

Research papers

Terrestrial end-Guadalupian crisis constrained by mid-latitude Permian palynological data from Jimsar, Junggar Basin, China

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ABSTRACT

The end-Permian mass extinction and the end-Guadalupian crisis are the most remarkable events in the Permian terrestrial ecosystem. To better understand the end-Guadalupian event in mid-latitude of Pangea in the Northern Hemisphere, palynological investigations are conducted on the terrestrial Permian deposits in the Dalongkou profile of Jimsar, northern Xinjiang, China. Two palynological assemblages are recognized in stratigraphic ascending order, the *Cordaitina subrotata*–*Striatoabietes lipidus*–*Protowellitschiapollis exoleucus* assemblage from the uppermost Lucaogou, Hongyanchi and the lower Quanzijie formations, and the *Kraeuselisporites spinulosus*–*Tuberculatosporites homotubercularis*–*Potonieisporites turpanensis* assemblage from the upper Quanzijie and lowermost Wutonggou formations. Based on the palynological data, the uppermost Lucaogou and Hongyanchi formations are assigned to the Roadian stage, and the lower Quanzijie Formation to the Capitanian stage, and the upper Quanzijie and lowermost Wutonggou formations to the Wuchiapingian stage. Thus, a Wordian-age hiatus is confirmed between the lower Quanzijie Formation and the Hongyanchi Formation on the basis of palynological evidence. The palynofloral succession shows a smooth transition between the Guadalupian and Lopingian palynofloras in the Dalongkou profile of Jimsar, in the Junggar Basin. The end-Guadalupian crisis resulted in a 17% loss of pollen species, indicating that the extinction was on the background level.

1. Introduction

The Permian was one of the most critical intervals in Earth's history (Lucas and Shen, 2018; Shen et al., 2019), marked by major biological crises at the Guadalupian–Lopingian boundary and the Permian–Triassic boundary (Stanley and Yang, 1994). The end-Permian mass extinction was selective even for marine benthos such as fusulines, rugose corals, brachiopods, and bryozoans (Stanley and Yang, 1994; Shi et al., 1999; Wang and Sugiyama, 2000; Isozaki et al., 2007; Hermann et al., 2011; Isozaki, 1997; Hallam and Wignall, 1999; Shen and Shi, 2002, 2009; Powers and Bottjer, 2007; Clapham et al., 2009; Wignall et al., 2011). The end-Guadalupian crisis was also considered severe for the terrestrial ecosystems, resulting in the transition from paleophytic to mesophytic vegetation which is recorded in Gondwana in the high latitudes of Southern Hemisphere and the North China plate in the sub-tropic (Shen, 1995; Retallack et al., 2006; Stevens et al., 2011).

However, the Permian terrestrial chronostratigraphy in North China

remains controversial, including the question of whether the hiatus between the Upper Shihhotse Formation and the Sunjiagou Formation covers the entire Guadalupian (Shen et al., 2019, 2022). The Permian stratigraphy in the Tarim, Turpan–Hami and Junggar basins in Xinjiang is also debated (Shen et al., 2019; Tang et al., 2022). This uncertainty has hampered investigations of the terrestrial end-Guadalupian crisis and the critical transitions in vegetation. The Upper Shihhotse Formation in Henan Province, North China, which yields the fossil plant *Chiropteris* (*Nystroemia*), has been assigned to the Guadalupian stage based on the zircon U–Pb dating of volcanic ash layers (Li et al., 2023a). In addition, fossil plants from the Pingdiquan Formation in the eastern Junggar Basin have been assigned to the Guadalupian, too (Huang et al., 2023). Thus, the Permian succession in North China and in the Junggar Basin, northwestern China, might record the vanishing of some species and the appearance of new species, and the transformation in vegetation from a paleophytic to a mesophytic flora during the Guadalupian–Lopingian transition. The Junggar Basin, which was located in mid-

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latitude Pangea in the Northern Hemisphere during the Permian, contained vegetation of the Angara flora, like the vegetation in Gansu, Inner Mongolia, and northeastern China (Huang, 1977, 1993, 1995; Zhu and Shen, 1977; Hu, 1980; Sun, 1989; Wu, 1993). The lithostratigraphy, biostratigraphy, paleontology, and geochemistry of the Permian–Triassic boundary have been investigated extensively (IGCAGS and IGXBGM, 1986; Cheng et al., 1997; Warts et al., 2000; Li et al., 2003; Hou, 2004; Pang and Jin, 2004; Foster and Afonin, 2005; Cao et al., 2008; Metcalfe et al., 2009; Yang et al., 2010; Wang et al., 2016; Wan et al., 2016); however, the Guadalupian–Lopingian transition is less well understood.

In this study, palynological assemblages from the Lucaogou, Hongyanchi, Quanzijie, and Wutonggou formations in the Dalongkou profile at Jimsar were studied. On the basis of these data, the geological ages of the formations are reconsidered, and the palynofloral changes during the Guadalupian–Lopingian transition are assessed. This new information enables us to better understand the end-Guadalupian crisis in mid-latitude Angara flora.

2. Geological setting

The Junggar Basin, located along the northern margin of the North Tianshan Mountains and the Bogda Mountains, covers an area of approximately $1.3 \times 10^5 \text{ km}^2$ (Imin et al., 2020). The basin is surrounded by the Kazakhstan block, the Siberian plate, and the Tarim plate (Kröner et al., 2008), and is an important tectonic unit in the Central Asian Orogenic Belt (Sengor et al., 1993; Windley et al., 2007; Briggs et al., 2007), one of the largest continental accretion belts on Earth (Li et al., 1992; Choulet et al., 2011; Xu et al., 2015). The Junggar terrane was located in the mid-latitude (30°N – 45°N) during the Permian (Zhao et al., 2018) and was attached to the southeast part of the Siberian plate (Olariu et al., 2022) (Fig. 1). During the middle and late Permian, when the Paleo-Asian Ocean was closing, the Junggar terrane collided with the North Tianshan and South Tianshan terranes as well as the Tarim plate, and the sedimentary setting of the Junggar Basin changed from a marginal continental sea to a terrestrial basin (Xiao et al., 2008, 2010; Olariu et al., 2022). Subsequently, the Junggar–Tarim united continent was integrated with the Jiamusi–Mongolia terrane and the North China plate (Huang et al., 2023).

The Permian deposits in the Junggar Basin are composed of the Cisuralian marine limestone containing brachiopod fossils and the Guadalupian–Lopingian siliceous sediments deposited in the lacustrine and fluvial environments, bearing plants, fresh-water bivalves, ostracods, conchostracans, fishes, amphibians, and reptiles (XBGM, 1999). The Permian succession studied herein is the Dalongkou profile, located 8 km south of the Santai Town, Jimsar County, northern Xinjiang, on the southern margin of the Junggar Basin (location of the base of the profile: $43^\circ57'22''\text{N}$, $88^\circ51'50''\text{E}$, 1111.29 m elevation; top of the profile: $43^\circ57'13''\text{N}$, $88^\circ51'40''\text{E}$, 1159.71 m elevation). The measured strata consist of the uppermost Lucaogou Formation (P_2l), the Hongyanchi Formation (P_2h), the Quanzijie Formation (P_{2-3q}), and the lowermost Wutonggou Formation (P_3w). The total thickness of the succession in the Dalongkou profile is 272.49 m (Figs. 1, 2). This locality is well known as a site that contains the terrestrial Permian–Triassic boundary, and was suggested as a candidate for the non-marine Permian–Triassic boundary global stratotype section and point (IGCAGS and IGXBGM, 1986; Cheng and Lucas, 1993; Liu, 1994; Metcalfe et al., 2009).

The strata in the Dalongkou profile starts from the uppermost part of the Lucaogou Formation in the core of the Dalongkou anticline. The upper part of the Lucaogou Formation is mainly composed of black and dark gray shale and carbonaceous shale, with a few intercalations of thin-bedded (0.10–0.25 m thick) argillaceous siltstone. This part of the succession is 26.75 m thick. Fifty palynological samples were collected from the uppermost Lucaogou Formation (sample numbers XDPS001 to XDPS050). The lacustrine fine-grained sediments in the Dalongkou profile are correlated with those of the type profile of the Lucaogou

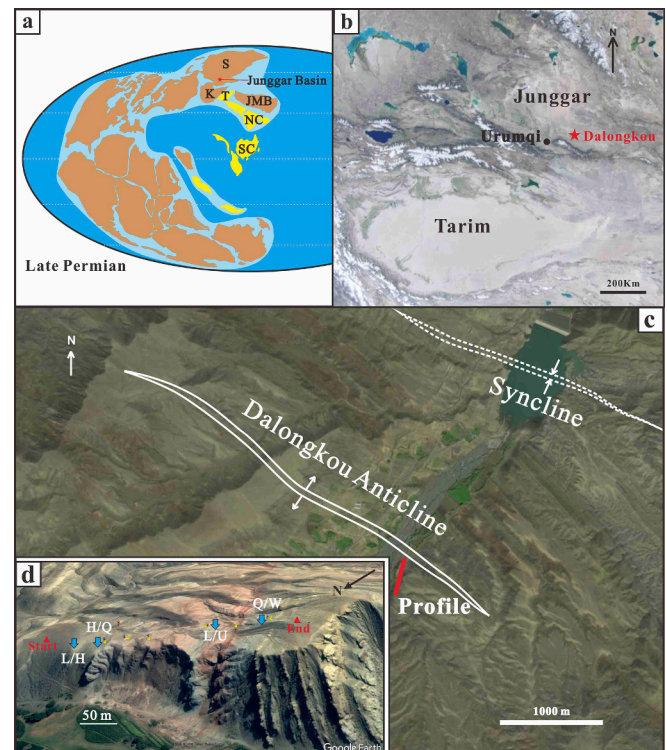


Fig. 1. Location and measured profile of Guadalupian and Lopingian transition at Dalongkou in Jimsar, northern Xinjiang, China. a. Reconstructed topography in Late Permian (Zhao et al., 2018). S: Siberian plate; K: Kazakhstan block; T: Tarim plate; NC: North China plate; SC: South China Plate; JMB: Jiamusi-Mongolia terrane. b, c, d. Location of the studied profile (red star and red line) in southern Junggar Basin. L/H: the boundary between the Lucaogou (P_2l) and Hongyanchi (P_2h) formations; H/Q: the boundary between Hongyanchi and Quanzijie (P_{2-3q}) formations; Q/W: the boundary between Quanzijie and Wutonggou (P_3w) formations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Formation at Cangfanggou in Urumqi. The formation at the type profile is 659.6 m thick and consists of black, dark gray, and brown shale, oil-shale, and siltstone, bearing ostracods (e. g., *Darwinula monitoria*), bivalves (e. g., *Anthraconauta pseudophilipsis*), fishes (*Chichia* sp., *Turfania* sp., *Tianshaniscus longipterus*), fossil plants, spores, and pollen (XBGM, 1999).

The Hongyanchi Formation is named after the locality Hongyanchi reservoir, south of Urumqi. The formation is 673.3 m thick at Hongyanchi, conformably overlies the gray shale and dolomite of the Lucaogou Formation, and consists of green and gray fine-grained sandstone, mudstone, shale and marlite, bearing bivalves, ostracods, conchostracans, fishes, and fossil plants (XBGM, 1999). At the Dalongkou profile, the Hongyanchi formation is 27.27 m thick and consists of thick-bedded grayish-yellow conglomerate that unconformably overlies the black laminated carbonaceous shale of the Lucaogou Formation. Fifteen palynological samples (XDPS051 to XDPS065) were collected from the Hongyanchi Formation.

The Quanzijie Formation is named after the Quanzijie Town, 25 km south of Jimsar. The formation is 183.26 m thick at the type profile, but 233.73 m thick at Dongwancun profile ($43^\circ53'10''\text{N}$, $89^\circ10'00''\text{E}$; Liu, 1994), 13 km north of Quanzijie Town. The Quanzijie Formation is 199.66 m thick at the Dalongkou profile, and its basement is a grayish-purple thick-bedded conglomerate that unconformably overlies on the green and black silty mudstone of the Hongyanchi Formation. The Quanzijie Formation is divided into a lower member (96.11 m thick) and an upper member (103.55 m thick). Sixty-eight samples (XDPS066 to XDPS133) were collected from the lower member and thirty-three

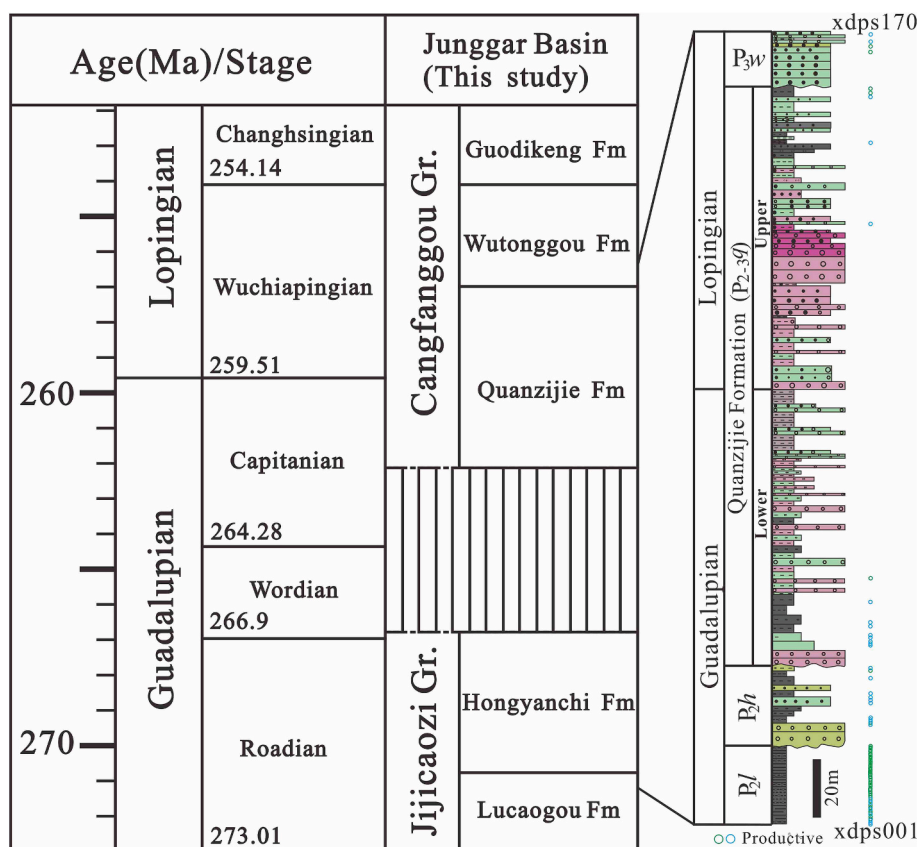


Fig. 2. Guadalupian and Lopingian stratigraphy and measured column at Dalongkou in Jimsar, northern Xinjiang, China.

samples (XDPS134 to XDPS166) from the upper member.

