Evolutionary history, biogeography, and extinction of the Cretaceous cheirolepidiaceous conifer, *Frenelopsis*

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ABSTRACT

Frenelopsis Schenk (family Cheirolepidiaceae†) was among the most widespread conifer genera and a dominant element of wetland ecosystems in low to mid-palaeolatitudes in the the Northern Hemisphere. It was also one of the more important peat-forming shrubs and trees generating extensive deposits of Cretaceous lignite. The genus became extinct at the end of the Cretaceous. Studies of the presence/absence and diversity of *Frenelopsis* allow us to analyse its evolutionary history, biogeography, and the consider the possible causes of its extinction. During the Early Cretaceous, the genus diversified, triggered by the rise of short-lived species and the constraint of endemism. The maximum diversity and species richness were attained in Barremian and Aptian times while the maximum number of global occurrences is documented during the Albian. In the Late Cretaceous, *Frenelopsis* species richness declined and the genus became progressively more restricted to the Tethyan archipelago in the context of the rise to dominance of angiosperms. In the Maastrichtian, the last representatives of *Frenelopsis* survived in the coastal wetlands of Iberia as a relictual plant. In northeast Iberia (present-day Pyrenees) the last occurrences from this genus are early to middle Maastrichtian in age and show an intriguing contrast between the abundance of vegetative remains and the lack of *Classopollis* pollen grains. These data suggest that at the end of its lineage, the plant was reproducing only vegetatively and that male sterility may have contributed to extinction.

1. Introduction

The Cheirolepidiaceae was a diverse and widespread Mesozoic conifer family. The earliest members date back to the early Late Triassic and, over 160 million of years, they developed highly variable growth habits and spread throughout a wide range of ecological niches (Alvin, 1982; Watson, 1988). They became particularly diverse in low latitudes but declined in many areas already by the early Late Cretaceous (Watson, 1988; van der Ham et al., 2003). Their latest representatives occurred in southernmost South America until the early Paleogene, surviving the Cretaceous/Paleogene (K/Pg) mass extinction for a short period (Barreda et al., 2012). The morphological and ecological plasticity of the family may explain their great evolutionary success and resistance to extreme environmental conditions. Moreover, there is

evidence that polyploidy might have been crucial for speciation within the Cheirolepidiaceae (Kürschner et al., 2013). The production of unreduced (i.e., diploid gametophytes pollen grains) and whole-genome doubling mechanisms (i.e., polyploidy) is widespread in living flowering plants, but is rare in other seed plant lineages (Stebbins, 1971; Leitch and Leitch, 2012). Another distinctive feature of the Cheirolepidiaceae is the structure of pollen wall of *Classopollis* Pflug emend. Srivastava, which is among the most complex in conifers (Srivastava, 1976; Alvin, 1982). Ovulate cones in *Frenelopsis* also reveal specialized tissues suggesting insect pollination (Labandeira et al., 2007). These particular features render it difficult to understand the origins and phylogenetic relationships of the Cheirolepidiaceae (Escapa and Leslie, 2017). Hence, Miller (1988) suggested that genus *Hirmeriella* Hörhammer, a type of cheirolepidiaceous ovulate cone, could be a sister clade to the

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Podocarpaceae or Cephalotaxaceae, whereas Alvin (1982) and Watson (1988) indicated putative relationships with the Cupressaceae. More recently, affinities to Araucariaceae and Podocarpaceae have also been proposed based on the presence of a tissue flap covering their seeds (Escapa et al., 2012). There is disagreement among palaeobotanists as to the Cretaceous genera that can be placed within the Cheirolepidiaceae. However, *Frenelopsis* Schenk, *Pseudofrenelopsis* Nath., *Tarphyderma* Archang. and Taylor, and *Tomaxellia* Archang. are unequivocally assigned to the family (Taylor et al., 2009).

Frenelopsis, with about 20 species, all restricted to the Cretaceous, achieved high diversity and widespread distribution (Mendes et al., 2010). *Frenelopsis* habits ranged from small shrubs to nearly 20-m-tall trees, and most of them showed evidence of xeromorphy in response to diverse ecological constraints (e.g., Watson, 1977, 1988; Gomez et al., 2001, 2002a; Axsmith and Jacobs, 2005; Bartiromo et al., 2012). For instance, in the Lower Cretaceous of Iberia, different species of *Frenelopsis* grew in a wide range of habitats including marine coastal mangroves and brackish marshes as well as freshwater floodplains and lakeshores, and probably underwent water stress due to variable salinity or seasonal aridity (Gomez et al., 2002a). *Frenelopsis* was particularly abundant and diverse in the Tethyan archipelago, and likely comprised large amounts of biomass that led these conifers to be one of the dominant peat-forming plants, precursors of coal (lignite), e.g., in the Cretaceous of Iberia (Gomez et al., 2001; Villalba-Breva et al., 2012) and probably elsewhere in the paratropical belt. In the present paper, we study the evolutionary and biogeographic history of *Frenelopsis* in order to better understand its origins, diversification and especially its extinction.

2. Description of vegetative and reproductive structures

2.1. Vegetative system

Frenelopsis is easily distinguished from fossil and living conifers by unique macro- and micro-morphological features (e.g., Gomez et al., 2002a, b). Leafy axes consist of jointed cylindrical units, each formed by two or three fused leaves forming relatively short, free, apical tips and extending to the base in a long sheath showing no suture between the leaves. These units are arranged in opposite-decussate phyllotaxy when leaves are two or whorled (rotating by approximately 60°) when there are three. In most species they branch punching a hole in one of the leaves (Daviero et al., 2001). Cuticles and especially the stomatal apparatuses provide the main significant characters to determine *Frenelopsis* species (e.g., Gomez et al., 2002a). Stomata are bordered by a thick stomatal rim and organized in longitudinal stomatal rows, more or less parallel along the leaf sheath, which converge toward the apex in each free tip. Guard cells are sunken and surrounded by a ring of four to six subsidiary cells each bearing one outer and often one inner papilla overhanging and closing the throat of the stomatal pit. Beyond morphological characters, *Frenelopsis* also appears to show its own chemotaxonomic cuticle features (Lafuente-Diaz et al., 2023).

2.2. Reproductive structures

Reports of cones bearing pollen grains are rarer than vegetative organs. Microsporangiate cones were found attached to leafy axes in *Frenelopsis oligostomata* Romariz emend. Alvin (Lauverjat and Pons, 1978), *F. alata* (Feistmantel) Knobloch (Kvaček, 2000), *F. turolensis* Gomez et al. (2002a), *F. ugnaensis* Gomez et al. (2002a) and *F. ramosissima* Fontaine emend. Watson (Axsmith and Jacobs, 2005). Male cones of *Frenelopsis* (e.g., *Classostrobus* Alvin et al.) show little morphological variability (Gomez et al., 2002a; Axsmith and Jacobs, 2005). They are small (3.5−13 mm long and 2.5−11 mm wide) and round to ellipsoidal or elongated. Their microsporophylls are triangular to rhomboidal, spirally arranged or peltate. The number of pollen sacs per microsporophyll is unknown for all aforementioned species.

Female cones were first described from the Cenomanian of Bohemia under genus *Alvinia* Kvaček, and were associated with *F. alata* (Kvaček, 2000). These ovuliferous cones are ovoid, larger (4.5 cm in diameter) than male cones and attached to a robust axis. The megasporophylls are large (up to 20 mm long) broadly rhomboidal, obtuse, with crenulate margins, and spirally arranged. A covering flap is distally attached to the adaxial surface of the scale. Each scale encloses a central, single seed. Kvaček (2000) suggested that the pollination of *Alvinia* was similar to that of the living representatives of *Agathis* Salisbury and *Araucaria* Jussieu. Likewise, the funnel-like pollen chamber in scales of *Alvinia* was lined by trichomes, which caught the *Classopollis* pollen. Then, pollen tubes grew from the pollen grains at the bottom of the funnel-like structure to the micropyle. Kvaček (2000) also hypothesized that propagation of *Alvinia* seeds might have been assisted by cone scales dispersed by wind as in extant *Araucaria*, *Cedrus* Trew or *Abies* Miller.

