Palynological reconstruction of the habitat and diet of *Iguanodon bernissartensis* in the Lower Cretaceous Morella Formation, NE Iberian Peninsula

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ABSTRACT

The recent discovery of iguanodontid remains from the new Palau-3 site in the Lower Cretaceous Morella Formation is the most complete non-articulated skeleton of *Iguanodon bernissartensis* on the NE Iberian Peninsula. To elucidate the paleoenvironment of the Palau-3 site, a palynological analysis was carried out on matrix samples collected from around the skeleton. The palynological assemblage is found to correspond to an upper Barremian age. While the assemblage is composed of bryophytes, pteridophytes, gymnosperms, freshwater algae, dinoflagellate cysts and fungal spores, the palynoflora is mostly dominated by the Cheirolepidiaceae conifer (*Classopollis*) and Anemiaceae fern (mainly *Cicatricosisporites*) families. The absence of angiosperm pollen in this flora is also noteworthy, as angiosperm remains have been recorded previously elsewhere in the Morella Formation. At the Palau-3 site, the fronds of Cyatheaceae and Anemiaceae ferns, as well as the foliage of the Cheirolepidiaceae conifers, may have been the major sources of nutrition of *I. bernissartensis* and other herbivorous iguanodontians. The paleobotany of the four major localities bearing *I. bernissartensis* remains in western Europe was surveyed to determine the habitat and feeding preferences of this styracosternan dinosaur. These localities are Bernissart (Belgium), Isle of Wight (England), Nehden (Germany), and Morella (Spain). In accordance to this survey, the habitat preferences of *I. bernissartensis* and association with specific plant communities show that this ornithopod species was adapted to a wide variety of paleoenvironments.

1. Introduction

The styracosternan dinosaur *Iguanodon* is one of the best studied ornithopods from the Lower Cretaceous of Europe. Since the genus was named by Mantell in 1825, numerous species of *Iguanodon* have been proposed, but it is currently acknowledged that this genus is represented by only two species, *Iguanodon bernissartensis* and *I. galvensis*. The stratigraphic and paleogeographic distribution of the type species, *I. bernissartensis*, is restricted to the Barremian−Aptian of Central and SW Europe (Fig. 1), with its southernmost occurrence in the Morella Formation near Morella on the NE Iberian Peninsula.

All Ornithischia are widely known for their specialized herbivorous diet (Müller and Garcia, 2020). However, based on skeletal and dental evidence, iguanodontians differed from other members of the clade (thryreophorans, marginocephalianas, non-iguanodontian ornithopods) in significant ways. For instance, the tooth enamel microstructure in this group is more complex, exhibiting a wavy pattern that increases abrasion resistance to plant feeding (Sander,

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1997, 1999, 2000). The species *Iguanodon bernissartensis* was a plant-eating dinosaur of about 13 m in length and about 3 tons in weight (Glut, 1997; Norman, 2004). A possible modern analog of this dinosaur is the African bush elephant (*Loxodonta africana*) which reaches dimensions up to 7.5 m and 6 tons and consumes more than 150 kg of fresh plant matter per day (Wilson and Reeder, 2005). In addition, tracks and bone beds have provided evidence that styracosternans developed gregarious behavior (Delair, 1982; Norman, 1987; Lockley, 1995; Glut, 1997; Lockley and Meyer, 2000). Therefore, plant communities would have a particular importance for a herd of *I. bernissartensis* in regard to quantity and nutritional quality.

From the Triassic to the Lower Cretaceous, herbivorous dinosaurs co-existed with a gymnosperm-dominated flora (Gee, 2010; Sander et al., 2010). It had formerly been thought that most of the Mesozoic gymnosperms such as cycadophytes, Ginkgoales, and Cheirolepidiaceae conifers would have been offered poor nutrition to herbivorous dinosaurs due to their tough bark, spiny foliage, and wealth of indigestible compounds (Tiffney, 1997). However, recent experimental work on the digestibility of the nearest living relatives of the Mesozoic flora has shown that gymnospermous foliage of conifers and ginkgophytes, and especially the above-ground shoots of the sphenophyte *Equisetum* would have provided as much or even more energy than angiosperm grasses and leaves do today (Hummel et al., 2008; Gee, 2011; Howell et al., 2023). Indeed, the most crucial parameter for a plant as food is considered to be its digestibility (Owen-Smith, 1988). By inference from the diets of large living herbivores, the enormous herbivorous dinosaurs would have been bulk feeders of plants that were difficult to digest, but available in the vegetation in large quantities (Demment and Van Soest, 1985; Hummel and Clauss, 2011).

Despite the importance of the vegetation for *Iguanodon bernissartensis* and its apparently restricted paleogeographic distribution (Fig. 1), the floral composition of its paleohabitat in the Morella area is still unclear. However, palynological studies have already proven to be an excellent method of providing taxonomic, paleoecological, and paleoenvironmental data in other nearby dinosaur-bearing sites (e.g., Santos et al., 2018; 2022a). Therefore, our work intends to: (1) reconstruct the plant communities inhabited by this styracosternan at the southernmost part of its paleogeographic range, (2) provide palynostratigraphical dating for this locality, and (3) compare the reconstruction of the Morella paleohabitat with those of other *I. bernissartensis*-bearing sites. Our work is based on the palynological study of matrix samples collected from around the most complete non-articulated skeleton of *I. bernissartensis* from a new locality, the Palau-3 site, on the NE Iberian Peninsula.

2. Geological setting

The Palau-3 site is located in a quarry less than 4 km south of the Morella locality in the region of Mas de Palau, in the northern part of the Castellón Province in northeastern Spain. The following exact
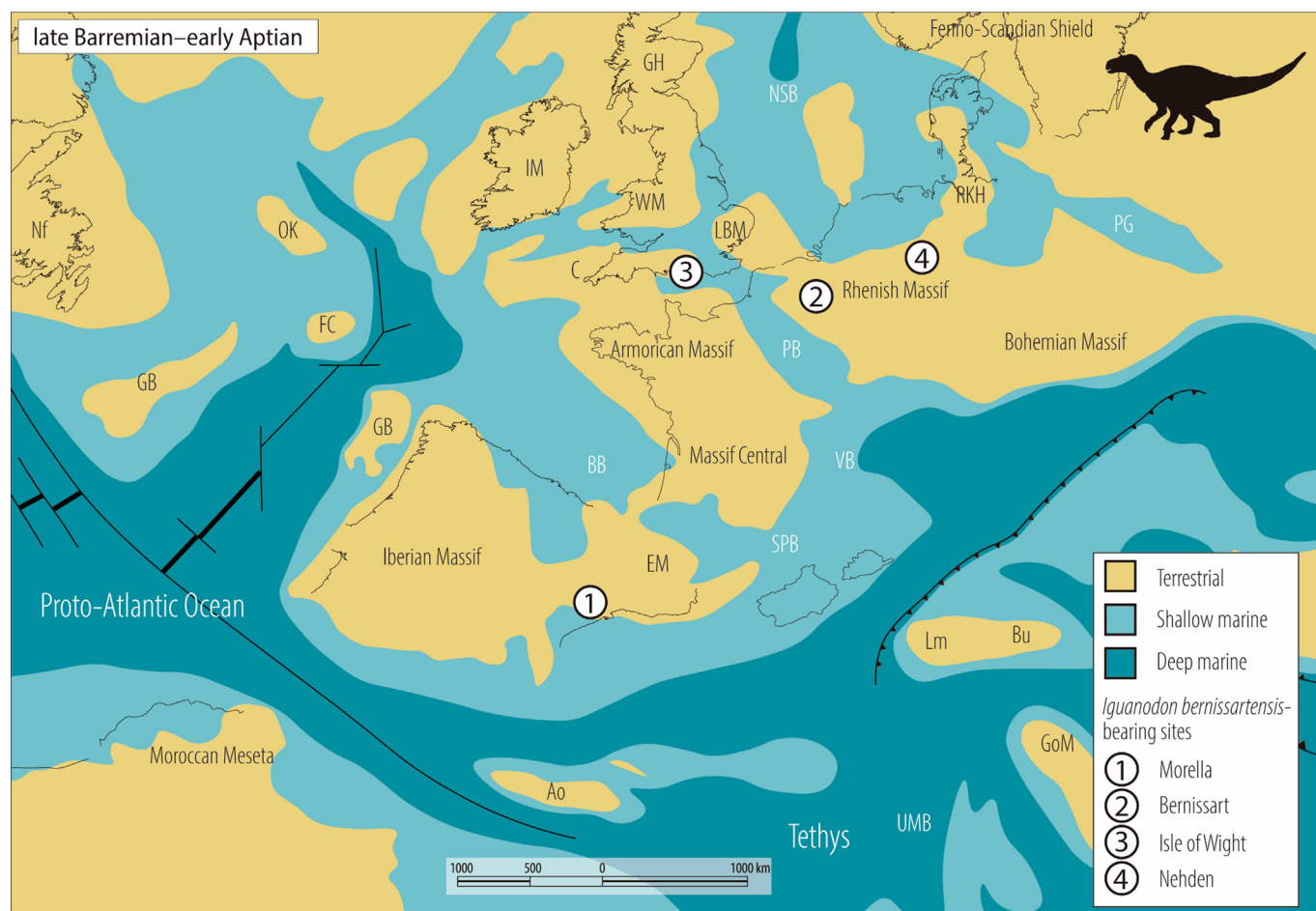

Fig. 1. Paleogeographical map of western Europe for the late Barremian−early Aptian interval (based on Masse et al., 2000; Cao et al., 2017). The location of the *Iguanodon bernissartensis*-bearing sites are highlighted with numbers. Abbreviations: Ao, Alboran. BB, Bay of Biscay. Bu, Bukk. C, Cornubia. EM, Ebro Massif. FC, Flemish Cap. GB, Great Bank. GB, Galicia Bank. GH, Grampian High. GoM, Golijia Massif. IM, Irish Massif. LBM, London-Brabant Massif. Lm, Licicum. Nf, Newfoundland. NSB, North Sea Basin. OK, Orphan Knoll. PB, Paris Basin. PG, Polish Graben. RKH, Ring Kobing-Fyn High. SPB, South Provence Basin. UMB, Umbria-Marche Basin. VB, Vocontian Basin. WM, Welsh Massif.

