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Plant diversity turnovers in the Triassic–Jurassic transition: evidence from the paleobotanical record of Argentina

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ABSTRACT

The Triassic–Jurassic transition was an important interval in Earth's history, which encompassed two great biotic crises: the End-Triassic mass extinction and the early Toarcian Oceanic Anoxic Event. The response of the terrestrial vegetation to these crises has been the subject of debate. In Argentina, a floristic turnover occurring in the Triassic/Jurassic boundary has been suggested, which led to the disappearance of corystoperms and peltasperms, and to a greater diversity of ferns, bennettitaleans, and conifers. Recent findings have thrown into question the previous evolutionary models. To understand the terrestrial plant turnovers during the Triassic–Jurassic transition in Argentina, we calculated diversity indexes, survivorship proportions, and origination and extinction rates, based on the megafossil record. The results indicate that, despite only one lineage disappeared in the Late Triassic (Pleuromeiaceae), there was an important but gradual vegetation change in the Triassic–Jurassic transition. Late Triassic diagnostic lineages extended into the Jurassic but most of them with few records and became extinct in the Early Jurassic. Floristic turnovers during the Jurassic can be correlated with paleoclimatic changes. The Osmundaceae, Dipteridaceae, and Bennettitales diversified in the Sinemurian. A taxa richness increase in the Toarcian is recognized, marked by a conifer diversification. In the Bathonian–Kimmeridgian interval, the conifers and bennettitaleans acquired greater importance. The dataset can be improved in the future by intensifying fossil sampling in order to obtain more robust and precise results.

Keywords: Mesozoic, South America, paleofloras, extinction

RESUMEN

Cambios en la diversidad de plantas en la transición del Triásico al Jurásico: evidencia del registro paleobotánico de Argentina.
La transición del Triásico al Jurásico fue un intervalo importante en la historia de la Tierra, que abarcó dos grandes crisis bióticas: la extinción masiva de fines del Triásico y el Evento Anóxico Oceánico del Toarciano Temprano. La respuesta de la vegetación a estas crisis ha sido objeto de debate. En la Argentina se ha sugerido un recambio en el límite Triásico/Jurásico, que llevó a la desaparición de corystopermas y peltaspermas, y a una mayor influencia de helechos, bennettitales y coníferas. Hallazgos recientes han puesto en duda los modelos evolutivos previos. Con el objetivo de comprender los cambios florísticos durante la transición del Triásico al Jurásico en la Argentina, calculamos índices de diversidad, proporciones de supervivencia y tasas de origen y extinción, a partir del registro megafosilífero. Los resultados indican que, aunque sólo un linaje desapareció en el Triásico Tardío (Pleuromeiaceae), se produjo un cambio de vegetación importante pero gradual en el límite Triásico–Jurásico. Los linajes diagnósticos del Triásico Tardío pasaron al Jurásico, pero la mayoría con pocos registros y se extinguieron en el Jurásico Temprano. Los cambios florísticos durante

el Jurásico pueden ser correlacionados con las fluctuaciones paleoclimáticas. Las Osmundaceae, Dipteridaceae y Bennettitales se diversificaron en el Sinemuriano. Se reconoce un aumento en la riqueza taxonómica en el Toarciano, marcado por la diversificación de las coníferas. En el Bathoniano–Kimmeridgiano adquirieron una mayor importancia las coníferas y bennettitales. El conjunto de datos podría ser mejorado en el futuro intensificando el muestreo de fósiles para obtener resultados más sólidos y precisos.

Palabras clave: Mesozoico, Sudamérica, paleofloras, extinción

INTRODUCTION

The Triassic–Jurassic transition, which extends from the Late Triassic through the Early Jurassic (~237 Ma to 174 Ma), was an important interval in Earth's history (Schoepfer et al. 2022). The End-Triassic mass extinction (ETME), at ~201.5 Ma, ranks among the 'Big Five' Phanerozoic mass extinctions (Raup and Sepkoski 1982, Bambach 2006). Significant losses have been recorded in all marine habitats and some terrestrial communities (Wignall and Atkinson 2020, and references cited therein). In addition, the Triassic–Jurassic transition encompasses a second-order mass extinction during the early Toarcian Oceanic Anoxic Event (T-OAE), at ~181 Ma (Harries and Little 1999, Schoepfer et al. 2022).

The ETME was triggered by Central Atlantic Magmatic Province (CAMP) magmatism (Marzoli et al. 1999), and the T-OAE by Karoo-Ferrar Large Igneous Province (KFLIP) magmatism (Pálfy and Smith 2000), both associated with the stepwise disintegration of the Pangean supercontinent (Schoepfer et al. 2022). Large outgassing of CO_2, CH_4, and SO_2, driven by CAMP, is believed to have triggered ETME through a series of cascading environmental perturbations, including changes in the global carbon cycle, rapid warming leading to "hyperthermic" climate events and increased continental weathering (Fox et al. 2022, and references cited therein).

Because there are few adequate fossiliferous sections globally, the ETME and the subsequent biotic recovery are not as well-known as other mass extinctions (Damborenea et al. 2017). However, in recent years it gained greater interest. Numerous publications increased our understanding of the event's causes, consequences, and extent (e.g. Bonis and Kürschner 2012, Haworth et al. 2012, Petersen and Lindström 2012, Blackburn et al. 2013, Bond and Wignall 2014, Pálfy and Kocsis 2014, van de Schootbrugge and Wignall 2016, Barbacka et al. 2017, Lindström 2021).

The impact of the ETME on terrestrial plants diversity is less understood than on terrestrial animals. Estimating the severity of the crisis in land plants is complicated by provinciality and conflicting records between extinctions based on fossil leaf taxa and those based on spores and pollen (Bond and Wignall 2014, Lindström 2016, Barbacka et al. 2017). Local extinctions in spore and pollen taxa vary globally between 17 and 73% and for most of the taxa that went extinct, the parent plant affinity is not fully resolved or even unknown (Lindström 2016). Likely, many of the spore-producing plants that disappeared at the end of the Rhaetian or in the earliest Hettangian were plants with ecological preferences that resulted in low preservation potential for their macroscopic remains, e.g. epiphytic plants or plants growing in sites with little potential for fast burial (Lindström 2021).

The response of the terrestrial vegetation to this crisis is debated with some authors suggesting that no abrupt floral extinction but gradual shifts took place across the Triassic–Jurassic transition (Lucas and Tanner 2015, Barbacka et al. 2017, Cascales-Miñana et al. 2016, 2018), while others present major turnovers (McElwain et al. 2007, Bonis and Kürschner 2012, de Jersey and McKellar 2013, Lindström et al. 2017, Gravendyck et al. 2020, Zhang et al. 2020). Macroflora records from East Greenland and southern Sweden show that the Late Triassic *Lepidopteris* flora was replaced by the Early Jurassic *Thaumatopteris* flora (Lundblad 1959, McElwain et al. 1999, 2007, Kustatscher et al. 2018). On the Southern Hemisphere record, the Triassic seed-fern dominated flora was replaced by a more complex flora with conifers (cheirolepids), bennettitaleans, and new seed-ferns during the Early Jurassic (Turner et al. 2009). In China, the Late Triassic *Dictyophyllum-Clathropteris* macroflora was substituted by the Early Jurassic *Ptilophyllum-Coniopteris* flora (Ye et al. 1986). In European successions, Rhaetian palynological assemblages are characterized by the abundance of the gymnosperm pollen *Ricciisporites tuberculatus* Lundblad —recently interpreted as produced by the peltasperm *Lepidopteris ottonis* (Goepp.) Schimp. by Vajda et al. 2023—, followed by a fern spore spike across the Triassic–Jurassic transition, and high abundances of *Classopollis* (Hirmerellaceae= Cheirolepidiaceae) in the Lower Jurassic successions (Götz et al. 2009, Larsson 2009, van de Schootbrugge et al. 2009, Bonis et al. 2009, 2010, Pieńkowski et al. 2012, Vajda et al. 2013). A fern spike was also identified within the Triassic–Jurassic sedimentary succession in North America, followed by the dominance of *Classopollis meyeriana* (Klaus) de Jersey in the Lower Jurassic successions (Olsen et al. 2002, Whiteside et al. 2007). In China, the Upper Triassic *Dictyophyllidites-Kyrtomisporis-Ovalipollis-Ricciisporites* palynological assemblage is replaced by the Lower Jurassic *Dictyophyllidites-Classopollis-Cycadopites* assemblage (Lu and Wang 1987, Wang et al. 2010). Rhaetian palynofloras from the Southern Hemisphere (New Zealand) are dominated by lycophyte spores and corystosperm pollen, followed by a high abundance of bryophyte spores in the uppermost Rhaetian, elevated osmundaceous fern spore quantity in the Hettangian, and profuse *Classopollis* occurrence in the Sinemurian (Akikuni et al. 2010, de Jersey and McKellar 2013). Similar stratigraphical abundance patterns were observed in eastern Australian records across the Triassic–Jurassic transition, with a large number of fern and bryophyte spores in the uppermost Rhaetian, and common cheirolepid pollen occurrences in the Hettangian and Sinemurian (de Jersey and McKellar 2013).

It was suggested that very few plant families became extinct during the End-Triassic crisis, as the seed ferns of the family Peltaspermaceae (McElwain and Punyasena 2007), and Umkomasiaceae (=Corystospermaceae) (Iglesias et al. 2011), being the overall balance of plant groups essentially similar in Hettangian and Rhaetian floras (Cascales-Miñana et al. 2018). For example, cheirolepid conifers originated before the Triassic/Jurassic boundary, and were affected by the extinction, but became markedly dominant in the Early Jurassic, up to >90% in many assemblages (Whiteside et al. 2007, Lindström 2016). However, in lower taxonomic levels, extinctions are estimated to be higher, with up to 95% of species locally in Greenland and Sweden (McElwain et al. 1999). In other parts of central Europe (e.g., Austria, Poland), plant diversity increased across the Triassic-Jurassic boundary, probably due to climatic warming resulting from redirected oceanic currents (Cascales-Miñana et al. 2018). The macroflora of Poland show no extinction event as the statistical analyses did not signal any significant difference in plant composition between the Rhaetian and Hettangian stages (Barbacka et al. 2017).

Other authors argued that the crisis among land plants at the end of the Triassic was profound from an ecological perspective (McGhee et al. 2013, Lindström 2016). In the United Kingdom and Austria, a replacement of Triassic broad-leaved forms with Jurassic narrow-leaved forms was seen, which may have been favored by the warming associated with increased atmospheric carbon dioxide levels (Belcher et al. 2010). In Greenland and Sweden, the sequences through the Triassic/Jurassic boundary reveal clear evidence of disruption to the vegetation: changing stomatal densities and carbon isotopes indicate a marked increase in atmospheric CO_2, and abundant fusain suggests extensive wildfires (McElwain et al. 1999). Combined mercury and teratology records demonstrate that terrestrial plants in Northwestern Europe were subject to mutagenesis correlative with CAMP volcanism. Thus, in addition to environmental stress from global warming and sulfuric acid deposition due to emissions from CAMP (Steinthorsdottir et al. 2011, 2018), mercury-induced phytotoxicity may have played a role in the demise of Late Triassic land plants (Lindström et al. 2019).

The rapidity of the event has also been discussed. Wignall and Atkinson (2020) showed that it can be resolved into two distinct, short-lived extinction pulses separated by a several hundred-thousand-year interlude phase, both consistent precisely with turnover and extinction losses in the palynological record in Europe. The first one coincides with the decline of conifer pollen and diversity reduction followed by the interlude phase, with assemblages dominated by fern spores. The second extinction corresponds to another abrupt palynological change, which is the loss of several pollen taxa, and the brief proliferation of *Classopollis* (Wignall and Atkinson 2020).

The biotic crisis related to the rapid global warming and oceanic oxygen deficiency during the early Toarcian Oceanic Anoxic Event (T-OAE) has long been considered a major event in the marine realm (Harris and Little 1999, Ullmann et al. 2014), and records of the effects on terrestrial ecosystems have remained scant. However, palynological studies of United Kingdom sequences have shown that during the T-OAE, terrestrial floras shifted from a high-diversity mixture of conifers, seed ferns, wet-adapted ferns, and lycophytes to a low-diversity assemblage dominated by cheirolepid conifers, cycads, and *Cerebropollenites*-producers, which were able to survive in warm, drought-like conditions, and despite a rapid recovery of vegetation after the T-OAE, the overall community composition remained notably different than that previous to the event (Slater et al. 2019).

In Argentina it has been suggested that, towards the Triassic/Jurassic boundary, a floristic turnover occurred, which led to the disappearance of Umkomasiales (=Corystospermales) and Peltaspermales, an impoverishment in Cycadales, Ginkgoales, and Gnetales, and to a greater abundance of ferns (e.g. Gleicheniaceae, Dipteridaceae, Osmundaceae), bennettitaleans, and conifers (e.g. Araucariaceae, Cupressaceae, Podocarpaceae) (cf. Artabe et al. 2007a, Iglesias et al. 2011). Concerning megafloras, about 50 taxa of ferns, bennettitaleans, and conifers originate in the Early Jurassic, different from those recorded in the Triassic (cf. Artabe et al. 2007a, Iglesias et al. 2011).

