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Amyelon bogdense sp. nov., a silicified gymnospermous root from the Changhsingian–Induan (?) in southern Bogda Mountains, northwestern China

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

[a] State Key Laboratory of Palaeobiology and Stratigraphy, Center for Excellence in Life and Paleoenvironment, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China [b] Geology and Geophysics Program, Missouri University of Science and Technology, Rolla, MO 65409, USA [c] Department of Palaeobotany and Palynology, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China [d] University of Chinese Academy of Sciences, Beijing 100049, China

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abstract

A silicified root, Amyelon bogdense Wan, Yang et Wang sp. nov., is described from the Changhsingian–Induan (?) Guodikeng Formation in south Taodonggou section, Turpan, Xinjiang Uygur Autonomous Region, northwestern China. The root consists of diarch protostele, primary xylem, secondary xylem, secondary phloem, and periderm. Primary xylem is exarch, with helical and scalariform thickenings on tracheidal walls. Secondary xylem is of the Agathoxylon-type, with alternately bi- to tetraseriate radial tracheidal pitting, uniseriate parenchymatous rays, and araucarioid cross-field pitting. Intercellular spaces occur between tracheids throughout the secondary xylem. Phloem is commonly compact. It is composed of radially aligned thick-walled cells, axial parenchyma and parenchymatous rays. Periderm consists of phelloderm, phellogen and phellem. Phelloderm cells are distributed external to the secondary phloem, with variable morphologies and sizes. Phellogen cells are commonly tabular and occasionally elongate. Phellem is distributed to the exterior of the phellogen, and is composed of 2–7, commonly 3–4 layers of radially arranged brick-shaped cells. Rootlets are elliptical to circular, less than 4 mm in diameter. Anatomical structures of rootlet are similar to those of the root. The arrangement of secondary xylem shows wedge-shaped spokes. Spaces between the secondary xylem spokes are either empty or filled with parenchyma. Some of the roots and rootlets have lenticel-like convex bodies. Lateral roots show no particular arrangement but appear to have been borne on only one side of the primary root. This is the first detailed report of the root anatomy with xylem and bark from the upper Paleozoic of the subangaran phytoprovince. The anatomical features differ from those of the previously studied stems in northwestern China, and provide additional information on the diversity of the subangaran flora.

1. Introduction

Root is a principal vegetative organ (Gifford and Foster, 1996), performing the function of anchorage, absorption and transport of minerals and water, and storage of photosynthate (Beck, 2010). Rooting structures are hypothesized to have evolved independently in all major groups of vascular plants during the Devonian (Raven and Edwards, 2001). Root anatomy and morphology of some representative genera from Paleozoic have been described (Williamson and Scott, 1894; Halket, 1932; Steidtmann, 1944; Beck, 1953; Cridland, 1964; Schopf, 1965, 1970, 1982; Rothwell and Whiteside, 1974; Rothwell, 1975; Russin, 1981; Li, 1986a, 1986b; Wang and Tian, 1993; Krings and Schultka, 2000; Decombeix et al., 2009). Although root anatomy reflects its origin, its subterranean environment, and its function (Beck, 2010), fossil roots have received much less attention than associated stems and reproductive organs (Raven and Edwards, 2001; Decombeix et al., 2009). One of the major reasons is that roots may be less readily fossilized than other vegetative organs.

* Corresponding author.
E-mail address: mlwan@nigpas.ac.cn (M. Wan).

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Amyelon (Williamson) Wang et Tian is one of the well-known Permo-Carboniferous roots that have been frequently reported since the nineteenth century. This genus is characterized by protostele or siphonostele with exarch primary xylem, secondary xylem with araucarian radial tracheidal pitting and two types of cross-field pitting, and occurrence of phloem and periderm (Williamson, 1874; Barnard, 1962; Cridland, 1964; Li, 1986a, 1986b; Wang and Tian, 1993). Amyelon was proposed to be referred to the family Cordaitaceae of Cordaitales due to its association with cordaitalean stems (Cridland, 1964). Whole-plant reconstructions of some cordaitalean plants from the Carboniferous and Permian coal balls supported the idea that this type of root has a cordaitalean affinity (Rothwell and Warner, 1984; Costanza, 1985; Trivett and Rothwell, 1985, 1988; Taylor, 1988; Stewart and Rothwell, 1993; Wang et al., 2003; Hilton et al., 2009a, 2009b). Although with a worldwide distribution, most species of Amyelon were reported from the tropical–subtropical Euramerica and Cathaysia, and rarely from the mid-latitude of Angara (Lepekhina, 1972).

Fossil woods are commonly found in the Paleozoic and Mesozoic in northwestern China (Zheng et al., 2008). Most previous researches on the permineralized materials have dealt with the stem (Zhang et al., 2007; Shi et al., 2014, 2017; Wan et al., 2014, 2016a, 2016b, 2016c, 2017a, 2017b, 2017c, 2018) and none with roots and their structures. In this contribution, we describe a new type of Amyelon from the Guodikeng Formation in the south Taodonggou section, southern Bogda Mountains, Xinjiang Uygur Autonomous Region, northwestern China. It is composed exclusively of diarch protostele with exarch primary xylem, Agathoxylon-type secondary xylem, secondary phloem and periderm. Rootlets of this species are unique with two radial wedge-shaped spokes. The anatomical structures of this new species contribute to a better knowledge of the fossil roots of gymnosperms.

2. Geological setting, material and methods

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 (Fig. 1, A, B; Yang et al., 2007, 2010; Obrist-Farner and Yang, 2015, 2016, 2017). The Tarlong–Taodonggou half graben, where the fossil roots were found, was located at the easternmost Kazakhstan Plate during the Permian (Fig. 1, C; Şengör and Natal'in, 1996; Ziegler et al., 1997; Scotese, 2001; Yang et al., 2010). It comprises the uppermost Carboniferous to Lower Triassic conglomerate, sandstone, shale, and minor limestone and volcanic rocks deposited in fluvial and lacustrine paleoenvironments (Yang et al., 2007, 2010).

