menispermoides</i> Jud & Gandolfo | Leaves | |
| | | | Nothofagaceae | <i>Dryophyllum australis</i> Berry | Leaves | Iglesias et al., 2007 |
| | | | Rhamnaceae | <i>Notiantha grandensis</i> Jud, Gandolfo, Iglesias & Wilf | Flowers | |
| | | <i>Suessenia grandensis</i> Jud, Gandolfo, Iglesias & Wilf | | Leaves | Jud et al., 2017 | |

| | | | | | | |
|---|----------------------------|--------------------|---|--|-----------------------|---------------------------------------|
| | | Rosaceae | Morphotype SA008 | Leaves | Iglesias et al., 2007 | |
| | | Sapindaceae | Morphotype SA043, SA052 | Leaves | Iglesias et al., 2007 | |
| | | Urticaceae | Morphotype SA051 | Leaves | Iglesias et al., 2007 | |
| MAASTRICHTI | Lefipán Fm. | Gymnosperms | Araucariaceae | cf. <i>Agathis</i> sp. | Leaves | Escapa et al., 2018 |
| | | | Podocarpaceae | <i>Retrophillum superstes</i> Wilf | Leafy branch | Wilf et al. 2017 |
| <i>Records from macrofloral localities NOT analyzed in this study</i> | | | | | | |
| DANIAN | Peñas Coloradas Fm. | | Boraginaceae | <i>Cordioxylon prototrichotoma</i> Brea & Zucol | Wood | Brea and Zucol 2006 |
| | Salamanca Fm. | Gymnosperms | Araucariaceae | <i>Dadoxylon pseudoparenchymatosum</i> Zamuner | Wood | Zamuner et al. 2000; Brea et al. 2005 |
| | | | Podocarpaceae or Cupressaceae | <i>Cupressinoxylon austrocedroides</i> Nishida <i>Cupressinoxylon artabeae</i> Ruiz | Wood | Ruiz et al., 2017 |
| | | | Podocarpaceae | <i>Podocarpoxyton multiparenchymatosum</i> Pujana & Ruiz | Wood | Ruiz et al. 2017 |
| | Angiosperms | Arecaeae | <i>Tripyllocarpa aestuaria</i> Gandolfo & Futey | Fruits | Futey et al., 2012 | |
| | | | <i>Palmoxylon patagonicum</i> Romero | Wood | Romero 1968 | |
| | | Myrtaceae | <i>Myrceugenia chubutense</i> Ragonese | Wood | Ragonese 1980 | |
| MAASTRICHTIAN | Lefipán Fm. | Gymno. | Araucariaceae | <i>Araucaria lefipanensis</i> Andruchow-Colombo, Escapa, Cúneo & Gandolfo | Leafy branch | Andruchow-Colombo et al. 2018a |
| | | Angio. | Unknown dicot | <i>Lefipania padillae</i> , Martínez | Leaves with cuticles | Martínez et al. 2018 |

Table 2. Shared palynological species among the Maastrichtian-Danian strata of the Lefipán Fm. San Ramón section and the Danian strata of the Palacio de los Loros and Bosque Ormachea collection localities. Compiled from Barreda et al. (2012) and Clyde et al. (2014).

| | Affinity | M-Lef | D-Lef | D-Sal |
|--|-----------------|--------------|--------------|--------------|
| <i>Ceratosporites equalis</i> Cookson & Dettmann 1958 | Selaginellaceae | X | x | x |
| <i>Clavifera triplex</i> (Bolkhovitina) Bolkhovitina | Gleicheniaceae | X | x | x |
| <i>Cyathidites minor</i> Couper 1953 | Unknown | X | x | x |
| <i>Cyathidites patagonicus</i> Archangelsky 1972 | Unknown | X | x | x |
| <i>Laevigatosporites ovatus</i> Wilson & Webster 1946 | Blechnaceae | X | x | x |
| <i>Retitriletes</i> <i>austrorivulites</i> (Cooks.) Dör., Kr. Mai & Schulz 1963 | Lycopodiaceae | X | x | x |
| <i>Polypodiidites speciosus</i> (Harris) Archangelsky 1972 | Polypodiaceae | | x | x |
| <i>Stereisporites</i> <i>antiquasporites</i> (Wilson & Webster) Dettmann 1963 | Sphagnaceae | x | x | x |
| <i>Trillites parvatus</i> Krutzsch 1959 | Dicksoniaceae? | | x | x |
| <i>Microcachrydites</i> <i>antarticus</i> Cookson 1947 | Podocarpaceae | x | x | x |
| <i>Phyllocladidites mawsonii</i> Cookson 1947 | Podocarpaceae | x | x | x |
| <i>Podocarpidites elegans</i> Romero 1977 | Podocarpaceae | x | x | x |
| <i>Podocarpidites rugulosus</i> Romero 1977 | Podocarpaceae | x | x | x |

| | | | | |
|--|----------------------|---|---|---|
| <i>Arecipites minutiscabratus</i> McIntyre 1968 | Arecaceae | x | x | x |
| <i>Haloragacidites harrisii</i> (Couper) Harris 1971 | Casuarinaceae | x | x | x |
| <i>Liliacidites variegatus</i> Couper 1953 | Liliaceae | x | x | x |
| <i>Liliacidites</i> <i>vermireticulatus</i> Archangelsky & Zamalao 1986 | Liliaceae | x | x | x |
| <i>Nothofagidites dorotensis</i> Romero 1973 | Nothofagaceae | | x | x |
| <i>Nothofagidites saraensis</i> Menéndez & Caccavari 1975 | Nothofagaceae | x | x | x |
| <i>Peninsulapollis gilli</i> (Cookson) Dettmann & Jarzen 1988 | Angio. Proteaceae | x | x | x |
| <i>Proteacidites sp. A</i> | Proteaceae | x | x | x |
| <i>Psilatricolporites sp.</i> | Unknown | x | x | x |
| <i>Rousea microreticulata</i> Archangelsky & Zamalao 1986 | Unknown | | x | x |
| <i>Senipites tercrassata</i> Archangelsky 1973 | Symplocaceae | x | x | x |
| <i>Triatriopollenites</i> <i>lateflexus</i> Archangelsky 1973 | Proteaceae? | x | x | x |
| <i>Tricolpites reticulatus</i> Couper 1953 | Gunneraceae | x | x | x |
| <i>Ulmoideipites patagonicus</i> Archangelsky 1973 | Ulmaceae | | x | x |

APPENDIX A.A. Number of specimens per Danian leaf morphotype after Iglesias et al., (2007). New morphotypes marked with *. Counts for the Salamanca Fm. Palacio de los Loros (PL1, PL2) and Peñas Coloradas Fm. Las Flores (LF) collections. Based on curated morphotype collections at MEF. Species after Iglesias et al., 2007.

| Leaf morphotype number | Exemplar specimen | PL1 | PL2 | LF | Species |
|------------------------|-------------------|-----|-----|-----|---|
| SA01 | MPEF-Pb-2020 | 3 | 10 | 0 | <i>Akania</i> sp. |
| SA02 | MPEF-Pb-2021 | 11 | 12 | 15 | |
| SA04 | MPEF-Pb-2022 | 40 | 21 | 87 | <i>Dryophyllum australis</i> |
| SA05 | MPEF-Pb-2023 | 12 | 10 | 4 | |
| SA08 | MPEF-Pb-2024 | 54 | 11 | 4 | |
| SA09 | MPEF-Pb-2025 | 210 | 174 | 51 | <i>Cissites patagonica</i> |
| SA10 | MPEF-Pb-2026 | 213 | 172 | 102 | <i>Laurophyllum piatnitzkyi</i> |
| SA14 | MPEF-Pb-2027 | 95 | 64 | 19 | " <i>Sterculia</i> " <i>acuminataloba</i> |
| SA16 | MPEF-Pb-2028 | 3 | 0 | 5 | |
| SA19 | MPEF-Pb-2029 | 63 | 21 | 11 | |
| SA20 | MPEF-Pb-2030 | 4 | 124 | 13 | |
| SA35 | MPEF-Pb-2031 | 12 | 20 | 7 | |
| SA39 | MPEF-Pb-2032 | 10 | 0 | 3 | <i>Paranymphea aristolochiaformis</i> |
| SA40 | MPEF-Pb-2033 | 4 | 1 | 0 | |
| SA41 | MPEF-Pb-2034 | 9 | 40 | 0 | |
| SA42 | MPEF-Pb-2035 | 25 | 4 | 21 | <i>Fagopyllum duseni</i> |
| SA43 | MPEF-Pb-3023 | 1 | 51 | 0 | |
| SA44 | MPEF-Pb-2037 | 69 | 5 | 12 | |
| SA45 | MPEF-Pb-2038 | 4 | 0 | 0 | |
| SA46 | MPEF-Pb-2039 | 56 | 7 | 0 | <i>Laurophyllum chubutensis</i> |
| SA47 | MPEF-Pb-2040 | 19 | 37 | 15 | |
| SA48 | MPEF-Pb-2041 | 105 | 5 | 18 | <i>Banaraphyllum ovatum</i> |
| SA49 | MPEF-Pb-2042 | 17 | 279 | 0 | " <i>Myrica</i> " <i>premira</i> |
| SA50 | MPEF-Pb-2043 | 0 | 8 | 0 | |
| SA51 | MPEF-Pb-2044 | 2 | 4 | 0 | |
| SA52 | MPEF-Pb-2045 | 1 | 0 | 0 | |
| SA53 | MPEF-Pb-3029 | 8 | 1 | 0 | |
| SA54 | MPEF-Pb-2046 | 0 | 10 | 0 | |
| SA55 | MPEF-Pb-2047 | 0 | 1 | 0 | |
| SA56 | MPEF-Pb-2048 | 5 | 3 | 5 | |
| SA57 | MPEF-Pb-2049 | 0 | 1 | 0 | |
| SA58 | MPEF-Pb-2050 | 2 | 9 | 1 | |
| SA59 | MPEF-Pb-2051 | 0 | 1 | 1 | |
| SA60 | MPEF-Pb-2052 | 2 | 0 | 0 | <i>Wilkinsoniphyllum menispermoides</i> Jud Jud et al., 2018 |
| SA66 | MPEF-Pb-3004 | 0 | 0 | 2 | |
| *SA68 | MPEF-Pb-3007 | 0 | 0 | 29 | |
| *SA69 | MPEF-Pb-3010 | 0 | 0 | 1 | |
| *SA70 | MPEF-Pb-3011 | 0 | 0 | 17 | |
| *SA73 | MPEF-Pb-3031 | 0 | 0 | 98 | |
| *SA74 | MPEF-Pb-3015 | 0 | 0 | 7 | |
| *SA75 | MPEF-Pb-3016 | 0 | 0 | 35 | |

| | | | | |
|-------|--------------|---|---|----|
| *SA76 | MPEF-Pb-3017 | 0 | 0 | 5 |
| *SA77 | MPEF-Pb-3018 | 0 | 0 | 10 |
| *SA78 | MPEF-Pb-3019 | 0 | 0 | 3 |

APPENDIX A.B. Maastrichtian leaf morphotypes and number of specimens per morphotype in the Lefipán Fm. LefW, LefL and LefE collections. Based on curated morphotype collections at MEF.

