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Originalarticle

# Sclerospiroxylonxinjiangensisnov.sp.,agymnospermouswoodfrom theKungurian (lowerPermian)southernBogdaMountains, northwestern China: Systematics and palaeoecology§

Mingli Wan [a,b], Wan Yang [b], Jun Wang [a,c,*]

[a] StateKeyLaboratoryofPalaeobiologyandStratigraphy,CenterforExcellenceinLifeandPaleoenvironment,NanjingInstituteofGeologyandPalaeontology, ChineseAcademyof Sciences,210008Nanjing,China [b] GeologyandGeophysicsProgram,MissouriUniversityofScienceandTechnology,65409Rolla,MO,USA
[c] UniversityofChineseAcademyofSciences,100049Beijing,China

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ABSTRACT

A newsilicifiedwood,SclerospiroxylonxinjiangensisWan,YangetWangnov.sp.,isdescribedfromthe Cisuralian(lowerPermian) Hongyanchi Formation in southeast Tarlong section, Turpan City, Xinjiang Uygur Autonomous Region, northwestern China. The fossil wood is composed of pith, primary xylem and Prototaxoxylon-type secondary xylem. The pith is solid, circular, heterocellular, with sclerenchyma and parenchyma. The primary xylem is endarch to mesarch, with scalariform thickenings on tracheid walls. The secondary xylem is pycnoxylic, composed of tracheids and parenchymatous rays. Growth rings are distinct. Tracheids have mostly uniseriate, partially biseriate araucarian pitting on their radial walls. Helical thickenings are always present on both the radial and the tangential walls. Rays are 2–14 cells high, with smooth walls. There are 2 to 7, commonly 2 to 4 cupressoid pits in each cross-field. Leaf traces suggest that S. xinjiangensis nov. sp. was evergreen with a leaf retention time of at least 15 years. Based on the sedimentological evidence, growth rings within the S. xinjiangensis nov. sp. could have been caused by seasonal climatic variations, with unfavorable seasons of drought or low temperature. Low percentage of latewood in each growth ring is probably due to the intensity of climatic seasonality and/or long leaf longevity.



## 1.Introduction

Cathaysia,Angara,EuramericaandGondwanafloras havebeen developedin China during the Carboniferous and Permian (Shen, 1995). Among them, the Angara flora was distributed in a large area of northern China, including northern Xinjiang, Gansu, and the Beishan and Abag Qi, Dong Ujimqin Qi and Xi Ujimqin Qi of Inner Mongolia, as well as the Da Khinggan Range, Xiao Khinggan Range, and Changbai mountains (Sun, 1989; Huang, 1995; Zhang et al., 2007). Permian floras from these areas are highly diverse as indicated by the collections of compression-impression foliage (Douand Sun, 1984, 1985a, 1985b; Liu and Yao, 1996a, 1996b), and permineralized specimens (Wan et al., 2014, 2016a, 2016b, 2017a).

However,mostofthefossilsarereportedfromtheupperPermian. FossilplantsfromtheearlyPermianAngaraFlorainnorthernChina

§ Correspondingeditor:EvelynKustatscher.

* Correspondingauthor.
E-mailaddress:jun.wang@nigpas.ac.cn(J.Wang).

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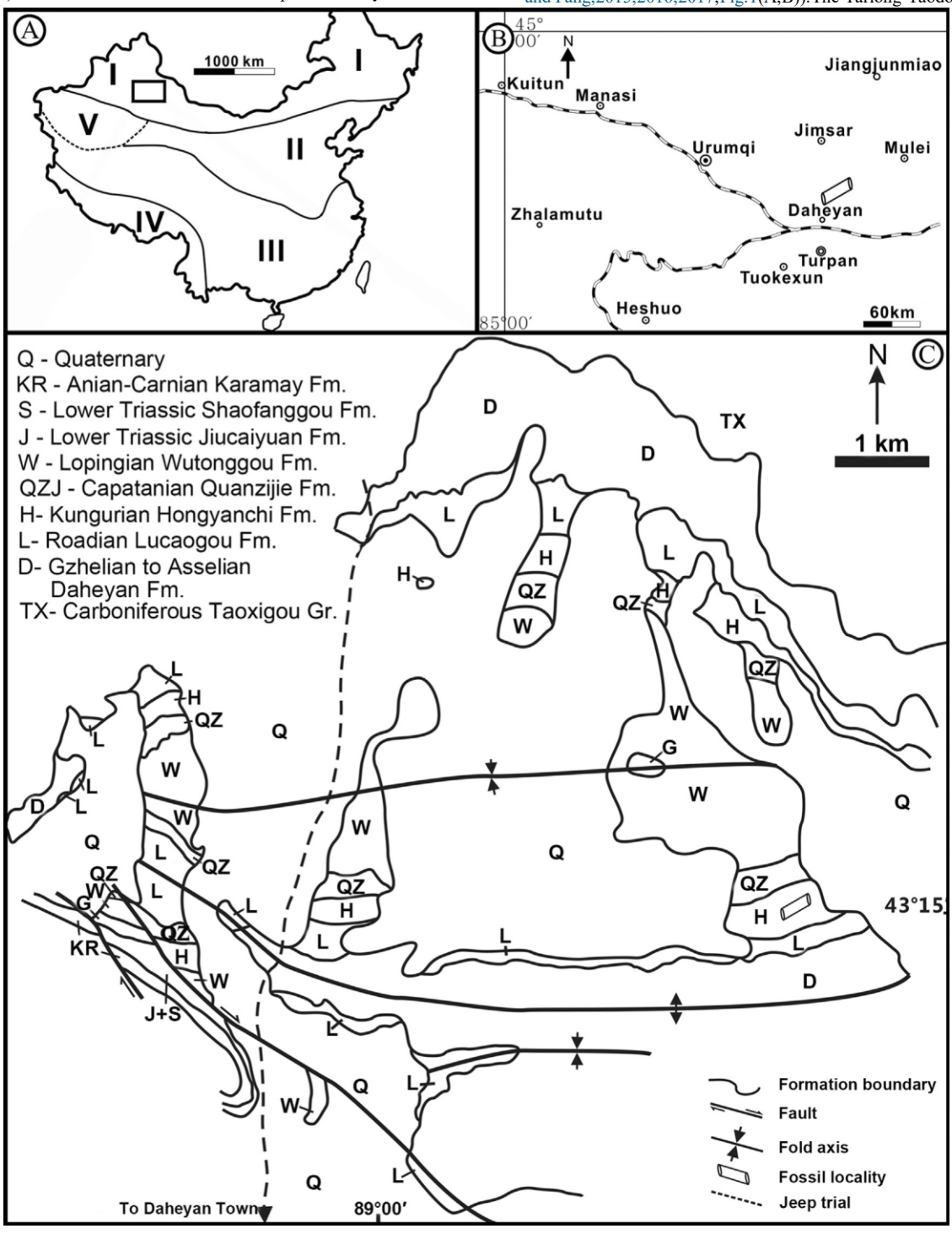
are assigned to the Crassinervia-Nephropsis-Zamiopteris assemblage (Huang, 1995), and thought to be low in diversity (Zhang etal., 2007). Early Permian plants in northern China are poorly understood compared with other locations of the Angaran palaeophytoprovince (Huang, 1995).

Northern Xinjiang Uygur Autonomous Region has been proven as a part of the Angaran palaeophytoprovince in the Permian (Meyen, 1981, 1982, 1997; Sun, 1989; Zhu et al., 2005). Cisuralian floras of this area remain incompletely understood (Huang, 1995). Little is known about the Cisuralian plant anatomy from silicified woods (Weietal., 2016), even in the entire northern China (Wan etal., 2017b, 2017d). In this contribution, we describe a new gymnospermous wood with coniferous affinity from the Hongyanchi Fm. in southeastern Tarlong section, southern Bogda Mountains, Xinjiang Uygur Autonomous Region, northwestern China (Fig. 1(A,B)). It is characterized by a heterogeneous pith, an endarch primary xylem, and a Prototaxoxylon-type secondary xylem. Frequent growth rings in the fossil wood suggest seasonal fluctuations caused by climatic and environmental stresses.