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coordinates of the site are: 40° 35′ 26.72″ N, 0° 7′ 32.73″ W, ETRS89 (Fig. 2). The Morella Formation crops out at the Palau-3 site and corresponds to the Morella sub-basin within the Maestrazgo Basin.

The Maestrazgo Basin belongs to the southern half of the Iberian Range, which is part of the Mesozoic Iberian Rift System. During Late Jurassic—Early Cretaceous times, a rifting cycle commenced after the break-up of Pangea and resulted in the opening of the Western Tethys and North Atlantic Oceans (Salas et al., 2001; Vera, 2001). This extensional tectonic phase led to the formation of the Mesozoic sedimentary basins with a predominance of shallow marine carbonates and occasional deltaic deposits along the Hauterivian—late Barremian interval (Salas, 1989; Salas et al., 1995), until the progressive opening of a shallow marine bay during the late Barremian—earliest Aptian (García-Penas et al., 2022).

The Morella Formation measures a maximum thickness of 80 m and consists of a sequence of deep red to greenish clays, sometimes sandy or silty, and sandstones with crossed stratification, and interbedded by sandy or biotitic limestones, generally in the upper part (Canérot et al., 1982, Fig. 3). Five facies associations were recognized that relate to marshy mud flats (Gàmez et al., 2003). The depositional environment of the Morella Formation is generally interpreted as a lower deltaic plain with high terrigenous input and tidal influence (Canérot et al., 1982; Salas, 1987; Salas et al., 1995; Gàmez et al., 2003). More recently, Santisteban et al. (2012) suggested that the Morella Formation would be affected by high-frequency cycles (30—80 ka), at least in its lower part, which is reflected in the alternation of red clays and marls. Each cycle would correspond to a transgressive—regressive parasequence within the different depositional sequences.

Many paleontological studies have been carried out on this formation since the last third of the nineteenth century. However, terrestrial vertebrate remains, specifically non-hadrosaurid styracosternan dinosaurs, are remarkable in this formation due to their abundance and biodiversity (Gasulla et al., 2022). In fact, the Mas de la Parreta quarry has produced a large proportion of the fossil faunal remains. Here, more than 2000 non-hadrosaurid styracosternan ornithopod dinosaur remains have been discovered within the last nearly two decades (Gasulla, 2015; Gasulla et al., 2022). In addition to the dinosaur remains, the Morella Formation has yielded evidence of a species-rich biota represented by abundant megafossil and microfossil plant remains, invertebrates, and diverse fauna of marine and other terrestrial vertebrates (Pérez-García et al., 2014a, 2014b; Quesada et al., 2019; Gasulla, 2015; Gasulla et al., 2022).

Regarding the microfossil flora, a number of paleopalynological studies have been carried out near the Barremian—Aptian boundary in the Iberian Peninsula. These were located in the following basins: Basque-Cantabrian Basin (Najarro et al., 2011; Barrón et al., 2015; Alonso et al., 2018; Rodríguez-Barreiro et al., 2018), Iberian Basin (Villanueva-Amadoz et al., 2014; Cors et al., 2015; Bueno-Cebollada et al., 2021), Lusitanian Basin (Groot and Groot, 1962; Trincão, 1990; Heimhofer et al., 2005, 2007; Mendes et al., 2018), and Algarve Basin (Berthou and Leereveld, 1990; Heimhofer et al., 2005, 2007; Mendes et al., 2023). In addition, other studies have focused on the megaflora which also aimed at reconstructing the plant communities of the Iberian Peninsula during the Barremian—Aptian (e.g., Friis et al., 2000; Gómez et al., 2001, 2020; Blanco-Moreno and Buscalioni, 2021).
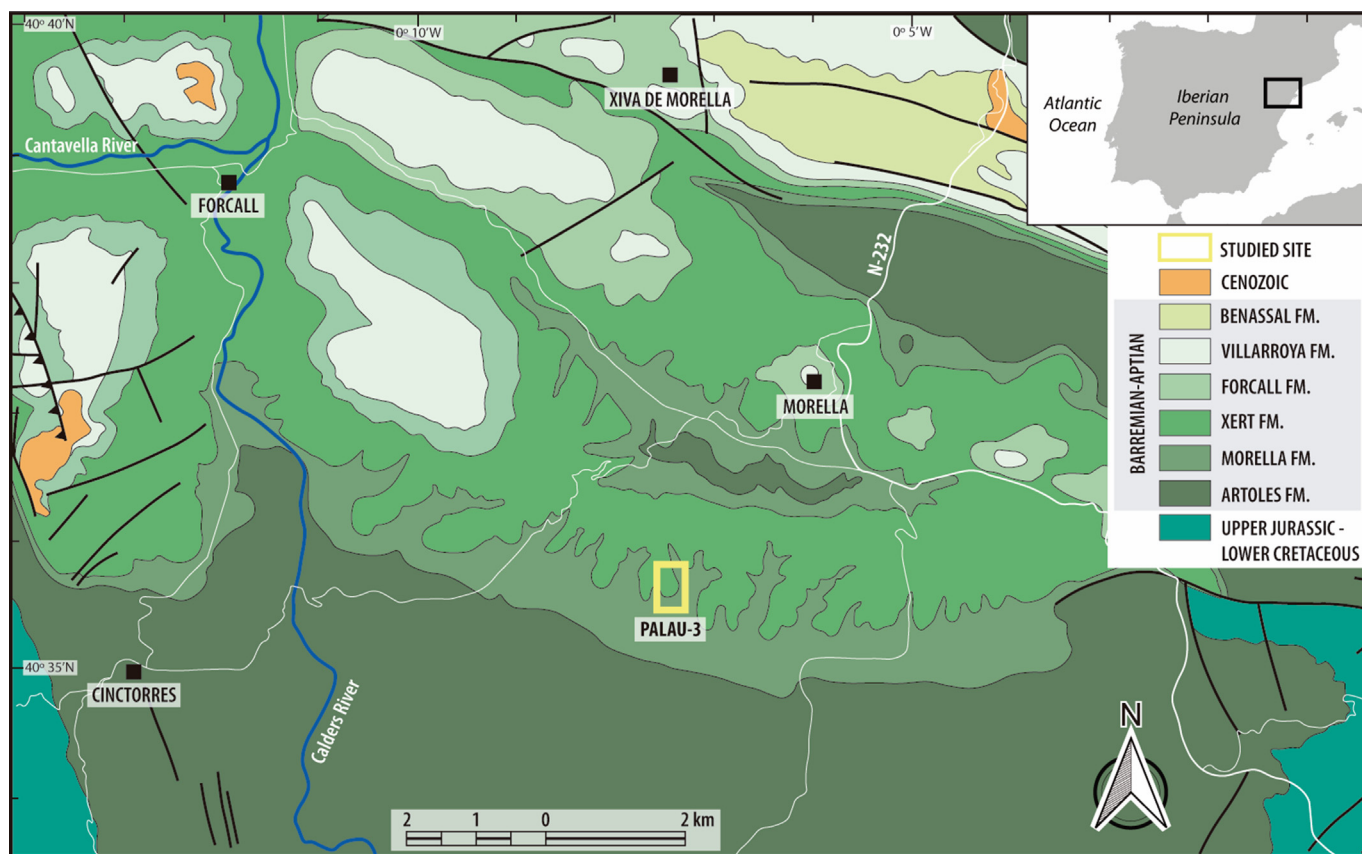

