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Neregato, R.; D'Apolito Junior, Carlos; Glasspool, I.j.; Wang, S.–j.; Liu, F.; Windslow, P.; Lu, J.; Shao, L.; Hilton, Jason

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**Palynological constraints on the provenance and stratigraphic range of
a Lopingian (late Permian) inter-extinction floral lagerstätte from the
Xuanwei Formation, Guizhou Province, China**

¹R. Neregato, ¹C. D’Apolito, ²I.J. Glasspool, ³S.-J. Wang, ⁴F. Liu, ¹P. Windslow, ^{1,5}J.
Lu, ⁵L. Shao and ¹J. Hilton

¹ School of Geography, Earth and Environmental Sciences, The University of
Birmingham, Edgbaston, Birmingham, B15 2TT, UK,

² Department of Geology, Colby College, Waterville, ME 04901-8858, USA,

³ State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, the
Chinese Academy of Sciences, Beijing 100093, P. R. China,

⁴ Nanjing Institute of Geology and Stratigraphy, the Chinese Academy of Sciences, 39
East Beijing Road, Nanjing, 210008, China,

⁵ State Key Laboratory of Coal Resources and Safety Mining, China University of
Mining and Technology (Beijing). Road Xueyuan, Beijing, 100083, China.

*Correspond authors: Rodrigo Neregato and Jason Hilton: School of Geography, Earth
and Environmental Sciences, The University of Birmingham, Edgbaston, Birmingham,
B15 2TT, UK.*

ABSTRACT

Late Permian (Lopingian) volcanoclastic lithologies from the Huopu Mine near Fuyuan,
Guizhou Province, SW China have yielded konservat lagerstätte-grade plant
macrofossils. These fossils derive from a stratigraphic interval bounded by the mid-
Capitanian extinction below and the end Permian extinction above and globally, few

anatomically preserved floras are known from this age. Due to practical constraints of active mining at the site, to date this konservat lagerstätte is only known from *ex situ* mine spoil. However, through the use of combined petrographic and palynologic analyses it has been possible to constrain the stratigraphic position, provenance and taphonomic history of these fossils, such that they are now known to have been deposited in a shallow marine setting as part of the lower member of the Xuanwei Formation during the Wuchiapingian. The palynological assemblage is of low abundance and diversity and is dominated by leptosporangiate (filicalean) fern spores with less common lycopsid and sphenopsid spores and gymnosperm pollen, and rare marine acritarchs and is suggestive of an ecologically pioneering rather than established flora. Given the Wuchiapingian age of the lagerstätte this flora has broader potential significance in that affords insights into pre-adaption and resilience to the profound environmental perturbations associated with the mid-Capitanian and end-Permian extinctions, which were key to long term survival into the Triassic.

Keywords: Xuanwei Formation, Wuchiapingian, fossil plant, volcanoclastic, biostratigraphy.

INTRODUCTION

The Permian aged floras of China provide important insights into the composition and evolution of wetland vegetation during the final stages of the Palaeozoic (Hilton *et al.*, 2001, 2004; Seyfullah *et al.* 2010; He *et al.* 2013a, 2013b), particularly as in Euramerica similar styled wetland floras had been extirpated, broadly coincident with the Carboniferous–Permian boundary (Hilton and Cleal, 2007; Tabor *et al.*, 2013).

The Late Permian Xuanwei Formation from SW China's easternmost Yunnan and westernmost Guizhou provinces (Fig. 1A-B) rests directly, but unconformably, upon the basalts of the Emeishan Large Igneous Province (LIP) (Fig. 1C). The Emeishan LIP has been correlated with the mid-Capitanian (formerly end-Guadalupian) mass extinction event (Wignall *et al.*, 2009) and plant fossils from this region have been instrumental in demonstrating linkage between the marine and terrestrial realms; plant fossils record a 24% species loss during this biotic crisis (Bond *et al.*, 2010; Bond and Wignall, 2014). Further, the Xuanwei Fm. in these areas is thought to have derived from the erosion of the Central Emeishan LIP basalts and their overlying tuffs (He *et al.*, 2007). Research suggests that this deposition continued throughout the remainder of the Lopingian (late Permian) and that the Permo-Triassic boundary extinction event interval was coincident with the deposition of the uppermost beds of the Xuanwei Fm., and preceded the deposition of the overlying earliest Triassic Feixianguan/Kayitou Formation (see: Wang *et al.*, 2011; Yu *et al.*, 2015).

The Xuanwei Fm. clearly occupies an important stratigraphic interval linking the mid-Capitanian biotic crisis and the Permo-Triassic boundary extinction event. This late Permian Formation preserves abundant compression and impression fossils from which a firm understanding of the composition and diversity of the regional flora has been developed (Zhao *et al.*, 1980, Yao *et al.*, 1980). However, it also preserves a palaeobotanical konservat lagerstätte (as per: Seilacher *et al.*, 1986). The fossils are preserved within a volcanogenic, epiclastic conglomerate comprised in part of tuffaceous material, hereafter just epiclastic conglomerate. Cellular details are preserved in high fidelity, through carbonate permineralized (Hilton *et al.*, 2004; Wang *et al.*, 2006; Seyfullah *et al.*, 2010; Wang *et al.*, in review), and provide details of plant anatomy unobtainable from contemporaneous compression and impression fossils.

To date studies on the anatomically preserved plants from the Xuanwei Formation lagerstätte remain in their infancy. Those from Huopu are the most informative as large blocks containing abundant plant material have been recovered from the locality whereas, from nearby localities only isolated specimens belonging to filicalean and marattialean ferns (Hilton *et al.*, 2004; He *et al.*, 2008, 2013b) have been recovered. The Huopu blocks yield an apparently diverse assemblage from which the species identified so far include gymnosperm stems and branches assigned to the pteridosperm *Callistophyton boyssetii* (Seyfullah *et al.*, 2009; Fig. 2A) and the coniferophyte *Xuanweioxylon scalariforme* (He *et al.*, 2013a; Fig. 2B-C), gymnosperm ovules including *Cardiocarpus huopuensis* (Wang *et al.*, 2006; Fig. 2D-E) and *Muricosperma guizhouensis* (Seyfullah *et al.*, 2010; Fig. 2F), and also heterosporous strobili and leaves assumed to belong to Noeggerathialean ferns (Wang *et al.*, in progress; Fig. 2G). Unfortunately, the precise stratigraphic occurrence of the Huopu material within the Xuanwei Fm. and its depositional environment remain unknown as these fossils have only been identified from loose blocks of epiclastic conglomerate contained in spoil from underground mining. Resolving these issues is important to better understand how these wetland taxa related to and were affected by the dramatic ecological changes that occurred during the Late Permian.

LOCALITY AND GEOLOGICAL INFORMATIONS

Blocks of epiclastic conglomerate sediment containing anatomically preserved plants were collected from mine spoil from Huopu coal mine, near Panxian in Guizhou Province, and Fuyuan in Yunnan Province, SW China (Wang *et al.*, 2006, in review; Figure 2) during field seasons in 2010-13. At this locality coal from the Xuanwei Formation is extracted in deep mines and as part of this process, spoil from rock units

adjacent to the economically viable coals are brought to the surface during the extraction process. Four main coals are documented as mineable across the Panguan Syncline, seams nos. 12, 17, 18 and 24 (Li *et al.*, 2012). Huopu is currently known to mine the Nos. 1, 3, 5, 7, 10, 12, 14, 17 coal seams, and of these extraction of the No. 17 coal seam is clearly important, the extraction of this typical "three soft coal" being fully mechanized (Liu *et al.*, 2014). This is comparable with the Dahe Mine about 10 miles to the southwest of Huopu where coal nos. 1+1, 2+1, 4, 7-10, 14 and 16 are worked (Feng and Quan, 2014). Correlating with Wang *et al.* (2011) this would indicate that the seams extracted occur across all three members of the Xuanwei Formation (lower, middle and upper), though the economically important no. 17 seam falls within the lower member.

The Xuanwei Formation is dominated by interbedded sandstones, conglomerates, mudstones and coals that formed primarily in terrestrial, fluvial, mire and proximal deltaic environments (Wang *et al.*, 2011), and has occasional volcanoclastic tuffaceous horizons that contain anatomically preserved fossil plants (Zhou *et al.*, 2000; Hilton *et al.*, 2004; Wang *et al.*, 2006; Zhang *et al.*, 2009, 2010; Dai *et al.*, 2010, 2014). Whereas the volcanoclastic horizons constitute konservat lagerstätten as they preserve fossil plants in exquisite cellular detail, some have also been designated as 'polymetallic ore beds' (Dai *et al.*, 2010). These 'ore beds' are pyroclastic in origin and occur primarily in the lower member of the Xuanwei Formation and can measure up to 10m in thickness. Their petrology, mineralogy, and geochemistry are similar to those of intra-seam alkali-tonsteins (usually only 3-5cm in thickness) (Dai *et al.*, 2010). Dai *et al.* (2010) also report that carbonization is very common in these volcanic breccias due to epigenetic hydrothermal fluids and illustrate fusinitic material.

The Xuanwei Formation rests unconformably on the Emeishan Basalt and was deposited during the Wuchiapingian to Changhsingian stages of the Permian (Wang *et*

al. 2011). The Formation represents the initial stages of denudation and sedimentary deposition of rocks from the Emeishan LIP. Stratigraphically above the Xuanwei Formation occur sediments of Triassic age (Wang *et al.*, 2011). In this geological context the Xuanwei Formation spans the interval between the mid–Capitanian extinction event that is coincident with onset of Emeishan volcanism (Wignall *et al.*, 2009) and the End–Permian mass extinction at the Permian–Triassic Boundary.

MATERIAL AND METHODS

Approximately 200g of fine grained, green coloured epiclastic conglomerate from Huopu coal mine (Fig. 2) containing abundant plant debris was selected from several representative blocks for palynological processing. Samples were fragmented using a geological hammer before being ground with pestle and mortar. This material was processed using standard HCL–HF–HCL acid maceration techniques, followed by zinc bromide heavy mineral separation (Batten, 1999). The organic residue was sieved using a 20 µm mesh. Because of the dominance of large charcoal fragments, the samples were swirled in a similar fashion to gold panning and the fine fraction collected and mounted in order to remove large chunks. The residue was strew mounted using Petropoxy 154.

Productive samples contain poorly-preserved palynomorphs of low thermal maturity (T.A.I. = 2+ to 3– using the scheme of Traverse, 2007) and as such oxidation was unnecessary. Slides were observed and photographed using a Zeiss Axioskope with transmitted light. Photographs were taken using a Canon EOS D40 digital SLR camera. Spore and pollen positions in the slides were marked using an England Finder. Image treatments and scale insertions, retrospectively, were done using Microsoft Office Picture Manager and Corel Draw version X6. Slides are deposited at the National

Museum of Plant History of China (NMPHC), Institute of Botany, Chinese Academy of Sciences, Beijing, China, under the accession numbers 72002–72008.