The Wutonggou Formation consists of grayish or yellowish-green sandstone, siltstone, and mudstone, usually with conglomerate at the base of sandstone beds. The boundary between the Wutonggou and Quanzijie formations is marked by a thick layer of coarse-grained pebbly sandstone. The lower part of the Wutonggou Formation is 18.82 m thick. Four palynological samples (XDPS167 to XDPS170) were collected from this formation (Fig. 2).

3. Materials and methods

A total of 170 samples were collected for palynological studies of the Dalongkou profile. The samples were treated with standard palynological procedures to extract and concentrate the organic residues of spores and pollen (Kaiser and Ashraf, 1974). For maceration, 50 g of sample was crushed, and treated with HCl (30%) and HF (40%) for 3–4 days to remove the calcium and silica, respectively. Subsequently, the samples were floated with ZnCl₂-mixed KI heavy liquid (2.2 g/cm³) and decolorized by HNO₃ for 5–6 days. A sieve (8-μm mesh) (BioDesign Inc. of New York, the United States) was used in all the steps to wash the residues with distilled water (Li et al., 2023b). The residues were transformed by gelatin to the slides, and observed, measured and photographed by an Olympus BX51 microscope with a cool CCD (ProgRes C5), and mounted on the stubs for scanning electron microscope (JEOL-6700F) observation. An England finder was used for positioning the pollen and spores. All slides and stubs are numbered with the prefix XDPS- and permanently housed in the Research Center of Paleontology and Stratigraphy, Jilin University, Changchun, China. A total of 4658 grains of pollen and spores were observed from 80 productive samples, from which 78 species in 40 genera were identified. Of these taxa, 20 species in 17 genera were described herein (Figs. 3, 4). Thirty-five samples that each yielded >100 grains of pollen and spores were

quantitatively analyzed; four samples (xdps18, xdps92, xdps166, xdps167) that each produced 71–92 grains were counted. The fossil images were edited using the software Helicon Focus (7.0.2) for focus stacking and the CorelDraw (X4) for cropping and rotation, without embellishment. The Software TILIA (2.1.1) was used for statistical analysis of pollen and spores.

4. Results

4.1. Systematic palynology

LYCOPHYTES

Order: SELAGINELLALES

Family: SELAGINELLACEAE

Genus: *Kraeuselisporites* (Leschik) Jansonius, 1964

Species: *Kraeuselisporites argutus* Hou et Wang, 1986

Fig. 3b

1986 *Kraeuselisporites argutus* Hou et Wang, Hou and Wang, p. 85, pl. 21, fig. 24 (holotype); pl. 25, fig. 27.

2017 *Kraeuselisporites argutus* Hou et Wang, Ouyang et al, p. 484, pl. 126, figs. 2, 3.

Description: The trilete spore is convexly sub-triangular in equatorial contour with rounded corners. Sinuous laesurae reach the sexine at the equator with a narrow labrum of 0.8 μm wide. The nexine is thick with a equatorial thickening of 4 μm wide. The sculpture of nexine is reticulate with several strong cone-spines, 4.6 μm in diameter and 1.9 μm in height. Sexine is thin, forming an equatorial cingulum of 4 μm wide. Sparse spines distribute on the distal surface and the equator, measuring 0.9–1.1 μm in diameter and 1.4–2.9 μm in height.

Comparison: The present material is characterized by strong cone-spines in the nexine and sparse high spines in the sexine, which are consistent with the holotype and other materials from the Lopingian

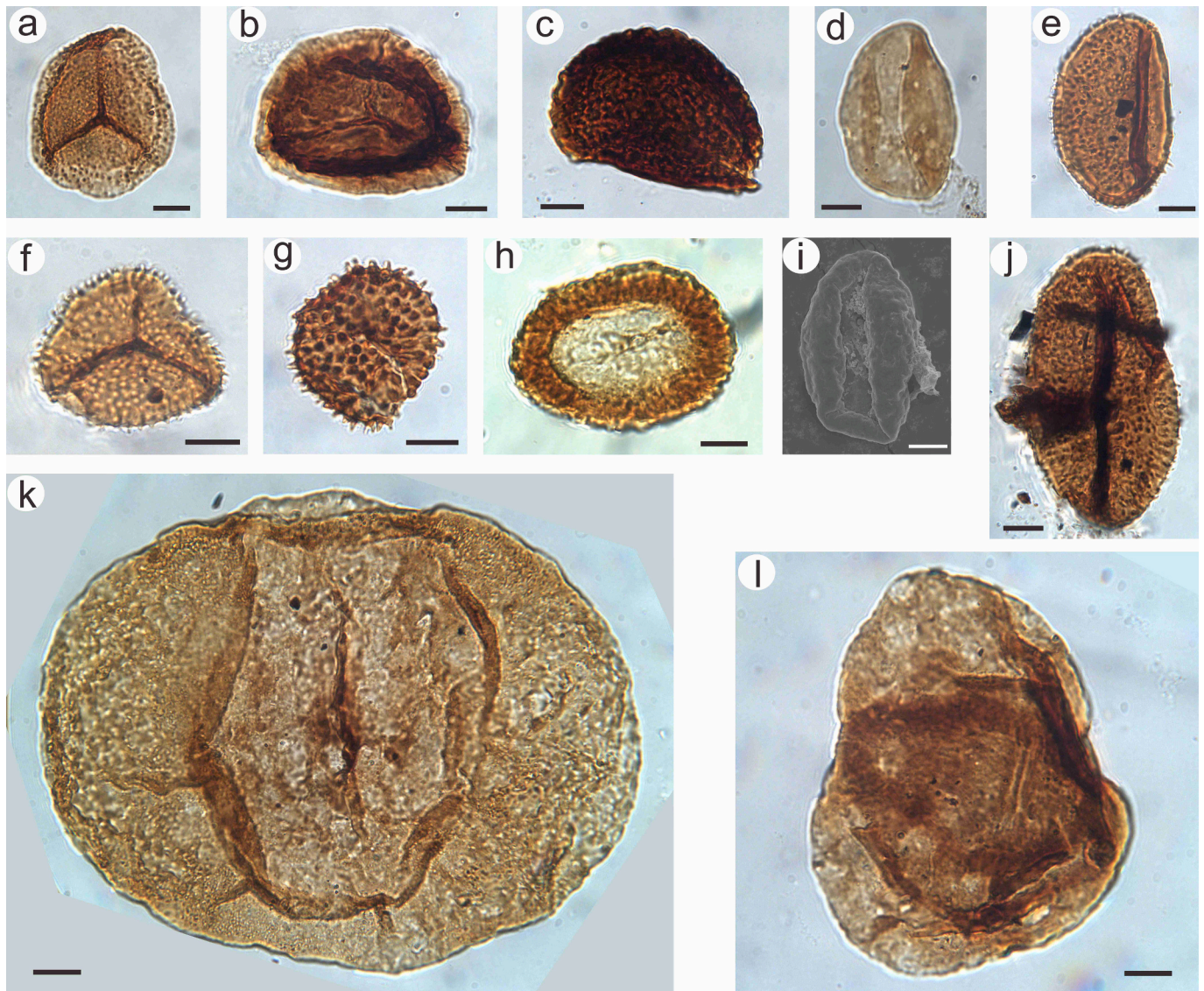


Fig. 3. Selected Guadalupian and Lopingian spores and pollen at Dalongkou in Jimsar, northern Xinjiang, China. a. *Kraeuselisporites spinulosus* (xdps165, G12-1); b. *Kraeuselisporites argutus* (xdps165, B41-1); c. *Schopfites phalacrois* (xdps166, B41-2); d, i. *Cycadopites retroflexus* (d-xdps45, B37-2; i-SEM-xdps24); e, j. *Tuberculatosporites homotubercularis* (e-xdps165, Q14-1; j-xdps166, F10-2); f. *Acanthotriletes rectispinus* (xdps165, L17-4); g. *Raistrickia obtusosetosa* (xdps167, P8-4); h. *Cordaitina subrotata* (xdps52, O22-4); k. *Potoniisporites turpanensis* (xdps168, H18-1); l. *Trochosporites reniformis* (xdps52, N30-3). Scale bar = 10 μ m.

Wutonggou Formation in Dalongkou of Jimsar, northern Xinjiang, China (Hou and Wang, 1986; Ouyang et al., 2017).

Stratigraphic horizon: upper Quanzijie Formation, Wuchiapingian.

Species: *Kraeuselisporites spinulosus* Hou et Wang, 1986.

Fig. 3a

1986 *Kraeuselisporites spinulosus* Hou et Wang, Hou and Wang, p. 85, pl. 21, figs. 22, 23 (holotype), 31.

1999 *Kraeuselisporites spinulosus* Hou et Wang, Ouyang and Norris, p. 31, pl. 4, figs. 6–8.

2003 *Kraeuselisporites spinulosus* Hou et Wang, Zhou, in Ouyang et al., pl. 16, fig. 1; pl. 102, fig. 11.

2017 *Kraeuselisporites spinulosus* Hou et Wang, Ouyang et al., p. 486, pl. 126, figs. 4, 9.

Description: The spore is trilete, $45 \times 46 \mu$ m in size, with a circular equatorial contour. The laesurae are straight, extending to the equatorial nexine. The labrum is 1.1μ m in width. The sexine is thin, forming an equatorial cingulum of $5\text{--}10 \mu$ m wide. The equatorial cingulum is covered by granules and spines that are $0.5\text{--}0.8 \mu$ m in diameter and $0.6\text{--}1.5 \mu$ m in height, respectively. The nexine is $1.3\text{--}2.0 \mu$ m thick,

bearing cone-spines and granules on distal and proximal surfaces, respectively. The cone-spines are acute, 0.8μ m in diameter and 0.5μ m in height.

Comparison: The present material is quite consistent with holotype from the Lopingian Wutonggou Formation at Dalongkou in Jimsar, northern Xinjiang, in having a cingulum and the dense small acute cone-spines on the nexine (Hou and Wang, 1986; Ouyang et al., 2017). However, the materials of the Lopingian Guodikeng Formation (Ouyang et al., 2017; Ouyang and Norris, 1999) are slightly different from the present material in having short laesurae.

Stratigraphic horizon: upper Quanzijie Formation, Wuchiapingian.

PTERIDOPHYTES

Order: ZYGOPTERIDALES

Family: ZYGOPTERIACEAE

Genus: *Raistrickia* (Schopf, Wilson and Bental) Potonié et Kremp, 1954

Species: *Raistrickia obtusosetosa* (Luber) Faddeeva, 1990

Fig. 3g

1941 *Azonotrilites obtusosetosus* Luber, in Luber and Waltz, p. 67, pl.

