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A Novel Gymnosperm Wood from the Lopingian (Late Permian) in Zhangzi, Shanxi, North China and Its Paleoecological and Paleogeographic Implications

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ABSTRACT: The Permian-Triassic transition saw extreme climatic changes that severely impacted the terrestrial ecosystem. Fossil plants, particularly fossil woods, are sensitive to climatic changes, and they, therefore, are unique materials revealing extreme environmental and climatic changes on land at that time. Abundant conifer woods were discovered in the Lopingian (Late Permian) strata of the Sunjiagou Formation in Shanxi Province, North China. The newly finding permineralized woods record the unique landscape of Lopingian North China. They represent a new conifer genus and species: *Shanxiopitys zhangziensis* gen. et sp. nov. Analyses of growth pattern and anatomical characteristics of the fossil woods indicate these trees grew under optimal growing conditions, and without seasonal growth cessation. However, climate signals from leaf fossils, vertebrate fossils and sedimentary evidences indicate a strongly seasonal climate in North China during the Lopingian. Thus, it is speculated that these trees likely lived in the gallery forests, which were distributed along the paleo-rivers within a seasonal landscape in the central North China block during the Lopingian.
KEY WORDS: *Shanxiopitys zhangziensis* gen. et sp. nov., wood, ecology, geography, gallery forest, Lopingian, North China.

0 INTRODUCTION

The combination of the Laurasia and Gondwana during the Late Paleozoic lead to the formation of the supercontinent Pangaea, and dramatically changed the global climate (Shi and Waterhouse, 2010; van der Voo, 1988). In the Permian, the termination of ice-age climates and the sea-level periodicity led to overall climatic warming (Montañez et al., 2007). The Permian successions in North China Block were formally regarded as continuous. However, Wu et al. (2021) suggested that there is a nearly 20 m. y. hiatus caused by tectonic movement spanning the Early Kungurian to the Mid-Guadalupian in North China. Moreover, the increasing global warming and aridification have completely changed the floras in the Permian North China (Wang et al., 2010; Stevens et al., 2011; Wu et al., 2021). Plants, particularly woods, are important indicators for terrestrial paleoclimate variations. In this paper, we describe the permineralized tree trunks and stems discovered in the Lopingian succession of the Sunjiagou Formation (formerly the Shiqianfeng Formation) in central North China. The exceptionally preserved woods provide new insights into the paleoclimate and landscape of the North China block during the Late Permian.

1 GEOLOGICAL SETTINGS, MATERIALS AND METHODS

The North China Block was calculated to be located between 15°N and 35°N in the latest Permian (Domeier and Torsvik, 2014). The Cisuralian sequence in North China was interpreted to be a prograding delta (Norin, 1922; Wu et al., 2021). From Early Kungurian to the Mid-Guadalupian (or later), the closure and/or subduction of the Paleo-Asian Ocean and its related tectonic convergence caused a long hiatus (Wang et al., 2022; Wu et al., 2021). The Lopingian Sunjiagou Formation overlies unconformably above the Asselian – Early Kungurian Upper Shihhotse Formation (Wu et al., 2021; Hu et al., 1990).

The Sunjiagou Formation is ~92 m in thickness in the research area. Its lower part is composed of purplish-reddish muddy siltstones, yellowish or greenish fine sandstones and

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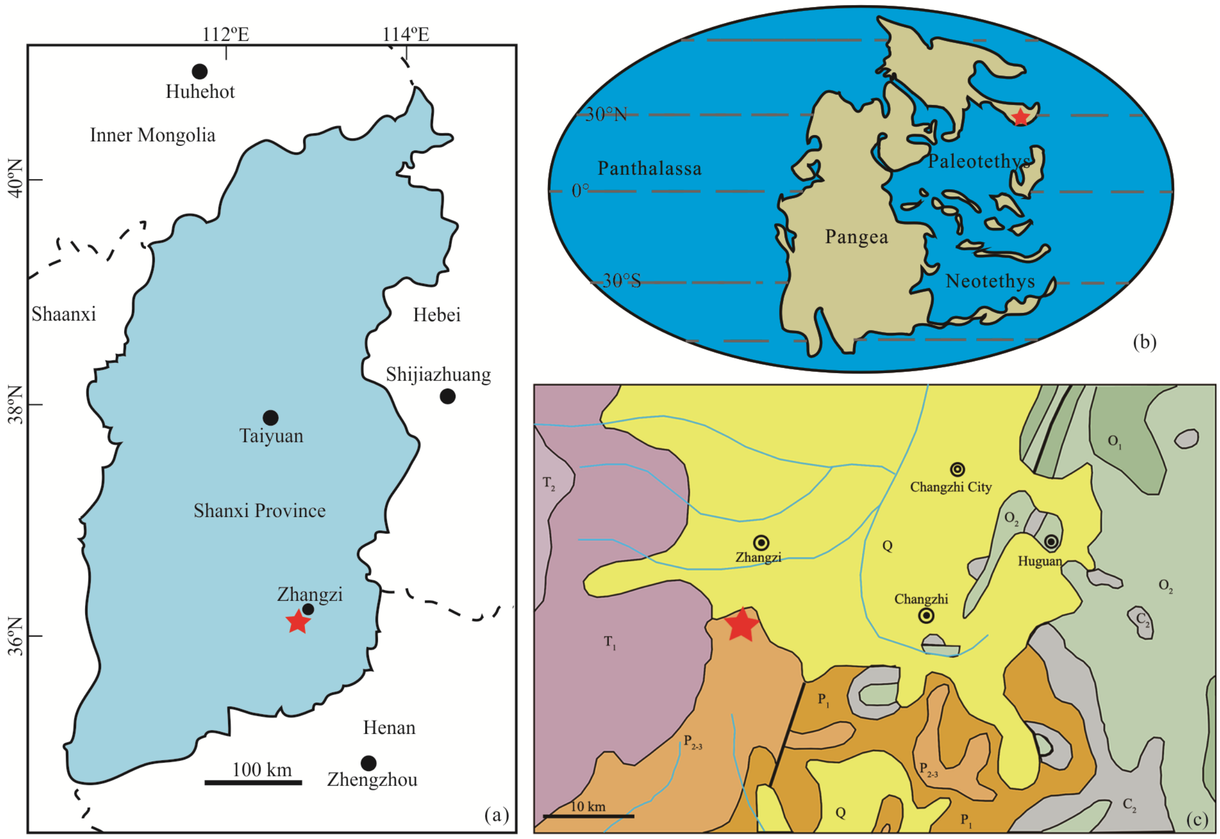

