Palynostratigraphical review of the K–Pg boundary from the Ibero-Armorican Island: New data from the Maastrichtian dinosaur outcrop Veracruz 1 (Pyrenees, NE Iberian Peninsula)

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ABSTRACT

The palynostratigraphy of the K–Pg boundary interval in SW Europe has been a subject of ongoing debate, despite numerous palynological studies in the region. To address this, we review previous publications and conduct analysis of new deposits to establish a palynostratigraphical chart. A total of 40 palynological studies within the Normapolles palynological province were reexamined to elucidate key taxa restricted to the Cretaceous (K-taxa), to the Maastrichtian–Danian interval (KPg-taxa) and those restricted to the Paleogene (Pg-taxa). Eventually, we propose 18 key taxa to differentiate a Maastrichtian from a Danian palynological assemblage within the Normapolles Province. Afterward, a palynostratigraphical analysis was carried out in Veracruz 1 (Aragonese Pyrenees), one of the more modern dinosaur-bearing sites of Europe. The palynological assemblage corresponded to an upper Maastrichtian age and was composed by pteridophyte spores, gymnosperms, angiosperms, dinoflagellate cysts, algae, and fungal spores. It was predominated by angiosperm pollen (Liliaceae, post-Normapolles, and triporate pollen). The plant communities in Veracruz 1 seem to be characterized by plants from an open coastal forest prevailed by Liliaceae flowering herbs and Juglandaceae/Myricaceae dicotyledonous trees and shrubs thriving in temperate-warm paleoclimate. The Gondwanan botanical influence was also supported by the presence of *Bacumorphomonocolpites* sp., as this taxon was previously recorded in other upper Maastrichtian deposits from Europe.

1. Introduction

The extinction event linked to the K–Pg boundary is one of the most debated and studied biotic crises from the past. Besides the asteroid impact 66 Ma ago in Chicxulub, Mexico (Alvarez et al., 1980, 1982), several destabilizing events occurred at the end of the Maastrichtian, such as climate change (Wilf et al., 2003; Self et al., 2006), volcanic activity in the Deccan Volcanic Province (Chenet et al., 2009), and marine regression (Miller et al., 2005). All

these, may have contributed to the extinction event linked to the K–Pg boundary. However, recent studies still consider the asteroid impact as the leading cause of the end-Cretaceous extinction event (Chiarenza et al., 2020; Dzombak et al., 2020; Lyons et al., 2020; Morgan et al., 2022). In any case, the result was the disappearance of nearly 70% of the living fauna on Earth (Jablonski, 1994). Non-avian dinosaurs, enantiornithine birds, pterosaurs, mosasaurs, plesiosaurs, and several crocodylomorphs, disappeared among other vertebrates (Bardet, 1994; Longrich et al., 2011, 2018; Brusatte et al., 2015; Puértolas-Pascual et al., 2016; Pérez-Pueyo et al., 2021a). In the oceans, the marine food chain, founded on coccolithophorids and foraminifera, was altered after the impact causing

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P. Martínez de Espronceda, I. Rodríguez-Barreiro, M. Pérez-Pueyo et al.

Cretaceous Research 154 (2024) 105757

the extinction of several taxa related to photic and higher trophic levels, such as ammonoids (D'Hondt, 2005).

However, the effect of the Chicxulub impact seems to have had less effect on the vegetation. Indeed, there was not any extinction at family level in any of the vascular plant groups recognized in the latest Cretaceous (Cascales-Miñana and Cleal, 2014). Even so, minor changes happened in the floral composition during this biotic crisis. In high-resolution palynological studies, a decrease in species diversity of microfloras has been observed, which is always less than 30% (Nichols, 2002; Hotton, 2002; Vajda and Raine, 2003; Nichols and Johnson, 2008). In some regions (*i.e.*, North America and New Zealand), similar paleoecological changes were observed (Vajda and Bercovici, 2014). First, right after the extinction of several plant species, a fungal spike occurred associated with the K−Pg boundary levels, suggesting an increased saprophytic activity enhanced by the abundant decomposing organic matter due to the cessation of photosynthesis (Vajda and McLoughlin, 2004; Sepúlveda et al., 2009; Vajda, 2012). Then, the subsequent proliferation of vegetation was first initiated by ferns, as indicates the spike of pteridophyte spores (*e.g.*, Vajda et al., 2001, 2004; Vajda and Raine, 2003; Nichols and Johnson, 2008; Bercovici et al., 2012). Subsequently, a recovery of angiosperms and conifer pollen took place (Sweet and Braman, 1992, 2001; Vajda et al., 2004; Bercovici et al., 2009).

The K−Pg boundary has been widely studied in the Northern Hemisphere, especially in North America, which includes some of the best examples of the Maastrichtian−Danian boundary as the continental Hell Creek Fm (Johnson et al., 2002). The fossil assemblages of this region are well known and have been studied extensively for many decades (*e.g.*, Pearson et al., 2002; Lyson and Longrich, 2011). Meanwhile, in the European region, the continental deposits from the so-called Ibero-Armorican Island (Spain, Portugal, and France) have been prospected during the last decades with remarkable results (Pereda-Suberbiola et al., 2009; Csiki-Sava et al., 2015; Fondevilla et al., 2019; Pérez-Pueyo et al., 2021a). The Maastrichtian−Paleocene Tremp Fm in Southern Pyrenees (NE Spain) represents a transitional to continental unit without significant sedimentary hiatuses (Oms et al., 2007; Riera et al., 2009). This unit also yields several sites with ichnites and vertebrate fossil remains of dinosaurs, crocodylomorphs, giant birds, and eggshells, being some of these the youngest Maastrichtian sites found in Europe so far (*e.g.*, Canudo et al., 2016; Díez-Canseco et al., 2016; Sellés et al., 2016; Pérez-Pueyo et al., 2021a, 2021b, Pérez-Pueyo, 2023).

Therefore, the Tremp Fm is a promising unit for studying the K−Pg extinction event on the Ibero-Armorican Island. Here, paleobotanical data has a particular interest since the K−Pg European floras seemed to have a different response compared to those present in the North American and New Zealand regions (Mayr et al., 1999; Vajda and Bercovici, 2014).

In this study, we analyze the palynology from the Maastrichtian Veracruz 1 site (Beranuy log, Southern Pyrenees, NE Spain) along with an exhaustive review of the previous continental palynological works in the Iberian Peninsula and the South of France (*i.e.*, the Ibero-Armorican Island) from a biostratigraphical perspective. The aims of this work are: 1) to elaborate a palynostratigraphical chart of the K−Pg boundary interval in the Ibero-Armorican Island; 2) to make a palynological dating of the recently discovered Veracruz 1 site; 3) to reconstruct the paleoecology of the Veracruz 1 site and its paleoenvironmental and paleoclimatological implications.

1.1. Geographic and geological context

The Beranuy log containing the site of Veracruz 1 is within the territory of the municipality of Beranuy and is located between the localities of Biascas de Obarra and Serraduy in the Ribagorza county (Southern Pyrenees, Huesca, Aragón, NE Spain) (Fig. 1A) (WGS84: 42° 22′ 06″ N; 0° 35′ 34″). The Pyrenees is an NNW-SSE Alpine mountain range between Spain and France formed due to the collision of the European and the Iberian plates during the latest Cretaceous to Miocene (Puigdefàbregas et al., 1986; Muñoz, 1992; Teixell, 1998, 2004; Sibuet et al., 2004). The thrust sheets of the orogeny controlled the development of several foreland basins (Chanvry et al., 2018; Muñoz et al., 2018), including the South-Pyrenean Basin (active between the Late Cretaceous and the Oligocene). The Beranuy outcrop studied here is located on the north flank of the Tremp Syncline, in an area also known as the Western Tremp Syncline (Fondevilla et al., 2019). The Tremp Syncline or Tremp-Graus Basin (Fig. 1A) is one of the sub-basins found in the South-Pyrenean Basin.

The sedimentary succession of the Tremp Syncline is composed of Upper Cretaceous marine deposits, followed by turbiditic and deltaic sediments (Santonian−Maastrichtian), and then by transitional and continental deposits (Maastrichtian−Paleocene) (Ardèvol et al., 2000; Gómez-Gras et al., 2016; Oms et al., 2016). The Maastrichtian−Paleocene Tremp Fm (Mey et al., 1968) (Fig. 1A, B), also known as Garumnian Facies or Garum Facies (Leymerie, 1868), is a heterogeneous and diachronous lithostratigraphic unit that represents coastal to continental deposits. This formation can be divided into four informal units recognizable throughout the South-Pyrenean Basin (Rosell et al., 2001): the 'Grey Garumnian' and the 'Lower Red Garumnian', dated as Maastrichtian; and the 'Vallcebre limestones and equivalents' and 'Upper Red Garumnian', which are Paleocene in age.