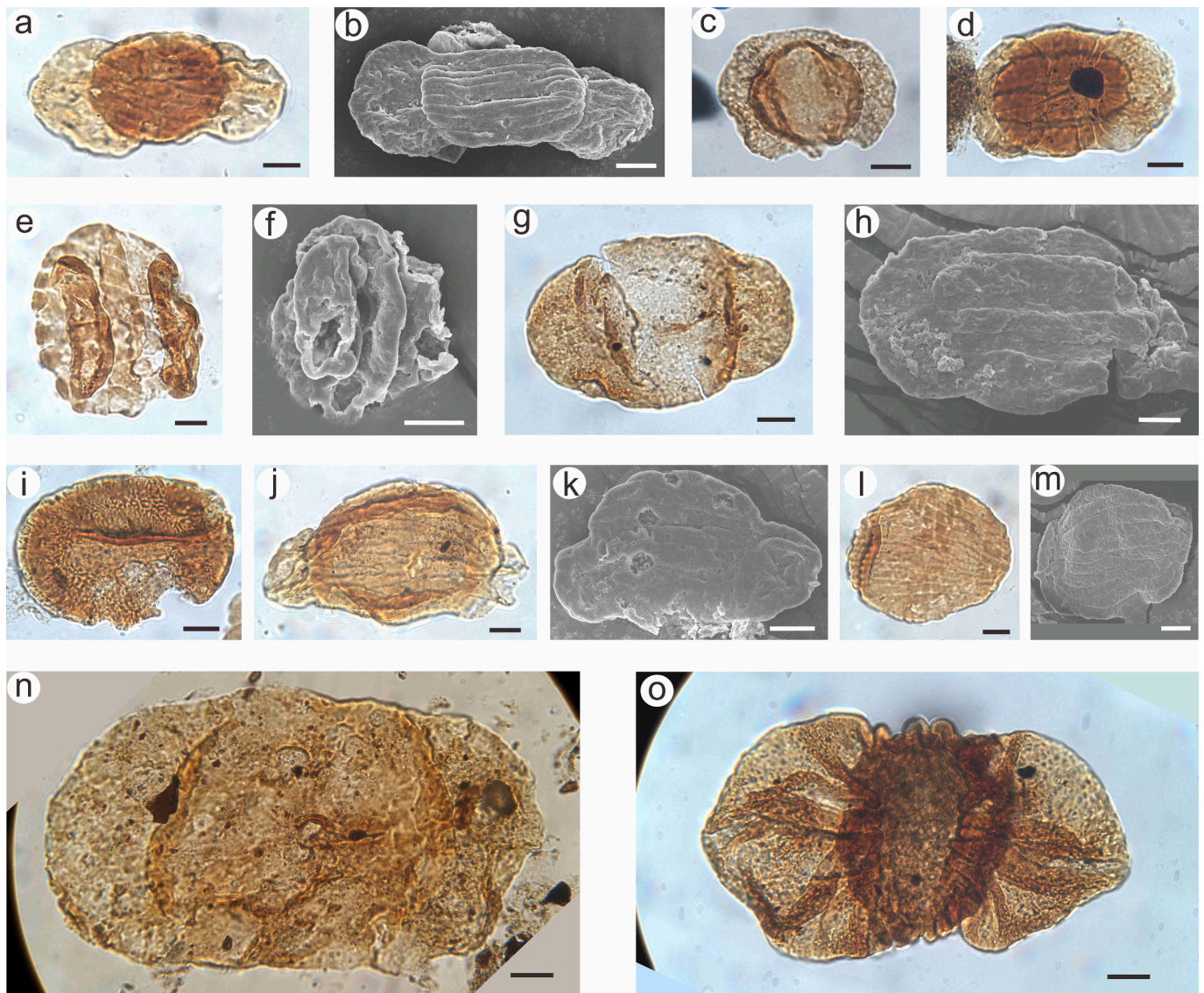


Fig. 4. Selected Guadalupian and Lopingian pollen at Dalongkou in Jimsar, northern Xinjiang, China. a, b. *Striatoabietes pachydermus* (a-xdps92, R29-2; b-SEM-xdps31); c. *Falcisporites* cf. *sublevis* (xdps168, K13-1); d, h. *Lunatisporites tersus* (d-xdps38, J13-1; h-SEM-xdps24); e, f. *Protowelwitschiapollis rhombos* (e-xdps52, P20-3; f-SEM-xdps24); g. *Klausipollenites schaubergeri* (xdps168, N15-2); i. *Samoilovitchisaccites chordens* (xdps46, J39-1); j, k. *Striatoabietes lipidus* (j-xdps31, L21-1; k-SEM-xdps31); l, m. *Vittatina subsaccata* (l-xdps41, I22-1; m-SEM-xdps24); n. *Vestigisporites complexus* (xdps48, Q23-1); o. *Vestigisporites elegantulus* (xdps167, G10-3). Scale bar = 10 μ m.

14, figs. 239a (holotype), 239b.

1990 *Raistrickia obtusosetosa* (Luber) Faddeeva, in Panova et al., pl. 26, fig. 12.

2003 *Raistrickia obtusosetosa* (Luber) Faddeeva var. *distans* Karamura, Zhou, in Ouyang et al., p. 200, pl. 6, figs. 26–28; pl. 101, fig. 3; pl. 102, fig. 6.

Description: Subcircular trilete miospore is $29 \times 33 \mu\text{m}$ in size. The laesurae reach the equator. The exine is $1.0\text{--}1.5 \mu\text{m}$ thick. Distal and equatorial surfaces bear bacula, spines, and clavae. The bacula and spines are $0.5\text{--}1.3 \mu\text{m}$ in diameter. The clavae are $2.4 \mu\text{m}$ in diameter and $0.8\text{--}2.5 \mu\text{m}$ in height.

Comparison: The present material is characterized by bacula, spines, and clavae, which are the same as the type material (Luber and Waltz, 1941) from the Permian Kemerovo Seam in Kuznetsk Basin, Russia, and the other material from the Guadalupian lower Wu'erhe Formation of Hebuksair and the Lopingian Wutonggou Formation of Dalongkou in Jimsar (Ouyang et al., 2003).

Stratigraphic horizon: lower Wutonggou Formation, Wuchiapingian.

Genus: *Schopfites* Kosanke, 1950

Species: *Schopfites phalacrois* Ouyang, 1986

Fig. 3c

1986 *Schopfites phalacrois* Ouyang, p. 45, pl. III, figs. 15 (holotype), 16, 17, 19, 20.

Description: The spore exhibits a simple trilete suture. The outline of the spore is semicircular in equatorial contour, $35 \times 53 \mu\text{m}$ in size. The laesurae extend to the inner margin of the equator, measuring three-quarters the length of the radius. The exine is $1 \mu\text{m}$ thick and is characterized by dense flat polygon verrucae, $2.0 \mu\text{m}$ in diameter and $1.2 \mu\text{m}$ in height.

Comparison: The present material is characterized by dense flat verruca on exine, consistent with the type material from the Lopingian Xuanwei Formation, Yunnan Province, southern China (Ouyang, 1986).

Stratigraphic horizon: upper Quanzijie Formation, Wuchiapingian.

Order: FILICALES

Family: BOTRYOPTERIDACEAE

Genus: *Acanthotriletes* (Naumova) Potonié et Kremp, 1955

Species: Acanthotriletes rectispinus (Luber) Hart, 1965

Fig. 3f

1941 *Azonotriletes rectispinus* Luber, in Luber et Waltz, p. 368, pl. 14, fig. 237.

1965 *Acanthotriletes rectispinus* (Luber) Hart, p. 144.

2003 *Acanthotriletes rectispinus* (Luber) Hart, Zhou, in Ouyang et al., p. 188, pl. 4, fig. 18; pl. 102, fig. 5.

Description: The spore is triangular in polar view and the sides are 33 μm long. The trilete marks are slightly split, extending to the inner margin of the equatorial contour, with raised labra measuring 0.9 μm wide. The exine is 0.9 μm thick. The distal surface and the equator are densely covered by small clavae and bacula, respectively. 48 bacula distribute on the equator, 0.5–1.4 μm in diameter and 1.0–1.7 μm height for each.

Comparison: The present material is similar to the type material (Luber and Waltz, 1941) from the Permian Kemerovo deposit of Kuznets Basin, Russia, except for long trilete marks; and its uniform ornamentation is consistent with the material from the Guadalupian Pingdiquan Formation in the Shaihuhe-Zhangpenggou well-area, northeast of Qitai, and the Lopingian Wutonggou Formation at Dalongkou in Jimsar (Ouyang et al., 2003). However, the specimens named *Acanthotriletes rectispinus* from the lower Dishuiquan Formation (Mississippian) in the Wucaiwan well-area, north of Jimsar (Ouyang et al., 2003, p.188, pl.8, fig. 2; pl.90, fig. 4) differ markedly from the type material and the present material in their much stronger cone-spines.

Stratigraphic horizon: upper Quanzijie Formation, Wuchiapingian.

Order: MARATTIALES

Family: MARATTIACEAE

Genus: *Tuberculatosporites* Imgrund, 1952

Species: *Tuberculatosporites homotubercularis* Hou et Wang, 1986

Fig. 3e, j.

1986 *Tuberculatosporites homotubercularis* Hou and Wang, p. 86, pl. 21, figs. 25, 26 (holotype).

2003 *Tuberculatosporites homotubercularis* Hou et Wang, Zhou, in Ouyang et al., pl. 18, fig. 1; pl. 102, fig. 17.

2017 *Tuberculatosporites homotubercularis* Hou et Wang, Ouyang et al., p. 635, pl. 136, figs. 16, 17.

Description: The spores are monolet, kidney-shaped in lateral view, and $52\text{--}69 \times 26\text{--}39 \mu\text{m}$ in size. The laesurae are obvious, with lengths of two-thirds of the long axis of the spore. The labra are 0.9–1.7 μm wide. The exine is 1.6–2.5 μm thick. The distal and equatorial surfaces are covered with dense cone-spines that are separated from each other. Spines are 0.5–1.0 μm in diameter, 0.5–1.8 μm in length, and 0.5–0.8 μm apart.

Comparison: The present material, characterized by cone-spines, is similar to the type material and other material from the Lopingian Wutonggou Formation at Dalongkou in Jimsar, Xinjiang (Ouyang et al., 2003, 2017; Hou and Wang, 1986).

Stratigraphic horizon: upper Quanzijie Formation, Wuchiapingian.

PTERIDOSPERMOPHYTES

Order: PELTASPERMALES

Family: PELTASPERMACEAE

Genus: *Striatoabieites* (Sedova) Hart, 1964

Species: *Striatoabieites pachydermus* Zhan, 2003

Fig. 4a, b.

2003 *Striatoabieites pachydermus* Zhan, in Ouyang et al., p. 361, pl. 65, figs. 1, 8, 10 (holotype); pl. 98, fig. 10.

Description: The bisaccate pollen is oval in the equatorial contour, $53\text{--}59 \times 24\text{--}29 \mu\text{m}$ in size. The corpus is subcircular or oval, $27\text{--}31 \times 24\text{--}29 \mu\text{m}$ in size. There are 8–10 taeniae, 2–3 μm wide for each and 0.3–1.3 μm apart. The exine is 0.7 μm thick. Sacci are larger than semicircular, $12\text{--}13 \times 19\text{--}29 \mu\text{m}$ in size. The bases of sacci are strongly folded.

Remarks: The present material is characterized by strong folds of sacci bases, which are consistent with the type material from the Pennsylvanian Chepaizi Formation in the areas of the Chepaizi and

Baikouquan wells at Karamay, and the Guadalupian Pingdiquan Formation in the area of Wucaiwan well of Jimsar, northern Xinjiang, China.

Stratigraphic horizon: upper Lucaogou Formation, Roadian; lower Quanzijie Formation, Capitanian.

Species: *Striatoabieites lipidus* (Zhang) Ouyang, 2017

Fig. 4j, k.

1983 *Sinosaccites lipidus* Zhang, p. 340, pl. 4, figs. 16, 17, 18(holotype), 32.

2017 *Striatoabieites lipidus* (Zhang) Ouyang et al., p. 766, pl. 161, figs. 3, 4, 6.

Description: The pollen grains are bisaccate and diploxylonoid, elliptical in equatorial contour, $57\text{--}71 \times 30\text{--}39 \mu\text{m}$ in size. The corpus is subcircular in equatorial contour, with 9–15 longitudinal taeniae, each 2–3 μm in width and 0.7–1.7 μm apart. The exine is 1 μm thick. The sacci are semicircular and smaller than the corpus, $6\text{--}12 \times 16\text{--}18 \mu\text{m}$ in size. The ventral bases of the sacci are more than two-thirds the width of the corpus. The exine is 0.7 μm thick.

Remarks: The material is characterized by small sacci and a large multi-striate corpus, consistent with the type material from the middle Permian Lucaogou Formation at Dalongkou in Jimsar, northern Xinjiang (Ouyang et al., 2017; Zhang, 1983).

Stratigraphic horizon: upper Lucaogou Formation, Roadian.

Genus: *Protowelwitschiapollis* Zhang, 1983

Type species: *Protowelwitschiapollis exilis* Zhang, 1983

Species: *Protowelwitschiapollis rhombos* Zhang, 1983

Fig. 4e, f.

1983 *Protowelwitschiapollis rhombos* Zhang, p. 333, pl. 3, figs. 4 (holotype), 25; pl. 5, fig. 24.

Description: The bisaccate pollen is $44\text{--}49 \times 49\text{--}50 \mu\text{m}$ in size. The corpus is rhombic in equatorial contour, $38\text{--}39 \times 49\text{--}50 \mu\text{m}$ in size. Six to eight parallel or convergent longitudinal taeniae are up to 5–7 μm wide for each and 0.7–1.3 μm apart. A transverse taenia on the distal surface of the corpus is 6–9 μm wide. The sacci are semicircular and distally inclined, $10\text{--}19 \times 26\text{--}38 \mu\text{m}$ in size. The ventral bases of sacci are half of the width of the corpus.

Comparison: The present material is consistent with the type material in having rhombic corpus and small distal inclined sacci. The present material is different from the *Hamiapollenites exilis* Koltchina, 1990 by the later having 8–12 proximal taeniae and 5–7 distal taeniae on the corpus (Koltchina, 1980, pp. 132–133, pl. 6, fig. 1).

Remarks: Ouyang et al. (2003) considered *Paucistriatopinites* Zauer ex Djupina, 1975 and *Protowelwitschiapollis* Zhang, 1983 to be invalid synonyms of *Hamiapollenites* Wilson, 1962. We do not agree with this emendation. *Hamiapollenites* Wilson, 1962 is characterized by 6–10 taeniae on the distal surface and 8–12 on the proximal surface (Wilson, 1962, p. 23, pl. 3, fig. 7). On the distal surface of *Paucistriatopinites* Zauer ex Djupina, 1975, a single taenia is present, whereas 2–4 taeniae are observed on the proximal surface (Djupina, 1975, p. 38, pl. 3, figs. 1–5). *Protowelwitschiapollis* Zhang, 1983 is characterized by 1 taenia on the distal surface and 8–12 taeniae on the proximal surface (Zhang, 1983, p. 332).

Stratigraphic horizon: upper Lucaogou Formation and Hongyanchi Formation, Roadian.

Genus: *Vittatina* (Samoilovich) Wilson, 1962

Species: *Vittatina subsaccata* Samoilovich, 1953

Fig. 4l, m.

1953 *Vittatina subsaccata* Samoilovich, p. 44, pl. 9, fig. 4 (holotype).

1965 *Vittatina subsaccata* Samoilovich, Hart, p. 51, fig. 114.

1969 *Vittatina subsaccata* Samoilovich, Bamber et Barss, pl. 4, fig. 18; pl. 5, fig. 1.

1975 *Vittatina subsaccata* Samoilovich, Djupina, pl. 7, figs. 1–7.

1976 *Vittatina subsaccata* Samoilovich, Faddeeva, pl. 1, figs. 20, 22.

1978 *Vittatina subsaccata* Samoilovich, Dybova-Jachowicz, pl. 9, figs. 7, 8, 10; pl. 10, figs. 1, 2.

1979 *Vittatina subsaccata* Samoilovich, Chuvashov et Djupina, pl. 35,

fig. 11.