## 2. Geological settings

The research area is located in the Tarlong-Taodonggou half graben, southern foothills of Bogda Mountains, bordering the northwestern margin of the Turpan-Hami Basin, Xinjiang Uygur Autonomous Region, northwestern China (Yangetal., 2007, 2010; Obrist-Farner and Yang, 2015, 2016, 2017; Fig. 1(A,B)). The Tarlong-Taodonggou half graben,




. 1. Maps showing the location of the study area. A. Early Permian phytogeoprovince map (modified after Shen, 1995). I: Angaran province in Junggar-Hinggan Region; II: Cathaysian province (North China province); III: Cathaysian province (South China subprovince); IV: Gondwana province; V: Euramerican province in Tarim Plate. B. Location of the collection site (wood stem symbol) in the Permian Angaran 'toprovince (Meyen, 1981, 1982, 1997; Sun, 1989). C. Geological map of the Tarlong Taodonggou area in Turpan-Hami Basin, southern Bogda Mountains, showing the fossil collection site (wood stem symbol) odified after Yangetal., 2010).

where the silicified woods were collected, was located at the easternmost Kazakhstan Plate during the Permian (Sengor and Natalin, 1996; Ziegler et al., 1997; Scotese, 2001; Yang et al., 2010; Fig. 2). Uppermost Carboniferous to LowerTriassicconglomerate,sandstone,shale,andminor limestoneandvolcanic rocks were deposited in fluvial and lacustrine palaeoenvironments (Yang et al., 2007,2010;Fig.1(C)).

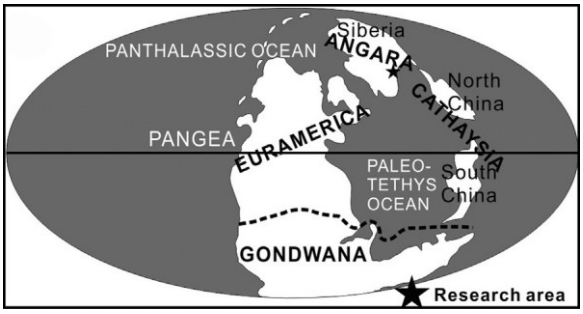



Fig. 2. Palaeogeographic map of Pangaea during the early Permian showing the fossil site (star) in the easternmost Kazakhstan Plate, mid-latitude NE Pangaea (Sengor and Natalin, 1996; Ziegler et al., 1997; Scotese, 2001; Lietal., 2004) (modified after Scotese, 2001).

Yangetal.(2010)definedtheHongyanchilow-ordercycle(LC) onthebasisof interpreted depositional environments and palaeoclimatic conditions. The Hongyanchi LC coincides with the Hongyanchi Fm. It is composed of medium-coarse sandstone, fine sandstone, thin-bedded siltstone and mudstone and shale deposited in fluvial, deltaic and deep lake environments. Its base is a transgressive surface overlain by deltaic deposits in SE Tarlong section. Its top is an erosional unconformity overlain by meandering stream deposits of the lower Quanzijie LC (Yang et al., 2010; Obrist-Farner and Yang, 2015, 2016, 2017). Macrofossil plants are rarely recorded from the Hongyanchi
Fm. in the Turpan-Hami Basin. So far, five species, including Walchia sp., Paracalamites sp., Rufloria ex. gr. derzawinii, Prynadaepteris anthrisifolia and Noeggerathiopsis sp., have been documented in the Hongyanchi Fm. (IPEDXPA and NIGPAS, 2003). The palynological assemblage was defined as the Acanthotriletes acinaeciformis–Cordaitina angustelimbatus–Urmites incrassatus Zone from the Hongyanchi Fm. (Ouyang et al., 2004). Previous biostratigraphic analyses attributed the Hongyanchi Fm. to the Wordian, middle Permian (Zhang, 1981; IGCAGS and IGXBGMR, 1986; Liaoetal., 1987; Zhuet al., 2005). Yang et al. (2010) proposed that the Hongyanchi LC would be Artinskian to Kungurian in age based on a U-Pb zircon dating (281.42 Ma) from a volcanic ash in profundal shale from the uppermost Hongyanchi LC in SE Tarlong. Fossil woods were collected from an interval 20 m below the volcanic ash bed. Therefore, their age is assigned to the Kungurian. The environment of the fossil-bearing sandstones and shales has been interpreted as a lacustrine delta (Yangetal., 2007, 2010), suggesting that the trees grew probably in a deltaic plain or in a nearby fluvial environment.

## 3. Material and methods

Nine individual stem fragments were collected from a single layer. All of them belong to one species based on their anatomical features. Transverse, radial and tangential surfaces of the fossil woods were cut and ground to 30 mm thickness for transmitted light microscopy. Thirty-seven thin sections have been made for all the nine samples. One sample (PB 22604) is designated as the holotype because of its well-preserved inner structures. The stem fragments were described using the terminology of Richter et al. (2004) and Philippe and Bamford (2008). A thin-section microscopic study of the stems indicates that they are well silicified. Large specimens were photographed with a Nikon D800 digital single-lens reflex camera. Images were taken using a Leica DM5000 compound microscope and a Leica DC500 digital microscope camera system. The fossil woods and their thin sections are stored in the Palaeobotanical Collection of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

## 4. Systematic palaeobotany

Division Fossil Gymnospermae
Genus Sclerospiroxylon (Prasad) emend. Zhangetal., 2007
Type species: Sclerospiroxylon marguerierae Prasad, 1982

Sclerospiroxylon xinjiangensis Wan, Yang et Wang nov. sp. Figs. 3–7

Derivation of the name: The specific epithet indicates that the fossil wood originated from the Xinjiang Uygur Autonomous Region.

Holotype: PB 22604, and the slides PB 22604–1 to PB 22604–9 (Figs. 4–7).

Type locality: Turpan City, Xinjiang Uygur Autonomous Region, China (Fig. 1).

Repository: Palaeobotanical Collection of Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Stratigraphic horizon: Hongyanchi Fm.; Kungurian, Permian.

Diagnosis: Stem eustelic. Pith solid, circular, heterocellular, with sclerenchyma and parenchyma. Thick-walled cells showing circular patterns in the middle part of the pith. Primary xylem strands endarchtomesarch. Tracheids of primary xylem with helical and scalariform thickenings. Secondary xylem pycnoxylic, composed of tracheids and parenchymatous rays. Tracheids rounded or polygonal, sometimes squarish in transverse section. Pitting on radial walls mostly uniseriate, rarely partially biseriate. When biseriate, pits alternately arranged. Bordered pits commonly circular, rarely flattened in outline with rounded to oval apertures, continuously arranged. Rays uniseriate, 2 to 14 cells high. Ray parenchymatous cells procumbent, rectangular. Cupressoid-type cross-field pitting. Each cross-field with 2 to 7, mostly 2 to 4 pits. Cross-field pits oval to circular, bordered with circular to elliptical apertures. Axial xylem parenchyma and ray tracheids absent.

Description: Fossil stem fragments are 10 to 16 cm in diameter and more than 1 m long in the field (Fig. 3(A–C)). They are either well preserved as cylinders or heavily compressed, in parallel with depositional beds. Some of them are fractured into numerous pieces (Fig. 3(A)). Cortex and peridermal structures are not preserved. The following description is based on the thin sections from the holotype specimen PB 22604.

Solid pith measures 1.8 4.7 cm in cross section (Fig. 4(A, B)). It is speculated to have been circular and estimated to be 2.5 cm in diameter in cross section. The heterocellular pith consists of parenchyma, thick-walled cells, and sclerenchyma (Figs. 4(B–E), 5(A–E)). Parenchymatous cells are mostly circular to polygonal in cross section (Fig. 4(C, D)); they are 25–130 mm in diameter. Large parenchymatous cells are commonly distributed in the periphery. Cell walls are commonly smooth, circular to elongated oval in radial section (Fig. 4(E)). Sclerotic cells are commonly dispersed in groups with 8 to 49 cells distributed throughout the pith (Figs. 4(D, E), 5(A–C), black arrows). Each sclerotic cell is circular to polygonal in both cross (Fig. 4(D), black arrows) and radial (Fig. 5(A, E), black arrows) sections.