All samples in this study were collected from the upper part of

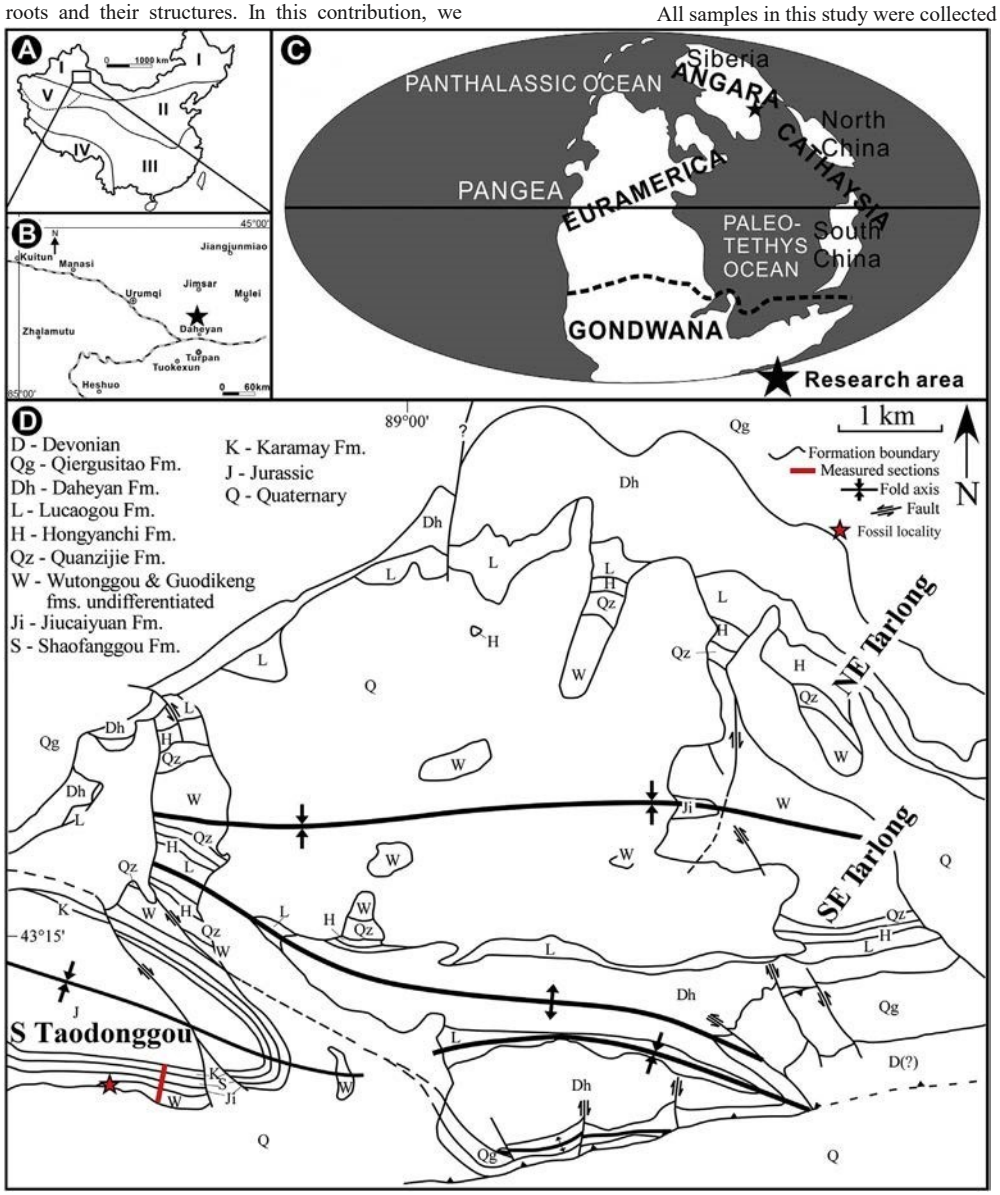


Fig. 1. Maps showing the location of study area. The late Permian phytogeoprovince map (A) is modified after Shen (1995); I – Angaran province in Junggar-Hinggan Region; II – Cathaysian provi (North China subprovince); III – Cathaysian province (South China subprovince); IV – Gondwana province; V –Angaran province in Tarim Plate. The collection site is shown by the black star in (which is in the Permian Angaran phytoprovince (Meyen, 1982, 1987; Sun, 1989). (C). Paleogeographic map of Pangaea during the Permian showing the fossil site (star) in the easternmost Kazakhs Plate at the mid-latitude NE Pangaea (Şengör and Natal'in, 1996; Ziegler et al., 1997; Scotese, 2001; Li et al., 2003), modifiedafter Scotese (2001). (D). Geological map of the Tarlong–Taodongg area in Turpan-Hami Basin, southern Bogda Mountains, showing the fossil collection site (red star), modified after Yang et al. (2010) and Obrist-Farner and Yang (2017). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Wutonggou low-order cycle in South Taodonggou section. The Wutonggou low-order cycle was defined by Yang et al. (2007, 2010) on the basis of long-term trends of interpreted depositional environments, tectonics and paleoclimatic conditions. The environments range from meandering stream, lacustrine deltaic, to lake margin; the climatic conditions are dominantly humid to subhumid; and the tectonic conditions are steadily subsiding (Yang et al., 2007, 2010; Thomas et al., 2011). The Wutonggou low-order cycle includes the Wutonggou and Guodikeng formations, and spans the Wuchiapingian, Changshingian and early Induan stages (XBGR, 1993; Cai, 1999; Yang et al., 2010). In a lithostratigraphic context, our fossil roots were collected from uppermost part of Guodikeng Formation. Previous biostratigraphy-based chronostratigraphy considered that the Guodingkeng Formation in northern Xinjiang could be diachronous, deposited during the Changhsingian to Induan (IGCAGS and IGXBGMR, 1986). During the last three decades, at least eight positions of Permian and Triassic boundaries within the Guodikeng Formation have been proposed on the basis of palynological, vertebrate zoological and geochemical data (IGCAGS and IGXBGMR, 1986; Ouyang and Norris, 1999; Hou, 2004; Li et al., 2003; Pang and Jin, 2004; Cao et al., 2008; Metcalfe et al., 2009; Kozur and Weems, 2011). In general, the exact Permian–Triassic boundary in Guodingkeng Formation of the research area is still controversial. Therefore, we assign the age of fossil roots described here as Changhsingian–Induan (?).

The description and discussion of anatomical features of the fossil roots in this study use the terminology of Richter et al. (2004), Evert (2006) and Angyalossy et al. (2016). A thin-section microscopic study of the roots indicates that they are well silicified. Thin section images were taken using a Leica DM5000 compound microscope and Leica DC 500 digital microscope camera system. The fossil roots and thin sections are stored in the Palaeobotanical Collection of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

3. Systematics

Division: Gymnospermae.

Genus:Amyelon Williamson emend. Wang et Tian, 1993.

Type species:Amyelon radicans (Williamson) Barnard, 1962.

Amyelon bogdense Wan, Yang et Wang sp. nov. (Plates I–VIII). Holotype: The specimen with catalog. PB 22881, and the slide PB 22881-1.

Paratype: The specimens with catalog. PB 22882–PB 22903, and the slides PB 22882-1 to PB 22903-1.

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

Type locality: South Taodonggou, Turpan, Xinjiang Uygur Autonomous Region, China.

Stratigraphic horizon: Guodikeng Formation.

Age: Changhsingian–Induan (?).

Etymology: The specific epithet refers to the specimens were collected, the Bogda Mountains.

Diagnosis: Root protostelic, bearing isolated or clusters of rootlets. Protostele diarch. Primary xylem exarch. Tracheids of primary xylem with helical and scalariform thickenings. Secondary xylem pycnoxylic, composed of radially arranged tracheids and parenchymatous rays. Tracheids rounded or polygonal, sometimes square in transverse section. Intercellular spaces present between tracheids. Radial pits uniseriate to tetraseriate, commonly triseriate, continuously and alternately arranged. Bordered pits circular to hexagonal in outline with rounded to oval apertures. Rays commonly uniseriate, rarely biseriate, 1–11 cells high, composed of procumbent parenchymatous cells. Cross-field pitting araucarioid-type. Each cross-field with 4–10, mostly 6–8 pits. Cross-field pits commonly circular, rarely oval, bordered with circular to elliptical apertures. Tangential tracheidal pits, axial parenchyma and ray tracheids absent. Secondary phloem composed of radially aligned thick-walled cells, axial parenchyma and parenchymatous

Plate I. Photographs showing the overview of the root axes of Amyelon bogdense sp. nov. from the Changhsingian–Induan (?) Guodingkeng Formation in South Taodonggou section, southern Bogda Mountains. (1). Transverse section of a fossil root axis, showing an elliptical shape with diarch stele (white arrows), secondary xylem (SX), and the bark (B). Black arrows point to three lateral root traces distributing only on the right side of the root. PB 22881-1; holotype. (2). Transverse section of a fossil root, showing the elliptical axis composed of diarch stele (white arrows), secondary xylem (SX), and the bark (B) without growth rings. PB 22882-1; paratype.

rays. Phelloderm composed of parenchymatous cells with rounded, polygonal and elongated shape, and in variable sizes transversely and radially. Phellem composed of regular, brick-shaped parenchymatous cells, forming a continuous layer around the outermost of root axis. Rootlet protostelic, with diarch protostele, exarch primary xylem, pycnoxylic secondary xylem, phloem and periderm. Secondary xylem arranging as two wedge-shaped spokes. Spaces between spokes empty or filled with parenchyma.

4. Description

Roots are abundant, and preserved in the sandstones without a particular orientation. They are preserved as either isolated roots with/ without lateral root traces (Plate I, 1, 2) or clusters composed of 2–5 axes (Plate II, 1, 3, 4, 5). Lateral root traces show an irregular arrangement but appear to have been borne on only one side of the primary roots (Plate I, 1). Traces of lateral root commonly occur in the bark (Plate VI, 5).

Individual roots are commonly irregularly elliptical in transverse section (Plate I, 1, 2). They range from 8 × 4 mm to 14 × 8 mm in area. Their primary vascular cylinder is protostelic, elongate in shape, with exarch protoxylem. Roots exhibit all their tissues preserved: primary xylem, secondary xylem, secondary phloem, phelloderm, phellogen and phellem. Bark including the tissues outside of the secondary