| Leaf Morphotype Number | Exemplar specimen | LefW | LefL | LefE |
|-------------------------------|--------------------------|-------------|-------------|-------------|
| LEF1 | MPEF-Pb-4915 | 1 | 0 | 0 |
| LEF2 | MPEF-Pb-4475 | 5 | 6 | 32 |
| LEF3 | MPEF-Pb-4916 | 1 | 1 | 0 |
| LEF4 | MPEF-Pb-4659 | 8 | 4 | 5 |
| LEF5 | MPEF-LW36 | 2 | 0 | 0 |
| LEF6 | MPEF-Pb-4662 | 1 | 1 | 2 |
| LEF7 | MPEF-Pb-4663 | 1 | 0 | 0 |
| LEF8 | MPEF-Pb-4929 | 0 | 2 | 0 |
| LEF10 | MPEF-Pb-4903 | 1 | 0 | 1 |
| LEF11 | MPEF-Pb-4880 | 1 | 0 | 4 |
| LEF12 | MPEF-Pb-4794 | 15 | 8 | 17 |
| LEF13 | MPEF-Pb-4702 | 1 | 0 | 0 |
| LEF15 | MPEF-Pb-4881 | 1 | 1 | 3 |
| LEF16 | MPEF-Pb-4389 | 4 | 1 | 3 |
| LEF17 | MPEF-Pb-4633 | 30 | 9 | 72 |
| LEF18 | MPEF-Pb-4479 | 1 | 0 | 11 |
| LEF19 | MPEF-Pb-4925 | 0 | 1 | 0 |
| LEF20 | MPEF-Pb-4266 | 11 | 10 | 42 |
| LEF21 | MPEF-Pb-4256 | 9 | 1 | 16 |
| LEF22 | MPEF-Pb-4711 | 0 | 0 | 1 |
| LEF23 | MPEF-LW10 | 1 | 2 | 0 |
| LEF24 | MPEF-Pb-4567 | 6 | 13 | 21 |
| LEF26 | MPEF-Pb-4586 | 1 | 0 | 0 |
| LEF27 | MPEF-Pb-4770 | 1 | 0 | 12 |
| LEF28 | MPEF-Pb-4603 | 2 | 1 | 0 |
| LEF29 | MPEF-Pb-4559 | 3 | 3 | 20 |
| LEF30 | MPEF-Pb-4834 | 14 | 3 | 3 |
| LEF32 | MPEF-Pb-4539 | 39 | 6 | 36 |
| LEF33 | MPEF-Pb-4519 | 0 | 2 | 4 |
| LEF34 | MPEF-Pb-4891 | 0 | 0 | 7 |
| LEF35 | MPEF-Pb-4656 | 1 | 0 | 0 |
| LEF36 | MPEF-Pb-4732 | 0 | 0 | 7 |
| LEF37 | MPEF-LW53 | 1 | 1 | 1 |
| LEF38 | MPEF-Pb-4742 | 8 | 9 | 32 |
| LEF39 | MPEF-Pb-4589 | 2 | 0 | 5 |
| LEF40 | MPEF-Pb-4849 | 1 | 0 | 6 |
| LEF41 | MPEF-Pb-4467 | 0 | 1 | 2 |

| | | | | |
|-------|--------------|----|----|-----|
| LEF42 | MPEF-Pb-4736 | 0 | 0 | 7 |
| LEF43 | MPEF-Pb-4808 | 1 | 0 | 3 |
| LEF44 | MPEF-Pb-4874 | 1 | 0 | 1 |
| LEF45 | MPEF-Pb-4898 | 1 | 3 | 1 |
| LEF46 | MPEF-Pb-4905 | 1 | 0 | 0 |
| LEF47 | MPEF-Pb-4932 | 0 | 0 | 3 |
| LEF48 | MPEF-Pb-4852 | 0 | 0 | 1 |
| LEF49 | MPEF-Pb-4928 | 0 | 0 | 1 |
| LEF50 | MPEF-Pb-4771 | 0 | 0 | 4 |
| LEF51 | MPEF-Pb-4751 | 1 | 2 | 2 |
| LEF52 | MPEF-Pb-4672 | 1 | 0 | 5 |
| LEF53 | MPEF-Pb-4920 | 2 | 2 | 0 |
| LEF54 | MPEF-Pb-4525 | 5 | 0 | 1 |
| LEF55 | MPEF-Pb-4835 | 4 | 1 | 5 |
| LEF56 | MPEF-Pb-4617 | 2 | 0 | 10 |
| LEF57 | MPEF-Pb-4112 | 38 | 20 | 103 |
| LEF58 | MPEF-Pb-4227 | 16 | 25 | 58 |
| LEF60 | MPEF-Pb-4717 | 1 | 0 | 1 |
| LEF61 | MPEF-Pb-4316 | 4 | 0 | 0 |
| LEF63 | MPEF-Pb-4917 | 1 | 8 | 0 |
| LEF64 | MPEF-Pb-4887 | 1 | 0 | 1 |
| LEF66 | MPEF-Pb-4802 | 1 | 0 | 3 |
| LEF67 | MPEF-Pb-4908 | 0 | 2 | 0 |

APPENDIX B. Characters coded for morphospace analysis, based on definitions of the Manual of Leaf Architecture (Ellis et al. 2009).

| | | | |
|----|---------------------------------|--------------------------|---|
| 1 | Blade characters | Size | Leptophyll:0; Nanophyll: 1; Microphyll: 2; Notophyll: 3; Mesophyll: 4; Macrophyll: 5; Megaphyll: 6 |
| 2 | | Margin | Entire: 0; Toothed dentate:1; Toothed serrate: 2; Toothed crenate: 3 |
| 3 | | Petiole insertion | Marginal: 0; Peltate excentric: 2 |
| 4 | | Shape | Elliptic: 0; Obovate: 1; Ovate: 2; Oblong: 3; Linear: 4 |
| 5 | | Medial symmetry | Symmetrical: 0; Asymmetrical: 1 |
| 6 | | Base symmetry | Symmetrical: 0; Asymmetrical: 1 |
| 7 | | Lobation | Unlobed: 0; Palmately lobed: 1; Pinnately lobed: 2; Mixed: 3 |
| 8 | | Max number of lobes | NA: 0; 1; 2; 3; |
| 9 | | Apex shape | Straight: 1; Convex rounded: 2; Convex truncate: 3; Acuminate: 4; Emarginate: 5; Lobed: 6 |
| 10 | | Apex angle | Acute: 0; Obtuse: 1 |
| 11 | | Base shape | Straight: 0; Concave: 1; Convex rounded: 2; Convex truncated: 3; Concavo-convex: 4; Complex: 5; Decurrent: 6; Cordate: 7; Lobate sagittate: 8 |
| 12 | | Base angle | Acute: 0; Obtuse: 1; Reflex: 2; Circular: 3 |
| 13 | Primary vein | Primary vein | Pinnate: 0; palmate actinodromous basal: 1; Palmate actinodromous suprabasal: 2; Palinactinodromous: 3; Acrodromous basal:4; Acrodromous suprabasal: 5 |
| 14 | | Number of basal veins | 0; 1; 2; 3; 4; 5; 6; 7; 8; 9; 10 |
| 15 | Agroptic veins | Agroptic veins | Absent: 0; Simple: 1; Compound: 2; May be both: 3 |
| 16 | Secondary vein framework | Secondary vein framework | Craspedodromous: 0; Semicraspedodromous: 1; Festooned seimcraspedodromous: 2; Eucamprodromous: 3; Simple brochidodromous: 4; Festooned brochidodromous: 5; Mixed: 6; Reticulodromous: 7 |
| 17 | | Major secondary spacing | Regular: 0; Irregular: 1; Decreasing proximally: 2; Gradually increasing proximally: 3; Abruptly increasing proximally: 4 |
| 18 | | Perimarginal veins | Absent: 0; Marginal: 1; Intramarginal: 2; |
| 19 | Intersecondary veins | Occurrence | Absence: 0; Presence: 1 |
| 20 | | Percurrent | NA: 0; Opposite: 1; Alternate: 2; Mixed: 3 |

| | | | |
|-------|---|--------------------------------------|--|
| 21 | Intercostal Tertiary Vein Fabric | Angle of percurrent tertiaries | NA: 0; Acute: 1; Obtuse: 2; Perpendicular: 3 |
| 22 | | Reticulate | NA: 0; Irregular: 1; Regular: 2; Composite admedial: 3 |
| 23 | | Ramified | NA: 0; Admedially ramified: 1; Exmedially ramified: 2; Transversely ramified: 3; Transversely freely ramified: 4 |
| 24 | Epimedial Tertiaries | Epimedial tertiary fabric | Opposite percurrent: 0; Alternate percurrent: 1; Mixed percurrent: 2; Ramified: 3; Reticulate: 4; Mixed: 5 |
| 25 | Tooth characters | Tooth spacing | NA: 0; Regular: 1; Irregular: 2 |
| 26 | | Number of orders of teeth | NA: 0; 1; 2; 3 |
| 27 | | Number of teeth per cm | NA:0 |
| 28 | | Sinus shape | NA: 0; Angular: 1; Rounded: 2 |
| 29-44 | | Tooth shapes (Absence:0; Presence:1) | cc/cv, cc/cc, cc/st, cc/fl, cv/cc, cv/cv, cv/st, cv/fl, st/fl, st/cv, st/st, st/cc, fl/st, fl/cv, fl/cc, fl/fl |
| 45 | | Principal vein in tooth | NA: 0; Present: 1; Absent: 2 |
| 46 | | Tooth type | NA: 0; Simple: 1; Glandular: 2; Spinose: 3 |

APPENDIX C. Coded character matrix for all Danian (prefix SA-) and Maastrichtian (prefix LEF-) morphotypes based on the character matrix in Appendix B.

| | C1 | C2 | C3 | C4 | C5 | C6 | C7 | C8 | C9 | C10 | C11 | C12 | C13 | C14 | C15 | C16 | C17 | C18 | C19 | C20 | C21 | C22 | C23 | C24 | C25 | C26 | C27 | C28 | C29 | C30 | C31 | C32 | C33 | C34 | C35 | C36 | C37 | C38 | C39 | C40 | C41 | C42 | C43 | C44 | C45 | C46 | | |
|--------|----|----|----|----|----|----|----|----|----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|---|
| SA1 | 3 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 6 | 0 | 0 | 3 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 5 | 2 | 1 | 3 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | | |
| SA2 | 3 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 4 | 0 | 6 | 0 | 0 | 3 | 2 | 0 | 1 | 2 | 0 | 1 | 3 | 0 | 0 | 0 | 1 | 1 | 2 | 2 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | | |
| SA4 | 3 | 3 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 3 | 2 | 0 | 0 | 2 | 1 | 4 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | | |
| SA5 | 3 | 2 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | 6 | 0 | 0 | 3 | 0 | 1 | 1 | 0 | 1 | 3 | 2 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | | |
| SA8 | 3 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 2 | 2 | 3 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | | |
| SA9A | 3 | 2 | 0 | 2 | 0 | 0 | 1 | 3 | 1 | 0 | 2 | 1 | 1 | 5 | 1 | 0 | 0 | 0 | 0 | 3 | 2 | 0 | 0 | 2 | 1 | 2 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 3 | | | |
| SA9B | 3 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 5 | 1 | 0 | 0 | 0 | 0 | 3 | 2 | 0 | 0 | 2 | 1 | 2 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 3 | | | |
| SA10A | 3 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 4 | 0 | 1 | 1 | 1 | 3 | 1 | 4 | 4 | 0 | 1 | 3 | 3 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| SA10B | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 4 | 1 | 1 | 1 | 3 | 3 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| SA014A | 4 | 0 | 2 | 2 | 0 | 0 | 1 | 5 | 0 | 0 | 2 | 3 | 1 | 5 | 0 | 4 | 0 | 2 | 1 | 3 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| SA014B | 4 | 0 | 0 | 2 | 0 | 0 | 1 | 5 | Na | Na | 2 | 1 | 2 | 3 | 0 | 4 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SA16 | 3 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 4 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SA19A | 4 | 0 | 0 | 1 | 0 | 0 | 1 | 4 | 1 | 0 | 7 | 2 | 1 | 7 | 1 | 6 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SA19B | 4 | 0 | 0 | 1 | 1 | 0 | 1 | 5 | 1 | 0 | 8 | 2 | 1 | 6 | 0 | 6 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SA20 | 3 | 2 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | 5 | 0 | 0 | 3 | 0 | 0 | 1 | 1 | 1 | 2 | 2 | 0 | 0 | 5 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | |
| SA35 | 4 | 2 | 0 | 2 | 0 | 0 | 1 | 5 | 1 | 0 | 8 | 2 | 1 | 5 | 2 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 1 | 1 | 2 | 4 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | |
| SA39 | 5 | 0 | 0 | 2 | 0 | 0 | 1 | 5 | 2 | 0 | 7 | 2 | 1 | 9 | 0 | 4 | 1 | 0 | 0 | 3 | 3 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| SA41 | 4 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 1 | 0 | 1 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SA42 | 2 | 3 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 6 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | Na | Na | Na | Na | Na | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | | |
| SA43 | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 5 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 3 | | |
| SA44 | 3 | 2 | 0 | 2 | 0 | 1 | 0 | 0 | Na | 0 | 5 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 1 | 2 | 2 | 0 | 0 | 2 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | | |

APPENDIX D. Detailed leaf architectural descriptions of Maastrichtian-Danian survivor pairs.

LF6-SA019

Reference specimens for LF6: MPEF-Pb-4662ab, MPEF-Pb-4761, MPEF-Pb-4660

Reference specimens for SA019: PL2 1245ab, PL1 527

Description: Blade size generally mesophyll, outline shape ovate to elliptic, medially and basally symmetrical. Margin entire. Petiole insertion marginal. Blades have a variable number of lobes, may be 3-5 lobed. Transitional forms between 3- and 5-lobed forms develop small lobules in proximal lobes that may incise deep enough to become small accessory lobes. Lobes may be simple or compound. Base shape may be rounded or concavo-convex, angle obtuse. Lobe apices with acute angles may be straight or slightly acuminate. Primary venation suprabasal actinodromous, primaries straight, 3-5 basal veins, most proximal primaries thinner. Secondary venation with excurrent attachment to primaries, proximally eucamptodromous transitions into brochidodromous in distal half of lobes. Agrophic veins simple. Intramarginal vein runs along the entire margin. Epimedial tertiary venation mixed percurrent, intercostal tertiary venation alternate percurrent. Fourth order venation weak, random reticulate.