RESULTS

PETROGRAPHIC ANALYSIS

Anatomically preserved plant-bearing lithologies within the Xuanwei Formation (Fig. 3) are heterolithic and dominated by pebble conglomerates of weathered igneous clasts in a medium–coarse grained, angular, quartz and feldspar-rich matrix. Individual pebble conglomerates (Fig. 3A) have a range of clasts of weathered basic to intermediate igneous rocks including fine- to medium-grained lithologies with randomly orientated, or flow aligned, plagioclase feldspar crystals, altered pyroxenes where the shape is preserved but has been replaced by carbonates, and occasional vesicles as well as micro–phenocrysts of plagioclase, which produce a trachytic texture, and larger phenocrysts of plagioclase. Igneous clasts vary from 7–40 mm in diameter and are pale–dark green (Fig. 3B–D). Conglomerates are matrix supported (Fig. 3A–B, E) and fine upwards into medium-grained sub–arkose and lithic sub–arkose (e.g. Fig. 3E). The arkose and lithic sub–arkoses can be weakly cross–bedded (Fig. 3E) to planar bedded and have individual beds from 0.5–30 mm thick. Although dominated by quartz and feldspar, they contain abundant glauconite that is recognised by its apple green colour and that gives a green colour to the rock when fresh. Glauconite grains are round–ovate and are from 0.3–1.5 mm in their long axis length (Figs. 3C–D, F). In petrological thin section they have a characteristic moderate relief, pleochroism and weak birefringence, and comprise a mosaic of fine grained crystals that attest to their authigenic origin.

Plant fossils are abundant within plant-bearing lithologies, occurring irregularly as finer grained detritus within the sub-arkoses and lithic arkoses or concentrated on bedding planes (Fig. 3E), or as larger clasts within the lithic arkoses (Fig. 3G) and conglomerates (Fig. 3A–B). The plant fossils are fragmentary, with larger plant clasts being rounded by taphonomic processes prior to deposition (Fig. 3A, F); plant clasts within the pebble conglomerates vary from a few millimetres in diameter to larger stems up to 10 cm in diameter and 30 cm long, and within the arkosic sediments are typically smaller and from 2–10 mm in diameter. Plant clasts are in many cases larger than the surrounding igneous clasts. Anatomical preservation of the fossil plants is facilitated by carbonate mineralization that occurred early in the diagenetic history of the lithology and prevented significant levels of organic decay prior to mineralization.

PALYNOLOGY

The macerations provided a well- to poorly-preserved, low abundance palynological assemblage dominated by fern spores but with rare gymnosperm pollen grains and marine acritarchs. Whereas identifiable specimens were limited in number, fragmentary and unidentifiable spores were common and unidentifiable plant debris and charcoal were abundant. The palynological diversity includes 15 spore genera (*Cyathidites*, *Leiotriletes*, *Waltzispora*, *Calamospora*, *Stenozonotriletes*, *Cyclogranisporites*, *Lophotriletes*, *Microbaculispora*, *Concavissimisporites*, *Verrucosisporites*, *Wilsonisporites*, *Dictyotriletes*, *Neoraistrickia*, *Laevigatosporites*, *Punctatosporites*) identifiable to 16 species, plus one indeterminate spore placed in open nomenclature, two pollen genera (*Circulina*, *Pteruchipollenites*) of which one is identifiable to species and four acritarch morphologies; *Michrystridium*, *Baltisphaeridium* and two indeterminate forms assignable respectively as Acanthomorph and Netromorph – see

Lei *et al.* 2013). A summary and description of each taxon is provided below along with an England Finder reference to a representative specimen on the slides.

Cyathidites Couper, 1953

Cyathidites breviradiatus Helby, 1966 (Fig. 4B)

Radially symmetric, trilete spore with a triangular amb. Sides concave with a slightly rounded apex. Trilete mark distinct with straight laesurae, measuring 6 μm in width, the rays extending to 1/2 the equatorial diameter. Exine laevigate, measuring approximately 1.0 μm in thickness. Equatorial diameter = 60 μm (EF: NMPHC 72006-M 25/2).

Cyathidites minor Couper, 1953 (Fig. 4A)

Radially symmetric, trilete spore with a triangular amb. Sides convex with a rounded apex. Trilete mark distinct with straight laesurae, measuring 4 μm in width, the rays extending to 2/3 the equatorial diameter. Exine laevigate, measuring less than 1.0 μm in thickness. Equatorial diameter = 33 μm (EF: NMPHC 72004-P 30/2).

Leiotriletes (Naumova) emend. Potonié & Kremp, 1954

Leiotriletes adnatoides Potonié & Kremp, 1955 (Fig. 4G)

Radially symmetric, trilete spore with a triangular amb. Sides straight to slightly concave with a rounded apex. Trilete mark distinct with straight, thick laesurae, the rays almost extending to the equatorial margin. Exine laevigate, measuring 1 μm in thickness. Equatorial diameter = 43 μm (EF: NMPHC 72007-M 49).

Leiotriletes adnatus (Kosanke) Potonié & Kremp, 1954 (Fig. 4C-D)

Radially symmetric, trilete spore with a triangular amb. Sides slightly convex to straight, with a rounded apex. Trilete mark distinct with straight laesurae, the rays extending to approximately 1/2 the equatorial diameter. Exine laevigate, measuring less than 1.0 μm in thickness. Equatorial diameter = 45-46 μm (EF: NMPHC 72002-V 28/4; EF: 3-O 39/1).

Leiotriletes exiguus Ouyang & Li, 1980 (Fig. 4F)

Radially symmetric, trilete spore with a triangular amb. Sides straight with rounded apex. Trilete mark distinct with straight, thin laesurae, the rays extending to 1/2 the equatorial diameter. Exine laevigate, measuring 2.0 μm in thickness. Equatorial diameter = 38 μm (EF: NMPHC 72006-O 43/1-2).

Leiotriletes spp. 1 (Fig. 4E)

Radially symmetric, trilete spore with a triangular amb. Sides convex, with a corroded rounded apex. Trilete mark distinct with straight laesurae, measuring 2 μm in width, the rays extending to the equatorial margin. Exine poorly preserved. Equatorial diameter = 45 μm (EF: NMPHC 72004-S 26/2).

Comment: This specimen is similar to *L. directus* Balme and Hennelly, 1956.

Waltzispora Staplin, 1960

Waltzispora albertensis Staplin, 1982 (Fig. 4I-J)

Radially symmetric, trilete spore with a triangular amb. Sides straight with a trapezoidal apex. Trilete mark distinct, laesurae straight, the rays extending to 1/2 the equatorial

diameter. Exine laevigate, measuring approximately 1-1.5 μm in thickness. Equatorial diameter = 40-53 μm (EF: NMPHC 72005-P 35/2; NMPHC 72008-G 30/1).

Waltzispora strictura Ouyang & Li, 1980 (Fig. 4H)

Radially symmetric, trilete spore with a triangular amb. Sides straight to concave, with a swollen apex. Trilete mark distinct with straight, thin laesurae, the rays extending to $\frac{1}{2}$ the equatorial diameter. Exine laevigate, measuring 1 μm in thickness. Equatorial diameter = 45 μm (EF: NMPHC 72006-W 42/1).

Calamospora Schopf, Wilson & Bentall, 1944

Calamospora pedata Kosanke, 1950 (Fig. 4K)

Trilete spore with an elliptical amb. Trilete mark distinct with straight, thick laesurae, the rays extending to approximately $\frac{2}{3}$ the equatorial diameter. Exine laevigate, measuring approximately 2 μm in thickness. Equatorial diameter = 45 μm (EF: NMPHC 72006-H 44/3).

Stenozonotriletes (Naumova) Potonié, 1958

Stenozonotriletes sp. 1 (Fig. 4L)

Radially symmetric, trilete spore with a sub-triangular to rounded amb. Trilete mark distinct with straight, thin laesurae, the rays extending to the equatorial margin. Exine laevigate, measuring less than 1 μm in thickness. Equatorial diameter = 20 μm (EF: NMPHC 72006- R 31/4).

Cyclogranisporites Potonié & Kremp, 1954

Cyclogranisporites aureus (Loose) Potonié & Kremp, 1955 (Fig. 4N)

Radially symmetric, trilete spore with a circular amb. Trilete mark distinct with straight, marginate laesurae, measuring 2.0 μm in width, the rays extending to 3/5 of the equatorial diameter. Exine measuring 1 μm in thickness, with an ornamentation formed by regularly distributed, inconspicuous grana measuring less than 0.5 μm in diameter. Equatorial diameter = 27 μm (EF: NMPHC 72006-U 42/1).

Comment: This taxon is a little smaller in comparison with other species assigned to *Cyclogranisporites*, but *C. aureus* is the only taxon to present a thin margo, as observed in this species.

Cyclogranisporites breviradiata de Jersey, 1960 (Fig. 4M)

Radially symmetric, trilete spore with a circular amb. Trilete mark distinct with straight, thin laesurae, the rays extending a little further than 3/5 of the equatorial diameter. Exine measuring approximately 1 μm in thickness, with an ornamentation formed by regularly distributed grana measuring less than 1 μm in diameter. Equatorial diameter = 54 μm (EF: NMPHC 72007-P 41/2).

Lophotriletes (Naumova) Potonié & Kremp, 1954

Lophotriletes paramictus Ouyang, 1986 (Fig. 4O-P)

Radially symmetric, trilete spore with a triangular amb. Sides slightly concave with a rounded apex. Trilete mark barely discernible. Exine ornamented with baculae and cones. Baculae measuring approximately 1.0 μm in diameter and 2.0-2.5 μm in height; cones measuring 1.0-1.5 μm in diameter and 1.5 μm in height. Some cones and baculae are basally joined forming a reticulum of muri measuring 1.0-2.0 μm in width. Distal

ornamentation is coarser than proximal. Exine measuring less than 1.0 μm in thickness. Equatorial diameter = 44 μm (EF: NMPHC 72007-H 38/2-4).

Microbaculispora Bharadwaj, 1962

Microbaculispora sp. 1 (Fig 4Q)

Radially symmetric, trilete spore with a triangular amb. Sides slightly convex with a rounded to flat apex. Trilete mark distinct with straight, thin laesurae, the rays extending to 3/5 of the equatorial diameter. Exine ornamented with uniformly distributed baculae measuring 1.0 μm in height and less than 1.0 μm in diameter. Baculae often anastomose distally to form rugulae. Equatorial diameter = 34 μm (EF: NMPHC 72008-J 45/3-4).

Comment: This specimen resembles *Microbaculispora gondwanensis* Bharadwaj 1962, but presents a smaller general size and has smaller baculae.

Concavissimisporites (Delcourt & Sprumont) Dettmann, 1963

Concavissimisporites aff. *apiverrucatus* (Couper) Döring (Fig. 5A)

Radially symmetric, trilete spore with a triangular amb. Sides strongly convex, with a rounded apex. Trilete mark distinct with straight, thin laesurae, the rays extending to the equatorial margin. Exine measuring 1.0 μm in thickness, ornamented with grana measuring approximately 0.3 μm in diameter. Equatorial diameter = 45 μm (EF: NMPHC 72006-T 43/4).

Verrucosisporites (Ibrahim) Potonié & Kremp, 1954

Verrucosisporites pergranulus (Alpern) Smith & Alpern, 1971 (Fig. 5B)

Radially symmetric, trilete spore with a circular amb. Trilete mark distinct with straight, relatively thick laesurae, the rays extending to the equatorial margin. Exine measuring 1.0 μm in thickness, ornamented with small verrucae measuring less than 2.0 μm in width and between 1.0-1.5 μm in height. Some of the verrucae are joined, forming a reticulum with muri less than 1.0 μm in width. Equatorial diameter = 50 μm (EF: NMPHC 72002-Q 49/1-2).

Verrucosisorites sp. 1 (Fig. 5C-D)

Radially symmetric, trilete spore with a circular amb. Trilete mark distinct with straight, thick laesurae and an irregular margo, the rays extending to the equatorial margin. Exine ornamented with sparse verrucae measuring 2.5-5.0 μm in diameter and 1.5-2.5 μm in height. Equatorial diameter = 38 μm (EF: NMPHC 72005-K 37).