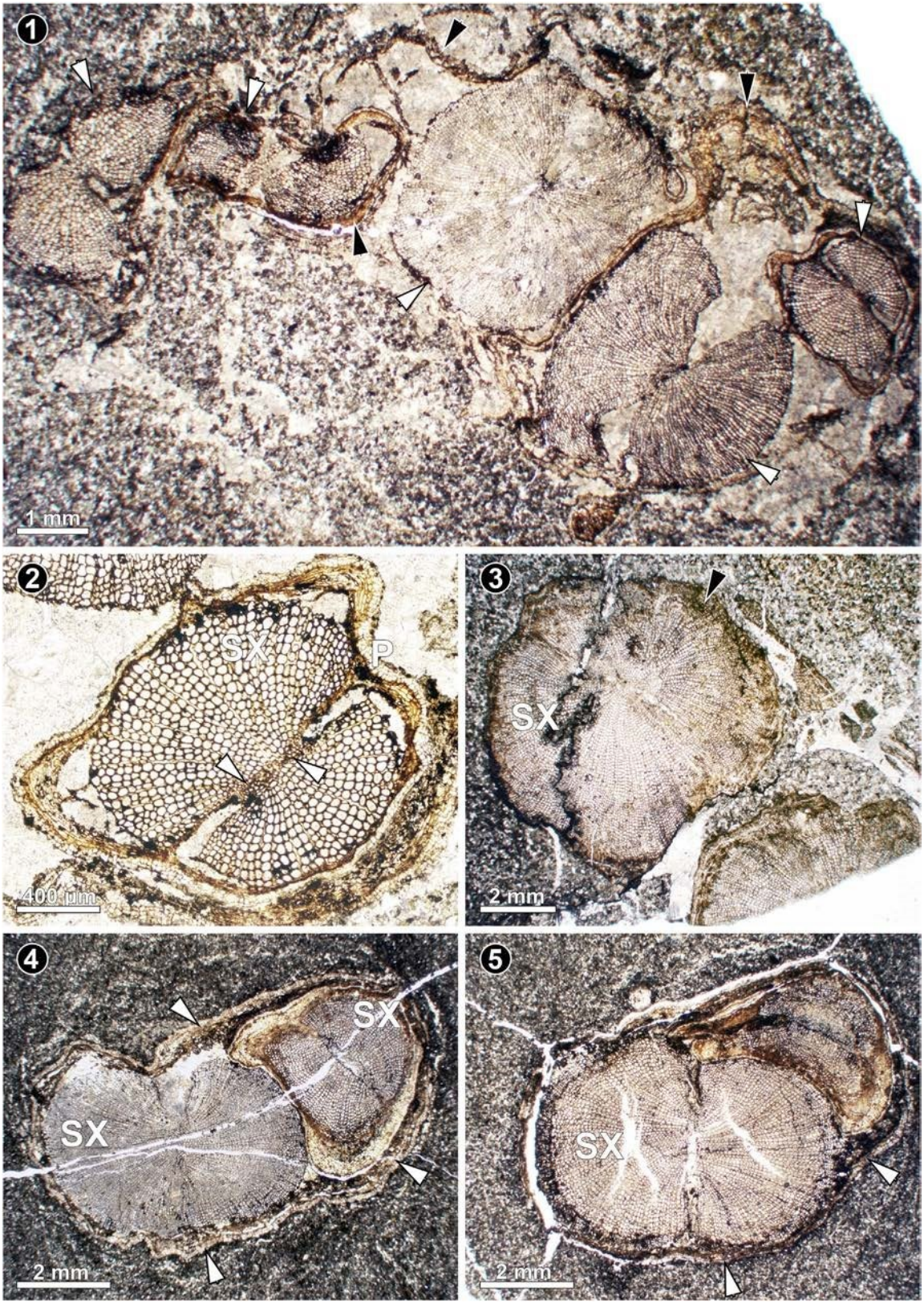


Plate II. Photographs showing rootlets of Amyelon bogdense sp. nov. from the Changhsingian–Induan (?) Guodingkeng Formation in South Taodonggou section, southern Bogda Mountains. (1) Transverse section of clusters of rootlets, showing five individual rootlets (white arrows) bundling by the periderm (black arrows). PB 22883-1; paratype. (2) Transverse section showing an enlargement picture of one rootlet with diarch stele (white arrows), secondary xylem (SX), and the periderm (P). The secondary xylem shows two wedge-shape spokes. Spaces between spokes are empty. PB 22883-1; paratype. (3) Transverse section showing a rootlet with a rounded shape (black arrow). PB 22884-1; paratype. (4) Transverse section showing two rootlets are bundling by the periderm (white arrows). PB 22885-1; paratype. (5) Transverse section showing two rootlets are bundling by the periderm (white arrows). PB 22886-1; paratype.

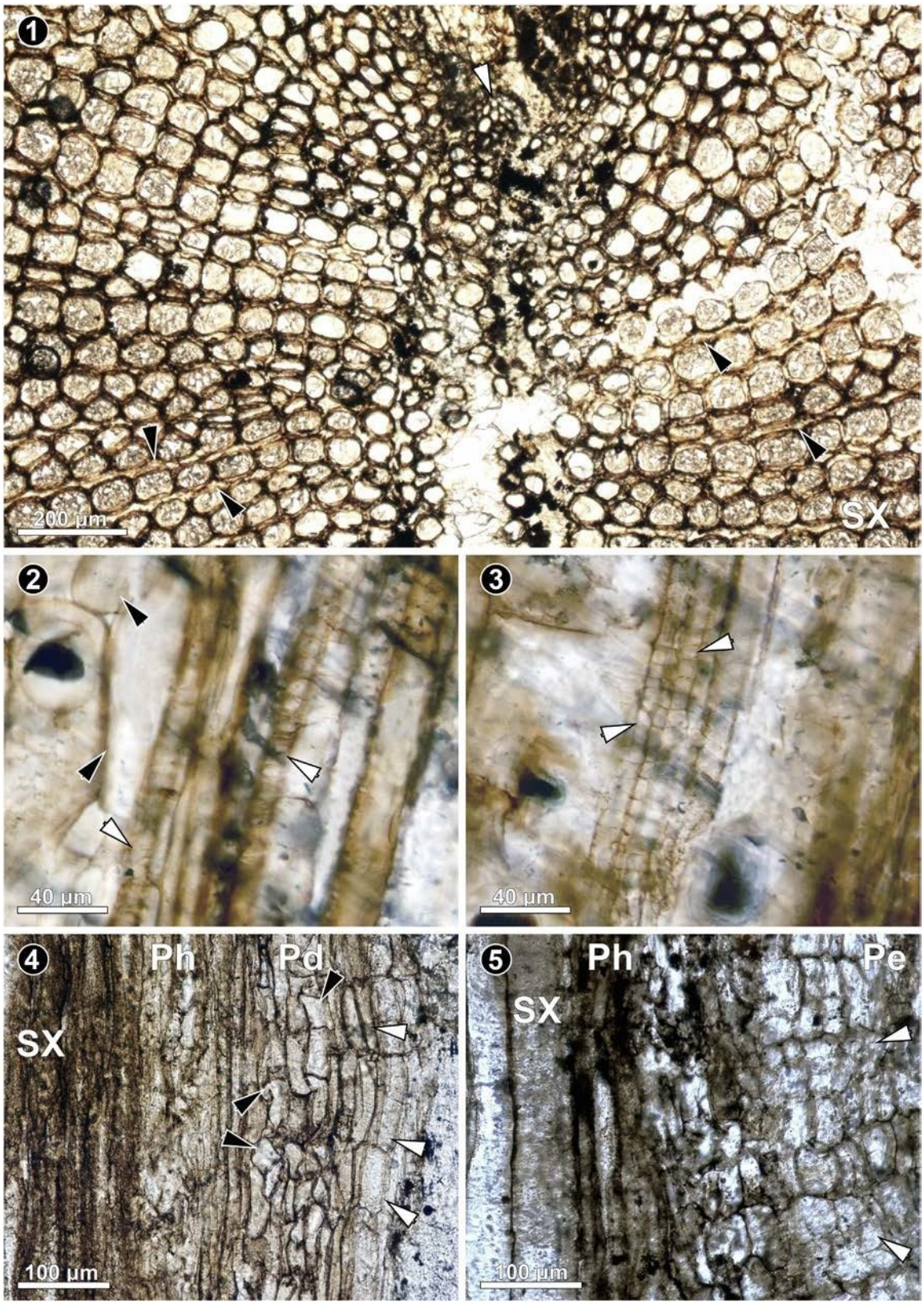


Plate III. Anatomical structures of Amyelon bogdense sp. nov. from the Changhsingian–Induan (?) Guodingkeng Formation in South Taodonggou section, southern Bogda Mountains.
(1) Transverse section of a root, showing the exarch primary xylem (white arrow), and the secondary xylem (SX) with parenchymatous rays (black arrows). PB 22886-1; paratype. (2) Radial section of a root, showing tracheids of primary xylem with helical thickenings (white arrows). Black arrows point to the neighboring parenchymatous cells probably from the spaces between secondary xylem spokes. PB 22887-1; paratype. (3) Radial section of a root, showing tracheids of primary xylem with scalariform thickenings (white arrows). PB 22887-1; paratype. (4) Radial section of a root, showing the distribution of secondary xylem (SX), secondary phloem (Ph), and phelloderm (Pd). Cells of phelloderm are variable in shape, ranging from polygonal (black arrows) to elongated (white arrows). PB

22888-1; paratype. (5) Radial section of a root, showing the distribution of secondary xylem (SX), secondary phloem (Ph), and phellem (Pe). Cells of phellem are brick-like and compactly arranged (white arrows). PB 22889-1; paratype.