However, in recent decades, new findings of plant megafossils and more accurate radiometric datings cast doubts on previously proposed evolutionary models. Based on their similarities in both macro- and micromorphology, a recent study considered *Alicurana* Herbst and Gnaedinger (an Early Jurassic cycad genus from Argentina) as a junior synonym of *Komlopteris* Barbacka emend. Slodownik et al., a genus assigned to a persistent lineage of post-Triassic corystosperms (Slodownik et al. 2023). *Lepidopteris* and *Dicroidium* lineages, dominant in Southern Hemisphere Triassic ecosystems, show a similar overall pattern of origination (Late Permian), diversification (late Early–Middle Triassic), and decline (Late Triassic), with relict occurrences during the Early Jurassic (Elgorriaga et al. 2019, Sagasti et al. 2019).

Few quantitative studies have been conducted on the Triassic–Jurassic megafloras of Argentina. Among them are the similarity analysis by Damborenea et al. (1975) on taphofloras from the Upper Triassic to the Lower Jurassic, and the contribution of Artabe et al. (2007a), which assesses diversity changes, extinction rates, and origination rates during the Middle Triassic to Early Jurassic interval.

The general purpose of this paper is to understand the terrestrial plant turnovers during the Triassic–Jurassic transition (End-Triassic Mass extinction event, the subsequent recovery, and the early Toarcian Oceanic Anoxic Event) in Argentina, based on megafossil records using a quantitative approach. Our results are compared with previous information and correlated with environmental and climatic changes. Though this analysis covers the Carnian–Berriasian time interval, it is mostly focused on the events occurring between the Rhaetian and the Oxfordian. Given that the information available about floristic changes in the Triassic–Jurassic transition is scarcer in the Southern Hemisphere than in the Northern Hemisphere, this work aims to provide data for the comprehension of plant evolution worldwide.

MATERIALS AND METHODS

Database assembly

In order to analyze the dynamics of the diversity of fossil plants in the Triassic–Jurassic interval in Argentina, a database was developed on the records of plant megafossils for the following lithostratigraphic units (formations), covering the time interval from the Carnian (Late Triassic) to the Berriasian (Early Cretaceous): Los Rastros and Ischigualasto (Ischigualasto-Villa Unión Basin); Carrizal (Marayes-El Carrizal Basin); Potrerillos, Cacheuta, and Río Blanco (Cuyo Basin); Chihuido, Llantenes, Paso Flores, Arroyo Malo, Lapa, El Freno, Nestares, Piedra del Águila, and Piedra Pintada (Neuquén Basin); Rancho de Lata (Frontal Cordillera); Santo Domingo (also known as Quebrada de Santo Domingo Formation, Northern Precordillera of La Rioja); Cerro Piche (North Patagonian Massif); unnamed formation at Cerro Bayo, Lonco Trapial, Cañadón Asfalto, and Cañadón Calcáreo (Cañadón Asfalto Basin); Roca Blanca, La Matilde, and Chon Aike (Deseado Massif); and Sprinhgill (Austral Basin) (Fig. 1). We considered the ages of each formation as indicated by the geochronological dating when available, or by biostratigraphic criteria when that information is controversial or not feasible. Based on radioisotopic information, the Los Rastros Formation is considered Carnian (234.47 ± 0.44 Ma; Mancuso et al. 2020), while the Ischigualasto Formation is Carnian to Norian (231.4 to 225.9 Ma; Rogers et al. 1993, Martínez et al. 2011). The Carrizal Formation is correlated with the Ischigualasto Formation through paleofloristic and palynological associations (Morel et al. 2015, Césari et al. 2021, Colombi et al. 2021), assigning it to the Upper Carnian. The available radiometric information from the Potrerillos Formation includes U-Pb SHRIMP ages, which date the central part of the unit as Carnian (230.3 ± 2.3 Ma) (Spalletti et al. 2008). The biostratigraphic analysis of Bodnar et al. (2020) suggested that the Cacheuta Formation was deposited during the Carnian–Norian interval, and the Río Blanco Formation, during the Norian. Volkheimer and Papu (1993) analyzed the microfloristic assemblages recorded from the upper levels of the Chihuido Formation, and they assigned the flora to the Norian stage. The Llantenes Formation, which underlies the Chihuido Formation, was assigned to the Norian–Rhaetian *Dictyophyllum tenuiserratum-Linguifolium arctum-Protocircoporoxylon marianaensis* (DLM) Biozone (Spalletti et al. 1999, Morel et al. 2003), thus we referred this lithostratigraphic unit to that interval. The Paso Flores Formation was also ascribed to the DLM Biozone (Spalletti et al. 1999, Morel et al. 2003) and recently Gnaedinger and Zavattieri (2021) proposed that its paleobotanical contents represents the youngest Triassic flora known in Argentina; as a consequence, here we inferred a Rhaetian age for this formation. The Rancho de Lata Formation was suggested to have been deposited from the Rhaetian to the Sinemurian, but it can be differentiated into two sections according to its palynoflora: a Rhaetian lower section and a Hettangian–Sinemurian upper section (Álvarez et al. 1994). The Lapa Formation was considered as Rhaetian–Hettangian according to its fossiliferous content and stratigraphic relationships (Spalletti et al. 1991, Gulisano and Gutiérrez-Pleimling 1995). The Santo Domingo Formation was regarded as latest Triassic–earliest Jurassic in age based on radiometric, paleomagnetic, and paleontological evidence (Caminos et al. 1995, Coughlin 2000, Vizán et al. 2013), corresponding with doubts to the Rhaetian–Hettangian interval. The El Freno Formation was suggested Hettangian–Sinemurian on the basis of its paleofloristic assemblages and stratigraphical relationships (Spalletti et al. 2007, Lanés et al. 2013, Gnaedinger et al. 2015). The most recent sedimentological, environmental, and paleobotanical data support a Sinemurian age for the Nestares Formation (Sagasti et al. 2019). The calculated U-Pb SHRIMP age for the time of deposition of the tuffs of the Piedra del Águila Formation is 191.7 ± 2.8 Ma (Sinemurian) (Spalletti et al. 2010). The Cerro Piche formation was restricted to the Sinemurian–Pliensbachian interval by a combined U-Pb/Hf isotope study (Falco et al 2021). For the Piedra Pintada Formation, we followed the stance of Damborenea and Manceñido (1993) who assigned it to the Lower Jurassic (Pliensbachian), latter followed by Martínez and Olivera (2016). The ages of the Cañadón Asfalto Basin units were considered according to U-Pb geochronology carried out by Cúneo et al. (2013), which indicates a Sinemurian to Pliensbachian age for the Las Leoneras Formation and its equivalents (e.g. the unnamed formation at Cerro Bayo), a Pliensbachian to Toarcian age for the Lonco Trapial Formation, a Toarcian to Aalenian age for the Cañadón Asfalto Formation (extended to Bajocian by Ruiz Gonzalez et al. 2024), and an Oxfordian to Kimmeridgian age for the Cañadón Calcáreo Formation. The Roca Blanca Formation lacks radiometric ages, but an Early Pliensbachian to Toarcian age was suggested based on the fossil flora contents (Herbst, 1965, Gnaedinger and Herbst 2009), which can be delimited by the 180.1 ± 1.5 Ma age of the overlying Cerro Leon Formation (Guido et al. 2004). The Bahía Laura Group comprises the interdigitated deposits of the Chon Aike and La Matilde formations. According to the ages obtained by De Barrio (1993) and Pankhurst et al. (1993), 162 ± 11 Ma and 168 ± 1.9 Ma respectively, the Bahía Laura Group can be dated as Bathonian to Oxfordian–Kimmeridgian. Based on U-Pb radiometric dating, Lovecchio and Naipauer (2022) determined Tithonian to Hauterivian maximum ages for the deposition of the Springhill Formation. This unit can be differentiated into two sectors with fossil plant assemblages: Lago Argentino (Tithonian) and western Austral Basin (Berriasian–Valanginian) (Del Fueyo et al. 2021, Tomas and Acuña 2022).

Some Upper Triassic and Jurassic formations were not included due to uncertainties in the age of the fossil-bearing levels. The Laguna Colorada Formation (El Tranquilo Basin, Santa Cruz Province), which has long been regarded as Norian in age mainly based on occurrences of the *Dicroidium* paleoflora, was recently assigned to the Sinemurian due to results of U-Pb geochronology from rocks intercalated with the vertebrate-bearing levels (Pol et al. 2021). Until now, a new interpretation of the age of the plant-fossil-bearing levels of the Laguna Colorada Formation has not been published ac-

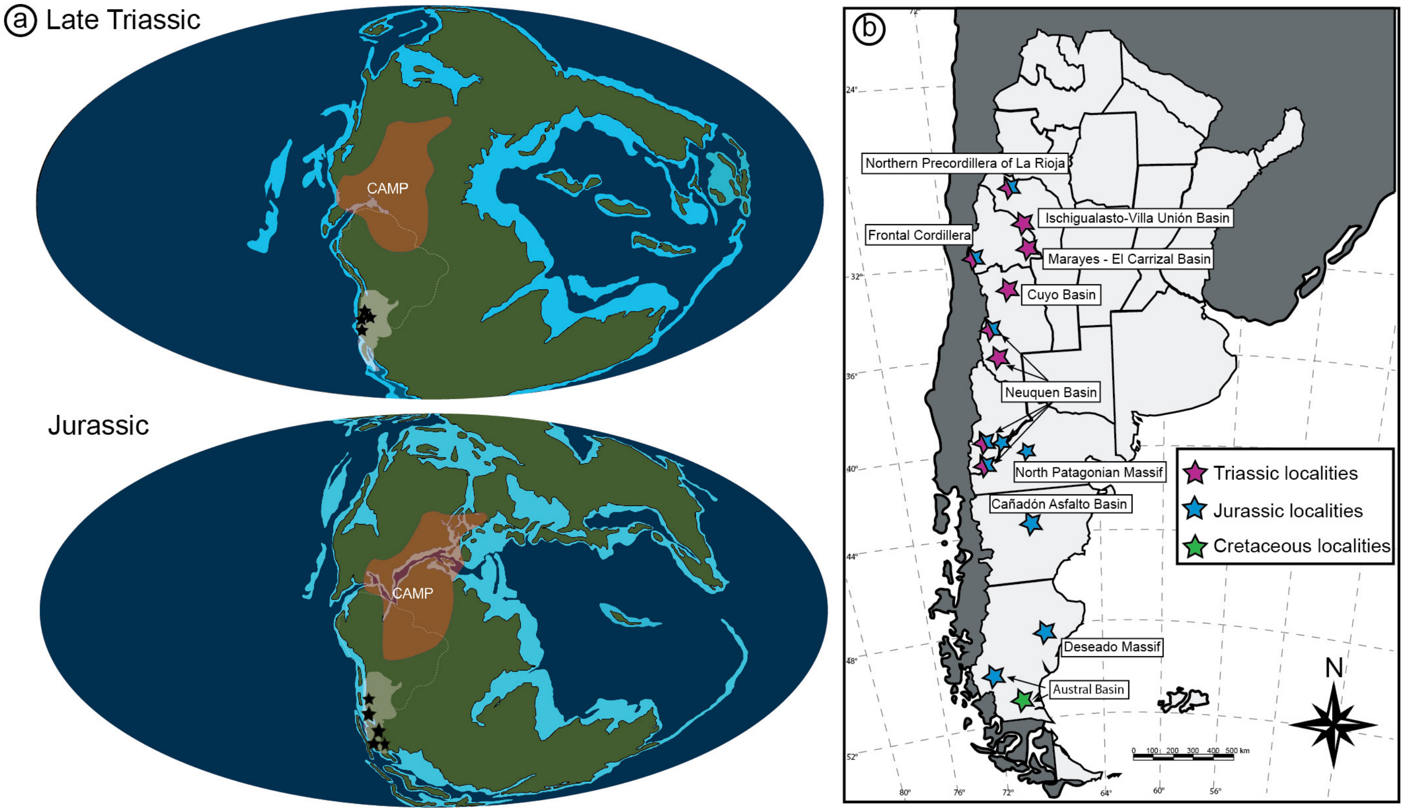

Figure 1. a) Paleogeographic maps of the Late Triassic and Jurassic, showing the locations of the Argentine basins included in the work (maps modified from http://www.scotese.com). b) Fossiliferous localities with Late Triassic, Jurassic, and Early Cretaceous floras analyzed in this work.

cording to the latest dating. The Cañadón Largo (El Tranquilo Basin, Santa Cruz Province), was inferred to be Ladinian–early Carnian in age because it underlies the Laguna Colorada Formation, previously assumed as Norian, and there is an important hiatus between them (Jalfin and Herbst 1995). Thus, the new age of the Laguna Colorada Formation will also change the inferred age of the Cañadón Largo Formation. The Cepeda Formation (Cuyo Basin, San Juan Province) is supposed to belong to the Upper Triassic, probably Carnian, but with doubts (Bodnar et al. 2019), and for that reason it was not considered for this analysis.

As many plant fossil assemblages were not precisely located stratigraphically along each formation, the age of each one is not known in detail. Accordingly, we had to consider that the age of each plant fossil assemblage was the same as that of the entire formation in which they occur. This may cause some imprecision in the calculated by-stage diversity, since several formations span long intervals, extending over more than one stage.