Wilsonisorites Kimyai, 1966

Wilsonisorites radiatus (Ouyang & Li) Ouyang, 1982 (Fig. 5E-F)

Radially symmetric, trilete spore with a circular amb and zona. Trilete mark distinct, the rays extending across the full width of the zona. Central body measuring 26 μm in diameter and the zona measuring 6 μm in width. Exine measuring 1.0 μm in thickness. Equatorial diameter = 35 μm (EF: NMPHC 72006-Y 31/4).

Neoraistrickia Potonié, 1956

Neoraistrickia sp. 1 Potonié, 1956 (Fig. 5G)

Spore subtriangular to circular. Trilete mark not preserved. Exine measuring 0.5 μm in thickness, ornamented with baculae measuring between 1.0-2.0 μm in diameter and 2.0-3.0 μm in height. Equatorial diameter = 50 μm (EF: NMPHC 72005-Q 48).

Laevigatosporites (Ibrahim) Dettmann, 1963

Laevigatosporites medius (Wilson & Coe) Schopf, Wilson & Bentall, 1944 (Fig. 5H)

Bilaterally symmetrical, monolete spore with an elliptical amb. Monolete mark straight, measuring 21 μm in length, this being about 1/2 of the longitudinal diameter. Exine laevigate, measuring approximately 2.0 μm in thickness. Spore measuring 45 x 46 μm (EF: NMPHC 72005-O 46/4).

Punctatosporites Ibrahim, 1933

Punctatosporites minutus Ibrahim, 1933 (Fig. 5I)

Bilaterally symmetrical, monolete spore with an elliptical amb. Monolete mark straight, measuring 31 μm in length, this being about 1/2 of the longitudinal diameter. Exine measuring 1.0 μm thickness, ornamented with grana measuring approximately 0.5 μm in diameter. Spore measuring 47 x 62 μm (EF: NMPHC 72002-V 52/3).

cf. *Punctatosporites* sp. (Fig. 5J)

Bilaterally symmetrical, monolete spore with an elliptical amb. Monolete mark not discernible. Exine measuring 1.0 μm thickness, ornamented with grana measuring less than 1.0 μm in diameter. Equatorial dimension 60 μm (EF: NMPHC 72001-P 45-1/3).

Pteruchipollenites Couper, 1958

cf. *Pteruchipollenites* sp. 1 (Fig. 5K-L)

Bilaterally symmetrical, longitudinally ellipsoid bisaccate pollen grain of the haploxylon-type. Central body sub-circular transversally, finely punctuate. Semi-circular sacchi, as wide as the central body and attached to it with a slightly concave fold. Grain measures 51-55 μm longitudinally and 31-36 μm transversely. Central corpus

measures 30-33 μm longitudinally and 33-36 μm transversely. Sacci measure 17-18 = μm longitudinally and 17-34 μm transversely, the distance between the sacci measures 17-18 μm (EF: NMPHC 72008-C 23/2; EF: NMPHC 72008-P 31/4).

cf. Circulina Maljavkina ex Klaus, 1963

cf. Circulina simplex Malyavkina, 1949 (Fig. 5M)

Subcircular pollen with a laevigate exine measuring 1.0 μm in thickness. Pollen grain measures 30 x 38 μm (EF: NMPHC 72005- D 36/4).

Spore indet. 1(Fig. 5N)

Spore with thin granular exine measuring 1.0 μm in thickness. Grana smaller than 1.0 μm in diameter. Apertural mark not preserved/discernible. Spore dimensions 70 x 34 μm (EF: NMPHC 72008-H 23/2).

Michrystridium Deflandre Sarjeant & StanvliFFE, 1994

Michrystridium cf. breve Jansonius (Fig. 5O)

Spherical acanthomorph acritarch, ornamented with spines measuring less than 2 μm in diameter and 3–4 μm in length. Spines join to form a reticulum between 4–7 μm in diameter. Cyst measuring 1.0 μm in thickness. Diameter = 22 μm (EF: NMPHC 72002-F 35/3).

Baltisphaeridium Eisenack, 1958

Baltisphaeridium cf. brevispinosum (Eisenack) Eisenack, 1959 (Fig. 5P)

Elliptical acanthomorph acritarch, ornamented with spines measuring 1 μm in diameter and 2.0 μm in length. Cyst measuring less than 1.0 μm in thickness. Dimension 35 x 48 μm (EF: NMPHC 72004-J 35/1).

Acanthomorph acritarch sp. 1 (Fig. 5Q)

Ovate acanthomorph acritarch, ornamented with spines measuring 2 μm in diameter and 4–6 μm in length. Dimensions 30 x 40 μm (EF: NMPHC 72006-R 48/1-2).

Netromorph acritarch sp. 1 (Fig. 5R)

Poorly-preserved elliptical netromorph acritarch, without appendages. Comparable with *Dictyotidium/Leiospheridium*. Dimension: 45 x 25 μm (EF: NMPHC 72008-K 37).

DISCUSSION

PETROGRAPHIC EVIDENCE FOR THE DEPOSITIONAL ENVIRONMENT OF THE PALAEOBOTANICAL LAGERSTÄTTE

The textural immaturity of the plant-bearing sediment and the abundance of igneous materials, including igneous clasts in pebble conglomerate and fresh quartz and feldspar crystals, are indicative of an epiclastic sediment re-worked from pre-existing igneous rocks such as the Emeishan Basalt that underlies the Xuanwei Formation (Figure 6) or a volcanoclastic deposit such as an ignimbrite (e.g. Zhong et al. 2014). From comparison with the work of He *et al.* (2007) the mafic-intermediate nature of the re-worked sediments may be suggestive of a position relatively low in the Xuanwei Fm., perhaps transitional between the authors' felsic 'Group 1' and mafic 'Group 2' sediments derived from erosion of the Central Emeishan LIP tuffs and their underlying basalts.

This might imply the occurrence of the epiclastic conglomerate in the lower member of the Xuanwei Fm. This interpretation is supported by regional geological surveys that include information from sub-surface outcrops and that document petrologically/lithologically similar tuffaceous sediments in this coal-bearing, conglomeratic sequence (Wang *et al.*, 2011).

The grain and clast size, textural immaturity, rounding of pebbles in the conglomerates and large size of the plant fossils suggest a comparatively high depositional energy and are comparable with lithologies from the lower conglomeratic member of the Xuanwei Fm. (especially as described by Shao *et al.*, 1994; Wang *et al.*, 2011). Such coarse conglomeratic and even sandy lithologies are absent from the upper member of the Formation as documented in nearby sections (e.g. Fig. 4 in Wang *et al.*, 2011). However, whereas the plant fossils suggest deposition within, or at least proximal to a terrestrial setting, the presence of authigenic glauconite indicates deposition under shallow marine conditions, below wave-base, in an area of low sedimentation (Kerr, 1977).

The lower member of the Xuanwei Fm. has been interpreted as a braided/fluvial setting, whereas the upper member has more of a marine influence including upper delta plain and inter-distributary bay facies (Wang *et al.*, 2011). The sedimentology of the lower conglomeratic member clearly indicates significant aggradation and given this activity, it is possible that multiple erosion/re-deposition events have occurred throughout the area. This is confirmed by the sequence stratigraphic analyses of Wang *et al.* (2011) who clearly document major changes in base level reported at this time (see: Fig. 10 of Wang *et al.* 2011). This gives rise to the possibility that the epiclastic conglomerate and the marine glauconite were originally deposited in discrete beds, subsequently both were eroded by a major aggradational event, and then finally

redeposited together due to their similar hydrodynamic characteristics. Regional sequence stratigraphic analyses indicate a mechanism by which this environmental mixing may have occurred: the K13 and K12 limestones in the lower part of the Longtan Formation are representative of marine transgressive events into the adjacent Xuanwei Formation (Wang et al., 2011) and broadly correlate with the lower part of the Xuanwei Formation. This mechanism would indicate initial deposition in a shallow marine, glauconite-forming environment with subsequent braided channel activity, due to sea level fall, resulting in sediment erosion and redeposition.

While the Huopu coal mine is part of the Liupanshui coal mining district, it is probably best compared with the Housuo coal mine in the Fuyuan coal mining district to which it is proximally located. At Housuo conglomerates are documented within the braided deltaic depositional system as alluvial deposits (Figure 6) and in this system glauconite has been documented in braided-delta plain, delta front and prodelta facies (Shao *et al.*, 1994; Wang *et al.* 2011). Shao *et al.* (1994) considered that environments within the lower member of the Xuanwei Formation that had a strong marine influence include delta channel and delta front facies demonstrated by the presence of marine algae and glauconite within the conglomeratic matrix, as well as calcite cements and imbricated clasts. With the exception of marine algae, though acritarchs such as *Baltisphaeridium* may be such, these features are similar to those of the fossil plant-bearing lithologies suggesting their source may have been within the delta channels or delta front facies.

Regarding the source area for channel systems in the Xuanwei Formation in the Huopu region, Figure 1C in Wang et al. 2011 shows palaeo-drainage channels regionally flowing from the NW to shallow marine systems to the SE, suggesting sources of igneous materials and plants came from the NW

PALYNOLOGICAL EVIDENCE FOR THE AGE OF THE PALAEOBOTANICAL LAGERSTÄTTE

Papers by Ouyang & Li (1980) and Ouyang (1982; 1986), who examined the 'Early Triassic' palynology of eastern Yunnan, Peng *et al.* (2006) and Yin *et al.* (2007), who studied sections at Zhejue and Chahe in westernmost Guizhou Province spanning the Late Permian and Early Triassic, provide a framework with which to compare the Huopu epiclastic conglomerate's palynology. Unitary Association analysis was attempted as a means of correlation, however, the low diversity and abundance of both the epiclastic conglomerate and the prior studies (Ouyang and Li, 1980, Peng *et al.*, 2006, Yin *et al.*, 2007) rendered the results poorly-significant statistically.

The palynological assemblage of the epiclastic conglomerate includes both well- and poorly-preserved pollen and spores, as well as acritarchs. The acritarchs offer further unequivocal evidence of a marine influence and support of the conclusions drawn from the petrographic identification of glauconite in the epiclastic conglomerate.

The pollen and spore composition is broadly similar to that previously noted from the Xuanwei Formation (Ouyang and Li, 1980; Ouyang, 1982; Peng *et al.*, 2006; Yin *et al.*, 2007) but is of even more limited diversity. Biostratigraphically, several of the genera (*Wilsonisporites* Kimyai, 1966, *Neoraistrickia* Potonié, 1956, and *Pteruchipollenites* Couper, 1958) recovered from the Huopu epiclastic conglomerate were considered by Ouyang (1982) as characteristically Mesozoic forms. Of these three genera only *Neiraistrickia* was identified by either Peng *et al.* (2006) or Yin *et al.* (2007) from Zhejue or Chahe, but therein from a latest Permian horizon (bed 66a).

Globally *Pteruchipollenites* Couper, 1958 is a long ranging genus reported from sediments of Westphalian to Cretaceous age (e.g. McGregor, 1965; Cesari, 2013) and first documented from the Jurassic of the UK (Couper, 1958). Spores from the epiclastic

conglomerate have been tentatively assigned to this genus, which Ouyang (1982; 1986) considered characteristic of Triassic age sediments in the western Guizhou and eastern Yunnan region, in part naming the Lower Triassic *Lundbladispora-Aratriporites-Pteruchipollenites* assemblage for it; *Pteruchipollenites reticarpus* being one of the major palynological components of the post-boundary Kayitou Fm (Table 3 in Ouyang, 1982). However, the genus has not otherwise been widely reported in the region, though other bisaccate grains are documented (see: Peng *et al.*, 2006; Yin *et al.*, 2007; Feng and Quan, 2014).

