

Latest Maastrichtian climate changes: Insights from high-resolution palynological data from the XHY2008 borehole, Jiayin, NE China

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ABSTRACT

The latest Maastrichtian was an important interval in Earth's history, characterized by global climatic fluctuations and significant biotic transitions. Understanding the climate and vegetation changes during this time is important for reconstructing the climatic perturbations during the pre-end-Maastrichtian mass extinction and elucidating the cause of the extinction. However, detailed reconstructions of terrestrial climate and vegetation changes remain limited due to the uneven preservation of palynomorphs and the scarcity of high-resolution palynological records. In this study, based on high-resolution palynological data from the Furao Formation in the XHY2008 borehole, Jiayin, Heilongjiang Province, Northeast China, three latest Maastrichtian palynological assemblages were identified, in ascending stratigraphic order: (1) the *Gabonispuris*–*Pinuspollenites*–*Aquilapollenites* assemblage; (2) the *Laevigatosporites*–*Monocolpopollenites*–*Ulmoidipites* assemblage; and (3) the *Osmundacidites*–*Pseudointegricarpus*–*Wodehouseia* assemblage. These assemblages provide key insights into the composition of latest Maastrichtian palynoflora and associated climatic changes. The data indicate that the latest Maastrichtian climate was warm and humid (i.e., subtropical) in the mid-latitudes of the Northern Hemisphere, which was typical of the Cretaceous greenhouse climate. However, two cooling and drying events were recognized based on quantitative analyses of the palynomorphs using principal component analysis and ecological affinity statistics. These two transient events involved changes from a subtropical–humid to temperate–subhumid climate in the last 34 kyr of the Cretaceous. These short-term climatic changes might record abrupt climatic perturbations during latest Maastrichtian cooling and enhance our knowledge on the frequency of climatic change.

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1. Introduction

The latest Maastrichtian was a climatically dynamic and biologically important interval in Earth's history that immediately preceded the catastrophic Cretaceous–Paleogene (K/Pg) mass extinction event (Macleod and Huber, 1996; Li and Keller, 1998a, 1998b; Keller, 2001; Schulte et al., 2010; Vajda and Bercovici,

2014; Barnet et al., 2017; Hull et al., 2020; Keller et al., 2020; O'Hara et al., 2022). This interval witnessed a series of rapid and extreme environmental perturbations (Keller et al., 2011; Renne et al., 2013; Zhang et al., 2018), including intensified Deccan Traps volcanism, disruptions to the global carbon cycle (McLean, 1985; Keller and Lindinger, 1989), a significant eustatic sea-level fall (Haq et al., 1987), and marked global cooling (Keller et al., 2011), all of which profoundly affected terrestrial and marine ecosystems (Stott and Kennett, 1990; Barrera, 1994; Nordt et al., 2002; Linnert et al., 2014; Vellekoop et al., 2019; Wang et al., 2024). The associated negative organic carbon isotopes ($\delta^{13}\text{C}_{\text{org}}$) imply there were complex interactions between atmospheric carbon input, biotic metabolism, and potential feedback

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mechanisms such as methane release or biomass combustion (Thomas, 2007). Given that it was the final phase of the long-lived Cretaceous greenhouse world (Skelton, 2003; Hay, 2011), late Maastrichtian climatic changes can provide key insights into how terrestrial ecosystems responded to abrupt environmental stressors. Palynological data serve as a high-resolution proxy for reconstructing vegetation dynamics and paleoclimatic conditions (Nichols and Jacobson, 1982; Nichols et al., 1986, 1992; Nichols, 2002, 2003; Samant and Mohabey, 2005, 2009; Samant et al., 2022, 2024), and can enhance predictions of ecosystem resilience and thresholds under current and future climate change scenarios (Wang et al., 2024).

Previous studies have investigated latest Maastrichtian climate changes. An episode of warming that occurred 450–100 kyr before the K/Pg boundary has been identified from a temperature increase of 2–5 °C in both the marine and terrestrial realms (Li and Keller, 1998b; Wilf et al., 2003; Woelders et al., 2017; Barnet et al., 2017; Hull et al., 2020; Gilabert et al., 2021; Nava et al., 2021; Gu et al., 2023; O'Connor et al., 2024). This latest Maastrichtian warming was followed by a gradual cooling towards the end-Cretaceous (Tobin et al., 2014; Petersen et al., 2016; Woelders et al., 2017; Keller et al., 2020; O'Connor et al., 2024). However, the most high-resolution paleoclimatic studies have focused mainly on geochemical data, such as clumped isotopes (Zhang et al., 2018), mercury (Hg) contents and isotopes (Keller et al., 2020; Gu et al., 2022), organic paleothermometer, the methylation index of 5-methyl branched glycerol dialkyl glycerol tetraethers (MBT⁵me), and carbon-isotopes (O'Connor et al., 2024). Due to differences in the preservation of various terrestrial palynomorph fossils and the poor temporal resolution, there have been few detailed studies of the climate change in the latest Maastrichtian based on high-resolution palynological data. In the Jiayin area of Heilongjiang Province, Northeast China, locality No.95 of the K/Pg boundary has been recognized based on continuous Upper Cretaceous to lower Paleogene lacustrine deposits with abundant, exceptionally well-preserved palynomorph assemblages, which provides a unique opportunity to study climatic changes during the latest Maastrichtian (Sun et al., 2002, 2003, 2005, 2011, 2014, 2021; Chen et al., 2004; Li et al., 2004; Markevich et al., 2006, 2011; Suzuki et al., 2010, 2011; Knittel et al., 2013; Sun, 2022).

In this study, we present high-resolution palynological data from the uppermost part of the Furao Formation (uppermost Maastrichtian) in the XHY2008 borehole in Jiayin, and present a reconstruction of the climatic changes just before the K/Pg boundary. Our findings contribute to a more refined understanding of the latest Maastrichtian climatic changes in a mid-latitude region of the Northern Hemisphere, and also enhance our understanding of the environmental dynamics leading up to the K/Pg mass extinction.

2. Geological background and stratigraphy

Jiayin is located in northern Heilongjiang Province, Northeast China, on the right bank of the Heilongjiang (Amur) River, south-east of the Zeya-Bureya Basin (Fig. 1A, 1B; Liang, 2015). To the southwest of Jiayin, the Songliao Basin is a major Mesozoic terrestrial petroliferous basin that is being investigated by the International Continental Scientific Drilling Program (ICDP). The basin contains sedimentary rocks that are >6500 m in thickness. A well-developed and continuous sequence of terrestrial deposits of Late Cretaceous to Paleocene age is distributed along the right bank of the Heilongjiang River in Jiayin. This sequence contains diverse and abundant fossils, including dinosaur bones and footprints, fossil woods, leaves, palynomorphs, ostracods, branchiopod

shells, fish bones and scales, and insects (Sun et al., 2002; Liang, 2015).

The Upper Cretaceous strata in the Jiayin area are divided into four formations in ascending stratigraphic order: the Yong'ancun Formation (K₂yn, Turonian–Coniacian), Taipinglingchang Formation (K₂tp, Campanian), Yuliangzi Formation (K₂yl, lower–middle Maastrichtian) and Furao Formation (K₂f, upper Maastrichtian). The Yuliangzi Formation is characterized by diverse dinosaur bones of early–middle Maastrichtian age, which are correlated to the Udurchukan Formation, and is dominated by fluvial sedimentary rocks, including grayish green and yellow conglomerates, gravelly sandstones, sandstones, and mudstones. The Furao Formation is dominated by lacustrine mudstones and deltaic fine-grained sandstones (Qu et al., 1997; Sun et al., 2002, 2005). A palynological study of the Furao Formation showed it can be correlated with the Middle Tsagan Formation (Bureya Formation) in the Zeya-Bureya Basin, which is consistent a late Maastrichtian age (Table 1) (Markevich et al., 2011; Knittel et al., 2013; Sun et al., 2014).

The Paleocene strata occur in the Wuyun Formation (Qu et al., 1997), which is divided into the Baishantou member in the lower part of the formation and a coal-bearing member in the upper part (Sun et al., 2002). The former member was assigned an early Danian age, whereas the latter is late Danian in age (Manchester et al., 1999; Sun et al., 2002, 2014).

The palynological samples analyzed in this study were collected from the XHY2008 borehole (129°35'14"E, 49°14'53"N), located near the Wuyun Town along the right bank of the Heilongjiang (Amur) River. The borehole penetrated Quaternary sediments through to lower Danian (Paleocene) and upper Maastrichtian (Upper Cretaceous) strata. The Maastrichtian and Danian deposits are continuous and fossiliferous. These strata record the nature of the vegetation in the latest Maastrichtian and the associated climatic conditions.

3. Materials and methods

All palynological samples analyzed in this study were collected from the XHY2008 borehole, located in the Jiayin area of Heilongjiang Province (Fig. 1C). A total of 183 samples were collected at intervals of 5 or 10 cm from the 22.10-m-thick core. Fifty-five samples are from the Furao Formation and 128 samples are from the Wuyun Formation. These samples are mainly light grayish-green or dark gray argillaceous mudstones and silty mudstones.

All samples were prepared following standard palynological procedures, as outlined by Traverse (2007). Each sample (50 g) was crushed to a particle size of <0.5 mm and treated with 18 % HCl for 24 h to remove carbonates, followed by 48 h with 40 % HF to dissolve silicate minerals. The residues were rinsed with distilled water until a neutral pH (Ph = 7) was reached. Heavy liquid flotation was undertaken with a mixed ZnCl₂–KI solution with a specific gravity of 2.2 g/cm³. An 8 μm mesh sieve was used to isolate organic residues and concentrate the palynomorphs. The palynomorphs were mounted in glycerin jelly on slides and sealed with nail polish. Pollen and spores on the slides were positioned using the England finder. All samples, slides, and scanning electron microscopy (SEM) stubs labeled with the prefix XHY2008- are housed at the Research Center for Paleontology and Stratigraphy, Jilin University, Changchun, China.

Optical microscopy observations were carried out with an Olympus BX-51 transmitted light microscope. Two slides were generally examined for each sample. While some samples were barren, others were highly productive, yielding up to >1200 grains of pollen and spores. Photomicrographs were captured with a 100 × oil immersion objective using a Weiscope digital camera

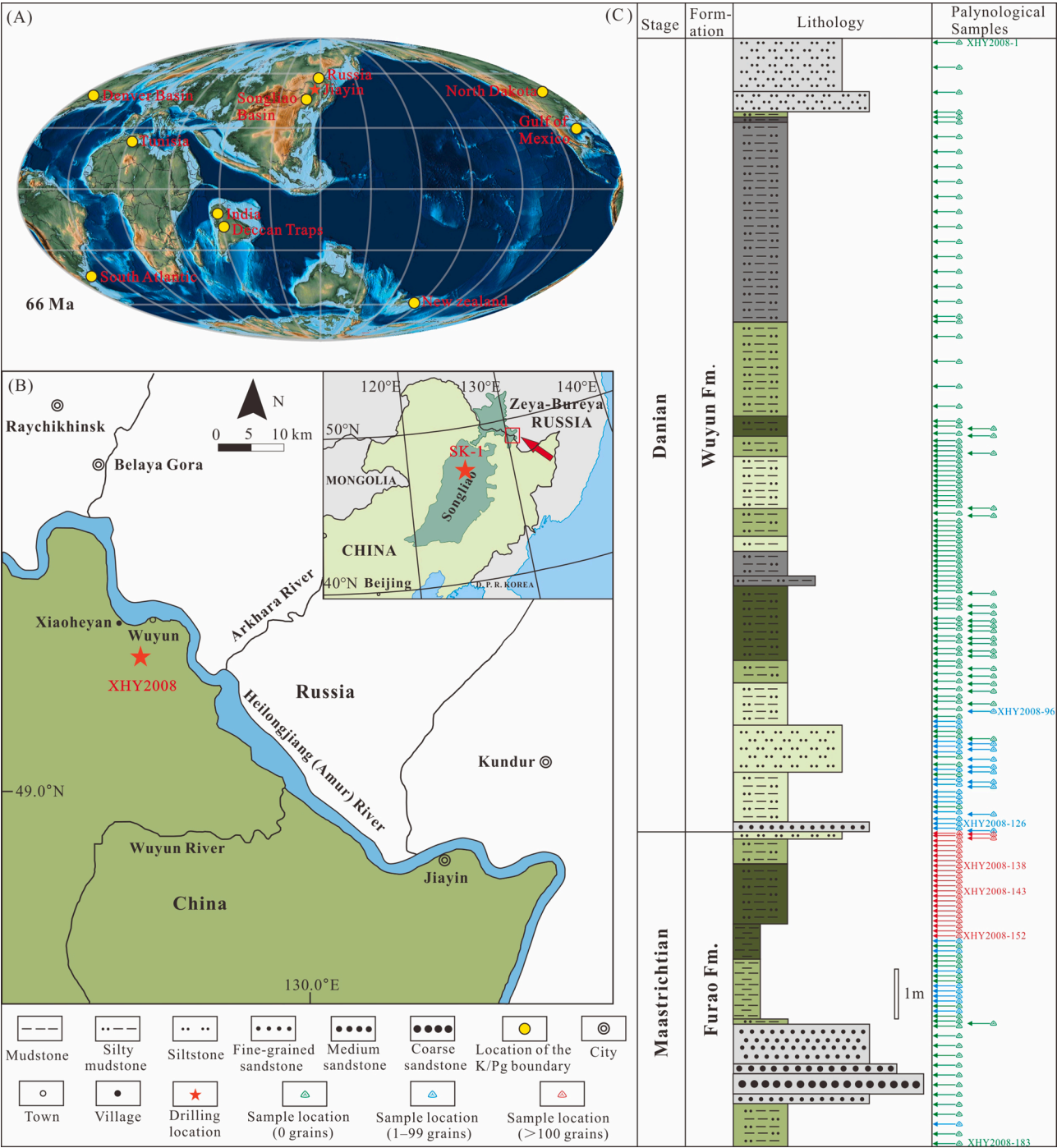


Fig. 1. Geographical and geological location of Jiayin in Heilongjiang Province. A. Reconstructed topography in the latest Cretaceous (after Scotese, 2014). B. Geographic map showing the location of the XHY2008 borehole (GPS coordinates: 129°35'14"E, 49°14'53"N) (after Sun et al., 2011). C. Stratigraphic horizons of the samples collected in the XHY2008 borehole in Jiayin.

Table 1
Correlation of the Upper Cretaceous in Jiayin of Heilongjiang (China) and the Zeya-Bureya Basin (Russia)

Formation	Chron. Stratigr.	Region	Zeya-Bureya Basin Russia	Jiayin of Heilongjiang China
Upper Cretaceous	Maastrichtian	U L- M	Bureya Formation Udurchukan Formation (Main dinosaur horizon)	Furao Formation Yuliangzi Formation (Main dinosaur horizon)



Fig. 2. Representative spores and pollen from the Furao Formation in the XHY2008 borehole (with the numbers recording the sample-slides and England Finder coordinates). Scale bar = 10 μ m (applicable to all specimens of the illustration).