In the database, we incorporated the number of specimens of each species recorded in each formation. All fossilization types and organs were included, but when there is a whole-plant concept, only the species which gives its name to the reconstruction was counted. Data were taken from published data in the reference list available in Supplementary Material 1.

The database was prepared in various steps using MS Excel and Google Sheets (Supplementary Material 2). First, data were compiled in MS Excel, resulting in: a 1/0 (presence/absence) matrix for species per formation; a table with the ages to which the formations are assigned; and a species dataset with taxa by formation and stage, including the taxonomic assignment from class to species and the age of the record. Then, an occurrence dataset was gathered for each stage, with the collection number and the references where samples were originally published or reported. Early and Late interval, and the lower and upper boundaries, were restricted by each stage. In those cases where the formation appeared in two stages, the record was multiplicated. This was indicated by adding a suffix to the collection number. The full table was compiled in one sheet and exported as a .csv file.

Repositories of specimens.

The sample number indicated in the database corresponds to their repository number according to the bibliography (see Supplementary Material 1). These repositories are:

-BA Pb (Colección Nacional de Paleobotánica del Museo Argentino del Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina)

-BAFC-Pb (Colección de Paleobotánica de la Facultad de Ciencias Exactas y Naturales de la Universidad de Buenos Aires, Buenos Aires, Argentina).

-CIRGEO-PB (Centro de Investigaciones en Recursos Geológicos, Buenos Aires, Argentina)

-CORD-PB (Museo de Paleontología de la Facultad De Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, Argentina)

-CTES-PB (Colección Paleontológica de la Universidad Nacional del Nordeste, sección Paleobotánica, Corrientes, Argentina)

-DNGyM (Dirección Nacional de Geología y Minería, Buenos Aires, Argentina)

-FMNH-P (Field Museum of Natural History, Paleobotany Collection, Chicago, USA)

-IANIGLA-PB (Colección de Paleobotánica del IANIGLA-CCT CONICET Mendoza, Mendoza, Argentina);

-LIL-PB (Colección Paleobotánica de la Fundación Miguel Lillo, Tucumán, Argentina)

-LPPB (División Paleobotánica, Museo de La Plata, La Plata, Argentina)

-MAPBAR (Museo Paleontológico Bariloche, Bariloche, Argentina)

-MCF-PBPH (Colección Paleontológica del Museo Municipal “Carmen Funes”, Plaza Huincul, Argentina)

-MCNAM-PB (Colección Paleobotánica del Museo de Ciencias Naturales y Antropológicas “Juan Cornelio Moyano”; Mendoza, Argentina)

-MHNSR-PB (Museo de Historia Natural de San Rafael, San Rafael, Argentina)

-MLP (División Paleontología Invertebrados, Museo de La Plata, La Plata, Argentina)

-MNBP (Colección del Monumento Natural Bosques Petrificados, Jaramillo, Argentina)

-MPEF-PB (Museo Paleontológico “Egidio Feruglio”, Trelew, Argentina)

-MPM-PB (Museo Padre Jesús Molina, Río Gallegos, Argentina)

-Pb (Hunterian Museum -Palaeobotany-, Glasgow, United Kingdom)

-PBSJ (Colección Paleobotánica del Museo de Ciencias Naturales de San Juan, San Juan, Argentina)

When the repository numbers were not provided, the specimens were mentioned without them. Some of the fossil specimens are illustrated in Figures 2–4.

Taxonomic assignments and systematic affinities

The supra-generic taxonomic assignments were made ac-

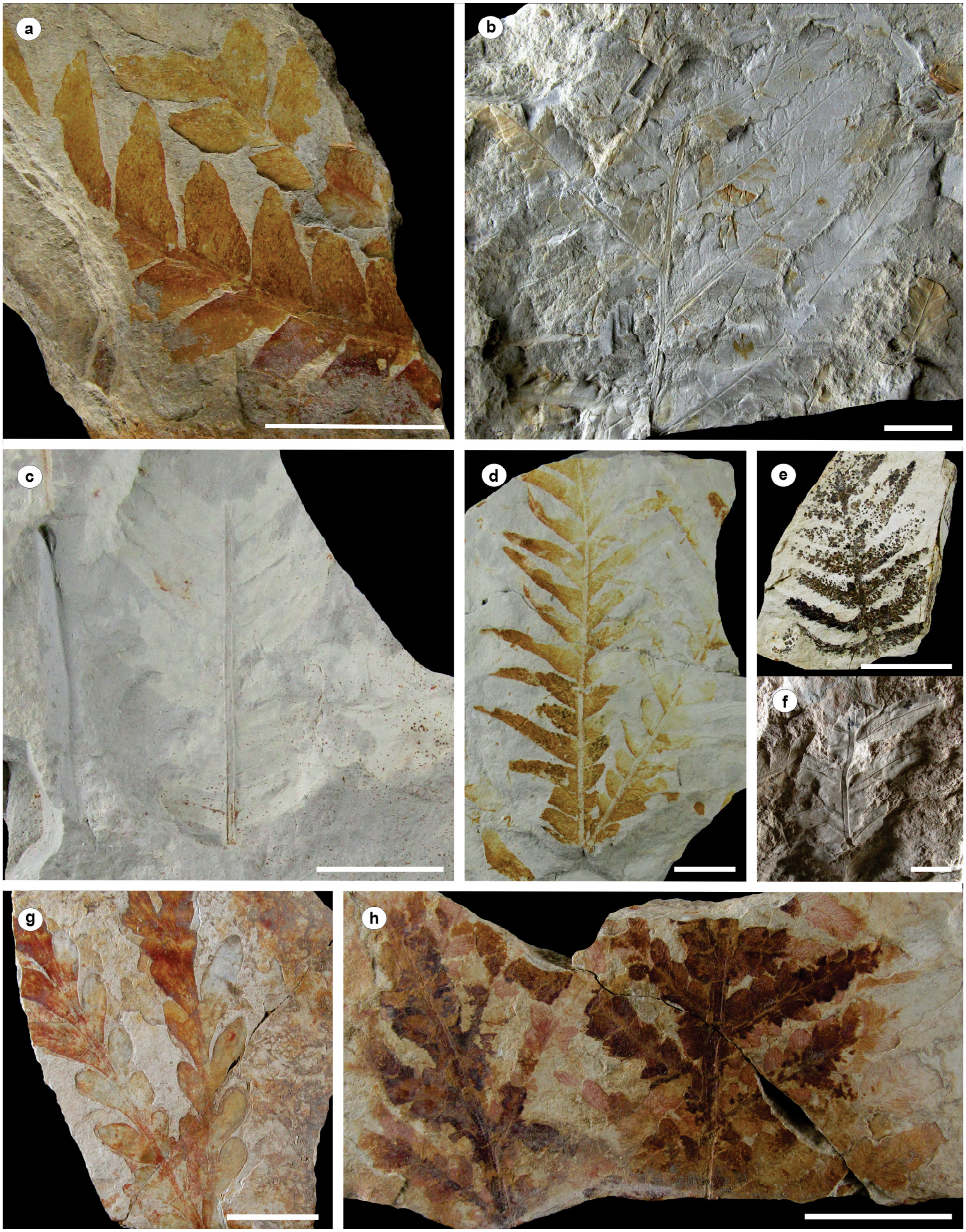

Figure 2. Representative flora of the Argentine Rhaetian. a) *Dicroidium odontopteroides* (Umkomasiaceae); Paso Flores Formation; LPPB 12519 (scale bar = 2 cm). b) *Cladophblebis kurtzi* (Osmundaceae); Paso Flores Formation; LPPB 12218 (scale bar = 2 cm). c) *Cladophblebis mendozaensis* (Osmundaceae); Paso Flores Formation; LPPB 12219 (scale bar = 2 cm). d) *Dicroidium lancifolium* (Umkomasiaceae); Paso Flores Formation; LPPB 12232 (scale bar = 2 cm). e) *Coniopteris harringtoni* (Dicksoniaceae?); Paso Flores Formation; LPPB 12222 (scale bar = 1 cm). f) *Dictyophyllum rothi* (Dipteridaceae); Paso Flores Formation; LPPB 12227 (scale bar = 2 cm). g) *Dicroidium crassum* (Umkomasiaceae); Paso Flores Formation; LPPB 12514 (scale bar = 1cm). h) *Zuberia sahnii* (Umkomasiaceae); Paso Flores Formation; LPPB 12520 (scale bar = 2 cm).

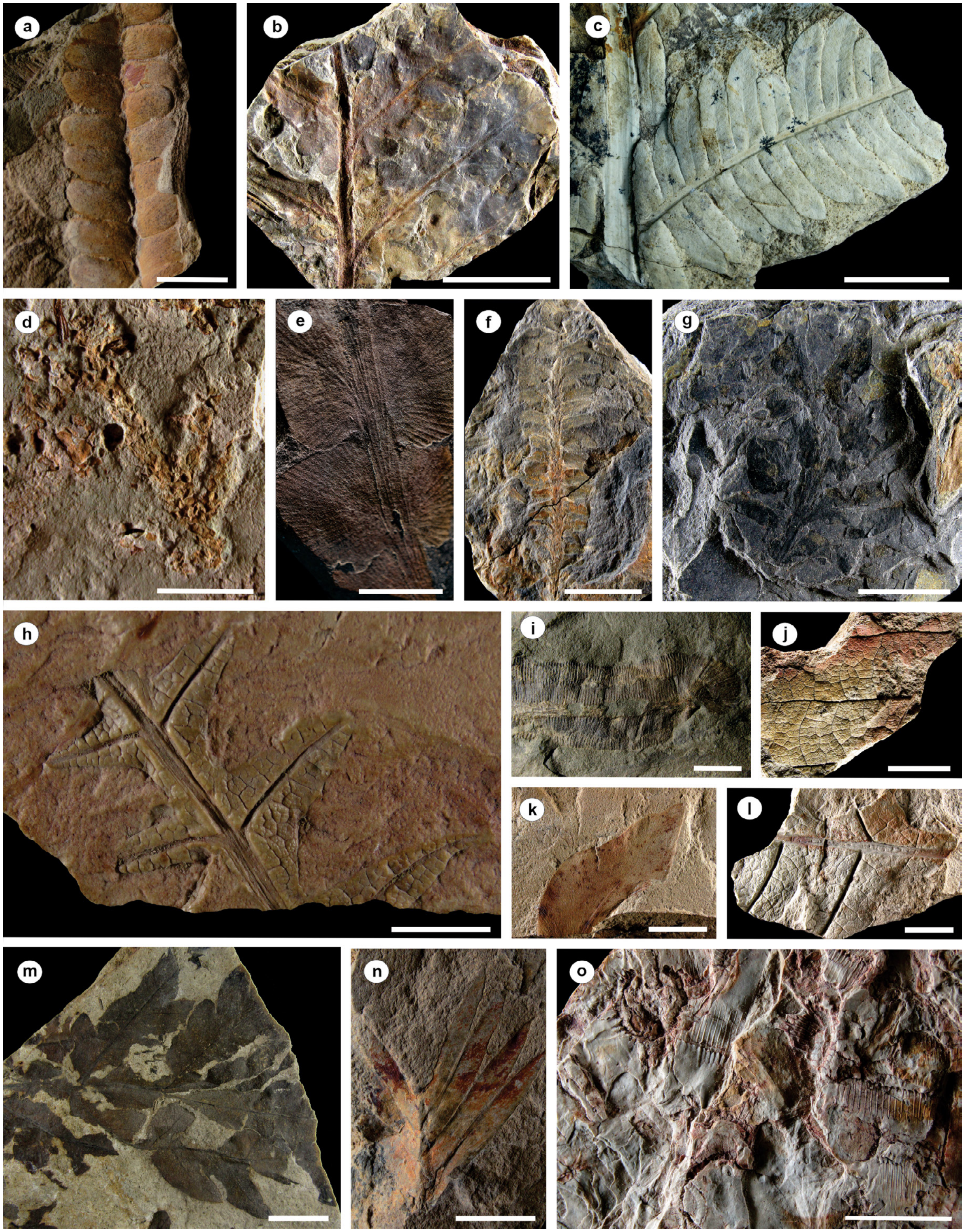

Figure 3. Representative flora of the Argentine Early Jurassic. a) *Otozamites albosaxatilis* (Bennettitales incertae sedis); Roca Blanca Formation; LPPB 6020 (scale bar = 1 cm). b) *Archangelskya protoloxoma* (Pteridosperm incertae sedis); El Freno Formation; LPPB 13200 (scale bar = 2 cm). c) *Cladophblebis antartica* (Osmundaceae); Nestares Formation; MAPBAR 5833 (scale bar = 2 cm). d) *Pagiophyllum* sp. (Coniferales incertae sedis); Lapa Formation; LPPB 12291 (scale bar = 2 cm). e) *Dicroidium odontopteroides* (Umkomasiaceae); Nestares Formation; MAPBAR 2317 (scale bar = 1cm). f) *Elatocladus conferta* (Coniferales incertae sedis); El Freno Formation; LPPB 13210 (scale bar = 1 cm). g) *Komlopteris artabeae* (Umkomasiaceae); Nestares Formation; LPPB 12263 (scale bar = 2 cm). h) *Dictyophyllum apertum* (Dipteridaceae); Piedra Pintada Formation; LPPB 3959 (scale bar = 1 cm). i) *Marattiopsis muensteri* (Marattiaceae); El Freno Formation; LPPB 13174 (scale bar = 1 cm). j) *Clathropteris obovata* (Dipteridaceae); Piedra Pintada Formation; LPPB 3983 (scale bar = 2 cm). k) *Sagenopteris nilssoniana* (Caytoniaceae); Piedra Pintada Formation; LPPB 5001 (scale bar = 2 cm). l) *Dictyophyllum rothi* (Dipteridaceae); Piedra Pintada Formation; LPPB 3953 (scale bar = 2 cm). m) *Goeppertella stipanicicii* (Dipteridaceae); Lonco Trapial Formation; LPPB 438 (scale bar = 2 cm). n) *Ptilophyllum aculifolium* (Bennettitales incertae sedis); El Freno Formation; LPPB 13203 (scale bar = 1 cm). o) *Equisetites patagonica* (Equisetaceae); Roca Blanca Formation; LPPB 5987 (scale bar = 2 cm).

