RESEARCH PAPER



A new thalloid liverwort: *Pallaviciniites sandaolingensis* sp. nov. from the Middle Jurassic of Turpan–Hami Basin, NW China

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Abstract Here we described a fossil thalloid liverwort from the Middle Jurassic Xishanyao Formation, Turpan-Hami Basin, China, preserved as a carbonized compression in greyish-green siltstones. The fossil thalloid liverwort is characterized by the long and strap-like thallus with a welldefined costa, entire margins and polygonal cells in the thallus wings. Following comparisons of the present fossil with extant and other related fossil liverworts, a new species, *Pallaviciniites sandaolingensis* sp. nov., is established in the subclass Pallaviciniineae, Pallaviciniales of the new classification system. It is probable that *Pallaviciniites sandaolingensis* grew on moist soils and rock surfaces near lakes and rivers in a humid and warm environment.

Keywords *Pallaviciniites* · Liverwort · Paleoecology · Turpan–Hami Basin · Middle Jurassic

Kurzfassung Hier beschreiben wir aus der mitteljurassischen Xishanyao-Formation des Turpan-Hami-Beckens in China ein fossiles thalloses Lebermoos, welches als kohliger Abdruck in grau-grünem Siltstein erhalten ist. Dieses Lebermoos ist durch einen langen,

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schlaufenähnlichen Thallus mit klar abgegrenzten Rippen, ganzen Rändern und polygonalen Zellen in den Thallusflügeln gekennzeichnet. Nach detailliertem Vergleich des vorliegenden Fossils mit heutigen und anderen fossilen Lebermoosen, wird die neue Art *Pallaviciniites sandaolingensis* sp. nov. innerhalb der Pallaviciniineae (Pallaviciniales der neuen Klassifikation) errichtet. Wahrscheinlich wuchs *P. sandaolingensis* auf feuchten Böden und Gesteinsoberflächen in der Nähe von Seen und Flüssen in einer humiden und warmen Umgebung.

Schlüsselworte Pallaviciniites · Lebermoose · Paläoökologie · Turpan-Hami-Becken · Mittlerer Jura

Introduction

Liverworts, with an extant diversity of about 6000-8000 species (Yano and Gradstein 1997; Gradstein et al. 2001; Crandall-Stotler et al. 2005; Heinrichs et al. 2005; Rubasinghe 2011), are considered the sister group to all other extant land plants (Qiu et al. 1998, 2006, 2007; Groth-Malonek and Knoop 2005). Liverworts have traditionally been classed into three groups based on growth form: (1) complex thalloid, (2) simple thalloid, and (3) leafy liverworts (Shaw and Renzaglia 2004). Over the past several years, however, the application of molecular methods has provided novel insights into liverwort classification (Crandall-Stotler et al. 2005; Frey and Stech 2005; Heinrichs et al. 2005, 2007; He-Nygrén et al. 2006), and the established classification into simple thalloid, complex thalloid, and leafy liverworts has been challenged (Crandall-Stotler et al. 2009). According to these results, liverworts are now subdivided into three major backbone clades: Haplomitriopsida, Marchantiopsida, and



Fig. 1 Map showing the fossil locality (indicated by the trifoliate leaf symbol) of Pallaviciniites sandaolingensis sp. nov

Jungermanniopsida (Davis 2004; Forrest and Crandall-Stotler 2004, 2005; Forrest et al. 2005; Heinrichs et al. 2005; Crandall-Stotler et al. 2009).

Simple thalloid liverworts are currently assigned to two subclasses, Pelliidae and Metzgeriidae of Jungermanniopsida (Crandall-Stotler et al. 2009). Simple thalloid liverworts are characterized by lacking internal or epidermal differentiations (Crandall-Stotler and Stotler 2000; Shaw and Renzaglia 2004; Rubasinghe 2011; Goffinet and Buck 2013). Liverwort fossils with a similar organization occurred relatively early in the fossil record. Riccardiothallus devonicus Guo et al. from the Lower Devonian of China has been suggested to represent the earliest megafossil evidence of liverworts (Guo et al. 2012). Metzgeriothallus sharonae Hernick, Landing and Bartowski from the Middle Devonian of eastern New York, USA, preserved with a sporophyte capsule (Hernick et al. 2008). Another thalloid liverwort fossil from the Upper Devonian (Frasnian) of New York was initially described as Hepaticites (Hueber 1961), but later was assigned to the new genus Pallaviciniites because of its close resemblance to the extant Pallavicinia (Schuster 1966).

In this paper, we present additional fossil thalloid liverworts from the Middle Jurassic of the Turpan–Hami Basin, Xinjiang. Based on a detailed comparison of thallus morphology and epidermis features, we introduce the new species *Pallaviciniites sandaolingensis* sp. nov.