Figure 1. Location of the fossil woods. (a) Location of Xianwengshan Fossil Wood Geopark. (b) Simplified paleogeographic reconstruction showing the location of North China Block. (c) Simplified geological map of the Xianwengshan Fossil Wood Geopark (O_1. Lower Ordovician; O_2. Middle Ordovician; P_1. Lower Permian; P_{2-3}. Middle and Upper Permian; T_1. Lower Triassic).

medium sandstones, overlain by the upper purple-reddish muddy siltstones and thin sandstones. The age of Sunjiagou Formation was assigned to Lopinggian (Wuchiapingian to Changhsingian) based on high-precision U-Pb chemical abrasion-isotope dilution-thermal ionization mass spectrometry (CA-ID-TIMS) geochronology of tuffs (Wu et al., 2021). The floral, palynological and magnetostratigraphic data also suggest that the Sunjiagou Formation are Lopingian in age (Stevens et al., 2011; Wang, 2010; Ouyang and Hou, 1999; Li, 1997).

More than 300 siliceous permineralized wood trunks and branches were discovered from the yellowish fine sandstones or medium sandstones of Sunjiagou Formation in the Xianwengshan Fossil Wood Geopark of Zhangzi County, Shanxi Province, China (Fig. 1). Three adjacent sections (Xiyu, Dongyu and Chongwazhang sections) in the geopark were logged (Fig. 2). We observed all the samples in the field and collected 21 samples. These fossil woods consist of 0.6–18 m long trunks or branches, 0.3–1.3 m in diameter (Fig. 3a). The branch scars show that the branchlets of the juvenile stem arrange spirally, and the branches of the mature trunk arrange in whorls. They are all heterochthonous burial and clearly represent the upper parts of the trees because they lack attached stumps. All the specimens were transported by streams and were deposited prostrate. The paleo-current evidence from trough trends in the sandstones yielding fossil woods shows a generally SE-NW oriented flow (317°).

Microscopic slides of the transverse, radial and tangential wood sections were made following the traditional techniques for permineralized woods: First, the samples were cut into appropriate sizes using a diamond saw and the top surface polished using a grinding wheel with carborundum grades of #240, #800 and #1200 in turn. The smooth top surface was then glued onto a glass slide with epoxy resin and the bottom surface ground down to a thickness of about 30 μm. The thin section was covered with abienic balsam. Slides were photographed with a Panasonic DMC-FZ28 digital camera. They were studied using a microscope Leica DM4000B. Photomicrographs were taken with a Nikon D300 digital camera. Images in figures are processed and stitched together by Adobe Photoshop CC. All the specimens and slides are housed in the Research Center of Palaeontology and Stratigraphy, Jilin University.

2 RESULTS

CLASS Coniferopsida Šternberg, 1820

ORDER Coniferales Šternberg, 1820

FAMILY Incertae sedis

GENUS *Shanxiopitys* gen. nov.

Genus diagnosis: pith of hollow type, periphery of the pith homogeneous with parenchyma cells. Primary xylem endarch. Tracheids with araucarian radial pitting and cupressoid or taxodioid cross-fields, with usually 1–5 oculipores.

Etymology: The generic name is derived from the Shanxi Province, where the type specimen was collected.

Holotype: The specimen SZH-11.