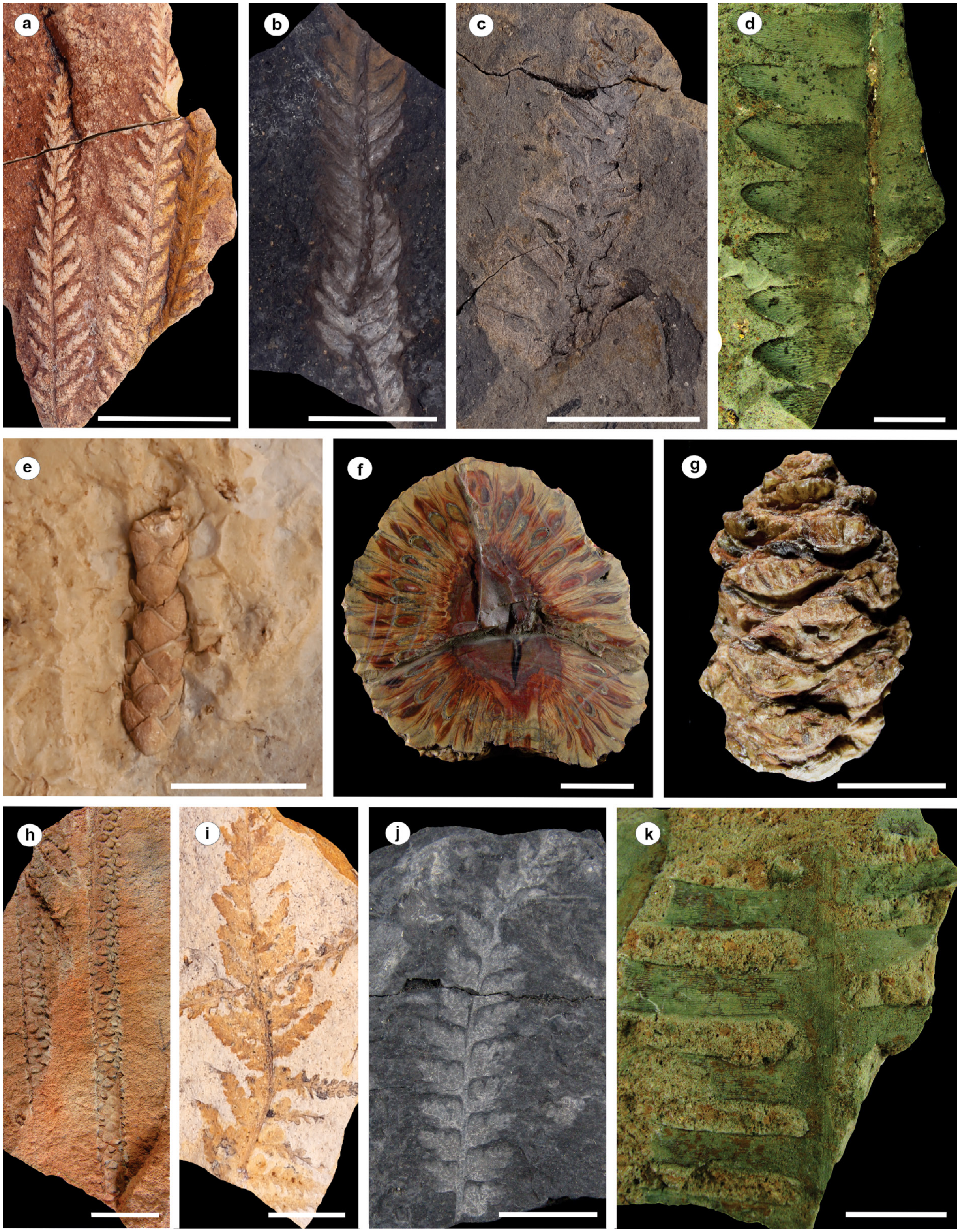

Figure 4. Representative flora of the Argentine Middle–Late Jurassic. a) *Korallipteris potrerillensis* (fern incertae sedis); Chon Aike Formation; MPM PB 15965 (scale bar = 2 cm). b) *Otozamites sanctae-crucis* (Bennettitales incertae sedis); Chon Aike Formation; MPM PB 15840 (scale bar= 2 cm). c) *Elatocladus conferta* (Coniferales incertae sedis); Chon Aike Formation; MPM PB 16000 (scale bar = 2 cm). d) *Dictyozamites latifolius* (Bennettitales incertae sedis); Chon Aike Formation; LPPB 11555 (scale bar = 2 cm). e) *Brachyphyllum lotenaense* (Coniferales incertae sedis); Chon Aike Formation; MPM PB 15982 (scale bar = 1 cm). f) ovulate cone of *Araucaria mirabilis* (Araucariaceae); La Matilde Formation; LPPB 8079 (scale bar = 2 cm). g) *Pararaucaria patagonica* (Hirmerellaceae); La Matilde Formation; LPPB 13748 (scale bar = 1 cm). h) leafy shoot of *Araucaria mirabilis* (Araucariaceae); La Matilde Formation; LPPB 13755 (scale bar = 2 cm). i) *Scleropteris vincei* (Tracheophyte incertae sedis); Chon Aike Formation; MPM PB 16006 (scale bar = 1 cm). j) *Coniopteris hymenophylloides* (Dicksoniaceae?); Springhill Formation; LPPB 11161 (scale bar = 1cm). k) *Pseudoctenis eathiensis* (Cycadales incertae sedis); Chon Aike Formation; LPPB 11543 (scale bar = 2 cm).

cording to those made in the references and updated in the corresponding cases (see References available as Supplementary Material 1). To organize the results concisely, some informal names of taxa were used, such as: pteridophytes (comprising free-sporing vascular plants, as lycophytes, sphenophytes, and ferns), pteridosperms or seed-ferns (containing peltasperms, corystosperms, petriellaleans, caytonialeans), cycadophytes (including cycadaleans, bennetitaleans, and nilssonialeans), and coniferophytes (grouping ginkgoaleans, czekanowskialeans, conifers, and gnetaleans).

We followed the most recently published and supported criteria for the affinity of each taxon, but there are still discrepancies or ambiguities with the systematic alliance of some genera that can lead to certain results to be carefully considered. One example is the genus *Cladophlebis*, which was usually assigned to the family Osmundaceae (see Van Konijnenburg-Van Cittert 1996, Artabe et al. 2007b), but its morphology also resembles that of Cyatheaceae or Schizaeceae among others (Skog and Dilcher 1994, Tidwell and Ash 1994). *Kurtziana* is a genus related both to the cycads (Artabe et al. 1991) or the seed-ferns (Bomfleur et al. 2011); however, we followed the first criterion because it is the most widely used in the Argentine Mesozoic literature. As both *Cladophlebis* and *Kurtziana* are taxa with several records in the Triassic–Jurassic of Argentina, they have relevance when limiting the temporal ranges of the lineages.

Another ambiguity related to the Triassic megafossil record of Coniferales (=derived conifers), which consists mainly of permineralized woods and leafy twigs, which are more equivocal than reproductive structures (see Bodnar et al. 2023). Consequently, the temporal ranges of Araucariaceae, Hirmerellaceae, and Cupressaceae could be narrowed if we adopt a more restricted proposal.

Calculated indices

The table (available as Supplementary Material 2) was then converted to .csv and imported in RStudio, where it was analyzed using DivDyn v.0.8.2 Package (Kocsis et al. 2019). Since this is an initial exploratory work, the equations provided in this package were used, following the premise of Kocsis et al. (2019) that studies are repeatable and can be continued by adding and improving information.

The value of species richness per stage was estimated based on the range-through assumption and including singletons, which are taxa described from only one collection and one stage. Species richness per stage of each plant lineage was estimated without the range-through assumption.

Diversity was estimated in each case by applying the DivDyn v.0.8.2 Package of the R software (Kocsis et al. 2019). The divDyn function calculates various metrics from occurrence data sets in the form of time series. Through this function, we calculated the following indexes of species and genera richness: Range-through diversity (divRT) (Newell 1952), Sampled-in-bin diversity (divSIB) (Miller and Foote 1996), and Corrected sampled-in-bin diversity (divCSIB) (Alroy et al. 2008). In this study, Range-through diversity considered all species or genera in the interval, that is, if a genus appeared in one geological interval and then disappeared later, one assumes that the species or genus existed for the entire time between its first and last known fossil occurrences, regardless of gaps that there may be on that geologic record. Sampled-in-bin diversity is the number of species or genera actually sampled in the focal bin or interval. It is a metric that avoids the range-interpolation bias, but it is more affected by changes in sampling intensity (Kocsis et al. 2022). Corrected sampled-in-bin diversity is a variant that corrects for residual error by assessing the proportion of species or genera found immediately before and after a sampling bin but not inside it (Alroy et al. 2008). Although this can be a convenient correction, it also increases the estimation error. Nevertheless, this is the least biased estimator for diversity (Kocsis et al. 2022). The diversity curves were compared with the number of occurrences in each time bin. For species diversity, we regarded the number of specimens of each species as occurrences, as provided by the references. For genera diversity, occurrences are the number of genera per formation, coming from the same collection. In this work, collections correspond to the references, as it is explained below.

We applied the function “ranges” to plot ranges and occurrence distributions through the Late Triassic–earliest Cretaceous interval and evaluated the First appearance data (FAD) and Last appearance data (LAD).

Extinction and origination rates at generic level were calculated with time-averaging by two methods: 1) per capita rates of Foote (1999) use the range-through assumption to establish ranges for the taxa in the dataset, the rate value expresses what proportion of the taxa decayed until the end of the interval or appeared at the beginning of the time-bin; and 2) ‘gap-filler’ rates (Alroy 2014), which is a different estimator of the per capita rates but will converge on them when sampling tends to completeness. We also estimated the proportions of survivorship at genus and species level using the “survivors” function, which calculates both forward and backward survivorship proportions from a given occurrence dataset. These are tools to visualize changes in the composition of a group over time (Raup 1978). The curves show how a once coexisting set of taxa, called a cohort, loses its participants (forward survivorship) as time progresses, or gains its elements as time is analyzed backward. Each value corresponds to a cohort in bin (a) and one other bin (b). The value expresses what proportion of the analyzed cohort (present together in bin a) is present in bin b.

Spearman Rank correlation coefficient was obtained to assess the correlations between the richness values and the number of collections where they occur. The collections refer to the fossil assemblages gathered by the same research team on a field trip (which coincides with the published reference). To assess the sampling biases across the different stages, sampling completeness was calculated using the three-timer sampling completeness function (Alroy 2008) at generic and specific levels.

RESULTS

Species richness

Figure 5a illustrates the Range-through diversity (divRT), Sampled-in-bin diversity (divSIB), and Corrected sampled-in-bin diversity (divCSIB) of species. During the Late Triassic, a severe reduction of the species richness is seen from the Carnian to the Norian, but in the Rhaetian, this decline was less pronounced (divRT and divCSIB) or even the values slightly increased (divSIB). The results indicate that the species richness in the Hettangian was reduced to half of the values recorded in the Rhaetian (divRT and divSIB), although according to (divCSIB) this reduction was much more moderate. The divRT and divSIB curves show that in the Sinemurian the number of species grew, but to less than observed in the latest Triassic. This pattern is not observed in divCSIB curve, which drops from the Hettangian to the Toarcian without clear peaks in the interval. If we consider the occurrences, the Sinemurian has a significantly higher value than the Hettangian, which could be influencing the observed increase in divRT and divSIB curves. However, this effect is not reflected in the divCSIB curve, as the latter is the least affected by sampling intensity. A decrease in species richness was documented from the Pliensbachian to the Bajocian in all the curves, and then an increase was recorded in the Bathonian and another in the Oxfordian. In the Tithonian, the species richness was strikingly reduced. During the Jurassic, species richness (per age) did not reach the Late Triassic values.