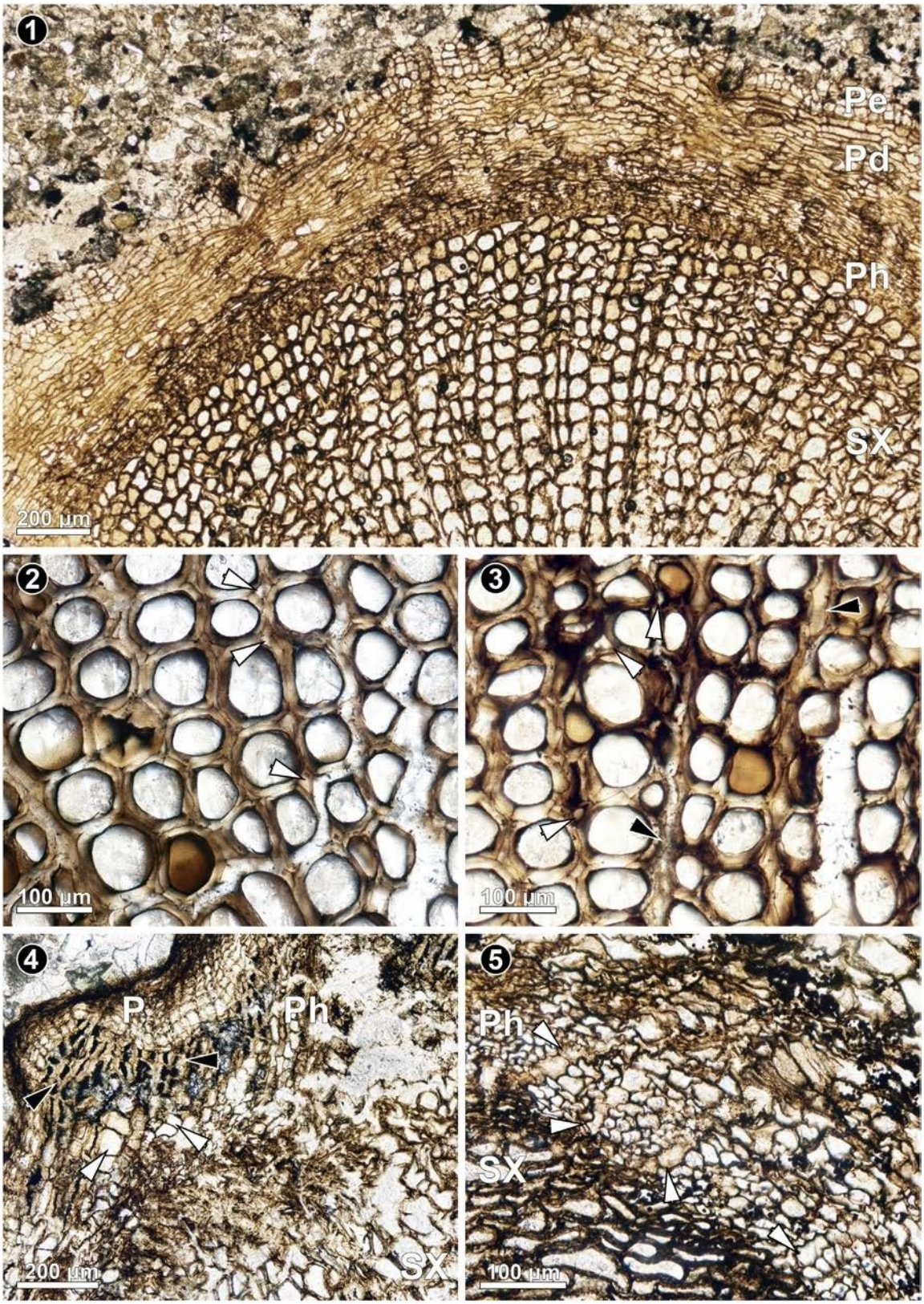


Plate IV. Anatomical structures of Amyelon bogdense sp. nov. from the Changhsingian–Induan (?) Guodingkeng Formation in South Taodonggou section, southern Bogda Mountains. (1) Transverse section of a root, showing the distribution of secondary xylem (SX), secondary phloem (Ph), phelloderm (Pd), and phellem (Pe). PB 22890-1; paratype. (2) Transverse section of a root, showing the shape of tracheids in the secondary xylem. White arrows point to the intercellular spaces between tracheids. PB 22891-1; paratype. (3) Transverse section of a root, showing tracheids with

intercellular spaces in the secondary xylem (white arrows). Black arrow point to parenchymatous cells. PB 22891-1; paratype. (4) Transverse section of a root, showing the distribution of secondary xylem (SX), secondary phloem (Ph), and periderm (P). White arrows point to the phloem parenchymatous cells. Black arrows point to cells in secondary phloem with opaque contents. PB 22892-1; paratype. (5) Transverse section of a root, showing the secondary xylem (SX), and the secondary phloem (Ph) with phloem rays (white arrows). PB 22893-1; paratype.

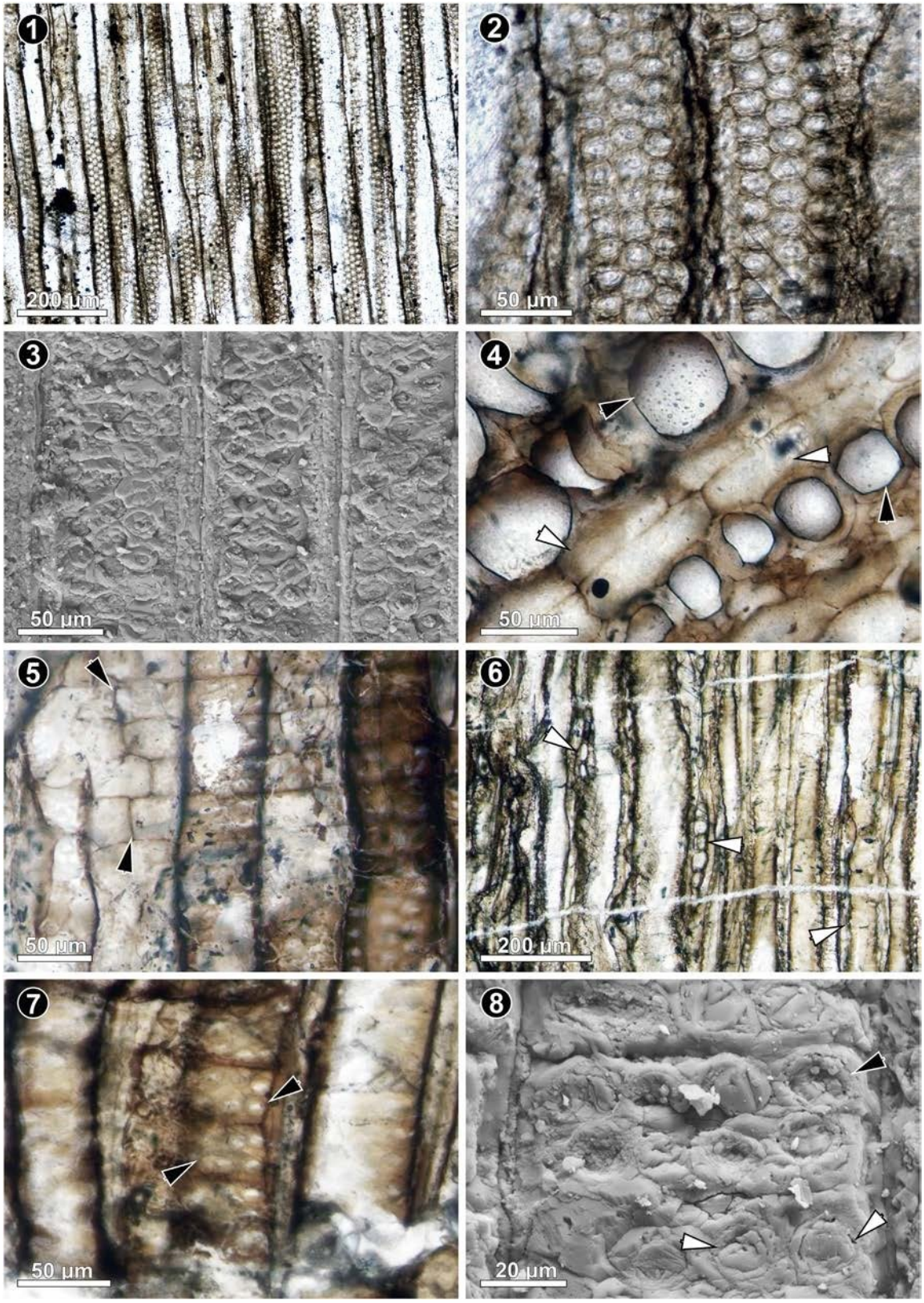
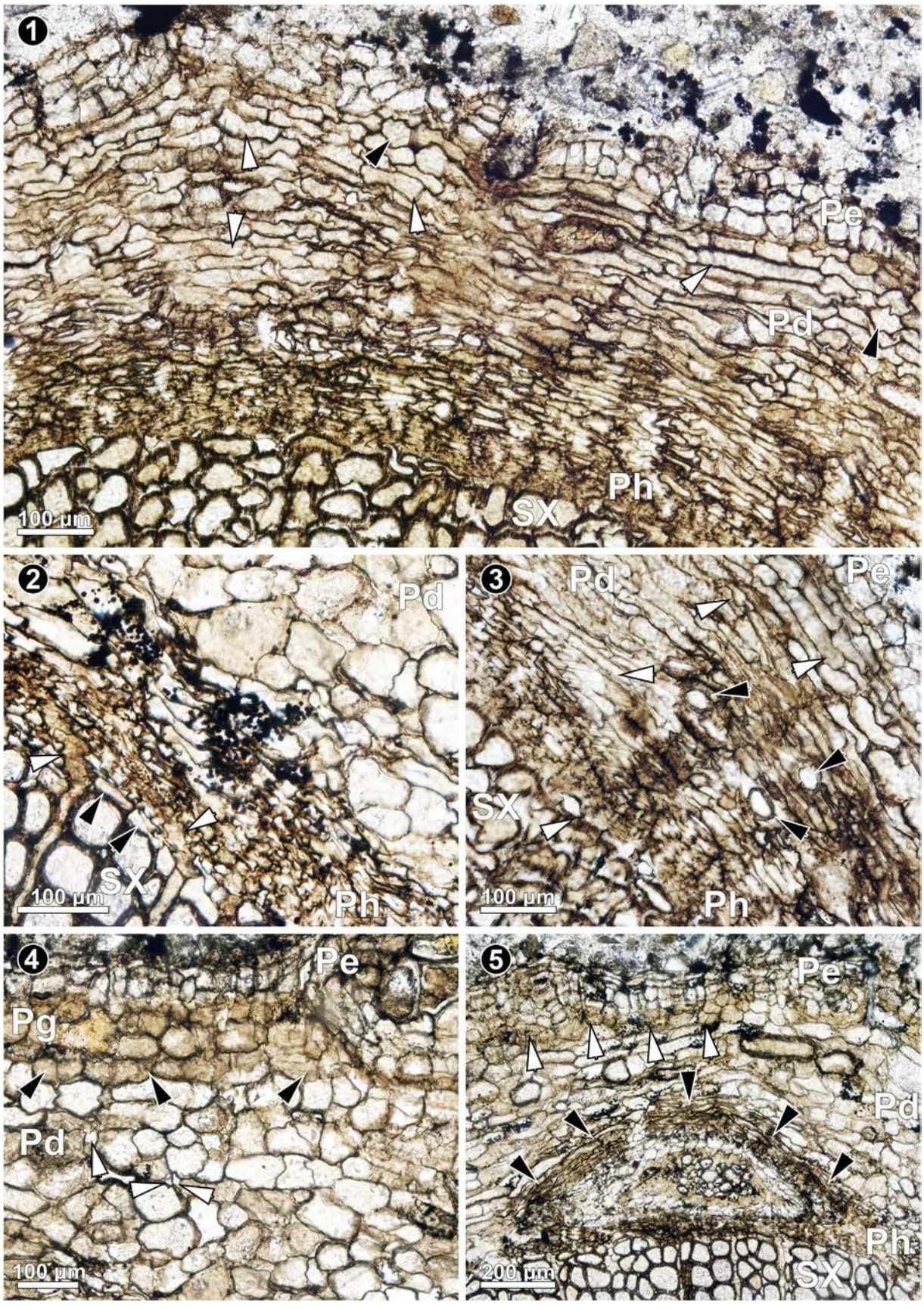