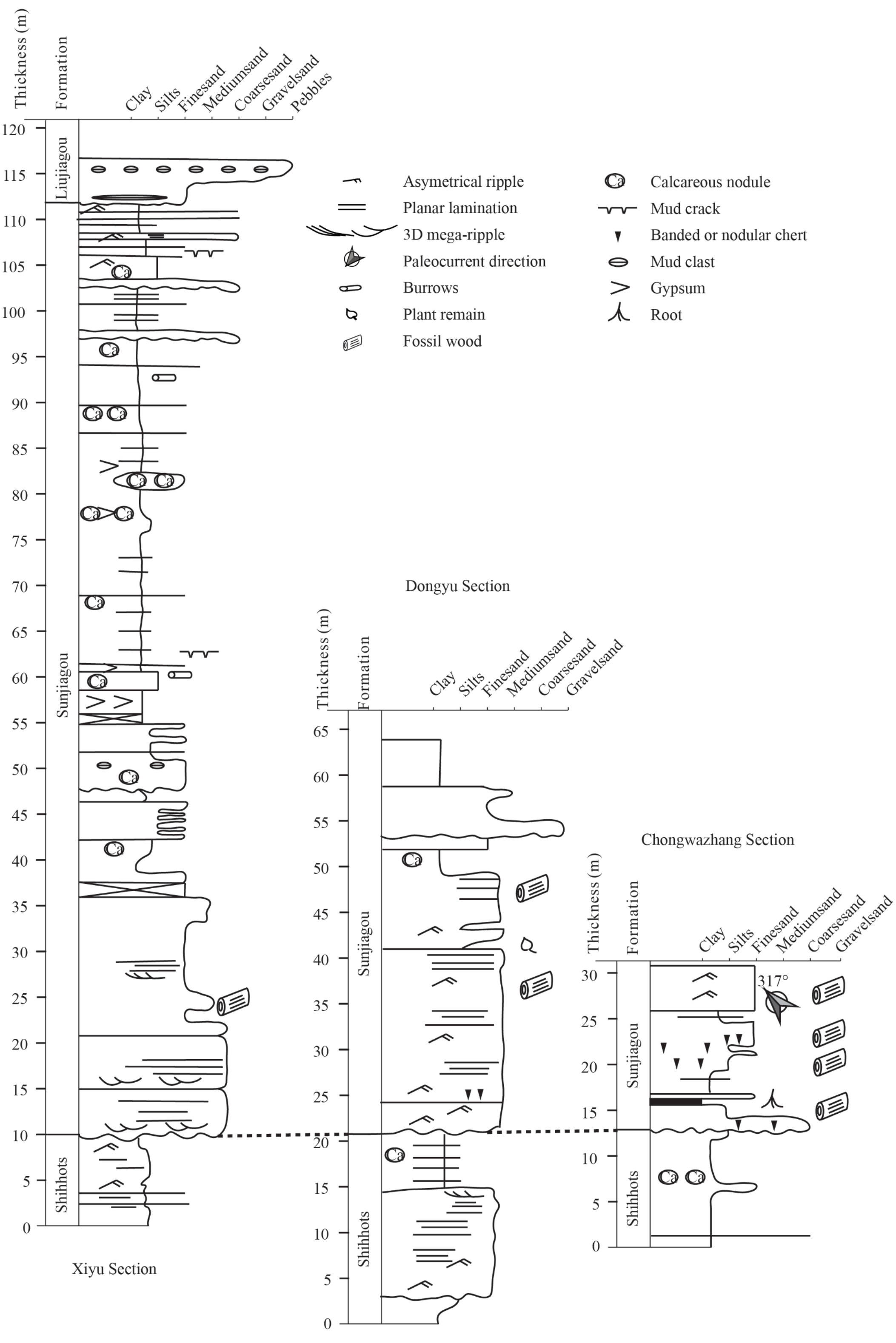

Figure 2. Sedimentological section for the Xianwengshan Fossil Wood Geopark where the samples were found.

Paratype: The specimen SZH-02.

Repository: All the specimens and slides are housed in the Key Laboratory for Evolution of Past Life and Environment in Northeast Asia, Jilin University, Changchun, China.

Type locality: Hezhi village, Zhangzi, Shanxi Province, PR China (Fig. 1).

Stratigraphic horizon and age: Sunjiagou Formation, Lopingian.

Etymology: The specific name is derived from the Zhangzi County, where the type specimen was collected.

Type species: *Shanxiopitys zhangziensis* gen. et sp. nov.

Shanxiopitys zhangziensis gen. et sp. nov.

Specific diagnosis: pith of hollow type, periphery of the pith homogeneous with parenchyma cells. Primary xylem endarch. Tracheids of primary xylem with helical, annular, and scalariform/reticulate thickenings. Secondary xylem homoxylic. Growth rings diffuse or inconspicuous. Araucarian radial pitting, 1–2 seriate (up to 4 seriate); xylem rays homogenous, uniseriate, rarely partially biseriate in 1–24 cells high or even more; 1–40 cells high; cross-field pits cupressoid or taxodioid type, 1–2, occasionally 3–5 in number. Resin canals and vertical parenchyma cells absent.

Description:

All the studied samples have the same anatomy. The pith is 1.0–3.5 cm (Fig. 3a). The pith parenchyma cells are distributed on the edge, circular in transverse section, max. A hundred μm in diameter (Figs. 3b, 3d). Intercellular spaces are invisible. The central part is hollow, many wizened parenchyma cells exist at the pith periphery (Figs. 3b–3e). The hollow-type pith may be a result of autolysis (self-digestion). Many scattered arthropod coprolites occur at the pith periphery and in the xylem (Figs. 3b, 3c). The primary xylem is endarch. Primary xylem tracheids, with helical, annular, and scalariform/reticulate thickenings, are 17–27 μm in diameter (Figs. 3e, 3f).

