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New Early Cretaceous palynology of the Southeastern Khorat Plateau, Northeastern Thailand: palaeobotanical, palaeoclimatic, and palynophytogeographical implications

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ABSTRACT
The Khorat Plateau, situated in northeastern Thailand and extending partially into Laos and Cambodia, was a thriving ecosystem during the Early Cretaceous. It harboured a diverse array of vertebrate fauna, including freshwater hybodont shark-like fish, actinopterygian fishes, turtles, crocodilians, theropod and sauropod dinosaurs, as well as bivalves. However, not many studies were focused on the flora of this ecosystem. This study focuses on palynological findings from the Sao Khua Formation in the southeastern Khorat Plateau. A total of 74 species from 43 genera were identified, forming an assemblage characterised by *Punctatisporites-Dicheiropollis-Classopollis*. Based on recent radiometric dating of detrital zircon grains, the Sao Khua Formation is as assigned to an age no younger than the mid to late Valanginian. As the result, the key taxa found in this formation have been calibrated and the age of the palynological assemblage is therefore Valanginian. The assemblage was dominated by pollen of Cheirolepidiaceae together with diversity of pteridophyte spores, suggesting a humid subtropical climate with periodic arid seasons. Comparative analysis with other palynological provinces places this area within the Eastern Tethys Province of the Pan-Tethys Realm.

KEY WORDS
Thailand,
Sao Khua Formation,
palynological assemblage,
Valanginian,
humid subtropical climate,
Eastern Tethys Province.

RÉSUMÉ

Nouvelles données palynologiques du Crétacé inférieur du sud-est du Plateau du Khorat, nord-est de la Thaïlande: implications paléobotaniques, paléoclimatiques et palynophytogéographiques.

Le plateau de Khorat, situé dans le nord-est de la Thaïlande et s'étendant partiellement au Laos et au Cambodge, était un écosystème prospère durant le Crétacé inférieur. Il abritait une variété importante d'espèces de vertébrés, incluant des poissons d'eau douce ressemblant à des requins hybodontes, des poissons actinoptérygiens, des tortues, des crocodiliens, des dinosaures théropodes et sauropodes, et des bivalves. Cependant, peu d'études se sont concentrées sur la flore de cet écosystème. Cette étude se concentre sur les découvertes palynologiques de la Formation Sao Khua dans le sud-est du Plateau de Khorat. L'assemblage palynologique, composé de 74 espèces réparties en 43 genres, est caractérisé par *Punctatisporites-Dicheiropollis-Classopollis*. Sur la base d'une datation radiométrique récente de grains de zircon détritiques, la Formation de Sao Khua n'est pas considérée comme plus jeune que le Valanginien moyen ou supérieur. Ainsi, les taxons clés trouvés dans cette formation ont été calibrés et l'assemblage palynologique est donc d'âge valanginien. Cet assemblage était dominé par des grains de pollen de Cheirolepidiaceae, ainsi que par une diversité de spores de fougères, impliquant un climat subtropical humide avec des saisons arides périodiques. L'analyse comparative avec les autres provinces palynologiques permet de considérer que cette région se situait dans la Province orientale de la Téthys, au sein du Domaine pan-téthysien.

MOTS CLÉS
Thaïlande,
Formation Sao Khua,
assemblage palynologique,
Valanginien,
climat subtropical humide,
Province de l'est de la Téthys.

INTRODUCTION

The Khorat Plateau is a vast plateau region situated in northeastern Thailand. Covering an approximate area of 155 000 square kilometres, this expanse is distinguished by its flat and arid terrain. The saucer-shaped plateau is divided by the Phu Phan Mountains into two basins: the northern Sakhon Nakhon Basin and the southern Khorat Basin. (Fig. 1). The Khorat Basin, one of the largest and well-exposed continental sedimentary basins in southeastern Asia, spans across eastern Thailand, western Laos, and northern Cambodia. The Early Cretaceous strata of the Khorat Basin, collectively known as the Khorat Group, comprise five formations (Fig. 1): the Phu Kradung Formation (Fm), Phra Wihan Fm, Sao Khua Fm, Phu Phan Fm and Khok Kruat Fm in ascending order (Racey & Goodall 2009). The Khorat Group has yielded a plethora of vertebrate fossils, including selachians, actinopterygians, sarcopterygians, temnospondyl amphibians, turtles, crocodyliformes, pterosaurs, non-avian dinosaurs, and birds (Manitkoon *et al.* 2022).

Among them, the Sao Khua Fm is famous for its abundant dinosaur fossils. Tetanuran non-avian theropods were found in the Sao Khua Fm, including the metriacanthosaur *Siamotyrannus* Buffetaut, Suteethorn & Tong, 1996, spinosaurid "*Siamosaurus*" Buffetaut & Ingavat, 1986, a possible second spinosaurid taxon "Phu Wiang spinosaurid B", megaraptoran *Phuwiangvenator* Samathi, Chanthasit & Sander, 2019, and coelurosaurian *Vayuraptor* Samathi, Chanthasit & Sander, 2019, ornithomimid *Kinnareemimus* Buffetaut, Suteethorn & Tong, 2009, an undetermined carcharodontosaurid from Phu Wang, and an undetermined tetanuran, and at least two sauropods, including the somphospondylan *Phuwiangosaurus* Martin, Buffetaut & Suteethorn, 1994, and an undetermined taxon (Tucker *et al.* 2022, and references therein). The authors also dated the Sao Khua Fm, from detrital zircon grains, as no younger than middle to late Valanginian.

Moreover, palynological fossils have been documented from the continental sediments of the Early Cretaceous, helping to determine the palynoflora of the Khorat Group formations (Racey & Goodall 2009). However, only twelve genera of spore and pollen fossils were found at the Sao Khua Fm (Racey *et al.* 1996; Racey & Goodall 2009). To address this gap, a detailed palynological study was conducted on five samples from the upper section of the Sao Khua Fm in Nam Yuen city, northeastern Thailand (Fig. 1). The new palynological data studied here provide valuable information to complete the regional palynostratigraphy and facilitate the reconstruction of the palaeovegetation and palaeoclimate of this area.

GEOLOGICAL SETTING

The Khorat Group (Fig. 2) represents the largest red-bed sequence on the Korat Plateau, but the age of each formation within the group remains controversial due to the absence of index fossils. The lowermost Phu Kradung Fm may extend into the Jurassic Period, whereas the Phra Wihan, Sao Khua, Phu Phan, and Khok Kruat formations are dated as "Early Cretaceous" (Racey *et al.* 1996; Carter & Moss 1999; Meesook 2000; Carter & Bristow 2003; Hasegawa *et al.* 2010).

The Sao Khua Fm is primarily composed of conglomeratic sandstone, siltstone, and claystone, as well as numerous palaeosol layers (Tucker *et al.* 2022). Facies analysis and architectural studies reveal that the sedimentation of Sao Khua Fm occurred within a floodplain setting fed by large meandering bedload-rich channels (Tucker *et al.* 2022). Multiple types

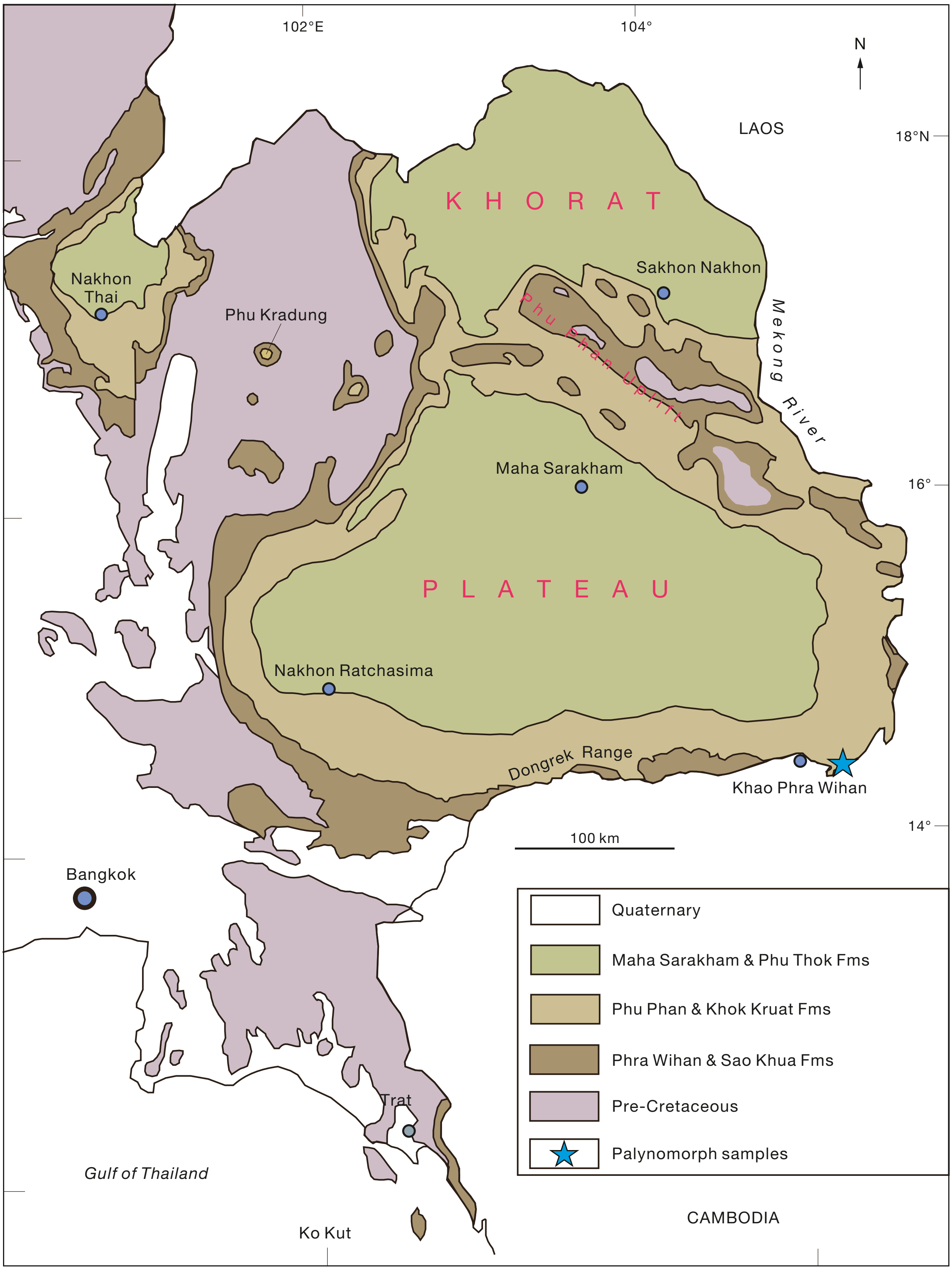

FIG. 1. — Synthetic geological map of eastern Thailand (after Meesook 2011).