LF18-SA008

Reference specimens for LF18: MPEF-Pb-4482, MPEF-Pb-4479, MPEF-Pb-4487

Reference specimens for SA008: PL1 587 +588, PL2 1029, MPEF-Pb-4030

Description: Danian blades range in size from microphyll to notophyll, but Maastrichtian forms are consistently microphyll in size. Here, only microphyll sized blades found in both Maastrichtian and Danian assemblages are described. Blades are ovate, medially and basally symmetrical. Petiole insertion marginal. Base shape straight to convex, obtuse. Apex shape rounded, acute. Pinnately lobed, lobes cv/cv with angular sinuses, proximal lobes compound with up to three orders, lobe complexity decreases distally until lobes become simple near blade apex. Lobe apices glandular. Primary venation pinnate, primary vein straight. One very thick primary divides suprabasally into a primary and two thickened basal secondaries. Agrophic veins simple if present, marginal vein present along entire blade margin. Secondaries straight, subopposite, craspedodromous, branching at lobe base where proximal branch continues straight and terminates at lobe

apex, distal branch curves and innerves supradjacent sinus where it branches again innerving margins. One secondary per lobe. Epimedial tertiary venation opposite percurrent, intercostal tertiary venation mixed percurrent. Higher order venation not preserved.

LF55 - SA078

Reference specimens for LF55: MPEF-Pb-4835ab, MPEF-Pb-4866, MPEF-Pb-4870ab,

Reference specimens for SA078: MPEF-Pb-3019

Description: Blade simple, size notophyll to mesophyll with entire margins. Ovate shape, basally and medially symmetrical. Marginal petiole insertion. Base shape concave, obtuse. Apex rounded, acute. Primary venation pinnate. Agrophic veins simple, thin marginal vein runs along entire margin. One basal vein. Secondary venation brochidodromous, secondaries opposite to subopposite, spacing gradually decreases apically but first two basal pairs may be irregularly spaced. Up to two, but generally one intersecondary vein per secondary vein. Epimedial tertiary venation mixed percurrent, intercostal tertiaries mixed alternate percurrent and random reticulate. Fourth order venation mixed alternate percurrent-random reticulate. Fifth order venation reticulate.

LF64 – SA035

Reference specimens for LF64: LW17, LL5ab, MPEF-Pb-4889ab

Reference specimens for SA035: MPEF-Pb-3007ab, MPEF-Pb-2031ab

Description: Blade sizes mesophyll to macrophyll, outline shape ovate, medially and basally symmetrical. Blades have a variable number of lobes, ranging from 3-5 lobes. In 3 lobed leaves, lobules are present. In 5-lobed leaves lobules have become incised enough to become smaller accessory lobes at the base of the leaf giving it a lobate base. Base shape may be lobate, truncate or rounded, with obtuse or reflex angles. Apex not preserved in any Maastrichtian specimens but in Danian specimens they are straight and acute. Petiole insertion marginal, petiole seems winged. Agrophic veins compound. Margin serrate. Primary venation basal actinodromous with generally 5 basal veins, proximal secondaries generally thinner. Secondary venation

craspedodromous, opposite to subopposite with excurrent attachment to midvein, terminating in spinose teeth along the margin. Epimedial tertiaries alternate percurrent, intercostal tertiaries mixed alternate-opposite percurrent. Teeth may be simple or compound, up to three orders of teeth. First order teeth are spinose, small, 1 compound tooth per cm. Teeth are hook shaped cc/cv, poorly developed at the base of the blade.

LF57 – SA020

Reference specimens for LF57: MPEF-Pb-4397ab, MPEF-Pb-4416

Reference specimens for SA020: MPEF-Pb-4019, PL2 182, MPEF-Pb-4021, PL2 2395

Description: Blades simple of notophyll size, shape ranges from narrow elliptic to ovate. Serrate margin. May be medially asymmetrical, bases are generally asymmetrical. Petiole insertion marginal. Base shape decurrent, acute. Apex straight to acuminate, acute. Primary venation pinnate, with a thick and straight primary vein. Agrophic veins absent, fimbrial vein running along entire margin present. Secondary venation craspedodromous to semicraspedodromous, opposite to subopposite secondaries with excurrent attachment to midvein terminate in tooth apices or may form weak loops from where a branch emerges and terminates in the tooth. Spacing does not increase or decrease proximally or apically. Epimedial and intercostal tertiary venation mixed percurrent. Fourth and fifth order venation random reticulate. Tooth shape and spacing very variable and may be asymmetric even within the same blade. In some cases, one side of the margin may be serrated while the other side has very sparse teeth. Teeth are small, glandular, ranging in shape from hook shaped to small and triangular, shapes may be cc/cv, st/st, cc/st, cv/cv. Teeth are separated by elongate rounded sinuses that run almost parallel to the midvein.

APPENDIX E.A. Reviewed Lefipán Fm.
specimens curated at the MEF.

| Locality | Field Number | Specimen Number MPEF-Pb | LEF morphotype |
|----------|--------------|-------------------------|----------------|
| LefW | | 4915 | 1 |
| LefW | | 4474 | 2 |
| LefW | | 4472ab | 2 |
| LefW | | 4473 | 2 |
| LefW | LW15 | | 2 |
| LefW | LW137 | | 2 |
| LefW | | 4389 | 4 |
| LefW | | 4906 | 4 |
| LefW | | 3190 | 4 |
| LefW | LW36AB | | 5 |
| LefW | LW87A-C | | 4 |
| LefW | LW102 | | 5 |
| LefW | LW107 | | 4 |
| LefW | LW132 | | 4 |
| LefW | LW88 | | 7 |
| LefW | LW11 | | 6 |
| LefW | | 4903 | 10 |
| LefW | LW68AB | | 9 |
| LefW | LW92AB | | 11 |
| LefW | LW93 | | 43 |
| LefW | | 4913 | 55 |
| LefW | LW111 | | 58 |
| LefW | LW121 | | 58 |
| LefW | | 4623 a-d | 12 |
| LefW | | 4624ab | 12 |
| LefW | | 4625 | 12 |
| LefW | | 4626 | 12 |
| LefW | | 4627 | 12 |
| LefW | | 4797 | 12 |
| LefW | | 4798 | 12 |
| LefW | | 4841ab | 12 |
| LefW | | 4860 | 12 |
| LefW | LW22 | | 12 |
| LefW | LW38ab | | 64 |
| LefW | LW39 | | 12 |
| LefW | LW42 | | 12 |
| LefW | LW46a-c | | 12 |
| LefW | LW62 | | 12 |
| LefW | LW70 | | 12 |
| LefW | LW72 | | 4 |
| LefW | | 4914 | 66 |
| LefW | LW13 | | 18 |
| LefW | LW50ab | | 58 |
| LefW | LW123 | | 13 |
| LefW | | 4651ab | 17 |
| LefW | | 4712 | 17 |
| LefW | | 4713 | 17 |
| LefW | | 4714 | 17 |
| LefW | | 4715 | 17 |

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|------|---------|--------|----|
| LefW | | 4716 | 17 |
| LefW | | 4718ab | 17 |
| LefW | | 4719 | 17 |
| LefW | | 4720 | 17 |
| LefW | | 4721 | 17 |
| LefW | LW5 | | 17 |
| LefW | LW14 | | 17 |
| LefW | LW26ab | | 17 |
| LefW | LW31ab | | 17 |
| LefW | LW34ab | | 17 |
| LefW | LW35ab | | 17 |
| LefW | LW41ab | | 37 |
| LefW | LW52 | | 17 |
| LefW | LW55ab | | 17 |
| LefW | LW65ab | | 17 |
| LefW | LW83 | | 17 |
| LefW | LW90 | | 17 |
| LefW | LW98 | | 17 |
| LefW | LW118 | | 17 |
| LefW | LW125 | | 17 |
| LefW | LW128ab | | 17 |
| LefW | LW129 | | 17 |
| LefW | LW95 | | 17 |
| LefW | LW104 | | 17 |
| LefW | LW105 | | 17 |
| LefW | | 4290ab | 20 |
| LefW | | 4291ab | 21 |
| LefW | | 4292ab | 21 |
| LefW | | 4293 | 21 |
| LefW | | 4294 | 21 |
| LefW | | 4295 | 20 |
| LefW | | 4298 | 21 |
| LefW | | 4299 | 21 |
| LefW | | 4301 | 20 |
| LefW | | 4302 | 21 |
| LefW | | 3189 | 20 |
| LefW | | 4288ab | 21 |
| LefW | | 4805 | 20 |
| LefW | LW110 | | 21 |
| LefW | LW126 | | 20 |
| LefW | LW27 | | 16 |
| LefW | | 3193 | 55 |
| LefW | | 4542 | 32 |
| LefW | | 4558 | 24 |
| LefW | | 4559 | 32 |
| LefW | LW30 | | 32 |
| LefW | LW53ab | | 4 |
| LefW | | 3188 | 31 |
| LefW | LW16 | | 31 |
| LefW | | 4931ab | 46 |
| LefW | | 4749 | 27 |
| LefW | LW21 | | 63 |
| LefW | LW97ab | | 27 |
| LefW | | 4545 | 24 |
| LefW | | 4547 | 32 |

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|------|--------|-----------------|----|
| LefW | LW66ab | | 32 |
| LefW | | 4621ab =4535 | 26 |
| LefW | | 4622 | 39 |
| LefW | | 4619ab | 39 |
| LefW | LW61ab | | 30 |
| LefW | LW75ab | | 55 |
| LefW | LW79ab | | 30 |
| LefW | LW80ab | | 30 |
| LefW | LW86 | | 30 |
| LefW | LW1 | | 30 |
| LefW | LW23 | | 30 |
| LefW | LW43 | | 30 |
| LefW | LW44 | | 30 |
| LefW | | 4901ab | 31 |
| LefW | | 4902 | 31 |
| LefW | | 4851 | 38 |
| LefW | | 4656ab | 53 |
| LefW | | 4904ab | 35 |
| LefW | LW85 | | 53 |
| LefW | | 4907 | 56 |
| LefW | LW3 | | 30 |
| LefW | | 4776ab | 15 |
| LefW | LW10 | | 38 |
| LefW | LW6 | | 38 |
| LefW | | 4552 | 54 |
| LefW | LW2-2 | | 54 |
| LefW | LW28 | | 54 |
| LefW | LW49ab | | 54 |
| LefW | LW54ab | | 24 |
| LefW | | 4748ab | 38 |
| LefW | LW19 | | 38 |
| LefW | LW67 | | 38 |
| LefW | | 4539 | 24 |
| LefW | | 4620 | 24 |
| LefW | LW71 | | 3 |
| LefW | | 4875 | 44 |
| LefW | LW4 | | 30 |
| LefW | LW9 | | 30 |
| LefW | LW24 | | 30 |
| LefW | LW74 | | 30 |
| LefW | LW76 | | 32 |
| LefW | LW120 | | 30 |
| LefW | | 4527ab | 40 |
| LefW | | 4905 | 46 |
| LefW | LW18 | | 46 |
| LefW | | 3194ab | 54 |
| LefW | LW45ab | | 51 |
| LefW | LW12 | | 32 |
| LefW | LW29 | | 32 |
| LefW | LW37ab | | 32 |
| LefW | LW59ab | | 32 |
| LefW | LW64ab | | 32 |
| LefW | LW69 | | 32 |
| LefW | LW73 | | 32 |
| LefW | LW82ab | | 32 |

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|------|--------|--------|----|
| LefW | LW84ab | | 32 |
| LefW | LW94ab | | 32 |
| LefW | LW103 | | 32 |
| LefW | LW133 | | 32 |
| LefW | | 4526ab | 32 |
| LefW | | 4528ab | 32 |
| LefW | | 4529ab | 32 |
| LefW | | 4530 | 32 |
| LefW | | 4531ab | 32 |
| LefW | | 4532ab | 32 |
| LefW | | 4533 | 32 |
| LefW | | 4536ab | 32 |
| LefW | | 4538 | 32 |
| LefW | | 4541 | 32 |
| LefW | | 4543 | 32 |
| LefW | | 4544 | 32 |
| LefW | | 4546 | 32 |
| LefW | | 4548 | 32 |
| LefW | | 4550 | 32 |
| LefW | | 4551 | 32 |
| LefW | | 4553 | 32 |
| LefW | | 4554 | 32 |
| LefW | | 4556 | 32 |
| LefW | | 4557 | 32 |
| LefW | | 4560 | 32 |
| LefW | LW58 | | 57 |
| LefW | | 4433ab | 57 |
| LefW | | 4379ab | 57 |
| LefW | | 4380 | 57 |
| LefW | | 4381ab | 57 |
| LefW | | 4387 | 57 |
| LefW | | 4549 | 57 |
| LefW | | 4806 | 57 |
| LefW | Lw48ab | | 57 |
| LefW | LW78 | | 57 |
| LefW | LW96 | | 57 |
| LefW | LW99 | | 57 |
| LefW | LW100 | | 57 |
| LefW | LW114 | | 57 |
| LefW | LW115 | | 57 |
| LefW | | 3192ab | 57 |
| LefW | | 4391 | 57 |
| LefW | | 4394ab | 57 |
| LefW | | 4395 | 57 |
| LefW | | 4396 | 57 |
| LefW | | 4398 | 57 |
| LefW | | 4399 | 57 |
| LefW | | 4400 | 57 |
| LefW | | 4804 | 57 |
| LefW | LW25ab | | 57 |
| LefW | LW32 | | 57 |
| LefW | LW47ab | | 57 |
| LefW | LW106 | | 57 |
| LefW | LW51 | | 24 |
| LefW | LW81 | | 38 |