2.3. Pollen

Cuticular studies of male cones attached to *Frenelopsis* axes have revealed pollen sacs containing great number of pollen grains with the distinctive morphology of the group *Circumpolles* (Pflug) Klaus (Barale et al., 1988). The genus *Classopollis* (Pflug) is the most characteristic of this extinct group (Jarzen and Nichols, 1996) and it is a very common Mesozoic pollen type produced by Cheirolepidiaceae, mainly in Jurassic and early Cretaceous palynological assemblages (Hluštík and Konzalová, 1976a,b; Alvin, 1977; Barale et al., 1988; Kvaček, 2000; Gomez et al., 2002a).

The pollen grains of *Classopollis* can be isolated or, more commonly, arranged in tetrads. These spheroidal grains have a circumpolar subequatorial groove that divide two unequal hemispheres. They are circular in polar view and rather elliptical in equatorial view with a small trilete mark in the proximal side and a distal circular cryptopore. The exine has scabrate or reticulate ornamentation with the smallest elements around the distal pore and the largest in the equatorial band.

Cheirolepidiaceae generally was anemophilous (but putative entomophily was reported by Labandeira et al., 2007), and produced large amounts of pollen. From an ecological viewpoint, the Cheirolepidiaceae inhabited both freshwater mires and coastal brackish wetlands. In the latter, their pollen grains are considered sensitive indicators of the sea level changes (Azéma et al., 1981). In the Cretaceous series of the western Portuguese Basin (Taugourdeau-Lanz et al., 1982), the palynological assemblages with large amounts of bisaccate pollen grains and low representation of *Classopollis* were indicative of transgressive periods. By contrast, these abundances reversed in regressive phases. This same pattern was observed in the Cenomanian-Turonian deposits of the Vendée (France) where the regressive phases correspond to an increase of *Classopollis* abundance (Azéma et al., 1981; Néraudeau et al., 2017). This may reflect the extension of *Frenelopsis*-dominated wetlands during these latter phases.

The fact that the pollen grains of *Classopollis* often appear grouped in tetrads indicates a negligible transport (Stuckins et al., 2017; Stuckins, 2022). This evidence and good preservation suggest autochthony and have been used altogether to infer proximity to the growth area.

3. Materials and methods

This study is based on a literature survey, which was used to construct a dataset of *Frenelopsis* global occurrences during the Cretaceous (Table 1). Only species that have been described based on cuticular characters and figured have been included in the analysis, while species described or reported only on the basis of general shoot morphology were not considered. The dataset includes information on the age, taxonomy, geographic location and references. The occurrences were plotted on seven global and four regional (Tethyan archipelago) palaeogeographic maps in order to display the biogeographic history of *Frenelopsis* during the Cretaceous. Species richness, origination and

Table 1

Dataset of *Frenelopsis* occurrences during the Cretaceous.

Age	Species	Taxonomy revisited	Country	Locality	Area/Region	Reference
Berriasian	*occidentalis*	*occidentalis*	Germany	Hildesheim	Lower Saxony	Watson and Alvin (1999)
Berriasian-Valangian	*malaiana*	*malaiana*	Malaysia	Maran	Pang	Smiley (1970); Lejal-Nicol (1987); Uyop and Che Aziz (2000)
Berriasian-Valangian	*malaiana*	*malaiana*	Malaysia	Panti	Pang	Smiley (1970); Uyop and Che Aziz (2000)
Valanginian	*teixeirae*	*teixerae*	Portugal	Sesimbra	Sesimbra	Rey (1972); Alvin and Pais (1978)
Valanginian	sp.	sp.	Portugal	S. Lourenço	Ericeira	Teixeira (1948); Rey (2006)
Valanginian to early Albian	sp.	sp.	Portugal	Zambujeiro	Cercal	Teixeira (1948); Rey (1993)
Hauterivian	sp.	sp.	Czech Republic	Beskyd Mts.	north Moravia	Hluštík (1978)
Hauterivian	sp.	sp.	France	La Crapaudière	Chapelle-aux-Pots	Carpentier (1933)
Hauterivian	sp.	sp.	France	Plaines	Pays de Bray	Carpentier (1933)
Hauterivian	*hoheneggeri*	*hoheneggeri*	Poland	Przenosza	Skrzydlna, Beskid Sredni	Reymanówna (1965); Reymanówna and Watson (1976)
Hauterivian	*hoheneggeri*	*hoheneggeri*	Poland	Wiśniowa	Beskid Srekid	Reymanówna (1965); Reymanówna and Watson (1976)
Hauterivian	*hoheneggeri*	*hoheneggeri*	Poland	Srekid	Beskid Srekid	Reymanówna (1965); Reymanówna and Watson (1976)
early Hauterivian	sp.	sp.	Portugal	S. Sebastião	Runa	Teixeira (1948); Rey (2006)
Hauterivian	*teixeirae*	*teixerae*	Portugal	Vale Cortiço clay pit	Torres Vedras	Rey (1993); Mendes et al. (2010); Lafuente-Diaz et al. (2023)
late Hauterivian-early Aptian	sp.	sp.	Spain	Vallazmorra	Hortezuelos, Santo Domingo de Silos	Sender et al. (2011)
Hauterivian - early Barremian	*hoheneggeri*	*hoheneggeri*	Poland	Lipnik	Bielsko	Schenk (1869); Reymanówna (1965)
Early Cretaceous	*sifloana*	*sifloana*	Sudan		Darfur	Watson and Alvin (1976); Watson (1983)
Hauterivian? - Barremian	*atlantica*	*atlantica*	Ireland	DSDP site 549	–	Batten et al. (2014)
Barremian	*hoheneggeri*	*hoheneggeri*	Czech Republic	Leipnik	Wernsdor	Reymanówna and Watson (1976); Carpentier (1937)
Barremian	*hoheneggeri*	*hoheneggeri*	Czech Republic, Austria, Croatia	Murk	Neutitschein; Wernsdorf	Reymanówna and Watson (1976); Carpentier (1937)
Barremian	sp.	sp.	Germany	Hildesheim	Lower Saxony	Lipps (1923); Carpentier (1937)
early Barremian	*rubiesensis*	*rubiesensis*	Spain	La Cabroa	Vilanova de Meià	Barale (1973); Barale et al. (1984)
early Barremian	*rubiesensis*	*rubiesensis*	Spain	La Pedrera de Meià	Vilanova de Meià	Gomez et al. (2002a)
late early Barremian	*choshiensis*	*choshiensis*	Japan	Choshi	Chiba Prefect., Honshu	Kimura et al. (1985); Chow and Tsao (1977)
late Barremian	*ugnaensis*	*ugnaensis*	Spain	Las Hoyas	Cuenca	Gomez et al. (2001, 2002a)
late Barremian	*ugnaensis*	*ugnaensis*	Spain	Uña	Cuenca	Gomez et al. (2001, 2002a)
early Aptian	*alata*	*alata*	Spain	Vallibona	Morella	Gomez et al. (2001); Aucour et al. (2008)
Barremian-Aptian	sp.	sp.	Czech Republic	–	–	Carpentier (1937)
late Aptian	sp.	sp.	France	Arnayon	–	Barale and Bréhéret (1995)
late Aptian	sp.	sp.	France	Etoile	–	Barale and Bréhéret (1995)
late Aptian	sp.	sp.	France	Ribeyret	–	Barale and Bréhéret (1995)
late Aptian-early Albian	*antunesii*	*antunesii*	Portugal	Carregueira mine	Juncal	Mendes and Kvaček (2022)
late Aptian	*cusanensis*	*profetiensis*	Italy	Peschera	Cusano Mutri	Bartiromo et al. (2012); Barral et al. (2019)
early-middle Aptian	*profetiensis*	*profetiensis*	Italy	Profeti	Campania	Bartiromo et al. (2009)
late Aptian to early Albian	sp.	sp.	Portugal	Almas do Juncal	Montemor-o-Velho	Pais and Trincão (1983); Dinis (2001)
late Aptian	sp	sp	Brazil	Nova Olinda	Araripe Basin	Kunzmann et al. (2006)
late Aptian - Albian	*ramosissima*	*ramosissima*	USA	Fredericksburg	Virginia	Berry (1910); Watson (1977); Upchurch and Doyle (1981)
late Aptian - Albian	*ramosissima*	*ramosissima*	USA	Baltimore	Maryland	Upchurch and Doyle (1981)
Aptian/Albian boundary	*ramosissima*	*ramosissima*	USA	Hood County	Texas	Axsmith and Jacobs (2005)
late Aptian-middle Albian	sp.	sp.	Portugal	Milheiro	Cercal	Teixeira (1948); Saporta and Choffat (1894)
late Albian	sp.	sp.	Portugal	Aguda	Azenhas do Mar	Reymanówna and Watson (1976); Hasenboehler (1981)
Aptian-Albian	*occidentalis*	*occidentalis*	Portugal	Almargem	Belas	Heer (1881); Saporta and Choffat (1894); Rey (1972); Alvin (1977); Watson (1988); Watson and Alvin (1999), Mendes et al. (2010)
early-middle Albian	sp.	sp.	Portugal	Cavadinha	Caranguejeira	Teixeira (1948); Dinis (2001)
early Albian	sp.	sp.	Portugal	Ceramic factory	Nazaré	Teixeira (1948); Dinis (2001)
early-middle Albian	sp.	sp.	Portugal	Pimenteira	Caranguejeira	Teixeira (1948); Dinis (2001)
late Albian	*alata*	*alata*	Portugal	Sítio	Nazaré	Alvin (1977); Dinis (2001)
early Albian	sp.	sp.	Portugal	Tavarede		Teixeira (1948); Dinis (2001)
Albian	sp.	sp.	Spain	La Cierva	Cuenca	Álvarez-Ramis (1981)
early-middle Albian?		sp.	Spain	Llosa del Bisbe	Valencia	Pla et al. (2008)
early-middle Albian	*turolensis*	*turolensis*	Spain	Rubielos de Mora	Rubielos de Mora	Gomez et al. (2002a)
middle-early late Albian	*justae*	*justae*	Spain	San Just	Teruel	Barral et al. (2019)