Plate V. Anatomical structures of Amyelon bogdense sp. nov. from the Changhsingian–Induan (?) Guodingkeng Formation in South Taodonggou section, southern Bogda Mountains. (1) Radial section of the secondary xylem, showing bi- to tetraseriate pitting on tracheidal walls. PB 22888-2; paratype. (2) Radial section of the secondary xylem, showing a detailed triseriate tracheidal pitting on tracheidal

walls. PB 22888-3; paratype. (3) Photomicrograph (SEM) of a radial section of the secondary xylem, showing a detailed triseriate tracheidal pitting on tracheidal walls. PB 22894; paratype. (4) Transverse section of the secondary xylem, showing the biseriate parenchymatous ray cells (white arrows) spanning two to four tracheids (black arrows). PB 22891-1; paratype. (5) Radial section of the secondary xylem, showing rectangular ray cells with very thin and smooth walls. White arrows points to vertical walls that are perpendicular to horizontal walls of the rays. PB 22895-1; paratype. (6) Tangential section of the secondary xylem, showing uniseriate rays. PB 22896-1; paratype. (7) Radial section of the secondary xylem, showing the araucarioid-type cross-field pitting. Black arrows point to pits arranged in two horizontal rows. PB 22894-1; paratype. (8) Photomicrograph (SEM) of a radial section of the secondary xylem, showing eight bordered pits in one field (black arrow) and three bordered pit (partially) in the adjacent field (white arrows). PB 22897; paratype.


1
Pe
Pd
Ph
SX
100 μm
2
Pd
SX
100 μm
Ph
3
Pd
Pe
SX
100 μm
Ph
4
Pe
Pg
Pd
100 μm
5
Pe
Pd
Ph
SX
200 μm

xylem is commonly compact forming a brown-colored band around the There are two exarch protoxylem poles in each root axis (Plate I, 1, 2; root axis (Plate I, 1, 2). Plate III, 1). The primary xylem either touches the secondary xylem or separates by several rows of parenchymatous cells (Plate III, 1, 2).

Tracheids of primary xylem are 6–32 μm in diameter. In longitudinal sections, tracheidal walls of primary xylem have helical and scalariform thickenings (Plate III, 2, 3).

The secondary xylem is composed of tracheids and parenchymatous rays. True growth rings are absent but growth interruptions (sensu Falcon-Lang, 2003) faintly occur. Tracheids are polygonal to circular in transverse section (Plate IV, 1, 2, 3). The radial diameters of tracheids vary from 30 to 107 μm (Plate IV, 2, 3). Tracheid walls are about 8–22 μm thick. Bordered pits on radial tracheidal walls are circular to hexagonal, contiguous, and with circular to oval apertures, bi- to tetraseriate, commonly triseriate (Plate V, 1, 2, 3). They are mostly alternately arranged. Intercellular spaces occur between tracheids throughout the secondary xylem (Plate IV, 2, 3). They are commonly polygonal to oval, and 5–11 μm in diameter. Rays are homogeneous and commonly uniseriate (Plate IV, 3; V, 6), rarely biseriate (Plate V, 4). They are 15–50 μm wide in transverse section (Plate IV, 3; V, 4). In radial section, parenchymatous ray cells are rectangular and range from 80 to 220 μm long and 20–45 μm high (Plate V, 5). Each ray cells spans 2–5, commonly 3–4 tracheids (Plate V, 4, 5). Cell walls of ray parenchyma are thin and sooth (Plate V, 4, 5). Rays are 1–11 cells high (Plate V, 6), and 5 cells high on average (n = 300). The cross-field pitting is araucarioid (sensu Richter et al., 2004). There are 4–10, mostly 6–8 pits in each cross-field (Plate V, 7, 8). Cross-field pits are oval to circular, bordered with circular to elliptically oval apertures, and commonly arranged in 2–3 horizontal rows.

Phloem is commonly compressed with crushed cells (Plate I, 1, 2). Primary phloem and vascular cambium have not been preserved. In a few well-preserved specimens, the secondary phloem is discernible (Plate IV, 1, 4, 5). It consists of radially aligned thick-walled cells, axial parenchyma and parenchymatous rays (Plate IV, 4, 5; VI 1, 2, 3, 4, 5). In transverse section, some crushed thick-walled cells are filled with opaque contents (Plate IV, 4). Other hollow thick-walled cells are presumed sieve cells due to their circular shape, but no sieve areas have been identified from both transverse and radial sections (Plate VI, 3). Axial phloem parenchymatous cells are commonly quadrangular to polygonal in transverse section (Plate IV, 3, 4). Phloem rays are dilated, continuous with the relatively narrower xylem rays (Plate IV, 4; VI, 2).

Periderm presents the phelloderm, phellogen and phellem (Plate VI, 1). Phelloderm is cells of variable in morphology and size in transverse section (Plate VI, 1, 2, 3). They are polygonal, circular, oval and elongated, and 10–120 μm in diameter. Elongated phelloderm cells are ranging from 20 × 5 μm to 175× 25 μm in area. In transverse section, phelloderm cells have numerous intercellular spaces among them (Plate VI, 4). In longitudinal section, phelloderm cells are both elongated and polygonal (Plate III, 4, 5). The thickness of phelloderm varies from 8 to 22 cell layers. In transverse section, phellogen consists of a few layers of thin-walled cells with a reduced radial diameter (Plate VI, 4, 5). Cells of phellogen are commonly tabular and occasionally elongate. Phellem is composed of 2–7, commonly 3–4 layers of radially arranged parenchymatous cells. Cells of phellem are commonly regular, brick-shaped, and densely arranged in transverse section (Plate VI, 1, 4, 5). In longitudinal section, they are prismatic and regular in size and shape (Plate III, 5).

Clusters of two to five rootlets are preserved as bounded by the same periderm band (Plate II, 1, 3, 4, 5). Rootlets are variably irregular in gross morphology, including circular (Plate II, 3) and elliptical (Plate II, 4, 5). The diameter of the circular rootlet is up to 7 mm (Plate II, 1, 3). Long axes of elliptical rootlets are ranging from 2 to 8 mm, and short axes are varying from less than 1 to 5.5 mm. Isolated rootlets are commonly elliptical, vary from 2.5 × 1.2 mm to 4.5 × 3 mm in size (Plate VII, 1, 2, 3). Rootlets are composed of primary xylem, secondary xylem, secondary phloem, phelloderm, phellogen and phellem, resembling to that of large roots (Plate VII, 1, 4). Primary xylem is protostelic, diarch and exarch (Plate VII, 1, 2, 3, 4). Secondary xylem consists of tracheids and parenchymatous rays. The arrangement of secondary xylem shows wedgeshaped spokes. Spaces between the secondary xylem spokes are commonly empty (Plates II, 1, 2; VII, 2, 3) but, in rare cases, these spaces are filled with parenchymatous cells. (Plate VII, 1, 4). These parenchymatous cells are connected to the primary xylem directly to the internal, and associated with phelloderm to the external (Plate VIII, 1, 4). Commonly, cells of the phloem are not preserved, leaving cavities between the secondary xylem and periderm (Plates II, 2; VII, 1).