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|------|---------|----------|----|
| LefW | LW124 | | 38 |
| LefW | LW33 | | 55 |
| LefW | LW117 | | 56 |
| LefW | | 4390 A | 58 |
| LefW | | 4232 | 58 |
| LefW | | 4235 | 20 |
| LefW | | 4233 | 58 |
| LefW | | 4234 | 58 |
| LefW | | 4236 | 58 |
| LefW | | 4238 | 58 |
| LefW | | 4245 | 58 |
| LefW | | 4297 | 20 |
| LefW | | 4289ab | 20 |
| LefW | | 4540 | 58 |
| LefW | | 4229a-c | 58 |
| LefW | | 4230ab | 58 |
| LefW | | 4231ab | 58 |
| LefW | | 4237 | 58 |
| LefW | | 3191 | 17 |
| LefW | | 4382 | 57 |
| LefW | | 4383 | 57 |
| LefW | | 4384 | 57 |
| LefW | | 4385 | 57 |
| LefW | | 4386 | 57 |
| LefW | LW122 | | 57 |
| LefW | LW89 | | 57 |
| LefW | LW108 | | 57 |
| LefW | LW116 | | 57 |
| LefW | LW119 | | 57 |
| LefW | LW131 | | 57 |
| LefW | LW134 | | 58 |
| LefW | | 4717ab | 60 |
| LefW | | 4378 | 16 |
| LefW | | 4389 | 16 |
| LefW | | 4391ab | 61 |
| LefW | | 4392ab | 61 |
| LefW | | 4397 | 61 |
| LefW | | 4803ab | 45 |
| LefW | LW40a-c | | 61 |
| LefW | LW112ab | | 20 |
| LefW | LW113ab | | 52 |
| LefW | LW127ab | | 16 |
| LefW | LW130ab | | 20 |
| LefW | | 4790 | 23 |
| LefE | | 4446 | 2 |
| LefE | | 4452 | 2 |
| LefE | | 4457 | 2 |
| LefE | | 4445 a-b | 2 |
| LefE | | 4448 a-b | 2 |
| LefE | | 4447 a-b | 2 |
| LefE | | 4450 a-b | 2 |
| LefE | | 4461 | 2 |
| LefE | | 4458 | 2 |
| LefE | | 4453 | 2 |
| LefE | | 4460 | 2 |

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|------|-----------------|----------|----|
| LefE | | 4455 | 2 |
| LefE | | 4454 | 2 |
| LefE | | 4449 a-b | 2 |
| LefE | | 4451 a-b | 2 |
| LefE | | 4459 | 2 |
| LefE | | 4456 | 2 |
| LefE | | 4462 | 2 |
| LefE | | 4495 a-b | 2 |
| LefE | | 4658 | 2 |
| LefE | | 4464 a-b | 2 |
| LefE | | 4468 | 2 |
| LefE | | 4469 | 2 |
| LefE | | 4822 | 2 |
| LefE | MD 148 a-b | | 2 |
| LefE | MD 144 a-b | | 2 |
| LefE | MD 145 a-b | | 2 |
| LefE | MD 147 | | 2 |
| LefE | MD 146 | | 2 |
| LefE | MD 149 | | 2 |
| LefE | | 4756 a-b | 4 |
| LefE | | 4757 | 4 |
| LefE | | 4659 | 4 |
| LefE | | 4657 | 4 |
| LefE | MD 131 | | 4 |
| LefE | | 4660 | 6 |
| LefE | | 4761 | 6 |
| LefE | | 4880 | 11 |
| LefE | | 4882 a-b | 11 |
| LefE | | 4611 | 12 |
| LefE | | 4608 | 37 |
| LefE | | 4607 | 12 |
| LefE | | 4612 | 12 |
| LefE | | 4606 a-b | 12 |
| LefE | | 4791 | 12 |
| LefE | | 4796 | 12 |
| LefE | | 4792 | 12 |
| LefE | | 4793 | 12 |
| LefE | | 4840 a-b | 56 |
| LefE | PLE-LF1 58 a-b | | 12 |
| LefE | MD 106 - MD 107 | | 12 |
| LefE | MD 108 | | 12 |
| LefE | | 4683 | 57 |
| LefE | | 4702 | 12 |
| LefE | | 4831 | 13 |
| LefE | | 4830 a-b | 13 |
| LefE | | 4876 | 13 |
| LefE | | 4832 | 32 |
| LefE | | 4877 | 12 |
| LefE | | 4878 | 12 |
| LefE | MD 100 | | 17 |
| LefE | MD49 | | 16 |

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|------|-----------------|----------|----|
| LefE | MD 105 | | 12 |
| LefE | | 4881 a-b | 15 |
| LefE | | 4313 a-b | 66 |
| LefE | | 4853 | 16 |
| LefE | | 4316 | 20 |
| LefE | | 4488 | 16 |
| LefE | | 4671 a-b | 17 |
| LefE | | 4814a-b | 25 |
| LefE | | 4628 a-b | 17 |
| LefE | | 4632 a-b | 17 |
| LefE | | 4645 | 17 |
| LefE | | 4649 | 17 |
| LefE | | 4646 | 17 |
| LefE | | 4647 | 17 |
| LefE | | 4633 a-b | 17 |
| LefE | | 4644 | 17 |
| LefE | | 4635 | 17 |
| LefE | | 4636 | 17 |
| LefE | | 4630 a-b | 17 |
| LefE | | 4629 a-b | 17 |
| LefE | | 4638 | 17 |
| LefE | | 4637 | 17 |
| LefE | | 4643 | 17 |
| LefE | | 4640 | 17 |
| LefE | | 4634 | 17 |
| LefE | | 4642 | 17 |
| LefE | | 4641 | 17 |
| LefE | | 4639 | 17 |
| LefE | PLE - LF15 4 | | 17 |
| LefE | | 4605 a-b | 36 |
| LefE | | 4708 | 17 |
| LefE | | 4710 | 17 |
| LefE | | 4709 | 17 |
| LefE | | 4707 | 17 |
| LefE | | 4705 | 17 |
| LefE | | 4703 a-b | 17 |
| LefE | | 4677 | 17 |
| LefE | | 4698 | 17 |
| LefE | | 4686 | 17 |
| LefE | | 4700 | 17 |
| LefE | | 4696 | 17 |
| LefE | | 4673 | 17 |
| LefE | | 4668 a-b | 17 |
| LefE | | 4672 a-b | 17 |
| LefE | | 4667 a-b | 17 |
| LefE | | 4681 | 17 |
| LefE | | 4760 a-b | 17 |
| LefE | | 4666 a-b | 17 |
| LefE | | 4669 a-b | 17 |
| LefE | | 4690 | 17 |
| LefE | | 4694 | 17 |
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| LefE | | 4701 | 17 |
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| LefE | | 4286 | 20 |
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| LefE | | 4257 a-b | 21 |
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| LefL | | 4754ab | 4 |
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| LefL | | 4663ab | 8 |
| LefL | | 4929 | 8 |
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| LefL | | 4758ab | 12 |
| LefL | | 4799 | 12 |
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| LefL | LL22ab | | 12 |
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| LefL | LL54 | | 20 |
| LefL | LL55ab | | 20 |
| LefL | LL17 | | 20 |
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| LefL | | 4246 | 58 |
| LefL | | 4242 | 58 |
| LefL | | 4253 | 58 |
| LefL | | 4244 | 58 |
| LefL | | 4241 | 58 |
| LefL | | 4252 | 58 |
| LefL | | 4249 | 58 |
| LefL | | 4239 | 58 |
| LefL | | 4909 | 58 |
| LefL | LL41 | | 58 |
| LefL | LL44 | | 58 |
| LefL | LL61 | | 58 |
| LefL | LL15 | | 58 |
| LefL | LL16 | | 58 |
| LefL | LL20 | | 58 |
| LefL | LL25 | | 58 |
| LefL | LL32ab | | 58 |
| LefL | | 4917 | 63 |
| LefL | | 4918 | 63 |
| LefL | | 4563ab | 63 |
| LefL | | 4924 | 63 |
| LefL | LL6ab | | 17 |
| LefL | | 4437ab | 57 |
| LefL | | 4726 | 57 |

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|------|------|--------|----|
| LefL | | 4388 | 57 |
| LefL | LL26 | | 57 |
| LefL | | 4401ab | 16 |
| LefL | | 4912 | 57 |
| LefL | | 4930 | 57 |

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|------|--|--------|----|
| LefL | | 4568 | 23 |
| LefL | | 4889ab | 47 |

APPENDIX E.B. Reviewed Salamanca Fm. specimens curated at MEF.

| Locality | Field Number | Specimen Number MPEF-Pb | Leaf Morphotype Number |
|----------|--------------|-------------------------|------------------------|
| PL1 | 1 | | SA14 |
| PL1 | 2 | | SA14 |
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| PL1 | 7 | | SA40 |
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| PL1 | 9 | | SA9 |
| PL1 | 10 | | SA9 |
| PL1 | 11 | | SA9 |
| PL1 | 12 | | SA8 |
| PL1 | 13 | | SA9 |
| PL1 | 14 | | SA44 |
| PL1 | 15 | | SA48 |
| PL1 | 16 | | SA44 |
| PL1 | 17 | | SA10 |
| PL1 | 19 | | SA10 |
| PL1 | 20 | | SA9 |
| PL1 | 21 | | SA39 |
| PL1 | 22 | | SA19 |
| PL1 | 23 | | SA10 |
| PL1 | 24 | | SA45 |
| PL1 | 25 | | SA48 |
| PL1 | 27 | | SA44 |
| PL1 | 28 | | SA9 |
| PL1 | 29 | | SA9 |
| PL1 | 30 | | SA9 |
| PL1 | 31 | | SA9 |
| PL1 | 32 | | SA42 |
| PL1 | 33 | | SA14 |
| PL1 | 35 | | SA41 |
| PL1 | 36 | | SA10 |
| PL1 | 37 | | SA48 |
| PL1 | 38 | | SA46 |
| PL1 | 40 | | SA10 |
| PL1 | 41 | | SA4 |
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| PL1 | 43 | | SA14 |
| PL1 | 44 | | SA14 |
| PL1 | 45 | | SA10 |
| PL1 | 46 | | SA8 |
| PL1 | 47 | | SA8 |
| PL1 | 48 | | SA9 |
| PL1 | 49 | | SA14 |
| PL1 | 50 | | SA4 |
| PL1 | 53 | | SA45 |
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| PL1 | 55 | | SA9 |
| PL1 | 56 | | SA4 |
| PL1 | 57 | | SA14 |
| PL1 | 58 | | SA10 |
| PL1 | 59 | 9818 | SA4 |

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| PL1 | 62 | | SA9 |
| PL1 | 63 | | SA10 |
| PL1 | 64 | | SA10 |
| PL1 | 65 | | SA19 |
| PL1 | 66 | | SA48 |
| PL1 | 67 | | SA44 |
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| PL1 | 77 | 4131 | SA49 |
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| PL1 | 79 | | SA20 |
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| PL1 | 83 | | SA49 |
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| PL1 | 89 | | SA46 |
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| PL1 | 93 | 9802 | SA10 |
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| PL1 | 120 | | SA19 |
| PL1 | 121 | | SA47 |

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|-----|-----|--|------|
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| PL1 | 123 | | SA46 |
| PL1 | 124 | | SA10 |
| PL1 | 125 | | SA10 |
| PL1 | 126 | | SA10 |
| PL1 | 127 | | SA10 |
| PL1 | 128 | | SA44 |
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| PL1 | 185 | | SA44 |
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| PL1 | 188 | | SA19 |

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| PL1 | 241 | | SA4 |
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| PL1 | 243 | | SA46 |
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| PL1 | 247 | | SA56 |
| PL1 | 248 | | SA9 |
| PL1 | 249 | | SA10 |

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| PL1 | 262 | | SA48 |
| PL1 | 263 | 6555 | SA10 |
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| PL1 | 265 | 4037 | SA9 |
| PL1 | 266 | 9806 | SA47 |
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| PL1 | 268 | | SA48 |
| PL1 | 269 | | SA48 |
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| PL1 | 289 | | SA19 |
| PL1 | 290 | | SA9 |
| PL1 | 291 | | SA41 |
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| PL1 | 307 | | SA10 |

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| PL1 | 328 | | SA10 |
| PL1 | 329 | | SA41 |
| PL1 | 330 | | SA48 |
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| PL1 | 365 | | SA42 |
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| PL1 | 367 | | SA10 |
| PL1 | 368 | 6557 | SA9 |
| PL1 | 369 | | SA10 |