Fig. 2. Detailed geological map of the study area showing the distribution of the Barremian—Aptian formations (based on Martín et al., 1972; Navarro Vázquez et al., 1972). Inset: Locality of the study area on the Iberian Peninsula.
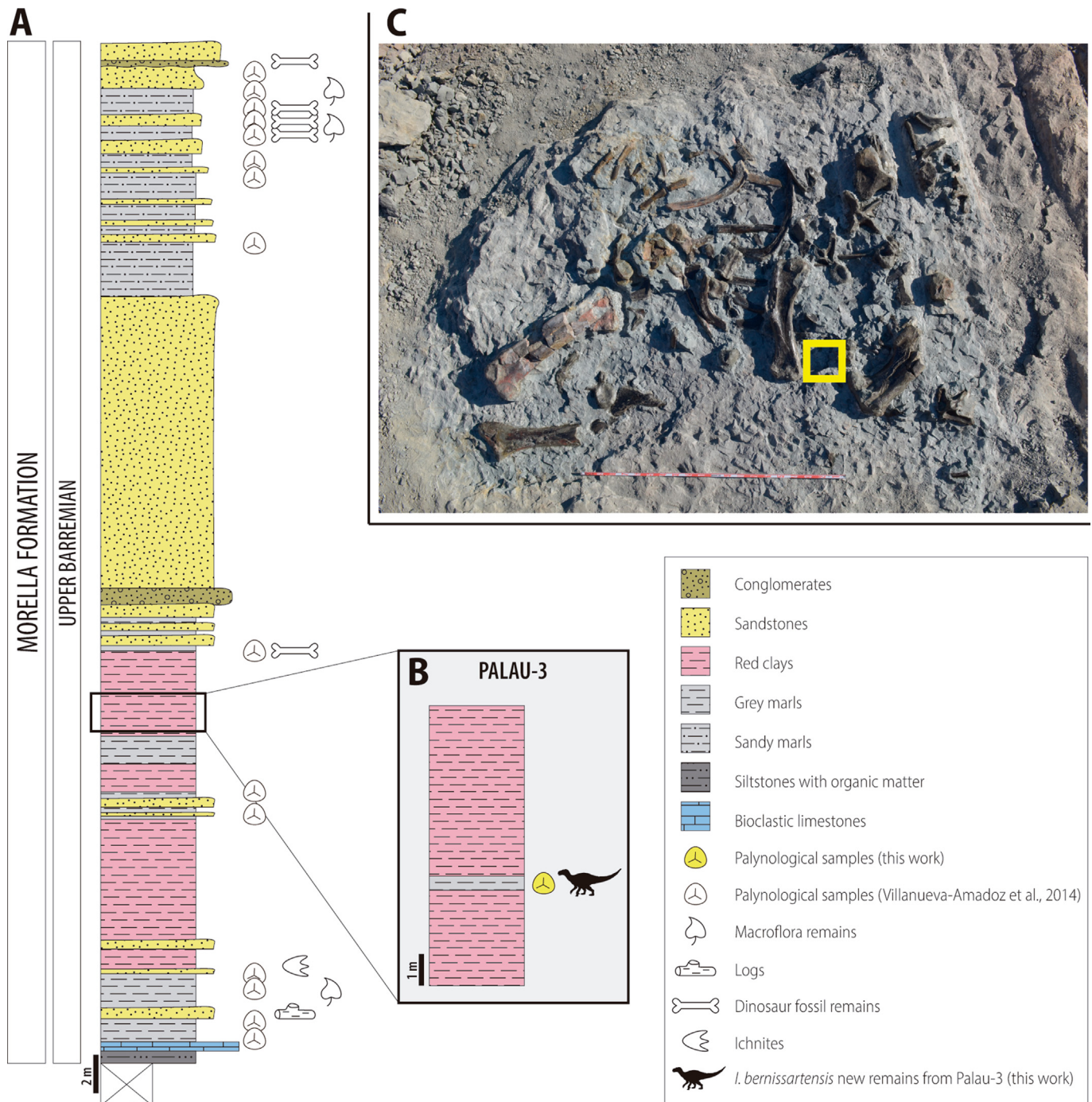
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Fig. 3. A. Composite stratigraphic column for the Morella Formation. Modified from Villanueva-Amadoz et al. (2014). B. Detail of the stratigraphic section at the Palau-3 site. C. Photo of the stratigraphic level at the Palau-3 site bearing the *I. bernissartensis* remains and the location of the palynological sample highlighted.

3. Materials and methods

The palynological sample investigated here was collected from the sediment matrix surrounding the skull of an *Iguanodon bernissartensis* from the Morella Formation. The dinosaur skull itself was excavated from the Palau-3 site in the Vega del Moll near the Morella locality, NE Iberian Peninsula. The palynological sample was processed in the palynological laboratory at the University of Vigo using the standard palynological HCl−HF−HCl techniques described by Wood et al. (1996). The acid digestion process consists of adding HCl and HF to remove carbonate and silicate minerals, respectively. A dispersing agent (a surfactant detergent) was subsequently added to facilitate filtering with a 5 μm sieve. The residues were smeared onto glass slides and observed with a Leica DM 2000 LED optical microscope equipped with LEICA ICC50 W digital camera. The illustrated specimens are indicated by fossil taxa name followed by sample number, slide number, and England Finder Reference. The palynological sample remnant, residues, and slides are stored in the laboratory of Dr. J.B. Diez (Department of Marine Geosciences and Territorial Planning, University of Vigo, Spain) with the prefix MP-3.

Quantitative analysis was based on more than 350 palynomorphs counted per slide (see Supporting Material for

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Table 1
List of the fossil palynological species recorded at the Palau-3 site near Morella, NE Spain. Except for those taxa for which the reference is highlighted (Filatoff, 1975; Yun, 1981; Abbink, 1998; Zippi, 1998), the botanical affinities are based on Zhang et al. (2021).

TAXA	BOTANICAL AFFINITIES	REFERENCES
Bryophytes		
Triporoletes incertus McIntyre and Brideaux, 1980	Ricciaceae	
Triporoletes reticulatus (Pocock, 1962) Playford, 1971		
Pteridophytes		
Aequitriradites spinulosus (Cookson and Dettmann, 1958) Cookson and Dettmann, 1961	Selaginellaceae	
Aequitriradites verrucosus (Cookson and Dettmann, 1958) Cookson and Dettmann, 1961		
Baculatisporites comaumensis (Cookson, 1953) Potonié, 1956	Osmundaceae	
Biretisporites potoniaei (Delcourt and Sprumont, 1955) Delcourt et al., 1963	Hymenophyllaceae	
cf. *Cibotiumspora juncta* (Kara-Murza, 1956) Zhang, 1978	Cyatheaceae	
Cibotiumspora jurienensis (Balme, 1957) Filatoff (1975)		
Cicatricosisporites abacus Burger, 1966	Anemiaceae	
Cicatricosisporites apiteretus Phillips and Felix, 1971		
Cicatricosisporites hallei Delcourt and Sprumont, 1955		
Cicatricosisporites hughesii Dettmann, 1963		
Cicatricosisporites striatus Rouse, 1962		
Concavissimisporites punctatus (Delcourt and Sprumont, 1955; Brenner (1963)	Lygodiaceae	
Costatoperforosporites fistulosus Deák, 1962	Anemiaceae	
Costatoperforosporites foveolatus Deák, 1962		
Crybelosporites pannuceus (Brenner, 1963) Srivastava, 1975	Marsileaceae	
Cyathidites australis Couper, 1953	Cyatheaceae	
Cyathidites minor Couper, 1953		
Deltoidospora sp.		
Densoisporites velatus Weyland and Krieger, 1953	Isoetales	
Interulobites triangularis (Brenner, 1963) Paden et al., 1971	Uncertain	
Klukisporites foveolatus Pocock, 1964	Lygodiaceae	
Leptolepidites major Couper, 1953	Lycopodiaceae - Selaginellaceae	Abbink, 1998; Filatoff, 1975
Leptolepidites psarosus Norris, 1969		
Matonisporites equiexinus Couper, 1958	Gleicheniaceae	
Patellasporites distaverrucosus (Brenner, 1963) Kemp, 1970	Selaginellaceae	
Pilosisporites brevibaculatus Döring, 1965	Lygodiaceae	
Pilosisporites trichopapillosus (Thiergart, 1949) Delcourt and Sprumont, 1955		
Plicatella bilateralis (Singh, 1971) Dörhöfer, 1977	Anemiaceae	
Undulatisporites undulapolus Brenner (1963)	Uncertain (pteridophyte)	
Gymnosperms		
Alisporites grandis (Cookson, 1953) Dettmann, 1963	Corystospermales	
Alisporites sp.		
Classopollis classoides (Pflug, 1953) Pocock and Jansonius, 1961	Cheirolepidiaceae	
Cycadopites sp.	Uncertain (gymnosperm)	
Ephedripites multicostatus Brenner (1963)	Ephedraceae	
Ephedripites sp.		
Algae		
Chomotriletes sp.	Oedogoniaceae	Zippi (1998)
Dinoflagellate cysts		
Pervosphaeridium truncatum (Davey, 1969) Below, 1982	Gonyaulacaceae	Yun Hyesu, 1981
Fungal spores		
Pluricellaesporites sp.	Uncertain (Fungi)	

palynological countings). Unless otherwise indicated, the biological affinities of the palynomorphs identified are based on the recompilation of botanical affinities by Zhang et al. (2021). Biodiversity was calculated from the Shannon-Wiener Index using the number of genera.

Our palynostratigraphical analysis was carried out with selected taxa with restricted ranges of Barremian–Aptian age. These ranges were based on previously published palynological studies on Northern Hemisphere sites, excluding remote locations in the Tethyan Realm (i.e., Antonescu, 1973; Burden, 1982, Burden and Hills, 1989; Batten, 1996; Mahmoud and Deaf, 2007; El-Noamani, 2018; Mendes et al., 2018). Unless otherwise indicated, only references with illustrations and unambiguous stratigraphic data were included.

4. Results

The palynological assemblage from the Palau-3 site shows a moderate level of biodiversity and a moderate grade of preservation (Table 1; Figs. 4–7). The assemblage is strongly dominated by Cheirolepidiaceae pollen (46 %, *Classopollis classoides*) and, in lower

frequency, Anemiaceae spores (22 %, mainly *Cicatricosisporites* spp.). However, spores of the pteridophyte families Cyatheaceae, Matoniaceae, Lycopodiaceae, and Selaginellaceae, and the bryophyte family Ricciaceae, as well as pollen of the conifer Podocarpaceae, are also found. The absence of angiosperm pollen in this assemblage is also noteworthy. In the case of marine palynomorphs, they are scarce (less than 2 %) and only represented by the Gonyaulacaceae family (*Pervosphaeridium truncatum*). A total of 27 fossil genera of spores, pollen, algae, and dinoflagellates form the palynological assemblage from the Palau-3 site.