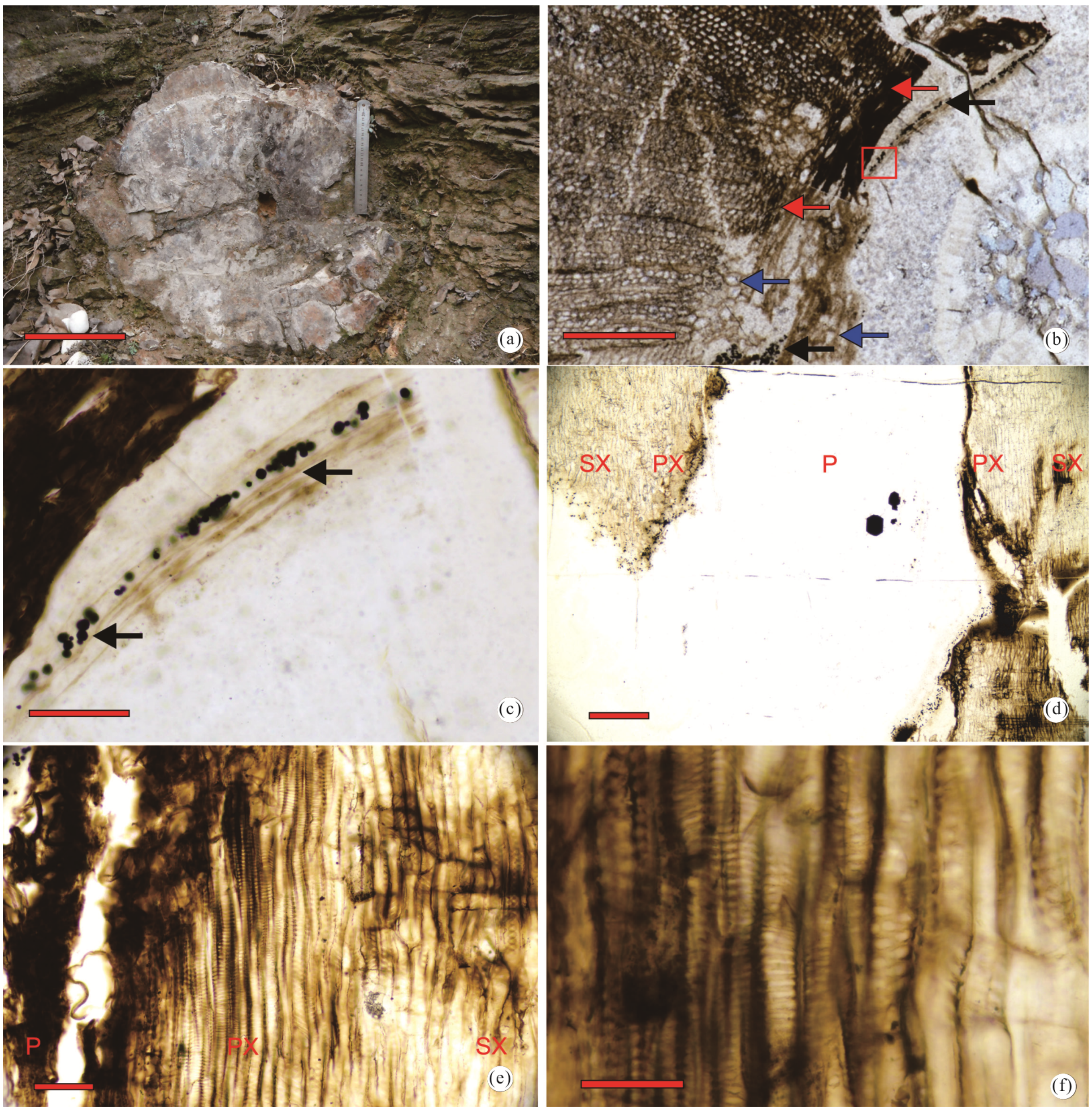

Figure 3. *Shanxiopitys zhangziensis* gen. et sp. nov. (a) Specimen SZH-01, scale bar = 20 cm; (b) transverse section (TS) showing the parenchyma cells (blue arrows) and the scattered arthropod coprolites (black arrows) in the pith, and the endarch primary xylem (red arrows) in the pith periphery, scale bar = 1 cm, specimen SZH-02; (c) TS showing the scattered arthropod coprolites (black arrows) in the pith (the red box in picture b), scale bar = 100 μm, specimen SZH-02; (d) radial section (RS) showing the hollow pith (P), primary xylem (PX) and secondary xylem (SX), scale bar = 500 μm, specimen SZH-02; (e) RS showing the close-up of the pith cells (P), primary xylem (PX) and secondary xylem (SX), scale bar = 100 μm, specimen SZH-02; (f) RS showing the primary xylem tracheids with helical, annular, and scalariform to reticulate thickenings, scale bar = 50 μm.

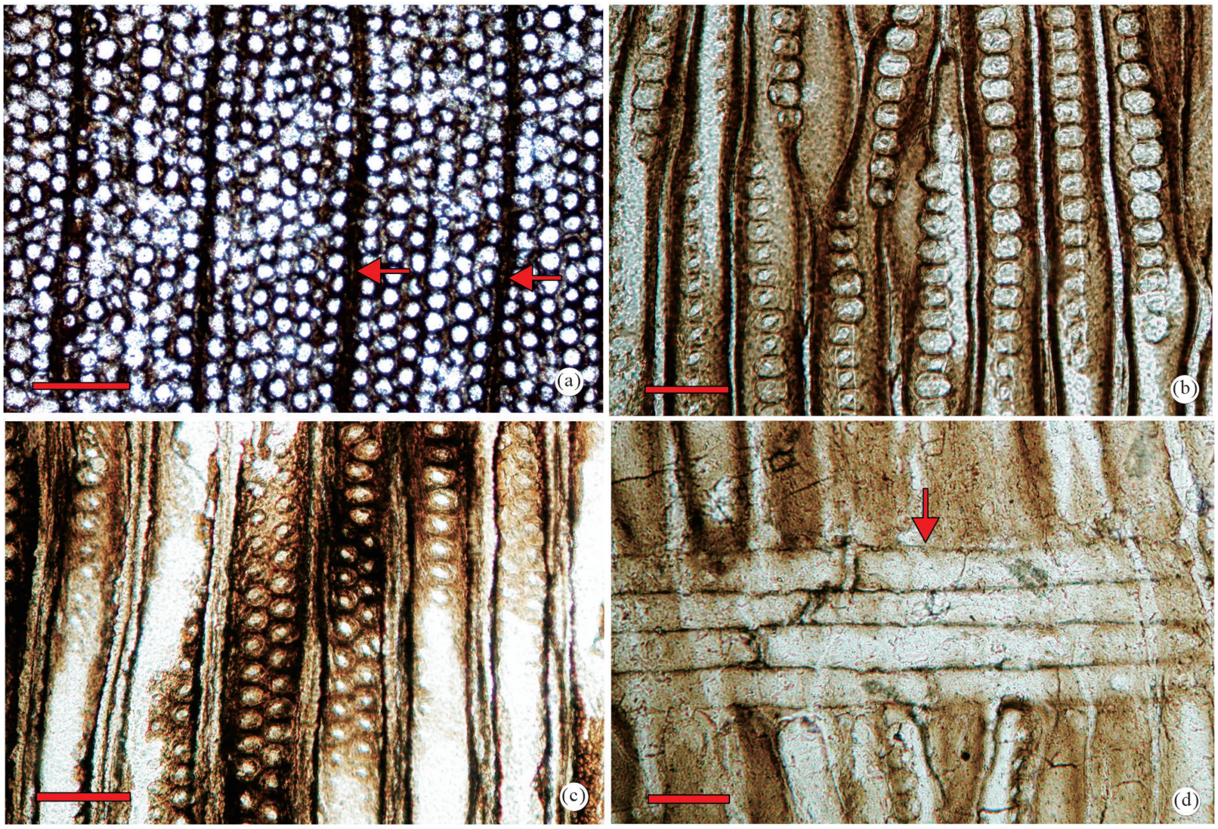

Figure 4. *Shanxiopitys zhangziensis* gen. et sp. nov. (a) TS showing the close-up of the tracheids and ray cells (red arrows), scale bar = 200 μm, specimen SZH-11. (b) Radial section (RS) showing uniseriate araucarioid bordered pits with circular or elliptical apertures on the radial walls of wood tracheids, scale bar = 40 μm, specimen SZH-11. (c) RS showing uniseriate or biseriate bordered pits with circular or elliptical apertures on the radial walls of wood tracheids. Scale bar = 40 μm. Specimen SZH-11. (d) RS showing the ray cells (red arrows), scale bar = 40 μm, specimen SZH-11.