The 'Grey Garumnian' (Fig. 1B) is a unit formed by gray marls and mudstones, with intercalations of sandstones, limestones, and coal beds. Fossils of plants, brackish and continental invertebrates, and vertebrates are frequent. The 'Grey Garumnian' was deposited in transitional paleoenvironments, including lagoon, marshes, and tidal mud flats (Nagtegaal, 1972; Eichenseer, 1988; Cuevas, 1992; Rosell et al., 2001; Riera et al., 2009; Díez-Canseco et al., 2014; Oms et al., 2016; Pérez-Pueyo, 2023). The age of the 'Grey Garumnian' varies throughout the basin due to its lateral relationship with the continental 'Lower Red Garumnian' (Ardèvol et al., 2000; Fondevilla et al., 2016), being younger (upper Maastrichtian) in the western part of the Tremp Syncline (*e.g.*, Pereda-Suberbiola et al., 2009; Canudo et al., 2016; Puértolas-Pascual et al., 2018) such as in the case of the studied Beranuy log including the Veracruz 1 site (Pérez-Pueyo, 2023).

The Veracruz 1 site is located in the uppermost part of the 'Grey Garumnian' unit (Fig. 1B), in a 2 m-thick level of dark gray organic-rich marly mudstones (Fig. 1B, C). They have abundant fossil remains and bioturbation, including plant rhizoliths (Pérez-Pueyo et al., 2019). In addition to planktonic foraminifera, charophyte gyrogonites, and charcoalified wood from wildfire, a diverse assemblage of invertebrates of mixed provenance (marine, transitional, and continental) has also been recovered from Veracruz 1, including bivalves, gastropods, decapod crustaceans (Pérez-Pueyo et al., 2022), bryozoans and serpulids. Besides, fossil remains of several groups of vertebrates have been recognized at the site, such as dinosaurs (hadrosauroid ornithopods and theropods), crocodylomorphs, Testudines, and Osteichthyes (Pérez-Pueyo et al., 2019). Eggshell fragments are also abundant at the Veracruz 1 site, being the type locality of *Pachykrokolithus excavatum* Moreno-Azanza, Pérez-Pueyo, Puértolas-Pascual, Núñez-Lahuerta, Mateus, Bauluz, Bádenas, and Canudo, 2022, a crocodylomorph ootaxa, probably related to continental eusuchian allodaposuchids, whose presence in the site has been suggested by the abundant record of isolated conical teeth (Moreno-Azanza et al., 2022; Pérez-Pueyo, 2023). By its sedimentological features and its mixed fossil
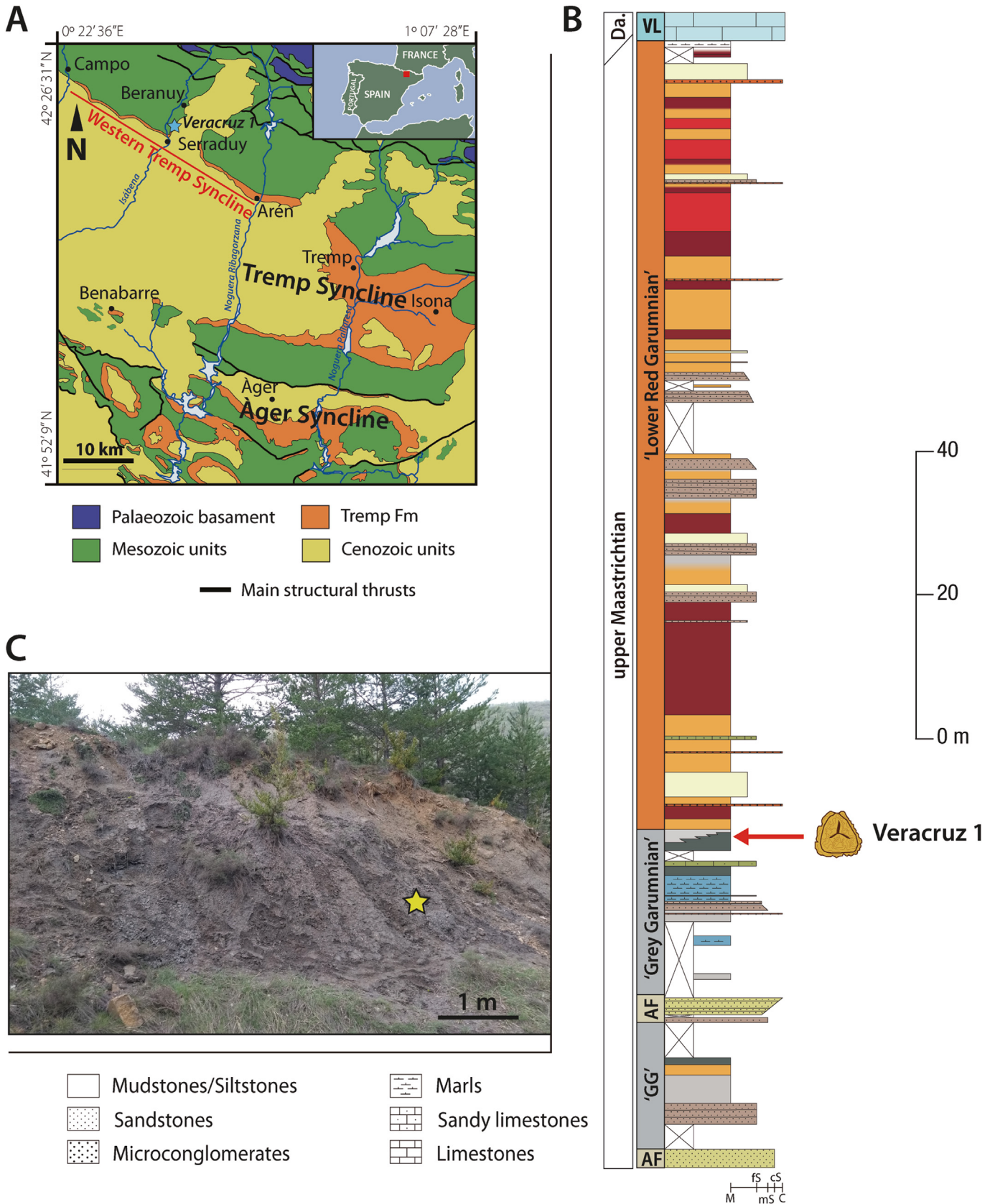
P. Martínez de Espronceda, I. Rodríguez-Barreiro, M. Pérez-Pueyo et al.

Cretaceous Research 154 (2024) 105757

Fig. 1. Geographic and geological setting of Veracruz 1 site (Huesca, Spain). A) Geological map of the Tremp and Àger synclines at the western part of the South-Pyrenean Basin. The blue star marks the location of Veracruz 1 (modified from López-Martínez and Vicens, 2012). B) Stratigraphic succession of the Mesozoic part of the Tremp Fm in the Beranuy log indicating the stratigraphic position of the Veracruz 1 site. AF: Arén Fm; GG: 'Grey Garumnian'; LG: 'Lower Red Garumnian'; VL: 'Vallcebre limestones and lateral equivalents'; M: mudstone; fS: fine sandstone; mS: medium sandstone; cS: coarse sandstone; C: conglomerate. C) General view of the Veracruz 1 site. The yellow star indicates the spot where the palynological sample was collected.

association, Veracruz 1 probably represents a small pond located in the area fringing the lagoon, with inputs coming from the continent, the lagoon itself, and the open sea (Pérez-Pueyo et al., 2019; Pérez-Pueyo, 2023).

1.2. State of the art of the K−Pg interval palynology

A consistent number of palynological studies were carried out across the K−Pg boundary interval on the Ibero-Armorican Island. At the same time, revisions of these works have been done during the last decades to detect any paleobotanical changes or trends which were able to determine a shift in plant communities during or after the K−Pg boundary. Over 20 palynological studies have been published in SW Europe (the Iberian Peninsula and southern France) within the Maastrichtian−Danian age interval (see Supplementary Material).

Pyrenees

The first approach to the palynology of the Tremp and Coll de Nargó synclines in the Pyrenean region was in Médus (1970), studying the "first lignite levels interbedded by limestones, right above the Aren's sandstones" (*i.e.*, the 'Grey Garumnian') in the Coll de Nargó section and the "lignites close to the Fuvelian located in the Maastrichtian−Danian boundary" (*i.e.*, basal 'Vallcebre Limestones') in the Suterranya section. The author makes no difference between the two assemblages, noticing that they are dominated by monocolpate pollen, with a remarkable presence of Arecaceae and *Trudopollis* pollen. Both assemblages were interpreted as an uppermost Maastrichtian age.

Another location studied in the Pyrenees was the Barranco de la Posa section by Kedves et al. (1985), corresponding to the upper half of the 'Grey Garumnian', showing an assemblage dominated by Cupressaceae and Palmae pollen and, in less proportion, *Cycadopites*, *Cupuliferoipollenites* and *Subtriporopollenites*. The assemblage would correspond to a lower Maastrichtian and the authors suggest a marked Gondwanan influence because of the high diversity of Palmae pollen and the abundance of *Cycadopites*.