In two radial thin sections, numerous hollow and thick-walled cells form a solid ellipsoid body with a major axis of 3.2 mm and a minor axis of 1.5 mm, in the middle part of the pith (Fig. 5(A)). Some parenchymatous cells and sclerenchyma are present in the inner (Fig. 5(C)) or marginal (Fig. 5(B)) part of the ellipsoid body. Some of the thick-walled cells are distorted into circular patterns in radial sections (Fig. 5(B–D)). Cell walls are commonly smooth, rarely dotted (Fig. 5(D)). Those hollow and thick-walled cells occurred casually in the pith of a single stem fragment. Their morphology and distribution in transverse sections cannot be traced due to preservation.

The primary xylem strands show an endarchtomesarch maturation (Fig. 6(A, B)). They are all in contact with the secondary

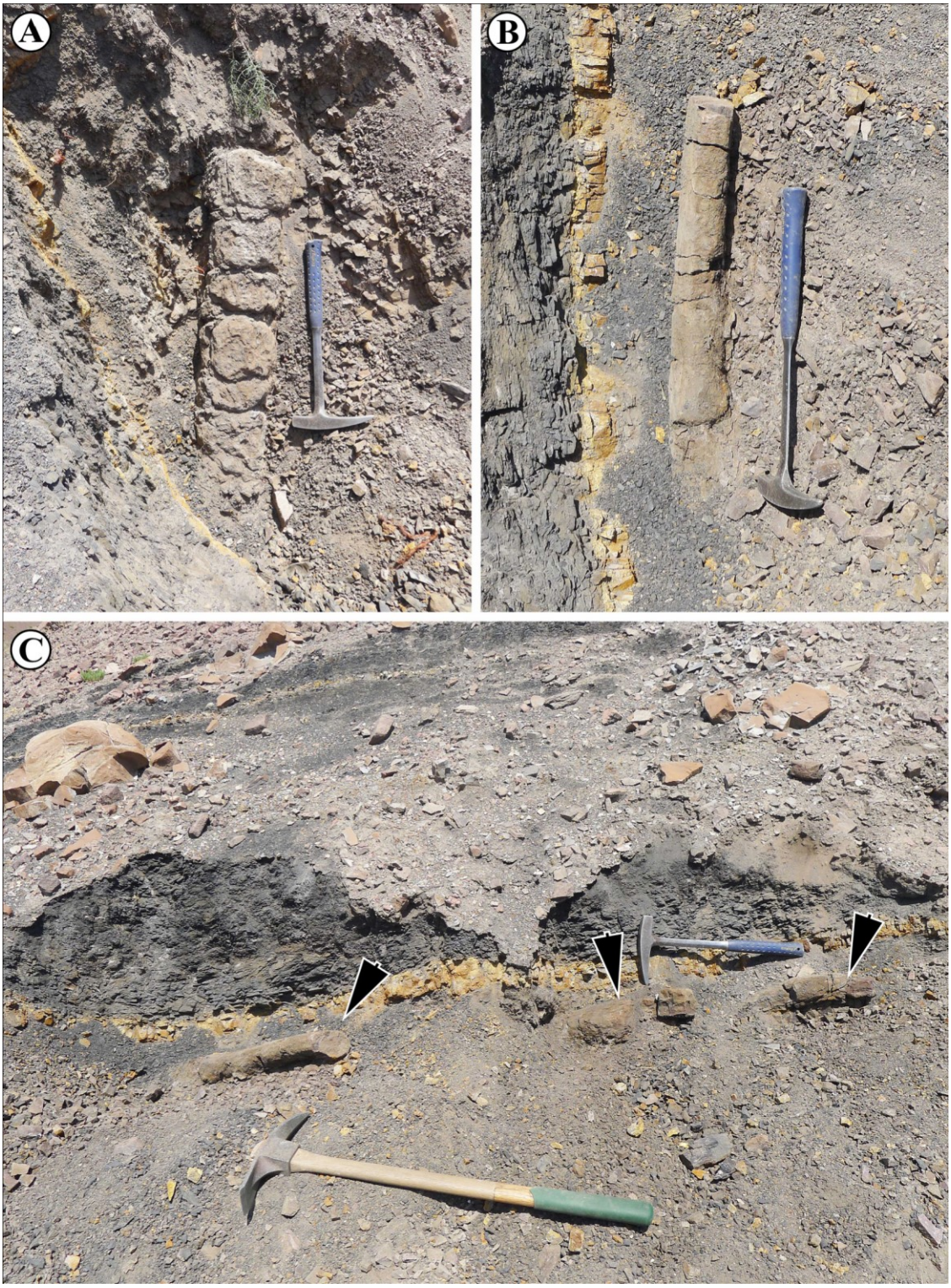



Fig. 3. Field photographs showing the original position of Sclerospiroxylon xinjiangensis nov. sp. from the Kungurian Hongyanchi Low-order Cycle, Tarlong-Taodonggou area, Turpan-Hami Basin, southern Bogda Mountains, NW China. A. Stem cylindrical, 15 cm in diameter, fractured into numerous pieces. B. Compressed fossil stem. C. Three fossil stems in a single layer. The hammer with a blue handle is ca. 35 cm long, and the pick is ca. 80 cm long.

xylem. Their tracheids are up to 35 mm in diameter and 700 mm in length. In longitudinal sections, the walls of protoxylem and metaxylem contain helical and scalariform thickenings (Fig. 6(C), white arrows).

The secondary xylem is composed of tracheids and parenchymatous rays. Growth rings are distinct and of various widths, up to 0.6 mm (Figs. 4(A), 6(D)). Boundaries of growth rings are well defined, distinctly visible by the presence of broad early wood with thinner cell walls and narrow late wood with thicker cell walls; the transition from early to late wood is gradual (Fig. 6(D), white arrow). Tracheids in early wood are more or less rounded to polygonal, in some instances squarish in cross section, about 20–