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| PL1 | 397 | | SA48 |
| PL1 | 398 | | SA48 |
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| PL1 | 403 | | SA10 |
| PL1 | 404 | | SA4 |
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| PL1 | 407 | 9799 | SA9 |
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| PL1 | 412 | | SA44 |
| PL1 | 413 | | SA19 |
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| PL1 | 418 | | SA48 |
| PL1 | 419 | | SA10 |
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| PL1 | 421 | | SA10 |
| PL1 | 422 | | SA48 |
| PL1 | 423 | | SA9 |
| PL1 | 424 | | SA10 |
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| PL1 | 428 | | SA9 |
| PL1 | 429 | | SA9 |
| PL1 | 430 | | SA48 |
| PL1 | 431 | | SA9 |

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| PL1 | 474 | | SA48 |
| PL1 | 475 | | SA44 |
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| PL1 | 479 | | SA49 |
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| PL1 | 484 | | SA49 |
| PL1 | 485 | | SA4 |
| PL1 | 486 | | SA44 |
| PL1 | 488 | | SA10 |
| PL1 | 489 | | SA46 |
| PL1 | 490 | | SA10 |
| PL1 | 491 | | SA46 |

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| PL1 | 494 | 9819 | SA9 |
| PL1 | 495 | | SA48 |
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| PL1 | 497 | | SA10 |
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| PL1 | 554 | | SA9 |
| PL1 | 555 | 9807 | SA4 |
| PL1 | 556 | | SA48 |

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| PL1 | 560 | | SA19 |
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| PL1 | 583 | | SA9 |
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| PL1 | 585 | | SA47 |
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| PL1 | 598 | | SA48 |
| PL1 | 599 | | SA9 |
| PL1 | 600 | | SA9 |
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| PL1 | 602 | | SA47 |
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| PL1 | 604 | | SA9 |
| PL1 | 605 | | SA9 |
| PL1 | 606 | | SA14 |
| PL1 | 607 | | SA10 |
| PL1 | 609 | | SA44 |
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| PL1 | 615 | | SA14 |
| PL1 | 616 | | SA14 |
| PL1 | 617 | | SA8 |
| PL1 | 618 | | SA10 |
| PL1 | 619 | | SA9 |

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| PL1 | 622 | | SA48 |
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| PL1 | 624 | | SA49 |
| PL1 | 625 | | SA53 |
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| PL1 | 630 | | SA8 |
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| PL1 | 644 | | SA48 |
| PL1 | 645 | | SA10 |
| PL1 | 646 | | SA48 |
| PL1 | 647 | | SA42 |
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| PL1 | 650 | | SA46 |
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| PL1 | 655 | | SA8 |
| PL1 | 656 | | SA10 |
| PL1 | 657 | | SA19 |
| PL1 | 659 | | SA44 |
| PL1 | 660 | | SA42 |
| PL1 | 661 | | SA10 |
| PL1 | 662 | | SA46 |
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| PL2 | 1120 | | SA9 |
| PL2 | 1120 | | SA10 |
| PL2 | 1121 | | SA47 |
| PL2 | 1122 | | SA9 |
| PL2 | 1125 | | SA10 |
| PL2 | 1126 | | SA19 |
| PL2 | 1127 | 9762 | SA20 |
| PL2 | 1129 | | SA9 |
| PL2 | 1130 | | SA20 |
| PL2 | 1131 | | SA53 |
| PL2 | 1132 | | SA9 |
| PL2 | 1133 | | SA35 |
| PL2 | 1134 | | SA9 |
| PL2 | 1135 | | SA9 |
| PL2 | 1136 | | SA9 |
| PL2 | 1137 | | SA9 |
| PL2 | 1138 | | SA10 |
| PL2 | 1139 | 9796 | SA9 |
| PL2 | 1140 | | SA10 |
| PL2 | 1141 | | SA9 |
| PL2 | 1142 | | SA10 |
| PL2 | 1143 | | SA10 |
| PL2 | 1144 | | SA20 |
| PL2 | 1145 | | SA10 |
| PL2 | 1148 | | SA9 |
| PL2 | 1149 | | SA9 |
| PL2 | 1150 | | SA10 |
| PL2 | 1151 | | SA10 |
| PL2 | 1152 | | SA14 |
| PL2 | 1153 | | SA9 |
| PL2 | 1153 | | SA51 |
| PL2 | 1154 | | SA47 |
| PL2 | 1155 | | SA9 |
| PL2 | 1155 | | SA14 |
| PL2 | 1156 | | SA9 |
| PL2 | 1156 | | SA9 |
| PL2 | 1159 | | SA9 |
| PL2 | 1159 | | SA49 |
| PL2 | 1160 | | SA9 |

| | | | |
|-----|------|------|------|
| PL2 | 1163 | | SA10 |
| PL2 | 1164 | | SA10 |
| PL2 | 1166 | | SA9 |
| PL2 | 1167 | | SA2 |
| PL2 | 1168 | | SA19 |
| PL2 | 1169 | | SA49 |
| PL2 | 1170 | | SA49 |
| PL2 | 1171 | | SA10 |
| PL2 | 1172 | | SA47 |
| PL2 | 1173 | | SA49 |
| PL2 | 1174 | | SA9 |
| PL2 | 1175 | | SA9 |
| PL2 | 1176 | | SA35 |
| PL2 | 1177 | | SA5 |
| PL2 | 1178 | | SA49 |
| PL2 | 1179 | 6566 | SA49 |
| PL2 | 1180 | | SA9 |
| PL2 | 1181 | | SA9 |
| PL2 | 1182 | | SA20 |
| PL2 | 1183 | | SA10 |
| PL2 | 1184 | | SA10 |
| PL2 | 1185 | | SA49 |
| PL2 | 1187 | | SA10 |
| PL2 | 1188 | | SA8 |
| PL2 | 1189 | | SA9 |
| PL2 | 1190 | | SA4 |
| PL2 | 1191 | | SA20 |
| PL2 | 1192 | | SA9 |
| PL2 | 1193 | 9778 | SA9 |
| PL2 | 1194 | | SA49 |
| PL2 | 1195 | | SA10 |
| PL2 | 1197 | | SA49 |
| PL2 | 1198 | | SA9 |
| PL2 | 1199 | | SA10 |
| PL2 | 1200 | | SA10 |
| PL2 | 1202 | 4010 | SA2 |
| PL2 | 1203 | | SA9 |
| PL2 | 1204 | | SA14 |
| PL2 | 1205 | | SA9 |
| PL2 | 1206 | | SA14 |
| PL2 | 1207 | | SA46 |
| PL2 | 1208 | | SA42 |
| PL2 | 1209 | 4011 | SA2 |
| PL2 | 1210 | | SA9 |
| PL2 | 1211 | | SA20 |
| PL2 | 1212 | | SA10 |
| PL2 | 1213 | | SA9 |
| PL2 | 1215 | | SA16 |
| PL2 | 1216 | | SA9 |
| PL2 | 1216 | | SA35 |
| PL2 | 1217 | | SA9 |
| PL2 | 1218 | | SA9 |
| PL2 | 1219 | | SA19 |
| PL2 | 1220 | | SA10 |
| PL2 | 1221 | | SA5 |
| PL2 | 1222 | | SA14 |
| PL2 | 1224 | | SA4 |
| PL2 | 1226 | | SA10 |

| | | | |
|-----|------|------|------|
| PL2 | 1228 | 9771 | SA14 |
| PL2 | 1229 | | SA35 |
| PL2 | 1230 | | SA9 |
| PL2 | 1231 | | SA9 |
| PL2 | 1232 | | SA10 |
| PL2 | 1234 | | SA1 |
| PL2 | 1235 | | SA48 |
| PL2 | 1236 | | SA9 |
| PL2 | 1237 | | SA19 |
| PL2 | 1238 | | SA4 |
| PL2 | 1239 | | SA2 |
| PL2 | 1240 | | SA9 |
| PL2 | 1241 | | SA9 |
| PL2 | 1242 | | SA9 |
| PL2 | 1243 | | SA10 |
| PL2 | 1244 | | SA10 |
| PL2 | 1245 | | SA19 |
| PL2 | 1246 | | SA9 |
| PL2 | 1247 | | SA9 |
| PL2 | 1248 | | SA10 |
| PL2 | 1251 | | SA9 |
| PL2 | 1252 | | SA9 |
| PL2 | 1253 | | SA41 |
| PL2 | 1254 | | SA50 |
| PL2 | 1255 | | SA1 |
| PL2 | 1256 | | SA20 |
| PL2 | 1257 | | SA9 |
| PL2 | 1257 | | SA9 |
| PL2 | 1258 | | SA48 |
| PL2 | 1260 | | SA49 |
| PL2 | 1261 | | SA47 |
| PL2 | 1262 | | SA20 |
| PL2 | 1263 | | SA58 |
| PL2 | 1264 | | SA9 |
| PL2 | 1265 | | SA10 |
| PL2 | 1266 | | SA9 |
| PL2 | 1268 | | SA9 |
| PL2 | 1269 | | SA9 |
| PL2 | 1270 | | SA10 |
| PL2 | 1271 | | SA58 |
| PL2 | 1272 | | SA9 |
| PL2 | 1273 | | SA49 |
| PL2 | 1275 | | SA10 |
| PL2 | 1276 | | SA9 |
| PL2 | 1277 | | SA10 |
| PL2 | 1278 | | SA14 |
| PL2 | 1279 | | SA16 |
| PL2 | 1280 | | SA9 |
| PL2 | 1281 | | SA41 |
| PL2 | 1282 | | SA49 |
| PL2 | 1283 | | SA20 |
| PL2 | 1285 | | SA49 |
| PL2 | 1286 | | SA19 |
| PL2 | 1287 | | SA16 |
| PL2 | 1288 | | SA9 |
| PL2 | 1289 | | SA9 |
| PL2 | 1290 | | SA16 |
| PL2 | 1291 | 9783 | SA49 |

| | | | |
|-----|------|------|------|
| PL2 | 1292 | | SA10 |
| PL2 | 1293 | | SA49 |
| PL2 | 1294 | | SA10 |
| PL2 | 1295 | | SA49 |
| PL2 | 1296 | | SA20 |
| PL2 | 1297 | | SA9 |
| PL2 | 1298 | | SA49 |
| PL2 | 1299 | | SA9 |
| PL2 | 1300 | | SA10 |
| PL2 | 1301 | | SA10 |
| PL2 | 1302 | 9794 | SA49 |
| PL2 | 1303 | | SA9 |
| PL2 | 1304 | | SA19 |
| PL2 | 1305 | | SA49 |
| PL2 | 1306 | | SA20 |
| PL2 | 1307 | | SA9 |
| PL2 | 1308 | | SA10 |
| PL2 | 1309 | | SA10 |
| PL2 | 1310 | | SA9 |
| PL2 | 1311 | | SA9 |
| PL2 | 1312 | | SA41 |
| PL2 | 1313 | | SA10 |
| PL2 | 1314 | | SA49 |
| PL2 | 1315 | | SA10 |
| PL2 | 1316 | | SA49 |
| PL2 | 1317 | | SA10 |
| PL2 | 1318 | | SA49 |
| PL2 | 1319 | | SA49 |
| PL2 | 1320 | | SA10 |
| PL2 | 1322 | | SA20 |
| PL2 | 1326 | | SA8 |
| PL2 | 1327 | | SA9 |
| PL2 | 1328 | | SA49 |
| PL2 | 1329 | | SA49 |
| PL2 | 1330 | | SA10 |
| PL2 | 1332 | | SA41 |
| PL2 | 1333 | | SA9 |
| PL2 | 1334 | | SA10 |
| PL2 | 1335 | | SA49 |
| PL2 | 1337 | | SA49 |
| PL2 | 1338 | | SA49 |
| PL2 | 1339 | | SA10 |
| PL2 | 1340 | | SA4 |
| PL2 | 1341 | | SA47 |
| PL2 | 1342 | | SA10 |
| PL2 | 1343 | | SA49 |
| PL2 | 1344 | | SA20 |
| PL2 | 1345 | | SA9 |
| PL2 | 1346 | | SA2 |
| PL2 | 1348 | | SA49 |
| PL2 | 1349 | | SA10 |
| PL2 | 1349 | | SA10 |
| PL2 | 1353 | | SA20 |
| PL2 | 1354 | | SA49 |
| PL2 | 1355 | | SA43 |
| PL2 | 1356 | | SA49 |
| PL2 | 1357 | | SA49 |
| PL2 | 1358 | | SA41 |