More recently, Fernández-Marrón et al. (2004) made a quantitative analysis of the abundance and diversity of the Campo section ('Lower Red Garumnian') and compared it to previous palynological data of the Fontllonga section from the Àger syncline (López-Martínez et al., 1999; Mayr et al., 1999). The results showed a consistent pattern along the K−Pg boundary where the most noticeable change is the increase in trilete spores during the uppermost Maastrichtian and its decrease in the Danian assemblages.

Later, Torices et al. (2012) focused their research on the Vicari section, encompassing the Arén and Tremp formations, where nine palynological samples were obtained along the 'Grey Garumnian' unit and the lower part of the 'Lower Red Garumnian' within the Tremp Fm. The authors found that the microflora here, shifts from an assemblage dominated by pteridophytes in the lower part of the 'Grey Garumnian', to a dominance of aquatic palynomorphs, both dinoflagellates and freshwater algae, in the upper part. Eventually, in the lower part of the 'Lower Red Garumnian', the assemblage is dominated by conifer pollen. They also found a clear decrease in the diversity throughout this interval.

Villalba-Breva et al. (2015) made a paleobotanical study (plant macro-fossil and palynology) from the lower part of the 'Lower Red Garumnian', in the stratotype of the Isona section. The palynological assemblage studied here showed a constant dominance of pteridophytes, while angiosperms and gymnosperms were less abundant.

Marmi et al. (2015) presented a study mainly focused on the plant macro-fossil record from the upper part of the 'Lower Red Garumnian' in Molí de Baró-1 section. The authors found a low-diversity palynological assemblage mainly dominated by angiosperm pollen (*i.e.*, Fagales). The macro-fossil remains showed a riparian plant community dominated by deciduous eudicots resembling extant willows, reed-like monocots, and palms (*Sabalites*).

In Marmi et al. (2016), an extensive study of the Maastrichtian Pyrenean deposits was made to propose an ecological model for the colonization during the Maastrichtian of NE Iberia. They provided new data from the Orcau-1 section, along with data from previous works of other areas (South Isona, Molí de Baró-1, Fontllonga, Campo, Fumanya, and La Posa). The palynological assemblage from Orcau-1 was dominated by angiosperm pollen mainly (Normapolles) and, in less proportion, *Triporoletes* pollen.

A few kilometers away towards the south, in the Àger Syncline, several palynological studies were carried out as well. First, Médus et al. (1988) made a combined biostratigraphical (palynology, charophytes, and fauna) and geochemical (iridium anomaly) study to establish the palynostratigraphy of the K−Pg boundary in non-marine deposits of the Pyrenees region. They sampled the Claret, Fontllonga, and Figols-Vallcebre sections (the latter form the Vallcebre Syncline). Besides the lack of the iridium anomaly, they found a smooth transition during the K−Pg boundary with the presence of early Cenozoic palynomorphs in the Maastrichtian levels and vice versa.

Later, López-Martínez et al. (1999) studied two palynological samples from the Fontllonga section below and above the K−Pg boundary interval. They found spore-dominated assemblages where angiosperm and gymnosperm pollen increased in the Danian sample. The authors also compared the diversity trend across the Late Cretaceous in other parts of Spain (Kedves et al., 1985; Álvarez-Ramis and Doubinger, 1994; Álvarez-Ramis et al., 1996).

The study presented by Mayr et al. (1999) made a micropaleontological and isotopic approach from the Fontllonga section as well, but focused on the Figuerola-La Massana Fm (equivalent to the 'Lower Red Garumnian' unit; Fondevilla et al., 2019). They found the following palynological evolution: 1) a dominance in trilete spores (mainly, Lycopodiaceae, Schizaeaceae, and Cyatheaceae), bisaccate and monocolpate pollen at the lower part of the Lower Red Garumnian; 2) an extraordinary peak in trilete spores at the upper Maastrichtian; 3) dominance of trilete spores, monocolpate and Normapolles-group (*Trudopollis* and *Romeinipollenites*) pollen before the K−Pg boundary; 4) in the Danian assemblage, trilete spores still have a significant presence but in less proportion, which is replaced by monocolpate, triporate (mainly *Subtriporopollenites* and *Triporopollenites*), and Normapolles-group pollen. The marine influence (scarce dinoflagellates) was only present in the Maastrichtian samples, and some interesting results were found regarding paleophytogeography: Gondwanan and Boreal influence was found in the uppermost Maastrichtian levels with the occurrence of *Bacumorphomonocolpites* and *Aquilapollenites*, respectively.

The Vallcebre Syncline also presents a few palynological studies in an eastern location. A study of megaspores was also carried out from the Tremp Fm in the Figols-Vallcebre section by Batten et al. (2011). The authors indicate that the fossil genera found suggest a freshwater wetland habitat. Additionally, a phytogeographic connection with North American paleofloras was observed as the megaspores found are typical from there (*Ghoshispora*, *Minerisporites*, and *Parazolla*).

Eventually, Villalba-Breva et al. (2012) made a combined study, including sedimentology, analysis of charophytes and plant macro-fossils, and palynology from the 'Grey Garumnian' unit in the Figols-Vallcebre section. The palynological results from the middle part of the 'Grey Garumnian' showed a dominance of conifer bisaccate pollen and pteridophytes. The plant macro-fossil remains demonstrate that the Maastrichtian coals from the Pyrenees would

P. Martínez de Espronceda, I. Rodríguez-Barreiro, M. Pérez-Pueyo et al.

Cretaceous Research 154 (2024) 105757

be formed by conifers (*Frenelopsis*) and palms (*Sabalites*) which might share the same paleoenvironment during this period.

Cantabrian Range

A few studies were done in this region. The first was a quantitative palynological analysis from the Quintanaloma Fm in the Sedano section of upper Campanian–lower Maastrichtian age (Médus, 1987). The assemblage showed a domination of Betulaceae pollen (*Interporopollenites* spp.) which was replaced by Typhaceae pollen (Typha-Sparganium, =*Emmapollis?*) during the Campanian–Maastrichtian boundary.

Later, Kedves (1996) studied an upper Santonian–Danian interval in the Quintanilla la Ojada section, corresponding with the Rioseco Facies (including Quintanaloma Fm) and Tubilla del Agua, Valdenoceda, Sobrepeña, and Escaño formations. The results showed a dominance of marine palynomorphs (dinoflagellate cysts) with the presence of angiosperm pollen (*Retitricolporites*, *Nudopollis*, and *Triatriopollenites*) for the upper Campanian–lower Maastrichtian interval. In the upper Maastrichtian–Danian assemblages, they were generally dominated by Normapolles. However, there is not differentiation between the Cretaceous and the Paleogene.

Iberian Range

Álvarez-Ramis and Doubinger (1994) studied a palynological assemblage from the calcareous deposits close to Guadalix de la Sierra in the NW Iberian Range. Unfortunately, the study does not indicate the name of the lithostratigraphic unit involved. However, according to their stratigraphical description, we suggest the calcareous deposits likely belong to the Valle de Tabladillo Fm (dolostones and marls). The palynological assemblage was dominated by Normapolles pollen. Although the palynological assemblage indicates an upper Campanian–Maastrichtian age, according to the authors, it should be considered that the Valle de Tabladillo Fm is usually considered to be Campanian in age (Alonso and Mas, 1982).

In the Lo Hueco site (SW Iberian Range), Peyrot et al. (2013) studied a palynological assemblage from the Villalba de la Sierra Fm with an age of Campanian–lower Maastrichtian age according to charophytes (Ramírez-Merino, 1989). The assemblage was dominated by monoporate pollen *Emmapollis?* spp. (primitive Typhaceae).

Eventually, Peyrot et al. (2020) made a palynological study from the Sierra Perenchiza Fm in two sections (Barranco del Agua and La Castellana) of the Chera Basin (southernmost Iberian Range). The palynological assemblages were diverse but mainly showed a dominance of angiosperm pollen, mainly Cyperaceae and Arecaceae pollen. The authors suggest an upper Campanian–?lower Maastrichtian age.

Aquitanian Basin

In Southern France, a significant amount of palynological studies were also conducted within the Aquitanian Basin. The palynology from the Maastrichtian GSSP in Tercis les Bains was intensively studied by Antonescu and Odin (2001), Méon (2001), and Siegl-Farkas (2001). Some focused on marine palynology but others on terrestrial palynomorphs. Eventually, a synthesis of these studies was made by Méon et al. (2001) with the following conclusions. The assemblages from the Campanian–Maastrichtian boundary were dominated by angiosperm pollen, where the Normapolles group has a significant presence. A proposal of some key taxa for the Campanian–Maastrichtian boundary interval: *Aveiropollenites triangulus* as a biomarker for the Campanian, the stratigraphical range of *Pseudoconvexipollis* sp. should be lowered down to the upper Campanian, and *Polaropollis* sp. 1, if it is not considered as a synonym of *Romeinipollenites laevigatus* could be restricted to the upper Campanian.