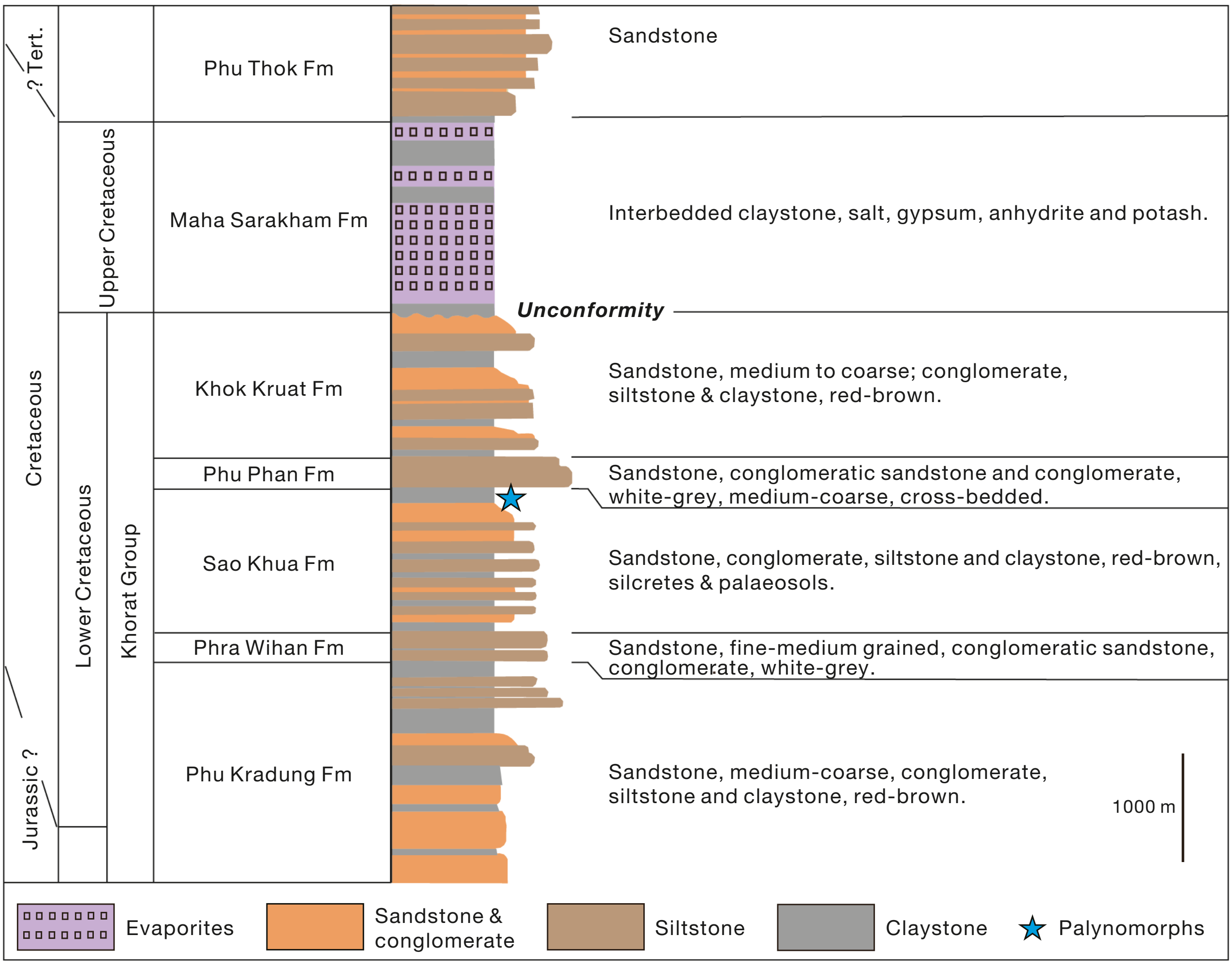

FIG. 2. — Cretaceous stratigraphic column in the Khorat Plateau, NE Thailand (after Meesook 2011).

of palaeosols were identified in this formation. Based on the characteristics and geochemical data of these palaeosols, palaeoclimate conditions suggest a predominantly stable humid subtropical climate, with a mean annual temperature of approximately 17-20°C and a mean annual precipitation of around 1000-1400 mm per year (Tucker *et al.* 2022). Based on radiometric dating of detrital zircons (via LA-IPC-MS), these authors considered that the middle part of the Sa Khua Fm was deposited no later than 133.8 ± 1.8 Ma (late Valanginian) and that the overlying Phu Phan Fm no later than 132.4 ± 2.0 Ma (lower Hauterivian). Consequently, the Sao Khua Fm is considered as no later than mid- to late Valanginian.

The outcrop from which the samples were collected is located 11.8 kilometres from Nam Yuen City, near the borders of Thailand, Laos, and Cambodia (Fig. 1). In this area, only the yellow-green siltstone at the top of the Sao Khua Fm crops out in a small valley near a temple, which located at 14°21'31"N, 105°12'34"E (Fig. 2). It is overlain by the reddish-brown calcareous, conglomeratic sandstone attributed to the base of the Phu Phan Fm, with a conformable contact between the two formations (Racey & Goodall 2009; Meesook 2011). Most of this area is a military restricted zone because it lies at the junction of Thailand, Myanmar, and Cambodia.

MATERIAL AND METHODS

A total of five palynological samples were collected from the yellow-green siltstone and mudstone beds of the Sao Khua Fm in Nam Yuen City (Figs. 1, 3A). Each sample was spaced 40 cm apart and identified as sk21, sk22, sk23, sk24, and sk25 from bottom to top. Plant macro-remains (Fig. 3B) can be observed within the yellow-green mudstone layer.

Each 50 g sample was crushed into grains smaller than 0.5 cm in diametre and subjected to treatment with HCl (10%) for 24 hours due to the high calcareous content, followed by HF (36%) for 48 hours, then treated with HCl (37.5%) for 24 hours again. To separate the organic residue from minerals and isolate the palynomorphs, a ZnCl-mixed KI heavy liquid with a density of 2.2 g/cm^3 along with an 8 μm sieve were used. Subsequently, the slides containing the palynomorph samples were examined under a Leica DM4000B microscope. Image processing was conducted using CorelDraw software. The botanical affinities of spores and pollen found in the Sao Khua Fm were summarized according to findings reported in previous studies and listed in Table 1.

All samples and slides are currently housed at the Research Center of Paleontology and Stratigraphy, Jilin University, China.

Table 1. — Palynomorphs identified in the Sao Khua Fm, with their botanical affinities and climate signal. References: **1**, Abbink *et al.* 2004; **2**, Alvin 1982; **3**, Atfy *et al.* 2019; **4**, Balme 1957; **5**, Balme 1995; **6**, Boulter & Windle 1993; **7**, Couper 1958; **8**, Dettmann 1963; **9**, Dettmann 1986; **10**, Dettmann *et al.* 1992; **11**, Filatoff 1975; **12**, Friis *et al.* 2004; **13**, Guignard *et al.* 2009; **14**, Harris 1979; **15**, Hubbard & Boulter 1997; **16**, Ji 1994; **17**, Van Konijnenburg-Van Cittert 1971; **18**, Van Konijnenburg-Van Cittert 1993; **19**, Krutzsch 1963; **20**, Li 1984; **21**, Liu *et al.* 2024; **22**, Mander 2011; **23**, Rodríguez-Barreiro *et al.* 2024; **24**, Santos *et al.* 2022; **25**, Song *et al.* 1986; **26**, Song *et al.* 1999; **27**, Traverse 2007; **28**, Trevisan 1971; **29**, Volkheimer *et al.* 2009; **30**, Weerakoon *et al.* 2021; **31**, Weyland & Krieger 1953; **32**, Wheeler *et al.* 2022; **33**, Yang *et al.* 2007; **34**, Ziaja 2006. Symbol: *****, grains less than 10. Abbreviation: **Gr.**, Grains.

	sk22	sk23		sk24		sk25		
Taxa	**Gr.**	**Gr.**	**%**	**Gr.**	**%**	**Gr.**	**Climate signal**	**Botanical affinity**
Ferns spore	–	50	31.06	72	19.89	–	–	–
Foraminisporis wonthaggiensis (Cookson & Dettmann) Dettmann, 1963	–	1	0.62	–	–	–	Warm and wet	Sphagnaceae (8, 19, 33)
Foraminisporis asymmetricus (Cookson & Dettmann) Dettmann, 1963	–	–	–	1	0.28	–	Warm and wet	Sphagnaceae (8, 19, 33)
Densoisporites sp.	–	–	–	1	0.28	–	Warm and wet	Pleuromeaceae/Selaginellaceae (5, 27, 31)
Foveosporites sp.	–	–	–	2	0.55	–	Warm and wet	Selaginellaceae (4, 5)
Neoraistrickia sp.	–	–	–	2	0.55	–	Warm and wet	Lycopodiaceae/Selaginellaceae (8, 10)
Verrucosisporites granatum (Bollkh.) Gao & Zhao, 1976	–	–	–	1	0.28	–	Warm and wet	Selaginellaceae (27, 33)
Verrucosisporites obscurilaesuratus Pocock, 1962	–	–	–	1	0.28	–	Warm and wet	Selaginellaceae (27, 33)
Verrucosisporites scitulus Yu & Zhang, 1982	–	–	–	1	0.28	–	Warm and wet	Selaginellaceae (27, 33)
Verrucosisporites sp.	–	3	1.86	–	–	–	Warm and wet	Selaginellaceae (27, 33)
Leptolepidites cf. *psarosus* Norris, 1969	–	1	0.62	–	–	–	Warm and wet	Lycopodiaceae (6, 11)
Leptolepidites verrucatus Couper, 1953	–	–	–	1	0.28	–	Warm and wet	Lycopodiaceae (6, 11)
Punctatisporites sp.	–	19	11.8	12	3.31	–	Warm and wet	Lepidocarpaceae (5)
Calamospora sp.	–	1	0.62	–	–	–	Warm and wet	Lycopodiaceae, Equisetales (5, 11)
Apiculatisporites sp.	–	1	0.62	–	–	–	Hot and wet	Lycopodiaceae, Selaginellaceae (11)
Baculatisporites sp.	–	–	–	1	0.28	–	Warm and wet	Pteridophyta, Osmundaceae (11)
Osmundacidites sp.	–	–	–	1	0.28	–	Warm and wet	Osmundaceae (5, 6, 7, 11)
Biretisporites potoniaei Delcourt & Sprumont, 1955	–	4	2.48	1	0.28	–	Warm and wet	Hymenophyllaceae (23)
Biretisporites punctatus Wan & Sun, 2014	–	–	–	1	0.28	–	Warm and wet	Hymenophyllaceae (23)
Biretisporites sp.	–	2	1.24	1	0.28	–	Warm and wet	Hymenophyllaceae (23)
Converrucosisporites minimus Yu & Miao, 1983	–	–	–	2	0.55	–	Hot and wet	Dicksoniaceae (5)
Cicatricosisporites cf. *paucistriatus* Han, 1983	–	–	–	1	0.28	–	Hot and wet	Anemiaceae (23)
Cicatricosisporites cf. *potomacensis* Brenner, 1963	–	–	–	1	0.28	–	Hot and wet	Anemiaceae (23)
Cicatricosisporites cf. *pseudoaurifer* (Bolkh.) Li,1959	–	–	–	2	0.55	–	Hot and wet	Anemiaceae (23)
Cicatricosisporites cf. *subrotundus* Brenner, 1963	–	–	–	1	0.28	–	Hot and wet	Anemiaceae (23)
Cicatricosisporites cuneiformis Pocock, 1964	–	–	–	1	0.28	–	Hot and wet	Anemiaceae (23)
Cicatricosisporites minutaestriatus (Bolkh.) Pocock, 1964	–	1	0.62	–	–	–	Hot and wet	Anemiaceae (23)
Cicatricosisporites paucistriatus Han, 1983	–	1	0.62	1	0.28	–	Hot and wet	Anemiaceae (23)
Cicatricosisporites solidus (Pu & Wu) Jia, 1986	–	–	–	1	0.28	–	Hot and wet	Anemiaceae (23)
Cicatricosisporites sp.	–	4	2.48	5	1.38	–	Hot and wet	Anemiaceae (23)
Concavissimisporites emarcidus Yu,1984	–	2	1.24	–	–	–	Hot and wet	Lygodiaceae (23)
Concavissimisporites punctatus (Delcourt & Sprumont) Brenner, 1963	–	–	–	6	1.66	–	Hot and wet	Lygodiaceae (23)
Concavissimisporites verrucosus Delcourt & Sprumont,1955	–	–	–	1	0.28	–	Hot and wet	Lygodiaceae (23)
Impardecispora apiverrucata (Couper) Venkatachala, Kar & Raza, 1969	–	–	–	4	1.1	–	Hot and wet	Cyatheaceae (1, 24)
Impardecispora cf. *breve* (Martynova) Yu, 1989	–	1	0.62	2	0.55	–	Hot and wet	Cyatheaceae (1, 24)
Klukisporites sp.	–	2	1.24	–	–	–	Hot and wet	Lygodiaceae (23)
Matonisporites?	–	–	–	1	0.28	–	Hot and wet	Gleicheniaceae (23)
Schizaeoisporites sp.	–	–	–	3	0.83	–	Hot and dry	Schizaeaceae (25, 26)
Todisporites major Couper, 1958	–	1	0.62	–	–	–	Warm and wet	Osmundaceae (11, 24)
Todisporites sp.	–	1	0.62	–	–	–	Warm and wet	Osmundaceae (11, 24)
Trilobosporites sp.	–	–	–	1	0.28	–	Hot and wet	Schizaeaceae (3, 11, 24, 29)
Pterisisporites minor Li, 1984	–	–	–	1	0.28	–	Hot and wet	Pteridaceae (20)
Pterisisporites undulatus Sung & Zheng in Sung & Li, 1976	–	–	–	3	0.83	–	Hot and wet	Pteridaceae (20)
Cyathidites australis Couper,1953	–	3	1.86	1	0.28	–	Hot and wet	Cyatheaceae (23)
Cyathidites minor Couper, 1953	–	1	0.62	–	–	–	Hot and wet	Cyatheaceae (23)
Deltoidospora irregularis (Pflug) Sung & Tsao, 1976	–	–	–	1	0.28	–	Hot and wet	Dipteridaceae, Matoniaceae (5, 6, 7, 13, 18, 22)
Deltoidospora sp.	–	–	–	1	0.28	–	Hot and wet	Dipteridaceae, Matoniaceae (5, 6, 7, 13, 18, 22)
Dictyophyllidites sp.	–	–	–	2	0.55	–	Hot and wet	Dipteridaceae, Matoniaceae (6, 7, 11, 13, 18)
Undulatisporites sp.	–	–	–	1	0.28	–	Hot and wet	Ophioglossaceae (25)
Laevigatosporites gracilis Wilson & Webster, 1946	–	–	–	2	0.55	–	Warm and wet	Ophioglossaceae (25)
Tenuicontactosporites cretacius Han, 1983	–	1	0.62	–	–	–	Hot and wet	Unknown

Table 1. — Continuation.