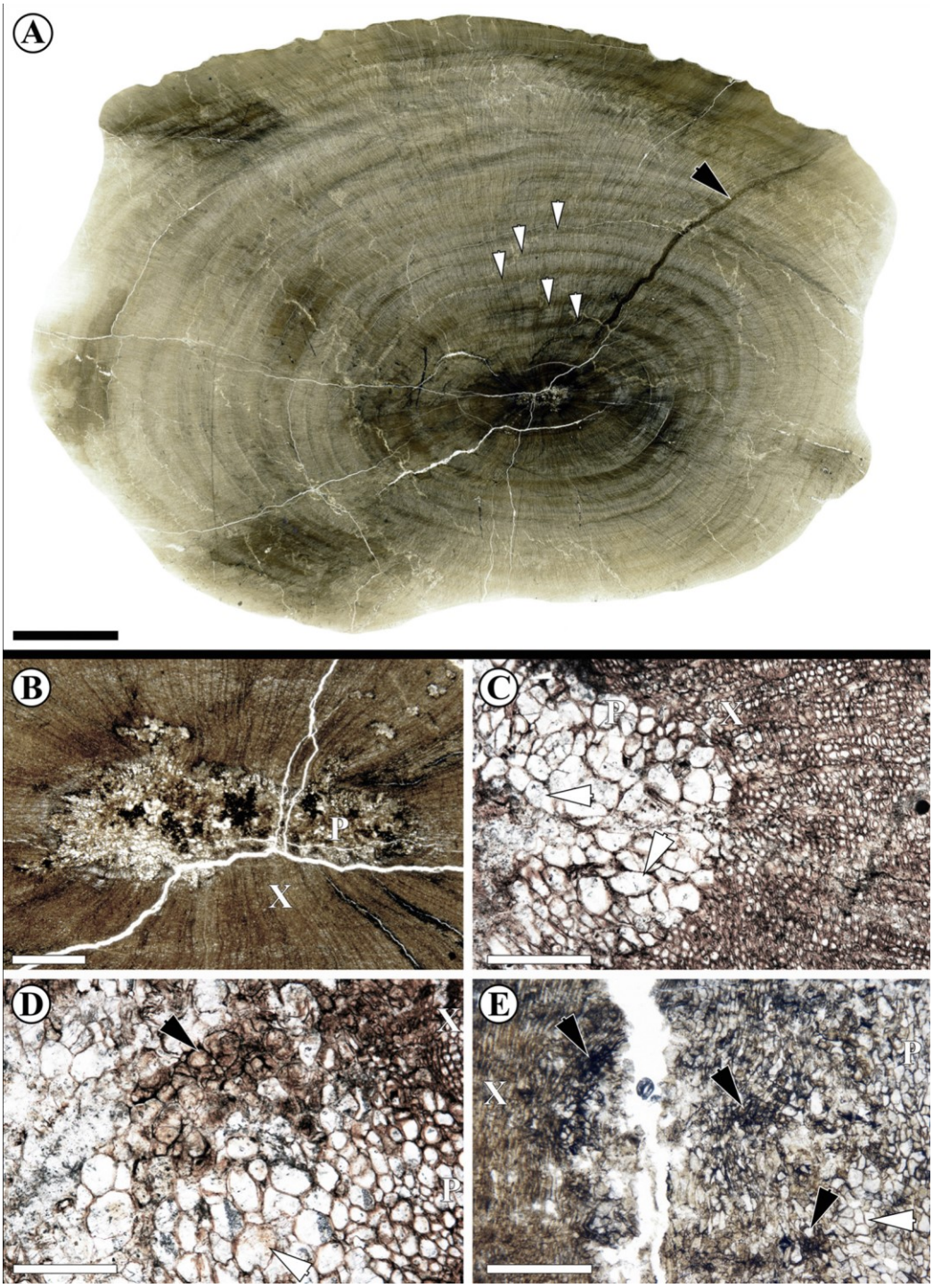



Fig.4.Photomicrographsshowingthegrossmorphologypithstructure ofSclerospiroxylonxinjiangensisnov.sp.(holotype;PB22604)fromtheKungurianHongyanchiLoworderCycle,Tarlong-Taodonggouarea, Turpan-HamiBasin,southernBogdaMountains,NWChina.A.Transversesectionofthefossilwood,showingtheoverviewoftheplant axiscontainingpithandxylem(slidePB22604–1).Growthringsareshownby whitearrows.Aleaftrace(blackarrow)horizontallypassesthroughthexylem.B.Transverse sectionofthefossilwood,showingtheheterocellularpith(P)andxylem(X)(slidePB22604–1).C.Transversesectionof thefossilwood,showingtheheterocellularpith(P) andxylem(X)(slidePB22604–1).Whitearrowspointtolargecirculartopolygonalparenchymatouscellsintheperipheralareaofthepith.D.Transversesectionof thefossil wood,showingtheheterocellularpith(P)andxylem(X)(slidePB22604–1).Blackarrowpointstothegroupedscleroticcells;whitearrowpointstolargecirculartopolygonal parenchymatouscellsinthe peripheralareaofthepith.E.Radialsectionofthefossilwood,showingthesolidheterocellularpith(P)andxylem(X)(slidePB22604–2).Black arrowspointtogroupedsclerenchyma.Scalebars:1cm(A),1mm(B), 200mm(C–E).

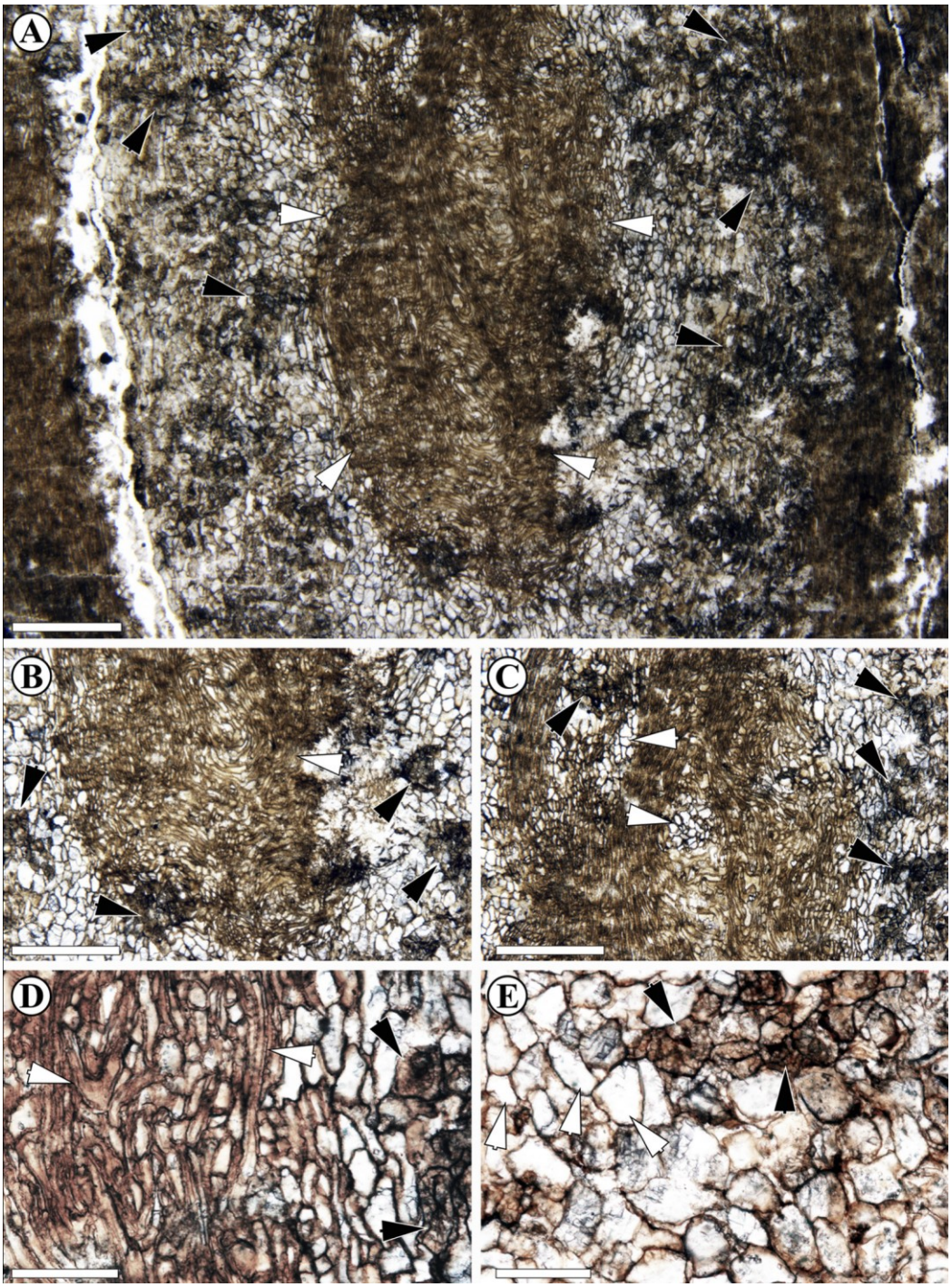



Fig. 5. Photomicrographs showing the pith structure of Sclerospiroxylon xinjiangensis nov. sp. (holotype; PB 22604) from the Kungurian Hongyanchi Low-order Cycle, Tarlong Taodonggou area, Turpan-Hami Basin, southern Bogda Mountains, NW China. A. Radial section of the fossil wood, showing the solid heterocellular pith (P) and xylem (X) (slide PB 22604–2). Black arrows point to grouped sclerenchyma; white arrows point to thick-walled cells forming a solid ellipsoid body with a major axis of ca. 3.2 mm and a minor axis of ca. 1.5 mm. B. Radial section of the fossil wood, showing the heterocellular pith with grouped sclerotic cells (black arrows); white arrow points to thick-walled cells forming a solid body (slide PB 22604–2). C. Radial section of the fossil wood, showing the heterocellular pith with grouped sclerotic cells (black arrows); white arrow points to the parenchymatous cells with the solid body formed by thick-walled cells (slide PB 22604–2). D. Radial section of the fossil wood, showing the heterocellular pith with distorted thick-walled cells (white arrows); black arrows point to the sclerotic cells (slide PB 22604–2). E. Radial section of the pith, showing circular to polygonal parenchymatous cells (white arrows) and sclerotic cells (black arrows) (slide PB 22604–2). Scale bars: 500 mm (A), 400 mm (B and C), 100 mm (D and E).