The secondary xylem was well preserved, it is pycnoxylic, with tracheids and parenchymatous rays. In the transverse section, the growth ring boundary is inconspicuous with only one row of latewood cells, or diffuse (Fig. 6). Resin duct and axial parenchyma are absent in all the specimens. Axial tracheids are circular or oval (Fig. 4a). The diameter of radial tracheid is 32–69 μm (average 52 μm) and that of tangential tracheid is 43 – 68 μm (average 52 μm); thickness of tracheid walls 6–9 μm (average 8 μm). Intercellular spaces between tracheas can be observed. Xylem rays usually consist of uniseriate cells. There are 1–9 seriates of tracheids between every two rays (Fig. 4a). The frequency of the ray is 3 – 6 in number in each millimeter.

In the radial section, the pits on the tracheid walls are bordered and subcircular or oblate in shape (flattening index = 0.72–0.97). They are arranged in uniseriate to biseriate contiguously (occasionally up to tetraseriate, < 1%). When uniseriate, they are contiguous; when multiseriate, pits are alternate (Figs. 3d, 3e). They are 15 × 13 to 23 × 15 μm (height × width) in size. The uniseriate pits often only occupy the midst of the radial tracheid wall with lateral margins of 4–10 μm and the biseriate pits often occupy the whole tracheid wall. Pores are circular or oblique oval. The ray cells are brick-like and usually span 1.5 to 7 tracheids (100–200 to 800 μm) (Fig. 4d). The horizontal and end walls of ray cells are both smooth. There is 1 (74%) or 2 (20%), occasionally 3 (4%), 4 (2%) or 5 (< 1%) oculipores in each cross-field unit (Figs. 5a, 5b). Oculipores are of cupressoid or taxodioid type, 8 – 13 μm in diameter (Figs. 5a, 5b).

In the tangential section, xylem rays are homogenous and uniseriate or locally biseriate (Figs. 5c, 5d). When biseriate, ray cells are opposite (Fig. 5d). They consist of circular or elliptical parenchyma cells. Rays 1 to 30, even up to 40 (Mean = 6) cells high and 14 – 17 per mm^2, 5 – 6 per mm. Ray cells are circular to rectangular, 24 × 22 to 33 × 29 μm in size.

Remarks: The anatomical features of *Shanxiopitys* gen. nov. closely resemble some extinct and extant gymnosperm woods that also display a small homogeneous pith, an endarch primary xylem and a thick pycnoxylic secondary xylem. Cycad has transfusion tissue and scleroid cells in a wide pith. *Shanxiopitys* differs from cycads in having a hollow-type pith with parenchyma cells at the periphery. Ginkgo has the irregular distribution of tracheids, the bending/crossing ends of tracheid elements, and the development of axial parenchyma cells (Feng et al., 2010). These characteristics are absent in the *Shanxiopitys*. Thus, we consider *Shanxiopitys* gen. nov. as a coniferophyte of uncertain systematic affinity. The pith of the *Shanxiopitys* gen. nov. is homogenous, composed only of parenchyma cells. The secondary xylem of the new taxon resembles the extant and fossil Coniferopsida woods and the representatives of fossils. These closely resemble those of other Permian woods (He et al., 2013).