Combined regions

Some of the aforementioned works integrated different regions. This is the case of Ashraf and Erben (1986), who compared the palynoflora from Spanish Tremp Fm in the Tremp Syncline (La Posa and Coll de Nargó sections) and the French Marnes rouges inferieures Fm(?) plus Facies Rognacien(?) in the Coriberes-Upper Aude Valley (Renne le Château and Albas sections) as well as Provence regions (Rousset section). The authors differentiated three different palynological assemblages: Palynozone A, the upper part of the lower Maastrichtian; Palynozone B, upper Maastrichtian; Palynozone C, Danian. According to the authors, the palynofloras shift from a tropical/subtropical (Palynozone A) to a subtropical/temperate (Palynozone B) and to, eventually, a temperate plant community (Palynozone C). A marked decrease in the diversity of pteridophytes (Cyatheaceae, Schizaeaceae, Gleicheniaceae, and Lycopodiaceae) seems to be present.

Médus (1972) made a palynological zonation of the Upper Cretaceous in SW France and NE Spain. Regarding the uppermost Cretaceous, the author correlates the Lower Rognacian facies in Provence with the Maastrichtian in Spain (i.e., Tremp Fm).

A comparison was also made between the Upper Cretaceous of the Lusitanian Basin (Portugal) and the Charentes region (SW France) (Médus, 1981). Most of the work is focused on Campanian deposits, but in the Charentes region, two Maastrichtian sections were studied, Archiac and Brossac sections. Both assemblages were dominated by Normapolles (Betulaceae, among others), and the authors highlighted the presence of the Normapolles group with an order of appearance. First, *Oculopollis*, *Lusatipollis*, *Papillopollis*, and *Trudopollis*, and later, the reappearance of the genera *Heidelbergipollis*, *Suemegipollis*, and *Interporopollenites*.

Eventually, to trace the K–Pg boundary, the assemblages from the Aix Basin and the Tremp Syncline were reexamined (Médus et al., 1992). According to the authors, the Maastrichtian–Danian palynological samples could be divided in two, the ones with Normapolles and the others with *Triporo-*, *Triatrio-*, *Intratripro-*, and *Subtriporopollenites* types. However, they also noticed that the latter group can also form part of the former assemblages, therefore being impossible to differentiate an uppermost Maastrichtian flora from a Danian one. Moreover, Médus et al. (1992) suggested a floristic/climatic change along the K–Pg boundary. The first, composed of three stages: 1) decrease and extinction of the Senonian Normapolles; 2) spread of the Danian flora, which issues from the lower Maastrichtian; 3) introduction of modern *Pinus* pollen grains and boreal-asiatic taxa (*Carya*, *Engelhardia*, *Nypa*, and forms referable to the *Restionaceae*).

2. Material and methods

2.1. Palynological revision

After an analysis of the previous data from the nearest *Aquilapollenites*, Normapolles, and Palmae provinces (Srivastava, 1978; Herngreen and Chlonova, 1981; Vajda and Bercovici, 2014) and a detailed revision of the palynological studies of deposits from SW Europe (see 1.2 and Supplementary material), a palynostratigraphical distribution of key taxa is proposed here for the K–Pg interval of the Normapolles Province, which will apply to the Ibero-Armorican Island. Unless indicated otherwise, just references properly illustrated and stratigraphically constrained were included.

Unlike in other regions, to differentiate Maastrichtian from Danian deposits, we suggest using the presence of 'K-taxa', 'KPg-

P. Martínez de Espronceda, I. Rodríguez-Barreiro, M. Pérez-Pueyo et al.

Cretaceous Research 154 (2024) 105757

taxa', and 'Pg-taxa', and to avoid the use of absence criteria. In our case, the 'K-taxa' are those which strictly disappear after the Cretaceous; the 'KPg-taxa' are those which are present in both Maastrichtian and Danian ages but give more stratigraphical detail (*i.e.*, upper Maastrichtian or lower Danian); the 'Pg-taxa' those which strictly first occur in Danian sediments. Besides the below, these taxa must have been recorded within the Normapolles Province before.

2.2. Palynological analysis

One palynological sample was collected from the Veracruz 1 site. The sample was collected selectively from the middle part of the gray organic-rich marly mudstones at the uppermost part of the 'Grey Garumnian' (Fig. 1B, C). The sample was processed in the laboratory of the University of Vigo using the standard palynological HCl−HF−HCl techniques described by Wood et al. (1996), consisting of acid digestion of HCl and HF to remove carbonate and silicate minerals. A dispersing agent was added subsequently to facilitate filtering. The residues were mounted on glass slides and were observed under a Leica DM 2000 LED optical microscope equipped with a LEICA ICC50 W digital camera. The illustrated specimens are indicated by fossil taxa name followed by sample number, slide number, and England Finder reference (see equivalence number to storage material in Supplementary material). The samples are stored in the Natural Science Museum of the University of Zaragoza (Spain) with codes from MPZ 2023/202 to MPZ 2023/250.

The palynostratigraphical dating was carried out after several selected taxa, restricted to the Maastrichtian−Danian age range. For this age calibration, studies from the Northern Hemisphere were taken into account (references in chart's figure caption), discarding remote locations of the Tethyan Realm. Again, unless indicated otherwise, only references properly illustrated and stratigraphically constrained were included.

3. Results

The palynological assemblage from the Veracruz 1 site has a good preservation level and great diversity (Table 1; Figs. 2 and 3). A total of 41 different morphogenera of spores, pollen, dinoflagellate cysts, algae, and fungal spores have been recovered. The palynological assemblage is characterized by a relative dominance of angiosperm pollen, more specifically, of Liliaceae (relative abundance of about 18%), Post-Normapolles group (17%), including *Trudopollis* or *Plicapollis*, and triporate pollen (13%), such as *Subtriporopollenites* and *Triatriopollenites*. Although plant-derived palynomorphs dominated the assemblage, marine markers are also present (less than 3% of relative abundance): dinoflagellate cysts (*e.g.*, *Sepispinula ambigua*, *Spiniferites* cf. *ramosus*) and brackish/freshwater algae (*e.g.*, *Chomotriletes fragilis*, *Ovoidites spriggii*).

4. Discussion

4.1. K−Pg palynostratigraphy from the Ibero-Armorican Island

The iridium anomaly is the best marker of the K−Pg boundary but it is often absent in terrestrial deposits. Therefore, in this kind of deposits, biostratigraphy plays an essential role. Detailed palynological studies have been performed in continental K−Pg deposits (*e.g.*, Nichols and Johnson, 2008; Vajda and Bercovici, 2014; Bercovici and Vellekoop, 2017). However, the differentiation between the latest Cretaceous and earliest Paleogene microfloras seems to be smooth, especially the further the study area is from

the Chicxulub impact. In regions like Europe, determining K−Pg key taxa may be challenging (Médus et al., 1988, 1992).

Many palynological studies on the K−Pg boundary interval have been conducted in North America, mostly recorded from the paleoshores of the Western Interior Seaway (Bercovici and Vellekoop, 2017, and references herein). The primary palynological approach to differentiate the Cretaceous from the earliest Paleogene in this region is the extinction of Cretaceous taxa (*i.e.*, absence criteria). It was defined as 'K-taxa' or 'K species', those that went extinct at the K−Pg boundary (Hotton, 2002; Nichols, 2002), formed mainly by *Aquilapollenites* pollen and other few distinctive palynomorphs. However, using absence criteria for dating may be risky as taphonomical bias should be considered. Moreover, some of these 'K-taxa' survive the K−Pg event and are present above for a short time although in very low abundance; that is why some authors recommend combining the use of these 'K-taxa' with relative abundance counting (Vajda and Bercovici, 2014; Bercovici and Vellekoop, 2017).

The Danian GSSP at El Kef section is also an interesting study location due to the detailed expression of the K−Pg interval. The palynological studies carried out there (Méon, 1990; Donze and Méon, 1997) showed a palynological assemblage formed by taxa from the Palmae and Normapolles palynological provinces. Most potential key taxa (Last Occurrence in Cretaceous and First Occurrence in Paleogene) found in Méon (1990) fossil-taxa distribution have longer temporal ranges. However, in the case of *Vadaszisporites urkuticus* and *Cicatricosisporites neumanii*, they both disappear right before the K−Pg boundary and have a distinctive appearance which may allow them to be 'K-taxa' from the El Kef.

The Ibero-Armorican Island was part of the Normapolles Province. Therefore, our study area does not present many key taxa recorded in the K−Pg deposits from North America or northern Africa (*i.e.*, El Kef). However, some of them do appear on the Ibero-Armorican Island. This is the case for the fossil-genus *Heliosporites*, *Liburnisporis*, and *Stellatopollis*, considered as 'K-taxa' from the *Aquilapollenites* Province (Hotton, 2002), and the fossil-genus *Vadaszisporites*, 'K-taxa' from El Kef (Méon, 1990). After the palynological studies from the Ibero-Armorican Island for the K−Pg, some authors suggested key taxa for this interval. Fernández-Marrón et al. (2004) propose *Pseudoromeinipollenites paleocenicus* as a Danian marker species. However, their assignation to the species is uncertain (*P.* cf. *paleocenicus*), and except for this work, it was not found in Danian sediments again. Médus et al. (1992) indicate that the K−Pg flora transition is smooth, and it is not possible to differentiate Maastrichtian from Danian deposits.