5. Discussion

5.1. Palynostratigraphy: age assignment of the Palau-3 site

Palynological dating is based here on the restricted temporal distribution of the following palynomorphs: *Cicatricosisporites abacus*, *Crybelosporites pannuceus*, and *Triporoletes incertus*. Although the marsileacean spore *Crybelosporites pannuceus* is a frequent element in Albian–Cenomanian palynological assemblages, its First Occurrence (FO) is recorded in the upper
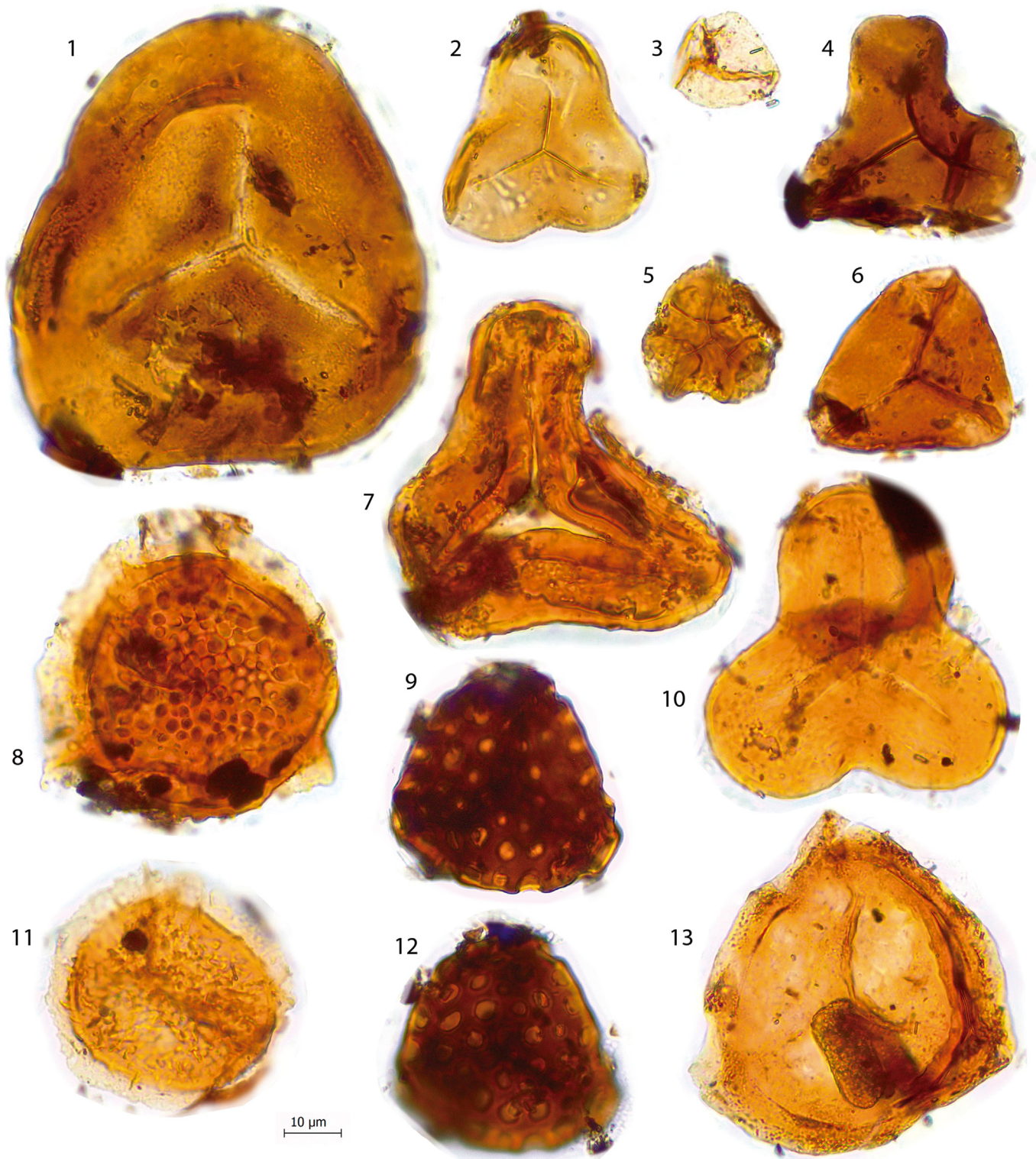
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Fig. 4. 1. *Cyathidites australis* (MP3-3-Q321); **2**. *Cyathidites minor* (MP3-2-P190); **3**. *Biretisporites potoniaei* (MP3-1-J301); **4**. cf. *Cibotiumspora juncta* (MP3-1-N483); **5**. *Cibotiusmpora jurienensis* (MP3-1-R143); **6**. *Deltoidospora* sp. (MP3-2-T343); **7**. *Matonisporites equiexinus* (MP3-1-O144); **8**. *Aequitriradites verrucosus* (MP3-3-M454); **9, 12**. *Klukisporites foveolatus* (MP3-3-J280) proximal and distal face, respectively; **10**. *Concavissimisporites punctatus* (MP3-3-L270); **11**. *Aequitriradites spinulosus* (MP3-3-G132); **13**. *Densoisporites velatus* (MP3-4-X150).
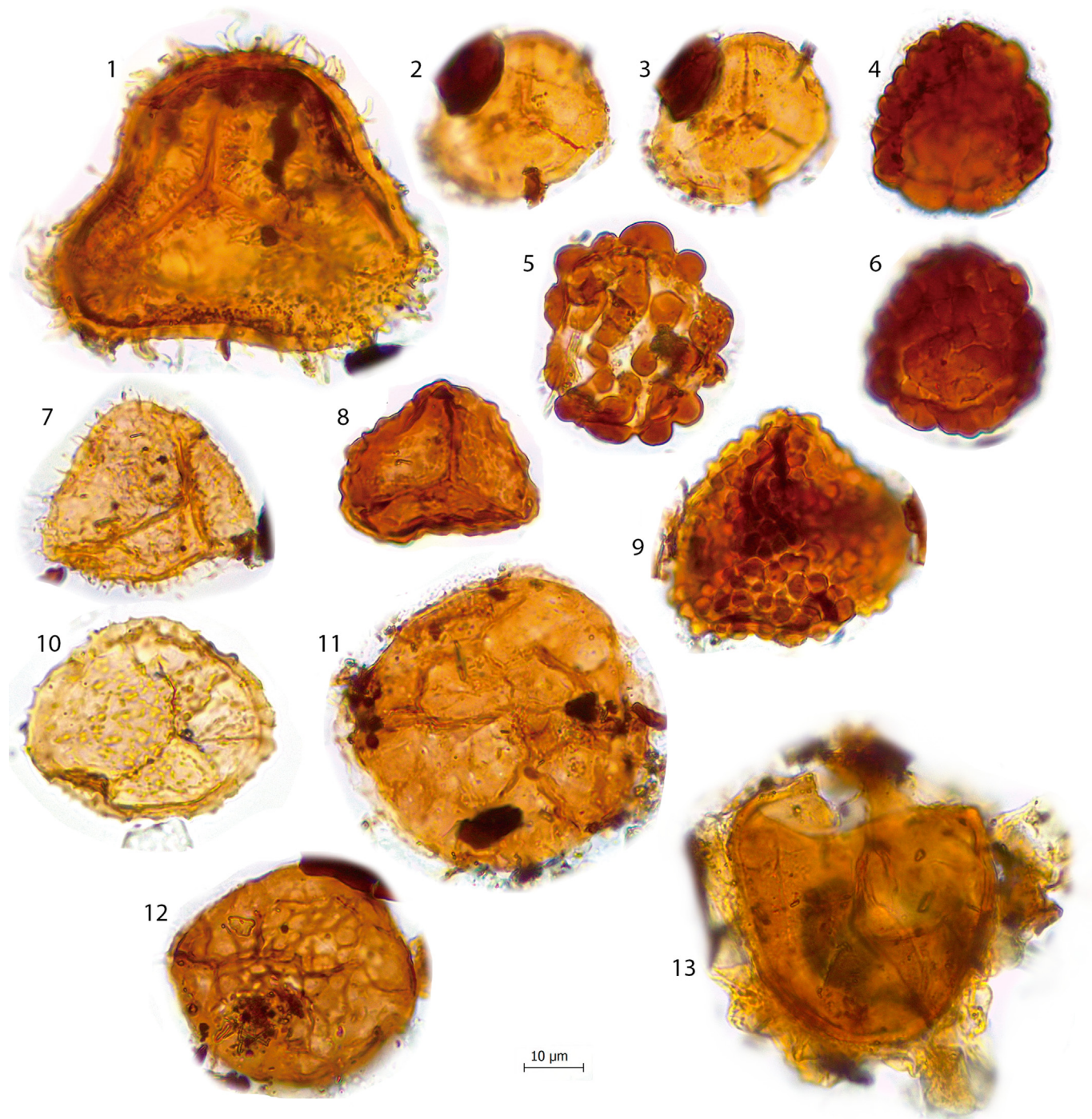
Fig. 5. 1. *Pilosisporites trichopapillosus* (MP3-3-L232); **2, 3.** *Interulobites triangularis* (MP3-1-N320) proximal and distal face, respectively; **4, 6.** *Patellasporites distaverrucosus* (MP3-4-L204) proximal and distal face, respectively; **5.** *Leptolepidites psarosus* (MP3-2-P270); **7.** *Pilosisporites brevibaculatus* (MP3-1-H143); **8.** Verrucated spore indet. (MP3-1-F182); **9.** *Leptolepidites major* (MP3-1-Q410); **10.** *Baculatisporites comaumensis* (MP3-4-V403); **11.** Triporoletes reticulatus (MP3-3-P353); **12.** *Triporoletes incertus* (MP3-1-O214); **13.** *Crybelosporites pannuceus* (MP3-4-N323).