A. *Cyathidites minor* Couper 1953, Slide No. XHY2008-134-1/J37-4; B. *Gleicheniidites senonicus* Ross 1949, Slide No. XHY2008-136-1/I41-3; C. *Alsophilidites arcuatus* (Bolchovitina) Xu et Zhang 1980, Slide No. XHY2008-136-1/M33-2; D. *Gabonisoris vigourouxii* Boltenhagen (1967), Slide No. XHY2008-152-1/K42-2; E. *Lygodiumsporites pseudomaximus* (Thomson et Pflug) Sung et Zheng 1978, Slide No. XHY2008-135-1/F25-3; F, G. *Laevigatosporites ovatus* Wilson and Webster 1946, F-Slide No. XHY2008-142-1/E40-1, G-Slide No. XHY2008-142-1/M38-2; H. *Sphagnumsporites antiquus* (Kruttsch) Chen 1983, Slide No. XHY2008-129-1/T35-2; I. *Hymenophyllumsporites* sp., Slide No. XHY2008-129-1/R39-2; J. *Gnetaceapollenites evidens* (Bolchovitina) Verbizkaja 1979, Slide No. XHY2008-142-1/K38-4; K. *Cyathidites* cf. *concavus* (Bolch., 1953) Dettmann (1963), Slide No. XHY2008-136-1/P35-2; L. *Osmundacidites wellmanii* Couper 1953, L-Slide No. XHY2008-129-1/F36-3, N-Slide No. XHY2008-133-1/I38-4; M. *Foveosporites cenomanicus* (Chlonova) Schvetzova 1976, Slide No. XHY2008-136-1/V34-2; O. *P. Rouseisporites reticulatus* Pocock 1962, O-Slide No. XHY2008-133-1/P41-1, P-SEM-Stub No. XHY2008-133; Q, R. *Ephedripites fusiformis* (Shakhmundes) Kruttsch 1970, Q-Slide No. XHY2008-129-1/K37-1, R-SEM-Stub No. XHY2008-137; S. *Ephedripites mingshuiensis* Yu, Guo et Mao 1983, Slide No. XHY2008-138-1/H42-4; T. *Taxodiaceapollenites hiatus* (Potonie) Kremp 1949, Slide No. XHY2008-135-1/P21-1.

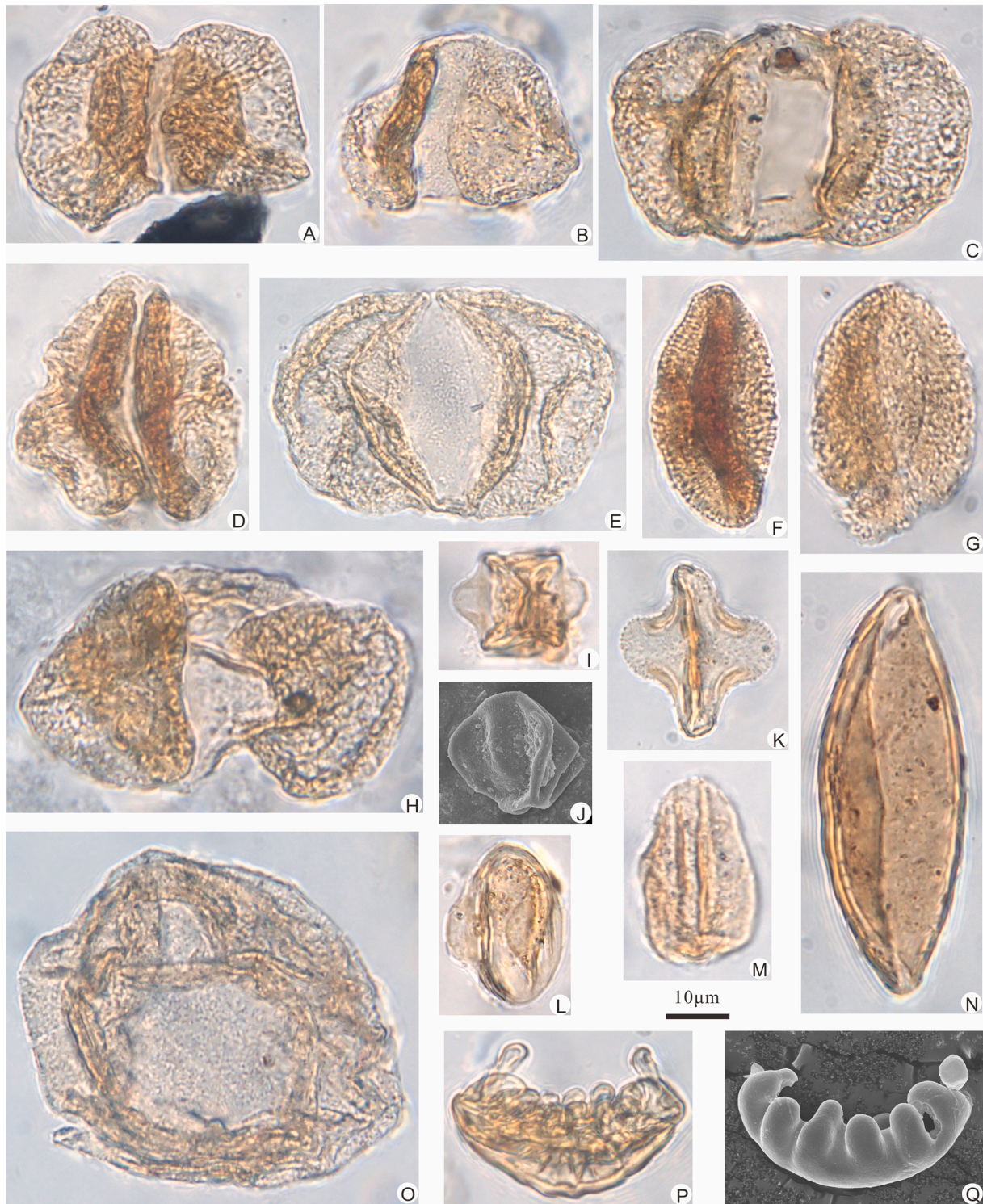


Fig. 3. Representative pollen from the Furao Formation in the XHY2008 borehole (with the numbers recording the sample-slides and England Finder coordinates). Scale bar = 10 μ m (applicable to all specimens of the illustration).

A. *Podocarpidites ellipticus* Cookson 1947, Slide No. XHY2008-135-1/O22-1; B. *Pinuspollenites microinsignis* (Krutzsch) Song et Zhong 1984, Slide No. XHY2008-143-1/N36-3; C. *Pinuspollenites labdacus* (Potonie) Raatz 1937, Slide No. XHY2008-135-1/P38-2; D. *Abietinaepollenites pactovae* (Krutzsch) Zhang 1999, Slide No. XHY2008-136-1/R34-2; E. *Alisporites bilateralis* Rouse 1959, Slide No. XHY2008-133-1/I41-2; F. *Liliacidites ellipticus* Nagy 1969, Slide No. XHY2008-136-1/G32-1; G. *Liliacidites creticus* (Norton) Mchedlishvili 1961, Slide No. XHY2008-150-1/B34-3; H. *Pinuspollenites* sp., Slide No. XHY2008-144-1/Q38-1; I, J. *Orbiculapollis lucidus* Chlonova 1961, I-Slide No. XHY2008-133-1/G39-1, J-SEM-Stub No. XHY2008-137; K. *Aquilapollenites insignis* (Norton) Mchedlishvili 1961, Slide No. XHY2008-133-1/U42-1; L. *Orbiculapollis globosus* (Chlonova) Chlonova 1961, Slide No. XHY2008-133-1/F38-4; M. *Monocolpopollenites* sp., Slide No. XHY2008-138-1/M42-1; N. *Ginkgocycadophytus* sp., Slide No. XHY2008-135-1/P23-1; O. *Araucariacites australis* Cookson 1947, Slide No. XHY2008-143-1/E34-3; P, Q. *Marsypiletes cretacea* Robertson 1973, P-Slide No. XHY2008-129-1/T40-3, Q-SEM-Stub No. XHY2008-133.

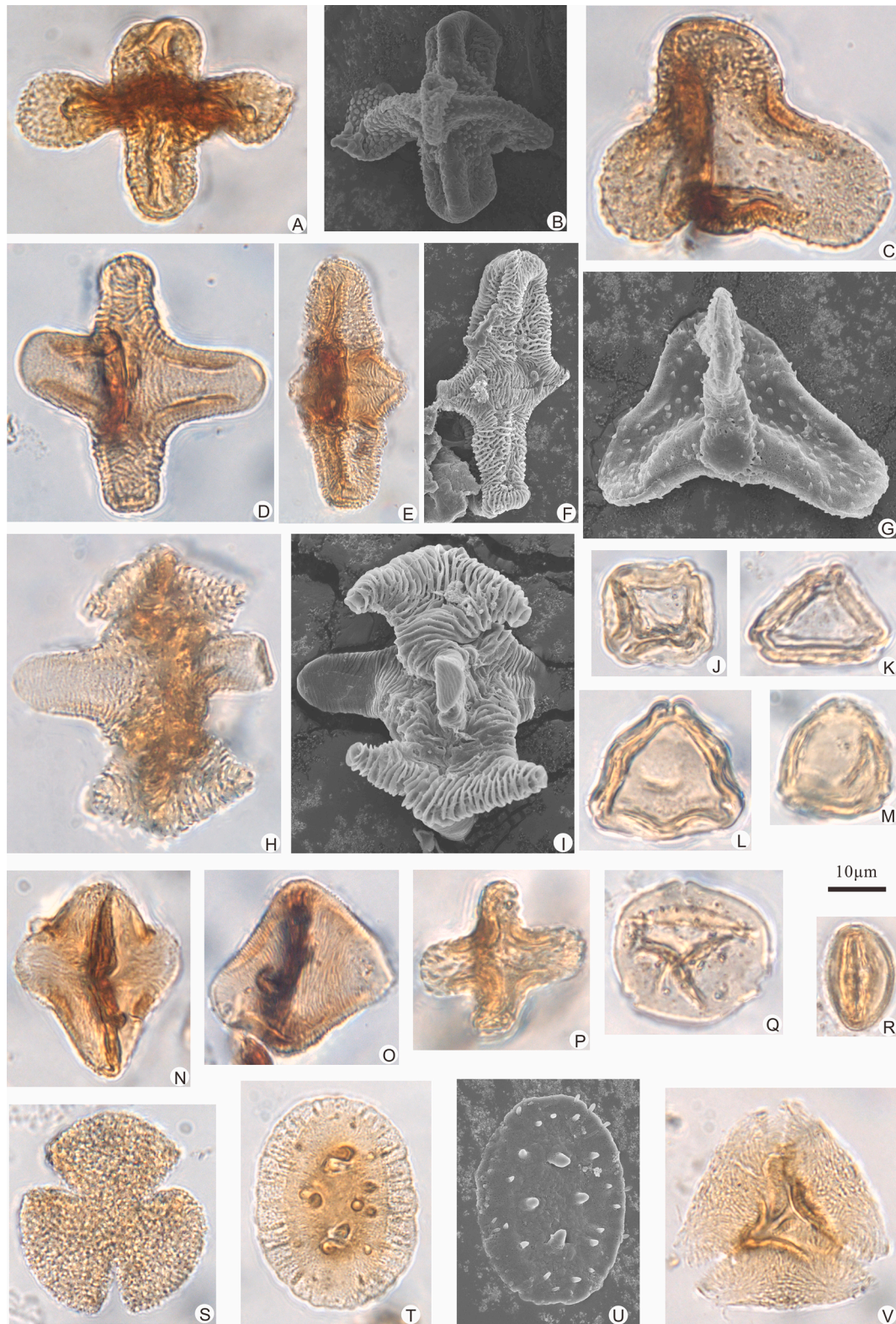


Fig. 4. Representative pollen from the Furao Formation in the XHY2008 borehole (with the numbers recording the sample-slides and England Finder coordinates).

Scale bar = 10 μ m (applicable to all specimens of the illustration).

A, B. *Aquilapollenites quadricretaceus* Chlonova 1961, A-Slide No. XHY2008-133-1/T40-4, B-SEM-Stub No. XHY2008-133; C, G. *Mancicorpus polaris* (Funkhouser) Stanley 1970, C-Slide No. XHY2008-152-1/M33-4, G-SEM-Stub No. XHY2008-133; D. *Aquilapollenites stelkii* Srivastava 1968, Slide No. XHY2008-143-1/H38-2; E, F. *Pseudointegricorpus clarireticulatus* (Samoilovitch) Takahashi and Shimono 1982, E-Slide No. XHY2008-133-1/U42-4, F-SEM-Stub No. XHY2008-133; H, I. *Pseudoaquilapollenites conatus* (Norton) Liu (1983), H-Slide No. XHY2008-129-1/I35-4, I-SEM-Stub No. XHY2008-133; J. *Ulmoideipites krempii* Anderson (1960), Slide No. XHY2008-142-1/E40-1; K. *Ulmoideipites tricostatus* Anderson (1960), Slide No. XHY2008-142-1/Q39-4; L. *Paraalnipollenites confusus* (Zakl.) Hills and Wallace 1969, Slide No. XHY2008-129-1/R39-1; M. *Betulaeipollenites bituitus* (Pot.) Potonie 1960, Slide No. XHY2008-150-1/S30-4; N.

(20,000 K pixels). Selected palynomorphs were observed with a SEM (JEOL JSM-6700F). Digital images were processed with Helicon Focus (7.0.2) and CorelDraw (2017) software. Amongst the 128 samples of the Wuyun Formation, twenty-four from the base of the formation contained palynomorphs, which enabled us to identify the K/Pg boundary. From the uppermost Furao Formation, thirty-three of fifty-five samples were productive, yielding 8089 identified grains of 85 genera and 207 species (see [Supplementary Appendix S1](#)). However, only twenty-four of these thirty-three samples containing >100 grains of pollen and spores were quantitatively analyzed. Stratigraphically-constrained cluster analysis was undertaken using the CONISS algorithm implemented in Tilia software (2.1.1). Principal components analysis (PCA) was carried out with CANOCO software ([Lepš and Šmilauer, 2003](#)) to transform the relative abundances of palynomorph taxa into environmental gradients, which facilitated the identification of the major climatic changes. A quantitative ecological analysis was applied based on the total number of species and individual specimens in each sample. According to their affinities, palynomorphs were classified into five climate zones and four humidity types, enabling the reconstruction of temperature and humidity over time. Collectively, these two methods provided reliable insights into the climatic changes during the latest Maastrichtian.

4. Results

4.1. Palynological assemblages

Three palynological assemblages were recognized according to their taxonomic compositions, in conjunction with variations in abundance and the CONISS results ([Figs 2–5](#)).

4.1.1. Gabonispuris–Pinuspollenites–Aquilapollenites assemblage

The *Gabonispuris–Pinuspollenites–Aquilapollenites* (GPA) palynological assemblage occurs in ten samples (XHY2008-152 to XHY2008-143), in the Furao Formation at depths of 25.10–24.20 m in the borehole. In total, 1536 grains were identified, which represent 61 genera and 114 species, including spores (20 genera and 35 species), gymnosperm pollen (18 genera and 34 species), and angiosperm pollen (23 genera and 45 species). The assemblage is dominated by angiosperm pollen, which comprised 22.56–67.38 % of the total grains in each sample, followed by spores (10.70–49.62 %) and gymnosperm pollen (10.19–27.82 %).