Taxa	sk22 Gr.	sk23 Gr.	sk23 %	sk24 Gr.	sk24 %	sk25 Gr.	Climate signal	Botanical affinity
Gymnosperms pollen	–	111	68.94	290	80.11	–	–	–
Araucariacites australis Cookson, 1947	–	6	3.73	2	0.55	–	Warm, semiarid-semihumid	Araucariaceae (5, 9, 17)
Araucariacites sp.	–	–	–	3	0.83	–	Warm, semiarid-semihumid	Araucariaceae (5, 9, 17)
Callialasporites dampieri (Balme) Sukh Dev, 1961	–	1	0.62	–	–	–	Warm, semiarid-semihumid	Araucariaceae (5, 6, 11, 15, 17)
Callialasporites trilobatus (Balme) Sckh Dev, 1961	–	–	–	1	0.28	–	Warm, semiarid-semihumid	Araucariaceae (5, 6, 11, 15, 17)
Psophosphaera grandis Bolkhovitina, 1956	–	–	–	1	0.28	–	Warm, semiarid-semihumid	Araucariaceae (16)
Psophosphaera undata (Bolkhovitina) Zhang,1978	–	–	–	2	0.55	–	Warm, semiarid-semihumid	Araucariaceae (16)
Psophosphaera sp.	–	–	–	1	0.28	–	Warm, semiarid-semihumid	Araucariaceae (16)
Classopollis sp.	*	15	9.32	33	9.12	*	Hot and arid	Cheirolepidiaceae (7, 14, 34)
Dicheiropollis etruscus Trevisan, 1971	–	81	50.31	215	59.39	*	Hot and arid	Cheirolepidiaceae (28)
Concentrisporites leptos Yu & Zhang, 1982	–	–	–	2	0.55	–	Cool and semihumid	Cupressaceae (1, 2, 24)
Concentrisporites opimus Yu & Zhang, 1982	–	–	–	2	0.55	–	Cool and semihumid	Cupressaceae (1, 2, 24)
Concentrisporites sp.	–	–	–	3	0.83	–	Cool and semihumid	Cupressaceae (1, 2, 24)
Perinopollenites limatus Lu & Wang, 1983	–	–	–	2	0.55	–	Cool and semihumid	Cupressaceae (1, 2, 24)
Exesipollenites sp.	–	–	–	1	0.28	–	Cool and semihumid	Cupressaceae (1, 2, 24)
Taxodiaceaepollenites sp.	–	5	3.11	1	0.28	–	Cool and semihumid	Cupressaceae (1, 2, 24)
Pinuspollenites minutus (Zakl.) Sung & Zheng,1978	–	–	–	1	0.28	–	Cool and semidry	Pinaceae (5)
Pinuspollenites sp.	–	–	–	1	0.28	–	Cool and semidry	Pinaceae (5)
Podccarpidites sp.	–	–	–	1	0.28	–	Cool and humid	Podocarpaceae (25, 30)
Cycadopites elongatus (Balkh.) Zhang, 1978	–	–	–	1	0.28	–	Hot and semiarid	Cycadales, Bennettitales, Ginkgoales (5, 11)
Cycadopites sp.	–	3	1.86	11	3.04	–	Hot and semiarid	Cycadales, Bennettitales, Ginkgoales (5, 11)
Eucommiidites sp.	–	–	–	4	1.1	–	Hot and semiarid	Cycadales, Gnetales (32)
Jugella rallus Yu, 1984	–	–	–	1	0.28	–	Arid	Ephedrales, Gnetales (12, 21)
Jugella sp.	–	–	–	2	0.55	–	Arid	Ephedrales, Gnetales (12, 21)
Caytonipollenites sp.	–	–	–	1	0.28	–	Warm and wet	Caytoniaceae (25)
Total	*	**161**	**–**	**362**	**100**	*		

RESULTS

The palynological recovery was excellent, four of the five samples (sk22, sk23, sk24, sk25) yielded spores and pollen grains. Notably, samples sk23 and sk24 showed diverse palynological richness, totalling 80 species and 46 genera (Table 1, Figs. 4-6). The composition of both sk23 and sk24 showed striking similarity, leading to the recognition of the *Punctatisporites-Dicheiropollis-Classopollis* assemblage. This assemblage is characterized by a predominance of gymnosperm pollen (68.32-80.11%), a low presence of pteridophyte spores (19.89-31.68%), and the absence of angiosperm pollen. Noteworthy gymnosperm pollen include *Dicheiropollis* Trevisan, 1971 (50.31-59.39%), *Classopollis* Pflug, 1953 (9.12-9.32%), as well as common types like *Araucariacites* Cookson ex Couper, 1953 (1.38-3.73%), *Cycadopites* Wodehouse, 1933 (1.86-3.31%), and *Taxodiaceaepollenites* Kremp ex Potonié, 1958 (0.28-2.48%). Additionally, sporadically appearing types include *Exesipollenites* sp., *Jugella rallus* Yu, 1984, *Jugella* sp., and *Callialasporites trilobatus* (Balme) Sckh Dev, 1961. Among pteridophyte spores, *Punctatisporites* Potonié & Gelletich, 1933 are the most abundant (3.31-11.80%), followed by *Cicatricosisporites* Potonié & Gelletich, 1933 (3.59-3.73%). Other significant types present in the assemblage encompass *Trilobosporites* sp., *Impardecispora* cf. *breve* (Martynova) Yu, 1989, *Impardecispora apiverrucata* (Couper) Venkatachala, Kar & Raza, 1969, *Schizaeoisporites* sp., *Densoisporites* sp., *Foraminisporis wonthaggiensis* (Cookson & Dettmann) Dettmann, 1963, *Foraminisporis* cf. *Asymmetricus* (Cookson & Dettmann) Dettmann, 1963, *Concavissimisporites emarcidus* Yu, 1984, *Concavissimisporites punctatus* (Delcourt & Sprumont) Brenner, 1963, *Leptolepidites* cf. *psarosus* Norris, 1969, *Leptolepidites verrucatus* Couper, 1953, *Pterisisporites minor* Li, 1984, *Pterisisporites undulatus* Sung & Zheng in Sung & Li, 1976, *Klukisporites* sp., *Foveosporites* sp., among others.

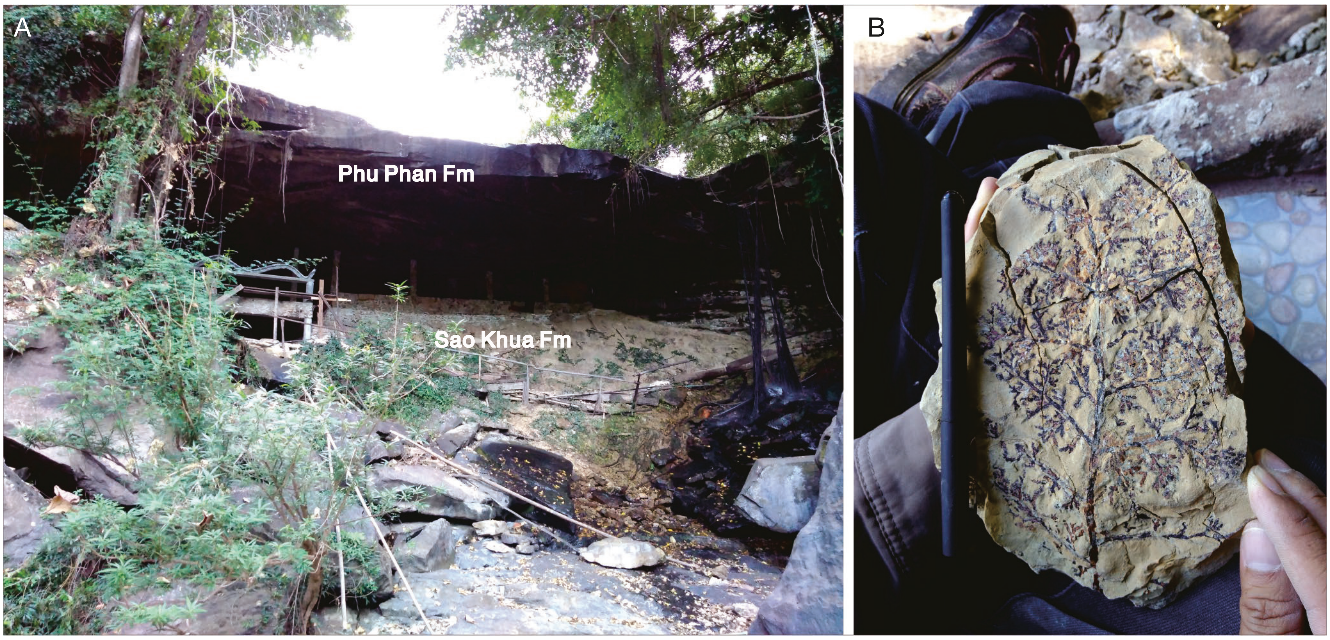

FIG. 3. — **A**, Outcrop of the upmost of the Sao Khua Fm in Nam Yuen City; **B**, *Cupressinocladus* Seward, 1919 (the pen is 15 cm in length). Photos: Xiao Shi.

DISCUSSION

AGE OF THE PALYNOASSEMBLAGE AND SAO KHUA FM

The age of the Sao Khua Fm has been discussed for several decades (Tucker *et al.* 2022, and references therein). Recently, U/Pb datings on detrital zircons recovered from the middle part of this formation and the overlying Phu Phan Fm allowed assigning the Sao Khua Fm to a mid to late Valanginian age (Tucker *et al.* 2022). This well-defined chronostratigraphy established with radiometric methods allows to calibrate the biostratigraphical ranges of some key palynological taxa of the Early Cretaceous.

The *Punctatisporites-Dicheiropollis-Classopollis* assemblage contains a variety of taxa with stratigraphical significance, such as *Cicatricosisporites* Potonié & Gelletich, 1933, *Trilobosporites* Potonié, 1956, *Impardecispora* Venkatachala, Kar & Raza, 1969, *Schizaeoisporites* Potonié ex Delcourt & Sprumont, 1955, *Densoisporites* Dettmann, 1963, *Foraminisporis* Krutzsch, 1956, *Concavissimisporites* Delcourt & Sprumont, 1955, *Leptolepidites* Couper, 1953, *Pterisisporites* Sun & Zheng, 1976, *Klukisporites* Couper, 1958, *Foveosporites* Balme, 1957, *Exesipollenites* Balme, 1957, and *Jugella* Mchedlishvili & Shakhmundes, 1973. However, many of them have long-ranging stratigraphical occurrences.

The main key species of the *Punctatisporites-Dicheiropollis-Classopollis* assemblage studied here is *Dicheiropollis etruscus* Trevisan, 1971. First identified by Trevisan (1971) in the Berriasian-Barremian Biancone Fm in Tuscany, Italy, *Dicheiropollis etruscus* has been found in various regions across Africa (Libya, Egypt, Morocco, Senegal, Ivory Coast, Gabon, Cameroon, Congo, Angola, Sudan, Chad, and South Sudan), South America (Venezuela, Brazil), and Asia (Yemen, Thailand, Cambodia, and China). Its predominant presence in the Berriasian-lower Barremian worldwide designates it as a valuable marker species for the Berriasian-lower Barremian stage in the northern Gondwana region (Fig. 7).