Materials and methods

Geological setting

The material was collected from the open-cast Sandaoling Coal Field, about 90 km northwest of Hami, Xinjiang Uygur Autonomous Region, Northwest China (43°07'N, 92°39'E; Fig. 1). The fossiliferous horizon is located in the northeastern Turpan–Hami Basin and belongs to the Xishanyao Formation. The age of the Xishanyao Formation exposed in Sandaoling is believed to be early Middle Jurassic (Liu 1994; Shang et al. 1999). The formation exposed in the fossil site is mainly composed of grey, greyish-green and greyish-black siltstones, sandstones, and intercalated by coal-bearing deposits. The present liverwort fossils occur in greyish-green siltstones.

Fig. 2 Gross morphology of *Pallaviciniites sandaolingensis* sp. nov. (**a-h**) and extant *Pallavicinia subciliata* for comparison (**i-k**). *Scale* bars = 5 mm. **a**, **b** Dense mats of thalli of *Pallaviciniites sandaolingensis*. Specimen nos. SDL-J₂-226, 329. **c**, **d** Thallus of *Pallaviciniites sandaolingensis* with a young branch (*arrows* show the young branch). Specimen no. SDL-J₂-275 (**a**, **b**). **e**, **h** Thallus of *Pallaviciniites sandaolingensis* with well-defined costa and entire margin. Specimen no. SDL-J₂-305 (**a**, **b**). **f**, **g** Relatively complete thallus of *Pallaviciniites sandaolingensis* with a gradually narrow base. Specimen no. SDL-J₂-093 (**a**, **b**). **i-k** Dense mats and individuals of extant *Pallavicinia subciliata* for comparison





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Fig. 3 Incomplete individuals of *Pallaviciniites sandaolingensis* sp. nov. (a–d) and general morphology of thallus wings of *Pallaviciniites sandaolingensis* (e, f) and of extant *Pallavicinia subciliata* for comparison (g, h). *Scale bars* a–d = 5 mm; e–h = 400 μm. a Incomplete individual of *Pallaviciniites sandaolingensis* with broad and well-defined costa. Specimen no. SDL-J₂-282. b–d Incomplete individuals of *Pallaviciniites sandaolingensis* with well-defined costa and entire margins. Specimen nos. SDL-J₂-048, 055, 090. e Thallus wings of *Pallaviciniites sandaolingensis* showing the well-defined costa and entire margin. f Thallus wings of *Pallaviciniites sandaolingensis* showing bifurcation. g Thallus wings of extant *Pallavicinia subciliata* showing the well-defined costa and entire margin for comparison. h Thallus wings of extant *Pallavicinia subciliata* showing bifurcation for comparison

The coal-bearing Xishanyao Formation is widely distributed in the Junggar and Turpan–Hami Basins (Sun et al. 2010; Dong 2012). Plant fossils and biostratigraphy of the Xishanyao Formation have been studied so far mainly in the Junggar Basin (Miao 2003, 2005, 2006; Ashraf et al. 2004; Sha and Jiang 2004; Sun et al. 2004, 2006, 2010; Nosova et al. 2011); by comparison, there are only few reports of plant macrofossils from this formation in the Turpan–Hami Basin (Dong 2012). Wu (1996) reported a new fossil liverwort *Metzgerites barkolensis* Wu from the Xishanyao Formation in the Turpan–Hami Basin. Liu (1994) and Shang et al. (1999) provided brief reports on the fossil plants from the Xishanyao Formation in the Sandaoling Coal Field; the dominant plants are ginkgoes and ferns (Shang et al. 1999).

Materials and preparation

Rock fragments with abundant plant remains were removed from the hand specimens and immersed in distilled water for 2 h. The fragments were then immersed in 10 % HCl solution until all the calcium carbonates were removed, then washed, and immersed in 46 % HF solution until the silica was removed. After washing in distilled water, the so-obtained plant fragments were treated with 5 % NaClO solution for 2 days, and finally cleaned in distilled water, embedded in glycerine jelly, mounted on slides, and observed under a Leica DM4000B light microscope at Lanzhou University.

The extant species *Pallavicinia subciliata* (Aust.) Steph. was collected from Yamaguchi, Japan, for comparison, and the material prepared following the method described by Li et al. (2014).

We employ the liverwort classification scheme introduced by Crandall-Stotler et al. (2009). All specimens and microscope slides are deposited in the Institute of Palaeontology and Stratigraphy, Lanzhou University, Gansu Province, China.