45 mm in diameter, arranged in regular radial files (Fig. 6(D)). They are long and fusiform with sharp or blunt ends. Radial pits are uniseriate (Fig. 6(E–H), white arrows), with rarely partially biseriate (Figs. 6(H), 7(A), black arrow). Tangential pits are absent. Bordered pits on radial tracheid walls are commonly rounded, rarely flattened (Fig. 6(G), black arrows), contiguous, with circular

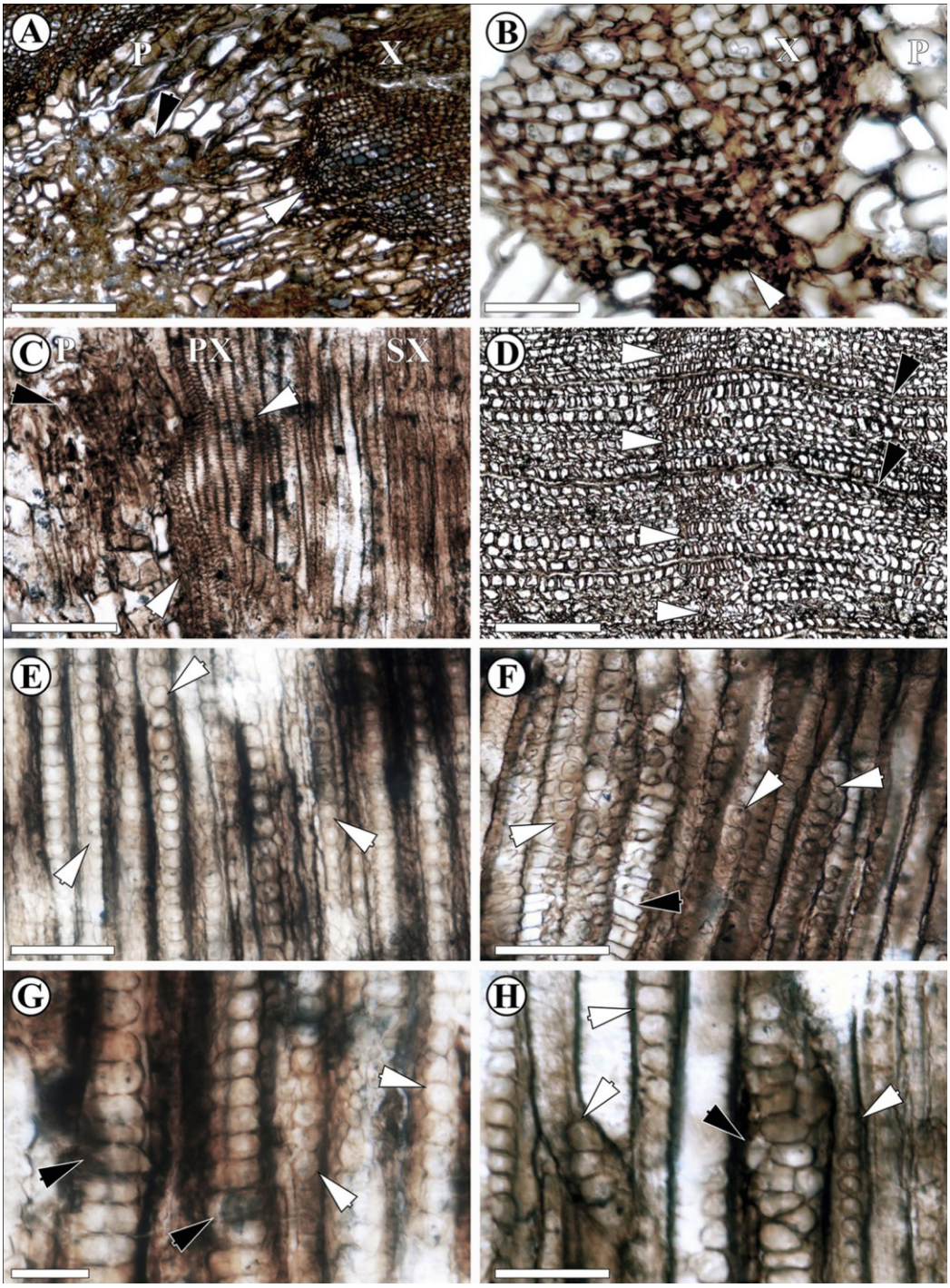



Fig. 6. Photomicrographs showing the xylem structure of Sclerospiroxylon xinjiangensis nov. sp. (holotype; PB 22604) from the Kungurian Hongyanchi Low-order Cycle, Tarlong-Taodonggou area, Turpan-Hami Basin, southern Bogda Mountains, NW China. A. Transverse section of the fossil wood, showing the heterocellular pith (P) and xylem (X) (slide PB 22604–1). Black arrows point to distorted thick-walled cells forming a solid body; white arrow points to the primary xylem. B. Transverse section of the fossil wood, showing the endarch primary xylem (white arrow) (slide PB 22604–1). C. Radial section of the fossil wood, showing the pith (P), primary xylem (PX) and secondary xylem (SX) (slide PB 22604–3). White arrows point to annular, helical and scalariform thickenings on walls of tracheids in primary xylem; black arrow points to the grouped sclerotic cells in the peripheral area of the pith. D. Transverse section of the xylem, showing the growth ring (slide PB 22604–1). White arrows point to the late wood composed of about 10 tracheids with thicker walls and smaller diameters; black arrows point to uniseriate rays. E. Radial section of the xylem, showing the uniseriate radial tracheidal pitting with contiguous and rounded pits (white arrows) (slide PB 22604–4). F. Radial section of the xylem, showing single helical thickenings on tracheidal walls (black arrow), and uniseriate radial tracheidal pitting with contiguous and rounded pits (white arrows) (slide PB 22604–4). G. Radial section of the xylem, showing the uniseriate radial tracheidal pitting with contiguous rounded (white arrows) and flattened pits (black arrows) (slide PB 22604–4). H. Radial section of the xylem, showing the uniseriate (white arrows) and partially biseriate (black arrows) radial tracheidal pitting with contiguous and rounded pits (slide PB 22604–4). Scale bars: 200 mm (A and D), 100 mm (C), 50 mm (B, E–H).