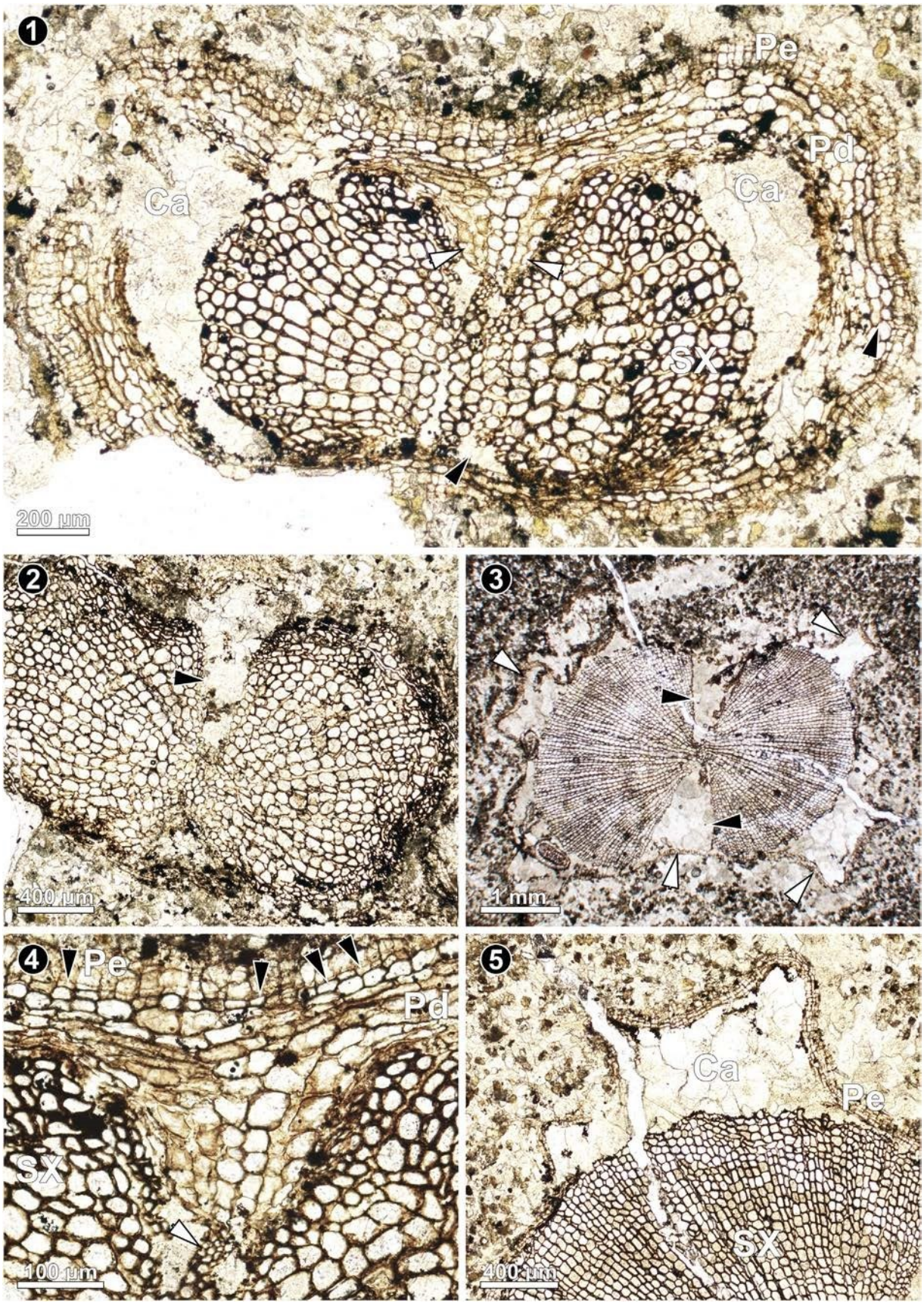
Some of the roots and rootlets show that the phellem has an irregular outline in transverse section, forming distinct convex bodies (Plates VII, 3, 5; VIII, 1, 2, 3). The convex bodies are commonly filled with secondary phloem and periderm cells (Plate VIII, 2, 3). They are about 1–2 mm wide at the base, and narrowing outward. Occasionally, convex bodies are quadrangular (Plate VII, 3, 5). Cells of secondary phloem in the convex bodies are highly extruded and distorted (Plate VIII, 3), or have not been preserved, leaving an empty space bounded by the phellem (Plates VII, 3, 5; VIII, 4, 5).

5. Comparison and discussion

Amyelon was erected for a Pennsylvanian root from coal balls by Williamson (1874) without a diagnosis. After examining Williamson's type slides and making slides of the topotype, Barnard (1962) first proposed a diagnosis for this genus, and assigned Amyelon radicans (Williamson) Barnard as the type species. However, in this diagnosis, Barnard (1962) emphasized the structure of the protostelic primary xylem and the secondary xylem with araucarian radial tracheidal pits and araucarioid cross-field pitting, and did not mentioned structures of the bark which were described in detail by Williamson (1874). The generic diagnosis of Amyleon has been emended several times with the accumulation of materials from the upper Paleozoic on different continents (Cridland, 1964; Li, 1986a; Wang and Tian, 1993; Wang et al., 2003). Based on the comprehensive study of materials from American Pennsylvanian coal balls, Cridland (1964) recombined Premnoxylon iowense Pierce et Hall to Amyelon iowense (Pierce et Hall) Cridland with a combination of aerenchyma, lenticels, periderm and medullated protosteles. Cridland (1964) added the characteristics of the cambium, phloem, periderm and cortex of mature roots, and anatomical features of rootlets to the diagnosis of Amyelon. The cross-field pitting was changed to "uniseriate and oblique" (Cridland, 1964). Li (1986a) pointed out that there is a contradiction between the generic diagnosis and A. iowense. In the diagnosis, Cridland (1964) attributed the radial tracheidal pitting to triseriate to pentaseriate. However, A. iowense has a uniseriate to pentaseriate radial pitting (Cridland, 1964, p. 187, 190, pl. 34, fig. 6). In addition, the "uniseriate and oblique" cross-field pitting proposed by Cridland (1964) is inconsistent with the

Plate VI. Anatomical structures of Amyelon bogdense sp. nov. from the Changhsingian–Induan (?) Guodingkeng Formation in South Taodonggou section, southern Bogda Mountains. (1) Transverse section of a root, showing the distribution of secondary xylem (SX), secondary phloem (Ph), phelloderm (Pd), and phellem (Pe). Secondary phloem cells are highly compact. White arrows point to the elongate phelloderm cells. Black arrow points to the polygonal phelloderm cell. PB 22890-1; paratype. (2) Transverse section of a root, showing the secondary xylem (SX), compact secondary phloem (Ph), and the phelloderm (Pd) with polygonal cells. White arrows point to phloem rays are continuous with xylem rays. Black arrows point to the probable vascular cambium. PB 22898-1; paratype. (3) Transverse section of a root, showing the distribution of secondary xylem (SX), secondary phloem (Ph), phelloderm (Pd), and phellem (Pe). Black arrows point to the thick-walled cells in the secondary

phloem. White arrows point to the elongate cells in the phelloderm. PB 22899-1; paratype. (4) Transverse section of a root, showing the phelloderm (Pd), phellogen (Pg), and phellem (Pe). Phelloderm cells are polygonal with intercellular spaces (white arrows). Phellogen cells are rectangular or polygonal in outline (black arrows). PB 22898-1; paratype. (5) Transverse section of a root, showing the secondary xylem (SX), phelloderm (Pd), phellogen (white arrows), and phellem (Pe). A lateral root trace is present in the secondary phloem with a roughly triangular outline (black arrows). PB 22899-1; paratype.


1
Pe
Pd
Ca
Ca
SX
200 μm
2
400 μm
3
1 mm
4
Pe
Pd
SX
100 μm
5
Ca
Pe
SX
400 μm

feature present in the type species (Li, 1986a). Wang and Tian (1993) to the specimens from the Cisuralian of North China, Wang and Tian suggested that the cortex could be either sloughed off during the early (1993) and Wang et al. (2003) provided the evidence that periderm development of the root or maintained to the mature stage. According could originate from both the pericycle and the outer cortex. As a result,

Wang and Tian (1993) emended the general diagnosis. This diagnosis was repeated by Wang et al. (2003) and Hilton et al. (2009a). However, under this diagnosis, the cross-field pitting, like in Cridland's (1964) revision, was changed to "uniseriate and oblique" (Wang et al., 2003; Hilton et al., 2009a).

Cross-field pitting is an important taxonomic characteristic in extant (Richter et al., 2004) and fossil (Pant and Singh, 1987; Philippe and Bamford, 2008) gymnospermous woods. However, this characteristic is not always well documented in Paleozoic woods. In addition, various types of cross-field pitting have been described from some single specimens (Decombeix et al., 2009; Wan et al., 2017d). Thus, Decombeix et al. (2009) proposed that the systematic implications of cross-field pitting of Paleozoic woods could be rather equivocal. To date, eight species of Amyelon have been erected from the Carboniferous and Permian worldwide (Table 1). In each species of Amyelon, the cross-field pitting type is discernible, and different from those in Gondwana glossopterid root Vertebraria with variable types (Decombeix et al., 2009). As a consequence, it is proposed that cross-field pitting is one of the anatomical features, rather than the only one, for differentiating various species of Amyelon. In the revision of Amyelon, Barnard (1962, p. 214) described the cross-field pitting of the type species, A. radicans, as "cross-field pits 6–12, half-bordered, cupressoid". According to the latest definition by Richter et al. (2004), the cross-field pitting of A. radicans can be described as araucarioid. This type of cross-field pitting are also reported in A. bovius Barnard, A. equivius Barnard, A. permiense Lepekhina, A. protopityoides (Felix) Lepekhina and A. xui Li (Barnard, 1962; Lepekhina, 1972; Li, 1986b). Unlike the species mentioned above, Amyelon iowense has a simple cross-field pitting, with at least three pits arranged vertically in each field (Cridland, 1964). In general, there are two types of cross-field pitting in the species of Amyelon, including araucarioid and, small simple pits. Therefore, we suggest that the araucarioid cross-field pitting should be added into the generic diagnosis. The araucarioid cross-field pitting of A. bogdense with 4–10, mostly 6–8 bordered pits in each cross-field which are arranged in two horizontal rows, and is most comparable to those of A. radicans, A. permiense and A. xui (Barnard, 1962; Lepekhina, 1972; Li, 1986a, 1986b).