When the diversity curve is compared with the occurrences (Fig. 5b), the stages in which the species richness was greater agree with those with larger number of records and collections. The Pliensbachian has the highest number of occurrences; however, the diversity curve slightly dropped in this stage. Spearman's rank correlation coefficient is 0.6433087,

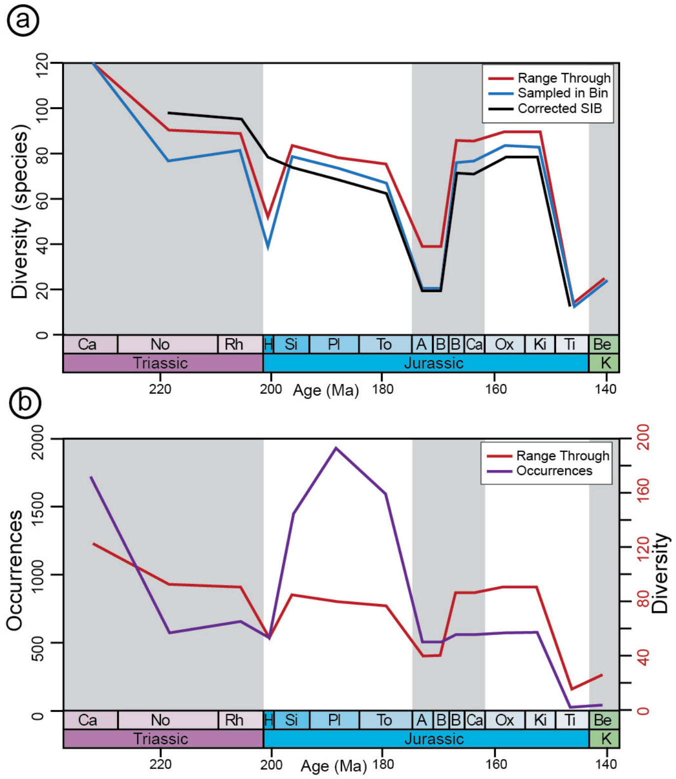

Figure 5. a) Diversity (richness) curves at species level in the Late Triassic–Late Jurassic interval of Argentina. b) Range-through diversity compared with the occurrences of each species per stage in Argentina. Black numbers: scale used for the occurrences; red numbers: scale used for the diversity curve.

Table 1. Values of three-timer sampling completeness of each stage for species and genera.

	Three timer sampling completeness	
Stage	Species	Genera
Carnian		
Norian	0,72727273	0,8
Rhaetian	0,8	0,85714286
Hettangian	0,45454545	0,64705882
Sinemurian	1	1
Pliensbachian	1	1
Toarcian	1	1
Aalenian	0,95238095	1
Bajocian	1	1
Bathonian	1	1
Callovian	1	1
Oxfordian	1	1
Kimmeridgian	1	1
Tithonian	1	0,625
Berriasian		

which indicates a moderate to high positive correlation between species richness and occurrences. The p-value equals 0.009672 (less than 0.05) which means that the correlation is statistically significant. The sampling completeness shows

Table 2. Species richness per plant lineage (without range through assumption) in each stage of the Late Triassic–earliest Cretaceous interval based on occurrences from Argentina. Abbreviations: Ca = Carnian, No = Norian, Rh = Rhaetian, He = Hettangian, Si = Sinemurian, Pl = Pliensbachian, To = Toarcian, Aa = Aalenian, Baj = Bajocian, Bat = Bathonian, Ca = Callovian, Ox = Oxfordian, Ki = Kimmeridgian, Ti = Tithonian, Be = Berriasian, i.s.= incertae sedis.

Plant group / Stage	Ca	No	Rh	He	Si	Pl	To	Aa	Baj	Bat	Cl	Ox	Ki	Ti	Be
Marchantiopsida i.s.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bryopsida i.s.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lycopodiaceae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuromeiaceae	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Isoetaceae	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0
Neocalamitaceae	4	1	0	1	3	0	0	0	0	0	0	0	0	0	0
Equisetaceae	1	1	1	1	4	5	3	1	1	2	2	3	3	0	0
Equisetales i.s.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asterothecaceae	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Marattiaceae	0	0	1	1	2	1	0	0	0	0	0	0	0	0	0
Osmundaceae	7	6	5	6	11	8	5	2	2	7	7	7	7	2	2
Gleicheniaceae	0	0	0	0	2	1	1	1	1	0	0	0	0	0	1
Dipteridaceae	0	2	6	4	11	13	7	0	0	2	2	2	2	0	0
Matoniaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Dicksoniaceae?	1	0	1	0	0	2	2	0	0	1	1	2	2	1	0
Ferns i.s.	0	0	0	0	0	2	2	0	0	1	1	1	1	0	0
Umkomasiaceae	31	16	13	1	3	0	0	0	0	0	0	0	0	0	0
Peltaspermaceae	7	0	0	0	0	0	2	2	2	0	0	1	1	0	0
Mattatielaceae	4	2	2	1	1	0	0	0	0	0	0	0	0	0	0
Petriellaceae	5	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Caytoniaceae	0	0	0	1	3	6	5	0	0	0	0	0	0	1	1
Pteridosperms i.s.	1	0	0	2	3	2	1	1	1	1	1	2	2	0	0
Zamiaceae	2	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Cycadales i.s.	5	3	4	0	0	0	0	0	0	2	2	2	2	0	1
Nilssoniaceae	1	3	3	0	1	0	0	0	0	0	0	0	0	0	0
Williamsoniaceae	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0
Benettitales i.s.	0	0	0	7	14	12	9	0	0	18	18	18	18	4	12
Cycadophyta i.s.	6	4	5	2	3	0	0	0	0	0	0	0	0	0	0
Ginkgoaceae	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0
Hamshawviaceae	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ginkgoales i.s.	11	6	8	0	0	1	1	0	0	1	1	1	1	0	2
Czekanowskiaceae	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Czekanowskiales i.s.	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Voltziaceae	5	3	4	1	1	0	0	0	0	0	0	0	0	0	0
Hirmeriellaceae	1	0	0	0	0	1	2	1	1	2	2	3	3	0	0
Araucariaceae	1	0	0	1	2	3	3	1	1	13	13	14	14	2	2
Cupressaceae	1	2	2	0	2	2	2	2	2	3	3	3	3	0	0
Podocarpaceae	3	4	4	1	1	0	0	0	0	4	4	4	4	0	0
Coniferales i.s.	0	6	7	4	4	6	9	5	5	14	14	15	15	3	4
Gnetales i.s.	10	5	3	0	0	1	1	0	0	0	0	0	0	0	0
Coniferophytes i.s.	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0
Gymmosperms i.s.	6	8	5	0	0	2	3	1	1	0	0	0	0	0	0
Tracheophytes i.s.	0	0	1	1	4	3	5	3	3	5	5	5	5	0	0
Total	**122**	**77**	**82**	**38**	**79**	**74**	**67**	**21**	**21**	**77**	**77**	**84**	**84**	**14**	**25**

scores higher than 0.9 in all the Jurassic stages except for the Hettangian, in which the lowest sampling completeness is recorded. That is the reason why the diversity decreases in this stage are less marked in CSIB metrics (Table 1, Fig. 5).

Regarding the species richness of each plant lineage (Table 2), the corystosperms (Umkomasiaceae) were the most diverse group in the Carnian, Norian, and Rhaetian, with 31, 16, and 13 species, respectively (see also Fig. 2). This family passed just as relicts to the Early Jurassic with four species (Table 2, Fig. 3). Other gymnosperm orders important during the Late Triassic were the Peltaspermales (Peltaspermaceae and Mattatiellaceae), Petriellales, Cycadales, Ginkgoales, and Gnetales. All these orders occurred in the Jurassic but only with very few species. During the Hettangian, the species richness of each recorded order or family did not exceed four species. The bennetittaleans, with 14 species, and the dipteridacean and osmundacean ferns, with 11, were the lineages with greatest specific richness in the Sinemurian (Table 2, Fig.3). The dipteridacean species richness decreased from the Toarcian onwards. On the contrary, osmundacean ferns diversified again in the Bathonian. A diminution of the bennettitalean richness is observed from the Pliensbachian, but they became the most diverse plant lineage during the Bathonian–Kimmeridgian. The modern conifer lineages showed a progressive diversification from the Sinemurian, and in the Oxfordian and Kimmeridgian, the Araucariaceae and Podocarpaceae were the most diverse conifer families (Table 2, Fig. 4). In the studied interval, the Marchantiopsida, Bryopsida, and the lycopodiacean lycophytes were recorded only in the Carnian, with one species each. Pleuromeiacean and isoetacean lycophytes were present in the Carnian–Norian and Bathonian–Kimmeridgian, respectively, also with one species each. Within sphenophytes, the family Equisetaceae shows species richness values quite stable from the Late Triassic to the Late Jurassic, with one to five species, while Neocalamitaceae (= Apocalamitaceae) reached four species in the Carnian, three in the Sinemurian, and disappeared afterward.

Genus richness

The calculated diversity curves (divRT, divSIB, and divCSIB; Fig. 6a) show a decrease between the Rhaetian and Hettangian, and a slight rise in the Sinemurian (divRT and divSIB) or in the Toarcian in the corrected-sample diversity (divCSIB). As in species richness, the Sinemurian has the greatest number of genera occurrences, which could influence the observed increase in divRT and divSIB curves. During the Jurassic, the genera richness did not reach the same levels as in the Rhaetian. Diversity increased in the Toarcian (divRT, divSIB, and divCSIB) and the Bathonian (divRT, and divCSIB) or Callovian (divSIB). A general diminution in genera richness was recorded after the Oxfordian (divRT, divSIB, and divCSIB). The stages with the greatest plant diversity in the Jurassic are different depending on the estimator: the Toarcian for the divRT, the Toarcian, Bathonian, Callovian, Oxfordian, and Kimmeridgian for divSIB, and the Oxfordian and Kimmeridgian for divCSIB diversity.

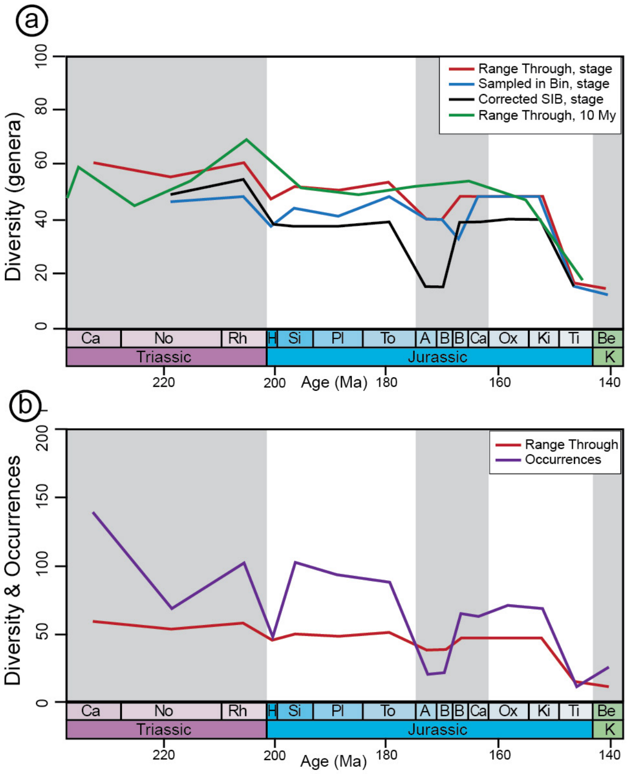

Figure 6. a) Diversity (richness) curves at genera level in the Late Triassic–Late Jurassic interval of Argentina; in green, range-through diversity with a 10-million-year bin resolution. b) Range-through diversity compared with the occurrences of each genus per stage in Argentina.

When the diversity curve is compared with the occurrences (Fig. 6b), the stages in which the genera richness was greater coincide with those with the largest number of records. Spearman's rank correlation coefficient gives a value of 0.4555421, which indicates a moderate positive correlation between the genera richness and occurrences. The p-value equals 0.08793 (greater than 0.05) which means that the correlation is not statistically significant. In summary, although there appears to be a moderate positive correlation between the two variables, it is not significant at the common threshold of 5% (p-value <0.05).

Comparing the diversity curves of different plant groups (Fig. 7–8), seed plants (Fig. 7) underwent a marked reduction of the genera richness between Rhaetian and Hettangian, and a general decrease from the Late Triassic to the Late Juras-

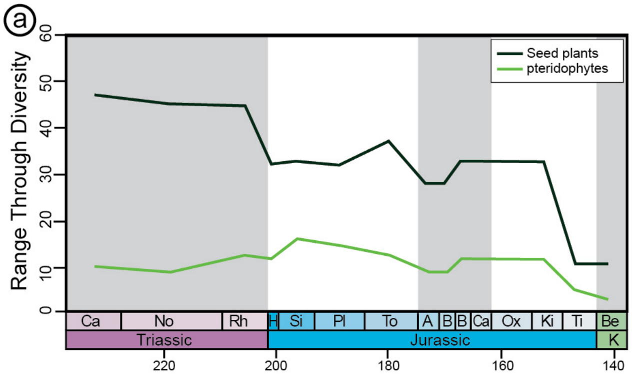

Figure 7. Comparison of the range-through diversity at generic level of the seed plants (gymnosperms) and pteridophytes or free-sporing vascular plants (lycophytes, sphenophytes, and ferns) in the Late Triassic–Late Jurassic interval of Argentina.

sic, while these trends were less significant for free-sporing vascular plants (pteridophytes). This last plant group went through genus-level diversification in the Sinemurian and Pliensbachian, impoverishment in the Aalenian-Bajocian, and a recovery from the Bathonian (Fig. 7, 8a). Within seed plants, the pteridosperms (Umkomasiales, Peltaspermales, Petriellales, Caytoniales, and incertae sedis pteridosperms) show a gradual reduction of the diversity from the Late Triassic to the Late Jurassic, with a mild recuperation during the Sinemurian and Toarcian (Fig. 8b). The divRT curve of cycadophytes (Cycadales, Nilssoniales, and Bennettitales) exhibits minor changes from the Late Triassic to the Late Jurassic, but with the major values in the Sinemurian and Bathonian to Kimmeridgian (Fig. 8c). The divSIB curve of this group also shows the peaks in the Sinemurian and Bathonian–Kimmeridgian, being, in this case, more noticeable. In both curves, a reduction of the cycadophyte genera richness is not recorded between the Rhaetian and Hettangian. The coniferophytes (Voltziales, Coniferales, Ginkgoales, Czekanowskiales, and Gnetales) genus-level diversity diminished in the Hettangian, progressively increased up to the Toarcian, and experimented a peak in the Bathonian–Kimmeridgian (Fig. 8d). The sampling completeness shows the highest values between the Sinemurian and the Kimmeridgian, and the lowest scores in the Hettangian and Tithonian (Table 1).