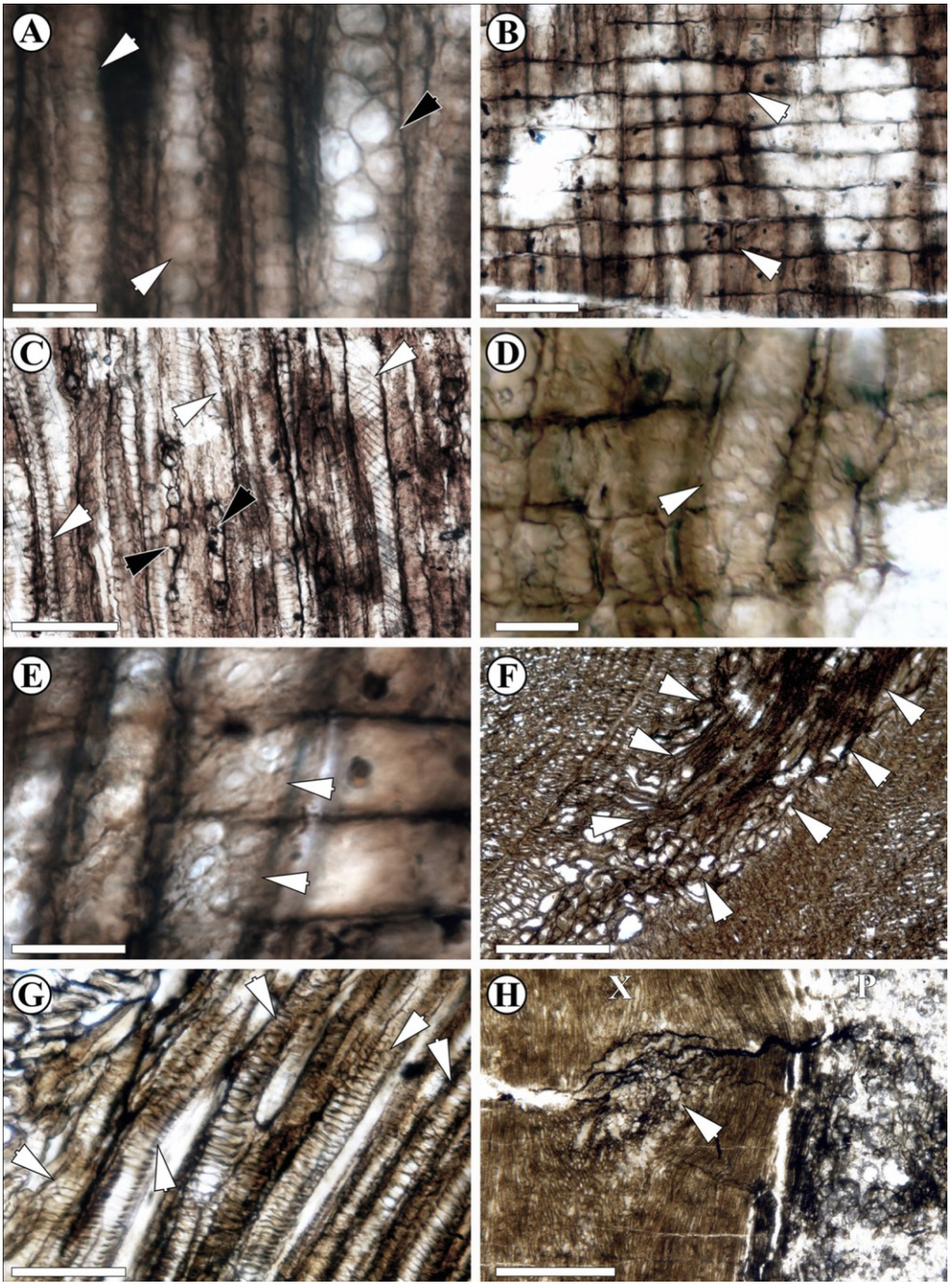



Fig. 7. Photomicrographs showing the xylem structure of Sclerospiroxylon xinjiangensis nov. sp. (holotype; PB 22604) from the Kungurian Hongyanchi Low-order Cycle, Tarlong-Taodonggou area, Turpan-Hami Basin, southern Bogda Mountains, NW China. A. Radial section of the xylem, showing the uniseriate (white arrows) and partially biseriate (black arrows) radial tracheidal pitting with contiguous and rounded pits (slide PB 22604–5). B. Radial section of the xylem, showing rectangular ray cells with smooth walls (slide PB 22604–6). White arrows points to vertical walls that are perpendicular to horizontal walls of the rays. C. Tangential section of the xylem, showing uniseriate rays (slide PB 22604–7). D. Radial section of the xylem, showing the cupressoid-type cross-field pitting (slide PB 22604–8). White arrow points to up to 7 pits arranged in a vertical column in a single cross-field. E. Radial section of the xylem, showing the cupressoid-type cross-field pitting (slide PB 22604–8). White arrows point to pits are of faint borders with elliptical apertures. F. Transverse section of the fossil wood, showing a leaf trace extending from the secondary xylem near the pith (white arrow) (slide PB 22604–1). G. Transverse section of the fossil wood, showing the leaf trace composed of tracheids with scalariform to reticulate thickenings (white arrows) (slide PB 22604–1). H. Tangential section of the fossil wood with pith (P) and xylem (X), showing a mesarch leaf trace near the pith (slide PB 22604–9). Scale bars: 20 mm (A, D and E), 50 mm (B and G), 100 mm (C), 200 mm (F), 400 mm (H).

to oval apertures. In biseriate parts, radial pits are mostly alternately arranged (Figs. 6(H), 7(A), black arrow). The spirals occurring on both radial and tangential tracheidal walls are single, clockwise or anticlockwise inclined at an angle of 20–708, running over or between the bordered pits (Figs. 6(F), 7(C)).

Rays are homogeneous and mostly uniseriate (Figs. 6(D), 7(B, C)). The parenchyma cells of rays are rectangular and range from 70 to 150 mm long and 20 to 35 mm high radially (Fig. 7(B)). Cell walls of ray parenchyma cells are smooth. The vertical walls are occasionally inclined at an angle of 40–608. In tangential sections, rays are 2–14 cells high (Fig. 7(C)), and 7 cells on average (n = 400). The cross-field

pitting is cupressoid sensu Richter et al. (2004). There are 2–7, commonly 2–4 pits in each cross-field (Fig. 7(D, E)). Cross-field pits are oval to circular, bordered with circular to elliptical apertures.

One leaf trace, circular in tangential section, occurs close to the pith (Fig. 7(H)), with a diameter of ca. 320 μm. It extends through at least 15 growth increments in cross section (Fig. 4(A), black arrow). The leaf trace is mesarch (Fig. 7(H)) and composed entirely of tracheids with scalariform to reticulate thickenings (Fig. 7(F, G)). The length of the leaf trace is more than 3.2 mm (Fig. 4(A), black arrow). Tracheids of leaf trace are 6–16 μm in diameter. Leaf traces are present in three other samples, showing similar anatomical features. They are persistent and commonly extending no less than 6 growth ring increments.

Remarks: It is noteworthy that there are numerous hollow thick-walled cells forming a solid ellipsoid body in the middle part of the pith (Fig. 5(A)). Some of the thick-walled cells are distorted, which are comparable to auxin swirls that have been described from the wood of fossil progymnosperms, equisetophytes and arborescent lycophytes (e.g., Rothwell et al., 2009). However, in S. xinjiangensis nov. sp. the hollow thick-walled cells occur in the middle part of the pith rather than in the secondary xylems. In addition, those hollow cells are different from tracheids due to the lack of secondary growth on cell walls. There are neither typical thickenings nor definite pits on their walls. It is proposed that these hollow thick-walled cells could be special transfusion tissues in the pith. This feature only occurs in two radial thin sections of the same specimen, and would not be a permanent, diagnostic character.

There are three lines of evidence which suggest that the persistent vascular trace corresponds to a leaf trace in S. xinjiangensis nov. sp. First, the vascular trace is composed entirely of cells with scalariform to reticulate thickenings on tracheidal walls (Fig. 7(G)), which are uncharacteristic of the more mature tissue one would expect to encounter in branches (Falcon Lang and Cantrill, 2001; Evert, 2006). Second, areas of the vascular 2 trace in tangential sections are stable (0.08–0.11 mm ). In cross

section, the width of the vascular trace is constant (Fig. 4(A)). These features make the vascular trace in our specimen similar to those in Araucariopitys sp., Podocarpoxylon sp., and Araucarioxylon sp. reported by Falcon-Lang and Cantrill (2001). Shi et al. (2017) described a coniferous branch from the Changhsingian-Induan Guodingkeng Fm. of Taoshuyuan section in Turpan-Hami Basin, which is less than 5 km away from current research area. Leaf traces in their branch have a similar size to those in S. xinjiangensis nov. sp. Third, branch trace commonly has a much larger size than that of a leaf trace (Falcon-Lang and Cantrill, 2001; Shi et al., 2017). It also exhibits a concentric outer layer of secondary xylem, which do not occur in leaf trace (Falcon-Lang and Cantrill, 2001).

