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Occurrence of *Sciadopitys*-like fossil wood (Coniferales) in the Jurassic of western Liaoning and its evolutionary implications

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The genus *Sciadopitys*, containing a single species (*S. verticillata*), is the only extant representative of the Family Sciadopityaceae (Coniferales), and is a remarkable living fossil. Although some leafy fossils have been ascribed to Sciadopityaceae, fossil xylem material with a close affinity to this family is very rare, and there have been no fossils found showing both pith and primary xylem structures, which are of great importance for wood identification. Thus, it has been difficult to use fossils for the understanding of wood anatomy evolution in the sciadopityaceous plants over geological time. In this note we briefly report on *Sciadopitys*-like fossil wood found in the Middle Jurassic of western Liaoning, which bears well-preserved *Protosciadopityoxylon*-type secondary xylem, endarch primary xylem and heterogeneous pith. This is the first report of fossil specimens of the Sciadopityaceae with such detailed preservation of wood structures. The discovery provides precise anatomical evidence for reconstructing the evolutionary history and geographical distribution of Sciadopityaceae, as well as contributing to understanding of the fossil diversity of the Jurassic Yanliao Flora in northern China.

conifer, Sciadopityaceae, anatomical structure, Tiaojishan Formation, Middle Jurassic, western Liaoning

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The living fossil *Sciadopitys* is a monotypic genus with a single species, *S. verticillata* (Thunb.) Sieb. et Zucc. endemic in Japan. This species was systematically assigned to the Family Taxodiaceae [1–4]. However, some authors insist on the establishment of the new Family Sciadopityaceae, on the basis of morphological, ontogenetic, karyological and immunological data [5–10]. Such a proposal has been accepted by many wood anatomists and botanists, and adopted in a number of publications on gymnosperm classification and systematics [11–14]. There is a close relationship between Cupressaceae (including former Taxodiaceae) and Sciadopityaceae in morphological aspects. Most molecular studies support the placement of Sciadopityaceae basal to a Cupressaceae plus Taxaceae clade [15,16].

Although *Sciadopitys* is limited in its current distribution, closely related fossils have been reported from Europe and North America, in addition to Japan. Fossil leaves of *Sciadopitys* and its allies are known to occur in the Jurassic to Upper Cretaceous of Europe [10–17]. Other fossil leaves referred to Sciadopityaceae are *Sciadopityoides* from the Late Jurassic and *Sciadopitophyllum* in the Late Cretaceous to Paleocene [18–21]. The fossil specimens "double needle leaf" documented by Florin [22,23] from the Tertiary hydrogenous coal in Germany were believed to be closely allied to or generically identical to *Sciadopitys* [24]. "*Sciadopitys*-like" leaves also have been described in the Late Jurassic to Early Cretaceous in Europe, including European Russia, such as *Tritaenia* Maegdefrau et Rudolf [25,26]. Well-preserved seed cones of the Sciadopytiaceae have been documented from the Upper Cretaceous in Japan

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[7,27].

The anatomical structures of secondary xylem of the living species, *Sciadopitys verticillata* have been studied in details [9,14,28,29]. The unique structure that distinguishes *Sciadopitys* from other conifers is the cross-field dominated by window-like pits and sub-taxodioid pits with extended pit apertures. Such characteristic anatomical structures are rarely documented in fossil xylem. Jurasky first described *Sciadopityoxylon* from the Tertiary of Germany [30]. The genus is characterized by uniseriate, separated and rounded bordered pits on radial walls, occasionally with biseriate and opposite pits. The cross-field pits are of both window-like and sub-taxodioid types. There are tracheids on the tangential walls, but spiral thickening and parenchyma are not present. The xylem rays are uniseriate, 1–6 cells high. Ray cells are smooth on the horizontal walls. Resin canals are absent [31,32]. Recently, two sciadopityaceous taxa, *Sciadopityoxylon* and *Protosciadopityoxylon*, have been recorded in Early Jurassic and Cretaceous deposits in northeast China [31–33] with generally similar secondary xylem. These two genera show the same window-like and sub-taxodioid cross-field pitting as in the living species, but are different in pits on the radial walls. Pits on the radial walls of *Protosciadopityoxylon* are uniseriate and close, or biseriate and alternate, while *Sciadopityoxylon* are uniseriate and separate, or biseriate and opposite. Pits on the radial walls of living *Sciadopitys* are uniseriate, seldom crowded [9]. The extant species *S. verticillata* is characterized by star-shaped pith and endarch primary xylem [9,29]. Previously, these anatomical features have been entirely unknown in fossil material. Here, we report on new fossil coniferous wood with Sciadopytiaceae affinity from the Jurassic of western Liaoning, China, characterized by having well preserved pith, primary xylem and secondary xylem. The specimens were found from the Middle Jurassic Tiaojishan Formation in the Changgao area, Beipiao City of western Liaoning. The Tiaojishan Formation is widely distributed in western Liaoning and northern Hebei and is represented by intermediate lava and pyroclastic rock, with intercalated basic volcanic rocks and sedimentary deposits. This formation has three sedimentary interbeds containing well preserved fossil plants. A number of plant fossils have been reported from this formation, including leaf impressions and compressions, seeds and fruits, permineralized fern rhizomes and fossil wood [34]. According to plant fossil assemblages and isotopic dating [35], the Tiaojishan Formation is considered to be Middle Jurassic in age.