| | | | |
|-----|------|------|------|
| PL2 | 1360 | | SA20 |
| PL2 | 1362 | | SA9 |
| PL2 | 1365 | | SA49 |
| PL2 | 1366 | | SA9 |
| PL2 | 1367 | | SA20 |
| PL2 | 1370 | | SA20 |
| PL2 | 1371 | | SA35 |
| PL2 | 1372 | | SA49 |
| PL2 | 1373 | | SA2 |
| PL2 | 1374 | | SA35 |
| PL2 | 1375 | | SA14 |
| PL2 | 1376 | | SA9 |
| PL2 | 1378 | | SA9 |
| PL2 | 1379 | | SA10 |
| PL2 | 1380 | | SA49 |
| PL2 | 1381 | | SA49 |
| PL2 | 1383 | 9763 | SA10 |
| PL2 | 1385 | | SA14 |
| PL2 | 1386 | | SA41 |
| PL2 | 1387 | 6567 | SA9 |
| PL2 | 1388 | | SA10 |
| PL2 | 1389 | | SA10 |
| PL2 | 1390 | 9777 | SA9 |
| PL2 | 1391 | | SA49 |
| PL2 | 1392 | | SA19 |
| PL2 | 1393 | | SA49 |
| PL2 | 1395 | | SA9 |
| PL2 | 1396 | | SA10 |
| PL2 | 1397 | | SA35 |
| PL2 | 1398 | | SA49 |
| PL2 | 1399 | | SA35 |
| PL2 | 1400 | | SA47 |
| PL2 | 1401 | | SA9 |
| PL2 | 1402 | | SA9 |
| PL2 | 1404 | | SA49 |
| PL2 | 1405 | | SA14 |
| PL2 | 1406 | | SA9 |
| PL2 | 1407 | | SA58 |
| PL2 | 1408 | | SA47 |
| PL2 | 1409 | | SA14 |
| PL2 | 1411 | | SA50 |
| PL2 | 1413 | | SA47 |
| PL2 | 1415 | | SA41 |
| PL2 | 1416 | | SA9 |
| PL2 | 1418 | | SA41 |
| PL2 | 1419 | | SA49 |
| PL2 | 1420 | | SA4 |
| PL2 | 1422 | | SA49 |
| PL2 | 1423 | | SA49 |
| PL2 | 1424 | | SA41 |
| PL2 | 1425 | | SA41 |
| PL2 | 1426 | | SA20 |
| PL2 | 1427 | | SA14 |
| PL2 | 1428 | | SA48 |
| PL2 | 1430 | | SA16 |
| PL2 | 1431 | | SA41 |
| PL2 | 1432 | | SA4 |
| PL2 | 1433 | | SA9 |

| | | | |
|-----|------|------|------|
| PL2 | 1434 | | SA9 |
| PL2 | 1435 | | SA9 |
| PL2 | 1436 | | SA9 |
| PL2 | 1437 | | SA9 |
| PL2 | 1438 | | SA49 |
| PL2 | 1439 | | SA9 |
| PL2 | 1440 | | SA10 |
| PL2 | 1441 | | SA10 |
| PL2 | 1442 | | SA10 |
| PL2 | 1443 | | SA14 |
| PL2 | 1444 | | SA1 |
| PL2 | 1445 | | SA47 |
| PL2 | 1446 | | SA4 |
| PL2 | 1447 | | SA9 |
| PL2 | 1448 | | SA4 |
| PL2 | 1451 | | SA41 |
| PL2 | 1452 | | SA41 |
| PL2 | 1453 | | SA49 |
| PL2 | 1454 | | SA43 |
| PL2 | 1455 | | SA10 |
| PL2 | 1456 | | SA49 |
| PL2 | 1457 | | SA9 |
| PL2 | 1459 | | SA47 |
| PL2 | 1461 | | SA16 |
| PL2 | 1462 | 9780 | SA9 |
| PL2 | 1465 | | SA10 |
| PL2 | 1466 | | SA46 |
| PL2 | 1467 | | SA41 |
| PL2 | 1468 | | SA2 |
| PL2 | 1470 | | SA9 |
| PL2 | 1471 | | SA10 |
| PL2 | 1472 | | SA47 |
| PL2 | 1474 | | SA50 |
| PL2 | 1475 | | SA10 |
| PL2 | 1475 | | SA10 |
| PL2 | 1476 | | SA9 |
| PL2 | 1477 | | SA9 |
| PL2 | 1478 | | SA14 |
| PL2 | 1480 | | SA58 |
| PL2 | 1481 | | SA1 |
| PL2 | 1482 | | SA16 |
| PL2 | 1484 | | SA43 |
| PL2 | 1485 | 9759 | SA14 |
| PL2 | 1486 | | SA55 |
| PL2 | 1487 | | SA9 |
| PL2 | 1488 | | SA9 |
| PL2 | 1489 | | SA35 |
| PL2 | 1490 | | SA19 |
| PL2 | 1491 | | SA9 |
| PL2 | 1492 | | SA4 |
| PL2 | 1493 | | SA9 |
| PL2 | 1494 | | SA9 |
| PL2 | 1495 | | SA9 |
| PL2 | 1496 | | SA9 |
| PL2 | 1497 | | SA9 |
| PL2 | 1498 | | SA2 |
| PL2 | 1499 | | SA9 |
| PL2 | 1500 | | SA19 |

| | | | |
|-----|------|------|------|
| PL2 | 1501 | | SA4 |
| PL2 | 1502 | | SA4 |
| PL2 | 1503 | | SA47 |
| PL2 | 1505 | | SA9 |
| PL2 | 1506 | | SA47 |
| PL2 | 1507 | 9761 | SA14 |
| PL2 | 1508 | | SA49 |
| PL2 | 1509 | | SA9 |
| PL2 | 1513 | | SA20 |
| PL2 | 1520 | | SA2 |
| PL2 | 1521 | | SA50 |

| | | | |
|-----|------|------|------|
| PL2 | 1523 | | SA10 |
| PL2 | 1524 | | SA51 |
| PL2 | 1550 | | SA9 |
| PL2 | 1580 | 9781 | SA41 |
| PL2 | 1694 | | SA46 |
| PL2 | 1883 | | SA19 |
| PL2 | 1884 | | SA9 |
| PL2 | 1981 | | SA9 |
| PL2 | 1982 | | SA58 |
| PL2 | 1983 | | SA4 |
| PL2 | 3721 | | SA43 |

APPENDIX E.C. Specimens from the Peñas Coloradas Fm. curated at MEF.

| Locality | Field Number | Specimen Number MPEF-Pb | Leaf Morphotype Number |
|----------|--------------|-------------------------|------------------------|
| LF | 1 | | SA68 |
| LF | 2 | | SA4 |
| LF | 3 | 9844 | SA74 |
| LF | 5 | | SA77 |
| LF | 6 | | SA4 |
| LF | 7 | | SA9 |
| LF | 8 | | SA4 |
| LF | 9 | | SA8 |
| LF | 9 | | SA75 |
| LF | 10 | | SA4 |
| LF | 11 | | SA75 |
| LF | 12 | | SA73 |
| LF | 13 | | SA10 |
| LF | 14 | | SA75 |
| LF | 15 | | SA10 |
| LF | 16 | | SA75 |
| LF | 17 | | SA48 |
| LF | 18 | | SA70 |
| LF | 21 | 9851 | SA9 |
| LF | 22 | | SA19 |
| LF | 23 | | SA75 |
| LF | 25 | | SA4 |
| LF | 25 | | SA73 |
| LF | 26 | 9870 | SA68 |
| LF | 27 | | SA9 |
| LF | 28 | | SA14 |
| LF | 29 | | SA73 |
| LF | 30 | 6545 | SA4 |
| LF | 31 | | SA4 |
| LF | 32 | | SA5 |
| LF | 33 | | SA73 |
| LF | 34 | | SA73 |
| LF | 35 | | SA73 |
| LF | 36 | | SA47 |
| LF | 37 | | SA20 |
| LF | 38 | | SA4 |
| LF | 39 | | SA10 |
| LF | 40 | 9855 | SA4 |
| LF | 41 | | SA73 |
| LF | 42 | | SA75 |
| LF | 43 | | SA73 |
| LF | 44 | | SA4 |
| LF | 46 | | SA48 |
| LF | 49 | | SA10 |
| LF | 50 | | SA4 |
| LF | 51 | | SA4 |
| LF | 52 | | SA35 |
| LF | 53 | | SA4 |
| LF | 54 | | SA73 |
| LF | 55 | 9865 | SA42 |
| LF | 56 | | SA73 |
| LF | 57 | 9864 | SA73 |

| | | | |
|----|-----|------|------|
| LF | 58 | 9852 | SA10 |
| LF | 59 | | SA2 |
| LF | 60 | | SA14 |
| LF | 61 | | SA4 |
| LF | 62 | 6546 | SA4 |
| LF | 63 | | SA44 |
| LF | 65 | | SA10 |
| LF | 66 | | SA73 |
| LF | 67 | | SA73 |
| LF | 68 | 9845 | SA75 |
| LF | 69 | | SA73 |
| LF | 70 | 9859 | SA68 |
| LF | 71 | | SA4 |
| LF | 72 | | SA4 |
| LF | 73 | | SA4 |
| LF | 74 | | SA19 |
| LF | 75 | | SA19 |
| LF | 76 | | SA56 |
| LF | 77 | | SA20 |
| LF | 77 | | SA44 |
| LF | 78 | | SA9 |
| LF | 79 | | SA10 |
| LF | 80 | | SA73 |
| LF | 81 | | SA4 |
| LF | 82 | | SA10 |
| LF | 83 | | SA77 |
| LF | 85 | | SA58 |
| LF | 86 | | SA10 |
| LF | 87 | | SA73 |
| LF | 88 | | SA14 |
| LF | 89 | | SA42 |
| LF | 90 | 6547 | SA42 |
| LF | 91 | | SA10 |
| LF | 92 | | SA10 |
| LF | 93 | | SA48 |
| LF | 95 | | SA14 |
| LF | 97 | | SA2 |
| LF | 99 | | SA2 |
| LF | 100 | | SA73 |
| LF | 102 | | SA10 |
| LF | 103 | | SA10 |
| LF | 104 | | SA75 |
| LF | 106 | | SA4 |
| LF | 107 | | SA4 |
| LF | 108 | | SA8 |
| LF | 109 | | SA10 |
| LF | 110 | | SA10 |
| LF | 111 | | SA10 |
| LF | 112 | 9871 | SA9 |
| LF | 113 | | SA10 |
| LF | 114 | 9868 | SA42 |
| LF | 115 | | SA48 |
| LF | 116 | | SA10 |
| LF | 119 | | SA73 |
| LF | 120 | | SA75 |
| LF | 121 | | SA4 |
| LF | 123 | | SA4 |
| LF | 124 | | SA9 |

| | | | |
|----|-----|------|------|
| LF | 125 | | SA75 |
| LF | 126 | | SA73 |
| LF | 127 | | SA9 |
| LF | 128 | | SA10 |
| LF | 129 | 9869 | SA14 |
| LF | 130 | | SA73 |
| LF | 132 | | SA68 |
| LF | 135 | | SA10 |
| LF | 136 | | SA10 |
| LF | 138 | | SA74 |
| LF | 139 | | SA4 |
| LF | 140 | | SA73 |
| LF | 141 | 6548 | SA42 |
| LF | 142 | | SA73 |
| LF | 144 | | SA5 |
| LF | 145 | | SA10 |
| LF | 146 | | SA73 |
| LF | 148 | | SA73 |
| LF | 149 | | SA68 |
| LF | 150 | | SA48 |
| LF | 151 | | SA9 |
| LF | 152 | | SA4 |
| LF | 153 | | SA44 |
| LF | 154 | | SA2 |
| LF | 155 | | SA48 |
| LF | 156 | | SA48 |
| LF | 157 | | SA75 |
| LF | 158 | | SA73 |
| LF | 161 | | SA10 |
| LF | 161 | | SA10 |
| LF | 162 | | SA47 |
| LF | 163 | | SA5 |
| LF | 164 | 9849 | SA47 |
| LF | 165 | | SA77 |
| LF | 166 | | SA9 |
| LF | 167 | | SA4 |
| LF | 167 | | SA9 |
| LF | 168 | | SA4 |
| LF | 170 | | SA73 |
| LF | 171 | | SA9 |
| LF | 172 | | SA20 |
| LF | 173 | | SA73 |
| LF | 174 | | SA75 |
| LF | 176 | | SA44 |
| LF | 177 | | SA4 |
| LF | 178 | | SA10 |
| LF | 179 | | SA73 |
| LF | 180 | | SA73 |
| LF | 181 | | SA2 |
| LF | 182 | | SA68 |
| LF | 183 | 9856 | SA10 |
| LF | 184 | | SA35 |
| LF | 185 | | SA9 |
| LF | 186 | | SA14 |
| LF | 187 | | SA9 |
| LF | 188 | | SA44 |
| LF | 189 | | SA10 |
| LF | 190 | | SA59 |