Occurrences

The number of occurrences of free-sporing vascular plants was much greater in the Pliensbachian than in other analyzed stages (Fig. 9a), with Dipteridaceae and Osmundaceae being the most representative families (Figs. 9a, 9b). The occurrences for Neocalamitaceae abruptly dropped in the Rhaetian and Hettangian and persisted up to the Sinemurian as relicts. The families Dipteridaceae, Osmundaceae, and Equisetaceae

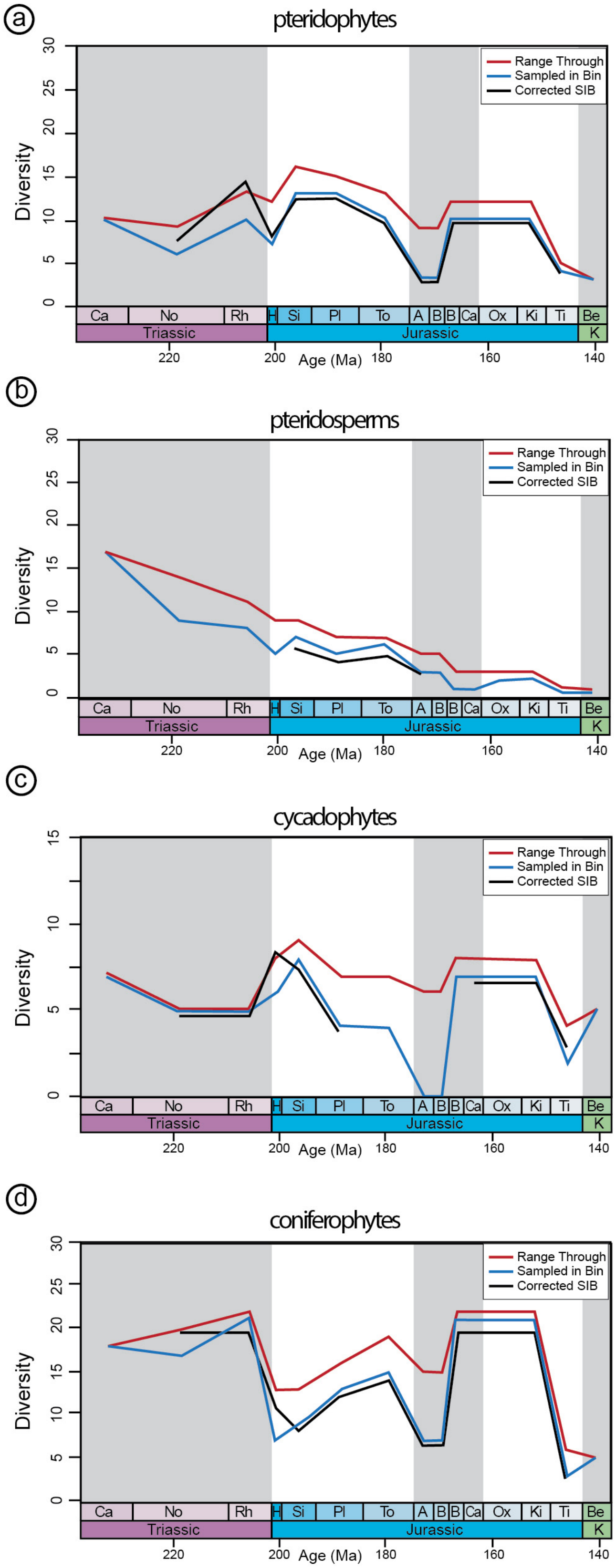

Figure 8. Diversity (richness) curves at genera level of different plant groups in the Late Triassic–Late Jurassic interval of Argentina. a) Pteridophytes. b) Pteridosperms or seed ferns. c) Cydadophytes. d) Coniferophytes. CSIB is interrupted when the values for three-timer sampling completeness are 1.

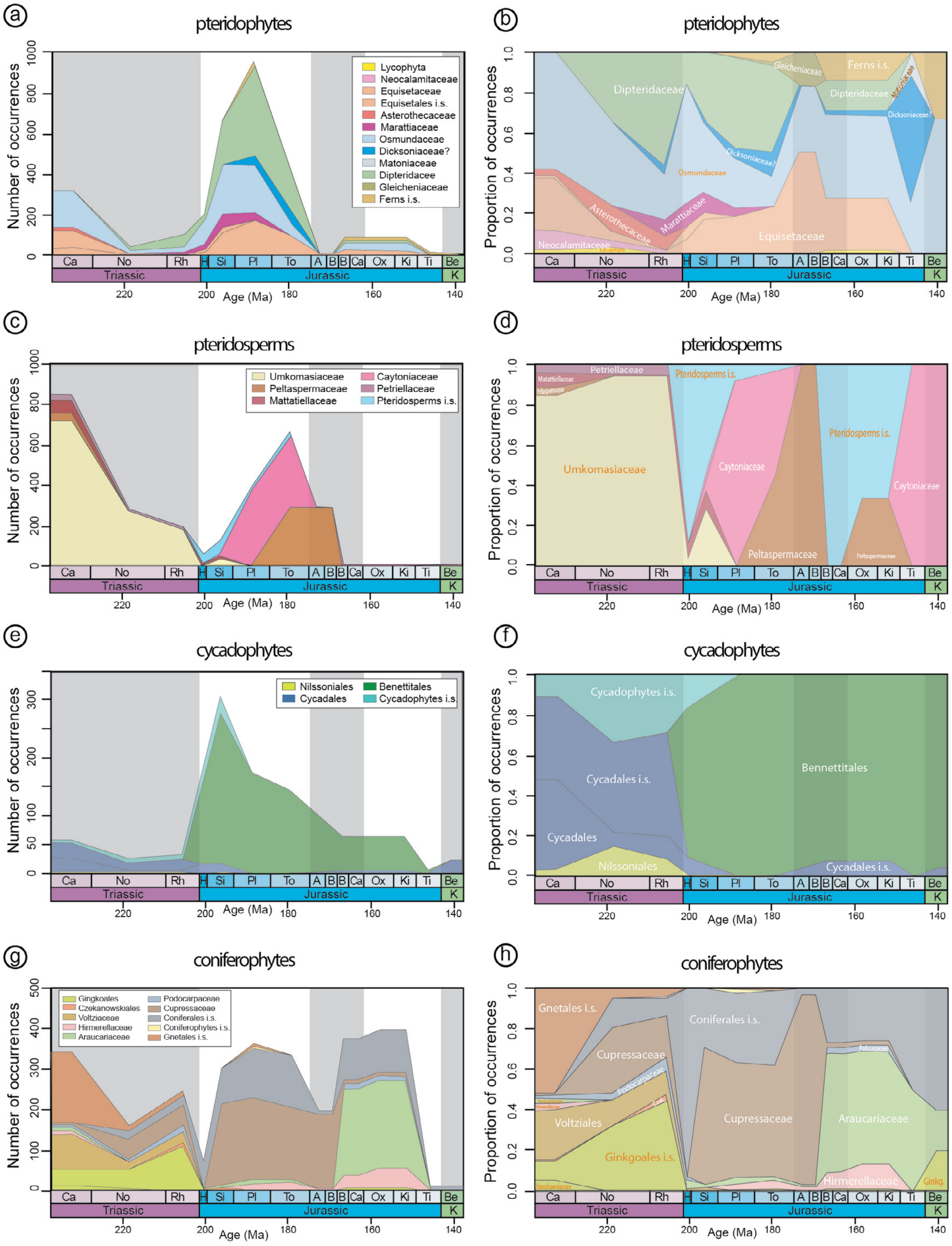

Figure 9. Number of occurrences and proportion of occurrences of each plant group in the Late Triassic–Late Jurassic interval of Argentina. a-b) Pteridophytes. c-d) Pteridosperms. e-f) Cycadophytes. g-h) Coniferophytes.

were the most frequent in the Early Jurassic (Figs. 4, 9a, 9b), whereas in the Middle Jurassic, the most common were the Osmundaceae. The number of pteridophyte records abruptly declined in the Late Jurassic. Considering the proportion of occurrences (Fig. 9b), Osmundaceae was a dominant family within ferns during almost all the studied interval, Dipteridaceae was important in the Rhaetian and Early Jurassic, Equisetaceae increased its representation throughout the Jurassic, and Gleicheniaceae was more relevant in the latest Early and earliest Middle Jurassic. As the few fern fossil records during the Tithonian correspond to specimens assigned to *Coniopteris*, which is a putative Dicksoniaceae genus, the importance of this family in the Late Jurassic is overrated. Lycophytes were very infrequent in the studied bin.

The occurrences of pteridosperms severely declined from the Carnian up to the Hettangian, increased from the Sinemurian up to the Toarcian, and dropped again from the Aalenian onwards (Fig. 9c). There is a reversal in the importance of the Umkomasiaceae in the Late Triassic, to the Caytoniaceae, Peltaspermaceae, and Matattiellaceae in the Jurassic (Fig. 9d).

The number of cycadophyte occurrences was greatest in the Early Jurassic (Fig. 9e). The proportion of records displays that the Cycadales were dominant in the Late Triassic, and from the Early Jurassic onwards the Bennettitales represented almost all the cycadophyte occurrences (Fig. 9f).

Within coniferophytes, the voltzian conifers, gnetaleans, and ginkgoaleans were common and dominant during the Carnian, but their importance considerably decreased from the Hettangian onwards (Figs. 9g, 9h). The proportion of occurrences of modern conifers (Coniferales) markedly increased from the Early Jurassic onwards. Cupressaceae had significance in the Early–Middle Jurassic, Araucariaceae was important during the Middle and Late Jurassic, and Hirmerellaceae (=Cheirolepidiaceae) acquired significance in the Late Jurassic (Figs. 9g, 9h).

Ranges and FAD-LAD

At species-level, a floral replacement is seen in the Early Jurassic (Fig. 10), with the appearance of several species that last for a short time and are successively replaced. A few taxa persist from the Late Triassic or Early Jurassic, but there is no long-term stability in the composition of plant communities.

Regarding the genera ranges (Supplementary Material 3), 43 genera disappeared through all the Late Triassic in Argentina. Although the genera *Hepaticites, Muscites, Protophyllocladoxylon,* and *Androstrobus*, are not present in the Jurassic or the first stage of the Cretaceous, they were described in younger Cretaceous or Cenozoic sequences from Argentina (Archangelsky 1965, Archangelsky and Villar de Seoane 2004, Puebla et al. 2012, Pujana 2022). Ten genera are singletons, present only in one stage. It is important to point out that *Lycopodites, Gontriglossa, Scytophyllum, Rissikianthus,* and *Protocircoporoxylon* are not considered singletons since these taxa were described in Early–Middle Triassic formations from Argentina (Coturel et al. 2016, Bodnar et al. 2019, Drovandi et al. 2020), despite that they are recorded in one stage of the studied interval. Excluding singletons and those that occur in the Cretaceous or Cenozoic, 29 genera had their last appearance in the Rhaetian.

Thirty-two genera appeared for the first time in the Early Jurassic in Argentina according to this study; from these, six genera were recorded in the Middle Triassic or in Triassic units not included in this work because their age is under discussion: *Rienitsia, Elatocladus, Desmiophyllum, Pelourdea, Pterophyllum*, and *Todites* (Troncoso et al. 2000, Zamuner et al. 2001). On the other hand, *Komlopteris* is a singleton genus as it was only present in the Sinemurian. From the 25 remaining taxa, seven appeared for the first time in the Hettangian, six in the Sinemurian, seven in the Pliensbachian, and four in the Toarcian.