The majority of the palynomorphs isolated from the epiclastic conglomerate are much more characteristically Permian than those documented above. Peng *et al.* (2006) provide a synoptic chart (their Fig. 7) of generic palynomorph range through the Late Permian and Early Triassic in western Guizhou and eastern Yunnan, including data from Ouyang (1986). Most of the taxa it provides data on were not recovered from the Huopu epiclastic conglomerate, however, *Leiotriletes* (Naumova) Potonié & Kremp, 1954, *Waltzispora* Staplin, 1960, *Calamospora* Schopf, Wilson & Bentall, 1944, *Cyclogranisporites* Potonié & Kremp, 1954 (n.b. appears to be tabulated as *Cyclogranulatisporites*), *Verrucosisporites* (Ibrahim) Potonié & Kremp, 1954, *Neoraistrickia*, *Lophotriletes* (Naumova) Potonié & Kremp, 1954, *Laevigatosporites* (Ibrahim) Dettmann, 1963 and *Punctatosporites* Ibrahim, 1933 were. In this region, these spore taxa are all demonstrated to be more abundant in the Permian than Triassic. In particular, *Waltzispora*, *Cyclogranisporites*, *Verrucosisporites*, *Neoraistrickia*, *Laevigatosporites* and *Punctatosporites* appear to be strong indicators of a Permian age, these genera not having been recorded from either of the westernmost Guizhou sections during the Triassic (Table 5, Peng *et al.*, 2006). Collectively these data suggest the epiclastic conglomerate to be characteristically Late Permian in age. Individual spore

species (*Cyclogranisporites aureus* (Loose) Potonié & Kremp, 1955, *Lophotriletes paramictus* Ouyang, 1986, *Calamospora pedata* Kosanke, 1950, *Leiotriletes exiguus* Ouyang & Li, 1980 and *Waltzispora strictura* Ouyang & Li, 1980) also support the Huopu epiclastic conglomerate as generally Permian in character.

In summary, despite the low diversity and poor-preservation of the palynoflora, its overall composition, being dominated by spores and with few pollen taxa, indicates a Late Permian age and supports the petrographic data as well as the stratigraphic range of the seams known to be mined at Huopu. The palynology is perhaps suggestive of the epiclastic conglomerate having derived from the lower member of the Xuanwei Formation, but this is not conclusive. However, it is possible that the lagerstätte assemblage, which includes palynotaxa such as *Pteruchipollenites*, may represent a predominantly lowland flora but containing more extensively transported and eroded upland elements, more typically associated with younger aged strata.

BOTANICAL AFFINITIES OF PALYNOTAXA AND DIVERSITY OF THE SOURCE FLORA

The affinities of pollen and spore taxa encountered in the Xuanwei Formation lagerstätte are shown in Table 1, which reveals the assemblage to be dominated by eusporangiate ('filicalean') fern spores including members of the Noeggerathiales (see Wang *et al.*, in review), but also including spores from lycophytes and sphenophytes, as well as gymnosperm pollen produced by pteridosperms. However, other dispersed taxa are of unknown affinity including *Stenozonotriletes*, *Wilsonisporites*, *Microbaculispora*, *Concavissimisporites* and *Circulina*, whereas others are associated with more than one plant group and are not indicative of a specific affinity; for instance dispersed species of *Laevigatosporites* may have been produced by lycophytes, sphenophytes including

Bowmaniales (Traverse 2007), or Marattialean ferns (Balme, 1995). The presence of spores affiliated with Noeggerathiales (*Cyclogranisporites*, *Laevigatosporites*) is unsurprising considering the recent documentation of their preserved strobili and leaves within the lagerstätte (Wang *et al.*, in review), with spores being nearly round or rounded triangular in shape, and being approximately 30 μm in diameter and having a smooth surface and a short trilete mark. However, the spores documented by Wang *et al.* (in review) were fragmentary and only identified from peel preparations from which they were unable to assign them to a *spora*–*dispersa* genus. The illustrations of *in-situ* microspores within a Noeggerathialean strobilus from the Xuanwei Formation (Wang *et al.*, in review) look most similar to *Leiotriletes* as documented here, with *Leiotriletes* considered to have been produced by the ferns Botryopteridales and Matoniaceae (Balme, 1995) or bryophytes and ferns including *Sermaya*, *Pecopteris*, *Botryopteris* and *Doneggia* (Traverse, 2007). Overall, the palynological composition of the lagerstätte is suggestive of a fern dominated pioneering plant community (e.g. DiMichele & Phillips, 2002), presumably related to the high energy and disturbed nature of the physical environment.

MACROFLORAL COMPOSITION

Although results on the macrofloral composition and diversity are only preliminary at this stage, the Huopu assemblage appears to lack typical wetland genera including lycophytes (*Lepidodendron*, *Achlamydocarpon*, *Sigillaria*, *Sigillariopsis*) and sphenophytes (*Calamostachys*, *Arthropitys*) that occur in the coal ball assemblage from the uppermost part of the Xuanwei Formation at Shuicheng (Tian and Zhang 1980; Tian and Wang, 1995; Hilton and Cleal, 2007; Wang *et al.*, 2009). The Huopu assemblage contains a diversity of gymnosperms including large, woody stems of the coniferophyte

Xuanweioxylon scalariforme (He et al., 2013a), small stems of the pteridosperm *Callistophyton boyssetii* (Seyfullah et al., 2009), as well as two kinds of large cardiocarpalean gymnosperm ovule of unknown affinity, namely *Cardiocarpus huopuensis* (Wang et al., 2006) and *Muricosperma guizhouensis* (Seyfullah et al., 2010). *Cardiocarpus huopuensis* and *Muricosperma guizhouensis* are distinct from the small ovules of Callistophytalean pteridosperms such as *Callospermarion* ovules belonging to the *Callistophyton* plant (Hilton et al., 2002; Seyfullah and Hilton, 2011). Noeggerathialean plants occur in contemporaneous compression/impression assemblages from the Xuanwei Formation (Zhao et al. 1980; Yao et al., 1980) and also occur in the epiclastic conglomerate, but are unknown from the stratigraphically younger coal-ball assemblage within the Xuanwei Fm. We have not yet identified cycads from the epiclastic conglomerate assemblage but they occur in both contemporaneous compression/impression assemblages (Yao et al., 1980) and coal-balls (Wang et al. 2011b). Our preliminary conclusion is that the epiclastic conglomerate flora is different from contemporaneous impression/compression assemblages which include abundant marattialean ferns and gigantopterids (Yao et al., 1980) and may be sampling a distinct source flora, potentially with a greater upland component.

TAPHONOMIC CONSIDERATIONS

The level of palynomorph preservation is extremely variable ranging from those with exceptional preservation to more abundant badly abraded specimens, suggesting a mixture of taphonomic pathways including recently deposited fresh taxa and more abraded and potentially re-worked taxa.

Permineralization of fossil plants in the Xuanwei Formation lagerstätten was facilitated by calcium carbonate with mineralization occurring rapidly after the plants

were deposited to prevent taphonomic decay. Carbonate mineralization of this kind is atypical of terrestrial sediments such as those that in general characterize the Xuanwei Formation (e.g. Wang *et al.*, 2011) but is characteristic of marine settings (Bateman *et al.*, 2000; Rothwell *et al.*, 2011; Spencer *et al.*, 2015). However, it also occurs associated with ash-producing volcanic activity in marginal marine lowland settings (Bateman and Scott, 1990). The Mississippian floras of Oxroad Bay in southern Scotland were covered by chemically unstable and porous volcanic ash or incorporated into sediments that reworked the ash, in which mineral saturated waters passed through the sediment and filled the void spaces with a carbonate cement that permineralized the fossil plants (Bateman & Scott, 1990, pg. 191). Whereas similar processes may have occurred in the Xuanwei lagerstätte, considering the abundance of eroded igneous lithoclasts and angular quartz and feldspar in the volcanoclastic sediment, the presence of glauconite indicates a stronger marine influence for which permineralization by marine carbonate is the most likely. The Jurassic aged marine palaeobotanical lagerstätten from Eathie (Rothwell *et al.*, 2011) and Berreraig Bay in Scotland (Bateman *et al.*, 2000; Spencer *et al.*, 2015) contain plant fossils that were rafted into proximal marine environments where they sank and underwent carbonate permineralization following diagenetic remobilisation of molluscan-aragonite as calcium carbonate (Bateman *et al.*, 2000).

Of interest is that both the sedimentary evidence and the palynological composition suggest the lagerstätte was deposited within the lower conglomeratic member of the Xuanwei Formation in a marine influenced setting. However, some of the palynomorphs may be considered more indicative of deposition in the upper member of the formation. Considering the composition of the spore and pollen assemblage that appears to represent a fern dominated pioneering plant community, this discrepancy

could be the consequence of taphonomy, potentially representing a stratigraphically early occurrence of upland species in the lower member of the formation that are in general more characteristic of the upper member of the formation. Such findings are not unheard of in the fossil record with Looy et al. (2014) documenting early occurring ‘Methuselah’ taxa, presumably demonstrating lineages survived but in places outside of lowland preservational basinal contexts. We conclude that it was likely that the palaeobotanical source for the lagerstätte was an upland flora that was initially eroded from a volcanic terrane by fluvial processes or a pyroclastic flow and was ultimately deposited in shallow marine settings. This source appears distinct from what is here interpreted as typical lowland floral composition of contemporaneous floras within the Xuanwei Formation (e.g. Yao et al. 1980; Zhao et al. 1980). Future fieldwork in this part of China needs to address the source of the plant bearing lagerstätte and undertake detailed sedimentological analysis of it to allow its mode of formation to be fully characterised. Zircon dating and charcoal analysis of the assemblage are now urgently required.

Summary considerations

The plant bearing lithologies comprise pebble conglomerates to sub-arkoses in which rounded basic-intermediate igneous clasts and anatomically preserved fossil plants are contained in a matrix of minerals dominated by angular quartz and feldspars and irregularly rounded glauconite. The presence of glauconite demonstrates deposition in a shallow marine setting with low sedimentation rates below wave base in which glauconite formed authigenically. Permineralization of the fossil plants appears to have been facilitated by marine carbonate, but mineralization associated with freshwater percolating through chemically unstable ashes at an earlier taphonomic stage cannot be

discounted. Further, the role of environment change cannot be discounted, potentially lowering sea level and reworking previously deposited marine sediments by fluvial processes, thus presenting a mixing of palaeo-environmental signals.

The palynological assemblage is of low abundance and diversity and is dominated by leptosporangiate (filicalean) fern spores with less common lycopsid and sphenopsid spores and gymnosperm pollen, and rare marine acritarchs. The spore and pollen assemblage is characteristic of an ecologically pioneering rather than established floral community suggesting in combination with sedimentary observations an ecosystem living in a disturbed volcanic setting consistent with recent exposure of the underlying lithologies of the Emeishan Basalt.

Compositionally the spore and pollen documented is most comparable with that previously recovered from the lower member of the Xuanwei Formation and suggests a Wuchiapingian (Lopingian) biostratigraphic age. However, it remains uncertain if select taxa represent contemporaneous occurrences of pioneering upland floral elements that are more typical of stratigraphically younger lowland settings that have been incorporated into a lowland context at an older stratigraphic stage. In-situ sampling or the source flora is required to ascertain its full ecological and stratigraphical significance.

The palaeobotanical lagerstätten represents the latest stages of Permian floral evolution before the onset of the ecological devastation of the end Permian extinction event. Greater confidence in determining the Wuchiapingian age of the Huopu lagerstätte allows greater understanding of the regional changes in diversity in the critical interval between the mid-Capitanian and end Permian extinctions, where pre-adaptation and resilience to profound environmental perturbations were undoubtedly key to survival into the Triassic.