1981 *Vittatina subsaccata* Samoilovich, Varjukhina, pl. 6, fig. 10; pl. 7, figs. 6, 7.

2003 *Vittatina subsaccata* Samoilovich, Zhan, in Ouyang et al., pl. 74, figs. 6–8, 10, 23.

2017 *Vittatina subsaccata* Samoilovich, Ouyang et al., pl. 164, figs. 1, 2, 7, 8, 35, 36.

Description: The striate pollen is oval in the equatorial contour, $50 \times 43 \mu\text{m}$ in size. The corpus is oval, with 14 longitudinal taeniae on the proximal surface. The taeniae are parallel to each other and convergent on both sides of corpus, about $1.3\text{--}3.0 \mu\text{m}$ wide and $0.7\text{--}0.8 \mu\text{m}$ apart. Sacci are slightly meniscus-shaped, $7\text{--}8 \times 24\text{--}28 \mu\text{m}$ in size.

Comparison: The present material is characterized by an oval corpus and small sacci, consistent with the holotype.

Stratigraphic horizon: upper Lucaogou Formation, Roadian.

Genus: *Lunatisporites* (Leschik) Jansonius, 1962

Species: *Lunatisporites tersus* Ouyang, 2003

Fig. 4d, h.

2003 *Lunatisporites tersus* Ouyang, in Ouyang et al., p. 410, pl. 50, figs. 5, 6, 7 (holotype), 8–11.

Description: The bisaccate pollen is elliptical in the equatorial contour, $49\text{--}57 \times 31\text{--}33 \mu\text{m}$ in size. The corpus is oval, $33\text{--}40 \times 30\text{--}33 \mu\text{m}$ in size. The exine is $1.1 \mu\text{m}$ thick. Four taeniae on the proximal surface, extending the entire corpus length, are up to $7\text{--}8 \mu\text{m}$ wide for each and $1.1\text{--}2.4 \mu\text{m}$ apart. The sacci are semispherical, $18\text{--}20 \times 28\text{--}29 \mu\text{m}$ in size. The ventral bases of sacci are less than one-third of the width of the corpus.

Comparison: The present material is characterized by four wide taeniae on the proximal surface of the corpus. This feature is consistent with the type material from the Cisuralian Jingou Formation and the Lopingian Wutonggou Formation in the Junggar Basin, Xinjiang (Ouyang et al., 2003).

Stratigraphic horizon: upper Lucaogou Formation, Roadian.

Order: CORYSTOSPERMALES

Family: UMKOMASIACEAE

Genus: *Klausipollenites* Jansonius, 1962

Species: *Klausipollenites schaubergeri* (Potonié et Klaus) Jansonius, 1962

Fig. 4g.

1954 *Pityosporites schaubergeri* Potonié et Klaus, p. 538, pl. 10, figs. 9 (holotype), 10.

1962 *Klausipollenites schaubergeri* (Potonié et Klaus) Jansonius, p. 55.

1986 *Klausipollenites schaubergeri* (Potonié et Klaus) Jansonius, Hou and Wang, p. 98, pl. 27, figs. 27, 28.

1999 *Klausipollenites schaubergeri* (Potonié et Klaus) Jansonius, Ouyang and Norris, p. 38, pl. 6, figs. 3–5.

2003 *Klausipollenites schaubergeri* (Potonié et Klaus) Jansonius, Ouyang, in Ouyang et al., p. 299, pl. 78, figs. 1–8, 28; pl. 103, figs. 26, 27.

Description: The pollen grain is bisaccate, oval in the equatorial contour, $59 \times 38 \mu\text{m}$ in size. The corpus is oval, $28 \times 38 \mu\text{m}$ in size. The exine is $0.7 \mu\text{m}$ thick. A single aperture is $13 \mu\text{m}$ long, in the middle of the corpus. The sacci are larger than subcircular, $12\text{--}16 \times 24\text{--}27 \mu\text{m}$ in size.

Comparison: The present material is consistent with type material (Potonié et Klaus, 1954) and the other material in northern Xinjiang, China (Hou and Wang, 1986; Ouyang and Norris, 1999; Ouyang et al., 2003).

Stratigraphic horizon: lower Wutonggou Formation, Wuchiapingian.

Genus: *Falcisporites* (Leschik) Klaus, 1963

Species: *Falcisporites* cf. *sublevis* (Luber) Ouyang et Norris, 1999

Fig. 4c.

Description: The bisaccate pollen is elliptical in the equatorial contour, $38 \times 26 \mu\text{m}$ in size. The corpus is oval, $24 \times 20 \mu\text{m}$ in size. The

exine is $0.3 \mu\text{m}$ thick. The sacci are larger than semicircular, $14\text{--}15 \times 21\text{--}24 \mu\text{m}$ in size, with a fusiform leptoma occupying up to half of the corpus.

Comparison: The present material is characterized by a fusiform leptoma that is similar to that of *Pemphygaletes sublevis* from the Permian strata of the western Pre-Urals of Russia (Luber and Waltz, 1941, p. 57, pl. 13, fig. 219). It is also close to *Falcisporites sublevis* (Luber) Ouyang et Norris (Ouyang and Norris, 1999, p. 42, pl. 6, figs. 14–17) from the Lopingian Guodikeng Formation in Dalongkou, northern Xinjiang; however, the sacci of the present material are connected with each other on the equatorial side.

Stratigraphic horizon: lower Wutonggou Formation, Wuchiapingian.

CONIFERS

Order: CORDAITALES

Family: CORDAITANTHACEAE

Genus: *Cordaitina* Samoilovich, 1953

Species: *Cordaitina subrotata* (Luber) Samoilovich, 1953

Fig. 3h

1953 *Cordaitina subrotata* (Luber) Samoilovich, pl. 2, fig. 10 (holotype).

1990 *Cordaitina stenolimbata* (Luber) Hou et Wang, p. 25, pl. 3, fig. 5.

1990 *Cordaitina subrotata* (Luber) Samoilovich, Hou and Wang, pl. 3, fig. 10.

2003 *Cordaitina subrotata* (Luber) Samoilovich, Wang, in Ouyang et al., p. 237, pl. 34, figs. 1, 2, 8, 10; pl. 101, fig. 7.

2017 *Cordaitina subrotata* (Luber) Samoilovich, Ouyang et al., p. 671, pl. 140, figs. 3, 4; pl. 161, fig. 22.

Description: Monosaccate pollen is subcircular in the equatorial contour, $42 \times 29 \mu\text{m}$ in size. The corpus is subcircular, $26 \times 17 \mu\text{m}$ in size. The radius is $12 \mu\text{m}$ long, slightly curving at the ends. The exine is $0.8 \mu\text{m}$ thick and reticulate. The lumina is $1.0 \mu\text{m}$ in diameter. The equatorial saccus is light brown, $6 \mu\text{m}$ wide.

Comparison: The present material is characterized by strong radiating creases in the saccus and wide limb, which are consistent with the characters of the type material (Samoilovich, 1953) from the Kungurian of the south Ural. The material named *Cordaitina stenolimbata* (Luber) (Hou and Wang, 1990) is consistent with the present material, and we agree with the assignment of *C. stenolimbata* to *C. subrotata* (Ouyang et al., 2003, 2017), which is widely distributed in the Guadalupian and Lopingian strata of Xinjiang and the Lopingian Upper Shihhotse Formation in Shanxi Province, China.

Stratigraphic horizon: Hongyanchi Formation, Roadian.

Order: VOLTZIALES

Family: UTRECHTACEAE

Genus: *Samoilovitchisaccites* Dibner, 1971

Species: *Samoilovitchisaccites chordens* Wang, 2003

Fig. 4i.

2003 *Samoilovitchisaccites chordens* Wang, in Ouyang et al., p. 257, pl. 28, figs. 1, 2, 6, 7 (holotype).

Description: Monosaccate pollen is elliptical in equatorial contour, $50\text{--}52 \times 30\text{--}35 \mu\text{m}$ in size. Corpus is elliptical too, $45\text{--}48 \times 20\text{--}22 \mu\text{m}$ in size. A ridge, $35\text{--}40 \times 1.5\text{--}2.0 \mu\text{m}$ in size, runs parallel to the longitudinal axis of the pollen. Equatorial saccus is $9\text{--}10 \mu\text{m}$ in width, with radial creases.

Comparison: The present pollen material is characterized by a ridge, which is consistent with the type material from Guadalupian Tiemulike Formation and Lucaogou Formation in Yining, northern Xinjiang.

Stratigraphic horizon: upper Lucaogou Formation, Roadian.

Genus: *Potonieisporites* Bharadwaj, 1954

Species: *Potonieisporites turpanensis* Hou et Wang, 1990

Fig. 3k.

1990 *Potonieisporites turpanensis* Hou et Wang, p. 26, pl. 6, fig. 19; pl. 7, fig. 1 (holotype).

2003 *Potonieisporites turpanensis* Hou et Wang, Wang, in Ouyang

et al., p. 254, pl. 26, figs. 1, 2, 4–8.

2017 *Potonieisporites turpanensis* Hou et Wang, Ouyang et al., p. 689, pl. 144, figs. 4, 7; pl. 160, fig. 40.

Description: The monosaccate pollen is oval in the equatorial contour, $124 \times 98 \mu\text{m}$ in size. The corpus is oval, $59 \times 85 \mu\text{m}$ in size. A short proximal suture in the middle part of the corpus is one-third of the length of the corpus. The exine is thin ($0.7 \mu\text{m}$ thick) with many irregular folds. The saccus encircles the equator and the distal surface of the corpus, $9\text{--}34 \mu\text{m}$ wide longitudinally and $8\text{--}32 \mu\text{m}$ transversely. The saccus base is thickened, $4 \mu\text{m}$ wide.

Comparison: The present material is the same as the type material from the Lopingian Wutonggou Formation in the Turpan Basin (Hou and Wang, 1990). This species is widely distributed in the Permian strata in the Junggar Basin and the Guadalupian Qipan Formation in the Tarim Basin.

Stratigraphic horizon: upper Lucaogou Formation, Roadian.

Family: ULLMANNIACEAE

Genus: *Vestigisporites* (Balme et Hennelly) Tiwari and Singh, 1984

Type species: *Vestigisporites rudis* Balme et Hennelly, 1955

Species: *Vestigisporites complexus* Ouyang, 2003

Fig. 4n.

2003 *Vestigisporites complexus* Ouyang, in Ouyang et al., p. 278, pl. 33, figs. 1, 6, 7 (holotype), 11, 14; pl. 40, fig. 11.

Description: The bisaccate pollen is elliptical in the equatorial contour, $116 \times 64 \mu\text{m}$ in size. The corpus is elliptical, $71 \times 64 \mu\text{m}$ in size. The surface of the exine is scabrous and exhibits an irregularly reticulate pattern characterized by an open, short aperture. The sacchi are larger than semicircular, $56\text{--}57 \times 20\text{--}23 \mu\text{m}$ in size, light brown in color, scabrous, with some folds.

Comparison: *Vestigisporites complexus* is characterized by the absence of distinct distal folds along the sacchi bases and the presence of an irregular fissure. The Dalongkou material is similar to the type material from the Guadalupian Pingdiquan Formation in Jimsar, northern Xinjiang.

Stratigraphic horizon: upper Lucaogou Formation, Roadian.

Species: *Vestigisporites elegantulus* Hou et Wang, 1986

Fig. 4o.

1986 *Vestigisporites elegantulus* Hou and Wang, p. 92, pl. 23, fig. 4 (holotype).

1986 *Vestigisporites dalongkouensis* Hou et Wang, Hou and Wang, p. 92, pl. 23, fig. 9.

2017 *Vestigisporites elegantulus* Hou et Wang, Ouyang et al., p. 709, pl. 148, fig. 13.

Description: The pollen is bisaccate and dumbbell-shaped in the equatorial contour, $101 \times 53 \mu\text{m}$ in size. The corpus is oval, $38 \times 53 \mu\text{m}$ in size. A single aperture on the middle of the corpus extends to the corpus edges. The sacchi are larger than the corpus, $27\text{--}30 \times 50\text{--}57 \mu\text{m}$ in size. The exine is thick (maximum $5.6 \mu\text{m}$) with equatorial thickening. The sacchi are larger than the corpus, with strong folds radiating from the sacchi base. The sacchi are intramicroreticulate or punctate, with lumina $0.7\text{--}1.7 \mu\text{m}$ in diameter.

Comparison: The Dalongkou material is the same as the type and other material from the Lopingian Wutonggou Formation at Dalongkou of Jimsar, northern Xinjiang.

Stratigraphic horizon: lower Wutonggou Formation, Wuchiapingian.

Order: CONIFERALES

Family: PODOCARPACEAE

Genus: *Trochosporites* Wilson, 1962

Species: *Trochosporites reniformis* Wilson, 1962

Fig. 3l.

1962 *Trochosporites reniformis* Wilson, p. 28, pl. 2, fig. 9 (holotype).

Description: The pollen is trisaccate and $69 \times 51 \mu\text{m}$ in size. The corpus is subcircular, $47 \times 37 \mu\text{m}$ in size. The sacchi are semicircular, $4\text{--}17 \times 28\text{--}40 \mu\text{m}$ in size. One of the three sacchi is much smaller than the others. The bases of the sacchi are slightly thickened, maximum $4\text{--}5 \mu\text{m}$ wide. The exine is thin, $0.7 \mu\text{m}$ thick.

Remarks: The present material is similar to the type from the Guadalupian Flowerpoint Formation of Okalahoma, USA.

Stratigraphic horizon: upper Lucaogou Formation, Roadian.

CYCADOPHYTES

Order: CYCADALES

Family: CYCADACEAE

Genus: *Cycadopites* (Wodehouse) Wilson et Wibster, 1946

Species: *Cycadopites retroflexus* (Luber) Hart, 1965

Fig. 3d, i.

1941 *Azoniales retroflexus* f. *cinctus* Luber, in Luber and Waltz, p. 179, pl. 16, fig. 252b (holotype).

1965 *Cycadopites retroflexus* (Luber) Hart, p. 107; text-fig. 258.