Barremian−lower Aptian of Portugal (Mendes et al., 2018). Moreover, it is also present in the Aptian: in the lower−upper Aptian of Egypt (Mahmoud and Deaf, 2007; El-Noamani, 2018) and the upper Aptian of North America (Burden, 1982, as *Perotrilites pannuceus*). Therefore, its presence in the Palau-3 site suggests a chronostratigraphic age no older than the upper Barremian. On the other hand, the Last Occurrence (LO) of *Cicatricosisporites abacus* is recorded in the lower Aptian of Romania (Antonescu, 1973) and North America

(Burden and Hills, 1989). In the case of *Triporoletes incertus*, its LO happens lower in the section, in the upper Barremian of England (Batten, 1996) and North America (Burden and Hills, 1989). Thus, according to the chronostratigraphic temporal ranges of the previous palynomorphs, an upper Barremian age is suggested for the Palau-3 palynological assemblage (Fig. 8).

In the Morella Formation, previous palynological dating had been carried out by Villanueva-Amadoz et al. (2014) who suggested
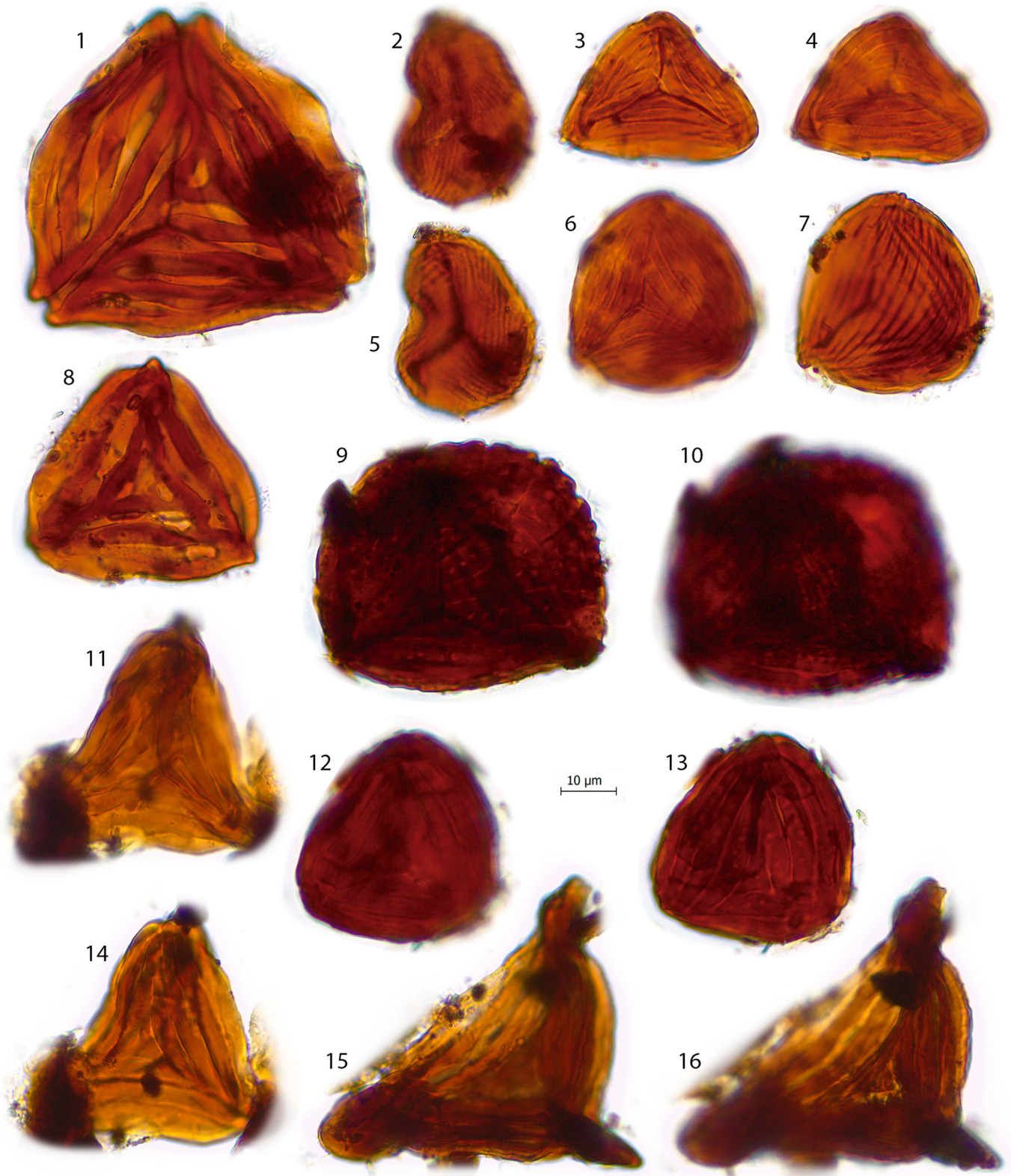
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Fig. 6. 1. *Cicatricosisporites hughesii* (MP3-3-M470); **2, 5.** *Cicatricosisporites hallei* (MP3-1-Q280) distal and proximal face, respectively; **3, 4.** *Cicatricosisporites striatus* (MP3-3-P254) proximal and distal face, respectively; **6, 7.** *Cicatricosisporites apiteretus* (MP3-1-K320) proximal and distal face, respectively; **8.** *Cicatricosisporites hughesii* (MP3-2-T382); **9, 10.** *Costatoperforosporites fistulosus* (MP3-1-Q293) proximal and distal face, respectively; **11, 14.** *Cicatricosisporites abacus* (MP3-1-L381) proximal and distal face, respectively; **12, 13.** *Costatoperforosporites foveolatus* (MP3-3-M153) proximal and distal face, respectively; **15, 16.** *Plicatella bilateralis* (MP3-3-Q120) proximal and distal face, respectively.
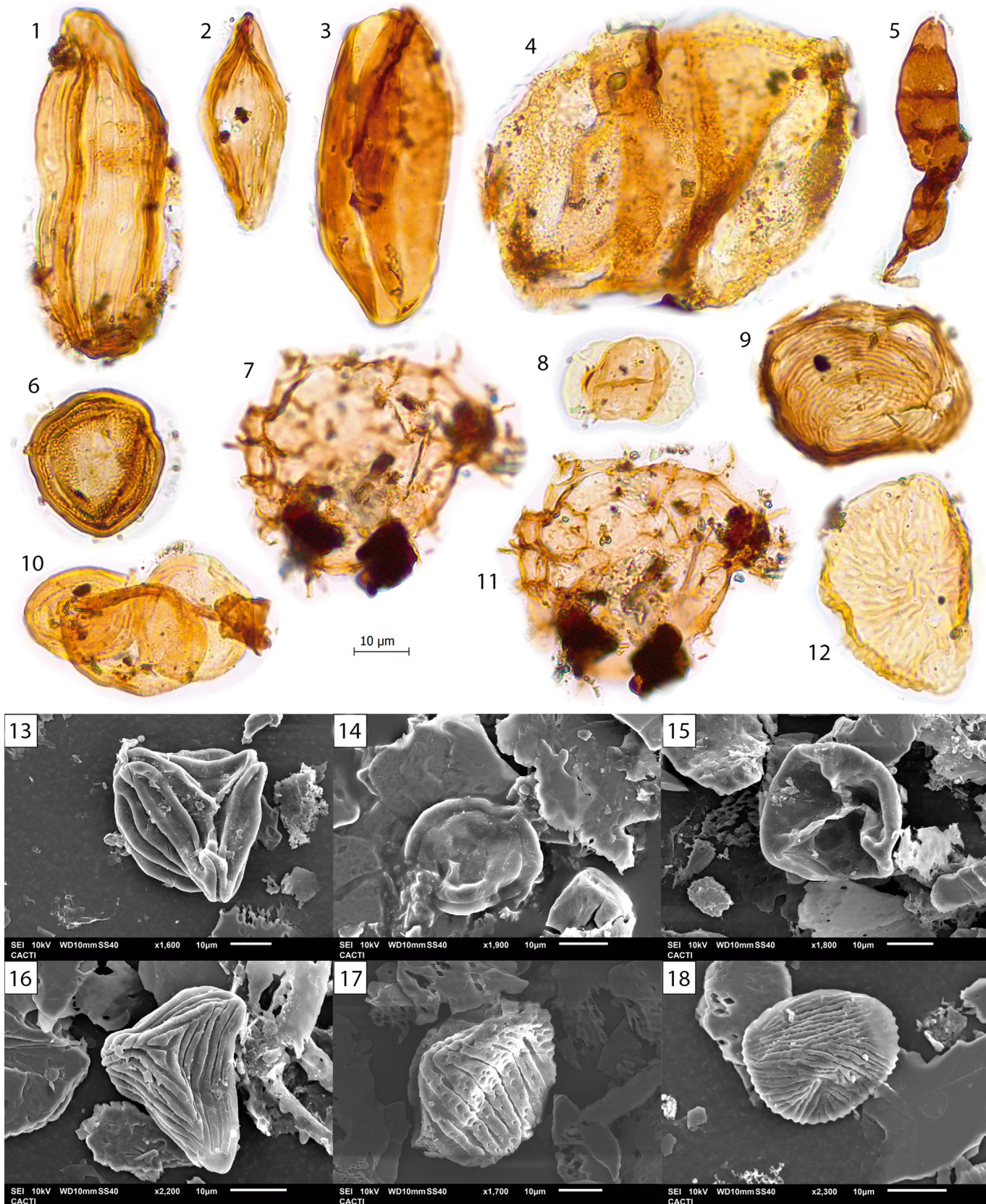
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Fig. 7. 1. *Ephedripites multicostatus* (MP3-1-N122); **2**. *Ephedripites* sp. (MP3-1-U420); **3**. *Cycadopites* sp. (MP3-1-F112); **4**. *Alisporites grandis* (MP3-4-G490); **5**. *Pluricellaesporites* sp. (MP3-1-T223); **6**. *Classopollis classoides* (MP3-2-Q300); **7, 11**. *Pervosphaeridium truncatum* (MP3-1-T293) apical and antapical part, respectively; **8**. *Alisporites* sp. (MP3-1-F394); **9**. *Chomotriletes* sp. (MP3-1-O173); **10**. Remain of *Classopollis classoides* tetrad (MP3-1-K173); **12**. Incertae sedis (MP3-2-G143). 13−18: Scanning electron micrographs of sporomorphs in the MP3 sample: **13**. Proximal face of *Cicatricosisporites hughesii*; **14**. *Classopollis* sp.; **15**. *Undulatisporites undulapolus*; **16**. *Cicatricosisporites abacus*; **17**. *Costatoperforosporites* sp.; **18**. Distal face of *Cicatricosisporites hallei*.