Table 1 (*continued*)

Age	Species	Taxonomy revisited	Country	Locality	Area/Region	Reference
late Albian- early Cenomanian	sp.	sp.	Portugal	Bairro	Alcanede	Teixeira (1948)
Cenomanian	sp.	sp.	Czech Republic	Bohdánkov	Bohemia	Velenovský and Viniklář (1926); Kvaček (2000)
Cenomanian	*alata*	sp.	Czech Republic	Brickkiln	Hloubètin, Praha	Hluštík and Konzalova (1976b)
Cenomanian?	sp.	sp.	Czech Republic	Drázdany	Moravia	Kvaček (2000)
Cenomanian	*alata*	*alata*	Czech Republic	Kamenná Panna clay pit	Horousany	Kvaček (2000)
Cenomanian	*harrisii*	*harrisii*	Tajikistan	Darvaz range	Bokodara gorge	Doludenko and Reymanówna (1978)
early late Cenomanian	*alata*	*alata*	Czech Republic	Pecinov quarry	Praha, near Rynholec	Uličný et al. (1997); Kvaček (2000)
early late Cenomanian	*alata*	*alata*	Czech Republic	Pecinov quarry	Praha, near Rynholec	Uličný et al. (1997); Kvaček (2000)
Cenomanian	sp.	sp.	Czech Republic	Peruc	–	Velenovský and Viniklář (1926); Carpentier (1937)
Middle Cenomanian	sp.	sp.	France	Brouillard quarry (Ecoufland)	Maine-et-Loire, Anjou	Broutin and Pons (1975), Pons (1979)
early Cenomanian	sp.	sp.	France	Charras	Charentes	Koeniguer (1981)
early Cenomanian	sp.	sp.	France	Île d'Oléron	Charente-Maritime	Koeniguer (1981)
early Cenomanian	sp.	sp.	France	La Revardière	Charentes	Koeniguer (1981)
Cenomanian	sp.	sp.	France	Monts-sur-Guesnes	Vienne	Lecointre and Carpentier (1938)
latest Albian-earliest Cenomanian	*alata*	sp.	France	Font-Benon Quarry	Archingeay and Renardières, Charente-Maritime	Aucour et al. (2008)
early Cenomanian	sp.	sp.	France	Rochefort	Charente-Maritime	Koeniguer (1981)
early Cenomanian	sp.	sp.	France	St. Clément	Charentes	Koeniguer (1981)
late Cenomanian	sp.	sp.	Italy	Colle di Moschenizza	Monfalcone, Gorizia	Tentor and Tentor (2007)
late Cenomanian	sp.	sp.	Portugal	Campolide	Alcântara	Saporta and Choffat (1894); Teixeira (1948)
middle Cenomanian	*occidentalis*	sp.	Portugal	Caranguejeira	Leiria	Choffat (1900); Crosaz-Galletti (1979); Callapez (1998)
middle Cenomanian	*occidentalis*	sp.	Portugal	Monsanto	Lisboa	Saporta and Choffat (1894); Teixeira (1948); Berthou (1973)
middle Cenomanian	sp.	sp.	Portugal	Murganhal	Caxias	Teixeira (1948); Berthou (1973)
late Cenomanian	sp.	sp.	Portugal	Padrão	Leiria	Teixeira (1948); Callapez (1998)
late Cenomanian	sp.	sp.	Portugal	Ratão	Alcântara	Saporta and Choffat (1894); Teixeira (1948)
late Cenomanian	sp.	sp.	Portugal	Vila Flor	Miranda do Corvo	Teixeira (1948); Cunha (1992)
Cenomanian?	sp.	sp.	Spain	–	Guadalix de la Sierra	Álvarez-Ramis (1981); Almendros et al. (1982)
Cenomanian-Turonian	sp.	sp.	Spain	Cerro de la Mesa quarry	Guadalix de la Sierra	Álvarez-Ramis (1981); Almendros et al. (1998)
middle-late Cenomanian	sp.	sp.	Spain	Fuentelespino de Haro	Cuenca	Álvarez-Ramis (1981)
Cenomanian-Campanian	sp.	sp.	Spain	Villadiego	Burgos	Álvarez-Ramis (1981)
Cenomanian/ Turonian?	*veneta*	*veneta*	Italy	Bonarelli	Belluno	Gomez et al. (2002b)
Cenomanian/ Turonian	sp.	sp.	Italy	Ca' Trenta di Schio	Vicenza	Pigozzo (2001); Gomez et al. (2002b)
Cenomanian/ Turonian	*alata*	sp.	Italy	Carcoselle	Possagno, Treviso	Bizzarini and Coccioni (1990); Pigozzo (2002); Gomez et al. (2002b)
Turonian	sp.	sp.	Portugal	Vila Verde	Tentúgal	Soares (1966); Callapez (1998)
Turonian-Coniacian	aff. *alata*	sp.	Czech Republic	Dymokury	Nymburk, Bohemia	Hluštík (1974)
Coniacian	*occidentalis*	sp.	Portugal	Verba	Vagos	Saporta and Choffat (1894)
Coniacian-Santonian	*königii*	sp.	Italy	Vernasso	Cividale and San Pietro de Natisone, Udine	Bozzi (1891); Gomez et al. (2002b)
Coniacian-Campanian	sp.	sp.	Germany	–	Westphalia	Hosius and von der Marck (1880); Carpentier (1937)
Coniacian-Campanian	sp.	sp.	Spain	Chotacabras quarry	Torrelaguna	Barale et al. (1988); Álvarez-Ramis et al. (1987)
Santonian to early Campanian	sp.	sp.	Portugal	Vale de Madeira	Poiares	Alvin (1977); Cunha and Reis (1995)
early Campanian-Maastrichtian	*occidentalis*	sp.	Portugal	Casal dos Bernardos	Alhadas	Lima (1900); Antunes and Pais (1978); Antunes and de Broin (1988); Cunha and Reis (1995)
early Campanian-Maastrichtian	sp.	sp.	Portugal	Taveiro	Coimbra	Antunes and Pais (1978); Antunes and de Broin (1988); Cunha and Reis (1995)
Campanian-Maastrichtian boundary	sp.	sp.	Spain	Fumanya Sud	Vallcebre	Riera et al. (2010), Villalba-Breva et al. (2012)
Campanian-Maastrichtian boundary	sp.	sp.	Spain	Mina Esquirol	Vallcebre	Riera et al. (2010)
Maastrichtian	aff. *occidentalis*	sp.	Portugal	Aradas	Aveiro	Teixeira (1948); Bernardes and Corrochano (1987); Antunes and de Broin (1988)
Maastrichtian	*occidentalis*	sp.	Portugal	Mataduços	Aveiro	Choffat (1900); Bernardes and Corrochano (1987); Moron (1981)