The spores consist of hepatophytes, mosses, lycophytes, and ferns, dominated by trilete spores, such as the ferns *Cyathidites* (0.37–18.80 %), *Leiotriletes* (1.07–11.29 %), and *Gabonispuris* (1.80–7.89 %). Other common spores include *Deltoidospora* (0–6.77 %), *Toroisporis* (0–4.84 %), and *Osmundacidites* (0–4.55 %). The dominant species are *Cyathidites minor* (0.37–17.29 %), *Gabonispuris vigourouxii* (1.80–7.89 %) ([Fig. 2D](#)), *Toroisporis minoris* (0–4.84 %), *Gleichenioidites senonicus* (0–3.70 %), *Foveosporites cenomanicus* (0–3.70 %), and *Deltoidospora microlepidoidites* (0–2.48 %). Monolet spores are represented by *Laevigatosporites* (0–3.76 %) of the Polypodiaceae. Given that the fern spores are not the dominant component in the palynological assemblage, but that the taxon *Gabonispuris* of Marsilaceae affinity is prominent, it was used as part of the name of the GPA assemblage.

The gymnosperm pollen is dominated by bisaccates, such as the conifers *Pinuspollenites* (0.83–10.00 %), *Podocarpidites* (0–5.26 %), and *Abiespollenites* (0.93–4.96 %), and the seed ferns *Alisporites* (1.20–6.35 %). Other commonly observed conifers include the aletes *Taxodiaceapollenites* (0–4.07 %), and bisaccates *Abietinaepollenites* (0–3.76 %) and *Cedripites* (0–2.63 %). The dominant gymnosperm species are the conifers *Pinuspollenites microinsignis* (0.83–8.18 %) ([Fig. 3B](#)) and *Taxodiaceapollenites hiatus* (0–4.07 %), and seed ferns *Alisporites bilateralis* (1.20–5.56 %). Other commonly occurring bisaccate conifers are *Podocarpidites minutus* (0–3.76 %), *Podocarpidites minisculus* (0–2.73 %), *Abietinaepollenites pactovae* (0–3.01 %), and *Abiespollenites editus* (0–2.38 %). The low proportion of monosulcate gymnosperms (i.e., *Monosulcites* [0–5.88 %] and *Ginkgocycadophytus* [0–2.67 %]), indicates a subordinate presence of Cycadales and Ginkgoales. The polyplicate pollen *Ephedripites* (0–0.60 %) is present, indicative of the presence of some Gnetidae. In general, *Pinuspollenites* is the most abundant among gymnosperms, which is a unique feature of the assemblage.

Angiosperm pollen is the most abundant component in the GPA palynological assemblage, comprising 22.56–67.38 % of the total grains. Amongst these, triprojectate pollen is dominant, and the main genera are *Aquilapollenites* (11.58–34.55 %), *Pseudoaquilapollenites* (0.83–28.70 %), and *Pseudointegricarpus* (0–16.30 %). Tricolporate *Xinjiangpollis* (0–7.27 %) and monocolpate *Marsypiletes* (0–6.45 %) are also relatively abundant. Other commonly occurring angiosperms include tricolpate *Tricolpites* (0–4.96 %) and *Tricolpopollenites* (0–4.28 %), and monocolpate *Monocolpopollenites* (0–3.74 %) and *Liliacidites* (0–2.96 %). The most abundant species are *Pseudoaquilapollenites conatus* (0–25.93 %), *Aquilapollenites stolkii* (1.20–19.83 %) ([Fig. 4D](#)), *Aquilapollenites absidatus* (2.26–14.97 %), *Aquilapollenites quadrilobus* (0.75–12.73 %), *Aquilapollenites quadricretaceus* (0.75–11.48 %), and *Pseudointegricarpus clarireticulatus* (0–16.30 %). Other frequently observed species are *Marsypiletes cretacea* (0–6.45 %), *Xinjiangpollis reticulatus* (0–5.45 %), *Tricolpites rugireticulatus* (0–4.96 %), and *Tricolpopollenites brevicolpatus* (0–2.67 %).

4.1.2. Laevigatosporites–Monocolpopollenites–Ulmoideipites assemblage

The *Laevigatosporites–Monocolpopollenites–Ulmoideipites* (LMU) palynological assemblage occurs in five samples (XHY2008-142 to 138), which are from the Furao Formation at depths of 24.10–23.70 m in the borehole. A total of 1227 grains were identified. They consist of 56 genera and 101 species, including spores (16 genera and 23 species), gymnosperm pollen (13 genera and 18 species), and angiosperm pollen (27 genera and 60 species). The assemblage is characterized by the dominance of angiosperm pollen, which comprise 52.07–83.85 % of the total grains in each sample, followed by spores (5.46–33.98 %) and gymnosperm pollen (3.11–15.70 %).

The spores consist of hepatophytes, mosses, lycophytes, and ferns, dominated by trilete spores, such as the ferns *Leiotriletes* (1.54–11.65 %), *Osmundacidites* (0–8.98 %), *Cyathidites* (0.62–8.26 %), *Deltoidospora* (0.34–2.48 %), *Gabonispuris* (0–2.91 %), and *Foveosporites* (0–3.31 %) of the Selaginellaceae. The dominant species are *Cyathidites minor* (0.62–6.80 %), *Foveosporites cenomanicus* (0–3.31 %), *Gabonispuris vigourouxii* (0–2.91 %), *Plicifera*

Aquilapollenites quadrilobus Rouse 1956, Slide No. XHY2008-129-1/R36-1; *O. Fibulapollis rombicus* (Samoil.) Stanley 1970, Slide No. XHY2008-133-1/D38-2; *P. Aquilapollenites attenuatus* Funkhouser 1961, Slide No. XHY2008-129-1/J38-3; *Q. Momipites triletipollenites* (Rouse) Nichols 1973, Slide No. XHY2008-142-1/O42-1; *R. Quercoidites yuqianensis* Sun 1989, Slide No. XHY2008-134-1/R39-3; *S. Tricolpites reticulatus* Cookson ex Couper 1953, Slide No. XHY2008-133-1/P38-2; *T. U. Wodehouseia spinata* Stanley 1961, T-Slide No. XHY2008-133-1/D41-4, U-SEM-Stub No. XHY2008-129; *V. Xinjiangpollis reticulatus* Wang, Sun et Zhao, 1990, Slide No. XHY2008-135-1/H40-3.

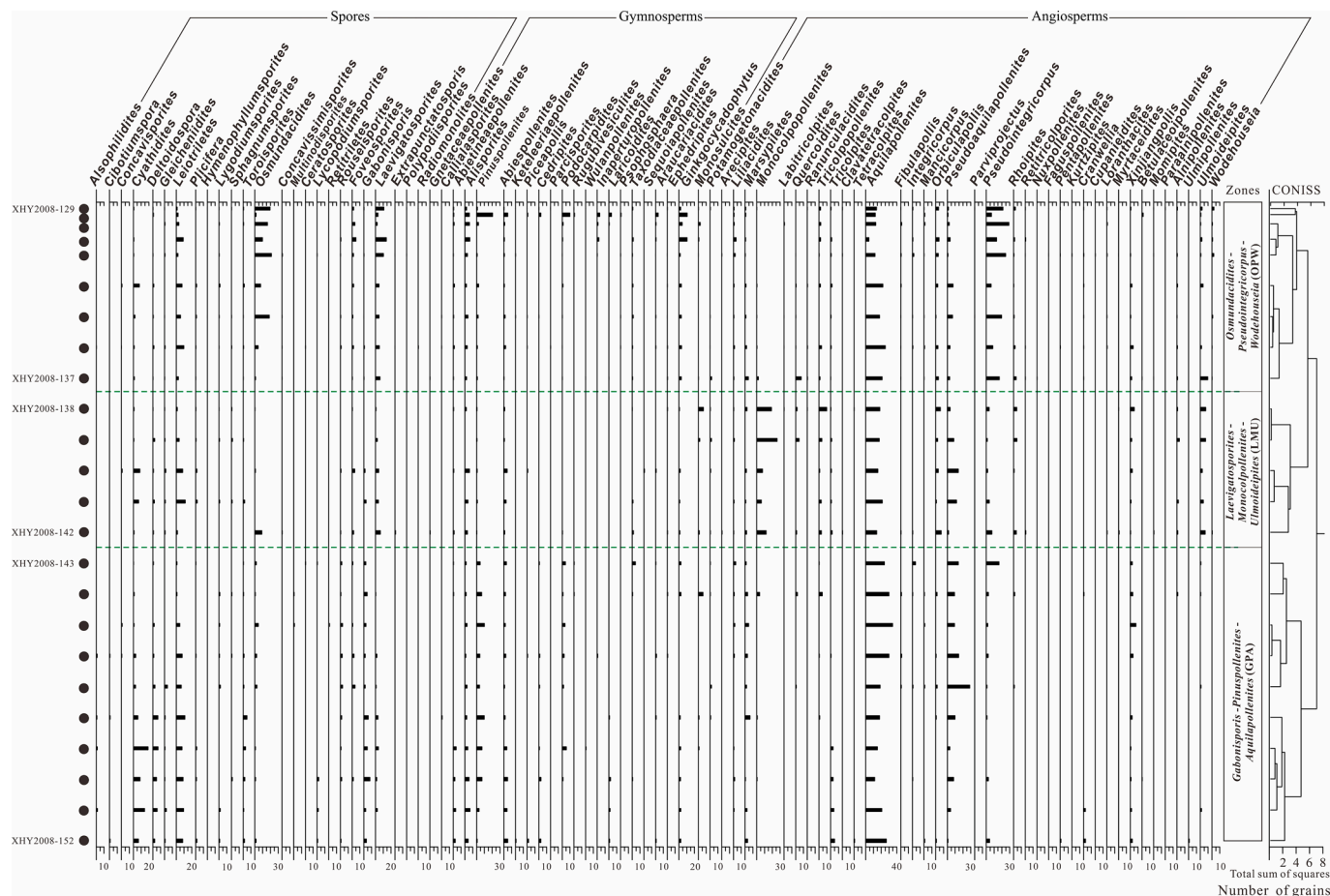


Fig. 5. Composition of the productive sample and palynological spectrum in the XHY2008 borehole in Jiayin, Heilongjiang, Northeast China.

delicata (0–1.94 %), *Toroisporis minoris* (0–1.94 %), *Deltoidospora microlepidoides* (0.34–1.94 %), and *Gleichenioides laetus* (0.17–1.65 %). Monolet spores are represented by *Laevigatosporites* (0.68–6.25 %) of the Polypodiaceae, which is dominated by *Laevigatosporites ovatus* (0–1.65 %) (Figs 2F, G). Given that the fern spores are secondary in the LMU assemblage, and the taxon *Laevigatosporites* of Polypodiaceae affinity is prominent in this palynological assemblage, it is used as part of the name of the LMU assemblage.

Gymnosperm pollen is represented mainly by the monosulcate *Monosulcites* (0–6.48 %), seed ferns *Alisporites* (0–5.79 %), and conifers *Abiespollenites* (0.62–4.13 %). The most abundant gymnosperms include the seed ferns *Alisporites bilateralis* (0–5.79 %) and alet conifers *Taxodiaceapollenites hiatus* (0–1.17 %). In addition, the monosulcate gymnosperm *Ginkgocycadophytus* (0–1.65 %) is indicative of a subordinate presence of Ginkgoales, and the polyplicates *Ephedripites* (0–0.39 %) and *Gnetaceapollenites* (0–0.39 %) are indicative of the presence of Gnetales.

The angiosperm pollen is predominantly triporate pollen, followed by monocolpate pollen. The dominant angiosperms are the monocolpate *Monocolpopollenites* (5.83–26.09 %), triporate *Aquilapollenites* (14.06–21.36 %), *Pseudoaquilapollenites* (1.56–14.05 %), *Pseudointegricarpus* (1.24–7.03 %), and *Orbiculapollis* (0.97–7.03 %), tricolpate *Tricolpopollenites* (0.83–9.90 %), and triporate *Ulmoidipites* (2.48–7.00 %). Common genera also include the tricolpate *Xinjiangpollis* (0.39–5.12 %), and *Rhoipites* (0–4.35 %), tricolpate *Quercoidites* (0–4.35 %), polyporate

Alnipollenites (0–3.11 %), and monocolpate *Marsypiletes* (0–2.39 %). The predominant species are *Monocolpopollenites* sp. (5.83–26.09 %) (Fig. 3M), *Pseudoaquilapollenites conatus* (0.78–12.40 %), *Aquilapollenites quadricretaceus* (1.37–11.57 %), *A. absidatus* (0.83–7.77 %), *A. quadrilobus* (1.65–7.34 %), *Pseudointegricarpus clarireticulatus* (1.24–7.03 %), *Tricolpopollenites brevicolpatus* (0–7.34 %), *Ulmoidipites krempii* (2.48–6.83 %) (Fig. 4J), and *Orbiculapollis lucidus* (0.97–6.25 %). Other common species include *Xinjiangpollis reticulatus* (0.39–4.10 %), *Quercoidites yuqianensis* (0–3.73 %), *Alnipollenites metaplasmus* (0–3.11 %), and *Marsypiletes cretacea* (0–2.39 %). Because the monocolpate *Monocolpopollenites* and triporate *Ulmoidipites* are relatively dominant, unlike in the GPA assemblage, they are used in the name of the LMU assemblage.

4.1.3. Osmundacidites–Pseudointegricarpus–Wodehouseia assemblage

The Osmundacidites–Pseudointegricarpus–Wodehouseia (OPW) palynological assemblage occurs in nine samples (XHY2008-137 to 129), which were collected from the Furao Formation at depths of 23.60–23.05 m in the borehole. A total of 5310 grains were identified. They consist of 79 genera and 184 species, including spores (22 genera and 49 species), gymnosperm pollen (21 genera and 42 species), and angiosperm pollen (36 genera and 93 species). The assemblage is characterized by the co-dominance of angiosperm pollen, which comprise 24.59–78.69 % of the total grains in each

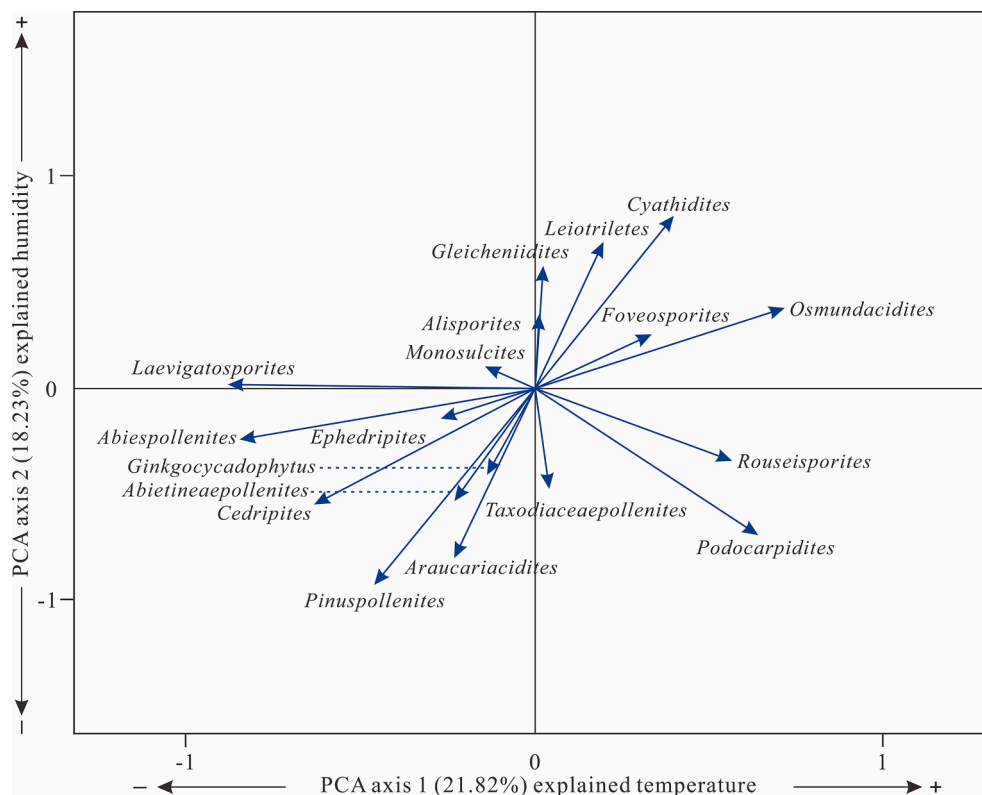


Fig. 6. Coordination plots of the main component analysis (PCA) showing the climate parameters in the XHY2008 borehole in Jiayin, Heilongjiang, Northeast China.

sample, and gymnosperm pollen (7.39–67.21 %), and a lower abundance of spores (8.20–38.89 %).