The secondary xylem of our wood is characterized by the mostly uniseriate araucarian pitting and helical thickenings on radial walls of tracheids. It is consistent with the genus Prototaxoxylon Kraüsel et Dolianiti (Kraüsel and Dolianiti, 1958; Pant and Singh, 1987). Fifteen species of Prototaxoxylon have been already described from the Pennsylvanian to the Jurassic (Shilkina, 1960; Gnaedinger, 2006; Wan et al., 2016b). Morphology and structure of pith and primary xylem are important in the classification of fossil wood (Lepekhina and Yatsenko-Khmelevsky, 1966; Lepekhina, 1972; Pant and Singh, 1987). Fossil woods with Prototaxoxylon-type secondary xylem and pith are commonly attributed to four genera including Taxopitys Kraüsel, 1928, Parataxopitys Maniero, 1951, Prototaxopitys Agashe, 1977, and Sclerospiroxylon (Prasad) emend. Zhang et al., 2007 (Kraüsel, 1928; Maniero, 1951; Agashe and Chitnis, 1971; Agashe, 1977; Prasad, 1982; Zhang et al., 2007). The occurrence of secretory cells and mesarch primary xylem in Taxopitys is different from the sclerenchyma and endarch to mesarch primary xylem in our fossil wood (Kraüsel, 1928). Parataxopitys is distinct from the current fossil wood in its exarch primary xylem (Maniero, 1951). Prototaxopitys has a homogeneous pith that differs from the heterogeneous pith in our fossil stem (Agashe and Chitnis, 1971; Agashe, 1977).

According to the structure of pith, primary and secondary xylem, our stem is assigned to Sclerospiroxylon (Prasad, 1982; Zhang et al., 2007), which has a secondary xylem of Prototaxoxylon type, endarch primary xylem, and heterogeneous pith with parenchyma and sclerenchyma. The type species S. marguerierae Prasad has vertical columns of sclerotic cells in the pith and 1–3 bordered pits in each cross-field (Prasad, 1982), whereas in our specimens, the sclerotic cells are grouped and distributed throughout the pith, and up to 7, commonly 2–4 bordered pits in each cross-field. S. neimongolense Zhang et al. from the Guadalupian Zhesi Fm. of Inner Mongolia has a pith morphology and structure similar to current materials (Zhang et al., 2007). However, its uni-to biseriate radial tracheid pitting is different from the mostly uniseriate pitting with partially biseriate pits on the radial walls of our wood. In addition, both S. marguerierae and S. neimengolense have uniseriate to biseriate pitting with circular, bordered pits on tangential tracheidal walls, which are absent in our wood. Based on the evidence and discussion mentioned above, we establish herein the new wood species S. xinjiangensis.

Fourteen Palaeozoic wood species within eight fossil genera have been documented so far from the Angaran palaeophytoprovince in northern China (Sze, 1934; Zhang and Zheng, 1984; Wang, 2000; Zhang et al., 2007; Zheng et al., 2008; Shi et al., 2014; Wan et al., 2014, 2016b, 2017a; Wei et al., 2016; Table 1). Most of them were collected from the Guadalupian and Lopingian. Six species have pith, primary and secondary xylem (Sze, 1934; Zhang et al., 2007; Shi et al., 2014; Wan et al., 2014, 2017a; Wei et al., 2016). S. xinjiangensis nov. sp. differs from all these fossil woods but S. neimengolense in the occurrence of sclerenchyma in the pith and helical thickenings on the tracheid walls of secondary xylem. The record of S. xinjiangensis nov. sp. provides additional information of biological diversity in the Permian of the Angara flora.

Late Palaeozoic tree trunks of substantial size that preserved a broad pith and pycnoxylic secondary xylem are widely reported across Angara, Cathaysia, Euramerica and Gondwana (e.g., He et al., 2013; Kurzawe et al., 2013a, 2013b; Falcon-Lang et al., 2014; Wan et al., 2014, 2016c, 2017c). Such fossils are mostly assigned to either cordaitalean or conifers (Wang et al., 2003; Hilton et al., 2009a, 2009b; Falcon-Lang et al., 2014). One of the characteristics of S. xinjiangensis nov. sp. is the occurrence of grouped sclerenchyma throughout the pith. Pith with sclerotic cells is common in extinct and extant conifers and in some pteridosperms (Doubinger and Marguerier, 1975; Galtier et al., 1992). Branches of the Late Pennsylvanian walchian Voltziales, such as Barthelia Rothwell et Mapes 2001, Emporia Mapes et Rothwell 2003, and Hanskerpia Rothwell et al., 2005, are documented possessing a pith with sclerotic nests (Rothwell and Mapes, 2001; Rothwell et al., 2005; Hernandez-Castillo et al., 2009a, 2009b, 2009c). Trunks that specifically show sclerotic cells in the pith have never been observed in Palaeozoic cordaitalean axes (Falcon-Lang et al., 2014).

Table 1
Comparisons among gymnospermous wood species from the Angara Flora in China.

| Species | Pith | Primary xylem | Secondary xylem | | | Type locality, horizone and age | References |
|---|---|---|---|---|---|---|---|
| | | | Pits on radial walls | Xylem rays | Cross-field pits | | |
| Sclerospiroxylon xinjiangensis nov. sp. | Solid and heterocellular, with parenchyma and scretory ducts – | Endarch and mesarch | Araucarian, uniseriate to tetraseriate | Uniseriate, 2 to 10 cells high cross-field | Cupressoid, commonly 2–4, up to 7 pits in each Xi Ujimqin Qi, Inner Mongolia; | Tarlong, Turpan, Xinjiang; Hongyanchi Fm.; Kungurian | This work |
| Agathoxylon sp. B | | | | Aarucarioid, 3–4 small pits 3–6 oval or circular | Zhexi Fm.; Guadalupian | Wan et al., 2017a | |
| Chapmanoxylon teilhardii Sze emend. Wang | Solid and heterocellular with parenchyma and sclereids Solid and heterocellular, with parenchyma, scretory ducts and sclerenchyma – | – | | non-bordered pits 4–12 bordered pits | Dalongkou, Jimsar, Xinjiang; | Wan et al., 2016b | |
| Chapmanoxylon xiuqiense Zhang et al. | | | Pits commonly uniseriate, rarely biseriate (alternate), contiguous, circular to elliptical; tangential pits uniseriate; spiral thickenings present | Cupressoid, 2–8 pits | Wutonggou Fm.; Wuchiapingian | | |
| Cordaioxylon houtoumiaoense Zhang et Zheng emend. Wang | | | | | Dalongkou, Jimsar, Xinjiang; | Wan et al., 2014 | |
| Ductoagathoxylon jimsarensis Wan et al. | | Endarch | Araucarian, uniseriate to biseriate, rarely triseriate | Aarucarioid, 5–22, mostly 6–12 pits | Wutonggou Fm.; Wuchiapingian | Zhang et al., 2007 | M. Wan et al. / Geobios 52 (2019) 85–97 |
| Prototaxoxylon uniseriale Prasad | Endarch and Araucarian, commonly uniseriate, mesarch partially biseriate, with taxinean | – | Araucarian, uniseriate to pentaseriate, bearing taxoid type third spiral thickenings | 1–2 circular–oval pits with faint borders | Turpan, Xinjiang; Wutonggou Fm.; Wuchiapingian | Zhang et al., 2007 | |
| | | Endarch | Araucarian, uniseriate to biseriate | | | Shi et al., 2014 | |
| Septomedullopitys sezi Wan et al. | | Endarch | Araucarian, uniseriate to pentaseriate | Simple, 1–2 pits | Sunite Zuo Qi, Inner Mongolia; | | |
| Sinopalaeospiroxylon baoligemiaoense Zhang et al. | | – | | Cupressoid or taxoid, 1 to 9 pits | Baoligemiao Fm.; Pennsylvanian | Zhang et al., 2007 | |
| | | | Araucarian, uniseriate to pentaseriate | | Xi Ujimqin Qi, Inner Mongolia; Zhexi Fm.; Guadalupian | | |
| Sclerospiroxylon neimongolense Zhang et al. | | Uniseriate, 2–14 cells high | | Cupressoid, 2 to 5 pits | | | |
| Xinjiangoxylon turpanense Shi et al. | | Uniseriate, 4–8 cells high Uniseriate, 1–6 cells high Uniseriate, 1–10 cells high Uniseriate, locally biseriate, up to 20 cells high | | Simple, 1–2 pits | Turpan, Xinjiang; Guodikeng Fm.; Changhsingian | | |
| Zalesskioxylon zhesiense Zhang et al. | – | tertiary spiral thickenings Uniseriate, up to 12 cells high | Araucarian, uniseriate to tetraseriate | Simple, 1–4 pits | Xi Ujimqin Qi, Inner Mongolia; | | |
| Solid, heterocellular with parenchyma, and grouped sclerenchyma – | Endarch | Uniseriate, 1–10 cells high | Araucarian, usually biseriate, occasionally triseriate | Hami, Xinjiang; Quanzijie Fm.; Guadalupian | Zhexi Fm.; Guadalupian | Wei et al., 2016 | |
| Solid, homocellular with parenchyma | Endarch | Araucarian, uniseriate to pentaseriate | | Urumchi, Xinjiang; Permian | | Sze, 1934; Wang, 2000 | |
| Solid, heterocellur with parenchyma – | – | Mixed, uniseriate to tetraseriate | Uniseriate to biseriate, up to 50 cells high Uniseriate to triseriate, 1 to 19 cells high Uniseriate, 1 to 25 cells high | Xi Ujimqin Qi, Inner Mongolia; Zhexi Fm.; Middle Permian | | Zhang and Zheng, 1984; Zhang et al., 2007 | |
| Solid and heterocelluar, with parenchyma, peripheral and grouped secretory ducts and cells – | | Uniseriate, 1 to 16 cells high | | | | Zhang and Zheng, 1984 | |