Table 1 (*continued*)

Age	Species	Taxonomy revisited	Country	Locality	Area/Region	Reference
Maastrichtian	*oligostomata*	*oligostomata*	Portugal	Olho de Agua, Esgueira	Aveiro, Beira Littorale	Romariz (1946); Broutin and Pons (1975); Alvin (1977); Lauverjat and Pons (1978); Bocherens et al. (1994)
Maastrichtian	*oligostomata*	*oligostomata*	Spain	Torrelaguna	Madrid	Álvarez-Ramis (1981); Álvarez -Ramis et al. (1987)
Maastrichtian	sp.	sp.	Spain	Pla de la Barranca	Vallcebre	Riera et al. (2010)
Maastrichtian	sp.	sp.	Spain	St. Corneli	Vallcebre	Riera et al. (2010)
Maastrichtian	sp.	sp.	Spain	Isona	Isona	Marmi et al. (2014)

Figueira da Foz.

extinction rates were estimated from stratigraphic ranges of 18 species of *Frenelopsis* based on the methods described by Foote (2000). Origination and extinction rates were calculated from the van Valen metrics (van Valen, 1984; Foote, 2000). In order to perform these estimations, the specimens have been grouped in time-homogeneous intervals (ca. 14 Ma duration).

4. Diversification and distribution of *Frenelopsis* in space and time

4.1. Berriasian–Hauterivian

Frenelopsis sp. remains have been reported from many European localities, including Poland, Czech Republic, Germany, France, and Portugal (Table 1). However, three species of *Frenelopsis* have been formally described from Berriasian to Hauterivian times in Europe (Figs. 1, 2A and 3A, Table 1). *F. occidentalis* is the oldest species and it has been documented from the Berriasian of Germany (Watson and Alvin, 1999). *F. teixeirae* occurred from the Valanginian to Hauterivian of Portugal (Alvin and Pais, 1978; Mendes et al., 2010) and *F. hoheneggeri* occurred in the Hauterivian of Poland (Reymanówna, 1965). In Africa, *Frenelopsis sifloana* is known from an unprecise stage in the Early Cretaceous of Sudan (Watson and Alvin, 1976; Watson, 1983). Here it has been provisionally included in this interval. In Asia, only one

species, *F. malaiana* Kon'no, was described in this interval, precisely in the Berriasian-Valanginian of western Malaysia (Smiley, 1970). The data available suggest that, from its origin, genus *Frenelopsis* was probably widespread, at least in a tropical to paratropical belt between 0° and 40° N ranging from the Tethyan archipelago to present southeastern Asia (Figs. 2 and 3A).