| | | | |
|----|-----|------|------|
| LF | 191 | | SA74 |
| LF | 192 | | SA14 |
| LF | 193 | | SA48 |
| LF | 194 | | SA75 |
| LF | 195 | | SA56 |
| LF | 196 | | SA10 |
| LF | 197 | | SA44 |
| LF | 198 | | SA44 |
| LF | 199 | | SA47 |
| LF | 200 | | SA73 |
| LF | 201 | | SA35 |
| LF | 201 | | SA75 |
| LF | 202 | | SA35 |
| LF | 203 | | SA2 |
| LF | 204 | | SA47 |
| LF | 205 | | SA10 |
| LF | 206 | 9860 | SA77 |
| LF | 207 | | SA16 |
| LF | 208 | | SA10 |
| LF | 209 | | SA73 |
| LF | 210 | | SA73 |
| LF | 211 | | SA75 |
| LF | 212 | | SA4 |
| LF | 213 | | SA73 |
| LF | 214 | 9139 | SA77 |
| LF | 215 | | SA4 |
| LF | 216 | 6549 | SA70 |
| LF | 217 | | SA10 |
| LF | 218 | | SA10 |
| LF | 219 | | SA4 |
| LF | 220 | | SA9 |
| LF | 221 | | SA4 |
| LF | 221 | | SA73 |
| LF | 222 | | SA70 |
| LF | 223 | | SA4 |
| LF | 223 | | SA76 |
| LF | 224 | | SA10 |
| LF | 224 | | SA10 |
| LF | 225 | | SA2 |
| LF | 227 | | SA47 |
| LF | 228 | 9873 | SA4 |
| LF | 228 | | SA10 |
| LF | 229 | | SA20 |
| LF | 230 | | SA47 |
| LF | 231 | | SA10 |
| LF | 231 | | SA35 |
| LF | 232 | | SA4 |
| LF | 233 | | SA4 |
| LF | 233 | | SA70 |
| LF | 234 | | SA73 |
| LF | 235 | | SA9 |
| LF | 235 | | SA47 |
| LF | 235 | | SA48 |
| LF | 236 | | SA9 |
| LF | 237 | | SA75 |
| LF | 238 | | SA74 |
| LF | 239 | | SA42 |
| LF | 240 | | SA73 |

| | | | |
|----|-----|------|------|
| LF | 241 | | SA10 |
| LF | 242 | | SA10 |
| LF | 243 | | SA73 |
| LF | 244 | 9847 | SA42 |
| LF | 245 | | SA4 |
| LF | 246 | | SA10 |
| LF | 246 | | SA75 |
| LF | 247 | | SA19 |
| LF | 248 | | SA68 |
| LF | 249 | | SA42 |
| LF | 250 | | SA10 |
| LF | 251 | | SA9 |
| LF | 252 | | SA74 |
| LF | 253 | | SA10 |
| LF | 254 | 9854 | SA20 |
| LF | 255 | | SA4 |
| LF | 256 | | SA14 |
| LF | 256 | | SA70 |
| LF | 257 | | SA10 |
| LF | 258 | | SA10 |
| LF | 259 | | SA19 |
| LF | 260 | | SA75 |
| LF | 262 | 9848 | SA14 |
| LF | 264 | | SA48 |
| LF | 265 | | SA42 |
| LF | 266 | | SA10 |
| LF | 267 | | SA9 |
| LF | 269 | | SA44 |
| LF | 270 | | SA4 |
| LF | 271 | | SA4 |
| LF | 272 | | SA8 |
| LF | 273 | | SA10 |
| LF | 275 | 9874 | SA9 |
| LF | 277 | | SA10 |
| LF | 278 | | SA4 |
| LF | 279 | 9843 | SA4 |
| LF | 280 | 9846 | SA73 |
| LF | 281 | | SA70 |
| LF | 282 | | SA10 |
| LF | 283 | | SA73 |
| LF | 284 | | SA48 |
| LF | 285 | | SA68 |
| LF | 286 | | SA10 |
| LF | 288 | | SA75 |
| LF | 289 | | SA10 |
| LF | 290 | | SA4 |
| LF | 292 | | SA4 |
| LF | 293 | 6568 | SA47 |
| LF | 294 | | SA10 |
| LF | 295 | | SA68 |
| LF | 296 | | SA75 |
| LF | 297 | | SA10 |
| LF | 298 | | SA4 |
| LF | 299 | | SA10 |
| LF | 300 | | SA75 |
| LF | 302 | 9858 | SA2 |
| LF | 303 | | SA10 |
| LF | 304 | | SA4 |

| | | | |
|----|-----|------|------|
| LF | 305 | 9876 | SA75 |
| LF | 306 | | SA2 |
| LF | 306 | | SA10 |
| LF | 307 | | SA77 |
| LF | 308 | | SA73 |
| LF | 309 | | SA73 |
| LF | 310 | | SA73 |
| LF | 311 | | SA68 |
| LF | 312 | | SA10 |
| LF | 313 | | SA73 |
| LF | 314 | | SA73 |
| LF | 315 | | SA14 |
| LF | 316 | | SA4 |
| LF | 317 | | SA73 |
| LF | 318 | | SA4 |
| LF | 320 | | SA73 |
| LF | 320 | | SA73 |
| LF | 321 | | SA10 |
| LF | 322 | | SA78 |
| LF | 323 | | SA48 |
| LF | 324 | | SA75 |
| LF | 325 | | SA14 |
| LF | 327 | | SA19 |
| LF | 328 | | SA10 |
| LF | 329 | | SA73 |
| LF | 330 | | SA73 |
| LF | 331 | | SA10 |
| LF | 333 | | SA73 |
| LF | 334 | | SA73 |
| LF | 335 | | SA73 |
| LF | 337 | | SA68 |
| LF | 338 | | SA73 |
| LF | 339 | | SA48 |
| LF | 340 | | SA2 |
| LF | 341 | | SA2 |
| LF | 342 | | SA68 |
| LF | 343 | | SA70 |
| LF | 344 | | SA42 |
| LF | 345 | | SA39 |
| LF | 346 | | SA4 |
| LF | 347 | | SA42 |
| LF | 348 | | SA10 |
| LF | 350 | | SA48 |
| LF | 351 | | SA68 |
| LF | 352 | | SA76 |
| LF | 353 | | SA10 |
| LF | 354 | | SA4 |
| LF | 355 | | SA4 |
| LF | 356 | | SA70 |
| LF | 357 | | SA39 |
| LF | 358 | | SA4 |
| LF | 359 | | SA10 |
| LF | 360 | | SA75 |
| LF | 361 | | SA10 |
| LF | 363 | | SA68 |
| LF | 367 | | SA70 |
| LF | 368 | 9127 | SA44 |
| LF | 369 | | SA10 |

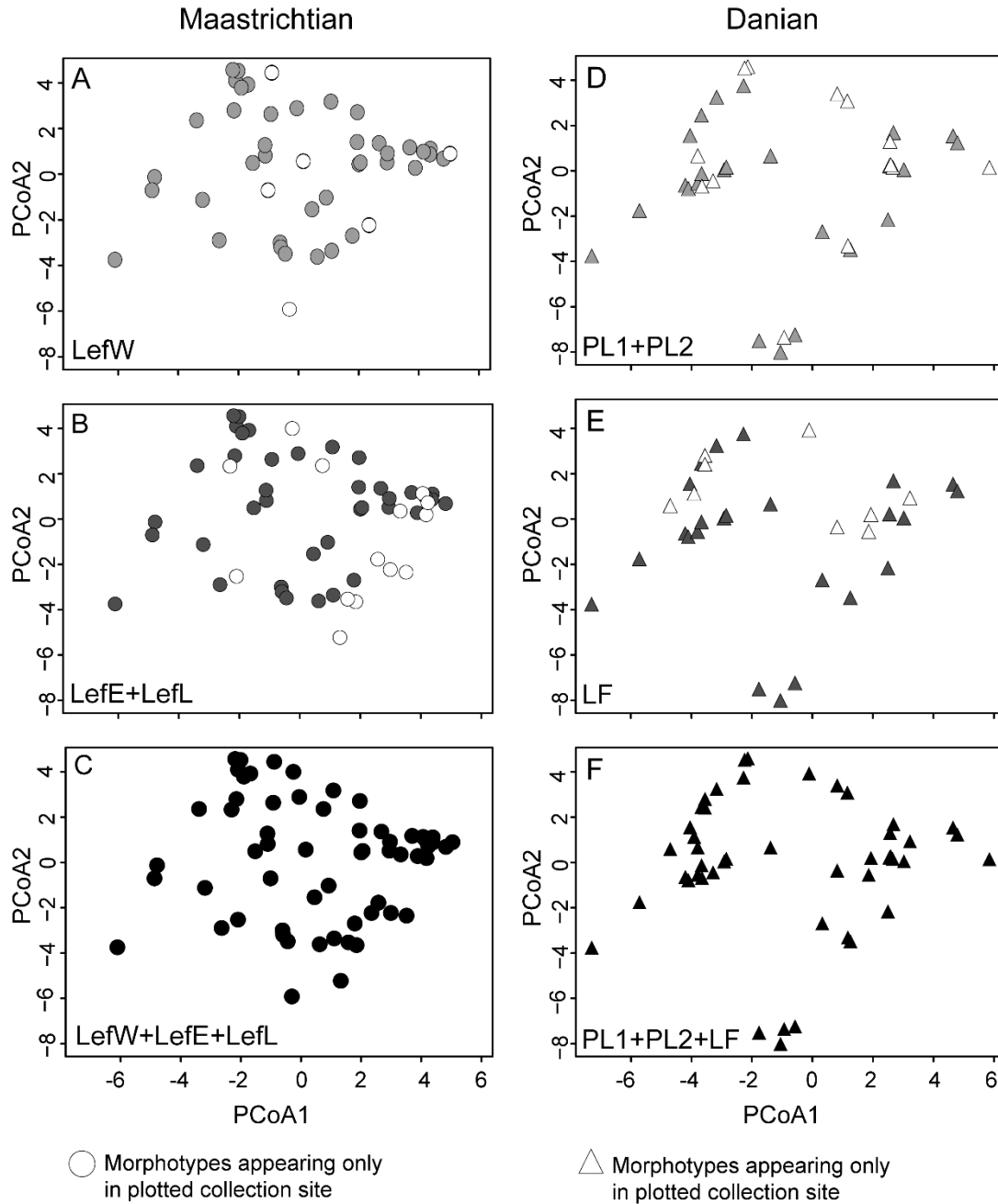
| | | | |
|----|---------|------|------|
| LF | 370 | | SA39 |
| LF | 371 | | SA4 |
| LF | 372 | | SA56 |
| LF | 373 | | SA73 |
| LF | 374=591 | 9875 | SA70 |
| LF | 375 | | SA10 |
| LF | 377 | | SA4 |
| LF | 378 | | SA68 |
| LF | 379 | | SA73 |
| LF | 380 | | SA48 |
| LF | 381 | | SA70 |
| LF | 382 | | SA70 |
| LF | 383 | | SA73 |
| LF | 384 | | SA68 |
| LF | 388 | | SA73 |
| LF | 389 | | SA35 |
| LF | 390 | | SA75 |
| LF | 391 | | SA9 |
| LF | 392 | | SA73 |
| LF | 393 | 9863 | SA4 |
| LF | 394 | | SA4 |
| LF | 395 | | SA75 |
| LF | 396 | | SA4 |
| LF | 397 | | SA70 |
| LF | 398 | | SA2 |
| LF | 399 | | SA20 |
| LF | 400 | | SA73 |
| LF | 402 | | SA10 |
| LF | 403 | | SA14 |
| LF | 403 | | SA19 |
| LF | 404 | 3019 | SA78 |
| LF | 405 | | SA73 |
| LF | 406 | | SA4 |
| LF | 407 | | SA18 |
| LF | 408 | | SA73 |
| LF | 409 | | SA4 |
| LF | 410 | | SA73 |
| LF | 411 | | SA10 |
| LF | 412 | | SA20 |
| LF | 413 | | SA10 |
| LF | 415 | | SA73 |
| LF | 416 | | SA68 |
| LF | 417 | | SA73 |
| LF | 418 | | SA75 |
| LF | 419 | | SA48 |
| LF | 420 | | SA47 |
| LF | 421 | | SA20 |
| LF | 422 | | SA10 |
| LF | 423 | | SA73 |
| LF | 424 | | SA4 |
| LF | 425 | 9857 | SA73 |
| LF | 427 | | SA47 |
| LF | 428 | | SA2 |
| LF | 429 | | SA73 |
| LF | 430 | | SA73 |
| LF | 432 | | SA10 |
| LF | 432 | | SA20 |
| LF | 434 | | SA73 |