The spores consist of hepatophytes, mosses, lycophytes, and ferns, and are primarily trilete spores, followed by monolet spores. The main trilete spores include the ferns *Osmundacidites* (1.03–21.30 %), *Leiotriletes* (1.25–9.78 %), and *Cyathidites* (0–7.77 %). The dominant trilete species are *Cyathidites minor* (0–6.47 %) (Fig. 2A) and *Osmundacidites wellmanii* (0–3.21 %) (Figs 2L, N). Moreover, the trilete *Foveosporites cenomanicus* (0–4.86 %) of the Selaginellaceae (Fig. 2M) is common. Monolet spores are represented by *Laevigatosporites* (2.33–13.89 %) of the Polypodiaceae and dominated by *Laevigatosporites ovatus* (0.65–4.83 %). Although the fern spores are the third most abundant type in the assemblage, *Osmundacidites* is the dominant fern taxon and is prominent in the palynological assemblage, thus it is included as a part of the name of the OPW assemblage.

The gymnosperm pollen is mainly represented by bisaccates, such as the conifers *Pinuspollenites* (0–20.49 %), *Abiespollenites* (0.33–4.92 %), and *Podocarpidites* (0–9.84 %), and the seed ferns *Alisporites* (1.94–6.25 %), along with the aletes conifers *Araucariacidites* (0–3.28 %), *Inaperturopollenites* (0–3.28 %), and *Laricoidites* (0–3.28 %). The dominant gymnosperms are the conifers taxa such as *Pinuspollenites microinsignis* (0–11.48 %), *Pinuspollenites minutus* (0–4.10 %), *Podocarpidites ellipticus* (0–4.92 %) (Fig. 3A), *Podocarpidites minutus* (0–3.28 %), *Laricoidites magnus* (0–3.28 %), and *Araucariacidites australis* (0–3.28 %), and the seed ferns *Alisporites bilateralis* (2.06–6.25 %) (Fig. 3E). In addition, some monosulcate *Ginkgocycadophytus* (1.56–10.66 %) of Ginkgoales, and polylicates *Ephedripites* (0–0.37 %) and *Gnetaceapollenites* (0–0.17 %) of Gnetales are present.

The angiosperm pollen consists predominantly of triprojectacite pollen, including *Pseudointegricarpus* (6.15–29.07 %),

Aquilapollenites (4.17–25.12 %) and *Pseudoaquilapollenites* (0.78–7.12 %), and the triporate *Ulmoideipites* (0–9.45 %). Other common taxa include the triprojectacite *Orbiculapollis* (0–4.17 %), monocolpate *Marsypiletes* (0–4.12 %) and *Liliacidites* (0.69–3.47 %), tricolpate *Xinjiangpollis* (0–3.71 %) and *Rhoipites* (0–3.26 %), tricolpate *Tricolpopollenites* (0–3.22 %), and periporate *Wodehouseia* (0–2.50 %). The most abundant species are *Pseudointegricarpus clarireticulatus* (6.15–29.07 %) (Figs 4E, F), *Aquilapollenites quadricretaceus* (2.27–8.72 %) (Figs 4A, B), *Aquilapollenites absidatus* (0–7.19 %), *Aquilapollenites quadrilobus* (0–7.12 %) (Fig. 4N), *Ulmoideipites krempii* (0–8.59 %), and *Pseudoaquilapollenites conatus* (0.58–6.80 %) (Figs 4H, I). Other common species include *Quercoidites yuqianensis* (0–4.81 %), *Marsypiletes cretacea* (0–4.12 %) (Figs 3P, Q), *Orbiculapollis lucidus* (0–3.47 %) (Figs 3I, J), *Xinjiangpollis reticulatus* (0–3.34 %) (Fig. 4V), *Wodehouseia spinata* (0–2.41 %) (Figs 4T, U), and *Liliacidites cf. variegatus* (0–2.08 %). Given that the triprojectacite *Pseudointegricarpus* is dominant, and the periporate *Wodehouseia* is mainly present in this assemblage, the OPW assemblage is named after these two genera.

4.2. Paleoclimatic conditions

4.2.1. Principal component analysis

The PCA ordination diagram based on the relative abundance of spore and pollen genera show that axis 1 accounts for 21.82 % of the variance in the palynological data, axis 2 accounts for 18.23 % (Fig. 6). This indicates that the abundance of each genus in every sample is controlled mainly by the environmental/climatic factors represented by the two axes.

Axis 1 appears to represent the paleo-temperature. Spores, such as *Rouseisporites* (hepatophytes), *Foveosporites* (Selaginellaceae), *Leiotriletes* (Leptosporangiopsida), *Osmundacidites*

(Osmundaceae), *Gleicheniidites* (Gleicheniaceae), and *Cyathidites* (Cyatheaceae), and pollen represented by *Alisporites* (Corystospermales) and *Taxodiaceapollenites* (Taxodiaceae), might be related to warm environments (Balme, 1995; Wang et al., 2005; Li et al., 2020; Yang et al., 2025), and exhibit positive values. In contrast, the conifers (*Abiespollenites*, *Cedripites*, *Pinuspollenites*, *Abietinaepollenites*, and *Araucariacidites*), Ginkgoales (*Ginkgocycadophytus*) and Gnetales (*Ephedripites*) pollen, which are commonly found in temperate zones (Wang et al., 2005; Li et al., 2020), tend to have negative values.

Axis 2 appears to be related to the humidity. Spores of *Foveosporites* (Selaginellaceae), *Leiotriletes* (Leptosporangiopsida), *Osmundacidites* (Osmundaceae), *Gleicheniidites* (Gleicheniaceae), and *Cyathidites* (Cyatheaceae), and pollen of *Monosulcites* (Cycadales) and *Alisporites* (Corystospermales), which thrive in humid environments (Dettmann, 1963; Boulter and Windle, 1993; Jin et al., 2020; Li et al., 2020; Yang et al., 2025; Zhang et al., 2025), tend to have positive values. In contrast, the xerophytic plants such as *Ephedripites* of the Gnetales and *Ginkgocycadophytus* of the Ginkgoales, as well as the mesophytic genera, including the conifers *Abiespollenites*, *Cedripites*, *Pinuspollenites*, *Abietinaepollenites*, *Araucariacidites*, *Podocarpidites*, and *Taxodiaceapollenites*,

which are adapted to arid or subhumid conditions (Balme, 1995; Gao et al., 1999; Bonis and Kürschner, 2012; Jin et al., 2020), might tend to have negative values.

The scores on axis 1 (temperature) were predominantly negative for the GPA assemblage, and became positive for the LMU and OPW assemblages. A distinct change to negative values occurred in the uppermost OPW assemblage (Fig. 7A). This might indicate a warming trend from the GPA assemblage through to the LMU and OPW assemblages, followed by a notable cooling at the end of the OPW assemblage.

The scores on axis 2 (humidity) exhibited two cycles (Fig. 8A). The first started with positive values in the lower part of the GPA assemblage, decreased in the middle, and became negative in the upper part. The other cycle included the LMU and OPW assemblages, with the axis 2 scores being highly positive in the lower part of the LMU assemblage, then decreasing gradually, and becoming negative in the upper part of the GPA assemblage.

4.2.2. Temperature analysis

Quantitative analyses were conducted on 24 palynological samples from the XHY2008 borehole, each of which yielded >100 grains of identifiable pollen and spores. Based on previous studies

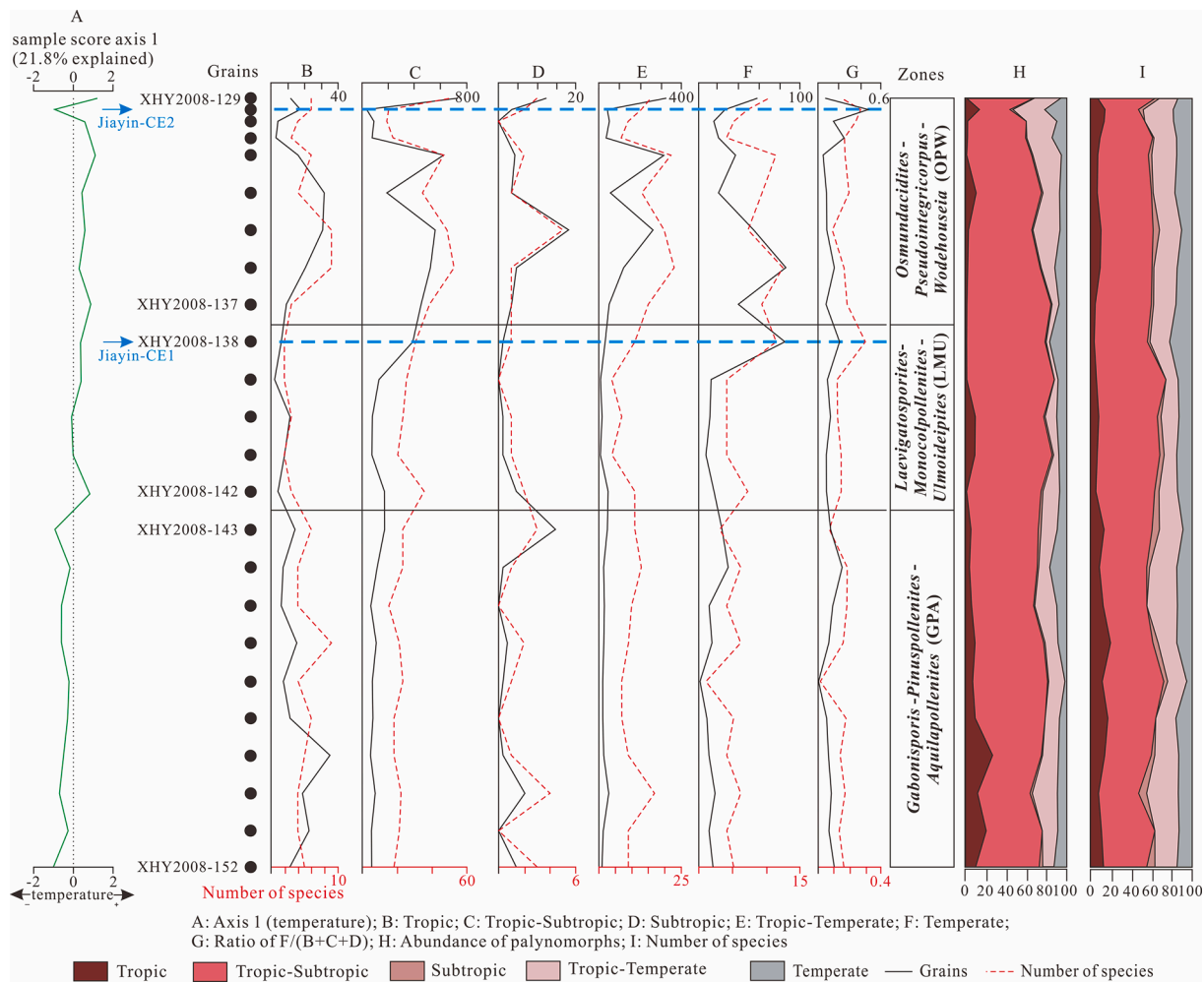


Fig. 7. Reconstructed temperature parameters based on the diversity and abundance of palynomorphs in the XHY2008 borehole in Jiayin, Heilongjiang, Northeast China. A. The scores on temperature curve of the PCA analysis; B. The distribution curve of the tropical taxa; C. The distribution curve of the tropical-subtropical taxa; D. The distribution curve of the subtropical taxa; E. The distribution curve of the tropical-temperate taxa; F. The distribution curve of the temperate taxa; G. The distribution curve of the ratio of temperate/(tropical + tropical-subtropical + subtropical); H. Composition of abundance of palynomorphs; I. Composition of species of palynomorphs.

(Srivastava, 1970; Jarzen and Norris, 1975; Jarzen, 1977; Balme, 1995; Gao et al., 1999; Song et al., 1999, 2000; Zhong et al., 2003; Abbink et al., 2004; Wang et al., 2005; Traverse, 2007; Jin et al., 2020; Li et al., 2020; Zhang et al., 2025), the botanical affinities, climatic zones, and humidity conditions of the palynological taxa were reconstructed for the XHY2008 borehole (Table 2).

In the 24 samples, the tropical taxa comprised 3.23–18.75 % of the total species and 0.92–25.56 % of the total grains in each sample, and the subtropical taxa comprised 0–7.55 % of the species and 0–4.81 % of the total grains. Tropical–subtropical taxa were the most dominant, comprising 34.88–64.10 % of the species and 28.69–82.61 % of the grains. The temperate taxa (2.78–17.74 % of the species; 0.93–21.31 % of the grains) were less abundant. The tropic–temperate taxa comprised 10.26–32.08 % of the species and 4.97–33.61 % of the grains (Table 3; Fig. 7).

The GPA assemblage was dominated by tropical–subtropical taxa (41.51–63.89 % of the species; 48.87–74.07 % of the grains), with subordinate tropic–temperate (18.75–32.08 % of the species; 12.30–25.26 % of the grains), tropical (7.55–18.75 % of the species;

3.74–25.56 % of the grains), and temperate (2.78–13.51 % of the species; 0.93–15.51 % of the grains) taxa. The subtropical taxa (0–7.55 % of the species; 0–4.81 % of the grains) were relatively scarce.

The LMU assemblage was dominated by tropical–subtropical taxa (48.39–64.10 % of the species; 66.94–82.61 % of the grains), and also contained some temperate (10.26–17.74 % of the species; 5.86–14.51 % of the grains) and tropic–temperate (10.26–17.95 % of the species; 4.97–17.58 % of the grains) taxa. An obvious change occurred at the end of the LMU assemblage, where the temperate taxa reached a maximum abundance (17.74 % of the species; 14.51 % of the grains) and the tropical–subtropical taxa dropped to a minimum (48.39 % of the species).