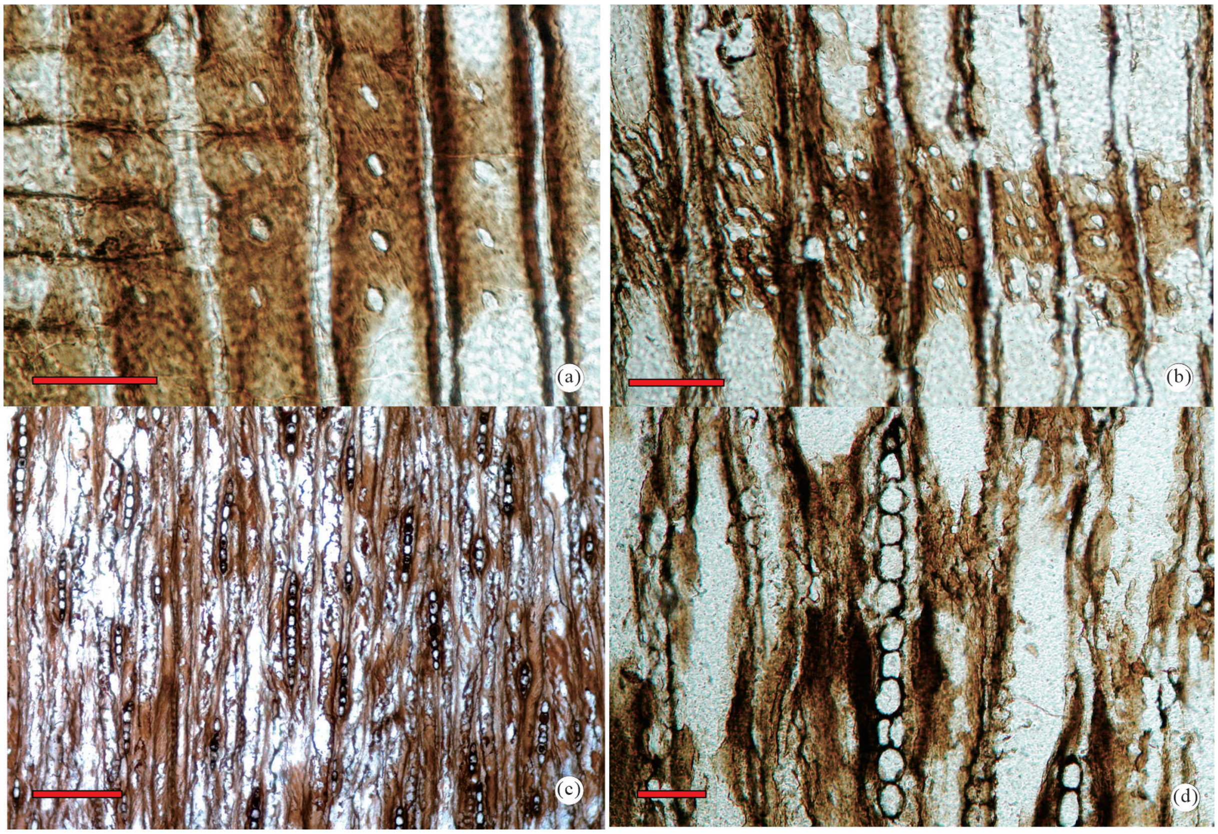

Figure 5. *Shanxiopitys zhangziensis* gen. et sp. nov. (a) RS showing the 1–2 oculipores in cross-field units, scale bar = 40 μm, specimen SZH-11; (b) RS showing the 2–4 oculipores in cross-field units, scale bar = 40 μm, specimen SZH-11; (c) Tangential longitudinal section (TLS) showing the homogenous and uniseriate or locally biseriate rays, scale bar = 200 μm, specimen SZH-11; (d) TLS showing the ray cells are uniseriate or locally biseriate, scale bar = 40 μm, specimen SZH-11.

The anatomy of pith is always regarded as a critical criterion for the classification of the gymnospermous woods (e.g.Shi et al., 2021, 2017, 2015,, 2014; Feng, 2012;Feng et al., 2012, 2010) and certain angiosperm woods (e.g., Mikesell and Schroeder, 1980; Metcalfe and Chalk, 1950; Haberlandt, 1914; Solereder, 1908). But the development of pith goes through different stages (Mikesell and Schroeder, 1980). Mature individuals show stable pith characteristics. The pith characteristics of *Shanxiopitys* gen. nov. are from the large mature trunks. The pith of all the samples are of hollow type. Therefore, the characteristics of the pith are very reliable.

So far, about 16 fossil pycnoxylic wood genera preserving pith and primary xylem have been previously described from the Upper Paleozoic of China (Wei et al., 2019). Among them, the pith is either solid or septate, and none of them is of hollow type. The current specimens resemble to three genera of them.

Chapmanoxylon Pant and Singh, 1987 was firstly described in the Permian West Bengal, India. It possesses a homogenous pith, an endarch primary xylem and an *Araucarioxylon*-type secondary xylem. The characteristics of *Shanxiopitys* gen. nov. is similar to the genus *Chapmanoxylon*. However, the present genus has cupressoid or taxodioid type cross-field pits (the cross-field with usually no more than four oculipores), instead of araucarioid-type cross-field pits (the cross-field with numerous oculipores (either cupressoid or taxodioid) which alternate and which are contiguous) in *Chapmanoxylon* (Philippe and Bamford, 2008; Philippe, 1995).

Ningxiaites Feng (2012) was firstly discovered from the Lopingian Sunjiagou Formation of Ningxia Hui Autonomous Region, North China. It is featured by a eustelic vascular system, thick pycnoxylic woody cylinder, and prominent helically arranged clusters of leaf traces. In the secondary xylem, isolated or vertically aligned axial parenchyma and inflated cells are present. That is different from the new taxon.

The fossil wood taxon *Plyophyllioxylon* Feng et al. (2012) was described from the Asselian Lower Shihhotse Formation of the Hulstai coalfield, Inner Mongolia Autonomous Region. Its pith is septate, and axial xylem parenchyma cells are present in the secondary xylem. These are different from *Shanxiopitys* gen. nov.

In conclusion, on the basis of the anatomical structures, we suggest that *Shanxiopitys* represents a new genus.

3 DISCUSSIONS

Growth-ring features provide a promising approach to better understanding the tree habit and its growing environment (e. g., Shi et al., 2017, 2015; Brea et al., 2011, 2008; Falcon-Lang, 2003, 2000a, b; Schweingruber, 1996, 1992). In *Shanxiopitys zhangziensis* gen. et sp. nov., the latewood cells do not differ greatly from earlywood cells, and the transition between the adjacent earlywood cells and latewood cells is very gradual (Figs. 6a, 6b); or locally, it has only one row of the latewood