Three well-preserved specimens in our collection belong to the new fossil wood taxon (PB21412–PB21414). The wood bears pith, primary xylem and secondary xylem. The pith is heterogeneous and irregularly stellate in shape (Figure 1a), which consists of parenchyma cells and small number of scattered sclerenchyma cells (Figure 1b). The most remarkable feature of the pith is the presence of dark nodules among the parenchyma cells (Figure 1c, arrow). These nodules are composed of clustered sclerenchyma cells. The primary xylem is endarch with metaxylem growing exocentrically. The radial wall pits on secondary xylem are of the transitional type; where uniseriate, the tracheids are circular and closely arranged (Figure 1d, left arrow); where biseriate, the tracheids are alternate and circular or polygonal (Figure 1d, right arrow). The cross-field pits contain both sub-taxodioid pits with extended pit aperture, and window-like pits. (Figure 1e,f). The ray cells are normally uniseriate, in places biseriate, with a height of 2–26 cells, and longitudinally elliptical in shape.

According to the anatomical structures of the secondary xylem, namely the transitional type pitting of the radial wall and mixed window-like pits and sub-taxodioid cross-field pits with extended pit apertures [14], the secondary xylem of our new fossil wood type should belong to the *Protosciadopityoxylon*-type of the Sciadopityaceae (Coniferales). The presence of detailed anatomical structures of pith and primary xylem enables us to establish a new morphogenus for the present specimens (detailed description to be published separately). It is the first time that *Sciadopitys*-like fossils with pith, primary xylem and secondary xylem have been found in the world. The present specimen has no doubt close systematic affinities to *Sciadopitys*, *Sciadopityoxylon* and *Protosciadopityoxylon* because it resembles, in many respects, the living genus and is generally similar to all three genera in the secondary wood structure. Two other coniferous genera, *Scotoxylon* (Seward et Bancroft) Vogellehner and *Yokoxylon* (Holden) Vogellehner [36], may be comparable with the specimens from western Liaoning, in having pith, primary and secondary xylem. The three genera share several characteristics in the primary xylem, but are different in pith and secondary xylem structures, especially in the features of cross-field pits. The secondary xylem of *Scotoxylon* is of the *Protojuniperoxylon*-type, whereas that of *Yokoxylon* is of the *Protocedroxylon*-type. They are not related to Sciadopityaceae with *Sciadopitys*- (or *Sciadopityoxylon*- and *Protosciadopityoxylon*-) type secondary xylem. The piths of both *Scotoxylon* and *Yorkoxylon* consist of homogeneous parenchyma cells, whereas the pith of the new morphogenus from Liaoning is heterogeneous and consists of parenchyma cells and scattered sclerenchyma cells. Comparing the new genus with *Sciadopityoxylon* and *Protosciadopityoxylon*, their secondary xylem is almost the same, especially the cross-field pitting, except for some minor differences in radial wall pits with *Sciadopityoxylon*. Pith and primary xylem structures of the new morphogenus from Liaoning are similar to *Sciadopitys*, namely that both genera show star-shaped pith and endarch primary xylem, which indicates a more close affinity. However, due to the lack of pith and primary xylem structures in *Sciadopityoxylon* and *Protosciadopityoxylon*, further comparisons among them are currently impossible. It is likely that some specimens referred to the *Protosciadopityoxylon*-type may be found to belong to the new morphogenus from Liaoning, if