After the revision of the previous palynological references from the *Aquilapollenites*, Normapolles, and Palmae provinces, several palynostratigraphical key taxa are proposed here for the Ibero-Armorican Island and, therefore, for the Normapolles Province (Fig. 4). The Ibero-Armorican palynological key taxa for the uppermost Cretaceous ('K-taxa') are numerous, diverse (pteridophyte spores and angiosperms), and taxonomically distinctive. They are formed by *Camarozonosporites insignis*, *Heliosporites kemensis*, *Liburnisporis* spp., *Stellatopollis* spp., *Vadaszisporites* spp., *Lusatisporis dettmannae*, *Trudopollis geometricus*, *T. granulosus*, and *T. lativerrucatus*. The Cretaceous−Paleogene key taxa ('KPg-taxa') are fewer but also provide helpful stratigraphical information. It is formed by *Trudopollis primigenius* (=*T. hojrupensis*; LO in the lower Danian), *Subtriporopollenites microconstans* (only found in the upper Maastrichtian), and others with their FO in the upper Maastrichtian (*Bacumorphomonocolpites* spp., *Rugulitriporites balinkaense*, *R. pflugii*, and *Subtriporoletes subporatus*). Unfortunately, the strictly Paleogene key taxa ('Pg-taxa') are scarce and sometimes not very distinct from other species ranging from the Cretaceous. Even so, the following would indicate a Danian age in

P. Martínez de Espronceda, I. Rodríguez-Barreiro, M. Pérez-Pueyo et al.

Cretaceous Research 154 (2024) 105757

Table 1
Relation of the palynological fossil species recorded in the Veracruz 1 site. Except for those taxa in which the reference is highlighted, the botanical affinities are based on Zhang et al. (2021).

Taxa	Botanical affinities	Additional references
Bryophytes		
Zlivisporis blanensis Pacltová, 1961	Ricciaceae	
Pteridophytes		
Biretisporites potoniaei (Delcourt and Sprumont, 1955) Delcourt et al., 1963	Hymenophyllaceae	
Camarozonosporites insignis Norris, 1967	Lycopodiaceae	
Cicatricosisporites sp.	Anemiaceae	
Concavissimisporites variverrucatus (Couper, 1958) Brenner, 1963	Lygodiaceae	
Cyathidites minor Couper, 1953	Cyatheales	
Dictyophyllidites sp.	Gleicheniaceae	
Echinatisporis longechinus Krutzsch, 1959	Selaginellaceae	
Klukisporites scaberis (Cookson and Dettmann, 1958) Dettmann, 1963	Lygodiaceae	
Lusatisporis dettmannae (Drugg, 1967) Srivastava, 1972	Selaginellaceae	
Matonisporites sp.	Gleicheniaceae	
Neoraistrickia cf. *robusta* Brenner, 1963	Selaginellaceae	
Neoraistrickia truncata (Cookson, 1953) Potonié, 1956		
Patellasporites distaverrucosus (Brenner, 1963) Kemp, 1970		
Gymnosperms		
Alisporites sp.	Corystospermales	
Araucariacites australis Cookson, 1947	Araucariaceae	
Cycadopites sp.	Cycadales	
Ephedripites multicostatus Brenner, 1963	Ephedraceae	
Inaperturopollenites sp.	Cupressaceae	
Angiosperms		
Bacumorphomonocolpites sp.	Arecaceae	Herngreen et al., 1986
Echimonocolpites sp.	Nymphaeaceae?	Ward, 1986
Emmapollis? sp.	Chloranthaceae?/Typhaceae?	Morley, 2001/Peyrot et al., 2013
Labraferoidaepollenites rurensis (Pflug and Thomson, 1953) Kedves and Russell, 1982	Myricaceae?	Kedves, 2000
Labrapollis labraferus (Potonié, 1931) Krutzsch, 1965	Undetermined Fagales	Batten, 1981
Liliacidites sp.	Liliaceae	Couper, 1953
Minorpollis sp.	Rhoipteleaceae	Friis et al., 2006
Oculopollis semimaximus Krutzsch, 1968	Undetermined Fagales/Juglandaceae?	Batten, 1981/Ferguson et al., 2007
Pandaniidites texus Elsik, 1968	Araceae/Pandanaceae	Stockey et al., 1997/Elsik, 1968
Plicapollis serta Pflug, 1953	Juglandaceae	Friis 1983
Pseudoplicapollis sp.	Undetermined Fagales	Batten, 1981
Rhoipites sp.	Malvaceae?	Hoorn et al., 2019
Rugulitriporites pflugii Kedves, 1982	Undetermined Fagales	Batten, 1981
Subtriporopollenites constans Pflug, 1953	Juglandaceae	
Subtriporopollenites microconstans Kedves and Herngreen, 1980		
Subtriporopollenites sympathicus Kedves and Herngreen, 1980		Daly and Jolley, 2015
Triatriopollenites cretacius Stanley, 1961	Myricaceae	
Triatriopollenites pseudorurensis Thomson and Pflug, 1953		
Triatriopollenites sp.		Daly and Jolley, 2015
Trudopollis granulosus Kedves and Herngreen, 1981	Juglandaceae	
Trudopollis parvotrudens Pflug, 1959		
Trudopollis pertrudens (Pflug in Thomson and Pflug, 1953) Krutzsch, 1967		Friis, 1983
Vacuopollis pflugii Kedves, 1979	Undetermined Fagales	Batten, 1981
Others		
Chomotriletes minor (Kedves, 1961) Pocock, 1970	Oedogoniaceae	Zippi, 1998
Fungal spores	Fungi	
Ovoidites parvus (Cookson and Dettmann, 1959) Nakoman, 1966	Zygnemataceae	Zippi, 1998
Sepispinula cf. *ambigua* (Deflandre, 1937) Masure in Fauconnier and Masure, 2004	Gonyaulacaceae	Islam, 1993
Spiniferites cf. *ramosus* (Ehrenberg, 1837) Mantell, 1854		Mantell, 1850

K−Pg boundary interval sediments: *Basopollis urkutensis*, *Thomsonipollis gracilis*, and *T. paleocenicus*.

4.2. Age assignment of the Veracruz 1 site

An upper Maastrichtian age is suggested for the Veracruz 1 palynological assemblage, according to the presence of the selected fossil-taxa *Bacumorphomonocolpites* sp., *Camarozonosporites insignis*, *Lusatisporis dettmannae*, *Pandaniidites texus*, *Rugulitriporites pflugii*, *Subtriporopollenites microconstans*, and *Trudopollis granulosus* (Fig. 5).

The fossil-genus *Bacumorphomonocolpites* is typical of the Maastrichtian−Paleocene of Gondwana (occurrences mainly found in Colombia, Venezuela, and Nigeria). However, it was seldom found in the Northern Hemisphere, only during the upper Maastrichtian. The record of *Bacumorphomonocolpites* sp. here is in the upper Maastrichtian of the Maastricht Fm in the Netherlands (Herngreen et al., 1986) and in the uppermost Maastrichtian of the Figuerola Fm in Spain (Mayr et al., 1999).