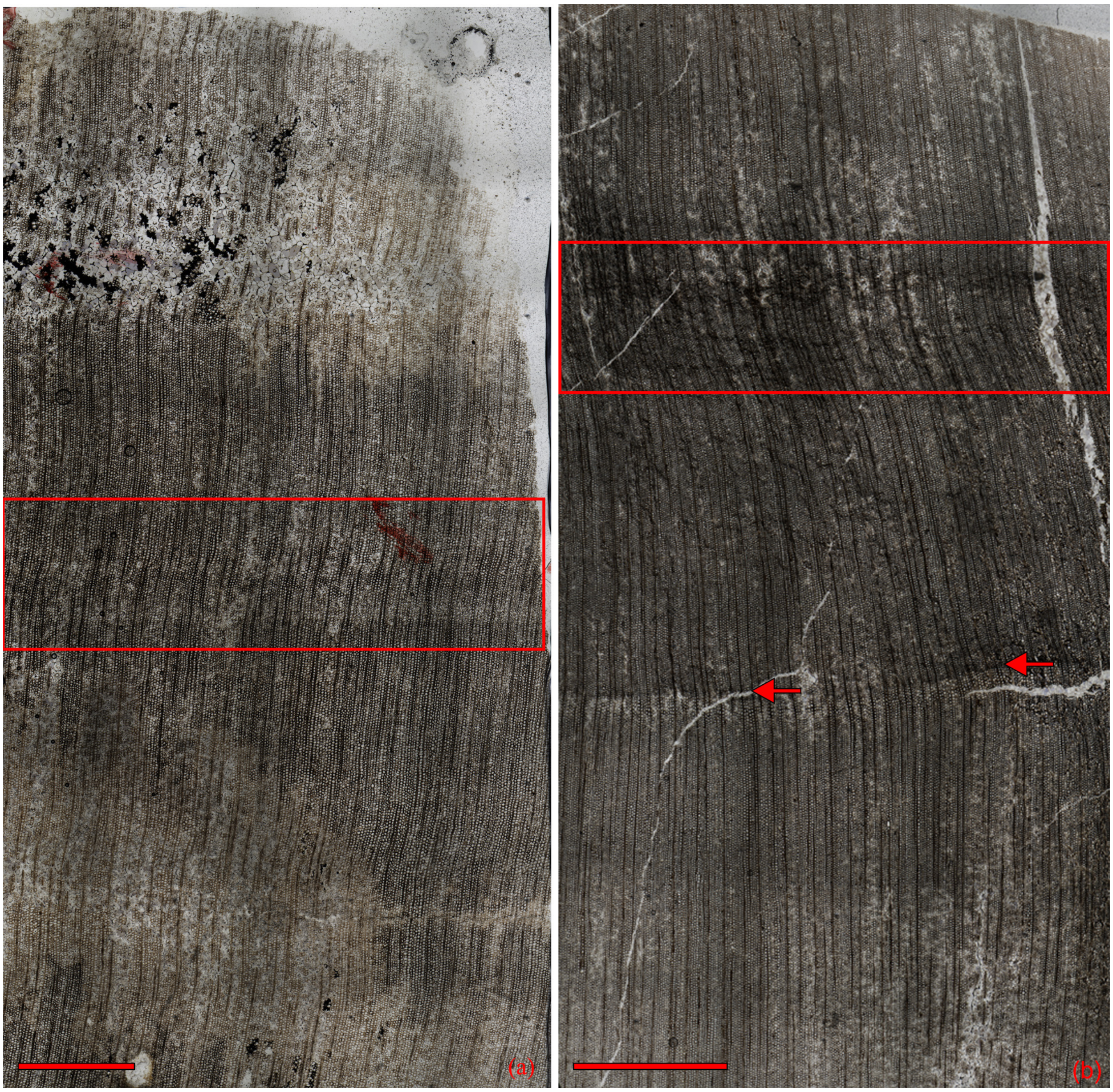

Figure 6. *Shanxiopitys zhangziensis* gen. et sp. nov. (a) TS showing the growth ring boundary is diffuse (red box), scale bar = 2 mm, specimen SZX-01; (b) TS showing the growth ring boundary is inconspicuous with only one row of latewood cells (arrows), or diffuse (red box), scale bar = 2 mm, specimen SZH-11.

cells (Fig. 6b). The presence of indistinct growth rings is typical in modern tropical and subtropical evergreen and semi-deciduous tree species (Tarelkin et al., 2016; Worbes, 1999). Thus, we speculate that *S. zhangziensis* gen. et sp. nov. was probably evergreen or semi-deciduous.

The trees show diffuse ring boundaries or a very low percentage of latewood. It indicates that the growing conditions are convenient and the cambium is never forced to cease growing for part of the year. Therefore, the growth-ring boundaries are diffuse or inconspicuous without any obvious change in cell wall thickness within a year. The latewood cells in the ring of the second year are still large, as the tree never enters dormancy and it continues to produce tracheids with thick walls at the end of the annual growing season (Speer, 2010; Worbes, 1999). Thus, the growth pattern of *S. zhangziensis* gen. et sp. nov. reveals that it grew in the environment developed under a warm humid climate condition without dry periods or of hydric stresses.

Wang (1993) reported the Asselian–Lopingian successional sequence of plant-communities in North China. Considered as a directional result of a great north wind migration of the pond-aquatic plant associations, the *Psygnophyllum* first occurred in a series of profiles of the Upper Shihhotse Formation in Shanxi Province. The unidirectional ascending trend of the flora turnover second boundary denotes the paleomonsoon activity. Most of the gymnosperms (*Psygmophyllum*, *Ullmannia*, "*Callipteris*", *Tatarina*, *Pseudovoltzia*, *Quadrocladus*, etc.) found in the Sunjiagou Formation show xeric cuticular texture, such as amphistomatic leaves with approximately the same number of stomata on both surfaces, thickened wall, sunken stomata, a much greater number of subsidiary cells arching over the aperture and dense hair or papillae, etc. (Wang and

Wang, 1986). These characteristics indicates that a strong wet-dry seasonality triggered by the mega-monsoon appeared in the Lopingian North China.

He et al. (2016) reported the *Gigantopteris dictyophylloides* Gu and Zhi in the Upper Shihhotse Formation of central Shanxi supporting it more likely formed under a seasonally dry climate. Moreover, the large tetrapod burrows from the Lopingian Naobaogou Formation of the Daqingshan Area, Inner Mongolia suggested the seasonal and semiarid or arid climate (Liu and Li, 2013).

The extensive red beds of Sunjiagou Formation were formerly interpreted forming in hot and arid climates (Parrish, 1995; Walker, 1976), or warm climates with wet-and-dry seasons (Parrish, 1998; Dubiel and Smoot, 1994). However, the growth pattern of *S. zhangziensis* gen. et sp. nov. reveals opposite results in Lopingian central North China. Sheldon (2005) believed that continental red beds can also form in warm, humid climates with good drainage and as such red color in itself does not indicate specific paleoclimatic features. Besides, mud cracks, gypsum beds, calcareous nodules and septarian nodules, usually formed in arid condition, were also found in the upper part of Sunjiagou Formation of the Xiyu Section (Fig. 7). In the other sections of North China, gypsum and numerous fine-grained aeolian sandstones were also reported (Wang and Chen, 2001; Wang and Wang, 1986;Norin, 1924, 1922). These demonstrated that Sunjiagou Formation was developed under an arid climate.