Arborescent seed ferns also exhibit a broad circular parenchymatous pith surrounded by a eustelic primary vascular system with numerous sympodial strands, and a thick development of wood (Galtier and Meyer-Berthaud, 2006). Compared to coniferous woods, pteridosperms commonly have higher and wider rays, and larger tracheid sizes (Galtier, 1988, 1992; Galtier and Meyer Berthaud, 2006). In addition, helical thickenings on secondary xylem tracheid walls have never been documented in pteridosperms. This specific anatomical feature is also found in the living Taxus and other conifers, especially in the Pinaceae (Zhang et al., 2007). Grouped sclerenchyma in the pith and helical thickenings on tracheidal walls of secondary xylems clearly distinguish S. xinjiangensis nov. sp. from other Palaeozoic pycnoxylic groups except for conifers. The affinity of S. xinjiangensis nov. sp. remains uncertain, due to the lack of knowledge about the type of leaves and reproductive structures that this stem bore. Compared to trunks and branches of fossil and living lignophytes, it shows a greatest similarity with conifers. Therefore, S. xinjiangensis nov. sp. is tentatively regarded to be of coniferous affinity.

## 5. Palaeoecological considerations

Presence of growth rings in S. xinjiangensis nov. sp. provides evidence for seasonal variations of local climate. Growth rings in S. xinjiangensis nov. sp. are characterized by very narrow late wood and higher proportion of early wood. This type of growth ring with lower percentage of late wood has been used as an indicator of intensity of climatic seasonality (e.g., Creber and Chaloner, 1984; Ash and Creber, 1992). This fits with all other available evidence. Based on the sedimentological record, great climatic variability persisted during the deposition of the Hongyanchi Fm. during the Artinskian–Kungurian (Yang et al., 2010). A shift from humid to semiarid climate is evident due to the highly-mature stacked vertic Calcisols in the uppermost Hongyanchi Fm. (Yang et al., 2010), underneath which our fossil wood specimens were collected. In addition, dropstones in deep shales suggest that the lakes were seasonally frozen (Yang et al., 2010). Macrofossil plants are rarely recorded from the Kungurian in Turpan-Hami Basin. The sporadic palaeobotanical record, including Walchia sp., Paracalamites sp., Rufloria ex. gr. derzawinii, Prynadaepteris anthrisifolia and Noeggerathiopsis sp., in addition to palynological data, also suggest seasonal climatic conditions developed in the Turpan-Hami Basin during the Cisuralian (Liu and Yao, 1996a; IPEDXPA and NIGPAS, 2003). Therefore, S. xinjiangensis nov. sp. would have lived under a condition with a periodic climatic stress. In this setting, the unfavorable seasons produced by drought or low temperature would be the most likely trigger for cambial dormancy and growth ring formation.

In addition to external climatic factors, growth ring morphology is strongly driven by endogenous influences (Falcon-Lang, 1999a, 1999b, 2000a, 2000b; Falcon-Lang and Cantrill, 2000, 2001). According to the observations of modern (Tomlinson, 1980; LaMarche et al., 1982) and fossil (Kumagai et al., 1995) evidence, it has been proposed that growth ring boundary markedness may not only be influenced by the intensity of climatic seasonality, but also be controlled by leaf longevity (Falcon-Lang, 1999b, 2000a, 2000b). In four specimens of S. xinjiangensis nov. sp., leaf traces with scalariform or reticulate thickened tracheids are found. They are persistent and commonly extending no less than 6 growth ring increments. One of them passes through ca. 15 ring increments before disappearing out of the plane of the section (Fig. 4(A)). Assuming that growth rings were formed annually, the fossil leaf trace data indicate that S. xinjiangensis nov. sp. was evergreen with long leaf retention times, in excess of 15 years. In modern evergreen conifers, the presence of several cohorts of living leaves maintains sufficiently high plant hormone which controls vascular cambium activity to permit year-round wood production provided that environmental conditions (temperature and water availability) are favourable for growth (Oribe and Kubu, 1997). It is hypothesized that in trees with high leaf retention times, young tracheid cells in the cambial zone are able to expand to their full size until just before the end of the growing season when environmental factors begin to limit growth (Falcon-Lang and Cantrill, 2000). As a consequence, S. xinjiangensis nov. sp. from the Kungurian of Turpan-Hami Basin possesses growth rings with narrow late wood and relatively subtle ring boundaries also probably due to the great leaf longevity. Growing under a seasonal climate, S. xinjiangensis nov. sp. shows a specific adaptive strategy. An evergreen habit would be advantageous under such climatically limited circumstances, as it would permit photosynthesis to start as soon as moisture or temperature levels exceeded the necessary threshold. Modern temperate evergreen conifers are able to tolerate a wide range of environmental and climatic variability in several ways, including restriction of metabolic activities, dormancy and reduction of respiration and transpiration, rather than loss of actively respiring or transpiring tissues (Parker, 1963; Mooney, 1969; Chabot and Hicks, 1982), so it is probable that the Kungurian conifers had similar functions.

## 6. Conclusions

A new wood species name, S. xinjiangensis, is proposed for a gymnospermous stem collected from the Kungurian (lower Permian) Hongyanchi LC in the southern Bogda Mountains, northwestern China. Details of anatomy of this permineralized fossil stem add to our knowledge of the diversity of the Angaran flora in the poorly known mid-latitude northeastern Pangaea. Grouped sclerotic cells in the pith, and helical thickenings on the tracheidal walls of the secondary xylem indicate S. xinjiangensis nov. sp. woods are of coniferous affinity. Growth rings in S. xinjiangensis nov. sp. are interpreted to have formed in response to a highly seasonal climate. According to the evidence of vertic Calcisols and palynological data, growth rings in S. xinjiangensis nov. sp. very likely have formed during the cool winter and dry season. Long leaf traces passed through up to 15 ring increments before disappearing suggest that S. xinjiangensis nov. sp. may have been produced by an evergreen tree, and maintained leaves for a relatively long time. The low percentage of late wood in growth rings in S. xinjiangensis nov. sp. was probably controlled by the intensity of climatic seasonality and/or influenced by the long leaf longevity.

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