Systematic paleontology

Class **Jungermanniopsida** Stotler and Crand.-Stotl., 1977

Subclass **Pelliidae** He-Nygrén, Juslén, Ahonen, Glenny and Piippo, 2005

Order **Pallaviciniales** W. Frey and M. Stech, 2005 Suborder **Pallaviciniineae** R. M. Schust., 1984 Genus *Pallaviciniites* R. M. Schust., 1966 *Pallaviciniites sandaolingensis* Li and Sun sp. nov. (Figs. 2a–h, 3a–f, 4a, b, d, e, g, h, j, k)

Etymology The specific epithet, *sandaolingensis*, refers to the type locality in the Sandaoling Coal Field.

Holotype SDL-J₂-093 (a, b) (Fig. 2f, g), a relatively complete thallus.

Paratypes SDL-J₂-048 (Fig. 3b); SDL-J₂-055 (Fig. 3d); SDL-J₂-089 (a, b); SDL-J₂-090 (Fig. 3c); SDL-J₂-226 (Fig. 2a); SDL-J₂-275 (a, b) (Fig. 2c, d); SDL-J₂-282 (Fig. 3a); SDL-J₂-305 (a, b) (Fig. 2e, h); SDL-J₂-329 (Fig. 2b).

Locality and horizon Sandaoling Coal Field, Turpan-Hami Basin, NW China; Xishanyao Formation, Middle Jurassic.

Diagnosis Plant thalloid and prostrate. Thalli long, straplike, branching irregularly. Margins entire. Costa well-defined, thickened, thallus wings unistratose. Cells in the central portion of the thallus wings hexagonal; cells of and adjacent to the costa elongated; cells near the thallus margins tetragonal to hexagonal, arranged in several longitudinal rows. Costa bearing unicellular, smooth, unbranched rhizoids.

Description The holotype (SDL-J₂-093) consists of a complete single individual (Fig. 2f–g). Some paratypes of *Pallaviciniites sandaolingensis* (SDL-J₂-282, 329) consist of dense mats of thalli (Fig. 2a, b). Thalli are long, dorsiventral, strap-like, and up to ca 50 mm long (Fig. 2b) and between 2.5 and 5.5 mm wide (Figs. 2h, 3a). They branch irregularly up to five times (Fig. 2b, f, g) and at angles between ca 30° and 75° (Fig. 2d, e, h). The margins are entire (Figs. 2d, h, 3b, c, e), and the base of thallus is with stipe (Fig. 2g). The costa is well-defined, about 0.7–2.2 mm wide, and several cells thick (Figs. 2e, h; 3d–f, 4a). A central strand is not clearly discernable. The thallus wings are apparently composed of a single layer of cells (Figs. 3e–f, 4a).

Cells in the central portion of the wings are hexagonal, relatively large, 26–49 μ m wide and 64–100 μ m long (Fig. 4d, e). Cells at the thallus margins are tetragonal to hexagonal, relatively small, 23–37 μ m wide and 25–56 μ m



◄ Fig. 4 Thallus wings and rhizoids of *Pallaviciniites sandaolingensis* sp. nov. (a, b, d, e, g, h, j, k) and of extant *Pallavicinia subciliata* for comparison (c, f, i). Scale bars a, $\mathbf{b} = 200 \ \mu\text{m}$; c, $\mathbf{f} - \mathbf{k} = 100 \ \mu\text{m}$; d $e = 50 \mu m$. a General morphology of thallus wings of *Pallaviciniites* sandaolingensis. b Dense mass of rhizoids of Pallaviciniites sandaolingensis along costa. c Hexagonal cells of wings of extant Pallavicinia subciliata for comparison. d Hexagonal cells of wings of Pallaviciniites sandaolingensis. e Close-up of d showing the thalluswing cells. f Tetragonal to hexagonal cells at the wing margin of extant Pallavicinia subciliata for comparison. g Tetragonal to hexagonal cells at the wing margin of Pallaviciniites sandaolingensis. h Elongate hexagonal cells adjacent to the costa of Pallaviciniites sandaolingensis, i Elongate cells of the costa of extant Pallavicinia subciliata for comparison. j Elongate cells of the costa of Pallaviciniites sandaolingensis. Cell shape cannot be recognized. k Unicellular and smooth rhizoids of Pallaviciniites sandaolingensis

long, and arranged in several longitudinal rows (Fig. 4g). Cells adjacent to the costa are elongate hexagonal and narrower than those in the central portion of the wing, 10–18 μ m wide and 30–54 μ m long (Fig. 4h). Cells of the costa appear to be elongated along the axis of the thallus (Fig. 4j), but their shape cannot be clearly recognized. Numerous rhizoids arise from the costa (Fig. 4b). They are unicellular, smooth and unbranched (Fig. 4j–k). Rhizoids occur in a tangled mass and their tips are broken off, so the complete length of individual rhizoid remains unknown.