The OPW assemblage was dominated by tropical–subtropical taxa (34.88–54.29 % of the species; 28.69–81.10 % of the grains), with an increased proportion of tropic–temperate taxa (17.02–30.23 % of the species; 8.59–33.61 % of the grains). The temperate (7.78–16.28 % of the species; 3.60–21.31 % of the grains), tropical (4.29–13.95 % of the species; 0.92–13.93 % of the grains), and subtropical (0–5.56 % of the species; 0–2.46 % of the grains)

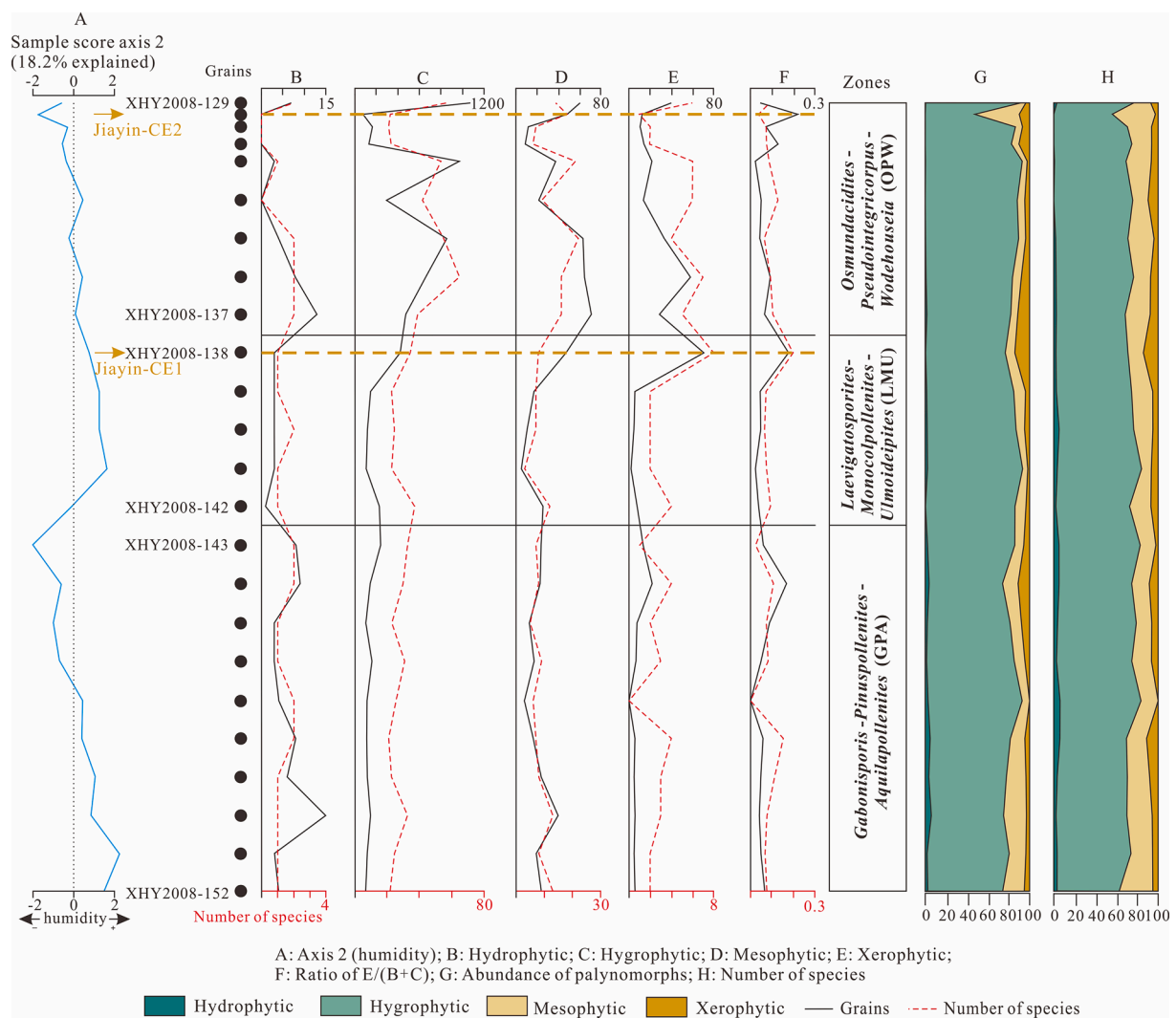


Fig. 8. Reconstructed humidity parameters based on the diversity and abundance of palynomorphs in the XHY2008 borehole in Jiayin, Heilongjiang, Northeast China. A. The scores on humidity curve of the PCA analysis; B. The distribution curve of the hydrophytic taxa; C. The distribution curve of the hygrophytic taxa; D. The distribution curve of the mesophytic taxa; E. The distribution curve of the xerophytic taxa; F. The distribution curve of the ratio of xerophytic/(hydrophytic + hygrophytic); G. Composition of abundance of palynomorphs; H. Composition of species of palynomorphs.

Table 2

Botanical affinities, humidity, and climate zone of dispersed palynofloras from the XHY2008 borehole in Jiayin, Heilongjiang, Northeast China.

Taxon	Botanical affinity	Humidity	Climatic Zone	References
<i>Rouseisporites</i>	Hepatophyta: Ricciaceae	Hygrophytic	Tropic–Temperate	Song (1986); Yang et al. (2007)
<i>Sphagnumsporites</i>	Bryophyta: Sphagnaceae	Hygrophytic	Tropic–Temperate	Raine et al. (2011); Li et al. (2020); Li et al. (2022)
<i>Lycopodiumsporites</i>	Lycophyta: Lycopodiaceae	Hygrophytic	Tropic–Temperate	Song et al. (2000); Zhang (2023)
<i>Retitritiles</i>	Lycophyta: Lycopodiaceae	Hygrophytic	Tropic–Temperate	Balme (1995); Abbink et al. (2004)
<i>Ceratosporites</i>	Lycophyta: Selaginellaceae	Hygrophytic	Tropic–Temperate	Cookson and Dettmann (1958); Lin (2020)
<i>Foveosporites</i>	Lycophyta: Selaginellaceae	Hygrophytic	Tropic–Temperate	Balme (1995); Zhang (2023)
<i>Osmundacidites</i>	Pteridophyta: Osmundaceae	Hygrophytic	Tropic–Temperate	Balme (1995); Li et al. (2020), 2022
<i>Concavisorites</i>	Pteridophyta: Dipteridaceae	Hygrophytic	Tropic–Subtropic	Van Konijnenburg-Van Cittert (1993); Li et al. (2020)
<i>Cibotiumspora</i>	Pteridophyta: Dicksoniaceae	Hygrophytic	Tropic	Filatoff (1975); Balme (1995); Li et al. (2020)
<i>Alsophilidites</i>	Pteridophyta: Cyatheaceae	Hygrophytic	Tropic	Song et al. (2000)
<i>Cyathidites</i>	Pteridophyta: Cyatheaceae	Hygrophytic	Tropic	Balme (1995); Wang et al. (2005); Li et al. (2020), 2022
<i>Deltoidospora</i>	Pteridophyta: Cyatheaceae	Hygrophytic	Tropic–Subtropic	Balme (1995); Abbink et al. (2004); Jin et al. (2020); Li et al. (2022)
<i>Gleicheniidites</i>	Pteridophyta: Gleicheniaceae	Hygrophytic	Tropic–Subtropic	Dettmann (1963); Boulter and Windle (1993); Jin et al. (2020)
<i>Plicifera</i>	Pteridophyta: Gleicheniaceae	Hygrophytic	Tropic–Subtropic	Song et al. (1999); Li et al. (2020)
<i>Leiotritiles</i>	Pteridophyta: Leptosporangiopsida	Hygrophytic	Tropic–Subtropic	Gao et al. (1999); Jin et al. (2020); Yang et al. (2025)
<i>Hymenophyllumsporites</i>	Pteridophyta: Hymenophyllaceae	Hygrophytic	Tropic–Subtropic	Song et al. (1999); Zhang (2023)
<i>Lygodiumsporites</i>	Pteridophyta: Lygodiaceae	Hygrophytic	Tropic	Song et al. (2000); Zhang et al. (2014); Jin et al. (2020)
<i>Toroisporis</i>	Pteridophyta: Lygodiaceae	Hygrophytic	Tropic–Subtropic	Song et al. (2000); Li et al. (2020)
<i>Concavissimisporites</i>	Pteridophyta: Lygodiaceae	Hygrophytic	Tropic	Song et al. (2000); Zhang (2023)
<i>Multinodisporites</i>	Pteridophyta: Pteridaceae	Hygrophytic	Tropic–Temperate	Song et al. (1999); Zhang (2023)
<i>Laevigatosporites</i>	Pteridophyta: Polypodiaceae	Hygrophytic	Tropic–Temperate	Song (1986); Balme (1995); Li et al. (2022); Yang et al. (2025)
<i>Extrapunctatosporis</i>	Pteridophyta: Polypodiaceae	Hygrophytic	Tropic–Temperate	Song et al. (1999); Yang et al. (2025)
<i>Polypodiisporites</i>	Pteridophyta: Polypodiaceae	Hygrophytic	Tropic–Temperate	Song et al. (1999); Yang et al. (2025)
<i>Radiomonolites</i>	Pteridophyta: Filicales	Hygrophytic	Tropic–Temperate	Song et al. (1999)
<i>Gabonisporis</i>	Pteridophyta: Marsilaceae?	Hydrophytic	Tropic–Subtropic	Song et al. (1999); Lin (2020)
<i>Alisporites</i>	Pteridospermophytes: Corystospermales	Hygrophytic	Tropic–Temperate	Balme (1995); Lin and Li (2018); Li et al. (2022)
<i>Inaperturopollenites</i>	Coniferophyta: Taxodiaceae	Mesophytic	Temperate	Balme (1995); Zhong et al., 2003; Jin et al. (2020)
<i>Taxodiaceapollenites</i>	Coniferophyta: Taxodiaceae	Hygrophytic	Subtropic	Zhong et al. (2003); Jin et al. (2020); Li et al. (2022); Yang et al. (2025)
<i>Sequoiapollenites</i>	Coniferophyta: Taxodiaceae	Hygrophytic	Subtropic	Song et al. (1999); Li et al. (2022)
<i>Abietinaepollenites</i>	Coniferophyta: Pinaceae	Mesophytic	Tropic–Temperate	Balme (1995); Song et al. (2000); Zhong et al. (2003); Lin (2020)
<i>Pinuspollenites</i>	Coniferophyta: Pinaceae	Mesophytic	Tropic–Temperate	Balme (1995); Zhong et al. (2003); Li et al. (2022); Yang et al. (2025)
<i>Abiespollenites</i>	Coniferophyta: Pinaceae	Mesophytic	Temperate	Song (1986); Li et al. (2022); Yang et al. (2025)
<i>Keteleeriaepollenites</i>	Coniferophyta: Pinaceae	Mesophytic	Subtropic	Gao et al. (1999)
<i>Piceapollis</i>	Coniferophyta: Pinaceae	Mesophytic	Temperate	Ji (1994); Song et al. (2000); Li et al. (2022)
<i>Cedripites</i>	Coniferophyta: Pinaceae	Mesophytic	Subtropic	Balme (1995); Li et al. (2022)
<i>Wulanpollenites</i>	Coniferophyta: Pinaceae	Mesophytic	Tropic–Temperate	Song et al. (2000); Li et al. (2022)
<i>Laricoidites</i>	Coniferophyta: Pinaceae	Mesophytic	Tropic–Temperate	Jin et al. (2020); Li et al. (2022)
<i>Parcisporites</i>	Coniferophyta: Podocarpaceae	Mesophytic	Tropic	Gao et al. (1999); Song et al. (2000); Lin (2020); Li et al. (2022)
<i>Podocarpidites</i>	Coniferophyta: Podocarpaceae	Hygrophytic	Tropic	Song (1986); Zhong et al. (2003); Lin (2020); Li et al. (2022)
<i>Rugubivesiculites</i>	Coniferophyta: Podocarpaceae	Mesophytic	Tropic	Song et al. (2000); Lin (2020); Li et al. (2022)
<i>Callialasporites</i>	Coniferophyta: Araucariaceae	Mesophytic	Tropic	Jin et al. (2020)
<i>Psophosphaera</i>	Coniferophyta: Araucariaceae	Mesophytic	Tropic–Temperate	Ji (1994); Zhong et al. (2003); Lin (2020); Li et al. (2022)
<i>Araucariacidites</i>	Coniferophyta: Araucariaceae	Mesophytic	Tropic–Subtropic	Dettmann, 1986; Balme (1995); Li et al. (2022)
<i>Gnetaceapollenites</i>	Gnetales	Hygrophytic	Tropic–Subtropic	Lin (2020); Hofmann et al. (2022)
<i>Ephedripites</i>	Ephedraceae	Xerophytic	Temperate	Balme (1995); Gao et al. (1999); Bonis and Kürschner (2012)
<i>Ginkgocycadophytus</i>	Ginkgophyta: Ginkgoales	Xerophytic	Temperate	Li et al. (2020)
<i>Monosulcites</i>	Cycadophyta: Cycadales	Xerophytic	Temperate	Balme (1995); Song et al. (1999); Wang et al. (2005); Jin et al. (2020)
<i>Potamogetonacidites</i>	Potamogetonaceae	Hydrophytic	Tropic–Temperate	Song et al. (1999); Han (2020)
<i>Arecipites</i>	Palmae	Hydrophytic	Tropic–Subtropic	Gao et al. (1999); Song et al. (1999)
<i>Monocolpopollenites</i>	Palmae	Hydrophytic	Tropic–Subtropic	Gao et al. (1999); Song et al. (1999)
<i>Liliacidites</i>	Liliaceae	Hydrophytic	Tropic–Temperate	Jarzen and Norris (1975); Gao et al. (1999); Song et al. (1999)
<i>Marsypiletes</i>	Undetermined	Undetermined	Undetermined	
<i>Ranunculacidites</i>	Ranunculaceae	Hydrophytic	Tropic–Temperate	Song et al. (1999)
<i>Labiaticolpites</i>	Labiatae	Hydrophytic	Tropic–Subtropic	Song et al. (1999)
<i>Quercoidites</i>	Fagaceae	Mesophytic	Tropic–Subtropic	Gao et al. (1999); Song et al. (1999)
<i>Tricolpites</i>	Hamamelidaceae	Mesophytic	Tropic–Subtropic	Gao et al. (1999)
<i>Tricolpopollenites</i>	Platanaceae	Undetermined	Undetermined	Song et al. (1999)
<i>Clavatetracolpites</i>	Undetermined	Undetermined	Undetermined	

Table 2 (continued)