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a Barremian age for the lower part of the formation, due to the presence of the dinocysts *Subtilisphaera terrula*, *Florentinia mantelli*, and *Oligosphaeridium abaculum*, as well as the spores *Cicatricosisporites hallei*, *C. hughesii*, *Klukisporites foveolatus,* and *Fisciniasporites potomacensis*. However, the occurrence of *Stellatopollis* sp. at the top of the section indicates that, at least the upper part, corresponds with the uppermost Barremian. This agrees with the upper Barremian age indicated by the palynological assemblage in our work.

The location of the Barremian–Aptian boundary in the Maestrazgo Basin has been an issue for many years. In the description of the lithostratigraphic units within the Maestrazgo Basin, the boundary was initially located at the transition between the Morella and Xert formations (Canérot et al., 1982). Later, it was thought its position was lower (below the Morella Formation), in the Artoles Formation (e.g.,; Salas, 1987; Salas et al., 1995; Embry et al., 2010), or at the boundary between these two formations (Gàmez et al., 2003), based mainly on charophytes, ostracods, benthic foraminifera, and geomagnetic polarity. However, more recently, the Barremian–Aptian boundary was suggested as occurring in the lowermost part of the Forcall Formation (above the Morella Formation) based on ammonoids (Moreno-Bedmar and García, 2011). This was eventually confirmed by the revision of the chronostratigraphy of the Maestrazgo Basin (Bover-Arnal et al., 2016) as a result of additional studies of ammonoids (García et al., 2014), palynology (Villanueva-Amadoz et al., 2014), charophytes (Pérez-Cano et al., 2020), as well as isotope dating (^{87}Sr/^{86}Sr from brachiopod, rudist, and oyster shells; Pascual-Cebrian, 2014; Bover-Arnal et al., 2016).

In addition, it has been recently recommended that the base of the Aptian be reconsidered in regard to the new Aptian GSSP candidate (Gorgo a Cerbara, Italy). According to Frau et al. (2018), the use of the reverse magnetochron CM0r as a primary marker should be questioned because the bio-, litho-, and chemostratigraphic records from SE France and Italy below and above this magnetochron seem to correspond with the *Martelites sarasini* ammonite zone (the latest ammonite zone of the Barremian). Indeed, in one of the latest versions of the chart from the International Commission on Stratigraphy (version 2022/02), the age of the base of the Aptian was updated to be ~121.4 Ma instead of the previous ~125.0 Ma. However, this sets up a conflict with the ammonite records in the Maestrazgo Basin, where the magnetochron CM0r coincides with the *Deshayesites oglanlensis* ammonite zone, above the *M. sarasini* zone (Bover-Arnal et al., 2016). For the sake of caution, to carry out the palynological dating here, we have based our analysis on a previous version of the ICS chart (v2021/10; Fig. 8).

5.2. Paleoecological reconstruction and paleoclimatical context

The Palau-3 palynological assemblage is dominated by Cheirolepidiaceae conifer pollen and a diversity of pteridophyte spores

(mainly Anemiaceae). It has been well-documented that *Classopollis* pollen was produced by Cheirolepidiaceae conifers (Hörhammer, 1933; Chaloner, 1962; Watson, 1988). Although Cheirolepidiaceae conifers, which went extinct at the end of the Cretaceous (Marmi et al., 2023), possessed a variety of growth habits and tolerated a wide variety of paleoenvironmental conditions, they had a preference for coastal environments, high temperatures, and semi-arid conditions (Alvin, 1982; Watson, 1988; Tosolini et al., 2015). Indeed, the dominance of Cheirolepidiaceae pollen may prove to be a good paleogeographic indicator, as Vakhrameev (1970) suggested that palynological assemblages that were highly dominated by *Classopollis* (>50 %) are characteristic of latitudes that were lower than 40°. In contrast, the high frequency of pteridophyte spores indicates wet conditions, as living ferns have high moisture requirements.

The Morella spore flora is dominated by Schizaeales (Anemiaceae) and, in lower frequencies, Cyatheales (Cyatheaceae), Gleicheniales (Matoniaceae), Lycopodiales (Lycopodiaceae), and Selaginellales (Selaginellaceae). The biogeography of these pteridophytes today is mostly pantropical, except for Cyatheales which occur in pantropical to temperate regions, with a preference for wet montane forests or cloud forests (Smith et al., 2006, 2008; Tryon and Tryon, 2012). In the fossil record, all of these spore-bearing fossil plants have been associated with humid environments such as marshes or riverbanks (Filatoff, 1975; Abbink et al., 2004).

The occurrence of bryophytes such as Ricciaceae liverworts is remarkable in the Morella plant community. Living Ricciaceae like *Riccia* are terrestrial or saxicolous, cosmopolitan, and grow in a wide range of habitats (Bischler-Causse et al., 2005), with a preference for those with high humidity such as flooded plains, lake margins, or ponds (Kıremıt et al., 2016; Santos Silva et al., 2018). The remains of this family in the plant megafossil record are scarce, but their paleoecological preferences are similar to the extant species of *Riccia*, as observed in recent evidence of Ricciaceae found in the Mesozoic of Spain linked to shallow freshwater pools (Santos et al., 2022b). Eventually, the occurrence of marine elements like the dinocyst *Pervosphaeridium*, however scarce, indicates a marine influence.

A previous palynological study from the Morella Formation (Villanueva-Amadoz et al., 2014) shows similar and consistent data from these deposits: an assemblage dominated by Cheirolepidiaceae, a great diversity of pteridophytes in lower frequencies, and the presence of marine elements (i.e., dinoflagellate cysts). However, a noteworthy difference can be found between the previous and Palau-3 palynological assemblages. Although, scarce and poorly-preserved, Villanueva-Amadoz et al. (2014) recorded angiosperm pollen (*Clavatipollenites*, *Retimonocolpites*, and *Stellatopollis*). Angiosperms usually occur at other upper Barremian sites from the Iberian Peninsula such as the Lusitanian (Heimhofer et al., 2005, 2007) and the Algarve basins (Heimhofer et al., 2005, 2007; Mendes et al., 2023). However, their presence up to the upper Aptian is stratigraphically
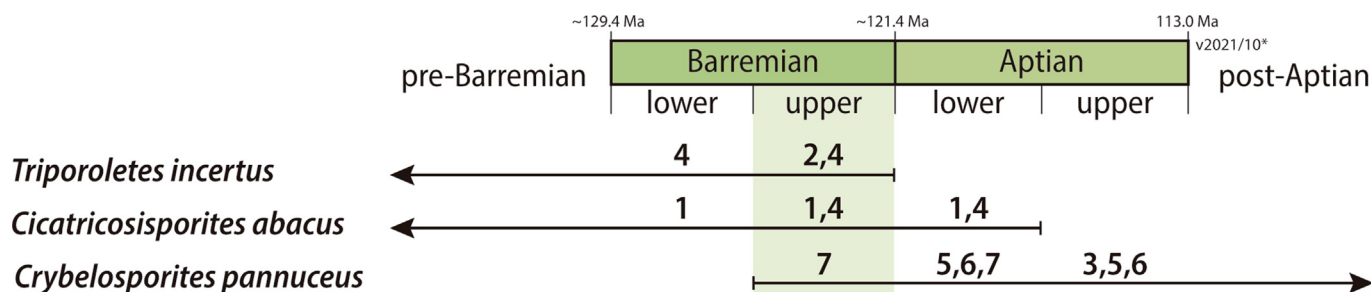

Fig. 8. Palynostratigraphical distribution of the selected taxa from the Palau-3 site. 1: Antonescu (1973); 2: Batten (1996); 3: Burden (1982); 4: Burden and Hills (1989); 5: El-Noamani (2018); 6: Mahmoud and Deaf (2007); 7: Mendes et al. (2018). *See discussion below.

discontinuous (several angiosperm barren intervals) and is marked by low diversity regardless of the paleoenvironment (Heimhofer et al., 2005, 2007). Therefore, the lack of angiosperms in the Palau-3 site may be related to an angiosperm barren interval or even due to taphonomical processes such as sorting during sediment transport.

Moreover, the sedimentological data suggests a transitional environment for the Morella Formation, more specifically, for a lower deltaic plain (Canérot et al., 1982; Salas, 1987; Salas et al., 1995; Gàmez et al., 2003). Most recently, a paleoecological reconstruction of the non-marine Barremian deposits from the Maestrazgo Basin was carried out based on charophytes (Pérez-Cano et al., 2022). Regarding the Morella Formation, three palaeoenvironmental zones were distinguished: 1) shallow marine subtidal areas with bivalves and echinoids, as well as tidal channels that may have been abandoned and become restricted ponds; 2) brackish supratidal lakes and ponds passing laterally either to lakeshore areas or to exposed floodplain areas; 3) floodplains with freshwater alkaline lakes with a high diversity of charophytes and greater terrigenous run-offs. Moreover, these authors suggest prevailing humid conditions in the Maestrazgo Basin during the early late Barremian based on the absence of evaporitic and dolomitic beds, and in agreement with previous suggestions for this time interval (Ruffell and Batten, 1990; Godet et al., 2008; Mutterlose et al., 2014).