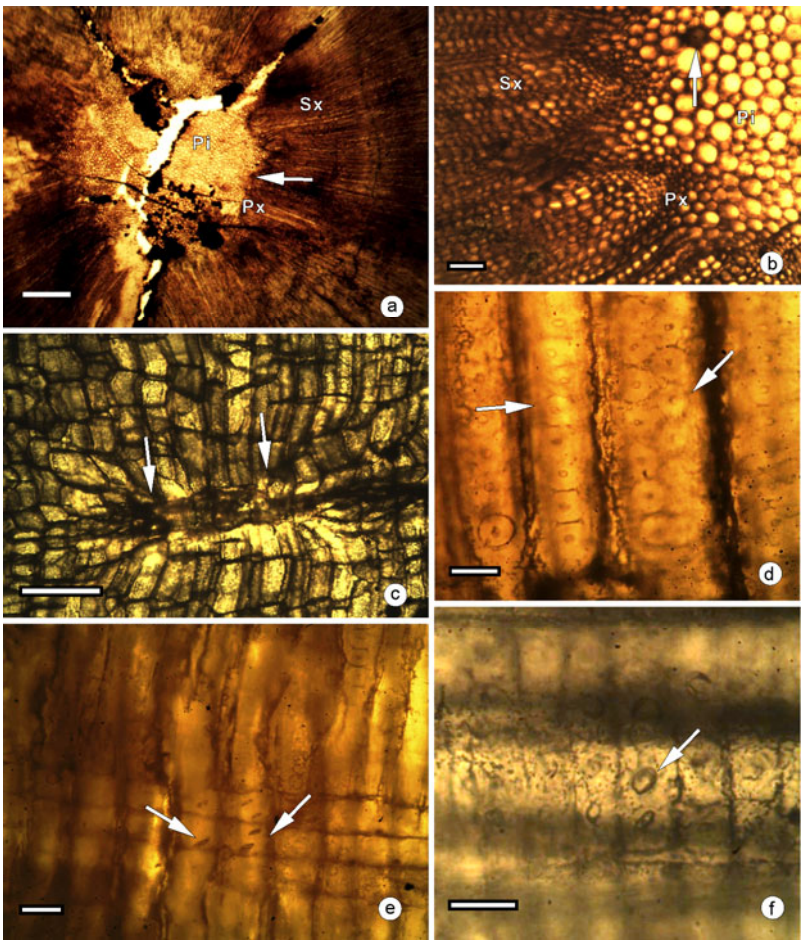

Figure 1 *Sciadopitys*-type fossils from the Middle Jurassic in Western Liaoning. a, Transverse section showing pith (Pi), primary xylem (Px) and secondary xylem (Sx), the arrow showing primary xylem. Scale bar = 1 mm. b, Transverse section showing parenchyma cells and small number of scattered sclerenchyma cells, the arrow indicating primary xylem and sclerenchyma cell. Scale bar = 100 μm. c, Radial section with nodules consists of clustered sclerenchyma cells (with arrows), surrounded by radial parenchyma cells. Scale bar = 500 μm. d, Radial section with radial wall pits uniseriate (left arrow), biseriate and alternate (right arrow) in arrangement (transitional type). Scale bar = 50 μm. e, f, Radial section showing cross-field pits (e: sub-taxodioid, scale bar= 62.5 μm; f: window-like, scale bar = 25 μm). Specimens and slides are preserved in Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

ever similar heterogenous pith and endarch primary xylem are detected.

The new morphogenus from Liaoning is similar to *Protosciadopityoxylon* in that it has transitional type tracheid pitting in the secondary xylem. Hence, it is relatively primitive, whereas the xylem structure of *Sciadopityoxylon* and *Sciadopitys* both belong to the living type. From a paleobiogeographic viewpoint, it is interesting that although the extant *Sciadopitys* is endemic in Japan, its ancestors may have existed in the Early and Middle Jurassic in China, flourished in the Jurassic and Cretaceous, and perhaps one of the groups then migrated from China to Western Europe and northwestern Canada. Because of significant changes in palaeoclimate and palaeoenvironment, sciadoptyaceous conifers became extinct in China, Europe and North American, but still survived in Japan since the Cretaceous [10]. The new *Sciadopitys*-type fossil wood from the Middle Jurassic of western Liaoning provides significant anatomical evidence for understanding the evolutionary link of sciadopityaceous wood fossils from the Early and Middle Jurassic, to Tertiary and living species. The discovery also increases our understanding of the fossil diversity of the Jurassic Yanliao Flora in northern China.

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