4.2. Barremian–Aptian

During this time interval, new species appeared in the Tethyan archipelago, such as *F. atlantica* Batten et al. in Ireland, *F. rubiesensis* Barale, *F. ugnaensis* Gomez et al. and *F. antunesi* Mendes et Kvaček in Iberia and *F. profetiensis* Bartiromo in exposed areas from the Apennine platform (Figs. 1, 2A and 3A; Table 1). In addition, *F. hoheneggeri* spread and colonised other areas of the archipelago (Figs. 2B–C, 3A, Table 1) such as present-day Croatia, Austria and the Czech Republic (Reymanówna and Watson, 1976; Carpentier, 1937). More occurrences were reported as *Frenelopsis* sp. from some islands of the archipelago, such as Iberia and France (Fig. 2B–C, 3A). In Asia, *F. choshiensis* Kimura et al. was restricted in Japan (Chow and Tsao, 1977; Kimura et al., 1985), while *F. ramosissima* Fontaine has been reported in the late Aptian of North America and lasted until early Albian (e.g., Upchurch and Doyle, 1981). Some of the species of the Tethyan archipelago (e.g., *F. atlantica* and *F. ugnaensis*) as well as the Asian *F. choschiensis* were likely endemic
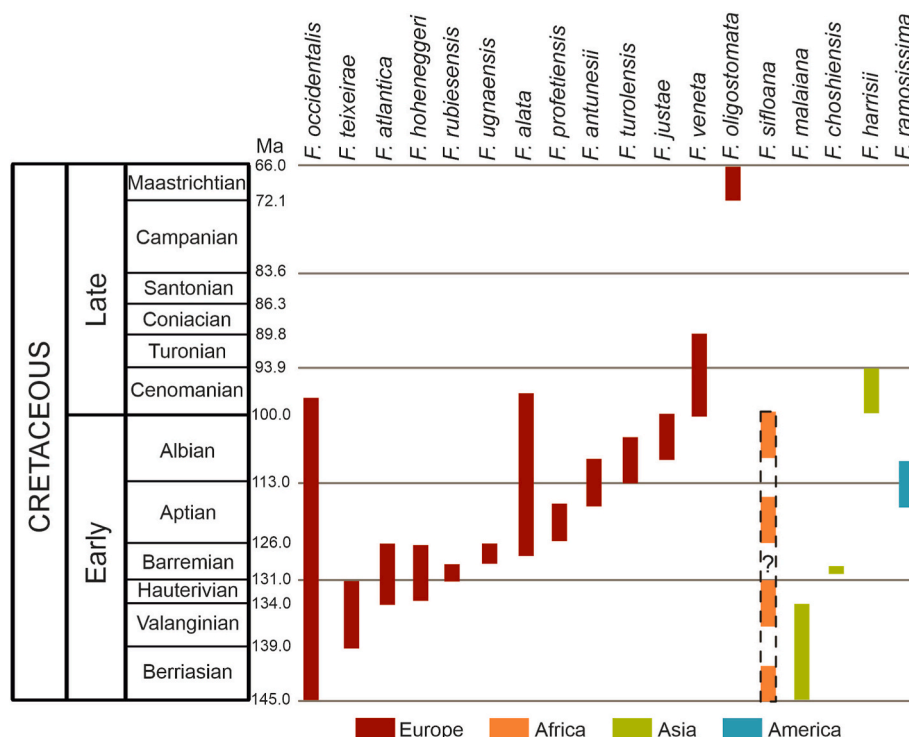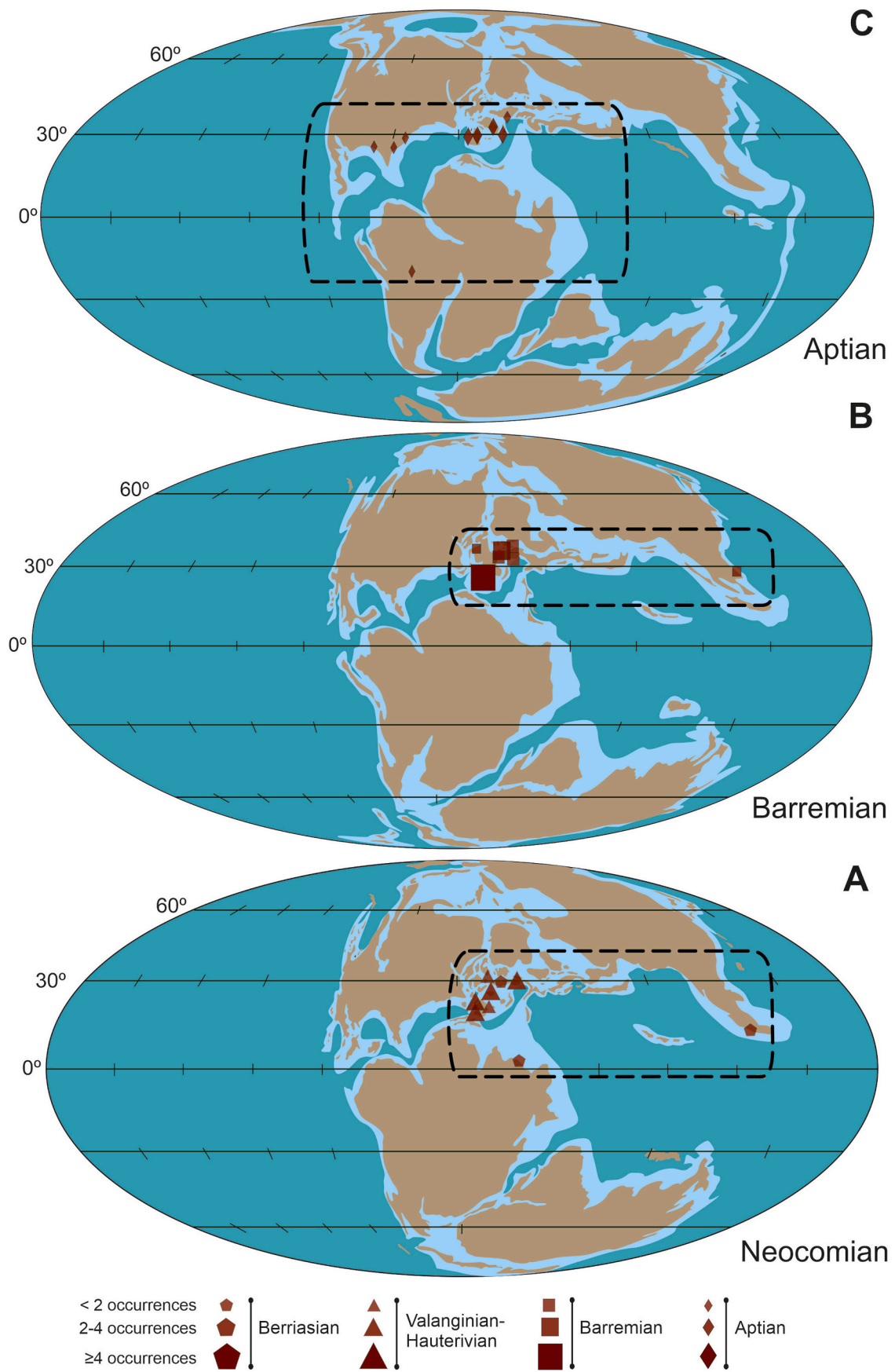

Fig. 1. Chronostratigraphic ranges of *Frenelopsis* species. The dashed line represents imprecise chronostratigraphic attribution within the range.

Fig. 2. Biogeography of *Frenelopsis* from the Berriasian to the Aptian plotted on global Early Cretaceous palaeogeographic maps. The dashed line represents the track line of *Frenelopsis* distribution. Palaeogeographic maps modified from https://deeptimemaps.com.
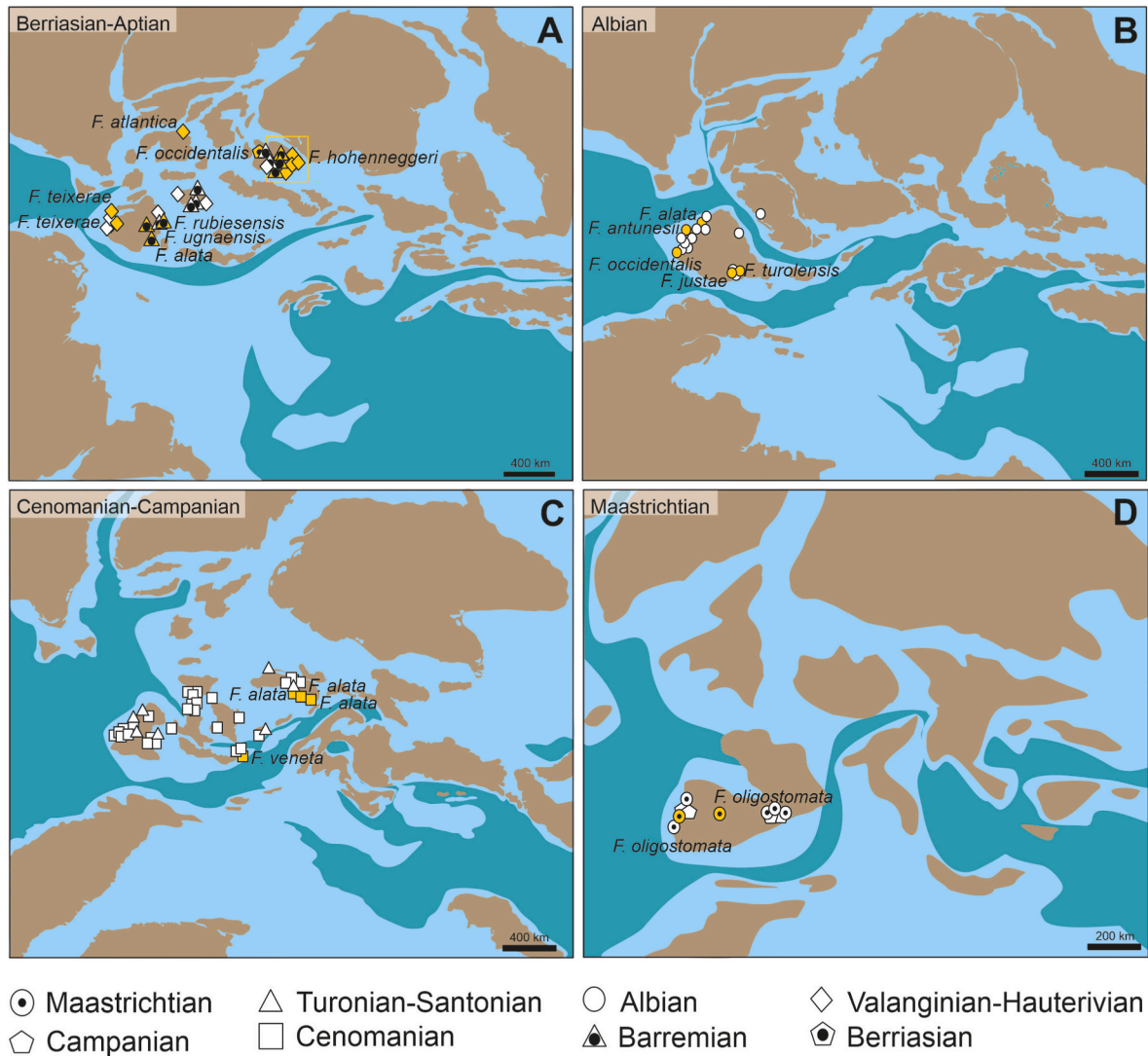
Fig. 3. Biogeographic distribution of *Frenelopsis* species in the Tethyan archipelago during the Cretaceous. In white *Frenelopsis* sp. occurrences, in orange *Frenelopsis* occurrences identified at the species level. Palaeogeographic maps modified from https://deeptimemaps.com.

and short-lived (Fig. 1). Available data (Fig. 2B–C, 3A, Table 1) suggest that the Tethyan archipelago was the area where *Frenelopsis* was more widespread during the Barremian–Aptian.