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REFERENCES

- Balme, B.E., 1995. Fossil in situ spores and pollen grains: an annotated catalogue. *Rev. Palaeobot. Palynol.* 87, 81–323.
- Bateman, R.M., Morton, N., Dower, B.L., 2000. Early Middle Jurassic communities in northwest Scotland: Paleoeological and paleoclimatic significance. In: Hall, R., Smith, P., Poulton, T. (Eds.), *Forum 6 (Proceedings of the Fifth International Symposium on the Jurassic System)*, GeoResearch TransTech Publications, Zurich, pp. 501–511.
- Bateman, R.M., Scott, A.C., 1990. A reappraisal of the Dinantian floras at Oxroad Bay, East Lothian, Scotland. 2. Volcanicity, palaeoenvironments and palaeoecology. *Trans. Roy. Soc. Edin.: Earth Sci.* 81, 161–194.

- Batten, D.J., 1999. Small palynomorphs. Pages 15–19 in T.P. Jones, N.P. Rowe (Eds), *Fossil Plants and Spores: Modern Techniques*. London: Geological Society.
- Bond, D.P.G., Wignall, P.B., 2014. Large igneous provinces and mass extinctions: An update. *Geol. Soc. Amer. Spec. Pub.* 505, doi:10.1130/2014.2505(02).
- Bond, D.P., Hilton, J., Wignall, P.B., Ali, J.R., Stevens, L.G., Sun, Y., Lai, X. 2010. The Middle Permian (Capitanian) mass extinction on land and in the oceans. *Earth-Science Reviews*, 102, 100-116.
- Césari, S., 2013. Palinología de la Formación Tupe (Paleozoico Superior), Sierra De Maz, Provincia de la Rioja. I. *Ameghiniana*, 21, 85–102.
- Couper, R.A., 1958. British Mesozoic microspores and pollen grains, a systematic and stratigraphic study. *Palaeontographica Abt. B* 103, 75–179.
- Dai, S., Zhou, Y., Zhang, M., Wang, X., Wang, J., Song, X., Jiang, Y., Luo, Y., Song, Z., Yang, Z., Ren, D., 2010. A new type of Nb (Ta)–Zr (Hf)–REE–Ga polymetallic deposit in the late Permian coal-bearing strata, eastern Yunnan, southwestern China: possible economic significance and genetic implications. *Int. J. Coal Geol.* 83, 55–63.
- Dai, S., Li, T., Seredin, V.V., Ward, C.R., Hower, J.C., Zhou, Y., Zhang, M., Song, X., Song, W., Zhao, C., 2014. Origin of minerals and elements in the Late Permian coals, tonsteins, and host rocks of the Xinde Mine, Xuanwei, eastern Yunnan, China. *Int. J. Coal. Geol.* 121, 53–78.
- DiMichele, W.A., Phillips, T.L., 2002. The ecology of Paleozoic ferns. *Rev. Palaeobot. Palynol.* 119, 143–159.
- Feng, Y., Quan, B., 2014. Study on the Late Permian palynological vegetation, ancient vegetation and paleoclimate of Fuyuan Coal Mine in Yunnan. *Chinese Sci. Papers Online*, CLC: Q914.81; P532.

- Hammer, O., Harper, D., Ryan, P., 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Paleontol. Elect.*, pp. 9.
- He, B., Xu, Y.G., Huang, X.L., Luo, Z.Y., Shi, Y.R., Yang, Q.J., Yu, S.Y., 2007. Age and duration of the Emeishan flood volcanism, SW China: geochemistry and SHRIMP zircon U–Pb dating of silicic ignimbrites, post-volcanic Xuanwei Formation and clay tuff at the Chaotian section. *Earth Planet. Sci. Lett.* 255, 306–323.
- He, J., Wang, S.J., Hilton, J., Shao, L., 2013a. *Xuanweioxylon* gen. nov.: novel Permian coniferophyte stems and branches with scalariform bordered pitting on secondary tracheids. *Rev. Palaeobot. Palynol.* 197, 152–165.
- He, X.Y., Wang, S.J., Hilton, J., Galtier, J., Li, Y.J., Shao, L., 2013b. A unique trunk of Psaroniaceae (Marattiales) — *Psaronius xuii* sp. nov., and subdivision of the genus *Psaronius* Cotta. *Rev. Palaeobot. Palynol.* 197, 1–14.
- He, X.Y., Wang, S.J., Hilton, J., Tian, B.L., Zhou, Y.L., 2008. Anatomically preserved marattialean plants from the Upper Permian of southwestern China: the trunk of *Psaronius panxianensis* sp. nov. *Plant Syst. Evol.* 272, 155–180.
- Hilton, J., Cleal, C.J., 2007. The relationship between Euramerican and Cathaysian tropical floras in the Late Palaeozoic: palaeobiogeographical and palaeogeographical implications. *Earth–Science Rev.* 85, 85–116.
- Hilton, J., Wang, S.J., Galtier, J., Glasspool, I.J., Stevens, L., 2004. An upper Permian permineralized plant assemblage in volcaniclastic tuff from the Xuanwei Formation, Guizhou Province, southern China, and its palaeofloristic significance. *Geol. Mag.* 141, 661–674.

- Hilton, J., Wang, S.J., Galtier, J., Li C.S., 2001. An Early Permian plant assemblage from the Taiyuan Formation of northern China with compression/impression and permineralized preservation. *Rev. Palaeobot. Palynol.* 114, 175–189.
- Hilton, J., Wang S.J., Zhu, W.Q., Tian, B., Galtier, J., Wei, A.H., 2002. *Callospermarion* ovules from the Early Permian of northern China: palaeofloristic and palaeogeographic significance of callistophytalean seed–ferns in the Cathaysian flora. *Rev. Palaeobot. Palynol.* 120: 301–314.
- Kerr, P.F., 1977. *Optical mineralogy*. McGraw–Hill College.
- Lei, Y., Servais, T., Feng, Q.L., He, W.L., 2013. Latest Permian arctarchs from South China and the *Micrhystridium/Veryhachium* complex revisited. *Palynology* 37, 325–334.
- Li, S., Tang, D., Xu, H., Yang, Z., 2012. The pore-fracture system properties of coalbed methane reservoirs in the Panguan Syncline, Guizhou, China. *Geoscience Frontiers* 3, 853–862.
- Liu, F.Q., Geng, X.W., Che, Y., Cui, X., 2014. The Adaptation Analysis of the Fully Mechanized Coal Mining Face of Huopu Mine’s Third Soft Coal Seam. *Adv. Mat. Res.* 1049, 335–338.
- Looy, C.V., Kerp, H., Duijnste, I.A.P., DiMichele, W.A., 2014. The Late Paleozoic ecological-evolutionary laboratory, a land-plant fossil record perspective. *The Sedimentary Record* 12(4), 4–10.
- McGregor, D.C., 1965. Triassic, Jurassic and Lower Cretaceous spores and pollen of Arctic Canada. *Geol. Surv. Canada Paper* 64, 1–10.
- Ouyang, S., 1982. Upper Permian and Lower Triassic palynomorphs from eastern Yunnan, China. *Can. J. Earth Sci.* 19, 68–80.

- Ouyang, S., 1986. Palynology of Upper Permian and Lower Triassic strata of Fuyuan district, eastern Yunnan. Beijing: Science Press [in Chinese with English abstract].
- Ouyang, S., Li, Z.P., 1980. Microflora from the Kayitou Formation of Fuyan district, E. Yunnan and its bearing on stratigraphy and palaeobotany. *In* Nanjing Institute of Geology and Palaeontology, Academia Sinica (Eds), Late Permian coal bearing strata and biota from western Guizhou and eastern Yunnan. Beijing: Science Press, pp. 123–183.
- Peng, Y., Yu, J., Gao, Y., Yang, F., 2006. Palynological assemblages of non-marine rocks at the Permian–Triassic boundary, western Guizhou and eastern Yunnan, South China. *J. Asian Earth Sci.* 28, 291–305.
- Rothwell, G.W., Stockey, R.A., Mapes, G., Hilton, J., 2011. Structure and relationships of the Jurassic conifer seed cone *Hughmillerites judii* gen. et sp. nov.: implications for the early evolution of cupressaceae. *Rev. Palaeobot. Palynol.* 164, 45–59.
- Seilacher, A., Reif, W.–E., Westphal, F., 1985. Sedimentological, ecological and temporal patterns of fossil lagerstätten. *Phil. Trans. Roy. Soc. Lond. B* 311, 5–23.
- Seyfullah, L.J., Hilton, J., 2011. Callistophytalean pteridosperms from the Permian floras of China. *Palaeontology* 54, 287–302.
- Seyfullah, L.J., Hilton, J., Liang, M.M., Wang, S.J., 2010. Resolving the systematic and phylogenetic position of isolated ovules: a case study from a new genus from the Upper Permian of China. *Bot. J. Linn. Soc.* 164, 84–108.

- Seyfullah, L.J., Hilton, J., Wang, S.J., Galtier, J., 2009. Anatomically preserved pteridosperm stems and petioles from the Permian floras of China. *Int. J. Plant Sci.* 170, 814–828.
- Shao, L., Zhang, P., Chen, D., Luo, Z., 1994. Braided delta depositional system and coal accumulation during early Late Permian period in eastern Yunnan and western Guizhou, southwest China. *Acta Sedimentologica Sinica* 12: 132–139 [in Chinese with English abstract].
- Spencer, A.R.T., Mapes, G., Bateman, R.M., Hilton, J., Rothwell, G.W., 2015. Middle Jurassic evidence for the origin of Cupressaceae: a palaeobotanical context for the roles of regulatory genetics and development in the evolution of conifer seed cones. *Am. J. Bot.* 102, 942–961.
- Tabor, N.J., DiMichele, W.A., Montañez, I.P., Chaney, D.S., 2013. Late Paleozoic continental warming of a cold tropical basin and floristic change in western Pangea. *Int. J. Coal Geol.* 119, 177–186.
- Tian, B.L., Zhang, L.W., 1980. Fossil atlas of Wangjiazhai mine region in Shuicheng, Guizhou. Coal Industry Press, Beijing [in Chinese].
- Tian, B.L., Wang, S.J., 1995. Paleozoic coal ball floras in China. In Li, X.X. (Ed.), *Fossil floras of China through the geological ages (English edition)*. Guangdong Science and Technology Press, Guangzhou, pp. 263–281.
- Traverse, A., 2007. *Paleopalynology (Second Edition)*. Topics in Geobiology, Vol. 28. Springer. 1–813.
- Wang, H., Shao, L., Hao, L.M., Zhang, P.F., Glasspool, I.J., Wheelley, J.R., Wignall, P.B., Yi, T.S., Zhang, M.Q., Hilton, J., 2011. Sedimentology and sequence stratigraphy of the Lopingian (Late Permian) coal measures in southwestern China. *Int. J. Coal Geol.* 85, 168–183.