2017 *Cycadopites retroflexus* (Luber) Hart, Ouyang et al., p. 795, pl. 167, figs. 11, 12, 17.

Description: The pollen grains are monosulcate, showing a prolate shape in the equatorial view, $31\text{--}37 \times 25\text{--}29 \mu\text{m}$ in size. The grains are truncated at their ends. The exine is smooth and $0.5\text{--}1.0 \mu\text{m}$ thick. The sulcate has a width of one-sixth to one-fifth of the pollen height and is wider at the two extremities.

Comparison: The present species is characterized by its truncate ends, consistent with the type material from the Cisuralian strata at Kuznetsk, Russia (Luber and Waltz, 1941) and material from the Lopingian Upper Shihhotse Formation of Ningwu, Shanxi Province, and the Guadalupian Lucaogou Formation at Yaomoshan, northern Xinjiang.

Stratigraphic horizon: upper Lucaogou Formation, Roadian.

4.2. Palynological assemblages

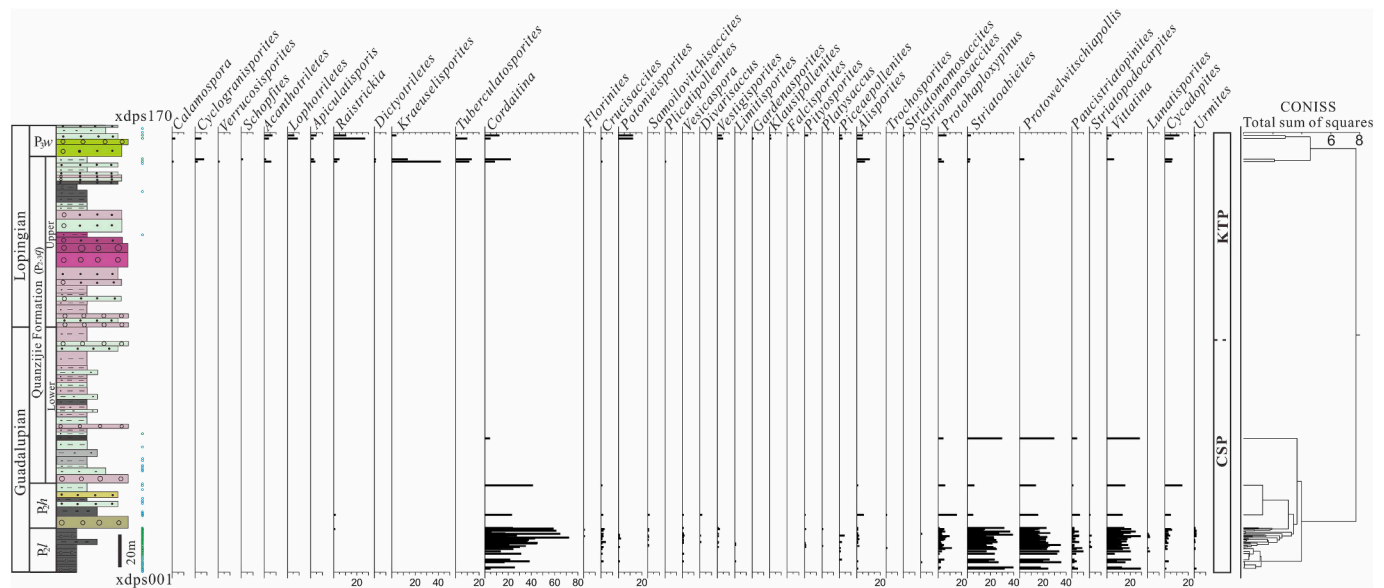
A total of 80 palynological samples are productive; however, only 39 samples are quantitatively analyzed. Two palynological assemblages are recognized in ascending order (Fig. 5).

4.2.1. *Cordaitina subrotata*–*Striatoabieites lipidus*–*Protowelwitschiapollis exolescus* assemblage (CSP)

This CSP assemblage is composed of 53 species in 25 genera in the horizon from the uppermost of the Lucaogou Formation and Hongyanchi Formation to the lower part of the Quanzijie Formation. The assemblage is characterized by abundance pollen. The only spores present in the assemblage are two species of *Raistrickia* seen in two samples, which comprise $0.83\text{--}0.99\%$ of the total grains in those samples.

In the assemblage, pollen constitute $98.67\text{--}100\%$ of the grains in each sample. The dominant components are *Cordaitina* ($2.95\text{--}72.28\%$), *Striatoabieites* ($4.96\text{--}39.64\%$), *Protowelwitschiapollis* ($2.19\text{--}35.64\%$), *Vittatina* ($2.39\text{--}29.13\%$), *Protohaploxypinus* ($0\text{--}15.72\%$), and *Cycadopites* ($0\text{--}14.76\%$). *Crucisaccites* ($0\text{--}3.96\%$) and *Alisporites* ($0\text{--}5.79\%$) are common. The most dominant monosaccate pollen types are *Cordaitina subrotata* ($1.58\text{--}39.64\%$), *C. stenolimbata* ($0\text{--}31.68\%$), *C. rotata* ($0\text{--}11.76\%$), *C. uralensis* ($0\text{--}5.77\%$), and *Crucisaccites ornatus* ($0\text{--}3.96\%$). Conspicuous taeniate pollen taxa are *Striatoabieites lipidus* ($1.26\text{--}24.78\%$), *S. pachydermus* ($0.98\text{--}14.16\%$), *Protowelwitschiapollis exolescus* ($1.00\text{--}24.75\%$), *P. exilis* ($0\text{--}16.55\%$), *Paucistriatopinites septatus* ($0\text{--}9.79\%$), *Vittatina subsaccata* ($0.83\text{--}18.87\%$), *V. costabilis* ($0\text{--}8.92\%$), *V. persecta* ($0\text{--}7.62\%$), and *Protohaploxypinus latissimus* ($0\text{--}4.95\%$). Other common species are *Alisporites communis* ($0\text{--}4.13\%$) and *Cycadopites caperatus* ($0\text{--}4.92\%$).

Sample XDPS-92 is the only sample from the lower part of the Quanzijie Formation that contains a relatively high abundance of pollen, although the sample contains only 71 grains of pollen representing 13 species in 6 genera. The dominant pollen types are *Striatoabieites* (29.58%), *Protowelwitschiapollis* (29.58%), and *Vittatina* (28.17%). The dominant species are *Striatoabieites lipidus* (21.13%), *S. pachydermus* (8.45%), *Protowelwitschiapollis exolescus* (21.13%), *P. exilis* (8.45%), *Vittatina subsaccata* (15.49%), *V. costabilis* (7.04%), *V. persecta* (4.23%), and *Cordaitina subrotata* (4.23%). As the dominant pollen types are consistent with those from the underlying Hongyanchi Formation and Lucaogou Formation, we assigned this sample to the CSP assemblage.



Pollen (36 species in 18 genera) in the assemblage are dominated by *Cordaitina* (4.88–22.22%), *Cycadopites* (5.71–12.38%), *Potonieisporites* (0–11.43%), *Alisporites* (4.88–11.11%), *Protohaploxylinus* (0–6.67%), and *Vittatina* (0–6.17%). The dominant monosaccate pollen are *Cordaitina subrotata* (0–14.81%), *C. stenolimbata* (2.86–4.94%), and *Potonieisporites turpanensis* (0–6.10%). The taeniate bisaccate pollen are dominated by *Alisporites stenoholcus* (1.90–6.17%) and *A. communis* (2.44–4.94%). Taeniate pollen include *Protohaploxylinus micros* (0–4.76%), *Vittatina subsaccata* (0–3.70%), and *Striatoobites pachydermus* (0–2.86%). Monosulcate pollen are represented by *Cycadopites*

[illegible]

sp. (1.90–6.10%) and *C. caperatus* (0–5.71%).

5. Discussion

5.1. Comparison of palynological assemblages in the Junggar Basin

Palynological investigations of Permian strata have been conducted in the Junggar Basin since the 1980s (Fig. 6). The assemblage in the oil shale of the Upper Jijicaozi Group (=Lucaogou Formation) in the Yaomoshan section, 3 km west of Urumqi, is composed of 42 species in 30 genera (Zhang, 1983), including *Acanthotriletes*, *Cordaitina*, *Potoniopsisporites*, *Hamiapollenites*, *Protowelwitschiapollis*, *Striatoabieites*, *Vittatina*, and *Cycadopites*. This assemblage is dominated by bisaccate taeniate pollen, as in the CSP assemblage of the present study; however, the abundance of monosaccate pollen in the CSP (e. g., *Cordaitina subrotata*, *C. stenolimbata*, *C. rotata*, *C. uralensis*, and *Crucisaccites ornatus*) indicates that the CSP assemblage is different from that of the Yaomoshan section. These monosaccate pollen species might be abundant in the upper horizons of the Lucaogou Formation (Fig. 5).

Hou and Wang (1986) reported the palynological assemblage named the *Kraeuselisporites*–*Lueckisporites* assemblage from the Lower Cangfengou Group (including the Quanzijie, Wutonggou and Guodikeng formations) at Dalongkou in Jimsar, northern Xinjiang, China (Hou and Wang, 1986). Subsequently, Hou and Wang (1990) reported four palynological assemblages in the southern Junggar Basin in stratigraphic ascending order, i.e. the *Cordaitina* - *Hamiapollenites*–*Vittatina* assemblage of the Lucaogou and Hongyanchi formations, the *Alisporites*–*Sulcatissporites*–*Protohaploxylinus* assemblage of the Quanzijie Formation, the *Kraeuselisporites*–*Potoniopsisporites*–*Sulcatissporites* assemblage of the Wutonggou Formation, and the *Limatulasporites*–*Alisporites*–*Lueckisporites* assemblage of the lower and middle part of the Guodikeng Formation (Hou and Wang, 1990).

The *Cordaitina*–*Hamiapollenites*–*Vittatina* assemblage (CHV) was delineated on the basis of eight samples from the Dalongkou profile. The assemblage is characterized by scarce spores (0.3–2.0%) and a high abundance of pollen (98.0–99.7%). The most common spore in the assemblage is *Punctatisporites* (0.3–0.6%); *Acanthotriletes*, *Verrucosiporites*, *Lophotriletes*, and *Tuberculatosporites homotubercularis* are very rare (Hou and Wang, 1990). The monosaccate pollen are dominated by *Cordaitina* and *Crucisaccites*, which constitute 5.5–66.4% of the assemblage; other genera include *Samoilovitchisaccites*, *Florinites*, and *Potoniopsisporites*. Taeniate bisaccate pollen (29.0–82.0%) are rather abundant, particularly *Hamiapollenites* (18.7–79.0%), *Protohaploxylinus* (1.1–24.0%), *Striatoabieites* (0.6–5.5%), and *Striatopodocarpites* (0.5–4.9%) (Hou and Wang, 1990). Generally, this assemblage is comparable with the CSP assemblage of the present study in that both are characterized by abundant taeniate bisaccate pollen.

The *Alisporites*–*Sulcatissporites*–*Protohaploxylinus* (ASP) assemblage was identified on the basis of five samples from the Quanzijie Formation in the Dalongkou profile. Although the contents of spores and pollen vary greatly between the lower two samples and the upper three samples, Hou and Wang (1986, 1990) still combined them into one assemblage. In the lower two samples, spores make up <5% of the assemblage, increasing to 10–25% in the upper three samples. The pollen in the lower two samples are dominated by taeniate bisaccate (57–66%) and monosaccate (12–30%) forms; those in the upper three samples are dominated by ataeniate bisaccate pollen (52–71%) and taeniate bisaccate pollen (9–28%). These marked changes were regarded as succession within the CHV assemblage (Hou and Wang, 1986). Because ataeniate bisaccate pollen are largely absent from the lower two samples of the ASP assemblage, it is most appropriate to assign the lower two samples from the lower Quanzijie Formation to the CHV assemblage, in the same way as we assigned sample XDPS-92 to the present CSP assemblage. Thus, the ASP assemblage is represented only by the three samples from the upper Quanzijie Formation. The common spores in the ASP and KTP assemblages are *Tuberculatosporites homotubercularis* and *Punctatisporites*

punctatus. The most abundant pollen species in the ASP assemblage are *Cordaitina uralensis* (1.0–13.0%), *Alisporites sublevis* (0.3–32.4%), *Hamiapollenites tractiferinus* (0.3–12.0%), *Vittatina vittifera* (0–3.7%), and *Cycadopites glaber* (0.6–4.2%). *Sulcatissporites* and *Protohaploxylinus* were subordinate. Therefore, the ASP assemblage can be correlated with the present KTP assemblage on the basis of the similarity in overall composition, dominant spores (e. g., *Tuberculatosporites*, *Raistrickia*), and dominant pollen (e. g., *Cordaitina*, *Alisporites*, *Protohaploxylinus*, *Vittatina*, and *Cycadopites*). However, the KTP assemblage differs from the ASP assemblage in that the abundant of *Kraeuselisporites spinulosus* and *Potoniopsisporites turpanensis* is greater in the former.

The *Kraeuselisporites*–*Potoniopsisporites*–*Sulcatissporites* assemblage (KPS) in the Wutonggou Formation at Dalongkou in Jimsar was identified from 13 samples. The spores (30–42%) are dominated by *Kraeuselisporites spinulosus* (0–35.7%) and *Tuberculatosporites homotubercularis* (0.6–25.6%). The pollen (41–65%) are composed of monosaccate (1.4–42.1%, mainly *Cordaitina* and *Potoniopsisporites*), ataeniate bisaccate (2.0–58.7%, including *Alisporites*, *Platysaccus*, *Sulcatissporites*, *Klausipollenites*, and *Vitreisporites*), and taeniate bisaccate (6.2–36.4%, mainly *Protohaploxylinus*, *Hamiapollenites*, and *Gardenasporites*). The KTP assemblage from the upper part of the Quanzijie Formation and the lowermost of the Wutonggou Formation is much more comparable to the KPS assemblage than the ASP assemblages in term of the high content of spores and the dominant species of spores and pollen species, while the rarity of *Sulcatissporites* and the high content of *Cycadopites* in the KTP assemblage indicate a transition from the ASP to KPS assemblages. This transition is consistent with the KTP assemblage having been recovered from a stratigraphic range that overlap the upper part of the ASP assemblage and the lower part of the KPS assemblage.