4.3. Albian−Cenomanian

During this time interval, the *Frenelopsis* species richness decreased. However, new but short-lived species appeared in particular islands of the Tethyan archipelago, where they were likely endemic. This is the case for the Albian *F. turolensis* and *F. justae* in eastern Iberia and the Cenomanian *F. veneta* Gomez et al. in emerged lands of the Friuli platform (Fig. 3B−C). In contrast, *F. alata*, which appeared in the previous interval, increased its biogeographic range to several islands of the archipelago, from western Iberia to the Bohemian Basin. During the Albian, another long-lived species, *F. occidentalis,* appeared in western Iberia (Portugal) and lasted until the Cenomanian. In Asia, *F. harrisii* Doludenko and Reymanówna occurred in the Tajikistan (Doludenko and Reymanówna, 1978) (Figs. 1 and 4B). In North America *F. ramosissima* persisted. The analysis of occurrences indicates that, during Albian and Cenomanian, *Frenelopsis* was again abundant and widespread in the Tethyan archipelago (Fig. 3B and C; Table 1), especially in a paratropical belt, between 25° and 40° northern palaeolatitudes (Fig. 3B−C).

4.4. Turonian−Santonian

During this time interval, a decrease in species richness occurred. The Friuli platform was still inhabited by *F. veneta*, which went extinct at the end of the Turonian (Gomez et al., 2002b). Other species, such as *F. alata* disappeared before the early Turonian. The number of occurrences of *Frenelopsis* sp. continued to be important in the Tethyan archipelago (Portugal, Spain, Italy, Czech Republic, Germany) but diminished in comparison to previous periods (Figs. 3, 4B and 6A; Table 1).

4.5. Campanian−Maastrichtian

Near the end of the Cretaceous, the new species *F. oligostomata* arose in western Iberia, where it inhabited coastal wetlands (Figs. 1, 3C−D, 4C and 5) (Mendes et al., 2010). Additionally, *Frenelopsis* sp. was very abundant in freshwater coastal habitats from northeastern Iberia (present-day South Pyrenees, Catalonia), where until the end of the early Maastrichtian it constituted a peat-forming plant, the peat turning after diagenesis into thick lignite deposits of the so called "Grey Unit" from the Tremp Formation (Villalba-Breva et al., 2012). The latest occurrences of *Frenelopsis* suggest that it was only restricted to the Iberoarmorican domain (Figs. 3D and 5), a large island composed of
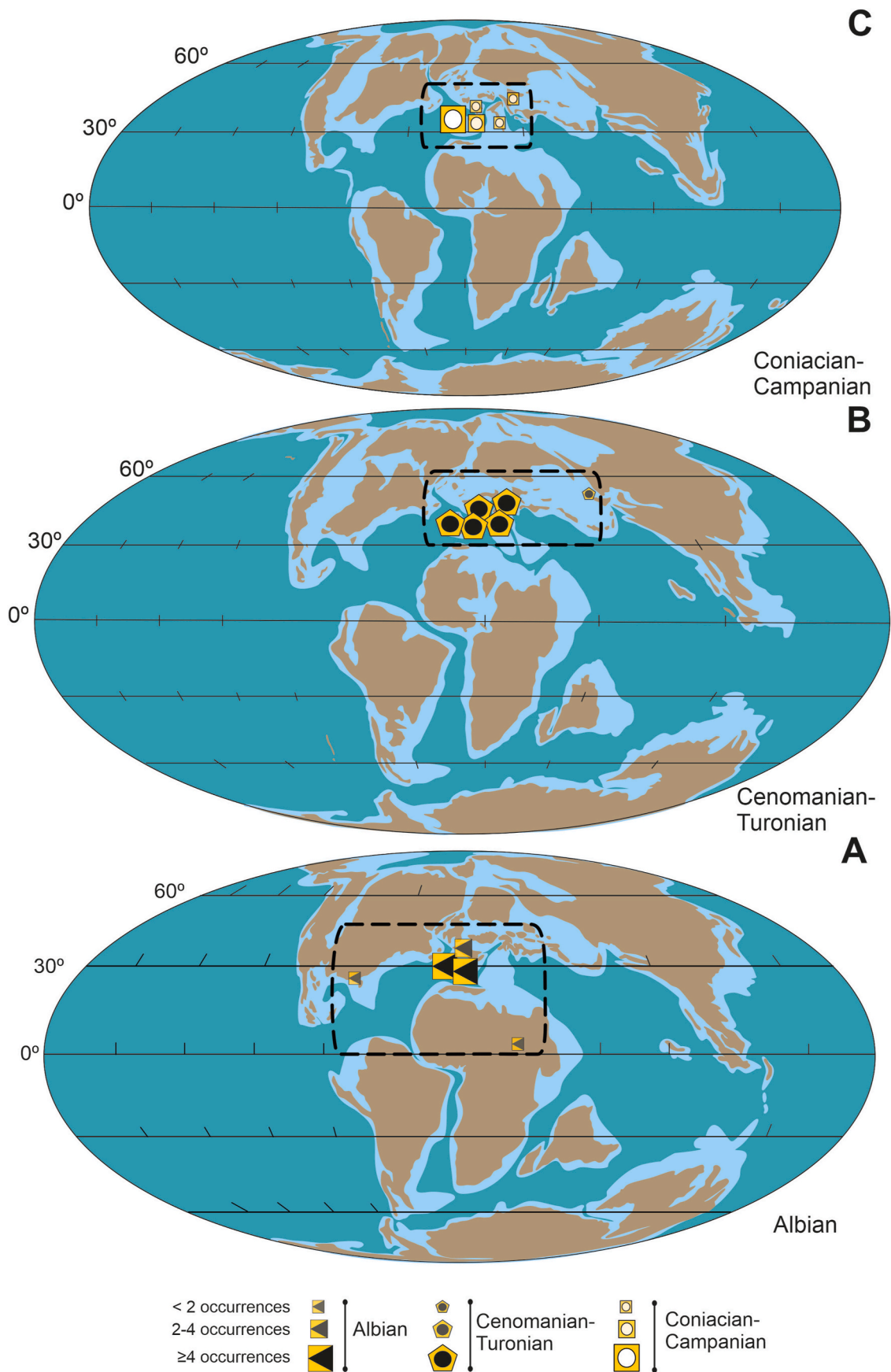
Fig. 4. Biogeography of *Frenelopsis* from Albian to Campanian, plotted on global Late Cretaceous palaeogeographic maps. The dashed line represents the track line of *Frenelopsis* biogeographic distribution. Palaeogeographic maps modified from https://deeptimemaps.com.
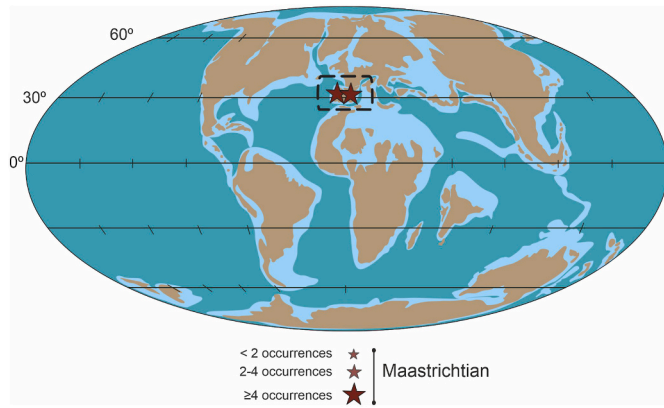
Fig. 5. Biogeography of *Frenelopsis* during the Maastrichtian, plotted on a worldwide palaeogeographic map at 80 Ma. The dashed line represents the track line of *Frenelopsis* biogeographic distribution. Palaeogeographic maps modified from https://deeptimemaps.com.

emerged lands of Iberia and parts of France that was located in the western edge of the southern Tethyan archipelago.