Initially discovered in Barremian deposits in northern Morocco (Hoculi 1981), subsequent findings have also revealed the presence of *Dicheiropollis etruscus* during the Berriasian-early Aptian age interval, co-occurring with angiosperms such as *Clavatipollenites hughesii*, *Stellatopollis* sp., *Retimonocolpites* sp., *Afropollis zonatus* Doyle, Jardiné & Doerenkamp, 1982, and *Afropollis operculatus* Doyle, Jardiné & Doerenkamp, 1982, and *Afropollis operculatus* (Gübeli, 1984). In the lower part of the Abu Gabra Fm in the Muglad Basin, South Sudan, *Dicheiropollis etruscus* has been identified with angiosperm pollen species like *Afropollis zonatus*, *Retimonocolpites variplicatus* Schrank & Mahmoud, 1998, and *Stellatopollis densiornatus* (Lima) Ward, 1986. The studies by Eisawi *et al.* (2012) and Cole *et al.* (2017) respectively determined the age of this palynological assemblage to be Berriasian-Barremian and Berriasian-lower Barremian. The evolutionary development stage of angiosperm pollen in this assemblage aligns closely with that of the angiosperm pollen found in conjunction with *Dicheiropollis etruscus* in northern Morocco (Gübeli *et al.* 1984), indicating that its geological age likely extends to the lower Aptian. Notably, *Dicheiropollis etruscus* has been observed together with dinoflagellate cysts in the upper Hauterivian-lower Barremian marine deposits in Libya and Egypt (Uwins & Batten 1988; Deaf *et al.* 2016), and in Yemen (Racey & Goodall 2009), its presence in marine deposits has been related to a timeframe ranging from upper Valanginian-lower Barremian, as determined by dinoflagellate cysts and acritarchs. In summary, while *Dicheiropollis etruscus* may have originated as early as the Late Jurassic and continued to the lower Aptian of the Early Cretaceous, its primary prevalence aligns with the Berriasian-lower Barremian.

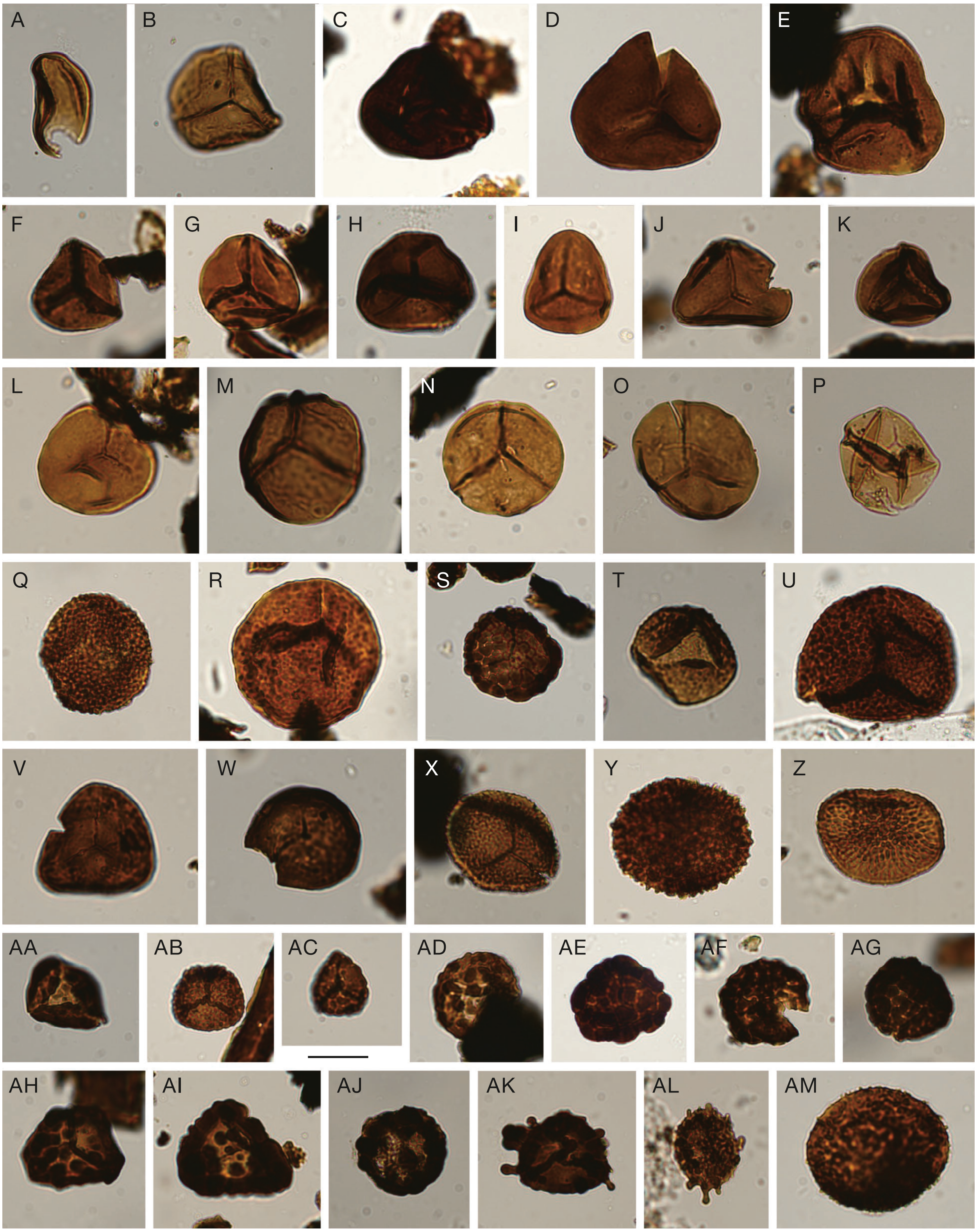

FIG. 4. — Selected palynomorph taxa. Specimen information (a/b) is comprised of the sample number (a), and slide number (b): **A**, *Laevigatosporites gracilis* Wilson & Webster, sk24/1; **B**, *Biretisporites* sp., sk23/1; **C**, *Cyathidites minor* Couper, sk23/1; **D**, **E**, *Cyathidites australis* Couper; **D**, sk24/1; **E**, sk23/1; **F**, *Biretisporites punctatus* Wan & Sun, sk24/2; **G**, **H**, *Biretisporites potoniaei* Delcourt & Sprumont; **G**, sk24/1, **H**, sk23/1; **I**, *Deltoidospora irregularis* (Pflug) Sung & Tsao, sk24/2; **J**, *Deltoidospora* sp., sk24/2; **K**, *Dictyophyllidites* sp., sk24/1; **L**, *Todisporites* sp., sk23/1; **M**, *Todisporites major* Couper, sk23/1; **N**, **O**, *Punctatisporites* sp., sk24/2; **P**, *Calamospora* sp., sk23/1; **Q**, *Verrucosisporites scitulus* Yu & Zhang, sk24/2; **R**, *Verrucosisporites obscurilaesuratus* Pocock, sk24/2; **S**, *Verrucosisporites granatum* (Bollkh.) Gao & Zhao, sk24/1; **T**, **U**, *Verrucosisporites* sp., sk23/1; **V**, *Undulatisporites* sp., sk24/1; **W**, *Tenuicontactosporites cretacius* Han, sk23/1; **X**, *Osmundacidites* sp., sk24/2; **Y**, *Baculatisporites* sp., sk24/2; **Z**, *Foraminisporis* cf. *asymmetricus* (Cookson & Dettmann) Dettmann, sk24/1; **AA**, **AB**, *Converrucosisporites minimus* Yu & Miao, sk24/1; **AC**, *Pterisisporites minor* Li, sk24/1; **AD**, *Leptolepidites* cf. *psarosus* Norris, sk23/1; **AE**, *Leptolepidites verrucatus* Couper, sk24/1; **AF**, **AG**, *Foveosporites* sp., sk24/2; **AH**-**AJ**, *Pterisisporites undulatus* Sung & Zheng in Sung & Li, sk24/2; **AK**, **AL**, *Neoraistrickia* sp., sk24/1; **AM**, *Apiculatisporites* sp., sk23/1. Scale bar: 20 µm. Photos: Yan Zhang and Chuanbiao Wan.

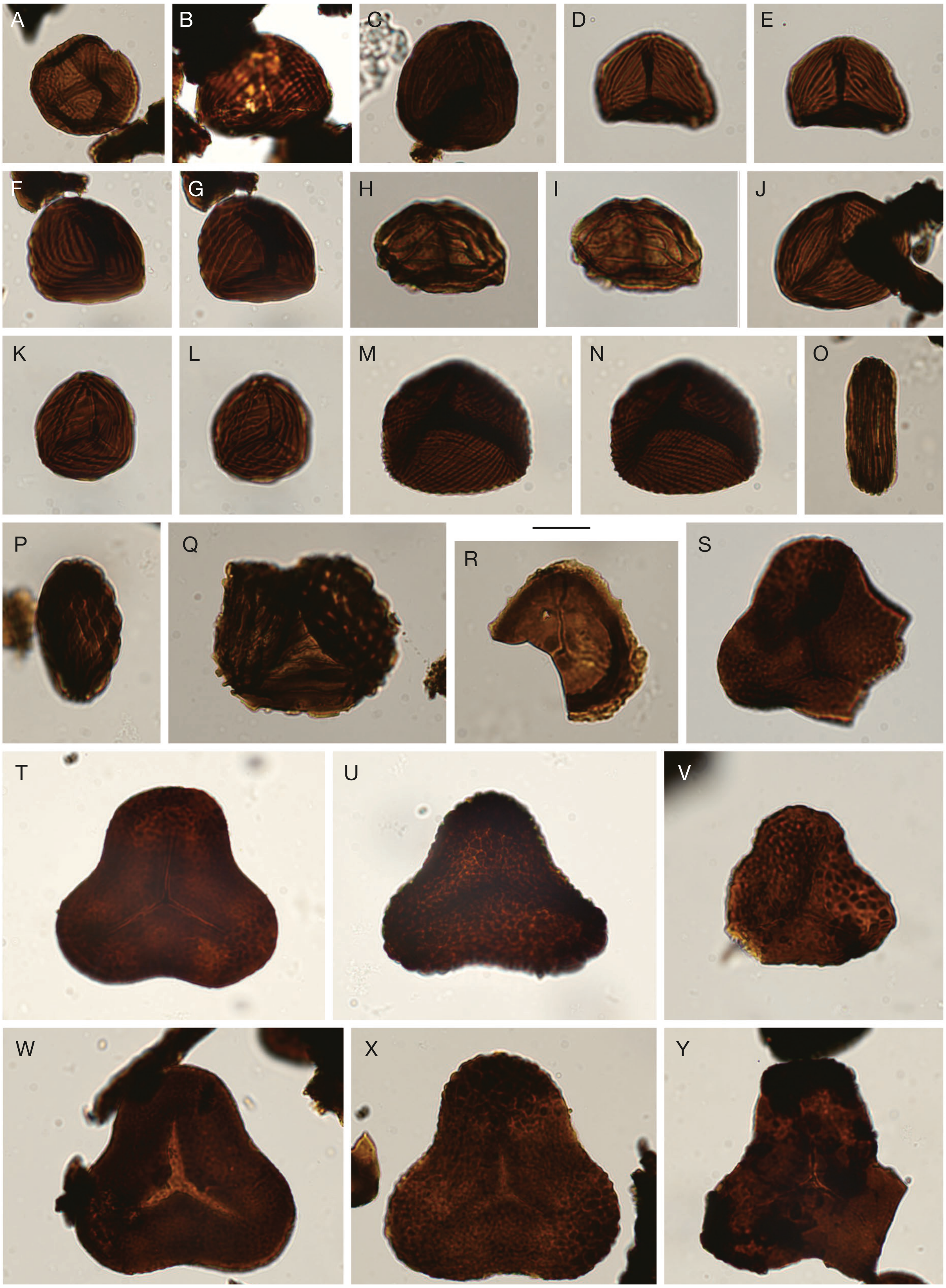

FIG. 5. — Selected palynomorph taxa. Specimen information (a/b) is comprised of the sample number (a), and slide number (b): **A**, *Cicatricosisporites solidus* (Pu & Wu) Jia, sk24/1; **B**, **M**, **N**, *Cicatricosisporites minutaestriatus* (Bolkh.) Pocock; **B**, sk23/1; **M**, **N**, proximal and distal face, respectively, sk24/2; **C**, *Cicatricosisporites* cf. *pseudoaurifer* (Bolkh.) Li, sk24/1; **D**, **E**, *Cicatricosisporites* sp., proximal and distal face, respectively, sk24/2; **F**, **G**, *Cicatricosisporites* cf. *pseudoaurifer* (Bolkh.) Li, proximal and distal face, respectively, sk24/1; **H**, **I**, *Cicatricosisporites* cf. *paucistriatus* Han, proximal and distal face,respectively, sk24/2; **J**, *Cicatricosisporites* cf. *potomacensis* Brenner, sk24/1; **K**, **L**, *Cicatricosisporites cuneiformis* Pocock, proximal and distal face, respectively, sk24/2; **O**, **P**, *Schizaeoisporites* sp., sk24/2; **Q**, *Cicatricosisporites paucistriatus* Han, sk24/1; **R**, *Densoisporites* sp., sk24/2; **S**, **T**, *Impardecispora* cf. *breve* (Martynova) Yu; **S**, sk24/1; **T**, sk24/2; **U**, *Concavissimisporites verrucosus* Delcourt & Sprumont, sk24/2; **V**, *Concavissimisporites emarcidus* Yu, sk23/1; **W**, *Concavissimisporites punctatus* (Delcourt & Sprumont) Brenner, sk24/2; **X**, *Impardecispora apiverrucata* (Couper) Venkatachala, Kar & Raza, sk24/1; **Y**, *Trilobosporites* sp., sk24/2. Scale bar: 20 µm. Photos: Yan Zhang and Chuanbiao Wan.