Amyelon bogdense is characterized by an exclusively diarch protostele. This feature makes it different from A. bovius, A. equivius, A. iowense, A. radicans and A. taiyuanense Wang et Tian which have more than two primary xylem poles (Barnard, 1962; Pierce and Hall, 1953; Cridland, 1964; Wang and Tian, 1993; Wang et al., 2003). Lepekhina (1972) described two species, A. protopityoides and A. permiense, from the Kuznetsk Basin of Russia, which belonged to the subangaran paleophytoprovince in the Permian (e.g., Meyen, 1987). Both have diarch primary xylems, araucarian radial pits, and araucarioid cross-field pitting, and lack of bordered pits on tangential walls of secondary xylem, which are similar to A. bogdense. Amyelon protopityoides has a secondary xylem comparable to Dadoxylon protopityoides Felix, which is characterized by one to eight rows of bordered pits alternately arranged on radial walls, and occasionally biseriate rays (Frentzen, 1931). Those are different from the bi- to tetraseriate radial tracheidal pitting and uniseriate rays in A. bogdense. Amyelon permiense differs from A. bogdense because the former has much more (up to 20) pits in each cross-field and lower (1–4 cells high) rays. The two species from the Permian of Russia, as well as A. bovius, A. equivius described by Barnard (1962) from the Mississippian of Scotland, are decorticated without any information of the phloem and periderm. Their absence of the bark prevents a further comparison with A. bogdense.

Amyelon iowense was originally described as Premnoxylon iowense by Pierce and Hall (1953). Phellem of A. iowense has an irregular outline with distinct convolutions, which was explained as lenticels (Cridland, 1964). Similar structures are also found in A. bogdense occurring occasionally and variably in shape. Amyelon iowense is characterized by the occurrence of a pith in the center of the root axis. Cridland (1964) pointed out that as the root grew in length, the protostele gave rise to a siphonostele by medullation of the metaxylem to form the pith. The protoxylem strands were retained at the margin of the pith where they lie adjacent to the secondary xylem. Therefore, Cridland (1964) recombined P. iowense to A. iowense with both protostele and siphonostele, which is distinguishable from A. bogense. In addition, the occurrence of aerenchymatous secondary phloem and phelloderm, and tangential tracheidal pitting in A. iowense makes it distinct from A. bogdense.

Amyelon taiyuanense was erected based on the materials of coal balls from the Cisuralian upper Taiyuan Formation in North China (Wang and Tian, 1993; Wang et al., 2003). It has a di- to tetrarch protostele which is different from the diarch protostele of A. bogdense. Cross-field pitting of this species has not been described. Its cortex could remain in large and mature root, whereas the cortex in A. bogdense commonly sloughs off during the development of periderm. Periderm of A. taiyuanense is generated from both pericycle and the periphery of the cortex, which is dissimilar to the deep origin of the periderm in other species of this genus including A. bogdensis. Li (1986a) described A. xui in coal balls from the Lopingian Wangjiazhai Formation in South China. The diarch protostele, exarch protoxylem, araucarian radial pitting, uniseriate rays, and araucarioid-type cross-field pitting in A. xui are comparable to those in A. bogdense. However, the occurrence of tangential tracheidal pitting and higher rays (up to 21 cells high) make this Cathaysian species distinguishable from A. bogdense.

One of the unique characteristics of Amyelon bogdense is the arrangement of secondary xylem into two radial wedge-shaped spokes in rootlets with diameters less than 4 mm (Plates II, 1, 2, 4; VII, 1, 2, 3). This feature has never been found in other species of Amyelon. Spaces between adjacent spokes are either filled with parenchymatous cells or empty. When present, parenchymatous cells are connected with the protoxylem directly to the internal, and are conjunct with the phelloderm to the external. The origination of these parenchyma is uncertain due to the limitation of material. Empty spaces that were named as lacunae by Decombeix et al. (2009) for the late Permian Antarctic Vertebraria roots, are common in our collections. Neish et al. (1993) found out Vertebaria root has two to nine spokes of secondary xylem, suggested that the formation of lacunae could be due to differential production of secondary xylem by the discontinuous vascular cambium. Parenchymatous cells in lacunae were disintegrated due to substantial structural pressure during the development of secondary growth, resulting in the empty spaces between the spokes of secondary xylem (Neish et al., 1993). This is probably the reason of the formation of empty spaces in A. bogdense. However, we cannot exclude the possibility that the transportation, chemical and fungal decaying, and feeding by herbivores may have formed the empty spaces. In larger roots with

Plate VII. Anatomical structures of Amyelon bogdense sp. nov. from the Changhsingian–Induan (?) Guodingkeng Formation in South Taodonggou section, southern Bogda Mountains. (1) Transverse section of a rootlet, showing an elliptical shape with diarch stele, exarch primary xylem, secondary xylem (SX), and the periderm composed of phelloderm (Pd) and phellem (Pe). Secondary xylem shows two wedge-shaped spokes. Spaces between the spokes are empty (black arrow) or filled with parenchymatous cells (white arrows). PB 229001; paratype. (2) Transverse section of a rootlet, showing an elliptical shape with two wedge-shaped spokes of secondary xylem. Spaces between the spokes are empty (black arrow). PB 22883-1; paratype. (3) Transverse section of a rootlet, showing an elliptical outline with two wedge-shaped spokes of secondary xylem. Spaces between the spokes are empty (black arrow). Phellem cells form irregular convex bodies to the external of secondary xylem (White arrows). Convex bodies are empty. PB 22901-1; paratype. (4) Transverse section of a rootlet, showing the exarch primary xylem (white arrow), secondary xylem (SX), and the periderm composed of phelloderm (Pd), phellogen (black arrows) and phellem (Pe). Spaces between the spokes are filled with parenchymatous cells. PB 22900-1; paratype. (5) Transverse section of a rootlet,

showing an empty polygonal convex body bundling by the phellem (Pe) to the external of secondary xylem (SX). Tissues between the secondary xylem and phellem are lost leaving empty cavities (Ca). PB 22901-1; paratype.

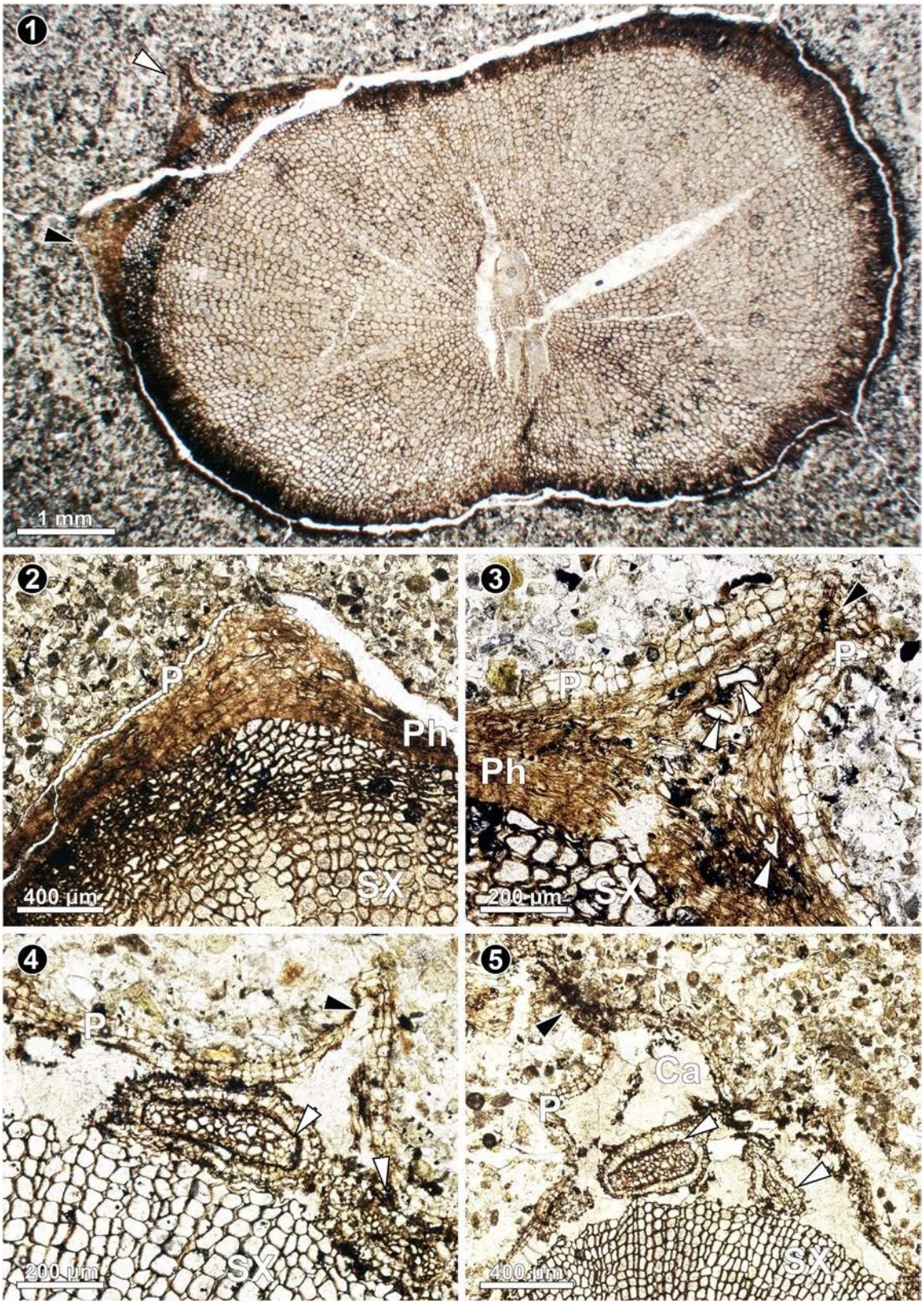


Plate VIII. Anatomical structures of Amyelon bogdense sp. nov. from the Changhsingian–Induan (?) Guodingkeng Formation in South Taodonggou section, southern Bogda Mountains.
(1) Transverse section of a root, showing an elliptical shape with two convex bodies (white and black arrows) to the external of secondary xylem. PB 22902-1; paratype. (2) Transverse section of a root, showing a detailed picture of secondary xylem (SX), highly compact secondary phloem (Ph), and periderm (P) with a convex body. PB 22902-1; paratype. (3) Transverse section of a root, showing a

detailed picture of secondary xylem (SX), highly compact secondary phloem (Ph), and periderm (P). White arrows point to thickwalled cells of the secondary phloem. Phellem cells form a horn-shaped convex body (black arrow). PB 22902-1; paratype. (4) Transverse section of a rootlet, showing a detailed picture of secondary xylem (SX) and phellem (Pe) with two lateral root traces (white arrows). Phellem cells form a horn-shaped convex body (black arrow). Tissues between the secondary xylem and phellem are lost leaving empty cavities. PB 22903-1; paratype. (5) Transverse section of a rootlet, showing a detailed picture of secondary xylem (SX) and phellem (Pe) with lateral root traces (white arrows). Phellem cells form an irregular convex body (black arrow). Tissues between the secondary xylem and phellem are lost leaving empty cavities (Ca). PB 22903-1; paratype.