Therefore, based on palynological and sedimentological evidence, the plant community of the Morella Formation during the late Barremian is reconstructed here as a coastal forest close to a deltaic plain. It was dominated by medium-height conifers (Cheirolepidiaceae) with sparse arborescent ferns (Cyatheaceae) and some taller conifers (Podocarpaceae), and carpeted by a diverse understory of herbaceous ferns (Anemiaceae, Matoniaceae, Lycopodiaceae, and Selaginellaceae) and liverworts (Ricciaceae). This flora grew under predominantly warm and humid conditions.

5.3. Habitat of Iguanodon bernissartensis *and diet implications*

Although *I. bernissartensis* has been widely studied over the years, there are only four areas where the occurrence of this iguanodontid has been confirmed: Bernissart (Belgium), Isle of Wight (UK), Nehden (Germany), and Morella (Spain). They were all located in a restricted W European region during Barremian−early Aptian time. Fortunately, there are paleobotanical studies that were carried out at the *I. bernissartensis* sites, allowing for the reconstruction of the plant communities at each of them.

5.3.1. Bernissart (Belgium)

The most important site is the Bernissart coal mine (Hainaut, Belgium), where dozens of complete skeletons were found during the late XIX century (Norman, 2004). The deposits correspond to the Sainte-Barbe Formation in the Mons Basin, which is composed of gray, sandy, lignitic clay with a high content of fossils (Robaszynski et al., 2002), with an upper Barremian to lowest Aptian age (Dejax et al., 2007; Yans et al., 2012). The paleoenvironment of this site was interpreted as a lake/swamp with marked seasonality and no marine influence.

The first paleobotanical studies from this site were carried out in the XIX and XX centuries (Dupont, 1878; Seward, 1900). The most recent palynological study by Dejax et al. (2007) found an assemblage with a wide variety of pteridophyte spores (mainly Cyatheaceae, Dicksoniaceae, Matoniaceae, and Lycopodiaceae), and in lower frequencies, pollen of Ephedraceae and of conifers (Araucariaceae and Sciadopityaceae). Later, a re-study of the paleobotanical megafossil remains of Bernissart defined four distinct communities in the area (Blanco-Moreno and Prestianni, 2021): 1) a submerged flora of freshwater algae; 2) a lake shoreline

community represented mainly by *Weichselia* and *Phlebopteris* ferns (Matoniaceae), and, to a lesser extent, *Ruffordia* (Anemiaceae); 3) a zone beyond the lake shoreline of other ferns such as *Hausmannia* and *Onychiopsis* (Dipteridaceae and Dicksoniaceae, respectively); 4) a community representing drier conditions consisting mainly of Matoniaceae, conifers (Araucariaceae and Sciadopityaceae), and *Taeniopteris*. Therefore, a rich plant community with different zones relative to the distance from the lake was inhabited by *I. bernissartensis*. Based on this reconstruction of habitat zones, the wide variety of herbaceous and arborescent ferns near the lake is remarkable, which consists of up to six different families with a prominent presence. The outer belt of forest vegetation was composed of plants with larger sizes and more tolerance for relatively drier conditions such as shrubs and conifers.

5.3.2. Isle of Wight (United Kingdom)

After the discovery at Bernissart, another *Iguanodon*-bearing site was found. A partial skeleton from Brook Chine in the Isle of Wight (UK) was described as a new *Iguanodon* species (*Iguanodon seelyi*) by Hulke (1882). Later, this species was considered to be a junior subjective synonym of *Iguanodon bernissartensis* (Norman, 2012). In addition to this partial skeleton, styracosternan fossil remains discovered at the Isle of Wight are derived from the Wessex (lower−?upper Barremian) and Vectis (upper Barremian−lower Aptian) formations. The Wessex Formation, in which several *Iguanodon bernissartensis* remains have been described, is a sedimentological formation that consists of an alternating varicolored sequence of mudstones and sandstones in which six major facies associations are recognized (Insole and Hutt, 1994). These major facies correspond to a low-relief alluvial plain related to a moderate-size meandering river system (Stewart, 1978).

Most fossil remains, however, come from the "plant debris bed" (Sweetman, 2011) interbedded all along the sequence with a characteristic horizon that bears fossil tree logs (i.e., the "Pine Raft"). The age of the Wessex Formation exposed on the Isle of Wight is Barremian, according to palynology, magnetostratigraphy, and carbon-isotope studies on fossil wood. The Barremian−Aptian boundary is thought to be located within the overlying Vectis Formation, while the Hauterivian−Barremian boundary lies close to the level of the "Pine Raft" (Kerth and Hailwood, 1988; Hughes and McDougall, 1990; Allen and Wimbledon, 1991; Robinson and Hesselbo, 2004). The climate during the deposition of the Wessex Formation is considered to have been warm with seasonal rainfall (Allen et al., 1998), although there was increased aridity upsection (Ruffell and Batten, 1990).

Several paleobotanical studies were carried out in the Wealden deposits on the Isle of Wight and on the southern mainland of England, on both microfossil and megafossil remains (Hughes, 1958; Batten, 1974; Oldham, 1976; Alvin et al., 1981; Alvin, 1983; Hughes and McDougall, 1990). The plant community consisted of a wide variety of pteridophytes, caytonialeans, cycadophytes, gingkophytes, conifers, and angiosperms. The Cheirolepidiaceae conifers seem to be a predominant element in both palynological (i.e., *Classopollis*) and plant megafossil (e.g., *Pseudofrenelopsis parceramosa*) floras. As a result, some authors have suggested that the local community was mainly represented by Cheirolepidiaceae together with a few associated species (Oldham, 1976; Alvin et al., 1981; Alvin, 1983). However, others suggest that the paleovegetation would have been more diverse, whereby the source of *Classopollis* pollen was a mangrove-type plant in the swamp forest (Batten, 1974; Hughes, 1975); we disagree with this interpretation because Classopollis producers are known from a wide range of paleoenvironments (Alvin, 1982; Watson, 1988; Abbink et al., 2004; Tosolini et al., 2018).

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In any case, based on all previous studies, an open forest of a diverse community of herbaceous and arborescent ferns (Anemiaceae, Cyatheaceae, Gleicheniaceae, and Matoniaceae), cycadophytes, and conifers (Cheirolepidiaceae and Araucariaceae) shaped the plant community growing on the Isle of Wight site at the time of deposition of the Wessex Formation. In addition, megaspores (possibly related to the aquatic fern family Salviniaceae) and a significant diversity of angiosperm pollen were found (Batten, 1974; Hughes and McDougall, 1990).

5.3.3. Nehden (Germany)

Juvenile skeletons and fragments of adults of several *I. bernissartensis* individuals were found in Nehden, Germany (Norman, 1987). This dinosaur site occurs in the clay infilling of a cavern system in a Devonian karst in a quarry located close to the Nehden locality in Sauerland, Germany. These clay deposits were interpreted as an extensive subterranean karst cave system influenced by an upland fluvial environment without any marine influence (Huckriede, 1982; Kampmann, 1983; Oekentorp, 1984; Clausen et al., 1989), although some authors suggest that there was a coastal shoreline nearby (i.e., Egge Embayment; Hölder and Norman, 1986).

The age of the deposits was first considered as belonging to an Aptian−Albian interval according to palynostratigraphy (Grebe, 1982) which was later narrowed down to the Aptian based on megaspores (Huckriede, 1982; Schultz and Noll, 1987). However, most of the palynomorphs from these studies have a long-range stratigraphical distribution, and the results were not conclusive. Subsequently, charophyte dating by Schudack (1987) suggested a Barremian age for the Nehden deposits, even though an upper Barremian−Aptian age was still adopted for this site in the following studies. In our opinion, the charophyte dating (Schudack, 1987) together with the presence of *Tricolpites* pollen (Grebe, 1982) would be indicative of an upper Barremian age for the Nehden deposits. According to mineralogical studies, the climate at the time of deposition would correspond to a warm climate with marked wet/dry seasons (i.e., Mediterranean climate) mainly based on the absence of kaolinite (Vortisch, 1983). Nevertheless, this interpretation would be inconsistent with the fossil flora found here (discussed below).

Several paleobotanical studies have been completed at the Nehden site. The first was a detailed palynological work in which two assemblages were described (Grebe, 1982). Both were similar in composition but had slight differences in the frequency of the most dominant groups. However, in both palynofloras, the important groups were the pteridophytes (widely diverse but mainly represented by Anemiaceae, Cyatheaceae, and Gleicheniaceae) and conifers (Cupressaceae, Pinaceae, and Podocarpaceae). Angiosperms were also present in low quantities, but noteworthy is the occurrence of *Tricolpites* pollen as the first record of tricolpate pollen happens in the upper Barremian (Scott et al., 1960; Brenner, 1963; Coiro et al., 2019); regardless of whether this was considered important by the author, its presence contributes to the dating of this site. Later, other multidisciplinary paleobotanical studies were carried out, such as palynomorphs, plant megafossil remains, charophytes, but also on insects (Huckriede, 1982; Kampmann, 1983; Schultz and Noll, 1987).