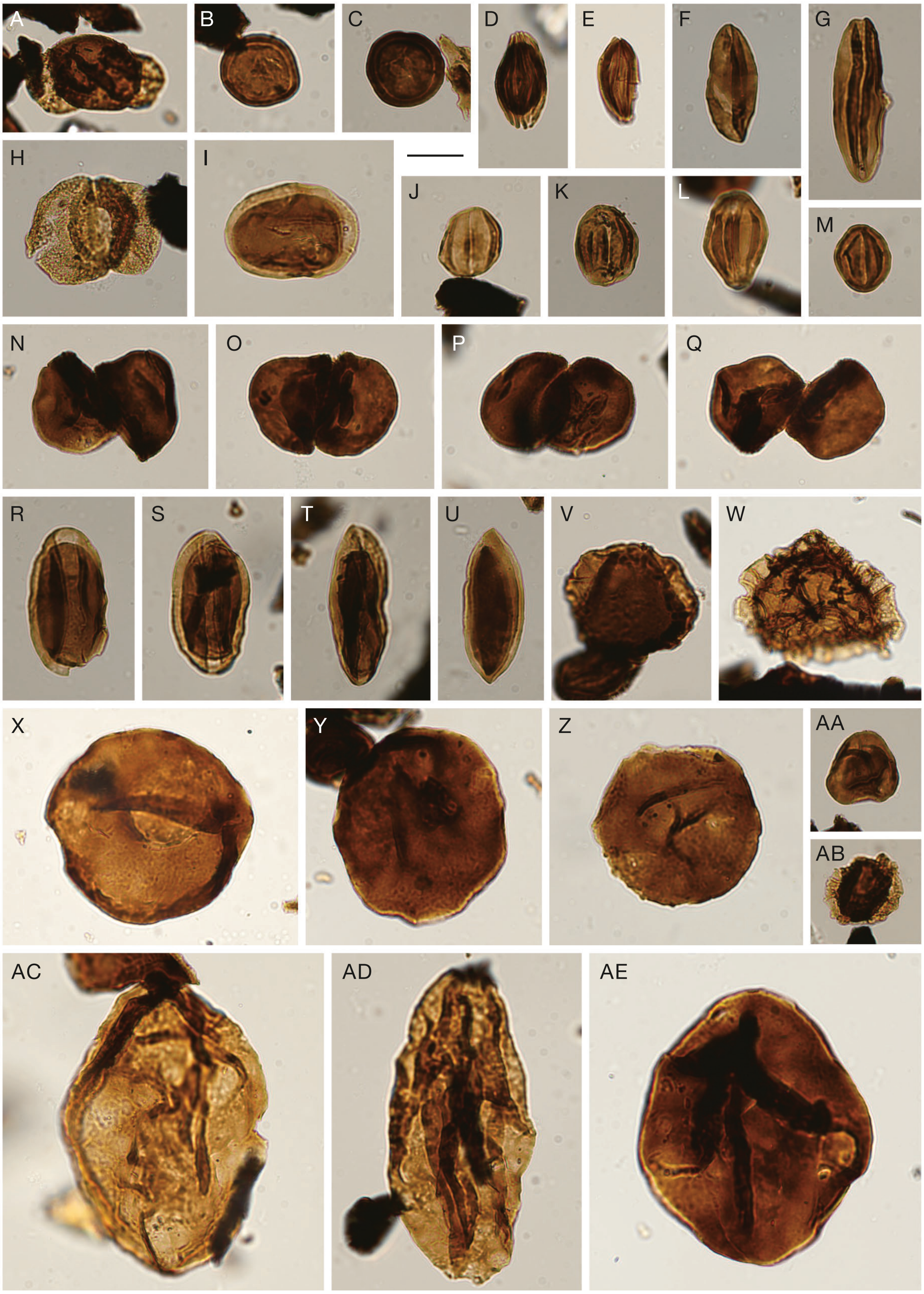

Fig. 6. — Selected palynomorph taxa. Specimen information (a/b) is comprised of the sample number (a), and slide number (b): **A**, *Pinuspollenites minutus* (Zakl.) Sung & Zheng, sk24/1; **B**, **C**, *Classopollis* sp.; **B**, sk24/2; **C**, sk24/1; **D**, *Jugella rallus* Yu, sk24/2; **E**, *Jugella* sp., sk24/1; **F**, *Cycadopites* sp., sk24/1; **G**, *Cycadopites elongatus* (Balkh.) Zhang, sk24/1; **H**, *Podocarpidites* sp., sk24/2; **I**, *Perinopollenites limatus* Lu & Wang, sk24/2; **J**-**M**, *Eucommiidites* sp.; **J**-**L**, sk24/1; **M**, sk24/2; **N**-**Q**, *Dicheiropollis etruscus* Trevisan; **N**, sk24/1; **O**-**Q**, sk24/2; **R**, **S**, *Concentrisporites opimus* Yu & Zhang; **R**, sk24/1; **S**, sk24/2; **T**, **U**, *Concentrisporites leptos* Yu & Zhang, sk24/2; **V**, *Callialasporites trilobatus* (Balme) Sckh Dev, sk24/1; **W**, *Callialasporites dampieri* (Balme) Sukh Dev, sk23/1; **X**-**Z**, *Araucariacites australis* Cookson; **X**, sk24/2; **Y**, sk24/1; **Z**, sk23/1; **AA**, *Exesipollenites* sp., sk24/2; **AB**, *Caytonipollenites* sp., sk24/1; **AC**, **AD**, *Psophosphaera undata* (Bolkhovitina) Zhang; **AC**, sk24/2; **AD**, sk24/1; **AE**, *Psophosphaera grandis* Bolkhovitina, sk24/1. Scale bar: 20 µm. Photos: Yan Zhang and Chuanbiao Wan.

Fig. 7. — The spatiotemporal distribution of *Dicheiropollis etruscus* Trevisan, 1971. References: **1**, Trevisan 1971; **2**, Hoculi 1981; **3**, Jardiné *et al.* 1974; **4**, Thusu & van der Eem 1985; **5**, Deaf *et al.* 2016; **6**, Mahmoud *et al.* 2019; **7**, Uwins & Batten 1988; **8**, Schrank 1992; **9**, Ied & Tahoun 2019; **10**, Gübeli *et al.* 1984; **11**, Salar-Cheboldaeff 1990; **12**, Hu *et al.* 2023; **13**, Doyle *et al.* 1977; **14**, Schrank 1992; **15**, Kaska 1989; **16**, Eisawi *et al.* 2012; **17**, Cole *et al.* 2017; **18**, Müller *et al.* 1987; **19**, Michels *et al.* 2018; **20**, Garcia *et al.* 2018; **21**, Racey & Goodall 2009; **22**, Lei 1993; **23**, Li & Liu 1994; **24**, Li 2000; **25**, Jiang *et al.* 2008; **26**, Guo *et al.* 2011; **27**, Lin & Li 2019; **28**, Li & Batten 2004; **29**, Zhang *et al.* 2019; **30**, Zhang 1995.

In eastern Asia, *Dicheiropollis* first appeared rarely in the Berriasian and then became more abundant during the Valanginian, reaching its peak in the Hauterivian-lower Barremian (Li 2000; Li & Batten 2004; Guo *et al.* 2011). The palynological assemblage corresponds closely to the *Dicheiropollis*-peak palynological assemblage established by Li & Batten (2004) in the Xueshan Fm at the Wenquan section in Qinghai, China. Both assemblages have a high abundance of *Dicheiropollis etruscus* and relatively abundant *Classopollis*, *Cicatricosisporites*, *Jugella*, among others, which are important for stratigraphic correlation. The age of the assemblage is likely similar, falling within the Valanginian-Hauterivian or Barremian. In this work, we provide a new occurrence in the middle to late Valanginian of Thailand, supported with independent age control.

The *Cicatricosisporites* genus often considered a Cretaceous marker (Batten 1996), may have first appeared in the Late Jurassic of Gondwana as discussed by Santos *et al.* (2021, 2022). However, their first occurrence in China was Berriasian (Pu & Wu 1982).

Eight identified species and one undetermined species are present in our assemblage. Among the *Cicatricosisporites* species found, *Cicatricosisporites* cf. *paucistriatus* Han, 1983 has been documented in the Hauterivian-Barremian Lengshuiwu Fm in Jiangxi, China (Yu & Han 1985). Other species such as *Cicatricosisporites* cf. *potomacensis* Brenner, 1963, *Cicatricosisporites* cf. *pseudoaurifer* (Bolkh.) Li, 1959, *Cicatricosisporites* cf. *subrotundus* Brenner, 1963, *Cicatricosisporites cuneiformis* Pocock, 1964, and *Cicatricosisporites* *solidus* (Pu & Wu) Jia, 1986 have been identified in Early Cretaceous strata in northern China (Pu & Wu 1982, 1985; Li 1984). *Cicatricosisporites minutaestriatus* is common in the Valanginian-Aptian, with less distribution in the Berriasian and Albian strata. (Yaroshenko & Aleksandrova 2015; Zhang *et al.* 2019).

Additionally, some species of the genera *Impardecispora*, have been recognized to be markers of the Jurassic-Cretaceous transition (Rodríguez-Barreiro *et al.* 2022). Notably, some of these species are more prevalent in the Early Cretaceous or exclusively found during that period. For instance, *Impardecispora apiverrucata*, present in the assemblage, is widespread in Late Jurassic-Early Cretaceous strata worldwide (Couper 1958; Tiwari & Tripathi 1995), with significant occurrences in China during the middle-late Early Cretaceous (Pu & Wu 1982; Song *et al.* 1986).

In the assemblage, *Schizaeoisporites*, *Foraminisporis*, and *Pterisisporites* are also present, appearing in Cretaceous and Cenozoic strata. The genus *Foraminisporis* is globally distributed in Cretaceous to Paleogene sediments (Burger 1993; Song *et al.* 2000; Valeria *et al.* 2024). Within this genus, two species are identified. *F. wonthaggiensis* is found in sediments of the Berriasian upwards and newer geological times (Dettmann 1963; Helby *et al.* 1987; Vallati 2001; Tripathi 2008), while *F.* cf. *asymmetricus* is commonly found in Early Cretaceous strata of China, particularly in the Hauterivian-Barremian strata (Pu & Wu 1982).

The gymnosperm pollen *Jugella* is present in Cretaceous strata. *Jugella rallus* was discovered in the Early Cretaceous deposits of Inner Mongolia, China (Miao *et al.* 1984).

Racey & Goodall (2009) reported on the palynological assemblage of the Sao Khua Fm in northeastern Thailand. In this assemblage, dominant taxa include *Dicheiropollis etruscus*, *Cicatricosisporites* spp., *Corollina* spp.? *Appendicisporites distocarinatus* Dettmann & Playford, 1968, and *Concavissimisporites punctatus*, while *Steriesporites* spp., *Cyathidites minor* Couper, 1953, *Exesipollenites tumulus* Balme, 1957, *Araucariacites australis* Cookson, 1947, *Convolutispora* spp., *Osmundacidites* spp., and *Leptolepidites verrucatus* Couper, 1953 are rare. The assemblage is dated to the Berriasian-lower Barremian. Despite only containing 12 palynomorph types, the main components are consistent with the present palynological assemblage. Therefore, the geological age of the Sao Khua Fm in Thailand is likely within the Berriasian-lower Barremian.

Reconstruction of Palaeovegetation and Palaeoclimate

Climatic and geographic conditions are widely acknowledged as the primary factors influencing botanical communities. Different palynological assemblages correspond to different climates and geographies. Spores and pollen, as the plant reproductive organs, are valuable tools for understanding the vegetation composition at a specific point in time (e.g. Weyland & Krieger 1953; De Jersey 1959; Dettmann 1986; Balme 1995; Traverse 2007; Bonis & Kürschner 2012; Wang *et al.* 2016; Slater *et al.* 2019). By analysing palynological assemblages and considering the ecological habitats of modern plants, palaeovegetational features provide insights into the palaeoclimate, palaeogeographical, and palaeodepositional environments and can be reconstructed (Table 1).

The components of the palynological assemblage studied in this work from the Sao Khua Fm, include bryophytes, lycophytes, sphenophytes, ferns, cycads, ephedrales, caytoniales, and conifers (Table 1).