Table 1
Comparison among the species of Amyelon Williamson emend. Wang et Tian.

Species	Primary xylem	Secondary xylem				Phloem	Periderm	Cortex	Type locality, horizon and age	References
		Radial pitting	Tangential pitting	Xylem rays	Cross-field pitting					
Amyelon bogdense sp. nov.	Exarch, diarch	Araucarian, bi- to tetraseriate, commonly triseriate, bordered pits rounded to hexagonal	Absent	Uniseriate, 1–11 cells high	Araucarioid, with 4–10, commonly 6–8 bordered pits in each field	Commonly compact; composed of thick-walled cells, axial parenchyma and parenchymatous rays	Composed of phelloderm, phellogen, and phellem; cells of phelloderm polygonal, rounded, oval and elongated in shape and variable in size; cells of phellem regular, brick-shaped, and radially and compactly arranged	Not preserved, probably slough off during the delevopment of periderm	South Taodonggou, Turpan, Xinjiang; upper Wutonggou Fm., Changhsingian to Induan (?)	The present paper
A. bovius Barnard	Exarch, tetrarch	Araucarian, bi- to tetraseriate, bordered pits hexagonal with horizontal oval apertures	Distant, scattered, rounded	Uniseriate, 1–38 cells high, mostly 1–3 cells high	Araucarioid, with 6–12 bordered pits in each field	Not preserved	Not preserved	Not preserved	Oxroad Bay, East Lothian, Scotland; Cementstone Group, upper Tournaisian	Barnard (1962)
A. equivius Barnard	Exarch, triarch	Araucarian, uni- to triseriate, bordered pits rounded and distant, with rounded apertures	Occassionally occurred, distant, scattered	Uniseriate, 1–9 cells high	Araucarioid, with 2–6 bordered pits in each field	Not preserved	Not preserved	Not preserved	Horse Roads Bay, Berwickshire, Scotland; Cementstone Group, upper Tournaisian	Barnard (1962)
A. iowense (Pierce et Hall) Cridland	Exarch, commonly tetrarch, sometimes triarch or diarch	Araucarian, uni- to pentaseriate	Occassionally occurred, uniseriate	Uniseriate, 1–8 cells high	Simple, with at least 3 pits arranging vertically in each field	Consisting of sieve elements, parenchyma, rays and fibers; outmost part of phloem aerenchymatous	Phelloderm extesive, aerenchymatous with long cells; phellem cells rectangular, tangentially elongated; lenticels present	Sloughed off during the delevopment of periderm	Ellis Mine, Mahaska County, Iowa; Desmoinesian, Pennsylvanian	Pierce and Hall (1953), Cridland (1964)
A. permiense Lepekhina	Exarch, diarch	Araucarian, uni- to tetraseriate	Absent	Uniseriate, 1–4 cells high, mainly 1–2 cells high	Araucarioid, with 4–20 bordered pits in each field	Not preserved	Not preserved	Not preserved	Kuznetsk Basin, Russia; Uskat River Fm., Lopingian	Lepekhina (1972)
A. protopityoides (Felix) Lepekhina	Exarch, diarch	Araucarian, with one to eight rows of bordered pits, alternately arranged	Absent	Commonly uniseriate, 1–10 cells high; rarely biseriate, 1–3 cells high	Type unknown, 2–7 pits in each field	Not preserved	Not preserved	Not preserved	Kuznetsk Basin, Russia; Usyatskoe Village Fm., Pennsylvanian-Cisuralian	Lepekhina (1972)

A. radicans (Williamson) Barnard	Exarch, diarch to tetrarch	Araucarian, bi- to pentaseriate, bordered pits rounded to hexagonal with oval and slightly inclined apertures	Distant, scattered, rounded	Uniseriate, 1–9 cells high	Araucarioid, with 6–12 bordered pits in each field	Compact	Phelloderm extesive and compact	Sloughed off during the delevopment of periderm	Pennsylvanian	Williamson (1874), Barnard (1962), Cridland (1964)
A. taiyuanense Wang et Tian	Exarch, diarch to tetrarch	Araucarian, bi- to hexagoseriate,	Absent	Uniseriate, 2–9 cells high	Not described	Composed of sieve elements, phloem parenchyma, phloem rays and fibers; thickness up to 0.8 mm	Composed of phelloderm, phellogen, and phellem; phelloderm cells irregularly arranged	Cortex divided into inner and outer part; inner cortex aerenchymatous and composed of plate collenchyma; cortex remaining in very large roots; exodermis existing at the periphery of the cortex	Xishan, Taiyuan City, Shanxi Province; Taiyuan Fm., Cisuralian	Wang and Tian (1993), Wang et al. (2003)

diameters greater than 4 mm, there are no wedge-shaped secondary xylem spokes. Therefore, it is hypothesized that immature A. bogdense consisted of wedges of wood separated by parenchyma, and became a complete cylinder of wood during its maturation. This growth process is comparable with that of Vertebraria described by Decombeix et al. (2009).

The Amyelon roots were known only as detached organs when Williamson (1872) first described them as Dictyoxylon Williamson belonging to conifers. Williamson (1874) revised his descriptions, and proposed a genus name associated with plants of Asterophyllites Brongniart or Sphenophyllum Brongniart. However, Renault (1879) described some roots with similar structures from France, and referred them to Cordaites Unger. This proposal was accepted by later researchers (e.g. Osborn, 1909; Scott, 1909; Seward, 1917; Halket, 1930; Wilson and Johnson, 1940). Andrews (1942) found the organic connection between the Amyelon-type root and the cordaitalean stem Pennsylvanioxylon nauertianum (Andrews) Costanza for the first time. This discovery prompted Cridland (1964) to suggest that Amyelon should be referred to the family Cordaitaceae of the Cordaitales. Later, more and more anatomical researches on coal balls have confirmed that Amyelon has a cordaitalean affinity (Rothwell and Warner, 1984; Costanza, 1985; Trivett and Rothwell, 1985, 1988; Taylor, 1988; Stewart and Rothwell, 1993; Wang et al., 2003; Hilton et al., 2009a, 2009b).

Cordaitalean plants occurred from Lower Mississippian to the end of Permian in the Angara kingdom (sensu Meyen, 1982; Meyen, 1987). Some of them, such as Rufloria, Noeggerathiopsis and Zamiopteris, represent locally significant, perhaps even predominant, components of the Angara flora (Meyen, 1987; Durante, 1995; DiMichele et al., 2001; Taylor et al., 2009). Meyen (1987) attributed families Cordaitaceae, Rufloriaceae and Vojnovskyaceae to the Cordaitales (equals to Cordaitanthales of Meyen). However, in comparison to those from Euramerica and Cathaysia, the Angaran cordaitalean plants generally remain poorly understood. Although a large number of gymnospermous woods had been described (e.g. Lepekhina, 1972), the anatomical structures of Angaran cordaitalean stems are still unknown (Meyen, 1987). Wan et al. (2017a) described a gymnospermous stem, Ductoagathoxylon jimsarensis Wan et al., from the Wuchiapingian in Dalongkou section in the northern Bogda Mountains, about 70 km away from Tarlong– Taodonggou sections. It possesses a similar Agathoxylon-type secondary xylem to A. bogdense. However, D. jimsarensis has a uni- to tetraseriate radial tracheidal pitting and much more bordered pits (up to 22) in each cross-field, which is different from our roots described here. Recently, in Tarlong–Taodonggou area, three species of silicified woods, including Septomedullopitys szei Wan et al., Turpanopitys taoshuyuanense Shi et al., and Xinjiangoxylon turpanense Shi et al., have been recorded from the upper Permian to Lower Triassic (Shi et al., 2014, 2017; Wan et al., 2014, 2016a, 2016b). However, all of them are detached specimens with uncertain affinities. These three species are characterized by a Protophyllocladoxylon-type secondary xylem with a window-like cross-field pitting (sensu Richter et al., 2004), which is obviously distinct from the Agathoxylon-type secondary xylem with araucarioid cross-field pitting of Amyelon bogdense. To date, fossil stems/branches with unequivocal araucarioid cross-field pitting have not been found in the southern Bogda Mountains. Furthermore, all of the specimens of A. bogdense in the research area are detached axis without any association with other fossil plants. They have different anatomical features from those of all the other stems previously studied in the same area. Therefore, the affinity of A. bogdense is still uncertain.

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