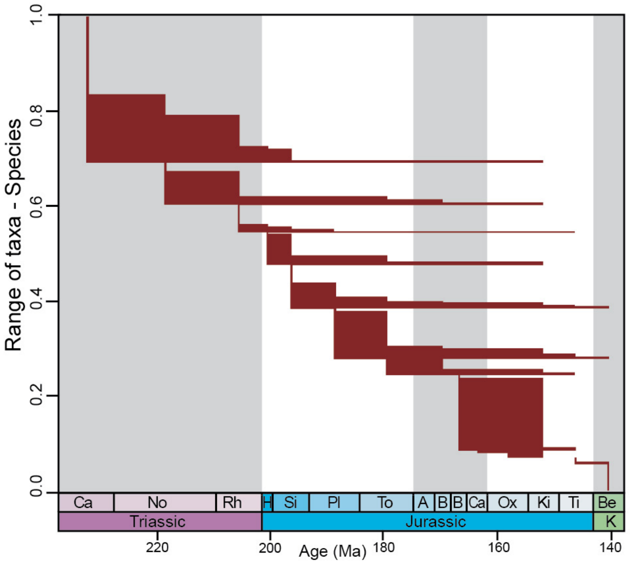

Figure 10. Patterns of FAD-LAD of fossil plant species in the Late Triassic–Late Jurassic interval of Argentina.

Finally, 46 genera present in the Argentine Triassic passed to the Jurassic; from these, 21 disappeared in the Early Jurassic.

Two lineages disappeared in the Late Triassic: the pleuromeiacean lycophytes, and the gymnosperm family Hamshawviaceae (Table 3). The families that first occurred in the Jurassic are the Gleicheniaceae, Caytoniaceae, and Williamsoniaceae in the Early Jurassic, the Isoetaceae in the Middle Jurassic, and the Matoniaceae in the Late Jurassic (Tab. 3).

Survivorship curves, and origination and extinction rates

In the ‘forward’ survivorship curves of plant genera, two different groups of cohorts can be recognized in the studied bin (Fig. 11a), one extending from the Late Triassic up to the Jurassic and the other spanning from the Jurassic up to the Early Cretaceous. The slopes of these curves for the Late Triassic cohorts are similar to those of the Early Jurassic and Middle Jurassic cohorts. The more pronounced slopes of the curves are observed between the Rhaetian and Hettangian,

Table 3. Temporal ranges of the plant lineages recorded in Argentine basins from the Late Triassic–earliest Cretaceous interval. Dotted lines indicate the temporal ranges deduced by data from older or younger sequences than the studied interval, not included in this analysis (see section "Ranges FAD-LAD" of Results). Abbreviations: Ca = Carnian, No = Norian, Rh = Rhaetian, He = Hettangian, Si = Sinemurian, Pl = Pliensbachian, To = Toarcian, Aa = Aalenian, Baj = Bajocian, Bat = Bathonian, Ca = Callovian, Ox = Oxfordian, Ki = Kimmeridgian, Ti = Tithonian, Be = Berriasian, i.s.= incertae sedis.

	Ca	No	Rh	He	Si	Pl	To	Aa	Baj	Bat	Ca	Ox	Ki	Ti	Be
Marchantiopsida i.s.	▨	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –
Bryopsida i.s.	▨	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –
Lycopodiaceae	▨	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –
Pleuromeiaceae	▨	▨													
Isoetaceae										▨	▨	– –	– –	– –	– –
Neocalamitaceae	▨	▨	▨	▨	▨										
Equisetaceae	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	– –	– –
Equisetales i.s.	▨														
Asterothecaceae	▨	▨	▨	▨	▨										
Marattiaceae			▨	▨	▨	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –
Osmundaceae	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Gleicheniaceae					▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Dipteridaceae	– –	– –	▨	▨	▨	▨	▨	▨	▨	▨	▨	– –	– –	– –	– –
Matoniaceae														▨	– –
Dicksoniaceae?	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	
Ferns i.s.							▨	▨	▨	▨	▨	▨	▨		
Umkomasiaceae	▨	▨	▨	▨	▨										
Peltaspermaceae	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		
Mattatielaceae	▨	▨	▨	▨	▨										
Caytoniaceae				▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Petriellaceae	▨	▨	▨	▨	▨										
Pteridosperms i.s.	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		
Zamiaceae	▨	▨	▨	▨	▨	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –
Cycadales i.s.	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Nilssoniaceae	▨	▨	▨	▨	▨										
Williamsoniaceae	– –	– –	– –	▨	▨	▨	▨	– –	– –	– –	– –	– –	– –	– –	– –
Benettitales i.s				▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Cycadophyta i.s.	▨	▨	▨	▨	▨										
Ginkgoaceae			▨	▨	▨	▨	▨								
Hamshawviaceae	▨	▨													
Ginkgoales i.s.	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Czekanowskiaceae	▨	▨	▨												
Czekanowskiales i.s.							▨	▨	▨						
Voltziaceae	▨	▨	▨	▨	▨										
Hirmeriellaceae	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		
Araucariaceae	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Cupressaceae	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		
Podocarpaceae	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	– –	– –
Coniferales i.s.		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Gnetales i.s.	▨	▨	▨	▨	▨	▨	▨								
Coniferophytes i.s.			▨	▨	▨	▨	▨								
Gymmosperms i.s.	▨	▨	▨	▨	▨	▨	▨	▨	▨						
Tracheophytes i.s.		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	

the Sinemurian and Pliensbachian, and the Kimmeridgian and Tithonian. The 'backward' survivorships show a more marked cohort emergence between Rhaetian and Hettangian, and between Bajocian and Bathonian (Fig. 11b).

The slopes of survivorship curves of species (Fig. 11c) tend to be steeper than those of genus curves, which is inherent

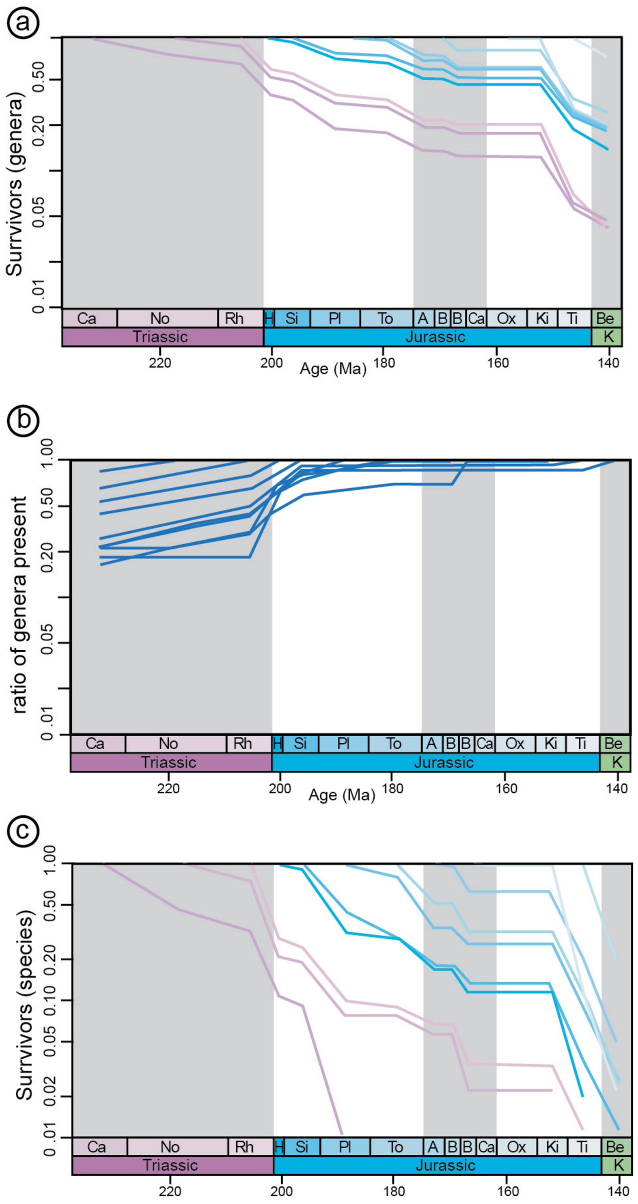

Figure 11. a) "Forward" survivorship proportion of plant genera in the Late Triassic–Late Jurassic interval of Argentina. b) "Backward" survivorship proportion of plant genera in the Late Triassic–Late Jurassic interval of Argentina. c) "Forward" survivorship proportion of plant species in the Late Triassic–Late Jurassic interval of Argentina.

to the method. All the species curves show abrupt inflections in the intervals in which the genera curves exhibit sharper slopes. It is noticeable a cohort with very marked slopes, extending from the Late Triassic and only to the Pliensbachian.

The extinction rates at the genus-level show the greatest values in the Rhaetian, the Toarcian, and between the Oxfordian and Kimmeridgian (Fig. 12a). The origination rates at genus-level show the greatest values in the Rhaetian, and Bathonian, and a less pronounced peak in the Pliensbachian (Fig. 12b). The peaks of extinction and origination in the Rhaetian show a floral replacement. The peaks of origination of the passages Pliensbachian/Toarcian and Bathonian/Callovian coincide with the lower values of extinction. In comparison with the diversity curves, the first is correlated with a slight decrease in diversity and the second with a clearer increase. The extinction and origination rates exhibit no values after the Kimmeridgian because of the absence of temporal definition of the paleofloras (see Discussion); for the same reason, there are no changes in the diversity between the Oxfordian and Kimmeridgian.

DISCUSSION

Sampling and taphonomical biases

This study comprised all fossil types without discrimination according to organs. While this inclusion approach may be subject to debate, it is essential to note that the fossilization type varies from one formation to another: while in some only permineralized logs are preserved, others only carry impressions-compressions of leaves. Being the plants modular organisms, each individual can produce a great number of leaves, branches, etc., that are preserved in the fossil record as disarticulated plant remains. For example, in a fossiliferous

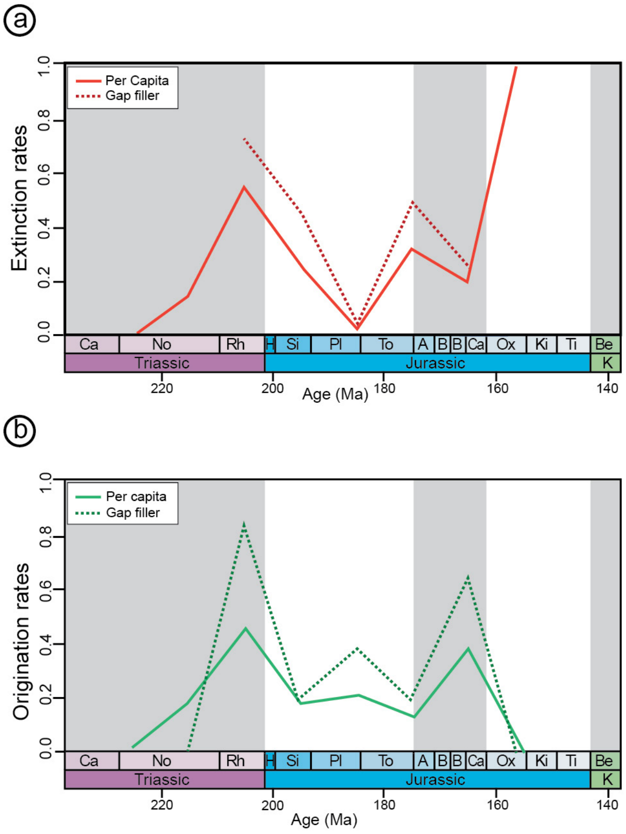

Figure 12. a) Extinction rates at genus-level in the Late Triassic–Late Jurassic interval of Argentina. b) Origination rates at genus-level in the Late Triassic–Late Jurassic interval of Argentina.

locality, a large number of fossil leaves belonging to deciduous trees may have been preserved by the nature of the original organ but not as a consequence of the number of individuals which lived in the plant community (see Serrano-Brañas and Reyes-Luna 2014). For this reason, if we restrict ourselves to one type of fossil or organ, we will not have enough information on some of the analyzed stages. From the Carnian to the Toarcian, the predominance of leafy branches and leaves (mostly preserved as impressions and compressions) over other plant organs is very clear, representing about 67-85% (Supplementary Material 4). Reproductive structures (preserved as impressions-compressions or permineralizations) are more abundant from the Pliensbachian to the Kimmeridgian; however, from the Aalenian onwards, they represent a significantly larger proportion of the total occurrences. On the other hand, the permineralized woods were more abundant in the Bathonian–Kimmeridgian interval, where they account for a quarter of the occurrences. In general, it can be observed that in stages with a lower proportion of fossilized leaves, the total number of occurrences also decreased, suggesting that leaves contribute more records than other plant organs. This is due to the intrinsic nature of plants, as they produce a large number of leaves throughout their lifetime, while they form only one stem. In comparison with the diversity curves, variations in the proportion of organ types and fossilization modes could be attributed to both taphonomic and taxonomic causes. For instance, fossiliferous sites with permineralized forests became very common from the Middle Jurassic onwards in Argentina, and in these locations, due to paleoenvironmental factors, impressions and compressions are uncommon. The greater abundance of fossil woods coincides with an increase in coniferophyte diversity (Fig. 8d), which are tree woody plants with large trunks.

Sampling biases in the paleobotanical record have been scarcely evaluated (Cleal et al. 2021, Pardoe et al. 2021). Our results show a high, positive correlation between species diversity and collections, but this correlation is lower at genera level. This means that increased sampling effort in the same locations may result in more species or morphological types. In paleobotany, the morphological species concept is applied, and variability within a species is only occasionally considered, and thus morphological combinations that minimally differ from already known ones are classified as new species.