All of these indicate that the Lopingian successions of North China were deposited in a strongly seasonal climate. However, the growth pattern of *S. zhangziensis* gen. et sp. nov. seems to contradict previous biotic features and sedimentary characteristics. In this case, the conifers may live in a unique ecosystem in a seasonally dry landscape.

Gallery forest is mostly narrow strips of forest along creeks or rivers in an otherwise unfrosted landscape (Veneklaas et al., 2005). The species and resources in the riparian ecosystems are distinct from those in the surroundings. The gallery forests offer shelter and a breeding ground for the species living in the savannas, grasslands, or deserts. The modern examples of gallery forests include Llanos ecoregion and Cerrado region in South America, Madagascar and Konza Prairie in the USA. The recognition of gallery forests in the geological period contributes to understanding the paleoenvironment and paleoecology in the Earth's history. We speculate that in the Lopingian central North China, the conifers living in narrow strips of forest along permanent creeks or rivers formed a unique gallery forest ecosystem in a seasonally dry landscape. In the dry season, the trees could get enough water supply, while those plants living at the margin of the gallery forest might suffer a seasonal dry condition and display xerophytic characteristics. The recognition of gallery forests in the geological period contributes to understanding the paleoenvironment and paleoecology in the Earth's history. This ecosystem is comparable with that of the Permian Tim Mersoi Basin in Niger, the Triassic Junggar Basin or the modern Lake Eyre Basin in Australia (Shi et al., 2021; Looy et al., 2016).

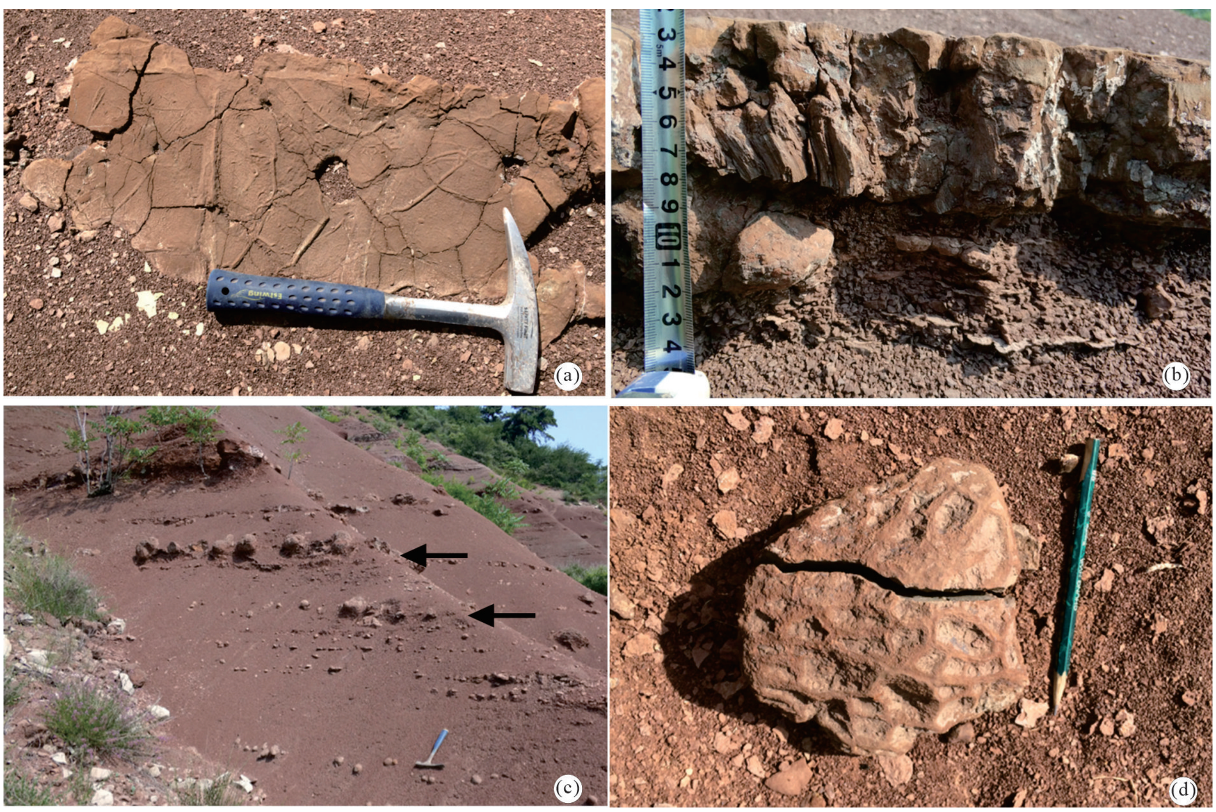

Figure 7. Representative field photographs, showing evidence of an arid climate during the Late Permian in North China Block. (a) Mud crack in the Sunjiagou Formation; (b) gypsum in the Sunjiagou Formation; (c) calcareous nodule beds (black arrows) in the Sunjiagou Formation; (d) septarian nodule in the Sunjiagou Formation. The hammer is 28 cm long and the diameter of the pencil is 0.5 cm.

4 CONCLUSION

In conclusion, the fossil woods found in the Xianwengshan Fossil Wood Geopark, Zhangzi County, Shanxi Province show a hollow-type pith, endarch primary xylem and pycnoxylic secondary xylem with Araucarian radial pitting and cupressoid/taxodioid-type cross-field pits, belong to a new taxon *Shanxiopitys zhangziensis* gen. et sp. nov. Their exceptional anatomical characteristics indicate these trees grew under optimal growing conditions without seasonal growth cessation. Combined with the leaf fossils, vertebrate fossils and sedimentary evidences, we speculate that there may exist gallery forests in the seasonal terrestrial basin in the Lopingian central North China. Further researches on sedimentology and *in-situ* stump fossils will be needed to illustrate the entire landscape in that period of North China.

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Conflict of Interest

The authors declare that they have no conflict of interest.

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