- Wang, S.J., He, X.Y., Shao, L.Y., 2011b. Cycad wood from the Lopingian (Late Permian) of southern China: *Shuichengoxylon tianii* gen. et sp. nov. *Int. J. Plant Sci.* 172, 725–734.
- Wang, S.J., Hilton, J., Liang, M.M., Stevens, L., 2006. Permineralized seed plants from the Upper Permian of southern China: a new species of *Cardiocarpus*. *Int. J. Plant Sci.* 167, 1247–1257.
- Wang, S.J., Sun, K.Q., Cui, J.Z., Ma, S.M., 2009. Fossil flora of China, Volume 1: Fossil plants from Coal Balls in China. Higher Education Press, China.
- Wang, S.J., Wang, J., Spencer, A.R.T., Bateman, R.M., Shao, L., Hilton, J., Submitted. Enigmatic Paleozoic Noeggerathiales were sophisticated eusporangiate ferns, not sphenopsids or progymnosperms. 1–16 pgs & 4 figs. *Am. J. Bot.*
- Wignall, P.B., Sun, Y.D., Bond, D.P.G., Izon, G., Newton, R.J., Veldrine, S., Widdowson, M., Ali, J.R., Lai, X.L., Jiang, H.S., Cope, H., Bottrell, S.H., 2009. Volcanism, mass extinction and carbon isotope fluctuations in the Middle Permian of China. *Science* 324, 1179–1182.
- Yao, Z.Q., Xu, J.T., Zheng, Z.G., Zhao, X.H., Mo, Z.G., 1980. On the biostratigraphy of the Permian and the boundary between the Permian and Triassic in western Guizhou–eastern Yunnan. Pages 1–69 in Nanjing Institute of Geology and Palaeontology, Academia Sinica, eds. Late Permian coal bearing strata and biota from western Guizhou and eastern Yunnan. Science Press, Beijing. [In Chinese]
- Yin, H., Yang, F., Yu, J., Peng, Y., Wang, S., Zhang, S., 2007. An accurately delineated Permian–Triassic Boundary in continental successions. *Sci. in China Ser. D: Earth Sci.* 50, 1281–1292.
- Yu, J., Broutin, J., Chen, Z.Q., Shi, X., Li, H., Chu, D., Huang, Q., 2015. Vegetation changeover across the Permian–Triassic Boundary in Southwest China:

- Extinction, survival, recovery and palaeoclimate: A critical review. *Earth Sci.- Rev.*, doi:10.1016/j.earscirev.2015.04.005
- Zhang, Q., Wang, D., Zhu, X., Zhang, Z., Zhu, C., 2009. Lead isotopic systematics for native copper-chalcocite mineralization in basaltic lavas of the Emeishan large igneous province, SW China: Implications for the source of copper. *Chinese J. Geochem.* 28, 1–18.
- Zhang, Z., Yang, X., Li, S., Zhang, Z., 2010. Geochemical characteristics of the Xuanwei Formation in West Guizhou: Significance of sedimentary environment and mineralization. *Chinese J. Geochem.* 29, 355–364.
- Zhao, X.H., Mo, Z.G., Zhang, S.Z., Yao, Z. Q., 1980. Late Permian flora from western Guizhou and eastern Yunnan. Pgs 70–122 *in* Nanjing Institute of Geology and Palaeontology, Academia Sinica, eds. Late Permian coal bearing strata and biota from western Guizhou and eastern Yunnan. Beijing: Science Press [In Chinese].
- Zhong, Y.T., He, B., Mundil, R., Xua, Y.G., 2014. CA-TIMS zircon U–Pb dating of felsic ignimbrite from the Binchuan section: Implications for the termination age of Emeishan large igneous province. *Lithos* 204: 14–19.
- Zhou, Y., Bohor, B.F., Ren, Y., 2000. Trace element geochemistry of altered volcanic ash layers (tonsteins) in Late Permian coal-bearing formations of eastern Yunnan and western Guizhou Provinces, China. *Int. J. Coal Geol.* 44, 305–3.

Fig. 1. A) Outline map of China showing province boundaries with Guizhou Province coloured dark grey. Dashed box indicates position of B. B) Enlargement from boxed area in A showing boundary region of Guizhou, Yunnan and Guangxi provinces, with cities and major towns indicated by solid circles, and coal mines working the Xuanwei Formation by hollow circles. Dashed line represents major roads. C) Summary lithostratigraphic correlation of the major Lopingian formations in Guizhou and Yunnan provinces (modified from Wang et al, 2011) showing approximate stratigraphic position of the Huopu lagerstätte.

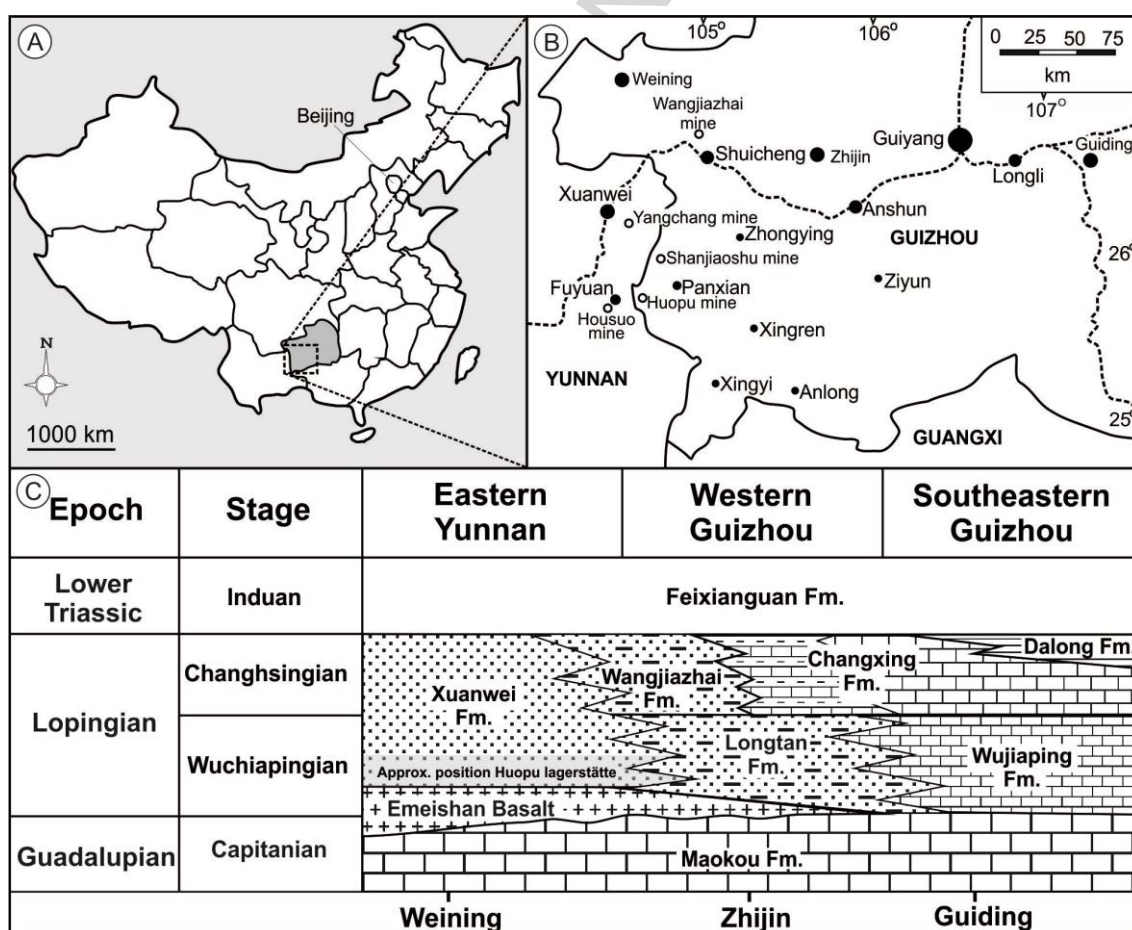


Fig. 2. Examples of the fossil plants preserved in the Huopu lagerstätte. **A)** Stem of the pteridosperm *Callistophyton boyssetii*. Scale bar = 1 mm. NMPHC slide BTop/6. **B)** Woody stem of the coniferophyte *Xuanweioxylon scalariforme*. P = pith; SX = secondary xylem; PL = peripheral loop. Arrows indicate leaf traces. Scale bar = 3 mm. NMPHC WP2L-0076. **C)** Enlargement of the sclerotic pith and inner part of the secondary xylem of *Xuanweioxylon scalariforme* (SX = secondary xylem; PL Peripheral loop; SC = Sclerotic pith). Scale bar = 500 μm . NMPHC WP2L-0082. **D)** Longitudinal section through the gymnosperm ovule *Cardiocarpus huopuensis* Wang et al. 2006 showing micropylar opening. Scale bar = 2 mm. NMPHC GPP2-003-F-0. **E)** near transverse section through *Cardiocarpus huopuensis* showing position of integumentary commissure in major plane. Sale bar = 2 mm. NMPHC GPP2-003I-1. **F)** Longitudinal section through the gymnosperm ovule *Muricosperma guizhouensis* Seyfullah et al. Scale bar = 1 μm . NMPHC GPP2-001-2. **G)** transverse section through an un-named heterosporous cone believed to belong to a noeggerathialean fern. Scale bar = 1 mm.