5. Discussion

### 5.1. Origins, diversification and decline of the genus Frenelopsis

Eighteen species of *Frenelopsis* have been analysed based on mega and micromorphological features of vegetative parts (Table 1, Fig. 1). The earliest records are from the Berriasian of Germany (Watson and Alvin, 1999) and Berriasian-Valanginian of Malaysia (Smiley, 1970; Uyop and Che Aziz, 2000). *Frenelopsis* could also be present in Africa (Sudan) but a detailed chronostratigraphic study is necessary to confirm this occurrence (Watson and Alvin, 1976; Watson, 1983). The present dataset suggests that *Frenelopsis* was already widely distributed from its

origins, at the beginning of the Cretaceous.

Frenelopsis diversified throughout the Early Cretaceous, as suggested by the number of occurrences, the number of species per unit of time and the mean standing diversity (Fig. 6A−C). However, it is noteworthy that the origination rate decreased between the Berriasian and Aptian and, especially, between the Albian and Santonian (Fig. 6D). From the Aptian interval onwards, the extinction rate exceeded the origination rate (Fig. 6D). The biogeographic range of *Frenelopsis* began to decrease during the Albian–Cenomanian, and during the Late Cretaceous it was confined to the Tethyan archipelago (Figs. 3B−C and 4A−C). All these results support the hypothesis that the decline of *Frenelopsis* could have already started during the late Early Cretaceous, coinciding with the rise to dominance of angiosperms and the expansion of megathermal forests from low to middle latitudes, which was driven by the mid-Cretaceous increase in global temperatures (Coiffard and Gomez, 2012; Coiffard et al., 2012). It is well documented that flowering plants colonised habitats in which *Frenelopsis* was previously dominant such as coastal wetlands, floodplains and freshwater swamps during the Albian−Cenomanian (Gomez et al., 2001, 2002a, 2004; Coiffard et al., 2006; Barral et al., 2016). Notwithstanding, during the Maastrichtian, at the end of its evolutionary history, *Frenelopsis* still formed important vegetations in coastal wetlands of Iberia, successfully competing with angiosperms, such as palms and monocot reeds (Villalba-Breva et al., 2012; Marmi et al., 2016).

5.2. The role of the Tethyan archipelago in Frenelopsis biogeography

At least half of the known species of *Frenelopsis* inhabited the Tethyan archipelago (Fig. 1−5, Table 1). Eustatic fluctuations, which characterised most of the Cretaceous, probably promoted first the isolation and later the spread of *Frenelopsis* populations in this area, enhancing allopatric speciation mechanisms. Some species, such as *F. teixeirae*, *F. justae*, *F. turolensis*, *F. ugnaensis*, *F. occidentalis* and *F. oligostomata* appear to have been endemic of Iberia (Fig. 3, Table 1). Other species, such as *F. profetiensis* and *F. veneta* were likely restricted to small,
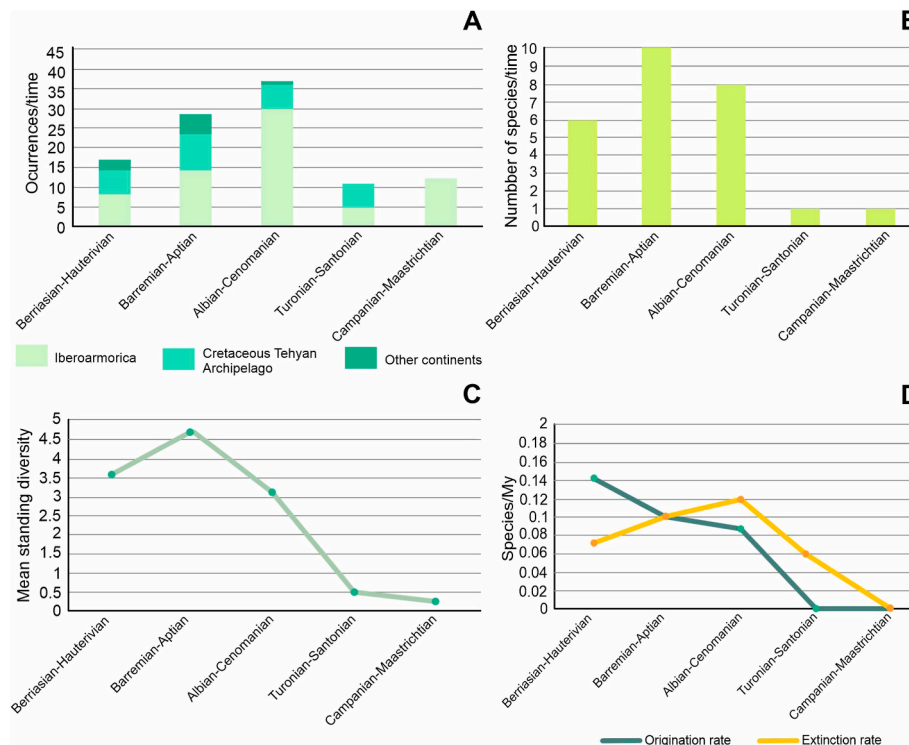
Fig. 6. Abundance and diversity of *Frenelopsis* during the Cretaceous. **A:** Total number of occurrences per time intervals (stages). **B:** Total number of species per time interval. **C:** Diversity curve. **D:** Curves of origination and extinction rates.

emerged areas in the Apennine and Friuli platforms (Gomez et al., 2002b; Bartiromo et al., 2009, 2012). This suggests that Iberia and other islands from the Apennine and Friuli platforms could be important areas for *Frenelopsis* speciation, favouring endemism and the divergence of short-lived species during most of the Cretaceous (Fig. 3). By contrast, other species had wider geographic ranges. This is the case of *F. alata* that spread from Iberia to the Bohemian and Friuli lands (Fig. 3). The biogeographic range of other species, such as *F. hoheneggeri,* is more difficult to interpret since many occurrences of this species lack sufficient cuticular data to be confirmed (Table 1).

All these data suggest that *Frenelopsis* was conspicuous in Iberia during the whole Cretaceous (Fig. 3). It seems clear that this palaeo-island played an important role in the radiation of the genus and provided refugia for these conifers during their Late Cretaceous decline, until holding its last representatives in the Maastrichtian.

5.3. Hypotheses on the extinction of Frenelopsis

The long-lasting evolutionary success of *Frenelopsis* throughout the Cretaceous in Europe was promoted by their ecological plasticity, high adaptability to environmentally constraints as well as strong competitiveness, having negative feedback on the richness and abundance of other taxa living in the same habitats (Gomez et al., 2002a; Barral et al., 2016). It appears that the diversification and rise to dominance of angiosperms in low and middle latitudes could have played an important role in the decline of *Frenelopsis* during the Late Cretaceous. However, even the last known *Frenelopsis* were still competing successfully with certain angiosperms, such as palms, in freshwater coastal swamps of Iberia (Villalba-Breva et al., 2012), before becoming extinct during the Maastrichtian. Another genus within the Cheirolepidiaceae crossed the Cretaceous/Paleogene boundary, and survivors of this family still played a significant role in Paleocene plant communities of southernmost South America (Barreda et al., 2012).