Other fossil taxa have their First Occurrence (FO) during the Maastrichtian. *Pandaniidites texus* is a typical taxon from the Cenozoic but has its FO in the Maastrichtian of North America (*e.g.*, Bergard, 1974; Potonié, 1975). However, in Europe, it was recently found in the upper Campanian−lower Maastrichtian deposits of the Villalba de la Sierra Fm in Spain (Peyrot et al., 2013). In the case of *Rugulitriporites pflugii*, its FO is in the upper Maastrichtian of the
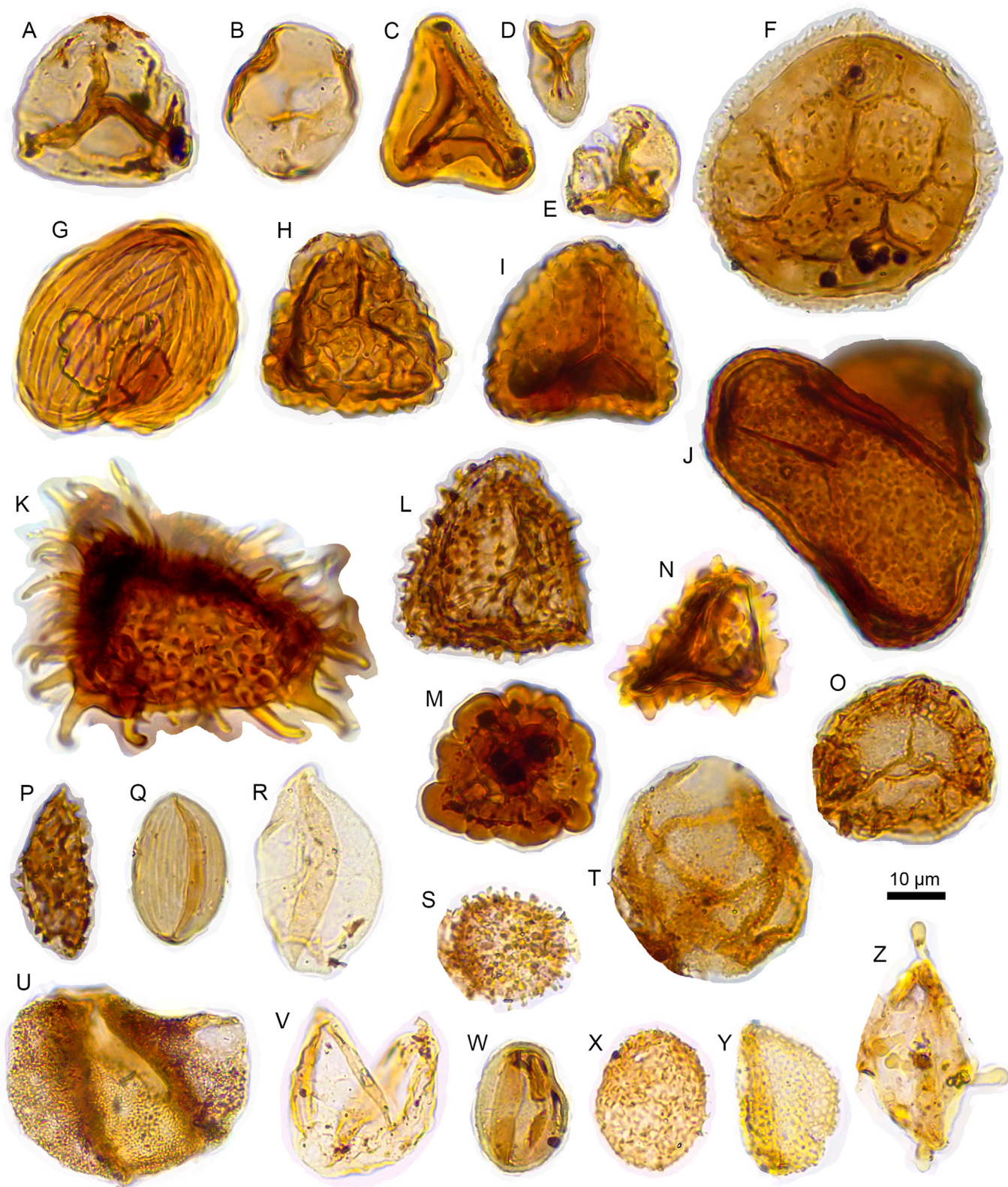
Fig. 2. Palynomorphs from the Veracruz 1 assemblage. A. *Biretisporites potoniaei* (VE1-2-K074); B. *Cyathidites minor* (VE1-2-J453); C. *Matonisporites* sp. (VE1-1-R412); D. *Dictyophyllidites* sp. (VE1-2-L344) E. *Dictyophyllidites* sp. (VE1-2-E361); F. *Zlivisporis blanensis* (VE1-3-O284); G. *Cicatricosisporites* sp. (VE1-3-L272); H. *Camarozonosporites insignis* (VE1-4-G233); I. *Klukisporites scaberis* (VE1-2-L223); J. *Concavissimisporites variverrucatus* (VE1-2-K152); K. *Echinatisporis longechinus* (VE1-4-Q104); L. *Neoraistrickia truncata* (VE1-2-K213); M. *Patellasporites distaverrucosus* (VE1-2-K221); N. *Neoraistrickia* cf. *robusta* (VE1-1-Q441); O. *Lusatisporis dettmannae* (VE1-4-O244); P. *Echimonocolpites* sp. (VE1-2-W162); Q. *Ephedripites multicostatus* (VE1-1-S454); R. *Cycadopites* sp. (VE1-1-D461); S. *Emmapollis?* sp. (VE1-1-L184); T. *Araucariacites australis* (VE1-1-S353); U. *Alisporites* sp. (VE1-2-Q214); V. *Inaperturopollenites* sp. (VE1-1-O311); W. *Rhoipites* sp. (VE1-3-N174); X. *Pandaniidites texus* (VE1-2-F262); Y. *Liliacidites* sp. (VE1-1-T423); Z. *Bacumorphomonocolpites* sp. (VE1-1-T294).
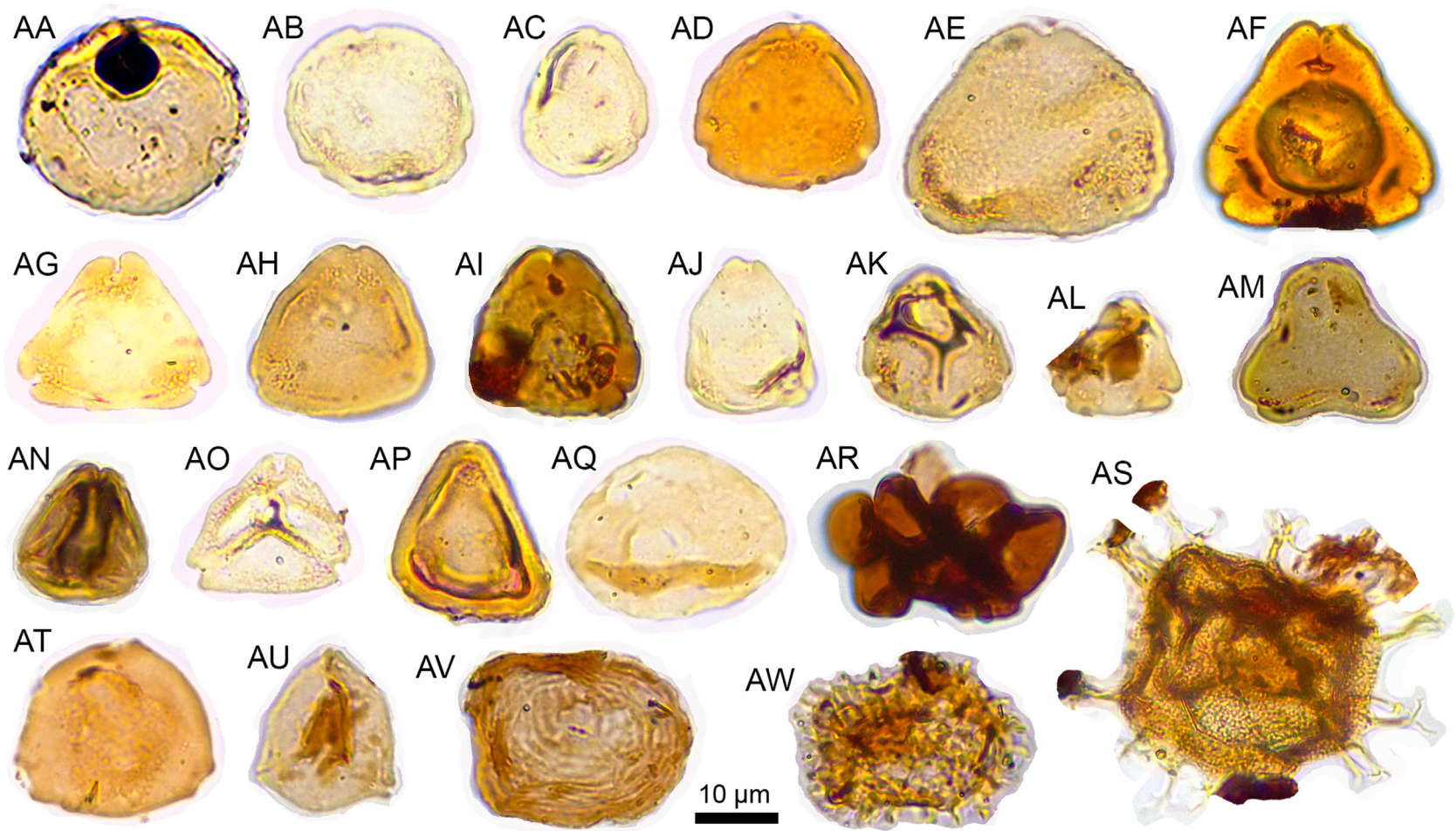
Fig. 3. Palynomorphs from the Veracruz 1 assemblage. AA. *Subtriporopollenites sympathicus* (VE1-2-C473); AB. *Subtriporopollenites constans* (VE1-1-K493); AC. *Subtriporopollenites microconstans* (VE1-1-P499); AD. *Triatriopollenites cretacicus* (VE1-1-Q212); AE. *Rugulitriporites pflugii* (VE1-2-F114); AF. *Oculopollis