Taxon	Botanical affinity	Humidity	Climatic Zone	References
<i>Tetracolpites</i>	Undetermined	Undetermined	Undetermined	
<i>Aquilapollenites</i>	Santalaceae?	Hygrophytic	Tropic–Subtropic	Jarzen and Norris (1975); Gao et al. (1999)
<i>Fibulapollis</i>	Santalaceae?	Hygrophytic	Tropic–Subtropic	Jarzen and Norris (1975); Gao et al. (1999)
<i>Integricarpus</i>	Santalaceae?	Hygrophytic	Tropic–Subtropic	Jarzen and Norris (1975); Gao et al. (1999)
<i>Mancicarpus</i>	Santalaceae?	Hygrophytic	Tropic–Subtropic	Jarzen and Norris (1975); Gao et al. (1999)
<i>Orbiculapollis</i>	Santalaceae?	Hygrophytic	Tropic–Subtropic	Jarzen and Norris (1975); Gao et al. (1999)
<i>Pseudoaquilapollenites</i>	Santalaceae?	Hygrophytic	Tropic–Subtropic	Jarzen and Norris (1975); Gao et al. (1999)
<i>Parviprojectus</i>	Santalaceae?	Hygrophytic	Tropic–Subtropic	Jarzen and Norris (1975); Gao et al. (1999)
<i>Pseudointegricarpus</i>	Santalaceae?	Hygrophytic	Tropic–Subtropic	Jarzen and Norris (1975); Gao et al. (1999)
<i>Rhoipites</i>	Anacardiaceae	Mesophytic	Tropic–Subtropic	Jarzen and Norris (1975); Gao et al. (1999); Song et al. (1999)
<i>Nuxpollenites</i>	Loranthaceae	Hygrophytic	Tropic–Temperate	Song et al. (1999)
<i>Faguspollenites</i>	Fagaceae	Hygrophytic	Tropic–Temperate	Jarzen and Norris (1975); Gao et al. (1999); Song et al. (1999)
<i>Pentapollenites</i>	Undetermined	Undetermined	Undetermined	
<i>Kurtzipites</i>	Undetermined	Undetermined	Undetermined	
<i>Cranwellia</i>	Loranthaceae	Hygrophytic	Tropic–Subtropic	Jarzen and Norris (1975); Gao et al. (1999); Song et al. (1999)
<i>Cupanieidites</i>	Sapindaceae	Hygrophytic	Tropic–Subtropic	Jarzen and Norris (1975); Gao et al. (1999); Song et al. (1999)
<i>Loranthacites</i>	Loranthaceae	Hygrophytic	Tropic–Subtropic	Jarzen and Norris (1975); Gao et al. (1999); Song et al. (1999)
<i>Myrtaceidites</i>	Myrtaceae	Hygrophytic	Tropic–Temperate	Gao et al. (1999); Song et al. (1999)
<i>Xinjiangpollis</i>	Undetermined	Xerophytic	Temperate	Yu (1981)
<i>Momipites</i>	Juglandaceae	Mesophytic	Temperate	Jarzen and Norris (1975); Gao et al. (1999); Song et al. (1999)
<i>Betulaceoipollenites</i>	Betulaceae	Mesophytic	Temperate	Jarzen and Norris (1975); Gao et al. (1999); Song et al. (1999)
<i>Paraalnipollenites</i>	Betulaceae	Mesophytic	Temperate	Jarzen and Norris (1975); Gao et al. (1999); Song et al. (1999)
<i>Alnipollenites</i>	Betulaceae	Mesophytic	Temperate	Jarzen and Norris (1975); Gao et al. (1999); Song et al. (1999)
<i>Ulmipollenites</i>	Ulmaceae	Mesophytic	Tropic–Temperate	Gao et al. (1999); Song et al. (1999)
<i>Ulmoideipites</i>	Ulmaceae	Mesophytic	Temperate	Gao et al. (1999); Song et al. (1999)
<i>Wodehouseia</i>	Undetermined	Undetermined	Undetermined	

taxa had a uniform abundance. An anomalous event was recorded in the uppermost OPW assemblage, with a large increase in the temperate taxa (16.28 % of the species; 21.31 % of the grains) and decrease in the tropical–subtropical taxa (34.88 % of the species; 28.69 % of the grains).

4.2.3. Humidity analysis

In terms of humidity, hydrophytic, hygrophytic, mesophytic, and xerophytic habitats were determined quantitatively for the 24 palynological samples from the XHY2008 borehole (Table 4).

The hydrophytic taxa, including the aquatic fern spores of the Marsiliaceae family (*Gabonispors*) and aquatic angiosperm pollen of the Potamogetonaceae family (*Potamogetonacidites*) (Zhou et al., 2023) accounted for 0–5.56 % of the total species and 0–7.89 % of the total grains in each sample. The hygrophytic taxa, including Hepaticae, Bryopsida, Lycopodiales, ferns, Liliales, and Santalales, were dominant (55.81–77.78 % of the species; 47.54–92.90 % of the grains). The mesophytic plants, such as Pinaceae, Araucariaceae, Anacardiaceae, and Juglandaceae, accounted for 9.09–41.86 % of the species and 3.79–41.80 % of the grains. The xerophytic types were rare or absent, ranging from 0 to 12.90 % of the species and 0–12.63 % of the grains (Fig. 8).

The GPA assemblage was dominated by hygrophytic plants (57.14–77.78 % of the species; 65.78–88.89 % of the grains), while the mesophytes were a secondary component (14.89–30.95 % of the species; 7.41–22.11 % of the grains). The hydrophytic and xerophytic types were minor constituents.

The LMU assemblage was also dominated by hygrophytic plants (61.29–75.76 % of the species; 68.09–87.38 % of the grains), and also contained mesophytes (9.09–19.05 % of the species; 4.85–11.18 % of

the grains) and xerophytes (5.13–12.90 % of the species; 1.94–12.63 % of the grains). An obvious change occurred at the end of the LMU assemblage, which was marked by a large increase in xerophytes (12.90 % of the species; 12.63 % of the grains) and abrupt decrease in the hygrophytes (61.29 % of the species; 68.09 % of the grains).

In the OPW assemblage, the hygrophytic types remained dominant (55.81–71.43 % of the species; 47.54–92.90 % of the grains), and the mesophyte abundance (14.29–41.86 % of the species; 3.79–41.80 % of the grains) increased significantly. The xerophyte (2.33–9.52 % of the species; 2.24–11.11 % of the grains) and hydrophyte (0–2.86 % of the species; 0–2.23 % of the grains) abundances were near-constant. A change also occurred in the uppermost OPW assemblage, with a distinct increase in the mesophytes (41.86 % of the species; 41.80 % of the grains) and a decrease in the hygrophytes (55.81 of the species; 47.54 of the grains).

5. Discussion

5.1. Comparison of the palynological assemblages in Jiayin

Palynological investigations of the Maastrichtian deposits in the Jiayin area have been ongoing since 1983 (Liu, 1983, 1990; Markevich et al., 2011; Sun et al., 2011, 2014). Liu (1983) reported an *Aquilapollenites spinulosus*–*Betulaceoipollenites* (AB) assemblage from the upper part of the Furao Formation, assigning it a Danian or latest Maastrichtian to Danian age. This assemblage was based on 12 samples collected from two profiles (Nanshan P14 and Baishantou P15) and four outcrops (BH5043, BH5044, BH5045,

Table 3
Quantitative analysis of the climatic zones of palynological taxa in the XHY2008 borehole in Jiayin of Heilongjiang, Northeast China.

Sample	Palynological Zone	Species(%)						Grains(%)					
		Tropic	Tropic–Subtropic	Subtropic	Temperate	Tropic–Temperate	Undetermined	Tropic	Tropic–Subtropic	Subtropic	Temperate	Tropic–Temperate	Undetermined
129	OPW	6.38	53.19	3.19	10.64	17.02	9.57	0.92	63.78	0.92	4.83	27.06	2.50
130		13.95	34.88	4.65	16.28	30.23	0.00	13.93	28.69	2.46	21.31	33.61	0.00
131		11.43	40.00	0.00	14.29	25.71	8.57	2.33	55.23	0.00	8.72	30.81	2.91
132		8.33	50.00	2.78	11.11	19.44	8.33	2.08	54.86	1.39	13.89	25.00	2.78
133		6.52	50.00	2.17	11.96	23.91	5.43	1.56	63.42	0.39	3.60	30.25	0.78
134		6.35	53.97	1.59	14.29	19.05	4.76	10.03	63.43	0.97	6.80	16.83	1.94
135		10.00	53.33	5.56	7.78	22.22	1.11	3.18	61.55	1.69	5.72	27.75	0.11
136	LMU	8.49	49.06	0.94	11.32	21.70	8.49	2.48	67.57	0.50	10.64	14.85	3.96
137		4.29	54.29	1.43	12.86	21.43	5.71	1.55	81.10	0.52	6.70	8.59	1.55
138		3.23	48.39	1.61	17.74	17.74	11.29	1.02	68.94	0.17	14.51	5.12	10.24
139		5.13	64.10	0.00	10.26	10.26	10.26	1.24	82.61	0.00	7.45	4.97	3.73
140		7.69	58.97	2.56	10.26	17.95	2.56	9.09	66.94	0.83	9.09	13.22	0.83
141		6.06	60.61	3.03	12.12	12.12	6.06	7.77	74.76	0.97	6.80	6.80	2.91
142		4.76	55.56	3.17	11.11	17.46	7.94	1.56	69.14	1.56	5.86	17.58	4.30
143	GPA	12.77	48.94	6.38	6.38	23.40	2.13	5.19	65.93	4.81	8.52	15.19	0.37
144		7.84	45.10	1.96	11.76	25.49	7.84	3.74	63.64	0.53	15.51	12.30	4.28
145		12.12	45.45	0.00	12.12	30.30	0.00	5.45	60.91	0.00	9.09	24.55	0.00
146		18.75	43.75	4.17	12.50	18.75	2.08	8.98	67.07	1.20	7.78	14.37	0.60
147		11.11	63.89	2.78	2.78	19.44	0.00	6.48	74.07	0.93	0.93	17.59	0.00
148		16.22	48.65	0.00	13.51	18.92	2.70	8.87	68.55	0.00	6.45	15.32	0.81
149		13.51	48.65	2.70	10.81	24.32	0.00	25.56	48.87	0.75	7.52	17.29	0.00
150		7.55	41.51	7.55	11.32	32.08	0.00	9.47	53.68	3.16	8.42	25.26	0.00
151		10.53	55.26	0.00	10.53	23.68	0.00	17.46	57.94	0.00	7.94	16.67	0.00
152		11.90	42.86	7.14	11.90	21.43	4.76	9.09	61.98	3.31	11.57	12.40	1.65

Table 4

Quantitative analysis of the living habitats of palynological taxa in the XHY2008 borehole in Jiayin of Heilongjiang, Northeast China.

Sample	Palynological Zone	Species(%)					Grains(%)				
		Hydrophytic	Hygrophytic	Mesophytic	Xerophytic	Undetermined	Hydrophytic	Hygrophytic	Mesophytic	Xerophytic	Undetermined
129	OPW	2.13	67.02	14.89	6.38	9.57	0.58	88.09	5.33	3.50	2.50
130		0.00	55.81	41.86	2.33	0.00	0.00	47.54	41.80	10.66	0.00
131		0.00	65.71	20.00	5.71	8.57	0.00	83.72	6.98	6.40	2.91
132		0.00	69.44	16.67	5.56	8.33	0.00	79.86	6.25	11.11	2.78
133		1.09	64.13	22.83	6.52	5.43	0.29	92.90	3.79	2.24	0.78
134	LMU	0.00	71.43	14.29	9.52	4.76	0.00	85.44	7.44	5.18	1.94
135		2.22	67.78	24.44	4.44	1.11	0.42	88.67	7.10	3.71	0.11
136		1.89	67.92	15.09	6.60	8.49	0.99	79.08	8.42	7.55	3.96
137		2.86	61.43	22.86	7.14	5.71	2.23	78.18	12.89	5.15	1.55
138		1.61	61.29	12.90	12.90	11.29	0.51	68.09	8.53	12.63	10.24
139	GPA	2.56	64.10	17.95	5.13	10.26	1.86	79.50	11.18	3.73	3.73
140		5.13	69.23	17.95	5.13	2.56	2.48	83.47	9.09	4.13	0.83
141		3.03	75.76	9.09	6.06	6.06	2.91	87.38	4.85	1.94	2.91
142		1.59	65.08	19.05	6.35	7.94	0.39	81.64	10.55	3.13	4.30
143		4.26	76.60	14.89	2.13	2.13	2.96	82.22	9.26	5.19	0.37
144		3.92	64.71	15.69	7.84	7.84	4.81	65.78	12.83	12.30	4.28
145		3.03	75.76	15.15	6.06	0.00	2.73	78.18	11.82	7.27	0.00
146		2.08	70.83	18.75	6.25	2.08	1.80	82.63	10.78	4.19	0.60
147		5.56	77.78	16.67	0.00	0.00	3.70	88.89	7.41	0.00	0.00
148		5.41	62.16	18.92	10.81	2.70	6.45	74.19	13.71	4.84	0.81
149		2.70	67.57	21.62	8.11	0.00	4.51	72.93	18.80	3.76	0.00
150		1.89	67.92	24.53	5.66	0.00	7.89	66.84	22.11	3.16	0.00
151		2.63	71.05	21.05	5.26	0.00	2.38	77.78	15.87	3.97	0.00
152		2.38	57.14	30.95	4.76	4.76	3.31	69.42	20.66	4.96	1.65

and BH5047). It included 77 genera and 92 species, and was dominated by angiosperms (18.10–84.70 % of the total grains) and gymnosperms (10.30–77.90 % of the total grains). The angiosperms were primarily represented by triporate pollen, which constituted an average of 30.80 % of the total grains. Common genera were *Triporopollenites* (0–18.30 %), *Paraalnipollenites* (0–9.30 %), *Caryapollenites* (0–6.80 %), *Betulaepollenites* (0–6.40 %), *Momipites* (0–5.50 %), *Comptonia* (0–5.00 %), *Maceopolipollenites* (0–4.40 %), *Ulmoideipites* (0–4.50 %), and *Betulaceipollenites* (0–2.30 %). The triporate pollen comprised an average of 10.20 % of the total grains and were dominated by *Aquilapollenites spinulosus*. The tricolpate and tricolporate pollen comprised an average of 6.40 % of the total grains. The polyporate pollen (average = 4.20 %) are mainly *Ulmipollenites* (0–7.30 %), *Alnipollenites* (0–2.00 %), *Juglanspollenites* (0–1.70 %), and *Ulmoideipites* (0–1.20 %). Gymnosperms were dominated by *Taxodiaceapollenites* (1.70–35.00 %) and *Inaperturopollenites* (3.30–19.00 %), while the bisaccate pollen of Pinaceae comprised 3.00–15.40 % of the total grains. Spores were dominated by monolete *Polypodiaceasporites* (0–41.90 %) (Liu, 1983).