The *Limatulasporites*–*Alisporites*–*Lueckisporites* (LAL) assemblage, identified from 16 samples in the lower and middle part of the Guodikeng Formation in the Dalongkou profile, is composed of spores (2.4–52.8%, dominated by *Limatulasporites fossulatus*, and pollen (62–80%) of monosaccate (0.4–3.8%), ataeniate bisaccate (33.2–59.2%) and taeniate bisaccate (2.4–43.0%). The main pollen taxa are *Alisporites*, *Pteruchipollenites*, *Klausipollenites*, *Limitisporites*, *Sulcatissporites*, *Protohaploxylinus*, *Gardenasporites*, *Striatopodocarpites*, *Lueckisporites*, *Taeniaesporites*, *Hamiapollenites*, *Vittatina*, and *Cycadopites*. The absence of *Tuberculatosporites* and the abundance of *Limatulasporites* and *Lueckisporites* in the LAL assemblage are different from the KPS assemblage and the KTP assemblage of the present study.

The Permian–Triassic transitional palynofloras at the Shichanggou in Urumqi, the Xiaoquangou in Fukang, and the Dalongkou in Jimsar were studied in detail (Qu and Wang, 1990; Ouyang and Norris, 1999; Metcalfe et al., 2009). The *Lundbladispora*–*Lunatisporites*–*Aratrisporites* assemblage (LLA) was established on the basis of three productive samples, two (AEA749, AEA751) from the upper Guodikeng Formation and one (AEA755) from the lower Jiucaiyuan Formation (Ouyang and Norris, 1999). The *Limatulasporites*–*Lundbladispora*–*Taeniaesporites*–*Equisetisporites* assemblage (LLTE) from the Jiucaiyuan Formation (Qu and Wang, 1990) can be entirely correlated with the LLA assemblage (Ouyang and Norris, 1999). The LLA and LLTE assemblages are assigned to the earliest Triassic.

Metcalfe et al. (2009) investigated several profiles covering the upper Quanzijie, Wutonggou, Guodikeng, and lower Jiucaiyuan formations at the Dalongkou in Jimsar and the Lucaogou in Urumqi, northern Xinjiang (Metcalfe et al., 2009). Based on two samples (sample 3405 from the upper Quanzijie Formation and sample 3395 from the upper Wutonggou Formation), the *Tuberculatosporites homotubercularis*–*Potoniopsisporites* sp. Q assemblage (TP) assemblage was established and characterized by *Tuberculatosporites homotubercularis* (= *Polypodioidites* sp.), *Kraeuselisporites spinulosus*, *Potoniopsisporites* sp. Q (= *P. turpanensis*) and *Sulcatissporites* spp. (Metcalfe et al., 2009; Afonin and Foster, 2005). Other species of spores in the TP assemblage include *Calamospora* sp. cf. *C. landiana*, *Osmundacidites senectus*, *O. wellmanii*, *Apiculatisporis cornutus*, *Didictriletes ericianus*, and *Lapposporites echinatus*. Other pollen

species include *Cordaitina uralensis*, *C. rotata*, *C. convallata*, *Coheniasaccites* sp., *Alisporites splendens*, *Vitreisporites signatus*, *Sulcatissporites* sp. B, *Scutasporites* sp. cf. *S. unicus* [most likely *Gardenasporites xinjiangensis* Hou et Wang, 1986 = *Scutasporites xinjiangensis* (Hou et Wang) Ouyang, 2003], *Protohaploxylinus* spp., *Hamiapollenites bullaeformis*, *Weylandites lucifer*, *Weylandites* sp., *Gnetaceapollenites multistriatus*, and *Vittatina* sp. cf. *V. costabilis*. The coexistence of *Tuberculosporites homotubercularis*, *Kraeuselisporites spinulosus*, and *Potonieisporites turpanensis* in the TP, ASP and KPS assemblages, and the present KTP assemblage, demonstrates the comparability of these assemblages.

The *Klausipollenites schaubergeri*–*Reduviasporonites chalas-tus*–*Syndesmorion stellatum* assemblage from the lower Guodikeng Formation and the *Lundbladispota foveata*–*Pechorospores disertus*–*Otynisporites eotriassicus* assemblage from the upper Guodikeng and lower Jiucuiyuan formations (Metcalfe et al., 2009; Afonin and Foster, 2005). The former can be correlated with the LAL assemblage from the middle and lower Guodikeng Formation (Hou and Wang, 1990), and the latter with the LLTE assemblage from the Jiucuiyuan Formation (Qu and Wang, 1990) or the LLA assemblage (Ouyang and Norris, 1999).

5.2. Geological age of palynological assemblages

5.2.1. *Cordaitina subrotata*–*Striatoabietes lipidus*–*Protowelwitschiapollis exoleucus* assemblage (CSP)

To assess the geological ages of the palynological assemblages, the geological distributions of all known species in the assemblage were compiled for the Dalongkou profile and other localities and horizons globally (Fig. 7).

The stratigraphic range of the CSP assemblage in the Dalongkou profile is from the uppermost Lucaogou Formation, through the Hongyanchi Formation, to the lower part of Quanzijie Formation. This range is normally assigned to the late Guadalupian and early Lopingian epochs (Cheng et al., 1997; Ouyang et al., 2004; Metcalfe et al., 2009); however, recent isotopic dating of the detrital zircons from coeval horizons in the Turpan-Hami Basin yielded an age of 281 Ma for red ash-fall beds in the uppermost Hongyanchi Formation (Yang et al., 2010). This new information resulted in a substantial revision of the Permian stratigraphic framework, with deposits regarded as Guadalupian in age (e.g., the Lucaogou and Hongyanchi formations) being assigned to the Cisuralian (Obrist-Farner and Yang, 2017; Shen et al., 2019; Wan et al., 2019; Tang et al., 2022). However, this reassignment was based solely on isotopic dating, without any biostratigraphic data.

The CSP assemblage is composed of 53 species in 25 genera, of which 48 species have been recorded (Fig. 7). Of these species, *Florinites luberae* has been recorded in the Kazanian strata in the Solikamsk Basin, Ural (Samoilovich, 1953; Hart, 1970), and in the Permian in the Junggar Basin (Fig. 8). *Divarisaccus cinctus* was reported in the Zhurinskii seam of Lenin deposits in the Kuznets Basin (Luber and Waltz, 1941). *Vesicaspora acrifera* and *Vestigisporites mellinus* occur in the Permian succession of the Kuznets Basin and the Artinskian strata of the Ural (Hart, 1965; Sivertseva, 1966), and have been recorded in the Pingdiquan and Wutonggou formations in the eastern and southern Junggar Basin (Ouyang et al., 2003). *Limitisporites expressus* was established on the basis of material from the Lower Permian of the Donets Basin and has been reported in the Hongyanchi Formation in the southern Junggar Basin; *Limitisporites pontiferrens* was established on the basis of material from the lower Shihhotse Formation in Shanxi, North China, and has been reported in the Jiamuhe Formation in the western Junggar Basin. *Platysaccus papilionis* is widely distributed in Permian strata from the Lucaogou Formation to the Guodikeng Formation in the southern Junggar Basin (Ouyang et al., 2003, 2017). *Trochosporites reniformis* was reported from the Kungurian-Rodian Flowerpot Formation of Oklahoma, USA (Wilson, 1962). *Striomonosaccites ovatus* occurs in the Tashikula Formation and the Pingdiquan Formation in the southern and eastern Junggar Basin (Ouyang et al., 2003). *Paucistriatopinites septatus*

has a stratigraphic range of Artinskian to Kungurian in Urals (Djupina, 1975). Four species of *Vittatina* were recorded from the Permian succession (Lucaogou, Hongyanchi, Quanzijie and Wutonggou formations) in the southern Junggar Basin (Ouyang et al., 2003, 2017). *Lunatisporites acutus* was reported from the Keuper (Upper Triassic) in Switzerland, however, it was distributed in the Lopingian in Europe and in the Guodikeng Formation in southern Junggar Basin (Ouyang et al., 2003). To sum up, there were ten species established from the Artinskian and Kungurian stages, eight species from the Guadalupian and Kazanian stages, three species from the Lopingian Stage, and one species from the Keuper (Upper Triassic).

The CSP assemblage in the Junggar Basin contains 20 endemic species. Eight species (*Vesicaspora pachyderma*, *Pityosporites evolutus*, *Striatoabietes pachydermus*, *Protohaploxylinus expletus*, *P. micros*, *Potonieisporites panjimensis*, *Samoilovitchisaccites chordens*, and *Cycadopites labiosus*) have stratigraphic range of Pennsylvanian to the Lopingian. A further ten species (*Vestigisporites complexus*, *Alisporites communis*, *A. stenoholcus*, *Striatoabietes lipidus*, *Protowelwitschiapollis elegetis*, *P. exilis*, *P. exoleucus*, *P. rhombos*, *Vittatina oviformis*, and *Lunatisporites tarsus*) have been recorded in the Permian strata. *Cordaitina brachytrileta* and *Striatopodocarpites lucaogouensis* were recorded only from the Lopingian (Wutonggou and Guodikeng formations).

Therefore, of the 48 known species in the CSP assemblages, thirty-one species have been recorded in the Permian strata, seven species in the Cisuralian and Guadalupian, eight species in the Guadalupian and Lopingian, and three species only in the Lopingian. Thus, the age of the CSP assemblage can be identified as Guadalupian.

Considering the vertical distributions of pollen and spores in the CSP assemblage, a vegetation loss is recorded at the base of the lower Quanzijie Formation, where 17 species in 13 genera were lost in the studied profile (Fig. 9). Of these, 7 species in 6 genera, (*Samoilovitchisaccites chordens*, *Vesicaspora pachyderma*, *Vestigisporites mellinus*, *Limitisporites expressus*, *L. cf. pontiferrens*, *Trochosporites reniformis*, and *Striomonosaccites ovatus*) have never been recorded in the horizons higher than the Hongyanchi Formation in the Junggar Basin. As the non-conformity between the Hongyanchi Formation and the Quanzijie Formation is widely accepted (Hou and Wang, 1986; Wu, 1993; XBGMR, 1999; Shen et al., 2019; Tang et al., 2022), we tentatively assign the uppermost Lucaogou Formation and the Hongyanchi Formation to the Roadian, and the lower Quanzijie Formation to the Capitanian (Fig. 2).

The CHV assemblage from the Lucaogou and Hongyanchi formations (Hou and Wang, 1990) is correlated with the Ufimian and Kazanian assemblages in the Cis-Ural area (Ouyang and Norris, 1999). The Ufimian stage was originally subdivided into the Solikamsk and Sheshma horizons, which were characterized by terrestrial-dominated red beds, i. e. the lower sequence of red sandstone and shale (Grunt, 2005; Lozovsky et al., 2009). The Kazanian deposits, which contain marine faunas of conodonts, foraminifers, ammonoids, and brachiopods, were correlated to the Roadian in the Boreal realm (Chernykh and Silantiev, 2004). Therefore, the Ufimian Stage was nested within the uppermost Kungurian Stage (sensu lato). Eurasian Permian palynological stratigraphy has been thoroughly summarized for the Euramerica and Angara botanical provinces (Hart, 1970). The palynological assemblages of the Ufimian and Kazanian stages in their stratotype sections show that most palynomorphs coexisted in both Ufimian and the Kazanian horizons (e. g., *Cordaitina uralensis*, *C. subrotata*, *Crucisaccites ornatus*, *Florinites luberae*, *Vittatina vittifera*, and *Protohaploxylinus latissimus*) (Utting et al., 1997); *Protohaploxylinus latissimus*, *P. perfectus*, *Vittatina vittifera*, and *V. rotunda* have even been recorded in the Urzhumskian (Gomankov and Danilova, 2015). Detailed investigations of the Ufimian, lower Kazanian and upper Kazanian palynostratigraphy showed that the only indicator of the Kazanian palynofloras was the presence of *Cyclogranisporites franklinii*, *Cordaitina vulgaris*, *Vitreisporites pallidus*, *Lueckisporites virkiae*, *Hamiapollenites erabi*, and *Weylandites cinnamatus* (Utting et al., 1997; Götz and Silantiev, 2015). However, two species (*Lueckisporites virkiae* and *Vitreisporites pallidus*) were recorded in the Lucaogou,