Comparison and discussion

Assignment to Pallaviciniites

The fossil specimens are thalloid gametophytes without differentiated leaves. They are assignable to Pelliidae or Metzgeriidae of Jungermanniopsida on the basis of their simple organization, unistratose wings, and the lack of hexagonal air chambers and ventral scales. Thalloid gametophytes of Metzgeriidae are characterized by unicellular setose hairs on the thallus margin and/or ventral surface of the costa (Crandall-Stotler et al. 2009; Gao and Wu 2010), which are absent in the fossils. Furthermore, the fossil specimens have entire margins and a well-defined costa, and some branches bear stipes. It is, therefore, reasonable to assign them to Pallaviciniineae of Pallaviciniales rather than members of the other two orders Fossombroniales and Pelliales of Pelliidae.

Compared to extant materials, the present fossil bears many resemblances to the extant *Pallavicinia subciliata* both on gross morphology (Fig. 2a, b, d, g, i–k) and cellular structures (Figs. 3d–h; 4c, d, f, g, i, j). The shared features are strap-like thalli, irregular branching, well-defined costa and similar cell patterns in particular thallus regions. Since several important diagnostic features, such as reproductive organs, however, have not been observed, we assign the material to the form genus *Pallaviciniites* included in the Pallaviciniineae.

Comparison with related fossil liverworts

Pallaviciniites sandaolingensis is characterized by having entire, smooth thallus margins compared to the serrate margins of the type species *P. devonicus* (Hueber 1961; Schuster 1966) and the undulating and crenulate margins of the recently described *Pallaviciniites*-like "Bryophyte 3" from the Triassic of Antarctica (Bomfleur et al. 2014).

Several fossil thalloid liverworts assignable to Jungermanniopsida have been reported in recent years. The thallus of *Riccardiothallus devonicus* from the Lower Devonian of Yunnan, China, lacks a costa (Guo et al. 2012), unlike the well-defined costa running down the midline of the thallus. *Metzgeriothallus sharonae* from the Middle Devonian (Givetian) of eastern New York State, USA, has a thallus with a single bifurcation at the apex, dark cells of the wings, and narrow cells along the margins (Hernick et al. 2008), whereas *Pallaviciniites sandaolingensis* branches several times (Fig. 2b, d, g) and has tetragonal to hexagonal marginal cells (Fig. 4e). The dark cells are also absent in the wings of *P. sandaolingensis*.

Riccardiopsis hsüi Wu and Li, Metzgerites barkolensis, M. exhibens Wu and Li, and M. yuxianensis Wu and Li are thalloid liverwort assignable to Jungermanniopsida from the Middle Jurassic of China. Riccardiopsis hsüi has a pinnate thallus (Wu and Li 1992) clearly different from Pallaviciniites sandaolingensis. Metzgerites barkolensis, M. exhibens, and M. yuxianensis are all characterized by a prominent costa several cells thick, and by a unistratose wing composed of polygonal cells. They differ from P. sandaolingensis in bearing hairs on the wing and/or the ventral surface of the costa (Wu and Li 1992; Wu 1996).

Paleoecology

The present fossil is preserved in the form of a complete thalli (Fig. 2c, d, f, g) with cellular details (Fig. 4a, d, e, g, h) and dense masses of fragile, unicellular rhizoids (Fig. 4b), with no indication of transport. We thus interpret the material to have been buried and preserved in situ. *Pallaviciniites sandaolingensis* occurs in thin layers of grey or greyish-green argillaceous siltstones. The Xishanyao Formation exposed in the Sandaoling Coal Field is mainly composed of grey and greyish-green siltstones intercalated with mudstones, sandstones, gritstones, and coal seams representing fluvial, lake-swamp sediments. In addition, the paleoclimate was humid and warm in the Middle Jurassic of the Sandaoling region (Liu 1990; Wang et al. 1994; Shang et al. 1999; Zhang et al. 2002; Miao 2005; Dong 2012). Extant species of Pallaviciniales are

globally distributed and typically occur in humid environments, such as wet rock surfaces, soils, or tussock near rivers or streams (Gao and Wu 2010).

Taking account of facies in which *Pallaviciniites sandaolingensis* was preserved, the mid-Jurassic paleoclimate of the Sandaoling region and the most typical habitats of extant Pallaviciniales species, it is probable that *P. sandaolingensis* grew on moist soils and rock surfaces near lakes and rivers in a humid and warm environment.

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