Gymnosperms were more abundant than pteridophytes, with conifers forming the main component of the vegetation (66.46-74.59%). Ferns (13.81-14.91%) and lycophytes (5.80-15.53%) were common components, while cycads (1.86-4.42%) constituted a relatively low proportion. Bryophytes, ephedrales, and caytoniales were rare (less than 1%). Within the conifers, Cheirolepidiaceae were the most developed (59.63-68.51%), with *Dicheiropollis* (50.31-59.39%) and *Classopollis* (9.12-9.32%) as prominent types. Araucariaceae (2.76-4.35%) and Cupressaceae (2.49-3.11%) were relatively common, while Pinaceae, and Podocarpaceae were rare (less than 2%). Ferns exhibited high diversity with the presence of several families, such as Anemiaceae, Schizaeaceae, Lygodiaceae, Gleicheniaceae, Osmundaceae, Hymenophyllaceae, Dicksoniaceae, Pteridaceae, Cyatheaceae, Dipteridaceae, and Ophioglossaceae. Lycophytes have a low diversity, primarily composed of Lepidocarpaceae (3.31-11.80%), with sporadic appearances of Selaginellaceae and Lycopodiaceae. The pollen composition (66.46-74.59%) of the mother plant is predominantly derived from coniferous species, including *Dicheiropollis*, *Classopollis*, *Araucariacites*, *Inaperturopollenites* Potonié, 1966, *Concentrisporites* Wall, 1965, *Psophosphaera* Naumova, 1939, *Taxodiaceaepollenites*, *Perinopollenites* Couper, 1958, *Pinuspollenites* Raatz, 1938, *Exesipollenites*, *Callialasporites* Dev, 1961, and *Podocarpidites* Cookson, 1947. This group constitutes the primary component of the flora. Additionally, the mother plant includes spores from herbaceous species (10.50-18.63%), such as *Punctatisporites*, *Pterisisporites*, *Biretisporites* Delcourt & Sprumont, 1955, *Undulatisporites* Pflug, 1953, *Schizaeoisporites*, *Deltoidospora* Miner, 1935, *Leptolepidites*, *Toroisporis* Krutzsch, 1959, *Leiotriletes* Naumova, 1937, *Foveosporites*, *Neoraistrickia* Potonié, 1956, *Converrucosisporites* Potonié & Kremp, 1954, *Laevigatosporites* Ibrahim, 1933, *Foraminisporis*, *Densoisporites*, and *Osmundacidites* etc. Shrubs (7.45-8.56%) and evergreen broad-leaved plants (3.31-3.73%) represent minor components of the flora.

Among the main components of the flora, Cheirolepidiaceae is the most developed and plays a decisive role in the reconstruction of the palaeovegetation and palaeoenvironment. The parent plants of *Classopollis* (Cheirolepidiaceae) were usually adapted to hot and (semi) arid climates and distributed in terrestrial or coastal ecological environments. Zhang (1995) speculated that one of the parent plants producing *Classopollis* pollen in Asia may be a dwarf tree or shrub. Both *Classopollis* and *Dicheiropollis* have the same complex outer wall structure observed under SEM (Zhang 1995). Trevisan (1971) speculated that both have drought and heat resistance. *Classopollis* are abundant in the conti-

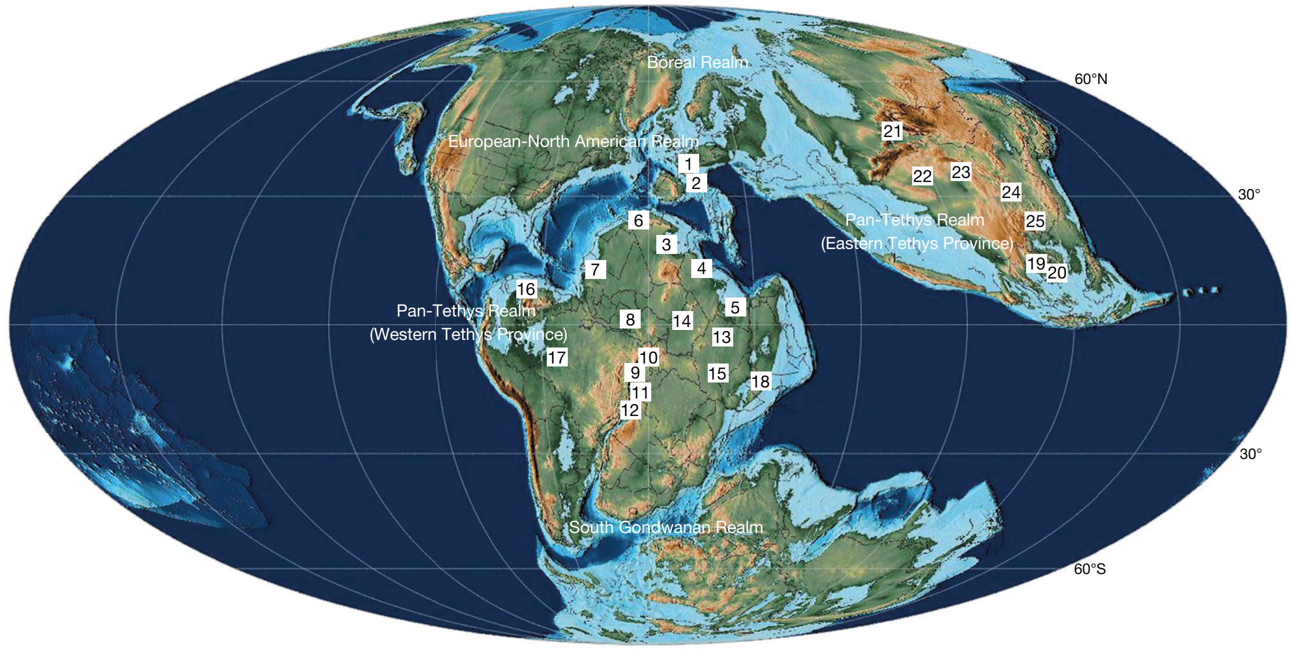

Fig. 8. — The distribution of *Dicheiropollis etruscus* Trevisan, 1971 in the Early Cretaceous (the palaeogeographical reconstruction is based on Scotese 2021). Countries: **1**, Italy; **2**, Switzerland; **3**, Algeria; **4**, Libya; **5**, Egypt; **6**, Morocco; **7**, Senegal; **8**, Côte d'Ivoire; **9**, Gabon; **10**, Cameroon; **11**, Congo; **12**, Angola; **13**, Sudan; **14**, Chad; **15**, South Sudan; **16**, Venezuela; **17**, Brazil; **18**, Yemen; **19**, Thailand; **20**, Cambodia; **21**, Xinjiang, China; **22**, Tibet, China; **23**, Qinghai, China; **24**, Sichuan, China; **25**, Yunnan, China.

nental sediments of the Early Cretaceous area of southern China (south of 40°N), but *Dicheiropollis* is absent. However, the abundance of *Dicheiropollis* distributed along the coast of the Tethys Sea, indicating that *Dicheiropollis* has a narrower environmental adaptation range than *Classopollis* and is mainly adapted to the littoral ecosystem.

In summary, the *Punctatisporites-Dicheiropollis-Classopollis* assemblage from the Early Cretaceous Sao Khua Fm, primarily composed of Cheirolepidiaceae, indicates that coniferous forests were the predominant vegetation in the Khorat Plateau of northwestern Thailand. In this environment, herbaceous and shrubby plants occupied a subordinate role, while evergreen broad-leaved plants were scarce. The paleolandscape was characterized by a coniferous forest ecosystem, reflecting particularly warm and semi-arid conditions (very likely in a littoral setting) within a tropical/subtropical climate.

The palynophytogeographic province

The palynological assemblage of the Early Cretaceous Sao Khua Fm on the Khorat Plateau yields abundant *Dicheiropollis etruscus* and *Classopollis*, and a moderate amount of *Araucariacites*, *Taxodiaceaepollenites*, *Ephedripites*, and *Eucommiidites*, while bisaccate pollen and spores are scarce. These characteristics are in line with those of the Northern Gondwana Province (Brenner 1976), Phytogeoprovince III (Srivastava 1978), and the West Africa-South America Province and Gondwana Province (*Dicheiropollis etruscus*/*Afropollis* Province) (Herngreen & Chlonova 1981; Herngreen *et al.* 1996).

Li & Batten (2011) proposed a new division of global palynophytogeographic regions after studying the Early Cretaceous palynoflora in China. Four realms are recognized, from north to south: The Boreal Realm, European-North American Realm, Pan-Tethys Realm, and South Gondwanan Realm (Fig. 8). The characteristic element of the Pan-Tethys Realm is *Dicheiropollis etruscus*, corresponding to Brenner's (1976) Northern Gondwana Province and Herngreen & Chlonova's (1981) West Africa-South American and Gondwana Province (or *Dicheiropollis etruscus*/*Afropollis* Province). Based on the abundance of *Dicheiropollis*, parts of China and Indochina are categorized in the Eastern Tethys Province of the Pan-Tethys Realm; southern Europe, South America, and northern Africa are grouped under the Western Tethys Province of the Pan-Tethys Realm. The palynological assemblage of the Sao Khua Fm is situated in the southernmost part of the Eastern Tethys Province in the Pan-Tethys Realm (Fig. 8).

CONCLUSIONS

The palynological investigation of the Sao Khua Fm in the southeastern Khorat Plateau, Thailand provides a deeper understanding of the palaeovegetation, palaeoclimate, and palynophytogeography. A total of 74 species from 43 genera have been identified, belonging to the *Punctatisporites-Dicheiropollis-Classopollis* assemblage. The age of the palynomorph assemblages is interpreted to be Valanginian. The evidence from palaeosols and the high diversity of spores indicate a humid subtropical climate at that time. However, the presence of abundant Cheirolepidiaceae pollen suggests periodic arid seasons, possibly associated with the Asian monsoon of the period. The Sao Khua Fm in Northern Thailand is characterized by a notable presence of *Dicheiropollis etruscus*, alongside various species of *Classopollis*, and typical pollen taxa, such as *Araucariacites*, *Inaperturopollenites*, *Ephedripites*, and *Eucommiidites*, among others. Bisaccate conifer pollen is rare, with a low percentage of spores, which is consistent with the typical flora of the Northern Gondwana province (or *Dicheiropollis etruscus*/*Afropollis* Province). Consequently, this assemblage represents a significant component of the flora within the Pan-Tethys Realm, situated in the southernmost part of the Eastern Tethys Province.

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REFERENCES

ABBINK O. A., VAN KONIJNENBURG-VAN CITTERT J. H. A. & VISSCHER H. 2004. — A sporomorph ecogroup model for the Northwest European Jurassic-Lower Cretaceous: concepts and framework. *Netherlands Journal of Geosciences/Geologie en Mijnbouw* 83: 17-38. https://doi.org/10.1017/s0016774600020436

ALVIN K. L. 1982. — Cheirolepidiaceae Biology,structure and paleoecology. *Review of Palaeobotany and Palynology* 37: 71-98. https://doi.org/10.1016/0034-6667(82)90038-0

ATFY H. E., MOSTAFA A., MAHER A., MAHFOUZ K. & HOSNY A. 2019. — Early Cretaceous biostratigraphy and palacoenvironment of the northern Western Desert, Egypt: an integrated palynological and micropalacontological approach. *Palacontographica* 299: 103-132. https://doi.org/10.1127/palb/2019/0064

BALME B. E. 1957. — Spores and pollen grains from the Mesozoic of Western Australia. Commonwealth Scientific and Industrial Research Organization. *Coal Research Section* 25: 1-48. https://doi.org/10.4225/08/585823888babf

BALME B. E. 1995. — Fossil in situ spores and pollen grains: An annotated catalogue. *Review of Palaeobotany and Palynology* 87: 81-323. https://doi.org/10.1016/0034-6667(95)93235-X

BATTEN D. J. 1996. — Upper Jurassic and Cretaceous miospores; *in* JANSONIUS J. & MCGREGOR D. C. (eds), *Palynology: Principles and Applications*. Volume 2. American Association of Stratigraphic Palynologists Foundation: 807-830.

BONIS N. R. & KÜRSCHNER W. M. 2012. — Vegetation history, diversity patterns, and climate change across the Triassic/Jurassic boundary. *Paleobiology* 38: 240-264. https://doi.org/10.1666/09071.1

BOULTER M. & WINDLE T. 1993. — A reconstruction of some Middle Jurassic vegetation in northern Europe. *Special Papers in Palaeontology* 49: 125-154.

BRENNER G. J. 1976. — Middle Cretaceous Floral Provinces and Early Migrations of Angiosperms, *in* BECK C. B. (ed.), *Origin and Early Evolution of Angiosperms*. Columbia University Press, New York: 23-47.