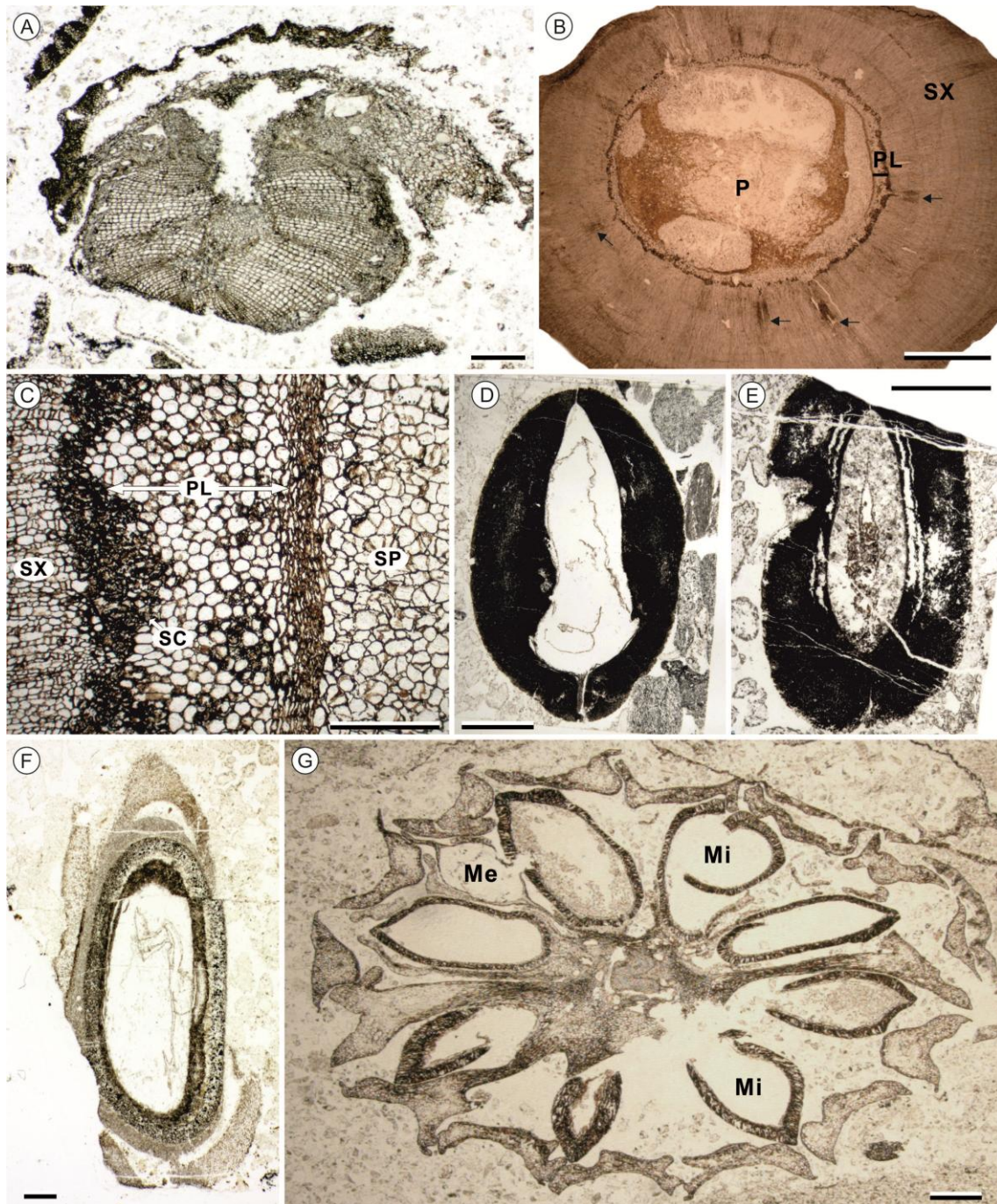


Fig. 3. Lithological features of the plant bearing epiclastic conglomerate at Huopu. **A)** Polished section through conglomeratic bed showing ovate to rounded, green, basic igneous clasts in arkosic matrix. Conglomerate fines up and has horizontally aligned long axes of clasts. Yellow arrows indicate fossil plant fragments. Scale bar = 5 mm. **B)** Rounded basic igneous clasts supported by an arkosic matrix. Yellow arrows indicate position of fossil plants. Scale bar = 5 mm. **C–D)** Pictomicrograph of igneous clast (bottom) and arkosic matrix (top) with C) in plane polarised light and D) in cross polarised light. Note elongate feldspars in the igneous clast, and green coloured, rounded minerals and the calcium carbonate cement. Scale bar = 500 μm . **E)** Polished section showing conglomeratic layer at bottom with laminated arkose above, examples of fossil plants indicated by yellow arrows, and basic igneous clasts by white arrows. Scale bar = 5 mm. **F)** Fresh surface of the arkose showing translucent-white feldspars, brown-light green carbonate, and bright green minerals. Scale bar = 1 mm. **G)** Polished section showing rounded and angular fossil plant (yellow arrows) and basic igneous (white arrows) clasts in arkosic matrix. Scale bar = 5 mm.

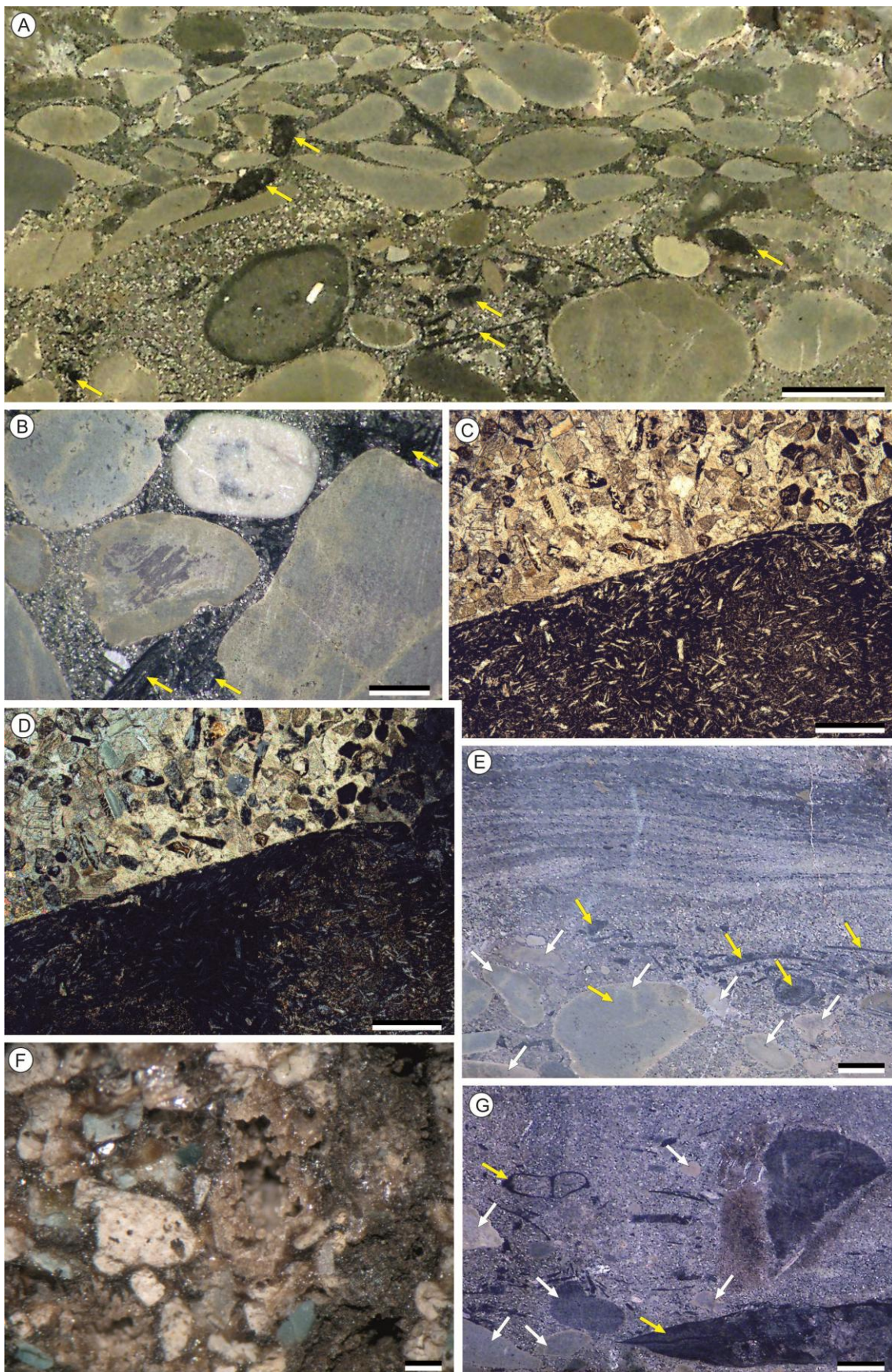


Fig. 4. Spores from the Xuanwei Formation palaeobotanical lagerstätte. All images same size; scale bar = 50 μm . **A)** *Cyathidites minor* Couper, 1953. **B)** *Cyathidites breviradiatus* Helby, 1966. **C–D)** *Leiotriletes adnatus* (Kosanke) Potonié & Kremp, 1954. **E)** *Leiotriletes* spp 1. **F)** *Leiotriletes exiguus* Ouyang & Li, 1980. **G)** *Leiotriletes adnatoides* Potonié & Kremp, 1955. **H)** *Waltzispota strictura* Ouyang & Li, 1980. **I–J)** *Waltzispota albertensis* Staplin, 1982. **K)** *Calamospora pedata* Kosanke, 1950. **L)** *Stenozonotriletes* sp. 1. **M)** *Cyclogranisporites breviradiata* de Jersey, 1960. **N)** *Cyclogranisporites aureus* (Loose) Potonié & Kremp, 1955. **O–P)** *Lophotriletes paramictus* Ouyang, 1986. **Q)** *Microbaculispora* sp. 1.

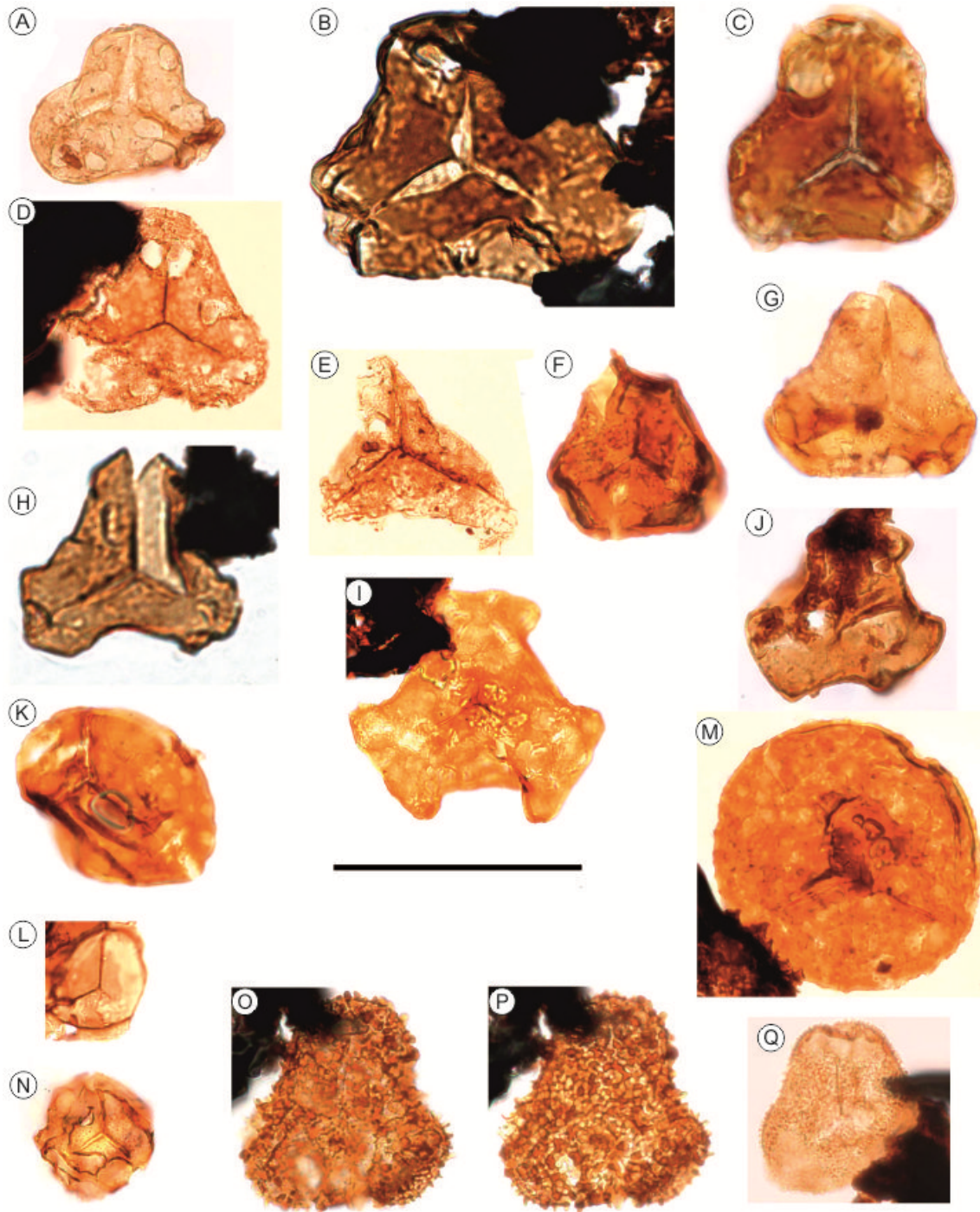


Fig. 5. Spores, pollen (A-N) and acritarchs (O-R) from the Xuanwei Formation palaeobotanical lagerstätte. All images same size; scale bar = 50 μm . **A)** *Concavissimisporites* aff. *apiverrucatus* (Couper) Döring. **B)** *Verrucosisporites pergranulus* (Alpern) Smith & Alpern, 1971. **C–D)** *Verrucosisporites* sp. 1. **E–F)** *Wilsonisporites radiatus* (Ouyang & Li) Ouyang, 1982. **G)** *Neoraistrickia* sp. 1 Potonié, 1956. **H)** *Laevigatosporites medius* (Ibrahim) Dettmann, 1963. **I)** *Punctatosporites minutus* Ibrahim, 1933. **J)** cf. *Punctatosporites* sp. 1. **K–L)** cf. *Pteruchipollenites* sp. 1. **M)** cf. *Circulina simplex* Malyavkina, 1949. **N)** Spore indet. sp. 1. **O)** *Michrystridium* cf. *breve* Jansonius. **P)** *Baltisphaeridium* cf. *brevispinosum* (Eisenack) Eisenack, 1959. **Q)** Acanthomorph acritarch sp. 1. **R)** Netromorph Acritarch sp. 1