semimaximus* (VE1-1-T393); AG. *Trudopollis pertrudens* (VE1-1-G364); AH. cf. *Labraferoidaepollenites rurensis* (VE1-1-C423); AI. *Trudopollis granulosus* (VE1-4-H251); AJ. *Trudopollis parvotrudens* (VE1-1-J112); AK. *Labrapollis labraferus* (VE1-2-O113); AL. *Minorpollis* sp. (VE1-4-U132); AM. *Vacuopollis pflugii* (VE1-2-W302); AN. *Pseudoplicapollis* sp. (VE1-2-P111); AO. *Plicapollis serta* (VE1-2-H441); AP. cf. *Labraferoidaepollenites rurensis* (VE1-2-C423); AQ. *Ovoidites spriggii* (VE1-1-J184); AR. Cluster of fungal spores (VE1-1-R403); AS. *Spiniferites* cf. *ramosus* (VE1-3-J082); AT. *Triatriopollenites pseudorurensis* (VE1-2-G431); AU. *Triatriopollenites* sp. (VE1-2-N542); AV. *Chomotriletes fragilis* (VE1-2-N323); AW. *Sepispinula* cf. *ambigua* (VE1-2-R413).
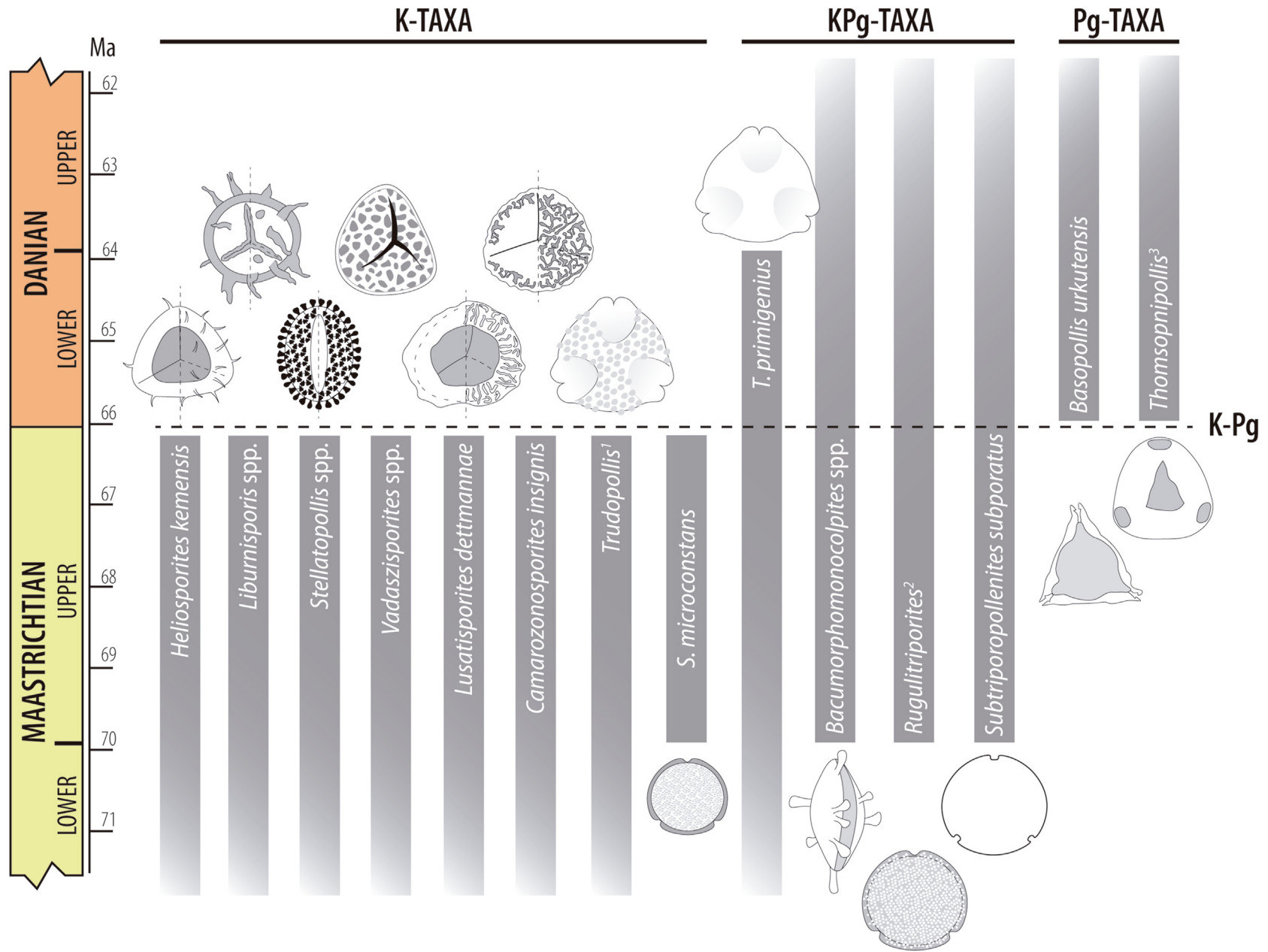
Fig. 4. Selection of terrestrial palynological key taxa for the K−Pg interval in the Normapolles Province. References used: Médus, 1970; Waanders, 1974; Herngreen et al., 1986; Siegl-Farkas, 1986; Siegl-Farkas, 1987; Méon, 1990; Méon, 1991; Médus et al., 1992; Mohsen, 1992a,b; Kedves, 1995; Mayr et al., 1999; Antonescu and Odin, 2001; Siegl-Farkas, 2001; Van Itterbeeck et al., 2005; Villalba-Breva et al., 2012; Peyrot et al., 2013; Marmi et al., 2016. 1: *Trudopollis geometricus*, *T. granulosus*, and *T. lativerrucatus*; 2: *Rugulitriporites balinkaense* and *R. pflugii*; 3: *Thomsonipollis gracilis* and *T. paleocenicus*.
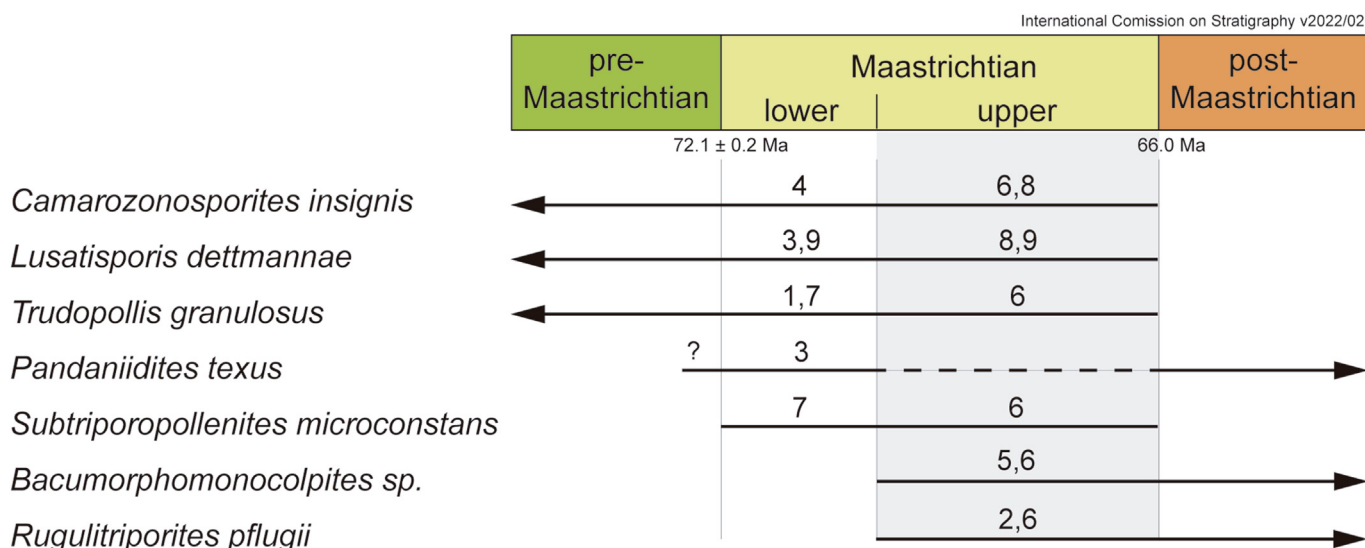
Fig. 5. The palynostratigraphic chart for the Maastrichtian of the selected fossil taxa from the Veracruz 1 assemblage based on previous Northern Hemisphere studies (Eastern North America, Europe, and North Africa), where those taxa are illustrated and well-identified. Southern France and the Iberian Peninsula: 1. Antonescu and Odin (2001); 2. Médus et al. (1988); 3. Peyrot et al. (2013); 4. Siegl-Farkas (2001); 5. Mayr et al. (1999). Others: 6. Herngreen et al. (1986); 7. Kedves and Herngreen (1980); 8. Méon (1991); 9. Waanders (1974).