Comparative analysis revealed that, although the AB, GPA, LMU, and OPW assemblages are all characterized by a dominance of angiosperms, which is consistent with angiosperm taxa dominating the floral assemblages at the end-Maastrichtian (Prasad et al., 2018), there are significant differences in their taxonomic compositions and relative abundances. In the GPA, LMU, and OPW assemblages, the angiosperms are predominantly *Santalaceae*? (*Pseudointegricarpus*, *Aquilapollenites*, *Pseudoaquilapollenites*, and *Orbiculapollis*), followed by *Ulmaceae* (*Ulmoideipites*), *Fagaceae* (*Quercoidites*), and monolete taxa (*Marsypiletes*) of uncertain botanical affinity. The gymnosperms are mainly represented by bisaccates with conifer affinity, with Ginkgoales being a secondary component. Spores are dominated by *Osmundaceae* (*Osmundacites*), followed by *Polypodiaceae* (*Laevigatosporites*). Some taxa occur in all of the AB, GPA, LMU, and OPW assemblages, including *Sphagnusporites*, *Osmundacites*, *Toroisporis*, *Gleichenioidites*, *Cyathidites*, *Deltoidospora*, *Pinuspollenites*, *Podocarpidites*, *Abietinaepollenites*, *Araucariacites*, *Taxodiaceapollenites*, *Ephedripites*, *Aquilapollenites*, *Integricarpus*, *Mancicarpus*, *Orbiculapollis*,

Tricolpites, *Ulmoideipites*, *Alnipollenites*, *Betulaceipollenites*, *Quercoidites*, and *Liliacidites*. The distinctive taxa in the AB assemblage include *Cicatricosisporites*, *Leptolepidites*, *Impardecispora*, *Todisporites*, *Divisisporites*, *Granulatisporites*, *Foveotrilletes*, *Microlepidites*, *Converrucosisporites*, *Salviniaspora*, *Polypodiaceasporites*, *Comptonia*, *Proteacidites*, *Gothanipollis*, *Plicapollis*, *Bratzevaea*, and some taxa typical of Cenozoic flora, such as *Magnolipollis*, *Sabalpollenites*, *Salixipollenites*, *Myricipites*, *Caryapollenites*, *Maceopolipollenites*, *Elgelhardtioipollenites*, *Juglanspollenites*, *Platycaryapollenites*, *Carpinipites*, *Ostryoipollenites*, *Anacolocidites*, *Chenopllis*, *Liquidambarpollenites*, *Platanoidites*, *Euphorbiacites*, *Tricolporopollenites*, and *Multiporopollenites*. In contrast, the unique taxa in the GPA, LMU, and OPW assemblages include *Leiotrilletes*, *Lygodiumsporites*, *Ceratosporites*, *Rouseisporites*, *Foveosporites*, *Gabonisporis*, *Laevigatosporites*, *Alisporites*, *Abiespollenites*, *Rugubivesiculites*, *Monosulcites*, *Potamogetonacidites*, *Marsypiletes*, *Monocolpopollenites*, *Tricolpopollenites*, *Fibulapollis*, *Pseudoaquilapollenites*, *Pseudointegricarpus*, *Rhoipites*, *Xinjiangpollis*, and *Wodehouseia*. They are all indicators of Late Cretaceous flora.

Therefore, the AB assemblage represents a transition from latest Maastrichtian to early Paleocene flora, which is characterized by a decline in typical Late Cretaceous taxa and the rise of Cenozoic taxa. For example, in the Jiayin area, the abundance of characteristic Late Cretaceous triporate taxa, such as *Aquilapollenites*, decreased, whereas the abundance of Paleogene triporate taxa such as *Betulaceipollenites*, increased. Therefore, the GPA, LMU, and OPW assemblages are confined to the late Maastrichtian, and correlated with the lower part of the AB assemblage (Table 5).

Markevich et al. (2011) identified the *Aquilapollenites stelkii*–*Pseudointegricarpus clarireticulatus* (AP) assemblage in three boreholes (XHY2005, XHY2006, and XHY2008) in the Jiayin area, and assigned it a late Maastrichtian age. This assemblage contains 69 genera and 105 species and is dominated by angiosperms (9.12–72.19 % of the total grains) and gymnosperms (13.96–33.70 % of the total grains). The angiosperms are mainly *Ulmaceae* (up to 25.00 %), *Aquilapollenites*, *Tricolpites*, *Quercites*, *Integricarpus*, *Orbiculapollis*, *Mancicarpus*, *Betulaceae*, and *Juglandaceae*. Gymnosperms are dominated by *Taxodiaceae* (up to 50.00 %),

Table 5

Comparison of palynological assemblages in the upper Maastrichtian and Danian Strata in Jiayin of Heilongjiang, Northeast China.

System	Stage	Formation	Liu (1983)	Markevich et al. (2011)	This paper
Paleogene	Danian	Wuyun	<i>Aquilapollenites spinulosus</i> - <i>Betulaceoipollenites</i> (AB)	<i>Triatriopollenites confusus</i> - <i>Aquilapollenites spinulosus</i> (TA)	
Upper Cretaceous	upper Maastrichtian	Furao		<i>Aquilapollenites stelkii</i> - <i>Pseudointegricarpus clarireticulatus</i> (AP)	<i>Osmundacidites</i> - <i>Pseudointegricarpus</i> - <i>Wodehouseia</i> (OPW) <i>Laevigatosporites</i> - <i>Monocolpopollenites</i> - <i>Ulmoideipites</i> (LMU) <i>Gabonispors</i> - <i>Pinuspollenites</i> - <i>Aquilapollenites</i> (GPA)

Cupressaceae, Ginkgoales, and *Pinuspollenites*. Spores are dominated by *Laevigatosporites*, *Leiotriletes*, and *Cyathidites*. There are some characteristic taxa in the AP assemblage, including *Marsipyletes cretacea*, *Tricolpites variexinus*, *Aquilapollenites stelkii*, *A. striatus*, *A. rigidus*, *Integricarpus bellum*, *Pseudointegricarpus clarireticulatus*, *Beaupreacidites*, Proteaceae, and Magnoliaceae. The *Triatriopollenites confusus*-*Aquilapollenites spinulosus* (TA) assemblage in the lower part of the Wuyun Formation was assigned to the Danian stage. The boundary between the TA and AP assemblages was set at a depth of 23.05–23.25 m in the XHY2008 borehole (Markevich et al., 2011), which is further constrained to a depth of 23.05 m by our data.

The GPA, LMU, and OPW assemblages have some key similarities with the AP assemblage, particularly in terms of the dominance of angiosperm pollen and taxonomic composition. However, differences in the relative abundances of certain taxa are likely due to the different sampling localities and sample sizes. In the GPA, LMU, and OPW assemblages, angiosperms are dominated by the triprojectacites, such as *Aquilapollenites*, *Pseudointegricarpus*, and *Pseudoaquilapollenites*, they are particularly abundant. Ulmaceae pollen is also prominent, especially in the LMU and OPW assemblages, although not uniformly dominant. The gymnosperms consist mainly of bisaccate pollen, including *Pinuspollenites*, *Alisporites*, *Podocarpidites*, and *Abiespollenites*. Taxodiaceae pollen is also present. The spores are primarily triletes, such as *Cyathidites*, *Leiotriletes*, and *Osmundacidites*, followed by the monolete *Laevigatosporites*.

5.2. Age of the palynoflora

Amongst the 85 genera and 208 species from depths of 25.10–23.05 m in the XHY2008 borehole, many are confined to the Upper Cretaceous in the worldwide, especially the species *Gabonispors vigourouxii*, *Aquilapollenites attenuatus*, *Aquilapollenites rigidus*, *Aquilapollenites stelkii*, *Parviprojectus reticulatus*, *Fibulapollis rombus*, *Pseudointegricarpus clarireticulatus*, *Integricarpus bellum*, *Orbiculapollis lucidus*, *Wodehouseia spinata*, *Marsipyletes cretacea*, *Pentapollenites dolium*, *Loranthacites macrosolenoides*, *Xinjiangpollis reticulatus*, and *Ulmoideipites krempii*.

Gabonispors vigourouxii was first reported from Upper Cretaceous in Gabon (Boltenhagen, 1967) and later recorded in high abundances in the regional palynoflora, which is mainly distributed in the tropical and subtropical humid environments near the equator to low latitude (Pérez, 1987; Vajda and Santivanez, 1999). *Gabonispors vigourouxii* has been documented in Upper Cretaceous from northwestern Bolivia, Colombia, Venezuela, Brazil, India, and China, where it is relatively common. In the XHY2008 borehole, *G. vigourouxii* occurs in the GPA, LMU, and OPW assemblages.

Aquilapollenites was first described by Rouse (1957) in Upper Cretaceous in Canada, and is widely regarded as a key indicator of Upper Cretaceous deposits. Subsequent studies have identified this genus in Upper Cretaceous in many regions, including western Siberia, western United States, Canada, Scotland (Isle of Mull), Japan (Hokkaido), Korea, Malaysia, India, Australia, central Africa, and eastern and northeastern China (Takahashi, 1967; Martin, 1968; Markevich, 1994; Gao et al., 1999; Nichols and Johnson, 2002; Yi and Batten, 2002; Mishra et al., 2019). However, rare Paleogene occurrences of *Aquilapollenites* are known from the Tantou Formation in western Henan Province, the Kongdian Formation in Shandong Province, and the Dainan Formation in Jiangsu Province (Han, 2020).

Both *Ulmipollenites* and *Ulmoideipites* are well-documented in Maastrichtian successions worldwide (Muller, 1981). *Ulmoideipites* was initially recognized in Upper Cretaceous–Paleocene strata in New Mexico (USA) and later recorded in western Siberia and the Russian Far East, as well as in Paleocene sediments of the Gulf of Mexico (Anderson, 1960; Markevich, 1994). It has been reported from the Maastrichtian Mingshui Formation in the Songliao Basin, the Nanxiong Formation in Guangdong Province, and the Taizhou Formation in Jiangsu Province, China (Guan, 1979; Gao et al., 1999; Liu et al., 2013). It has also been recorded in Paleocene strata in the Jiangnan Basin and the Paleocene Fushun Formation in Liaoning Province (Liu, 1983).

Integricarpus was generally restricted to the Upper Cretaceous, particularly the Coniacian Stage. However, it is abundant in the Maastrichtian–Danian Chirymyskaya Formation in Yakutia, Russia (Gao et al., 1999).

Pseudointegricarpus clarireticulatus (Samoil.) Takah. is known to occur in late Maastrichtian deposits in the Zeya–Bureya Basin in the Amur–Heilongjiang River region (Tekleva et al., 2015). It is of Maastrichtian age in northern China, the Sakhalin Islands, and Russia.

Wodehouseia spinata is another key index taxon and first appeared in middle to upper Maastrichtian deposits (Srivastava, 1969; Wiggins, 1976; Sweet, 1994; Braman and Sweet, 1999; Sweet and Braman, 2001). It is abundant in uppermost Cretaceous of the Rocky Mountains region and rare in lower Paleocene deposits in the northern United States and Canada (Nichols and Sweet, 1993), but absent in Paleocene Series in the Denver Basin, USA (Nichols and Fleming, 2002).

In summary, the sampled core from the XHY2008 borehole is late Maastrichtian in age, based on the palynological association.

Markevich et al. (2011) placed the K/Pg boundary in the XHY2008 borehole in Jiayin, Northeast China, between sample 5 (23.05 m) and sample 14 (23.25 m), based on the disappearance of *Aquilapollenites*, *Integricarpus bellum*, *Pseudointegricarpus clarireticulatus*, *Parviprojectus reticulatus*, *Fibulapollis rombus*, *Rhoipites crassus*, and *Wodehouseia spinata* in sample 5 (23.05 m).

The present study identified five samples at depths of 23.20–23.05 m that contained *Aquilapollenites*, *Pseudointegricorpus clarireticulatus*, *Fibulapollis rhombicus*, and *Wodehouseia spinata*, such as sample 129 (23.05 m). However, the presence of *Triatriopollenites confusus* was not confirmed in sample 129 (23.05 m) in this study. Therefore, we also assign sample 129 (23.05 m) to the Maastrichtian.

The SK-1 borehole of the Cretaceous Continental Scientific Drilling (CCSD-SK-1) project in the Songliao Basin, Northeast China (Wan et al., 2013), yielded a deposition rate of ~60.13 mm/kyr for the second member of the Mingshui Formation in a 190-m-thick deposit that was dated at 68.74–65.58 Ma (Wan et al., 2013). Given the similarity in sedimentary facies between the Maastrichtian Mingshui Formation in the Songliao Basin and the Furao Formation in Jiayin, Northeast China, both were dominated by lacustrine mudstones and deltaic fine-grained sandstones (Sun et al., 2002, 2005; Li et al., 2011; Wan et al., 2013), we suggest they had a similar deposition rate of ~60 mm/kyr. Consequently, the depth interval from 25.10 to 23.05 m in the XHY2008 borehole, which hosts the GPA, LMU, and OPW palynological assemblages, could represent ca. 34 kyr of deposition. Therefore, the palynological interpretation of this study focuses exclusively on the end-Maastrichtian climatic changes.

5.3. Climatic conditions

5.3.1. Latest Maastrichtian climatic changes

The Cretaceous had a strong greenhouse climate (Wang et al., 2024), with elevated global temperatures that allowed forest ecosystems to flourish even in the high-latitude Arctic (Spicer and Herman, 2010; Sun et al., 2016). Multiple independent paleothermal proxies from both marine and terrestrial archives provide evidence for significant global climatic perturbations leading up to the K/Pg boundary. These include the latest Maastrichtian warming event (LMWE) and subsequent end-Maastrichtian cooling (Li and Keller, 1998b; Hull et al., 2020). Based on $\delta^{13}\text{C}$ values of terrestrial paleosol carbonates in the Tornillo Basin, Texas, USA, the LMWE lasted for ca. 0.5 Myr and featured a temperature increase from 20.0 to 22.0 °C (Nordt et al., 2003). In the western United States, the organic paleothermometer $\text{MBT}^{5\text{me}}$ and the carbon-isotope composition of two K/Pg-spanning lignites indicated ~3 °C of warming during the final ca. 100 kyr of the Maastrichtian (O'Connor et al., 2024). Marine sedimentary records corroborate this warming event, indicating a global mean temperature increase of ~2 °C (Gu, 2023). At the mid-latitude South Atlantic Deep Sea Drilling Project Site 525, high-resolution stable isotope data indicate that the LMWE persisted for ca. 34 kyr, with the temperature of the intermediate water mass increasing by 2–3 °C (Li and Keller, 1998b). Additional records from the same site show that high-resolution benthic stable isotope data record global warming of ~2.5–5.0 °C that occurred 150–300 kyr before the K/Pg boundary (Barnet et al., 2017). On Seymour Island, Antarctica, clumped isotope temperature data indicate a temperature increase of 7.8 ± 3.3 °C at the end-Cretaceous (Petersen et al., 2016). $\delta^{18}\text{O}$ data for planktic foraminifera in the North Atlantic reveal a temperature increases of up to 6 °C (MacLeod et al., 2005).

Following the LMWE, a marked cooling trend is evident. The end-Maastrichtian climate was characterized by an obvious decrease in temperature (from 22 °C to 17.6 °C), based on terrestrial paleosol carbonate clumped isotope data in the Tornillo Basin, Texas, USA (Nordt et al., 2003). A comparable cooling of ~5–10 °C was recorded during the end-Maastrichtian in both the western United States (O'Connor et al., 2024) and Northeast China (Zhang et al., 2018). At the mid-latitude South Atlantic Deep Sea Drilling Project Site 525, stable isotope data showed that the intermediate

and surface water temperatures decreased by an average of 2.1 °C and 1.4 °C, respectively, during the final 100 kyr of the Maastrichtian (Li and Keller, 1998b). In the North Atlantic at 35°N, the organic geochemical palaeothermometer TetraEther index of tetraether consisting of 86 carbon atoms (TEX_{86}) revealed a significant cooling of ~7 °C during the Maastrichtian (Linnert et al., 2014). This rapid cooling in the last 100 kyr (Wilf et al., 2003) before the K/Pg boundary led to global temperatures decreasing back to or below the pre-warming level (Zhang et al., 2018; Vellekoop et al., 2019; Hull et al., 2020; O'Connor et al., 2024).