BURGER D. 1993. — Early and middle Cretaceous angiosperm pollen grains from Australia. *Review of Palaeobotany and Palynology* 78: 183-234. https://doi.org/10.1016/0034-6667(93)90065-3

CARTER A. & MOSS S. J. 1999. — Combined detrital-zircon fission-track and U-Pb dating: A new approach to understanding hinterland evolution. *Geology* 27: 235-238. https://doi.org/10.1130/0091-7613(1999)027%3C0235:CDZFTA%3E2.3.CO;2

CARTER A. & BRISTOW C. S. 2003. — Linking hinterland evolution and continental basin sedimentation by using detrital zircon thermochronology: a study of the Khorat Plateau Basin, eastern Thailand. *Basin Research* 15 (2): 271-285. https://doi.org/10.1046/j.1365-2117.2003.00201.x

COLE J. M., ABDELRAHIM O. B., HUNTER A. W., SCHRANK E. & ISMAIL M. S. B. 2017. — Late Cretaceous spore-pollen zonation of the Central African Rift System (CARS), Kaikang Trough, Muglad Basin, South Sudan: angiosperm spread and links to the Elaterates Province. *Palynology* 41 (4): 547-578. https://doi.org/10.1080/01916122.2017.1303795

COUPER R. A. 1958. — British Mesozoic microspores and pollen grains. A systematic and stratigraphic study. *Palaeontographica* 103: 75-179.

DE JERSEY N. J. 1959. — Jurassic spores and pollen grains from the Rosewood Coalfield. *Queensland Government Mining Journal* 60: 346-366.

DEAF A. S., HARDING, I. C. & MARSHALL, J. E. A. 2016. — Early Cretaceous palynostratigraphy of the Abu Tunis 1x borehole, northern Western Desert, Egypt, with emphasis on the possible palaeoclimatic effect upon the range of *Dicheiropollis etruscus* in North Africa. *Palynology* 40: 25-53. https://doi.org/10.1080/01916122.2014.993480

DETTMANN M. E. 1963. — Upper Mesozoic microfloras from southeastern Australia. *Proceedings of the Royal Society of Victoria* 77: 1-148.

DETTMANN M. E. 1986. — Early Cretaceous palynoflora of subsurface strata correlative with the Koonwarra Fossil Bed, Victoria (Australia). *Memoirs of the Association of Australasian Palaeontologists* 3: 79-110.

DETTMANN M. E. & CLIFFORD H. T. 1992. — Phylogeny and biogeography of *Ruffordia*, *Mohria* and *Anemia* (Schizaeaceae) and *Ceratopteris* (Pteridaceae): Evidence from in situ and dispersed spores. *Alcheringa* 16: 269-314.

DETTMANN M. E., MOLNAR R. E., DOUGLAS J. G., BURGER D., FIELDING C., CLIFFORD H. T., RANCIS J., JELL P., RICH T., WADE M., RICH P. V., PLEDGE N., KEMP A. & ROZEFELDS A. 1992. — Australian Cretaceous terrestrial faunas and floras: biostratigraphic and biogeographic implications. *Cretaceous Research* 13: 207-262. https://doi.org/10.1016/0195-6671(92)90001-7

DOYLE J. A., BIENS P., DOERENKAMP A. & JARDINÉ S. 1977. — Angiosperm pollen from the pre-Albian lower Cretaceous of equatorial Africa. *Bulletin des centres de recherches exploration-production Elf-Aquitaine* 1: 451-473.

EISAWI A., IBRAHIM A. B., ABDELRAHIM O. B. & SCHRANK E. 2012. — Palynozonation of the Cretaceous to Lower Paleogene strata of the Muglad Basin, Sudan. *Palynology* 36 (2): 191-207. https://doi.org/10.1080/01916122.2011.633634

FILATOFF J. 1975. — Jurassic palynology of the Perth Basin, Western Australia. *Palaeontographica* 154: 1-113.

FRIIS E. M., PEDERSEN K. R. & CRANE P. R. 2004. — Araceae from the Early Cretaceous of Portugal: Evidence on the emergence of mono-cotyledons. *Proceedings of the National Academy of Sciences* 101: 16565-16570. https://doi.org/10.1073/pnas.040717410

GAO R. Q., ZHAO C. B., QIAO X. Y., ZHENG Y. L., YAN F. Y. & WAN C. B. 1999. — *Cretaceous Oil Strata Palynologiy from Songliao Basin*. Geological Publishing House, Beijing, 373 p.

GARCIA G. G., GARCIA A. J. V. & HENRIQUES M. H. P. 2018. — Palynology of the Morro do Chaves Formation (Lower Cretaceous), Sergipe Alagoas Basin, NE Brazil: Paleoenvironmental implications for the early history of the South Atlantic. *Cretaceous Research* 90: 7-20. https://doi.org/10.1016/j.cretres.2018.03.029

GÜBELI A., HOCHULI P. A. & WILDI W. 1984. — Lower Cretaceous turbiditic sediments from the Central Rif chain (Northern Marocco). Palynology, stratigraphy and palaeogeographic setting. *Geologische Rundschau* 73, 1081-1114. https://doi.org/10.1007/bf01820889

GUIGNARD G., WANG Y. NI Q., TIAN N. & JIANG Z. 2009. — A dipteridaceous fern with in situ spores from the Lower Jurassic in Hubei, China. *Review of Palaeobotany and Palynology* 156: 104-115. https://doi.org/10.1016/j.revpalbo.2008.09.004

GUO X. P., WANG D. N., DING X. Z., ZONG W. M. & ZHOU W. 2011. — Early-Middle Cretaceous Sporopollen Assemblages and New Progress on Biogeography in the Northern Part of Tarim Basin. *Geological Review* 57 (6): 870-880.

HARRIS T. M. 1979. — *The Yorkshire Jurassic Flora*. V. *Coniferales*. British Museum (Natural History), London, 134p.

HASEGAWA H., IMSAMUT S., CHARUSIRI P., TADA R., HORIUCHI Y. & HISADA K. I. 2010. — Thailand was a desert during the mid-Cretaceous: Equatorward shift of the subtropical high-pressure belt indicated by eolian deposits (Phu Thok Formation) in the Khorat Basin, northeastern Thailand. *Island Arc* 19 (4): 605-621. https://doi.org/10.1111/j.1440-1738.2010.00728.x

HELBY R., MORGAN R. & PARTRIDGE A. D. 1987. — A palynological zonation of the Australian Mesozoic. *Association of Australasian Palaeontologists* 4: 1-94.

HERNGREEN G. F. W. & CHLONOVA A. F. 1981. — Cretaceous microfloral provinces. *Pollen et Spores* 23 (3-4): 441-555.

HERNGREEN G. F. W., KEDVES M., ROVNINA L. V. & SMIRNOVA S. B. 1996. — Cretaceous palynofloral provinces: a review, *in Palynology: Principles and Applications*. Volume 3. American Association of Stratigraphic Palynologists Foundation: 1157-1188.

HOCULI P. A. 1981. — North Gondwana floral elements in lower to middle Cretaceous rocks of the Southern Alps (southern Switzerland, northern Italy). *Review of Palaeobotany and Palynology* 35: 337-358.

HU Y., HU J., DU Y. B., LU H. N., YANG N., WANG L. & XU H. H. 2023. — Early Cretaceous palynofloras from the Bongor basin, Chad, and their palaeoenvironmental and palaeoclimatic significances. *Journal of African Earth Sciences* 198: 104793. https://doi.org/10.1016/j.jafrearsci.2022.104792

HUBBARD R. N. L. B. & BOULTER M. C. 1997. — Mid Mesozoic floras and climates. *Palaeontology* 40 (1): 43-70.

IED I. M. & TAHOUN S. S. 2019. — A Cretaceous sporomorph palynozonation and the palaeobiogeography of northern Egypt. *Palynology* 43 (3): 467-482. https://doi.org/10.1080/01916122.2018.1437091

JARDINÉ S., BIENS P. & DOERENKAMP A. 1974. — *Dicheiropollis etruscus*, un pollen caractéristique du crétacé inférieur Afro-Sudaméricain. *Sciences géologiques, bulletins et mémoires* 27: 87-100.

JI L.M. 1994. — The Provincialzation Position and Paleoclimate of the Early Cretaceous Microflora in the Minhe Basin, Gansu Province. *Acta Sedimentologica Sinica* 12 (2): 133-142.

JIANG D. X., WANG Y. D. & WEI J. 2008. — Palynoflora and its environmentals significance of the Early Cretaceous in Baicheng Xingjiang Autonomous Region. *Journal of Paleogeography* 10 (1): 77-86.

KASKA H. V. 1989. — A spore and pollen zonation of Early Cretaceous to Tertiary nonmarine sediments of Central Sudan. *Palynology* 54: 79-90.

KRUTZSCH W. 1963. — *Atlas der mittel-und jungtertiären dispersen Sporen-und Pollen-sowie der Mikroplanktonformen des nördlichen Mitteleuropas*. Lieferung 2. Veb. Deutscher Verlag der Wissenschaften, 141 p.

LEI Z. Q. 1993. — The discovery and significance of the late Jurassic sporopollen assemblage in peninsular Thailand, *in International Symposium on Biostratigraphy Of Mainland Southeast Asia: facies & paleontology*: 361-374.

LI J. G. & BATTEN D. J. 2004. — Early Cretaceous palynofloras from the Tanggula Mountains of the northern Qinghai-Xizang (Tibet) Plateau, China. *Cretaceous Research* 25: 531-542. https://doi.org/10.1016/j.cretres.2004.04.005

LI J. G. & BATTEN D. J. 2011. — Early Cretaceous palynofloral provinces in China: western additions. *Island Arc* 20 (1): 35-42.

LI W. B. 1984. — Palynology of Early Cretaceous of Jiaohe Basin, Jilin Province. Memoirs of Nanjing Institute of Geology and Palaeontology, *Academia Sinica* 19: 67-125.

LI W. B. 2000. — Early Cretaceous palynoflora from northern Tarim Basin. *Acta Palaeontologica* 39 (1): 28-45.

LI W. B. & LIU Z. S. 1994. — The Cretaceous palynofloras and their bearing on stratigraphic correlation in China. *Cretaceous Research* 15: 333-365. https://doi.org/10.1006/cres.1994.1021

LIN M. Q. & LI J. G. 2019. — Late Jurassic-Early Cretaceous palynofloras in the Lhasa Block, central Xizang, China and their bearing on palaeoenvironments. *Palaeogeography, Palaeoclimatology, Palaeoecology* 515: 95-106. https://doi.org/10.1016/j.palaeo.2018.05.038

LIU G. F., LIU R., WANG N., XU M. J. & DANG H. L. 2024. — Response to palaeoclimate by Early Cretaceous terrestrial organic-rich shales in the Yin'e Basin: Evidence from sporopollen, n-alkanes and their compound carbon isotopes. *Palaeogeography, Palaeoclimatology, Palaeoecology* 637: 112031. https://doi.org/10.1016/j.palaeo.2024.112031

MAHMOUD M. S., DEAF A. S., TAMAM M. A. & KHALAF M. M. 2019. — Revised (miospores-based) stratigraphy of the Lower Cretaceous succession of the Minqar-IX well, Shushan Basin, north Western Desert, Egypt: Biozonation and correlation approach. *Journal of African Earth Sciences* 151: 18-35. https://doi.org/10.1016/j.jafrearsci.2018.11.019

MANDER L. 2011. — Taxonomic resolution of the Triassic-Jurassic sporomorph record in East Greenland. *Journal Micropalaeontology* 30: 107-118. https://doi.org/10.1144/0262-821X11-012

MANITKOON S., DEESRI U., LAUPRASERT K., WARAPEANG P., NONSRIRACH T., NILPANAPAN A., WONGKO K. & CHANTHASIT P. 2022. — Fossil assemblage from the Khok Pha Suam locality of northeastern, Thailand: an overview of vertebrate diversity from the Early Cretaceous Khok Kruat Formation (Aptian-Albian). *Fossil Record* 25 (1): 83-98. https://doi.org/10.3897/fr.25.83081

MEESOOK A. 2000. — Cretaceous environments of northeastern Thailand. *Cretaceous Environments of Asia* 17: 207-223. https://doi.org/10.1016/s0929-5446(00)80034-5

MEESOOK A. 2011. — Cretaceous, *in* RIDD M., BARBER A. & CROW M. (eds), *The Geology of Thailand.* Geological Society of London, 169-184.

MIAO S. J., YU J. X., QU L. F., ZHANG W. P., ZHANGF Q. B. & ZHANG D. H. 1984. — *Paleontological Atlas of North China.* Volume 3. Geological publishing house, Beijing, 857 p.