The methodological scope varies in each research included in this analysis. Some references (here considered as collections) are studies focused on one to three species with a very large number of specimens of each taxon (see for example, Escapa et al. 2008, 2015, Elgorriaga et al. 2015, 2019, Choo et al. 2016, Contreras et al. 2019) while other papers aims are floristic analyses, where there are comparatively fewer specimens for many more taxa (see for example, Petriella and Arrondo 1984, Spalletti et al. 1991, 2010, Morel et al. 1999, 2013). This could affect sampling completeness.

Another issue that may affect the index is the bias produced by the wide time ranges of the Jurassic formations. While the Triassic formations are better constrained in age, and even an intra-formational analysis could be performed, the Jurassic formations with their respective floras artificially span several stages.

Another analyzed bias in the estimation of past diversity has been the type of environments in which plant fossils are preserved. Plant preservation potential in surface environments increases dramatically in the presence of surface water bodies, high water tables, or with rapid burial to below the vadose zone, which are circumstances more frequently present in humid-climate environments than in arid or semi-arid environments and where sedimentation rates are high and, as a consequence, wetland floras preserved in basinal environments during humid climatic intervals dominate much of the plant fossil record (Channing and Edwards 2013). On the other hand, specific richness tends to be greater in the wetter biomes (McNeely 2003), hence a larger number of plant-remains in the humid intervals would only overstate a diversity increase which would have actually occurred.

In our results, there is a correlation between the diversity and the number of formations per stage, but in some stages, this relation is not so evident. For instance, there are only two units (i.e. Chon Aike and La Matilde Formations) from the Bathonian–Callovian, which are among the stages with greatest diversity; nevertheless, La Matilde Formation is one of those with the largest number of outcrop sites of the Argentine Jurassic and its paleoflora has been studied unceasingly since 1924 by several authors (resulting in 31 collections).

Despite the estimated plant diversity could appear as essentially the result of sampling bias, Capel et al. (2022) noted that the number of localities may co-vary with abundance and diversity, and so diversity may not be just a response to heterogeneous sampling or lack of fossiliferous localities. For example, the records of plant macrofossils after an extinction event can be scarce as plants were not as widespread as they were later in the recovery interval. In this study, the RT and SIB diversity Hettangian decrease and the increase in the Pliensbachian (and their corresponding drop and climb of occurrences) can be an example. In fact, the low number of localities probably reflects actual low plant abundance and diversity of the vegetation, implying a redundancy effect. The concomitant increase in diversity and number of localities probably also reflects the progressive colonization of the plants after the extinction event (Capel et al. 2022).

Comparison with previous studies

A major floristic change in Argentina towards the Triassic/Jurassic boundary was suggested, leading to the disappearance of the Umkomasiales and Peltaspermales, the impoverishment of the Ginkgoales, and an increase in the diversity of ferns, Bennettitales, and conifers (Artabe et al. 2007a, Iglesias et al. 2011). According to the most recent findings, included in this contribution, Umkomasiales and Peltaspermales (Peltaspermaceae and Mattatielaceae) reached the Early and Late Jurassic, respectively. During the Early Jurassic, Ginkgoales declined, while derived conifers, Bennettitales, and ferns of the families Osmundaceae and Dipteridaceae diversified.

In their reviews of Mesozoic floras, Artabe et al. (2007a) and Iglesias et al. (2011) stated that the Argentine Triassic flora comprised 86 genera and 238 species, from which only 28 species survived in the Jurassic. Although it is not explicit in their contribution, Artabe et al. (2007a) elaborated diversity curves of species richness under the range-through assumption, based on an absence/presence matrix of species using Past software (Artabe pers. comm.). Our study shows that from 166 species present in the Late Triassic, only 26 Triassic species survived into the Jurassic, but at the genus-level the survival is greater (from 87 genera present in the Late Triassic, 48 passed to the Jurassic). Artabe et al. (2007a) recorded 131 species in the Carnian (BNP Biozone) and 54 in the Norian (OL Biozone), while in our analysis we recorded 122 species in the Carnian, and 77 species in the Norian. These discrepancies may be due to the new interpretation about the age of some units and the new paleobotanical data published since those authors carried out their investigation in 2007 (see Introduction, and Material and Methods). Artabe et al. (2007a) and Iglesias et al. (2011) also asserted that 27 genera appeared for the first time in the Early Jurassic and that Jurassic floras are characterized by a low diversity. Our results show that in the Early Jurassic 24 genera appeared for the first time and that, although the Jurassic diversity was lower than the Carnian one, the species and genus richness values of some Jurassic ages were comparable to those of the Norian and Rhaetian.

Quattrochio et al. (2007) suggested that the megafloras of the Middle and Late Jurassic of Argentina showed an impoverishment in the number of species compared with the Early Jurassic. Our estimations exhibit high diversity in Middle Jurassic megafloras and a decrease in diversity afterward.

Regarding the controversy about the abrupt or gradual extinction of the terrestrial vegetation across the Triassic–Jurassic transition, at the lineage level only the Pleuromeiaceae became extinct, but there was an important change in the dominance of the groups. Despite the most abundant groups in the Late Triassic (Neocalamitaceae, Dipteridaceae, Osmundaceae, Umkomasiaceae, Cycadales, Ginkgoales, Voltziaceae, and Gnetales, Fig. 2) passed through the Jurassic, most of them passed as relicts (Neocalamitaceae, Umkomasiaceae, Ginkgoales, Voltziaceae, and Gnetales) or with less dominance (Cycadales). Only Dipteridaceae and Osmundaceae diversified during the Jurassic. According to our database, several genera considered diagnostic of the Argentine Triassic survived as relict forms to the Early Jurassic: *Neocalamites* (Neocalamitaceae), *Rietnisia* (Asterothecaceae), *Dicroidium* (see Fig. 3e), *Rhexoxylon* (Umkomasiaceae), *Rochipteris* (Petriellaceae), *Dejerseya* (Matatiellaceae), *Heidiphyllum* (Voltziaceae), *Kurtziana* (Cycadales), or even to the Late Jurassic *Lepidopteris* (Peltaspermaceae). Most lineages and genera that go through the Triassic/Jurassic boundary became extinct in the Early or Middle Jurassic. The extinction rates indicate a peak at the Rhaetian; however, the origination rates also have high values indicating a turnover. The slopes of the survivorship curves between Rhaetian and Hettangian are pronounced. Taking our results with caution due to the sampling biases, we can see that there was an important floristic change in the Triassic/Jurassic transition, but it is not so abrupt, and several taxa became extinct gradually during the Late Triassic, between 230 Ma and 202 Ma, before the T/J boundary and afterward in the Jurassic.

After the end-Triassic, the terrestrial ecosystems appear to have recovered by late Hettangian time in several areas of the world (Austria, UK, Denmark, Greenland, Arctic Canada, Australia, and New Zealand), with the return of common to abundant woody plants (Lindström 2016). In Argentina, the richness values and occurrences were low for all plant groups in the Hettangian as seen in our analysis. However, it is important to recognize that sampling at this stage remains the least comprehensive. Recovery can be inferred in the Sinemurian since an important increase in diversity of pteridophytes, seed ferns, and cycadophytes was recorded. Ferns, which are considered colonizer taxa commonly found in disturbed environments (Zhou et al. 2021), were more abundant and diverse (at species and family levels) in the Sinemurian of Argentina, which could be an indication that they accompanied the ecosystem recovery. The coniferophytes showed an important diversification from the Pliensbachian.

Regarding the early Toarcian Oceanic Anoxic Event, we noticed an increase of overall diversity at species- and genus-level in the Toarcian, in particular of the seed plants, with a major contribution of the derived conifers. However, given the nature of our data, the information from the Toarcian is insufficient, as the materials may come from layers both below and above the event. A peak of the extinction rate curves was observed in the Toarcian and the diversity fell in the Aalenian, and these changes might be linked to the Toarcian crisis.

Paleoclimatic discussion

The Rhaetian was characterized by a warm, wet climate with a definite seasonality (Parrish 1993). A peak of species and genera richness, both in pteridophytes and gymnosperms, is observed in Argentina.

The Early Jurassic climate was characterized by global warming, more intense than the present: average summer temperatures exceeded 35 °C in low-latitude regions of western Pangea, where eolian sandstones testify to the presence of vast deserts (Chandler et al. 1992). High rainfall rates were associated primarily with monsoons that originated over the warm Tethys Ocean, characterizing an overall paleoclimate for the Jurassic (Chandler et al. 1992). The climatic conditions at the beginning of the Early Jurassic (Hettangian) were similar to those of the Late Triassic, and the Pliensbachian to Toarcian was a time of global warming, probably driven by the Karoo magmatism (Holz 2015). For Argentina, warm (-temperate) and humid conditions during the Sinemurian and increasing warmth and aridity from the Late Pliensbachian to the Toarcian were suggested (Volkheimer et al. 2008a). Our results indicate a diversity reduction in the Hettangian, and during the Sinemurian a diversification of pteridophytes (especially Osmundaceae and Dipteridaceae) and cycadophytes (bennettitaleans) (Fig. 3). The family Osmundaceae and the genus *Otozamites* are indicative of wet and warm climates (Van Konijnenburg-Van Cittert 2002, Wang et al. 2008). The Pliensbachian appears as an interval with an overall diversity-decline and a decline of seed ferns, but a slight increase in fern and conifer diversity.

The Early Toarcian global warming trend is marked by an oceanic anoxic event (Holz 2015). A change from wet (fern-dominated) to warmer and seasonally dry landscapes during the Toarcian was interpreted from palynological data from Denmark (Wade-Murphy et al. 2006), and plant fossils have also been interpreted to reflect short-term warming in the Toarcian of Siberia (Vakhrameev 1991). The Toarcian was one of the moments of the Jurassic with highest overall diversity at the genus level for Argentina as can be seen from our analysis. A diversification in seed plants (mainly coniferophytes), but a reduction in the genus richness of ferns, agrees with the floristic change in other parts of the world and drier conditions. At the Toarcian, there is an extinction-rate peak in Argentine megafloras. Considering that there is no precise dating of each plant fossil assemblage, the age of this peak needs to be adjusted to determine its relationship to the Early Toarcian crisis.

For the Early Bajocian, Hesselbo et al. (2003) characterized strongly seasonal arid and weakly seasonal arid climates. Our data show a decrease in plant diversity and occurrences in the Aalenian and Bajocian.

Migration of marine fauna and isotopic thermometry pointed out drastic cooling during the early Late Callovian, suggesting continental ice formation at this time (Holz 2015). Dromart et al. (2003) designated this episode the “Callovian Ice Age”; hence, the Middle Jurassic seems to display one of the coldest climates of the entire Mesozoic. For Argentina, Volkheimer et al. (2008b) suggested warm and relatively humid climatic conditions during the Middle Jurassic due to the mega- and microfloras with high percentages of the thermophilic Hirmerellaceae (=Cheirolepidiaceae), associated with Araucariaceae, which need relatively humid conditions. Consistent with the present analysis, in the Bathonian–Callovian, the overall diversity was high in every plant group except for the seed ferns, and as in the previous studies, with a major representation of Osmundaceae, Bennettitales, Araucariaceae and a minor importance of the Hirmerellaceae (Fig. 4). The Araucariaceae maintained a preference for subtropical or mesothermal conditions (Kershaw and Wagstaff 2001); therefore, it cannot be ruled out that the climate was temperate in this interval.

More recent papers corroborate the Oxfordian–Kimmeridgian warming and the more humid paleoclimatic conditions towards the Tithonian (e.g. Wierzbowski et al. 2013). In the Oxfordian–Kimmeridgian interval, a mild increase in species diversity is seen, but at genus-level this is imperceptible. In the Oxfordian, the extinction rates reached the highest values, and the origination rates, the lowest values. This might be exaggerated by the lack of a precise age definition of the plant-fossil strata from the formations included in that bin (i.e. Chon Aike and La Matilde). This lack of precision results in origination rates of zero and extinction rates greater than one, making it impossible to graph in Figure 12. A decrease in floral diversity towards the Tithonian was observed, but as the number of total occurrences was also very few for that stage in Argentina (25 occurrences, one formation with two collections), these results should be taken with caution.

CONCLUSIONS

We carried out a detailed characterization of the megafloras of the Triassic–Jurassic transition, based on recent advances in the knowledge of the Late Triassic and Jurassic of Argentina. This analysis offers guidance for future collection and analytical efforts to address knowledge gaps in plant fossil assemblages from intervals and localities with scarce or imprecise records. The dataset generated in this work can be improved by updating, modifying, or adding new information in the future and in this way the results obtained will be more robust.

The obtained curves of diversity, and origination and extinction rates, display fluctuations along the Triassic–Jurassic transition, but there is no absolute certainty that these patterns precisely align with globally dated events. In Argentine megafloras, the End-Triassic and Early Toarcian mass extinctions are reflected more as gradual turnovers than as abrupt crises. Several lineages that were dominant during the Triassic survived up to Sinemurian, but taxa that will become more important in Jurassic and Early Cretaceous floras emerged after the Triassic/Jurassic boundary.

The Sinemurian was an interval in which ferns and bennettitaleans diversified, which can be related to the previous interpretation of a wet climate during the Sinemurian for Argentina. In the Toarcian, an increase in conifer diversity and a decrease in fern richness, might be correlated with the reduction in humidity proposed for this stage. The greater importance of the Osmundaceae, Araucariaceae, and Bennettitales, from the Bathonian onwards coincided with the warmer and wetter climates suggested for the Bathonian–Kimmeridgian interval.

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