One may wonder why this did not happen for *Frenelopsis*. Evidence could come from the Maastrichtian of northeastern Iberia, where *Frenelopsis* leafy axes are very abundant and the accumulation of these remains formed the peat precursory of large amounts of lignite in the Tremp and Vallcebre basins, Catalonia (Villalba-Breva et al., 2012). Among the latest known records of *Frenelopsis* from Iberia are those reported from the lower Maastrichtian of Fumanya and Mina Esquirol, in the Vallcebre Basin (Villalba-Breva et al., 2012) (Fig. 7) and the middle Maastrichtian of Isona, in the Tremp basin (Marmi et al., 2014). However, while some Early Cretaceous palynofloras from Iberia reached up to 80−90% of *Classopollis* (Solé de Porta et al., 1994; Gomez et al., 2001), these characteristic pollen grains were almost absent in the Iberian Maastrichtian, e.g., Vallcebre Basin, Coll de Nargó Basin and

Tremp Basin (Médus, 1970, 1972; Fernández-Marrón, 2009; Villalba-Breva et al., 2012). The only locality where *Classopollis* was mentioned as an extremely rare element of the palynological assemblage was Barranc La Posa in the Tremp Basin (de Porta et al., 1985). To explain the absence of *Classopollis* in latest Cretaceous pollen assemblages and the mismatch with rich *Frenelopsis* megafossil assemblages of the same outcrops, Friis et al. (2011) and Villalba-Breva et al. (2012) suggested taphonomic biases or low production of *Classopollis* pollen by the source plants. However, taphonomic bias is a rather improbable situation to explain the absence of pollen in coastal wetlands, where transport through tractive currents was reduced and other types of transport, such as floatation, could hardly make the abundant and thick-walled *Classopollis* pollen grain completely disappear from the palynofloras. Thus, the second hypothesis gains probability. *Frenelopsis* relictual populations of Iberia might have been affected by low pollen production or even male sterility, being these factors the *coup de grace* that led to extinction. In fact, high number of *Classopollis* pollen tetrads with abortive or malformed individual pollen grains have been recognized from uppermost Triassic to Lower Cretaceous deposits (e.g., Stuckins, 2022; Galasso et al., 2023). For instance, in the middle Jurassic deposits from Neuquén Basin (Argentina), the malformations of *Classopollis* grains are significantly high i.e., 2.8–8.4% in tetrads and 30.9–57.7% of individual grains (Jin et al., 2020; Stuckins, 2022). The production of aborted pollen grains from *Classopollis* increases in particular time intervals during the Early Cretaceous (Kürschner et al., 2013; Galasso et al., 2023).

Male sterility has been suggested as a possible cause for the decline of some extant conifer species. For instance, unreduced and abortive pollen grains are thought to have led to the endangered Mediterranean cypress, *Cupressus dupreziana* A. Camus, to natural extinction (Pichot and Maâtaoui, 2000; Maâtaoui and Pichot, 2001). Similarly, the decline of Taiwanese populations of the Cupressaceae *Taiwania cryptomerioides* Hayata are attributed to male sterility (Chen et al., 2006). More precisely, the latter authors explained that in *T. cryptomerioides* sterile microspores remained as tetrads due to the absence of callose in the tetrad cross walls.

In order to test the hypothesis of extinction through male sterility in *Frenelopsis* it is necessary to increase the search for fossil *Classopollis* in the Maastrichtian of Iberia and document if pollen malformations, such as tetrads with abortive grains, or other morphologically recognizable teratologies occur.

6. Conclusions

The compilation of over a century of taxonomic, biogeochemical and palaeoecological studies about the extinct conifer *Frenelopsis* allows us to
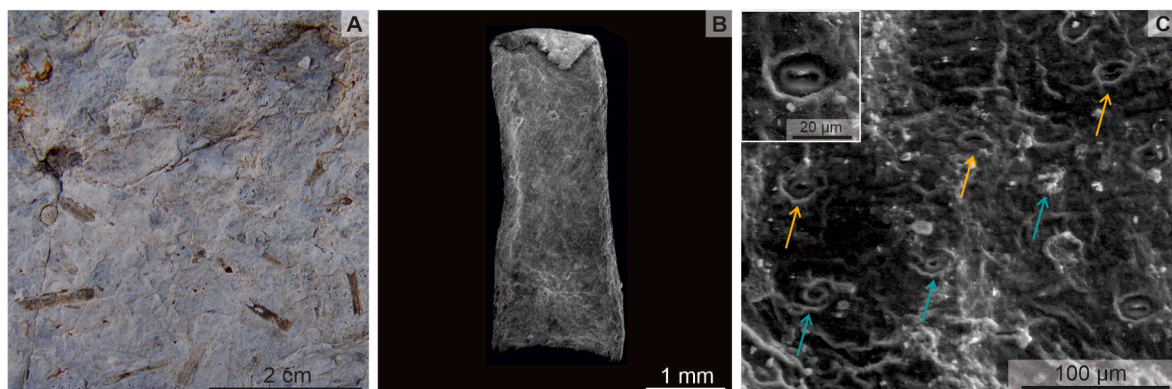
Fig. 7. Vegetative remains of *Frenelopsis* sp. from the Maastrichtian of Mina Esquirol (Catalan Pyrenees, Spain). **A:** Abundant *Frenelopsis* vegetative shoots almost covering completely the base of a coal seam (only a few cuticles are preserved). **B:** Detail of internode showing one free tip of leaf folded down. **C:** SEM picture of cuticle showing two rows of stomata aligned (arrows) and detail of a stomatal apparatus (insert) showing rim around sunken stomata. Papillae are not preserved, which renders it difficult determination at the species level.

reconstruct its evolution in terms of diversity and species richness, biogeographic history and to infer about the causes of its extinction.

The oldest record of *Frenelopsis* dates back to Berriasian. From the beginning of its history (Berriasian−Hauterivian), *Frenelopsis* was well distributed in the Tethyan archipelago and soon extended to Asia in the paratropical climatic belt of the Northern Hemisphere. In the Aptian it reached North and South America, while the stage when *Frenelopsis* colonized Africa remains to be documented with more precision. Until the Aptian the species richness and standing diversity of *Frenelopsis* increased, while the maximum number of occurrences is reported from Albian-Cenomanian times. The Tethyan archipelago was the area with more species and occurrences. Particularly Iberia was the one of the most important diversity hotspots and hold many endemic species, such as *F. teixeirae*, *F. ugnaensis*, *F. justae* or *F. turolensis*.

After the Cenomanian the species richness and the number of occurrences of *Frenelopsis* drastically diminished and its biogeographic range became constrained to the Tethyan archipelago. This trend exacerbated in the Maastrichtian, when *Frenelopsis* only survived relict in the Iberian paleoisland. The last occurrence in coastal wetlands of the middle Maastrichtian of the Tremp Basin (Catalan Pyrenees) may be considered a refuge for this genus. Populations were significant enough to constitute the main peat-forming plant from the Pyrenean Maastrichtian coal, exploited in gallery and opencast mines until the past century, while its pollen (*Classopollis*) was almost absent. This suggests that male sterility could have been one of the main causes of its extinction before the K/Pg boundary, while another closely related genus survived this boundary shortly in South America. Future palynological studies about the importance of malformations and frequency of abortive pollen grains of *Classopollis* in the last populations of *Frenelopsis* could help to test this hypothesis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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