| | | | |
|----|-----|------|------|
| LF | 436 | | SA73 |
| LF | 437 | | SA73 |
| LF | 438 | | SA4 |
| LF | 439 | | SA44 |
| LF | 441 | | SA19 |
| LF | 442 | | SA75 |
| LF | 443 | | SA4 |
| LF | 444 | | SA70 |
| LF | 445 | | SA77 |
| LF | 446 | | SA10 |
| LF | 447 | | SA20 |
| LF | 448 | | SA73 |
| LF | 449 | 9853 | SA19 |
| LF | 451 | | SA4 |
| LF | 452 | | SA4 |
| LF | 452 | | SA56 |
| LF | 455 | | SA73 |
| LF | 456 | | SA10 |
| LF | 457 | | SA74 |
| LF | 460 | | SA5 |
| LF | 461 | | SA10 |
| LF | 464 | | SA4 |
| LF | 465 | | SA73 |
| LF | 467 | | SA4 |
| LF | 470 | | SA10 |
| LF | 471 | | SA73 |
| LF | 473 | | SA14 |
| LF | 477 | | SA2 |
| LF | 478 | | SA10 |
| LF | 479 | | SA10 |
| LF | 480 | | SA10 |
| LF | 482 | | SA73 |
| LF | 483 | | SA68 |
| LF | 484 | | SA73 |
| LF | 485 | 9872 | SA10 |
| LF | 486 | 6550 | SA14 |
| LF | 488 | | SA68 |
| LF | 489 | | SA73 |
| LF | 490 | | SA10 |
| LF | 491 | | SA47 |
| LF | 492 | | SA73 |
| LF | 494 | | SA68 |
| LF | 495 | | SA47 |
| LF | 497 | | SA73 |
| LF | 498 | | SA19 |
| LF | 499 | | SA20 |
| LF | 500 | | SA70 |
| LF | 502 | | SA68 |
| LF | 503 | | SA10 |
| LF | 504 | | SA35 |
| LF | 505 | | SA68 |
| LF | 506 | | SA10 |
| LF | 506 | | SA73 |
| LF | 507 | | SA4 |
| LF | 508 | | SA73 |
| LF | 509 | | SA68 |
| LF | 510 | | SA4 |
| LF | 510 | | SA16 |

| | | | |
|----|-----|------|------|
| LF | 511 | | SA73 |
| LF | 512 | | SA10 |
| LF | 513 | | SA73 |
| LF | 514 | | SA44 |
| LF | 515 | | SA4 |
| LF | 515 | | SA76 |
| LF | 516 | | SA10 |
| LF | 517 | | SA68 |
| LF | 518 | | SA73 |
| LF | 519 | | SA75 |
| LF | 520 | | SA10 |
| LF | 521 | | SA73 |
| LF | 523 | | SA14 |
| LF | 524 | 6551 | SA48 |
| LF | 525 | | SA4 |
| LF | 526 | | SA9 |
| LF | 527 | | SA4 |
| LF | 529 | | SA75 |
| LF | 530 | | SA68 |
| LF | 532 | | SA73 |
| LF | 533 | | SA9 |
| LF | 534 | | SA10 |
| LF | 535 | | SA10 |
| LF | 536 | | SA73 |
| LF | 537 | | SA47 |
| LF | 538 | | SA16 |
| LF | 539 | | SA14 |
| LF | 540 | | SA20 |
| LF | 540 | | SA68 |
| LF | 541 | | SA4 |
| LF | 542 | | SA4 |
| LF | 543 | | SA73 |
| LF | 544 | | SA10 |
| LF | 545 | | SA73 |
| LF | 546 | 6552 | SA14 |
| LF | 547 | | SA10 |
| LF | 548 | | SA75 |
| LF | 549 | | SA9 |
| LF | 550 | | SA68 |
| LF | 551 | | SA14 |
| LF | 552 | | SA4 |
| LF | 553 | | SA4 |
| LF | 557 | | SA77 |
| LF | 558 | | SA47 |
| LF | 560 | | SA16 |
| LF | 563 | 9850 | SA10 |
| LF | 564 | | SA4 |
| LF | 566 | | SA10 |
| LF | 567 | | SA77 |
| LF | 568 | | SA4 |
| LF | 569 | | SA73 |
| LF | 571 | | SA16 |
| LF | 571 | | SA70 |

| | | | |
|----|-----|------|------|
| LF | 572 | | SA73 |
| LF | 573 | | SA4 |
| LF | 574 | | SA4 |
| LF | 575 | | SA4 |
| LF | 576 | | SA10 |
| LF | 577 | | SA73 |
| LF | 579 | | SA10 |
| LF | 580 | | SA20 |
| LF | 581 | | SA19 |
| LF | 583 | | SA10 |
| LF | 585 | | SA4 |
| LF | 586 | | SA68 |
| LF | 587 | | SA75 |
| LF | 588 | | SA70 |
| LF | 589 | | SA73 |
| LF | 592 | | SA4 |
| LF | 593 | | SA76 |
| LF | 595 | | SA76 |
| LF | 596 | | SA68 |
| LF | 596 | | SA75 |
| LF | 597 | | SA75 |
| LF | 598 | | SA73 |
| LF | 599 | | SA77 |
| LF | 600 | | SA10 |
| LF | 602 | | SA9 |
| LF | 603 | | SA10 |
| LF | 604 | | SA10 |
| LF | 605 | | SA10 |
| LF | 606 | | SA73 |
| LF | 607 | | SA10 |
| LF | 608 | | SA48 |
| LF | 609 | | SA56 |
| LF | 610 | | SA2 |
| LF | 611 | | SA44 |
| LF | 614 | | SA10 |
| LF | 616 | | SA75 |
| LF | 617 | | SA4 |
| LF | 618 | | SA4 |
| LF | 619 | | SA10 |
| LF | 620 | 6553 | SA10 |
| LF | 621 | | SA9 |
| LF | 623 | | SA73 |
| LF | 625 | | SA14 |
| LF | 626 | | SA73 |
| LF | 627 | | SA8 |
| LF | 628 | | SA10 |
| LF | 629 | | SA78 |
| LF | 630 | | SA4 |
| LF | 631 | | SA9 |
| LF | 632 | | SA4 |
| LF | 633 | | SA74 |
| LF | 634 | | SA4 |
| LF | 811 | | SA10 |

APPENDIX F. Lefipán, Salamanca and Peñas Coloradas fms. morphospaces subdivided by macrofloral composition in each assemblage and overall Maastrichtian and Danian assemblages. **A.** Morphospace occupied by morphotypes present in collection LefW. Morphotypes occurring only in LefW highlighted in white. **B.** Morphospace occupied by morphotypes present in collection horizon LefE + LefL- Morphotypes occurring only in this horizon highlighted in white. **C.** Morphospace occupied by all Maastrichtian morphotypes. **D.** Morphospace occupied by morphotypes present Salamanca Fm. PL1+PL2 collections. Morphotypes occurring only in Salamanca Fm. highlighted in white. **E.** Morphospace occupied by morphotypes present in Peñas Coloradas Fm. LF collection. Morphotypes occurring only in Peñas Coloradas Fm. highlighted in white.



APPENDIX G. Measures of disparity calculated for individual Maastrichtian and Danian macrofloral assemblages, and all Maastrichtian and Danian morphotypes. Salamanca Fm. PL1+PL2 localities grouped based on their almost equivalent floral composition as seen in Figure 6. Lefipán Fm. LefE+LefL localities grouped because they are collected along the same stratigraphic horizon.

| | Sum of ranges PCoA 1-4 | Hypercube vol. | Avg. pairwise distance | Max. pairwise distance |
|------------------------------|-----------------------------------|-----------------------|-----------------------------------|-----------------------------------|
| LF | 40.80 | 9877.35 | 8.58 | 14.14 |
| PL1+PL2 | 42.87 | 11746.23 | 8.79 | 14.70 |
| All Danian | 42.87 | 11746.23 | 8.58 | 14.70 |
| LefW | 38.88 | 8691.23 | 7.71 | 12.69 |
| LefE+LefL | 37.97 | 7958.47 | 7.75 | 12.81 |
| All Maastrichtian | 38.88 | 8691.23 | 7.63 | 12.81 |

APPENDIX H. A. Percentage of missing data for each character used to construct the macrofloral morphospaces.

| Character | % of missing data |
|--------------------------------|--------------------------|
| Max size | 0.0 |
| Margin | 0.0 |
| Petiole insertion | 2.8 |
| Shape | 0.0 |
| Medial symmetry | 0.0 |
| Base symmetry | 3.8 |
| Lobation | 0.0 |
| Max number of lobes | 0.0 |
| Apex shape | 28.3 |
| Apex angle | 14.2 |
| Base shape | 7.5 |
| Base angle | 2.8 |
| Primary vein | 0.0 |
| Number of basal veins | 8.5 |
| Agrophic veins | 0.0 |
| Secondary vein framework | 0.0 |
| Major secondary spacing | 0.0 |
| Perimarginal veins | 0.9 |
| Intersecondary veins | 3.8 |
| Percurrent | 8.5 |
| Angle of percurrent tertiaries | 8.5 |
| Reticulate | 9.4 |

| | |
|---------------------------|-----|
| Ramified | 9.4 |
| Epimedial tertiary fabric | 8.5 |
| Tooth spacing | 0.0 |
| Number of orders of teeth | 0.0 |
| Number of teeth per cm | 0.0 |
| Sinus shape | 0.0 |
| cc/cv | 0.9 |
| cc/cc | 0.9 |
| cc/st | 0.9 |
| cc/fl | 0.9 |
| cv/cc | 0.9 |
| cv/cv | 0.9 |
| cv/st | 0.9 |
| cv/fl | 0.9 |
| st/fl | 0.9 |
| st/cv | 0.9 |
| st/st | 0.9 |
| st/cc | 0.9 |
| fl/st | 0.9 |
| fl/cv | 0.9 |
| fl/cc | 0.9 |
| fl/fl | 0.9 |
| Principal vein in tooth | 1.9 |
| Tooth apex | 0.9 |

APPENDIX H. B. Percentage of missing data for each morphotype used to construct the macrofloral morphospaces.

| Morphotype | % of missing data |
|-------------------|--------------------------|
| SA1 | 0.0 |
| SA2 | 0.0 |
| SA4 | 0.0 |
| SA5 | 0.0 |
| SA8 | 0.0 |
| SA9A | 0.0 |
| SA9B | 0.0 |
| SA10A | 0.0 |
| SA10B | 0.0 |
| SA14A | 0.0 |
| SA14B | 4.3 |
| SA16 | 0.0 |
| SA19A | 0.0 |
| SA19B | 0.0 |
| SA20 | 0.0 |
| SA35 | 0.0 |
| SA39 | 0.0 |
| SA41 | 0.0 |
| SA42 | 10.9 |
| SA43 | 0.0 |
| SA44 | 2.2 |
| SA45 | 0.0 |
| SA46 | 0.0 |
| SA47 | 0.0 |
| SA48 | 0.0 |
| SA49 | 0.0 |
| SA50 | 2.2 |
| SA51 | 0.0 |
| SA52 | 0.0 |
| SA54 | 0.0 |
| SA55 | 13.0 |
| SA56 | 0.0 |
| SA57 | 4.3 |
| SA58 | 0.0 |

| | |
|-------|------|
| SA59 | 0.0 |
| SA60 | 0.0 |
| SA63 | 0.0 |
| SA66 | 4.3 |
| SA68 | 0.0 |
| SA69 | 4.3 |
| SA70 | 0.0 |
| SA73 | 0.0 |
| SA74 | 2.2 |
| SA75 | 0.0 |
| SA76 | 2.2 |
| SA77 | 2.2 |
| SA78 | 4.3 |
| LF1 | 50.0 |
| LF2 | 0.0 |
| LF3 | 13.0 |
| LF4 | 10.9 |
| LF5 | 15.2 |
| LF6 | 2.2 |
| LF7 | 15.2 |
| LF8 | 0.0 |
| LF9 | 10.9 |
| LF10 | 17.4 |
| LF11 | 0.0 |
| LF12 | 0.0 |
| LF13 | 0.0 |
| LF15 | 19.6 |
| LF16 | 0.0 |
| LF17A | 2.2 |
| LF17B | 0.0 |
| LF18 | 0.0 |
| LF19 | 0.0 |
| LF20 | 0.0 |
| LF21 | 6.5 |
| LF22 | 2.2 |

| | |
|------|------|
| LF23 | 0.0 |
| LF24 | 0.0 |
| LF26 | 0.0 |
| LF27 | 4.3 |
| LF32 | 0.0 |
| LF33 | 4.3 |
| LF34 | 0.0 |
| LF35 | 10.9 |
| LF36 | 0.0 |
| LF37 | 2.2 |
| LF38 | 0.0 |
| LF39 | 6.5 |
| LF40 | 0.0 |
| LF41 | 6.5 |
| LF42 | 17.4 |
| LF43 | 2.2 |
| LF44 | 0.0 |
| LF45 | 4.3 |
| LF46 | 0.0 |
| LF47 | 0.0 |
| LF48 | 0.0 |
| LF49 | 2.2 |
| LF50 | 6.5 |
| LF51 | 0.0 |
| LF53 | 0.0 |
| LF54 | 2.2 |
| LF55 | 0.0 |
| LF56 | 4.3 |
| LF57 | 0.0 |
| LF58 | 0.0 |
| LF60 | 2.2 |
| LF63 | 4.3 |
| LF64 | 4.3 |
| LF66 | 4.3 |
| LF67 | 0.0 |