Maastricht Fm in the Netherlands (Herngreen et al., 1986), and the Tremp Fm in Spain (Médus et al., 1988).

The fossil taxa *Subtriporopollenites microconstans* has been recorded only within Maastrichtian successions so far. Its FO is in the lower Maastrichtian of the Gulpen Fm (Kedves and Herngreen, 1980), while its Last Occurrence (LO) is in the upper Maastrichtian of the Maastricht Fm (Herngreen et al., 1986), both in the Netherlands.

Several fossil taxa have their LOs during the upper Maastrichtian. *Camarozonosporites insignis* has its youngest record on the upper Maastrichtian of the Maastricht Fm in the Netherlands and the El Haria Fm in Tunisia (Herngreen et al., 1986; Méon, 1991). The youngest record for *Lusatisporis dettmannae* is on the Maastrichtian of the Monmouth Gp (Tinton, Red Bank, Navesink, and Mt. Laurel formations) in the Atlantic coast of the U.S.A. as *L. circumundulatus* (Waanders, 1974) and on the upper Maastrichtian of the El Haria Fm in Tunisia as *Psilatriletes circumundulatus* (Méon, 1991). The LO of *Trudopollis granulosus*, is in the upper Maastrichtian of the Maastricht Fm in the Netherlands (Herngreen et al., 1986).

Numerous datings have been made for the Tremp Fm in the past. However, the geographical location of the 'Grey Garumnian' unit should be taken into account as there is a lateral change with other units within the Tremp Basin, which, in general, are younger westwards and northwards (Villalba-Breva and Martín-Closas, 2013), as in the case of the 'Grey Garumnian' in the Western Tremp syncline (Canudo et al., 2016; Puértolas-Pascual et al., 2018; Pérez-Pueyo, 2023), where Veracruz 1 site locates.

The previous biostratigraphical studies were focused on foraminifera, charophytes, and rudists. First, the rudist *Hippurites radiosus* level at the top of the Arén Fm (below the Tremp Fm) indicates a lower Maastrichtian age between 71.7 and 70.8 Ma (Vicens et al., 2004; Caus et al., 2016). However, this rudist horizon has not been found in the western part of the Tremp Basin so far.

The foraminifera content of the Tremp Fm was studied in the area between Tremp-Isona (central-eastern Tremp Basin). Here, the 'Grey Garumnian' yielded scarce foraminifera, with poor biostratigraphic value. However, at the lower part of the overlaying 'Lower Red Garumnian', foraminifera of the *Pseudoguembelina palpebra* biozone are present, thus indicating a lower Maastrichtian age (Díez-Canseco et al., 2014). In the westernmost sector of the basin (Serraduy), foraminifera have been only found in the 'Lower Red Garumnian'. These foraminifera have signs of reworking (Pérez-Pueyo, 2023); however, because of the presence of the specimens of *Pseudoguembelina hariaensis*, at least an upper Maastrichtian age can be suggested as the FO of this fossil-taxa is 67.3 Ma corresponding with the upper part of chron C30n (Puértolas-Pascual et al., 2018).

The charophyte studies were done in the Vallcebre (Catalonian Pyrenees) and the Tremp basins. In the area of Vallcebre, the 'Grey Garumnian' would correspond to the *Peckichara cancellata* (upper Campanian—lower Maastrichtian) biozone (Vicente et al., 2015), while in the central-easternmost part of the Tremp Basin the 'Grey Garumnian' yielded a charophyte assemblage with a broader range (upper Campanian—upper Maastrichtian). However, the occurrence of *Peckichara sertulata* in the easternmost sections indicates a lower Maastrichtian.

A correlation with magnetostratigraphic studies is also possible. From east to west, the 'Grey Garumnian' unit seems to correspond with the polarity chron C31r (lower Maastrichtian) in the Vallcebre Basin (Oms et al., 2007) and easternmost Tremp Basin (Fondevilla et al., 2016) while 'the Grey Garumnian' unit in the western Tremp Basin (where the Veracruz 1 site locates), corresponds to the polarity chron C29r (upper Maastrichtian), which encompasses 400 ky before the K—Pg boundary (Puértolas-Pascual et al., 2018; Pérez-Pueyo, 2023).

Therefore, our palynological age assignment of the Veracruz 1 site at the uppermost part of the 'Grey Garumnian' as an upper Maastrichtian is consistent with the previous data for the westernmost part of the basin. This supports the idea that the deposits in the western Tremp syncline area are younger than their equivalents in eastern locations.

4.3. Paleoenvironment and paleoecology

The presence of both marine and brackish/freshwater paly-nomorphs is consistent with the sedimentological interpretation of this site as a small pond located in the margin of a coastal lagoon environment, where the primary input of sediment was from the land, but with marine influence also present.

The palynological assemblage from the Veracruz 1 site is mainly represented by angiosperms, specifically *Liliacidites*, Normapolles group, and other triporate pollen. The botanical affinity of *Liliacidites* pollen is Liliaceae (Couper, 1953) which are perennial herbs with flowers. In the case of the Normapolles-group and tri-porate pollen, they are often related to Juglandaceae/Myricaceae (Friis, 1983; Manchester, 1989), which are flowering trees and shrubs where the extant ones belong to the walnut/bayberry families. Therefore, the plant community at the fringe of the lagoonal deposits of the upper Maastrichtian 'Grey Garumnian' unit studied here, would have been formed mainly by a seaside forest of Juglandaceae/Myricaceae trees and shrubs (walnut and bayberry-like) with a flowering understory of Liliaceae herbs. Moreover, is remarkably the presence of *Emmapollis*-like pollen (*Emmapollis?* sp.), which is suggested to have typhacean botanical affinities (Peyrot et al., 2013). The *Emmapollis?* sp. found in Veracruz 1 are identical to those identified as *Emmapollis?* sp. 2 found in the upper Campanian−lower Maastrichtian of central Spain (Peyrot et al., 2013).

Today, Liliaceae herbs are common in steppes and mountain meadows of the Northern Hemisphere. However, they are widely distributed along diverse ecological conditions but temperate cli-mates (Simpson, 2019). The extant Juglandaceae/Myricaceae plants often thrive in similar conditions, with temperate riverside and coastal environments. Nevertheless, Daly and Jolley (2015) differ-entiated the best-suitable environments for each Normapolles type. On the one hand, *Plicapollis*, *Subtriporopollenites*, and *Trudo-pollis* pollen would be related to Juglandaceae and correspond to warmer and drier conditions (Friis, 1983; Daly and Jolley, 2015). On the other hand, other Normapolles pollen related to Myricaceae, such as *Triatriopollenites*, whose presence is fewer yet consistent and diverse, would correspond to cooler and wetter conditions (Daly and Jolley, 2015). In our case, all of these co-occurrences, together with Liliaceae, could suggest that they are indicative of a temperate-warm climate for this area. According to climate modeling and fossil plant evidence, the general paleoclimatology of the Ibero-Armorican Island during the Maastrichtian would be subtropical with a mean annual surface temperature of 24−28 °C (Golovneva, 2000; Hunter et al., 2008). Indeed, some authors sug-gest that this region was located at the southern border within the Northern Mid-Latitude Warm Humid belt (Chumakov et al., 1995; Hay and Floegel, 2012). However, low-scale climatic changes should be taken into account for this period (Wilf et al., 2003; Self et al., 2006).

The Veracruz 1 assemblage is clearly dominated in terms of abundance and diversity by palynomorphs from the Normapolles Province (Herngreen et al., 1996), consistent with its geographical location. However, a Gondwanan influence was observed with the presence of palynomorphs from the Palmae Province (*e.g.*, *Bacu-morphomonocolpites*). This seems to occur only during the late Maastrichtian, as Laurasian occurrences of *Bacumorphomono-colpites* were also found in the uppermost Maastrichtian of the Iberian Peninsula (Mayr et al., 1999) and in the upper Maastrichtian of the Netherlands (Herngreen et al., 1986). Gondwanan influence was not rare for the Iberian Peninsula, as it was already noticed in several paleontological studies within Cretaceous successions (*e.g.*,

Villanueva-Amandoz et al., 2010; Vila et al., 2022). The mix of palynomorphs from these two areas seems to indicate that during the Mesozoic, the Iberian Peninsula was a recurrent transition zone between Gondwana and Laurasia. Nevertheless, this Gondwanan influence reached higher paleolatitudes (more than 50°N) during the late Maastrichtian (Herngreen et al., 1986).

5. Conclusions

Even after many years of investigations, the location of the K−Pg boundary in Europe's continental record is problematic due to the absence of the iridium anomaly. The revision of the palynological studies from the Ibero-Armorican Island for this period has allowed us to propose a palynostratigraphic chart with several key taxa restricted to the Maastrichtian ('K-taxa'), to the Danian ('Pg-taxa'), and others providing a more detailed location within the Maastrichtian−Danian range ('KPg-taxa').

A new palynological analysis from one of the more modern dinosaur-bearing sites of the Ibero-Armorican Island, the Veracruz 1 site (Pyrenees, NE Spain), has provided the following conclusions: 1) the Veracruz 1 palynological assemblage supports an upper Maastrichtian age; 2) the plant communities were mainly composed by angiosperms, more specifically by an understory of Liliaceae flowering herbs together with Juglandaceae/Myricaceae trees and shrubs; 3) the paleoclimatology and paleoenvironment are consistent with a temperate-warm climate within a seaside forest close to a lagoon; 4) our data confirm Gondwanan influence during the late Maastrichtian in Europe.

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P. Martínez de Espronceda, I. Rodríguez-Barreiro, M. Pérez-Pueyo et al.

Cretaceous Research 154 (2024) 105757

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2023.105757.