5.3.2. Climate reconstruction

During the Late Cretaceous, the Jiayin region and Songliao Basin in Northeast China were located in the East Siberian Province of the Siberian-Canada floral realm (Vakhrameev, 1991) or the boreal floral realm (Guo, 1983), or the mesophytic palynofloral region (Zhang, 1993), which had a subtropical to warm temperate climate (Sun, 1979).

Leaf-margin analyses of samples from North Dakota, USA (48°N) suggested the latest Maastrichtian mean annual temperature (MAT) was 12.5–14.8 °C (Wilf et al., 2003), which corresponds to a warm temperate climate (Cuming et al., 1981). In contrast, Denali, Alaska, USA (74°N) yielded an early Maastrichtian MAT of ~7 °C using the climate leaf analysis multivariate program (CLAMP) (Spicer and Herman, 2010), which corresponds to a cool temperate climate (Cuming et al., 1981). A projection of the palaeolatitude of Jiayin (~49°N) onto the Maastrichtian latitudinal temperature gradient curve (Spicer and Herman, 2010) yields an estimated MAT of ~14 °C, similar to that of North Dakota and consistent with a warm temperate climate.

Previous studies of latest Maastrichtian climatic changes have focused largely on geochemical records and plant macrofossils. In contrast, the present study provides high-resolution insights based on palynological analysis. Our palynological data showed that the average abundance of the tropical and subtropical taxa reached 62.53 % of the total species and 71.28 % of the total grains, while the temperate taxa accounted for only 11.48 % of the species and 8.74 % of the grains. These values suggest a subtropical or even tropical climate, although the tropical taxa are only 9.37 % of the species and 6.63 % of the grains, much lower than in the tropical climate zone (Zhao et al., 1992; Gao et al., 1999). As such, it is reasonable to assign the Jiayin area to a subtropical climate zone during the end-Maastrichtian.

5.3.3. Cooling events

Two discrete episodes of cooling were recognized, the Jiayin-CE1 and Jiayin-CE2 cooling events, which occurred in the uppermost LMU (23.70 m) and OPW (23.07 m) palynological assemblages, respectively.

The Jiayin-CE1 cooling event was characterized by an obvious increase in temperate taxa and a significant decrease in tropical and subtropical taxa within the uppermost LMU palynological assemblage. The content of temperate taxa increased by 7.48 % of the species and 7.06 % of the grains, indicating a transition to a warm temperate climate. The newly emerging species in the temperate zone were *Ephedripites mingshuiensis*, *Ramunculacidites vulgaris*, *Xinjiangpollis bellus*, *Xinjiangpollis* sp. and *Alnipollenites verus*. At this time, the tropical-subtropical taxa decreased by 15.71 % of the species and 13.67 % of the grains. The taxa with a decreased content were mainly *Monocolpopollenites*, *Pseudoaquilapollenites*, *Quercoidites*, *Leiotriletes*, *Deltoidospora*, and *Laevigatosporites*. One tropical-subtropical species, *Toroisporis brevidivisus*, disappeared. Therefore, the data support the interpretation that the Jiayin-CE1 cooling event produced a warm temperate climate.

The Jiayin-CE2 cooling event was recorded in the uppermost OPW palynological assemblage and was characterized by a pronounced increase in temperate taxa accompanied by a substantial decrease in tropical to subtropical taxa. The temperate taxa increased by 12.59 % of the grains, while the tropical–subtropical taxa decreased by 26.54 % of the grains, indicative of a warm temperate climate. The tropical–subtropical taxa, including *Pseudointegricorpus*, *Pseudoaquilapollenites*, *Leiotriletes*, *Loranthacidites*, *Aquilapollenites*, and *Mancicorpus*, decreased by 5.12 % of the total species. Some tropical–subtropical species, such as *Fibulapollis rombicus*, *Gleichenioidites laetus*, *Labitricolpites pachydermus*, and *Toroisporis minoris*, disappeared. This indicates a change to a warm temperate climate.

In terms of humidity, our palynological data show that the average content of the hydrophytic and hygrophytic taxa reached 69.81 % of the total species and 80.65 % of the total grains, whereas the xerophytic taxa accounted for only 6.11 % of the species and 5.44 % of the grains. The ratio of xerophytic to hydrophytic and hygrophytic grains varies between 0 and 0.22, indicating a humid climate (Zhao et al., 1992; Gao et al., 1999). However, two episodes of drying climate were recognized in association with the two cooling events.

The Jiayin-CE1 drying event was characterized by a distinct increase in xerophytic taxa and a pronounced decrease in hydrophytic and hygrophytic taxa. The content of xerophytic pollen increased by 7.77 % of the total species and 8.90 % of the total grains, while the hygrophytic taxa decreased by 2.81 % of the species and 11.41 % of the grains. The ratio of xerophytic to hydrophytic and hygrophytic taxa increased by 0.13 for the species and 0.14 for the grains, suggesting a drying event. Typical xerophytic taxa that appeared in the samples were *Ephedripites mingshuiensis*, *Xinjiangpollis bellus*, and *Xinjiangpollis* sp. In contrast, major decreases occurred in the hygrophytes, including *Monocolpopollenites*, *Pseudoaquilapollenites*, *Alnipollenites*, *Liliacidites*, *Leiotriletes*, *Deltoidospora*, *Sphagnumsporites*, *Lygodiumsporites*, *Gleichenioidites*, *Plicifera*, and *Laevigatosporites*.

Similarly, the Jiayin-CE2 cooling event was accompanied by an increase in xerophytic taxa and an abrupt decrease in hygrophytic taxa, indicative of a drying event. The content of xerophytic pollen grains increased by 4.26 % of the grains, and the mesophytes increased by 21.86 % of the species and 34.82 % of the grains. The hygrophytes decreased by 9.90 % of the species and 36.18 % of the grains. The ratio of xerophytic to hydrophytic and hygrophytic taxa increased by 0.15 of the grains, again indicating a drying event. Seven hygrophytic species were absent: *Foveosporites cenomanicus*, *Fibulapollis rombicus*, *Loranthacidites macrosolenoidites*, *Gleichenioidites laetus*, *Lygodiumsporites pseudomaximus*, *Toroisporis minoris*, and *Labitricolpites pachydermus*.

These two cooling and drying events have been recognized in two other boreholes (XHY2005 and XHY2006) in the Jiayin area. In XHY2005, the palynological data show that the average content of tropical and subtropical pollen and spores reached 85.61 % of the grains, while the temperate taxa were only 7.51 % of the grains, indicating a subtropical or even tropical climate. However, tropical taxa were only 4.02 % of the grains, which is much lower than in the tropical climate zone (Zhao et al., 1992; Gao et al., 1999). As such, a subtropical climate is more appropriate. Two cooling events were recognized at depths of 20.30 and 20.90 m, respectively. In terms of humidity, the average content of hygrophytic taxa reached 73.40 % of the grains, while xerophytes were only 5.97 % of the grains. The ratio of xerophytic to hydrophytic and hygrophytic grains varies from 0.01 to 0.18, indicating a humid climate (Zhao et al., 1992; Gao et al., 1999), although two drying events were also recorded, which correlate with those in the XHY2008 borehole (Fig. 9).

In XHY2006, the palynological data show that the average content of tropical and subtropical pollen and spores reached 87.81 % of the grains, while the temperate taxa comprise only 8.30 % of the grains. The tropical taxa only comprise 14.81 % of the grains, which is again lower than that in the tropical climate zone (Zhao et al., 1992; Gao et al., 1999). Therefore, a subtropical climate existed during the end-Maastrichtian cooling. Two cooling events

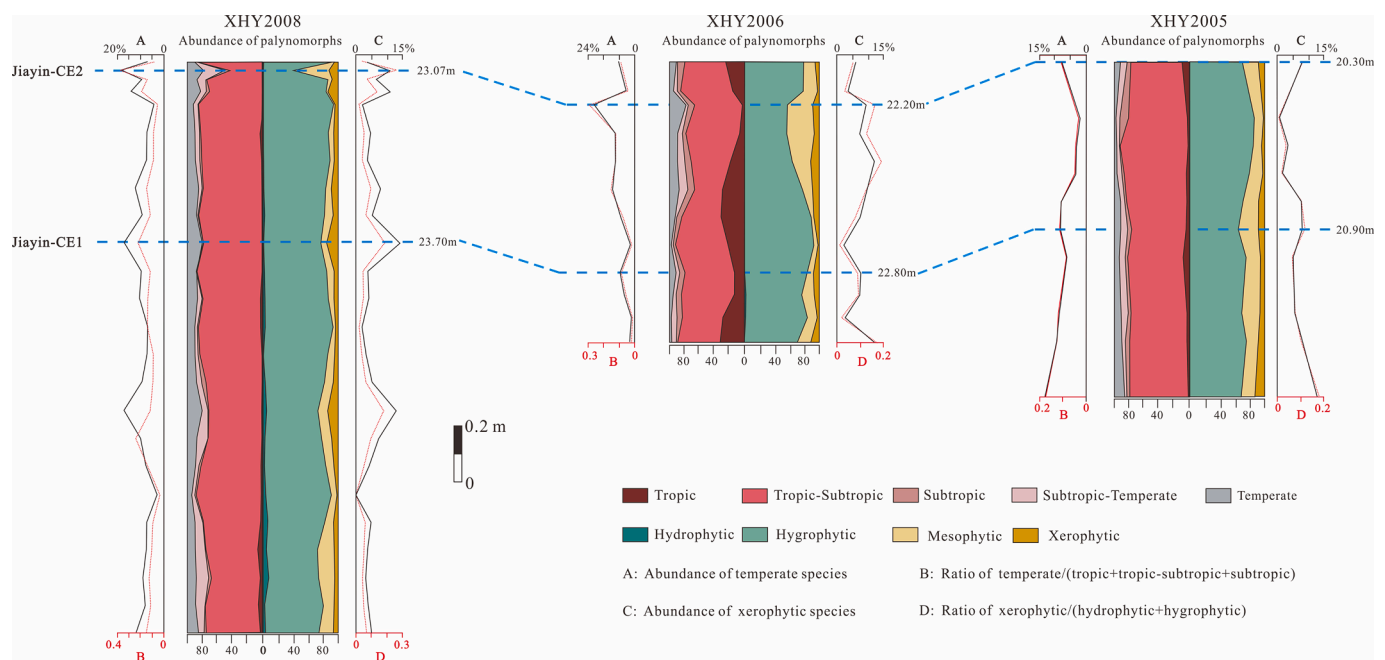


Fig. 9. Reconstructed climate zones and humidity based on the abundance of palynomorphs at XHY2005, XHY2006, and XHY2008 boreholes in Jiayin, Heilongjiang, Northeast China. A. The distribution curve of abundance of temperate species; B. The distribution curve of the ratio of the temperate/(tropical + tropical–subtropical + subtropical); C. The distribution curve of abundance of xerophytic species; D. The distribution curve of the ratio of xerophytic/(hydrophytic + hygrophytic).

are recorded at 22.20 and 22.80 m, respectively. The average content of hygrophytic pollen and spores reached 76.50 % of the grains, whereas the xerophytes are only 7.36 % of the grains. The ratio of xerophytic to hydrophytic and hygrophytic grains ranges from 0.02 to 0.19, indicative of a humid conditions with subhumid pulses during the cooling events (Fig. 9).

From a broader perspective, variable cooling and drying events occurred across different regions during the latest Maastrichtian and Danian. Palynological data from the SK-1 borehole in the Songliao Basin have revealed a distinct cooling and drying event in the latest Maastrichtian, as evidenced by a significant increase in the *Ephedripites* content by 51.75 % of the grains, which reaches a content of 59.34 % of the grains (Li et al., 2011). This cooling and drying event was characterized by a dominance of *Ephedripites* of the Gnetales (*Ephedra*) and decline in *Cyathidites* of the Cyatheaceae, indicative of a change to arid conditions. Similarly, high-resolution palynological data for the Hell Creek Formation in southwestern North Dakota, USA, also document a distinct cooling and drying event during the latest Maastrichtian. This event was characterized by an increase in gymnosperms by 7.50 % of the grains to a content of 13.00 % of the grains and a corresponding decrease in Pteridophyte and Bryophyte spores by 5 % and 6 % of the grains, respectively (Nichols and Johnson, 2002). In India, evidence comes from the Hakim and Shriwas boreholes, where a similar climatic shift is marked by the dominance of *Ephedripites* spp., which comprises 51.0 % of the grains in the assemblage. These taxa are closely related to the xerophytic shrubs of the family Ephedraceae (Thakre et al., 2024), indicative of desert to semi-arid and seasonally dry climatic conditions (Graham, 1999). Complementary mineralogical data for associated carbonaceous clays revealed a dominance of smectite and smectite/chlorite interlayer clays, indicating fluctuating depositional environments ranging from humid to semi-arid (Thakre et al., 2017). This is consistent with the latest Maastrichtian aridification trends identified from palynological and mineralogical evidence in Saurashtra, Gujarat, India (Samant et al., 2014). In the South Atlantic, a similar cooling event is recorded by a significant decrease in the content of *Senegalinium* complex and trilete spores and persistently low terrestrial palynomorph concentrations (10–15 % of the grains) during the latest Maastrichtian (Woelders et al., 2017). In addition, coeval cooling events just prior to the K/Pg boundary have been documented in several independent archives: (1) bulk-carbonate $\delta^{18}\text{O}$ data from the Walvis Ridge (ODP Site 1262); (2) sea-surface-temperature trends reconstructed from TEX₈₆ data at Bajada del Jagüel; and (3) molluscan $\delta^{18}\text{O}$ records from Seymour Island, Antarctica (Woelders et al., 2017). These findings support the interpretation that the end-Maastrichtian cooling and drying events were global rather than regional in nature. The high-resolution palynological record for the Jiayin area provides more details of these two cooling and drying events during the latest Maastrichtian.

6. Conclusions

Three latest Maastrichtian palynological assemblages, the *Gabonispuris*–*Pinuspollenites*–*Aquilapollenites* assemblage, the *Laevigatosporites*–*Monocolpopollenites*–*Ulmoideipites* assemblage, and the *Osmundacidites*–*Pseudointegricorpus*–*Wodehouseia* assemblage in stratigraphic ascending order were recognized based on the high-resolution palynological data from the Fura Formation in the XHY2008 borehole in Jiayin, Heilongjiang Province, Northeast China. This provides valuable insights into the reconstruction of climatic changes during latest Maastrichtian based on the palynological data.

The latest Maastrichtian climate was generally a warm and humid subtropical climate in the mid-latitude of Northern

Hemisphere, indicating a greenhouse climate in Jiayin, Heilongjiang Province, Northeast China. However, two cooling and drying events were recognized during the last 34 kyr before the K/Pg boundary, based on quantitative analyses of pollen and spores by the method of principal component analysis and ecological affinity statistics. These events led to climate conditions changing from humid subtropical to subhumid temperate. These short-term climatic changes might record abrupt climatic perturbations during latest Maastrichtian cooling.

CRediT authorship contribution statement

Jiahui Yu: Writing – original draft, Software, Investigation, Formal analysis, Conceptualization. **Yuewu Sun:** Writing – review & editing, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Eugenia V. Bugdaeva:** Writing – review & editing. **Valentina S. Markevich:** Writing – review & editing.

Declaration of competing interest

The authors declare that they have no competing interests. All authors have approved this manuscript, and no author has financial or other contractual agreements that might cause conflicts of interest.

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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.2025.106270>.