Taxa	Age					Palynoflora																					
						Angara									Euramerica					Cathaysia		Gondawana					
	C ₁	C ₂	P ₁	P ₂	P ₃	A		B			C	D	E	F			G			H	I	J	L	M			
						a1	a2	b1	b2	b3				f1	f2	f3	g1	g2	g3					m1	m2		
<i>Cyclogranisporites staplinii</i>						+	+	+		+	+																
<i>Calamospora deusirugosus</i>						+			*																		
<i>Schopfites phalacrois</i>						+																	*				
<i>Acanthotriletes microspinosus</i>						+		+						+	+	+							+				
<i>Acanthotriletes rectispinus</i>						+			+	+				*													
<i>Apiculatisporis xiaolongkouensis</i>						+			*										+								
<i>Kraeuselisporites argutus</i>						+			*																		
<i>Kraeuselisporites spinulosus</i>						+			*									+									
<i>Tuberculatosporites homotubercularis</i>						+			*																		
<i>Potonieisporites turpanensis</i>						+		+	*								+	+									
<i>Plicatipollenites cf. densus</i>						+	+																				
<i>Vestigisporites elegantulus</i>						+			*	+	+																
<i>Vestigisporites turgidus</i>						+	+			*																	
<i>Gardenasporites delicatus</i>						+																		*			
<i>Klausipollenites schaubergeri</i>						+			+			+			+		+		+		+	+		+	+	*	
<i>Falcisporites cf. sublevis</i>						+			+			+			*							+	+				
<i>Striatomonosaccites ellipticus</i>						+	+																				
<i>Raistrickia alligodonta</i>						+	+		+		+			*													
<i>Raistrickia obtusosetosa</i>						+	+		+		+			*													
<i>Cordaitina rotata</i>						+	+	+	+	+	+			*		+	+	+				+	+				
<i>Cordaitina stenolimbata</i>						+	+	+	+	+	+			*		+						+	+				
<i>Cordaitina subrotata</i>						+	+	+	+	+	+			*			+					+	+				
<i>Cordaitina uralensis</i>						+	+	+	+	+	+			+	*		+	+	+			+	+				
<i>Crucisaccites ornatus</i>						+	+		+	+	+			*													
<i>Crucisaccites variosulcatus</i>						+	+		+	+	+	+		*													
<i>Potonieisporites panjimuensis</i>						+	+				*																
<i>Vestigisporites complexus</i>						+	+			*		+															
<i>Pityosporites evolutus</i>						+	+		+			+															
<i>Alisporites communis</i>						+	+		*		+	+															
<i>Alisporites stenoholcus</i>						+	+		+	*																	
<i>Protohaploxypinus expletus</i>						+	+	*				+															
<i>Protohaploxypinus latissimus</i>						+	+			+	+	+			*			+									
<i>Protohaploxypinus micros</i>						+	+																		*		
<i>Protohaploxypinus minor</i>						+	+		+								+	+								*	
<i>Striatoabietes pachydermus</i>						+	+	*																			
<i>Striatoabietes lipidus</i>						+	+		*																		
<i>Protowelwitschiapollis exoleucus</i>						+	+	+	*		+							+									
<i>Vittatina costabilis</i>						+	+		+	+	+								*			+					
<i>Vittatina persecta</i>						+	+		+	+				+	*												
<i>Vittatina subsaccata</i>						+	+		+	+	+			*			+	+					+				
<i>Cycadophites caperatus</i>						+	+		+	+	+	+				*	+	+				+					
<i>Cycadophites labiosus</i>						+	+	*										+									
<i>Cycadophites retroflexus</i>						+	+		+	+							*					+					
<i>Urmites incrassatus</i>						+	+		+	+				*				+									
<i>Cordaitina brachytrileta</i>						+			*																		
<i>Florinites luberae</i>						+		+	+	+	+	+	+	+	*		+	+									
<i>Samoilovitchisaccites chordens</i>						+						*															
<i>Vesicaspora cf. acrifera</i>						+			+	+	+	+		*	+	+											
<i>Vesicaspora pachyderma</i>						+		*			+																
<i>Vestigisporites mellinus</i>						+			+	+	+			*													
<i>Limitisporites expressus</i>						+			+					*													
<i>Limitisporites cf. pontiferrens</i>						+		+															*				
<i>Platysaccus papilionis</i>						+		+	+	+		+					+		+	+		+				*	
<i>Divarisaccus cinctus</i>						+		+	+	+	+	+		*													
<i>Trochosporites reniformis</i>						+														*							
<i>Striomonosaccites ovatus</i>						+		+		+														+		*	
<i>Protowelwitschiapollis elegetis</i>						+			*																		
<i>Protowelwitschiapollis exilis</i>						+			*			+															
<i>Protowelwitschiapollis rhombos</i>						+			*			+															
<i>Paucistriatopinites septatus</i>						+									*												
<i>Striatopodocarpites lucaogouensis</i>						+			+	*																	
<i>Vittatina oviformis</i>						+		+	*			+															
<i>Vittatina vittifera</i>						+		+	+	+	+				*		+					+					
<i>Lunatisporites acutus</i>						+			+											+							
<i>Lunatisporites tersus</i>						+		*	+	+		+															

Note: + occurrence * type horizon

Fig. 7. Geological distribution of identified palynological species in the Dalongkou Profile in Jimsar, northern Xinjiang, China. A: The present data, a1. *Cordaitina subrotata*–*Striatoabietes lipidus*–*Protowelwitschiapollis exoleucus* assemblage (CSP), a2. *Kraeuselisporites spinulosus*–*Tuberculatosporites homotuberculis*–*Potonieisporites turpanensis* assemblage (KTP); B: Southern Junggar Basin (Hou and Wang, 1986, 1990; Ouyang et al., 2003, 2017), b1. Tashikula Formation (P₁), b2. Lucaogou and Hongyanchi Formations (P₂), b3. Quanzijie, Wutonggou, and Guodikeng Formations (P₃); C: Pingdiquan Formation (P₂) in eastern Junggar Basin (Ouyang et al., 2003); D: Lower Wuerhe Formation (P₂) and Tiemulike Formation (P₂) in western Junggar Basin (Ouyang et al., 2003); E: Linxi Formation (P₃) in northeastern China (Zhang et al., 2020, 2022); F: Russia, f1. Kungurian (P₁) in Kuznetsk Basin (Luber and Waltz, 1941), f2. Kazanian (P₂) in Solikamsk Basin (Samoilovich, 1953), f3. Capitanian (P₂) in Kuznetsk Basin (Samoilovich, 1953); G: Tarim Basin, g1. Keziliqiman and Qipan Formations (P₁) (Wang, 1985; Zhu, 1997), g2. Kalundaer Formation and Biyouliet Group (P₂) (Huang et al., 2004), g3. Duwa Formation (P₃) (Hou, 1990); H: Flowerpot Formation (P₁), Oklahoma, USA (Wilson, 1962); I: Zechstein (P₃) in West Europe (Gibson and Bodman, 2021; Gibson and Wellman, 2021); J: Upper Shihhotse and Sunjiagou Formations (P₃) in North China (Gao, 2008; Hou and Ouyang, 2000); L: Xuanwei and Longtan Formations (P₃) in South China (Ouyang, 1986; Ouyang et al., 2017); M: Gondwana, m1–Palynofloral assemblage-III and IV (P₂) (Aggarwal et al., 2019), m2–Palynofloral assemblage-V (P₃) (Aggarwal et al., 2019).

[illegible]

Fig. 8. Stratigraphic correlation of Permian in Junggar Basin and related areas.

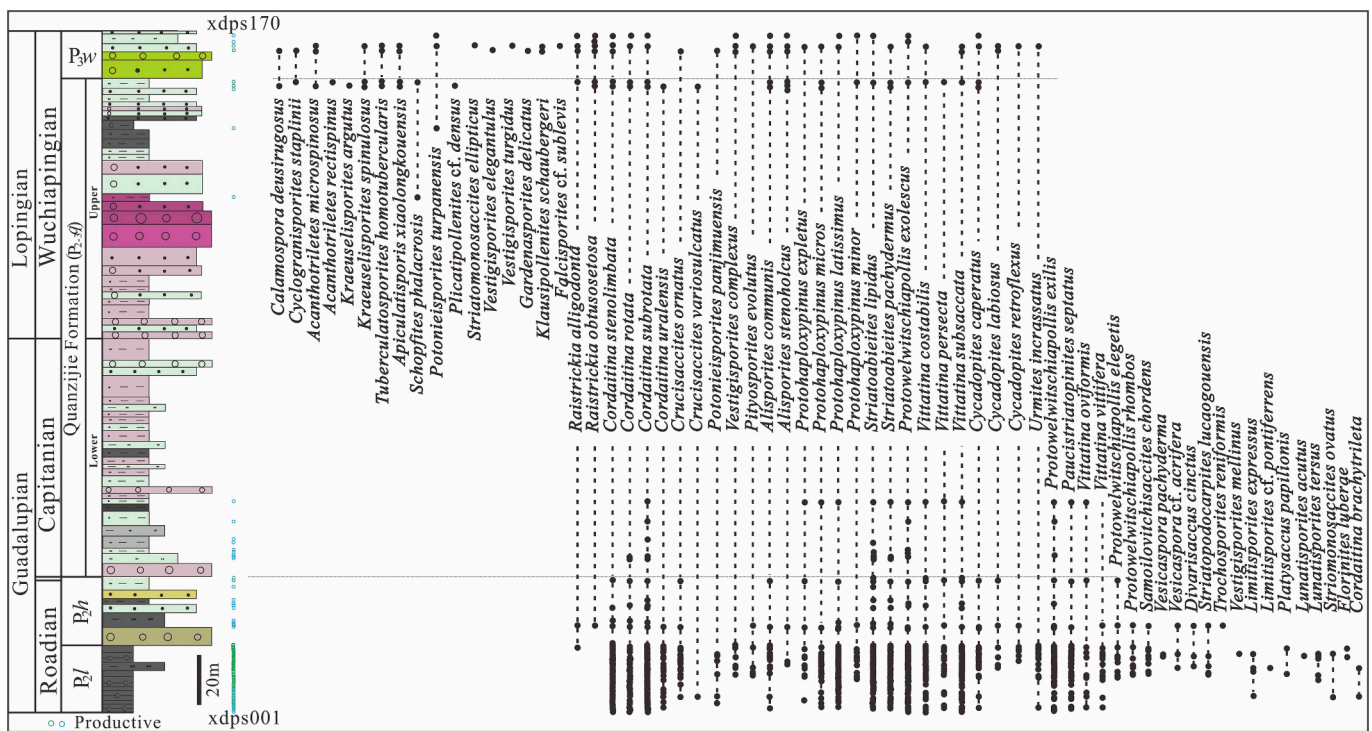


Fig. 9. Distribution of selected species during the Guadalupian-Lopingian transition in the Dalongkou profile in Jimsar, northern Xinjiang, China.

Quanzijie, Wutonggou and Guodikeng formations in the Junggar Basin (Hou and Wang, 1990; Ouyang et al., 2003, 2017). *Trochosporites reniformis*, which occurs in the Hongyanchi Formation, was reported from the Flowerpot Formation of Oklahoma, which is assigned to the Kungurian-Roadian transition (Johnson, 2021). *Raistrickia alligodonta* and *R. obtusosetosa*, which occur in the Hongyanchi Formation, also occur in the Kazanian and Tatarian strata on the Russian platform (Olferev, 1974; Molin et al., 1986; Dryagina, 1988; Faddeeva, 1990; Koloda and Kanev, 1996). Therefore, the CHV assemblage is Kungurian to Guadalupian in age. However, the present CSP assemblage from the uppermost of the Lucaogou Formation, Hongyanchi Formation and lower Quanzijie Formation is slightly stratigraphically higher than the CHV assemblage; thus, we assigned the uppermost Lucaogou Formation and Hongyanchi Formation to the Kazanian or Roadian. As the KTP

assemblage from the upper Quanzijie and lowermost Wutonggou formations is assigned to the Wuchiapingian, and there is a hiatus at the base of the Quanzijie Formation, it is reasonable to assign the lower Quanzijie Formation to the Capitanian (Fig. 2).

5.2.2. *Kraeuselisporites spinulosus*–*Tuberculatosporites homotubercularis*–*Potonieisporites turpanensis* assemblage (KTP)

The KTP assemblage was extracted in the horizons from the uppermost Quanzijie Formation to the lower Wutonggou Formations, which are normally assigned to the Lopingian (Hou and Wang, 1986, 1990; Ouyang and Norris, 1999; Ouyang et al., 2003; Yang et al., 2010). The assemblage consists of 55 species in 29 genera, including 44 identifiable species (Fig. 7). Of these species, 27 also occur in the CSP assemblage (see above), and 17 species are known only in the KTP assemblage.

Cyclogranisporites staplinii has been recorded in the Pennsylvanian Bond Formation in Illinois, USA (Peppers, 1964), and in Carboniferous and Permian strata in northern Xinjiang (Ouyang et al., 2003). *Acanthotriletes microspinosus* has been documented from Lopingian rocks in Yunnan, South China, and *Acanthotriletes rectispinus* has been reported from the Carboniferous and Permian rocks in northern Xinjiang (Ouyang, 1986; Ouyang et al., 2003). *Schopfites phalacrosis* and *Gardenasporites delicatus* have been recorded in the Lopingian Xuanwei Formation in Yunnan (Ouyang, 1986). *Klausipollenites schaubergeri* occurs in the upper Permian Christina horizon in Australia (Potonié and Klaus, 1954) and is widely distributed in the Zechstein deposits in the German Basin (Gibson and Wellman, 2021; Gibson and Bodman, 2021) and the upper Permian strata on the Russian platform (Kyrbezhkova, 1970; Maheshwari, 1997). The species also occurs in the Guodikeng Formation at Dalongkou profile in the Junggar Basin (Ouyang and Norris, 1999), in the Sunjiagou Formation in Tianjin and Shanxi in North China (Hou and Ouyang, 2000; Zhu et al., 2002), and in the Linxi Formation in Inner Mongolia and Songliao Basin, in Northeast China (Zhang et al., 2020, 2022). *Falcisporites sublevis* has been reported in the Permian strata of the Solikamsk Basin, Russia (Luber and Waltz, 1941), and in the Quanzijie, Wutonggou, Guodikeng formations at the Dalongkou profile (Ouyang et al., 2003; Ouyang and Norris, 1999). *Calamospora densirugosus*, *Apiculatisporis xiaolongkouensis*, *Kraeuselisporites argutus*, and *K. spinulosus* have been recorded in the Wutonggou Formation at Dalongkou (Hou and Wang, 1986). *Tuberculatosporites homotubercularis* occurs in the Wutonggou and Guodikeng formations at Dalongkou (Hou and Wang, 1986; Ouyang and Norris, 1999). *Potonieisporites turpanensis* occurs in the Permian strata in the Junggar Basin. *Vestigisporites turgidus* has been reported in the Cisuralian-Guadalupian in the southern Junggar Basin (Ouyang et al., 2003). *Schopfites phalacrosis* and *Gardenasporites delicatus* have been recorded in the Xuanwei Formation in Yunnan, South China (Ouyang, 1986). This formation has been assigned to the Wuchiapingian stage on the basis of isotopic dating of the underlying Emeishan basalts (Zhong et al., 2014; Shen et al., 2019). During the late Permian, *Klausipollenites schaubergeri* was widely distributed in the Angara, Euramerica, Cathaysia, and Gondwana. Considering all this information, the KTP assemblage is assigned to the Wuchiapingian.