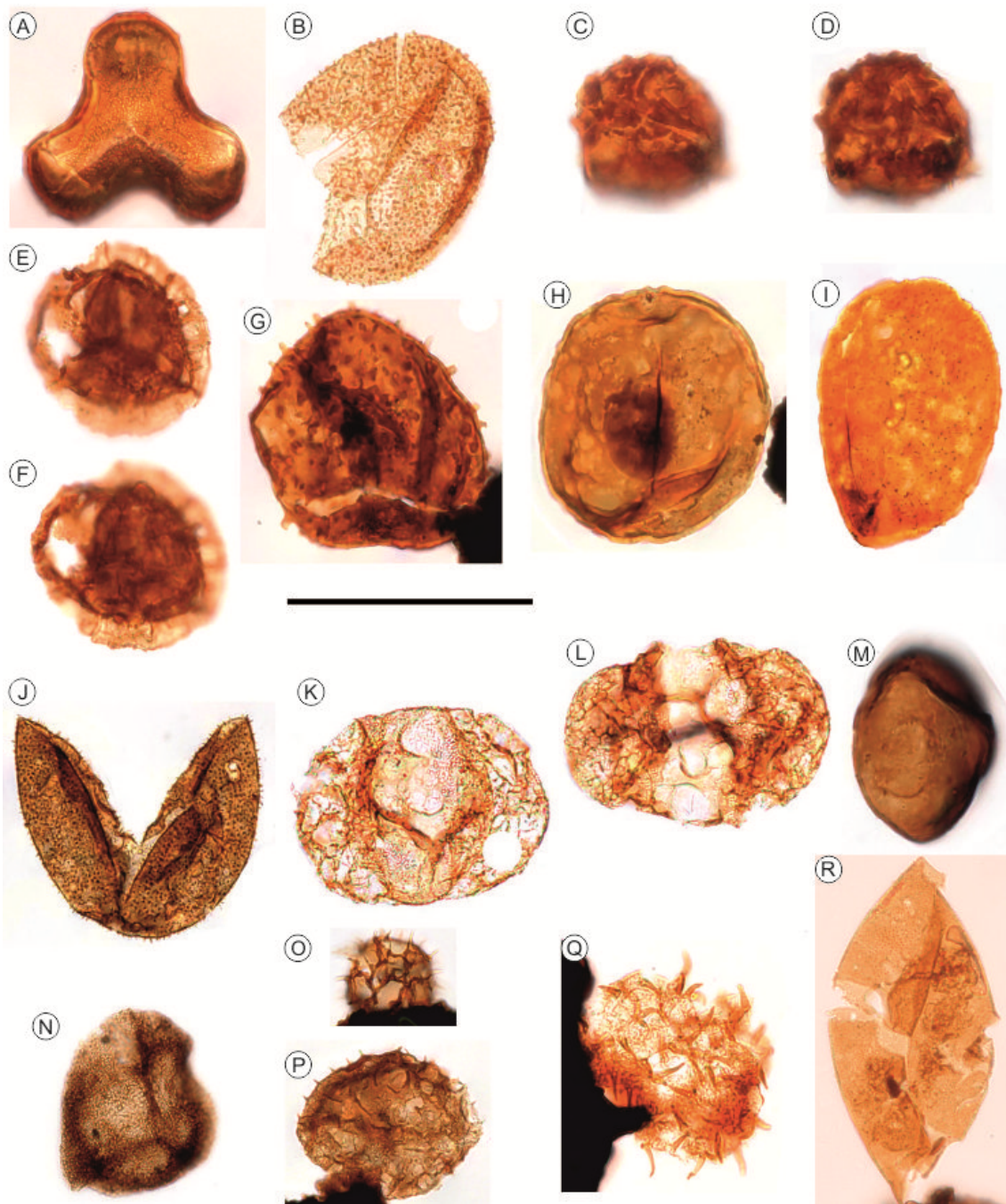


Fig. 6) Summary sedimentary log through the lower member of the Xuanwei Formation at Housuo showing position of two thick conglomerates with imbricate clasts and plant fossils and roots in the '1st alluvial system' of Wang et al. (2011). Figure modified from Wang et al. (2011).

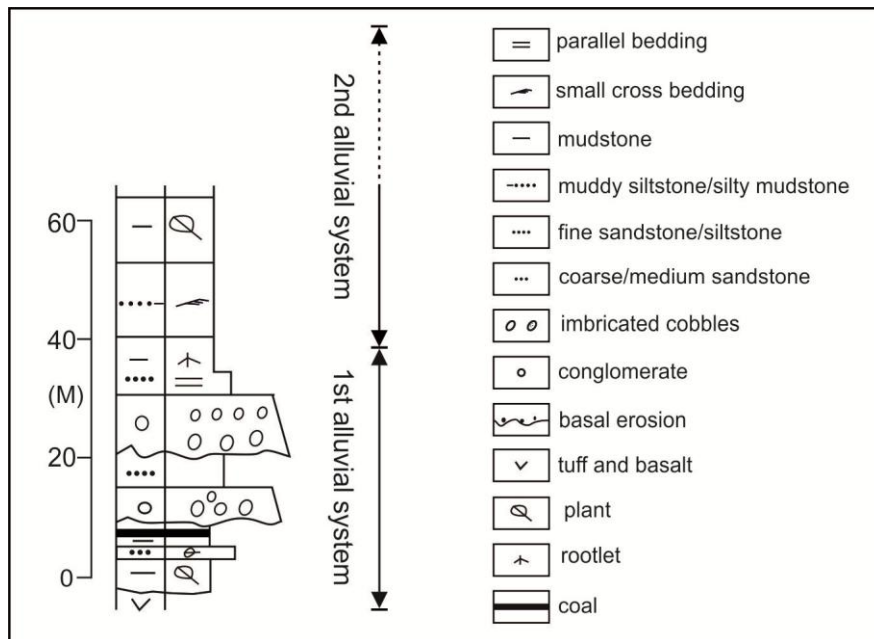
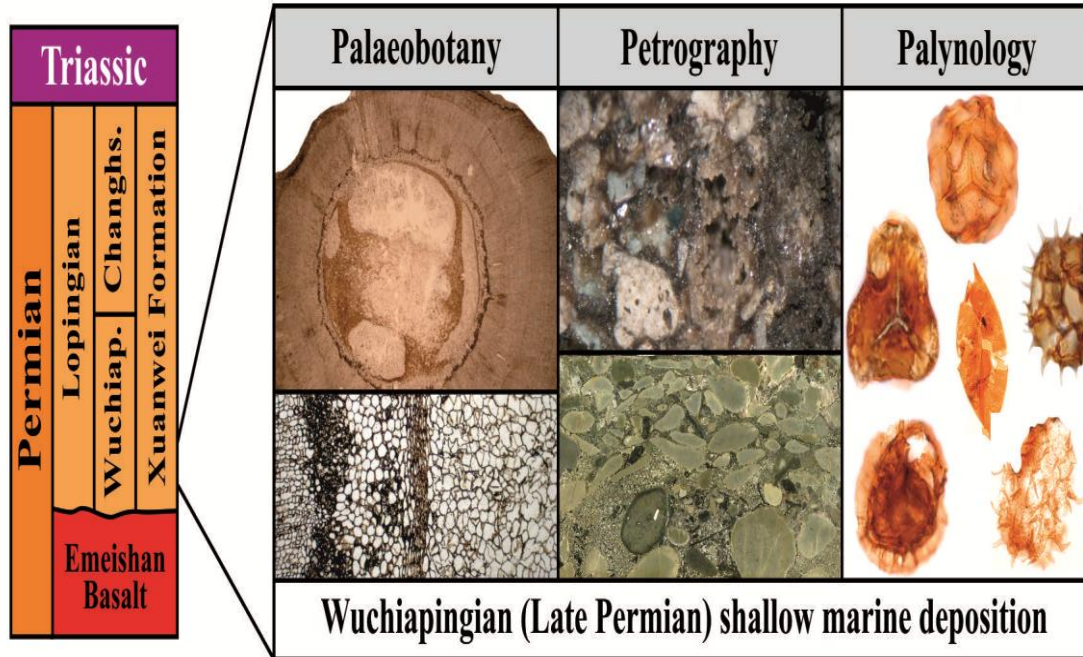


Table 1. Botanical affinities of the spore and pollen encountered in the Xuanwei Formation lagerstätte (modified from Balme (1995) and Traverse (2007)).

Genus	Botanical affinity	
	Balme (1995)	Traverse (2007)
<i>Cyathidites</i>	Gleichiniaceae, Dicksoniaceae, Cyatheaceae, Schizeaceae, Polypodiaceae	Dicksoniaceae (<i>Coniopteris</i>)
<i>Leiotriletes</i>	Zygopteridales, Botryopteridales, Matoniaceae	Bryophyte, Ferns (<i>Sermaya</i> , <i>Pecopteris</i> , <i>Botryopteris</i> , <i>Doneggia</i>)
<i>Waltzispota</i>	-	-
<i>Calamospora</i>	Selaginellales, Equisetopsida, Scoleopteris	<i>Calamites</i> , Marattiales (<i>Scoleopteris</i>)
<i>Stenozonotriletes</i>	-	-
<i>Cyclogranisporites</i>	Bryophyte, Selaginellales, Equisetopsida, Noeggerathiales, <i>Cycadopsida</i> , Marattiales (<i>Pecopteris</i> , <i>Scoleopteris</i>)	Marattiales (<i>Pecopteris</i> , <i>Acitheca</i> , <i>Scoleopteris</i>)
<i>Lophotriletes</i>	Botryopteridales	<i>Botryopteris</i>
<i>Microbaculispora</i>	?	?
<i>Concavissimisporites</i>	?	?
<i>Verrucosisporites</i>	Botryopteridales, Marattiales, Filicales, <i>Cycadopsida</i>	Botryopteridales, <i>Biscalitheca</i> , <i>Scoleopteris</i> , <i>Eoangiopteris</i> , <i>Millaya</i>
<i>Wilsonisporites</i>	-	-
<i>Dictyotriletes</i>	Ferns?	Ferns (Botryopteridales) and fern-like plants (<i>Phillipopteris</i>)
<i>Laevigatosporites</i>	Lycopsida (<i>Sigillariaceae</i>), Bowmanitiales, Marattiales (<i>Asterotheca</i> , <i>Marattia</i> , <i>Pecopteris</i> , <i>Scoleopteris</i>), Noeggerathiales	Lycopsida, <i>Bowmanites</i> , <i>Sphenophyllum</i>
<i>Punctatosporites</i>	Ferns (<i>Zeilleria</i> , <i>Asterotheca</i> , <i>Grandeuryella</i> , <i>Marattia</i> , <i>Pecopteris</i> , <i>Scoleopteris</i>)	<i>Pecopteris</i> , <i>Scoleopteris</i> , <i>Dizeugotheca</i>
<i>Pteruchipollenites</i>	Gymnosperm; Pteridosperms, <i>Pteruchus</i>	Pteridosperm (<i>Pteruchus</i>)
<i>Circulina</i>	-	-

Graphical abstract

Age and provenience of the Huopu konservat lagerstätte



ACCEPTED

Highlights

- 1) Inter-extinction (mid-Capitanian and Permo-Triassic) floral lagerstätte
- 2) Wuchiapingian age for the Huopu lagerstätte from Guizhou Province, SW China
- 3) Mix of transported pioneering plant spores/pollen and marine acritarchs
- 4) Konservat lagerstätte permineralized by carbonate in shallow marine setting