MICHELS F. H., SOUZA P. A. & PREMAOR E. 2018. — Aptian-Albian palynologic assemblages interbedded within salt deposits in the Espírito Santo Basin, eastern Brazil: Biostratigraphical and paleoenvironmental analysis. *Marine and Petroleum Geology* 91: 785-799. https://doi.org/10.1016/j.marpetgeo.2018.01.023

MÜLLER J., DI GIACOMO E. D. & VAN ERVE A. W. 1987. — A palynological zonation for the Cretaceous, Tertiary, and Quaternary of Northern South America. *American Association of Stratigraphic Palynologists, Contribution Series* 19: 7-76.

PU R. G. & WU H. Z. 1982. — Sporo-Pollen from the Late Mesozoic Beds in Eastern Heilongjiang Province. *Bulletin of the Shenyang Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences* 5: 338-456.

PU R. G. & WU H. Z. 1985. — Sporopollen Assemblages and their stratigraphical significance of the Hingganling and Zhalainuoer Groups in Hingganling Region, Northeast China. *Bulletin of the Shenyang Institute of Geology and Mineral Resuorces, Chinese Academy of Geological Sciences* 11: 47-113.

Racey A., Love M. A., Canham A. C., Goodhall J. G. S., Polachan S. & Jones, P. D. 1996. — Stratigraphy and reservoir potential of the Mesozoic Khorat Group, north eastern Thailand: Part 1, Stratigraphy and Sedimentary Evolution. *Journal of Petroleum Geology* 19 (1): 5-39.

Racey A. & Goodall J. G. 2009. — Palynology and stratigraphy of the Mesozoic Khorat Group red bed sequences from Thailand. In: Buffetaut, E., Cuny, G., Le Loeuff, J., Suteethorn, V. (eds), Late Palaeozoic and Mesozoic Continental Ecosystems in SE Asia. *Geological Society*, Special Publications, London, 315: 69-83. https://doi.org/10.1144/SP315.6

Rodríguez-Barreiro I., Santos A. A., Arribas M. E., Mas R., Arribas J., Villanueva-Amadoz U., Fernández-Baldor F. T. & Diez J. B. 2022. —The Jurassic-Cretaceous transition in the West Cameros Basin (Tera Group, Burgos, Spain): sedimentological and palynostratigraphical insights. *Cretaceous Research* 139: 105300. https://doi.org/10.1016/j.cretres.2022.105300

Rodríguez-Barreiro I., Santos A. A., Villanueva-Amadoz U., Gasulla J. M., Escaso F., Ortega F., Gee C. T. & Diez J. B. 2024. — Palynological reconstruction of the habitat and diet of *Iguanodon bernissartensis* in the Lower Cretaceous Morella Formation, NE Iberian Peninsula. *Cretaceous Research* 156: 105804. https://doi.org/10.1016/j.cretres.2023.105804

Salard-Cheboldaeff M. 1990. — Intertropical African palynostratigraphy from Cretaceous to Late Quaternary times. *Journal of African Earth Sciences* 11: 1-24. https://doi.org/10.1016/0899-5362(90)90072-M

Santos A. A., Jain S. & Diez J. B. 2021. — Upper Jurassic palynology from the Blue Nile Basin (Ethiopia). *Review of Palaeobotany and Palynology* 285: 104361. https://doi.org/10.1016/j.revpalbo.2020.104361

Santos A. A., Piñuela L., Rodríguez-Barreiro I., García-Ramos J. C. & Diez J. B. 2022. — Jurassic Palynology from "The Dinosaur Coast" of Asturias (Lastres Fm., Northwestern Spain): Palynostratigraphical and Palaeoecological Insights. *Biology* 11: 1695. https://doi.org/10.3390/biology11121695

Schrank E. 1992. — Nonmarine Cretaceous correlations in Egypt and northern Sudan: palynological and palaeobotanical evidence. *Cretaceous Research* 13: 351-368. https://doi.org/10.1016/0195-6671(92)90040-W

Scotese C. R. 2021. — An atlas of Phanerozoic paleogeographic maps: the seas come in and the seas go out. *Annual Review of Earth and Planetary Sciences* 49: 679-728. https://doi.org/10.1146/annurev-earth-081320-064052

Slater S. M., Twitchett R. J., Danise S. & Vajda V. 2019. — Substantial vegetation response to Early Jurassic global warming with impacts on oceanic anoxia. *Nature Geoscience* 12 (6): 462-467. https://doi.org/10.1038/s41561-019-0349-z

Song Z. C., Liu G. W., Li W. B., Jia B. L. & Hua R. H. 1986. — *Early Cretaceous palynological assemblages from Eren Basin, Inner Mongolia, China. Cretaceous Ostracod and Sporo-Pollen Fossils of Eren Basin, Inner Mongolia, China*. Anhui Science and Technology, Publishing House, Hefei: 106-334.

Song Z. C., Shang G. Y., Liu Z. S., Huang P., Wang X. F., Qian L. J., Du B. A. & Zhang D. H. 2000. — *Fossil Spores and Pollen of China*. Volume 2. The Mesozoic spores and pollen. Science Press, Beijing, 710 p.

Song Z. C., Zheng Y. H., Li M. Y., Zhang Y. Y., Wang W. M., Wang D. N., Zhao C. B., Zhou S. F., Zhu Z. H. & Zhao Y. N. 1999. — *Fossil spores and pollen of China*. Volume 1. Late Cretaceous Tertiary spores and pollen. Science Press, Beijing, 910 p.

Srivastava S. K. 1978. — Cretaceous spore-pollen floras: a global evaluation. Biological Memoirs 3 (1), *Palaeopalynology Series* 5: 1-130.

Thusu B. & van der Eem J. G. L. A. 1985. — Early Cretaceous (Neocomian-Cenomanian) palynomorphs. *Journal of Micropalaeontology* 4 (1): 131-150.

Tiwari R. S. & Tripathi A. 1995. — Palynological assemblages and absolute age relationship of intertrappean beds in the Rajmahal Basin, India. *Cretaceous Research* 16 (1): 53-72. https://doi.org/10.1006/cres.1995.1004

Traverse A. 2007. — *Paleopalynology*. Dordrecht: Springer Science & Business Media 1-813. https://doi.org/10.1007/978-1-4020-5610-9

Trevisan L. 1971. — *Dicheiropollis*, a pollen type from Lower Cretaceous sediments of southern Tuscany (Italy). *Pollen et Spores* 13 (4): 561-596.

Tripathi A. 2008. — Palynochronology of Lower Cretaceous volcano-sedimentary succession of the Rajmahal Formation in the Rajmahal Basin, India. *Cretaceous Research* 29: 913-924. https://doi.org/10.1016/j.cretres.2008.05.008

Tucker R. T., Hyland E. G., Gates T. A., King M. R., Roberts E. M., Foley E. K., Berndt D., Hanta R., Khansubha S., Aswasereelert W. & Zanno L. E. 2022. — Age, depositional history, and paleoclimatic setting of Early Cretaceous dinosaur assemblages from the Sao Khua Formation (Khorat Group), Thailand. *Palaeogeography, Palaeoclimatology, Palaeoecology* 601: 111107. https://doi.org/10.1016/j.palaeo.2022.111107

Uwins P. J. R. & Batten D. J. 1988. — *Early to mid-Cretaceous palynology of northeast Libya. Subface Palynostratigraphy Northeast Libya*: 215-257.

Valeria S. P. L., Loinaze P., Césari S. N., Giordano S. R., Stach N. H. & Ansa A. 2019. — Palynological analysis of a Lower Cretaceous subsurface succession from the south flank of the Golfo San Jorge Basin, Argentina. *Cretaceous Research* 97: 94-106. https://doi.org/10.1016/j.cretres.2019.01.008

Valeria S. P. L., Magdalena L., Agustín R. R., José O. A. & Nicolás F. 2024. — New palynological record for the Puesto Albornoz Formation (Golfo San Jorge basin, Argentina): Stratigraphic and paleoenvironmental implications. *Journal of South American Earth Sciences* 135: 104804. https://doi.org/10.1016/j.jsames.2024.104804

Vallati P. 2001. — *Bioestratigrafía (Palinología) del Cretácico tempranoy medio en Patagonia septentrionaly central*. PhD thesis, Universidad Nacional de la Patagonia San Juan Bosco, 278 p.

Van Konijnenburg-Van Cittert J. H. 1971. — In situ gymnosperm pollen from the Middle Jurassic of Yorkshire. *Acta Botanica Neerlandica* 20: 1-96. https://doi.org/10.1111/j.1483-8677.1971. tb00688. x

Van Konijnenburg-Van Cittert, J. H. 1993. — A review of the Matoniaceae based on in situ spores. *Review of Palaeobotany and Palynology* 78 (3-4): 235-267. https://doi.org/10.1016/0034-6667(93)90066-4

Van Konijnenburg-Van Cittert J. H. & Van der Burgh J. 1989. — The flora from the Kimmeridgian (Upper Jurassic) of Culgower, Sutherland, Scotland. *Review of Palaeobotany and Palynology* 61: 1-51. https://doi.org/10.1016/0034-6667(89)90060-2

Volkheimer W., Gallego O. F., Cabaleri N. G., Armella C., Narváez P. L., Silva Nieto D. G. & Páez M. A. 2009. — Stratigraphy, palynology, and conchostracans of a Lower Cretaceous sequence at the Cañadón Calcáreo locality, Extra-Andean central Patagonia: age and palaeoenvironmental significance. *Cretaceous Research* 30: 270-282. https://doi.org/10.1016/j.cretres.2008.07.010

Wang D. N., Wang X. R. & Ji Q. 2016. — The Palynoflora Alternation and the Paleoclimate Change at the Turning Time between Late Jurassic and Early Cretaceous in Northern Hebei and Western Liaoning. *Acta Geoscientica Sinica* 37 (4): 449-459.

Weerakoon W. A. P., Joshi H., Aggarwal N., Jha, N., Jayasena H. A. H., Yakandawala D., Chandrajith R., Ratnayake N. P. & Tiwari P. 2021. — Late Jurassic-Early Cretaceous palynostratigraphy and palaeoclimate in the Andigama Basin, Sri Lanka. *Journal of Asian Earth Sciences* 6: 100067. https://doi.org/10.1016/j.jaesx.2021.100067

WEYLAND H. & KRIEGER W. 1953. — Die Sporen und Pollen der Aachener Kreide und ihre Bedeutung fur die Charakterisierung des mittleren Senons. *Palaeontographica* B: 2-29.

WHEELER A., SHEN J., MOORE T. A., MOROENG O. M. & LIU J. 2022. — Palaeoecology and palaeoclimate of an Early Cretaceous peat mire in East Laurasia (Hailar Basin, Inner Mongolia, China). *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology* 599: 111050. https://doi.org/10.1016/j.palaeo.2022.111050

YANG X. J., LI W. B. & BATTEN D. J. 2007. — Biostratigraphic and palaeoenvironmental implications of an Early Cretaceous miospore assemblage from the Muling Formation, Jixi Basin, northeast China. *Cretaceous Research* 28 (2): 339-347. https://doi.org/10.1016/j.cretres.2006.07.008

YAROSHENKO O. P. & ALEKSANDROVA G. N. 2015. — Lower Cretaceous palynological assemblages of the Levashi Formation in the Aimaki section of Central Dagestan. *Stratigraphy and Geological Correlation* 23 (1): 24-44. https://doi.org/10.1134/S0869593814060070

YU J. X. & HAN X. P. 1985. — *Cretaceous spore-pollen of Jiangxi*. Geological Publishing House, Beijing, 1-200.

YU J. X., ZHANG Z. L. & ZHOU S. F. 1985. — The Discovery of a New Monosulcate Pollen- *Zhonghuapollis* gen. nov. and Its Startigraphical Significance. *Acta Botanica Sinica* 27 (5): 532-537.

ZHANG M. Z., DAI S., HEIMHOFER U., WU M. X., WANG Z. X. & PAN B. T. 2014. — Palynological records from two cores in the Gongpoquan Basin, central East Asia – Evidence for floristic and climatic change during the Late Jurassic to Early Cretaceous. *Review of Palaeobotany and Palynology* 204: 1-17. https://doi.org/10.1016/j.revpalbo.2014.02.001

ZHANG M. Z., HOU X. W., DU B. X., JI L. M., DU Z. & WANG S. 2019. — The first palynological records from the Lower Cretaceous of the northern Sichuan Basin, China: Palynostratigraphical and paleoenvironmental significance. *Journal of Asian Earth Sciences* 174: 177-188. https://doi.org/10.1016/j.jseaes.2018.12.005

ZHANG W. P. 1995. — Occurrence of *Dicheiropollis* form the Anning Formation in the Fumin Basin, Yunnan and its significance. *Acta Micropalacontologica Sinica* 12 (1): 39-49.

ZIAJA J. 2006. — Lower Jurassic spores and pollen grains from Odrowąż, Mesozoic margin of the Holy Cross Mountains, Poland. *Acta Palaeobotanica* 46: 3-83.

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