The *Alisporites*–*Sulcatisporites*–*Protohaploxylinus* assemblage in the Quanzijie Formation and the *Kraeuselisporites*–*Potonieisporites*–*Sulcatisporites* assemblage in the Wutonggou Formation (Hou and Wang, 1990) have been correlated with the Tatarian succession of the Russian plate (Ouyang and Norris, 1999). The Tatarian succession is composed mainly of continental red-beds that formed in delta plain, fluvial, and lacustrine environments in a regressive setting (Gorbatkina and Strok, 1984), and is normally subdivided into (in stratigraphic ascending order) the Urzhumskian, Vishkilskian, and the Vyatskian horizons (Gomankov, 1997). The Urzhumskian and Vishkilskian (Severodvinskian) have generally been assigned to the Wordian and Capitanian (Guadalupian), and the Vyatskian is retained in the Wuchiapingian (Henderson et al., 2020). The palynofloras of the Tatarian sequence in Russia have been divided into four zones: Zone I roughly corresponded to the Urzhumskian; Zone II to the lower part of the Severodvinskian; Zone III to the upper Severodvinskian and lower Vyatskian; and Zone IV to the upper Vyatskian. *Lueckisporites virkkiae* was the characteristic element of Zone I and *Scutaspites unicus* was first observed in Zone III; however, these two species are widely distributed in the Wutonggou Formation and the lower Guodikeng Formation in the Junggar Basin. *Klausipollenites schaubergeri* was recorded in the Vetlugian, which overlies the Vyatskian, in association with the Early Triassic *Lunatisporites* and *Lundbladispora*.

Therefore, the correlation between the ASP and KPS assemblages and the Tatarian palynofloras needs to be more firmly established, because the Tatarian palynofloras cannot be distinguished in any essential way from those of the Kazanian (Gomankov, 1998). However, the KTP assemblage might be correlated with the Tatarian Zone III on the basis of the presence of *Raistrickia*, *Schopfites*, and *Klausipollenites schaubergeri*.

The absence of *Lueckisporites virkkiae* in the KTP assemblage might reflect ecological or climatic reasons (Ouyang and Norris, 1999).

6. The end-Guadalupian crisis

Since the recognition of the end-Guadalupian crisis as a mass extinction event (Stanley and Yang, 1994), the paleontology, geology, and geochemistry of the interval have been extensively investigated. The volcanism of the Emeishan large igneous province and the nadir of sea level in the Paleozoic are regarded as the most important factors leading to the global changes in the organic and inorganic realms (Chen and Shen, 2019). High contents of dibenzofuran, indicating a collapse of terrestrial vegetation, has been reported in the Guadalupian-Lopingian transition in the Penglaitan GSSP (Kaiho et al., 2023). The Kamura cooling event and the collapse of photosymbiosis were evidenced by the appearance of mid-latitude brachiopods in the tropical areas and the extinction of the unique tropical-adapted fauna during the mid-Capitanian (Shen and Shi, 2002; Isozaki and Aljinović, 2009; Isozaki et al., 2011). The mid-Capitanian extinction of the Cathaysia flora was marked by a loss of 56% of macrofossil plant species in the middle Upper Shihhotse Formation in North China (Stevens et al., 2011). In contrast, in the palynological record from this formation in the Linxing area, Shanxi Province, North China, only *Gulisporites* disappeared in the middle of the Upper Shihhotse Formation (Wei et al., 2022); however, *Gulisporites cochlearius* also occurs in the Kayitou Formation (Changhsingian-Induan stages) in Yunnan Province, South China (Ouyang, 1982). The end-Guadalupian extinction of the Cathaysia flora occurred between deposition of the Upper Shihhotse Formation and the Sunjiagou Formation in North China, with an extinction rate as high as 96.3% on the species level for the macroflora (Wang, 1989). On terrestrial Gondwana, the end-Guadalupian extinction is recognized by the disappearance of fossil leaves *Gangamopteris ovata*, *Palaeovittaria kurzi*, *Lanceolatus communis*, *Glossopteris damudica*, *G. decipiens*, *G. formosa*, *Noeggerathiopsis* sp., and *Lepidophyllum* sp. at Portal Mountain, Antarctica (Retallack et al., 2006); in eastern Australia, the crisis was marked by the loss of a few plants at the generic and species levels (Fielding et al., 2023). However, palynological studies in the Godavari Graben, southern India, indicate that only three genera (*Horridiriletes*, *Ibisporites*, and *Tiwarisporites*) become extinct during the end-Guadalupian crisis (Jha and Aggarwal, 2011; Mishra and Singh, 2018; Aggarwal et al., 2019). These findings show that the effects of end-Guadalupian and mid-Capitanian crises on terrestrial vegetation differed spatially and between macroflora and palynoflora. A similar difference has been reported for the end-Permian mass extinction in Australia, which is marked by 97% species-level extinction in fossil leaf data but only 19% taxonomic loss at the genus/or family levels in fossil pollen (Retallack, 1995; McElwain and Punyasena, 2007).

The present palynological data for the middle and upper Permian succession in the Dalongkou profile show an obvious change between the Guadalupian and Lopingian palynofloras (Fig. 9). Twenty-one pollen species from the Guadalupian uppermost Lucaogou and Hongyanchi formations were not detected in the Lopingian upper Quanzijie and lowermost Wutonggou formations in this study. Ten species of them (*Cordaitina brachytrileta*, *Platysaccus papilionis*, *Divarisaccus cinctus*, *Protowelwitschiapollis elegetis*, *P. exilis*, *P. rhombos*, *Striatopodocarpites lucaogouensis*, *Vittatina vittifera*, *Lunatisporites acutus*, and *L. tersus*) occur in the Lopingian Wutonggou and Guodikeng formations in the Junggar Basin. Two species (*Florinites luberae* and *Vesicaspora cf. acrifera*) occur in the Lopingian Linxi Formation in Inner Mongolia. Only nine species in eight genera (*Samoilovitchisaccites chordens*, *Vesicaspora pachyderma*, *Vestigisporites mellinus*, *Limitisporites expressus*, *L. cf. pontiferrens*, *Trochospores reniformis*, *Striomonosaccites ovatus*, *Vittatina oviformis*, and *Paucistriatopinites septatus*) have been recorded in neither the KTP assemblage nor Lopingian palynofloras globally. Consequently, among the 53 species within the CSP assemblages, 9 species have become

extinct. The extinction rate stands at 17%, notably lower than that of mass extinctions, which surpass 75%; and this is regarded as a background extinction.

The extinction patterns of taxonomic and ecologic selection are direct record of processes during background and mass extinction. Clapham and Payne (2011) reported that the end-Permian (Changhsingian) mass extinction was a physiologically selective crisis, and the Capitanian extinction exhibited similar physiological selectivity too. Background extinction selectivity is consistently significant with the geographic range. Narrowly distributed taxa are at significantly greater risk of extinction during the background intervals in the Kungurian–Wuchiapingian (Clapham and Payne, 2011). It is generally agreed that background extinction is an ongoing feature in most ecosystems, with typically a few species in decline and a few that are expanding (Wiens et al., 2012). The present end-Guadalupian extinction of pollen proves the end-Guadalupian extinction was taxonomically selective (Chen and Shen, 2019).

7. Conclusion

Detailed palynological investigation of the Guadalupian and Lopinian strata at Dalongkou in Jimsar, northern Xinjiang, China, was performed to determine the age of the uppermost Lucaogou, Hongyanchi, Quanzijie, and lowermost Wutonggou formations, and to discuss the end-Guadalupian crisis on terrestrial vegetation. Two palynological assemblages are recognized in stratigraphic ascending order, the *Cordaitina subrotata*–*Striatoabietes lipidus*–*Protowelwitschiapollis exoleusculus* assemblage from the uppermost Lucaogou, Hongyanchi and lower Quanzijie formations and *Kraeuselisporites spinulosus*–*Tuberculatosporites homotubercularis*–*Potonieisporites turpanensis* assemblage from the upper Quanzijie and lower Wutonggou formations. On the basis of palynological data, the uppermost Lucaogou Formation and Hongyanchi Formation are assigned to the Roadian, the lower Quanzijie Formation is assigned to late Capitanian, and the upper Quanzijie and lower Wutonggou formations are Wuchiapingian stage. A hiatus (missing of Wordian) between the Lower Quanzijie Formation and the Hongyanchi Formation is identified. The coexistence of *Schopfites phalacrosis*, *Tuberculatosporites homotubercularis* and *Gardenasporites delicatus* provides reliable age-links between the upper Quanzijie and lower Wutonggou formations in northern Xinjiang and the Xuanwei Formation in Yunnan. The end-Guadalupian extinction is taxonomically selective on terrestrial vegetation, and 17% extinction rate indicates a background extinction.

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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Appendix A. List of identified taxa in the Dalongkou profile in Jimsar, northern Xinjiang

TRILETE SPORES

Kraeuselisporites argutus Hou et Wang, 1986
Kraeuselisporites spinulosus Hou et Wang, 1986
Kraeuselisporites sp.
Calamospora deusirugosus Hou et Wang, 1986
Cyclogranisporites staplinii (Peppers) Peppers, 1970
Cyclogranisporites sp.
Verrucosisporites sp.
Raistrickia alligodonta (Andrejeva) Dryagina, 1990
Raistrickia obtusosetosa (Luber) Faddeeva, 1990
Schopfites phalacrosis Ouyang, 1986
Acanthotriletes microspinosus (Ibrahim) Potonie et Kremp, 1955
Acanthotriletes rectispinus (Luber) Hart, 1965
Acanthotriletes sp.
Lophotriletes sp.
Dictyotriletes sp.
Apiculatisporis xiaolongkouensis Hou et Wang, 1986
Apiculatisporis sp.
 Monolete spores
Tuberculatosporites homotubercularis Hou et Wang, 1986
Tuberculatosporites sp.

POLLEN

ATAENITE MONOSACCITES

Cordaitina brachytrileta Hou et Wang, 1990
Cordaitina rotata (Luber) Samoilovich, 1953
Cordaitina stenolimbata (Luber) Hou et Wang, 1990
Cordaitina subrotata (Luber) Samoilovich, 1953
Cordaitina uralensis (Luber) Samoilovich, 1953
Florinites luberae Samoilovich, 1953
Crucisaccites ornatus (Samoilovich) Dibner, 1971
Crucisaccites variosulcatus Djupina, 1971
Potonieisporites panjimuensis Wang, 2003
Potonieisporites turpanensis Hou et Wang, 1990
Potonieisporites sp.

Samoilovitchisaccites chordens Wang, 2003
Plicatipollenites cf. *densus* Srivastava, 1970

TAENIATE MONOSACCITES

Striatomonosaccites ellipticus Wang, 2003
Striatomonosaccites ovatus Bharadwaj, 1962

TAENIATE BISACCATES

Protohaploxypinus expletus Hou et Wang, 1990
Protohaploxypinus latissimus (Luber et Waltz) Samoilovich, 1953
Protohaploxypinus micros Hart, 1964
Protohaploxypinus minor (Klaus) Hou et Wang, 1986
Striatoabietes lipidus (Zhang) Ouyang, 2003
Striatoabietes pachydermus Zhan, 2003
Striatopodocarpites lucaogouensis Zhan, 2003
Protowelwitschiapollis elegetis Zhang, 1983 = *Hamiapollenites elegantis* (Zhang, 1983) Ouyang, 2017
Protowelwitschiapollis exilis Zhang, 1983 = *Hamiapollenites* cf. *exoleusculus* (Zhang, 1983) Hou et Wang, 1990
Protowelwitschiapollis exoleusculus Zhang, 1983 = *Hamiapollenites exoleusculus* (Zhang, 1983) Hou et Wang, 1990
Protowelwitschiapollis rhombos Zhang, 1983 = *Hamiapollenites rhombos* (Zhang, 1983) Zhan, 2003
Paucistriatopinites septatus Djupina, 1975 = *Hamiapollenites septatus* (Djupina, 1975) Zhan, 2003
Vittatina costabilis Wilson, 1962
Vittatina oviformis Wang, 2003
Vittatina persecta Zauer, 1960
Vittatina subsaccata Samoilovich, 1953
Vittatina vittifera (Luber) Samoilovich, 1953
Lunatisporites acutus Leschik, 1955

Lunatisporites tersus Ouyang, 2003

ATANIATE BISACCATES

Vesicaspora cf. *acrifera* (Andreyeva) Hart, 1965

Vesicaspora pachyderma Wang, 2003

Vesicaspora sp.

Falcisporites cf. *sublevis* (Luber) Ouyang et Norris, 1999

Klausipollenites schaubergeri (Potonié et Klaus) Jansonius, 1962

Alisporites communis Ouyang, 2003

Alisporites stenoholcus Ouyang, 2003

Divarisaccus cinctus (Luber, 1941) Wang, 2003

Platysaccus papilionis Potonié et Klaus, 1954

Vestigisporites complexus Ouyang, 2003

Vestigisporites elegantulus Hou et Wang, 1986

Vestigisporites mellinus Sivertseva, 1966

Vestigisporites turgidus Ouyang, 2003

Limitisporites expressus (Kruzina) Ouyang, 2003

Limitisporites cf. *pontiferrens* (Kaiser) Ouyang, 2003

Gardenasporites delicatus Ouyang, 1986

Piceapollenites sp.

Pityosporites evolutus Ouyang, 2003

POLYSACCATES

Trochosporites reniformis Wilson, 1962

Trochosporites sp.

MONOSULCATES

Cycadopites caperatus (Luber) Hart, 1965

Cycadopites labiosus Ouyang, 2003

Cycadopites retroflexus (Luber) Hart, 1965

Cycadopites sp.

Urmites incrassatus Djupina, 1974

Appendix B. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.revpalbo.2025.105445>.

Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

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