At the Nehden site, several zones of vegetation were distinguished (Huckriede, 1982; Kampmann, 1983). In the upper part, plants that are adapted to drier conditions, represented by Ginkgoales and conifers, were present. Then, there was a transitional area dominated by bald cypresses of Cupressaceae (such as *Taxodium sciadopityites*) and Araucariaceae conifers. The next zone consisted of wetlands characterized by an enormous variety of pteridophytes consisting of herbaceous, arborescent, and climbing ferns, the most prominent families having been highlighted by Grebe (1982). Eventually, the fourth zone was formed by a freshwater flora dominated by aquatic ferns and green algae. Interestingly, possible fruits of the angiosperm families Cyperaceae (sedges) and Caprifoliaceae (honeysuckles) were also found. Moreover, a wide variety of megaspores occur here, supporting the presence of aquatic ferns (Batten, 1974).

There seems to be a clear discrepancy between the fossil flora and the previously interpreted climate at the Nehden site. Today's Mediterranean climate is extremely arid during the dry season which lasts more than half of the year. Moreover, Mediterranean floras are drought-tolerant. In contrast, most of the fossil flora at the Nehden site consisted of hygrophytes that require high moisture all year round. The more obvious discrepancies involve the Cupressaceae (*Taxodium sciadopityites*) and Araucariaceae that grew in the transitional area between the uplands and wetlands in Nehden (Kampmann, 1983). According to Huckriede (1982), these plants would have been able to resist the drier conditions of a Mediterranean climate because the wet season would bring enough water to maintain lakes and swamps the rest of the year, allowing hygrophytes to thrive in the neighboring wet soils. However, neither *Taxodium* nor Araucariaceae grow in such hot and dry climates today, even if they survive in regions with a pronounced wet season. In summary, there are several factors that point out that the paleoclimatic conditions in Nehden at the time of deposition were not quite as hot and extremely arid as is found in a true Mediterranean climate: 1) the presence of hygrophyte plants; 2) the assignment of a Mediterranean climate to Nehden, mainly due to the "absence of kaolinite" (Vortisch, 1983); and 3) recent paleoclimatic models suggesting a temperate and humid climate for the Nehden area (Hay and Floegel, 2012; Burgener et al., 2023). For all these reasons, a warm and humid subtropical to warm-temperate climate is more likely to have prevailed in the Nehden site during the late Barremian−early Aptian.

5.3.4. Morella (Spain)

In the Morella area on the northeastern Iberian Peninsula, there are more than eight sites where partial or complete skeletons of *I. bernissartensis* have been identified with confidence (Gasulla et al., 2022). All of them occur within the Morella Formation, which bears a fossil plant community dominated by medium-size Cheirolepidiaceae conifers and, in lesser abundance, arborescent Cyatheaceae ferns, Podocarpaceae conifers, and diverse herbaceous ferns such as Anemiaceae, Matoniaceae, Lycopodiaceae, and Selaginellaceae. This plant paleoecosystem thrived in a warm and humid climate during the late Barremian (see 5.2.).

5.3.5. General overview

In summary, the four sites containing *Iguanodon bernissartensis* remains, although very close in age (Barremian−lower Aptian), were deposited in a wide variety of paleoenvironments (Fig. 1, Table 2): a lake/swamp system (Bernissart), an open forest associated with a fluvial environment (Isle of Wight), a fluvial/swamp system (Nehden), and a coastal forest (Morella). The abundance of *I. bernissartensis* remains in all of the faunal assemblages dominated by styracosternan dinosaurs (Verdú et al., 2017; Gasulla et al., 2022; Lockwood et al., 2021) in which this species occurs suggests that it had a great capability to adapt to diverse environments, which would explain its great ecological success within the Cretaceous dinosaur communities in what is today Europe. However, the paleoclimate at all four sites seems to be consistent with predominantly warm and wet conditions.

Similarly, the plant communities occurring at these paleoenvironments were frequently alike in taxonomic composition. This is the case especially between floras on the Isle of Wight and at

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Table 2
Main characteristics of the habitats of the *Iguanodon bernissartensis*-bearing sites.

Site	Formation	Horizon	Paleoenvironment	Paleoclimatology	Paleoecology	Main botanical families
Bernissart (W Belgium)[a]	Sainte-Barbe Fm. (Mons Basin)	upper Barremian −lower Aptian	Lake/swamp	Warm and humid with high seasonality	Margin lake community dominated by herbaceous and arborescent ferns	Anemiaceae (herbaceous fern) Cyatheaceae (arborescent fern) Matoniaceae (herbaceous fern)
Isle of Wight (S England)[b]	Wessex Fm. (Wessex Basin)	Barremian	Alluvial plain	Warm with seasonal rainfalls increasing aridity towards the top	Open forest dominated by Cheirolepidiaceae conifers and diverse herbaceous and arborescent ferns	Cheirolepidiaceae (conifer) Schizaeaceae (herbaceous fern) Cyatheaceae (arborescent fern) Gleicheniaceae (herbaceous fern) Matoniaceae (herbaceous fern)
Nehden (W Germany)[c]	Clay infill of a Devonian karst	upper Barremian	Fluvial system	Warm and humid with high seasonality	Plant community with diverse herbaceous and arborescent ferns and conifers	Anemiaceae (herbaceous fern) Cyatheaceae (arborescent fern) Gleicheniaceae (herbaceous fern) Podocarpaceae-Pinaceae (conifer) Cupressaceae (conifer)
Morella (NE Spain)[d]	Morella Fm. (Maestrazgo Basin)	upper Barremian	Tidal flat	Warm and humid	Coastal open forest dominated by Cheirolepidiaceae conifers and herbaceous ferns	Cheirolepidiaceae (conifer) Anemiaceae (herbaceous fern) Cyatheaceae (arborescent fern)

[a] Botanical references: Dejax et al. (2007); Blanco-Moreno and Prestianni (2021).
[b] Botanical references: Hughes (1958); Batten (1974); Oldham (1976); Alvin et al., 1981; Alvin (1983); Hughes and McDougall (1990).
[c] Botanical references: Grebe (1982); Kampmann (1983).
[d] Botanical references: Villanueva-Amadoz et al. (2014); this work.

Morella, where the Cheirolepidiaceae conifers played a significant role in these assemblages, and especially between Bernissart and Nehden, where pteridophytes were common. However, at all of the sites, the diversity of the herbaceous and arborescent ferns is remarkable. The fern flora was dominated by the families Anemiaceae and Cyatheaceae, which may have played a major role in the diet of *I. bernissartensis*.

Angiosperm-dominated floras were not observed until the mid-Cretaceous of North America and Europe (Friis et al., 2011) after a rapid radiation which led to a floristic change displacing mainly cycadophytes and pteridophytes (Lidgard and Crane, 1988). The Iberian Peninsula seems to have been a key area for the diversification of angiosperms, especially western Iberia (Heimhofer et al., 2005, 2007; Friis et al., 2010, 2011), as the first angiosperm-dominated floras were found in this region during the late Cenomanian represented by Normapolles pollen related to Fagales (Solé de Porta, 1978; Thurow et al., 1988; Peyrot et al., 2008; Rodríguez-Barreiro et al., in press). Evidence of angiosperms at the *I. bernissartensis*-bearing sites, while commonly present, is always scarce. Therefore, it seems that angiosperms did not play a major role in the diet of *I. bernissartensis*.

As bulk feeders, the ornithopods would have had to ingest and masticate as much plant matter as quickly and efficiently as possible each day. Like other large, herbivorous dinosaur groups such as sauropods, they would have consumed a variety of plants, although they may targeted the more nutritious plant groups (Gee, 2011) or have been limited to the plants growing in the area. Taller ornithopods with a facultatively bipedal stance, such as iguanodontians, would have been able to feed on plant foliage that was borne several meters above ground, such as the fronds of arborescent ferns or the leaves on the lower branches of conifer trees (cf. Sander et al., 2010; Gee, 2011). According to plant digestibility experiments (Hummel et al., 2008; Gee, 2011; Howell et al. 2023), herbaceous and arborescent ferns (including Anemiaceae and Cyatheaceae) would have been moderately nutritious for herbivores, while *Equisetum* sphenophytes and the foliage of conifers such as the Araucariaceae and Cheirolepideaceae would have been higher quality, favored sources of food. In our study, the most commonly found food plants documented in the Morella palynoflora as co-occurring with *I. bernissartensis* are thus the conifer trees of the Cheirolepidiaceae, low-growing ferns of the Anemiaceae, and the arborescent ferns of the Cyatheaceae.

6. Conclusions

New *Iguanodon bernissartensis* remains were discovered in the dinosaur-bearing site of Palau-3, consisting of the most complete non-articulated skeleton of this species on the Iberian Peninsula. Based on the palynological analysis of the *I. bernissartensis*-bearing deposits in the Morella Formation, the following conclusions can be made here: 1) the Palau-3 palynological assemblage is upper Barremian in age; 2) the paleoenvironment is reconstructed as a coastal open forest thriving under a warm and humid climate; 3) these Early Cretaceous plant communities were dominated by Anemiaceae and Cyatheaceae ferns, as well as by Cheirolepidiaceae conifers.

A survey of Cretaceous paleobotanical studies from all the sites with *I. bernissartensis* remains shows a preference for certain habitats, which may reflect their dietary preferences. These ornithopods were adapted to a wide variety of paleoenvironments within a restricted area of the archipelagos found in the westernmost Tethyan margin during the Early Cretaceous (Barremian−early Aptian) in what is today western and central Europe. These paleoenvironments are generally interpreted as warm and wet. Moreover, *I. bernissartensis* appears to be linked to plant communities dominated by arborescent and herbaceous ferns of the Anemiaceae and Cyatheaceae families, as well as by Cheirolepidiaceae conifers. Anemiaceae and Cyatheaceae fronds, and the foliage of the Cheirolepidiaceae trees were thus likely to have been the main sources of nutrition for *I. bernissartensis* and other iguanodontians in this region.

Data availability

Data will be made available on request.

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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.2023.105804.