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SPECIALIZED ADHESIVE PAD OF A CLIMBING PTERIDOSPERM FROM PERMIAN PEAT-FORMING FOREST (WUDA, INNER MONGOLIA)

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Abstract: *Certain pteridosperm tendril adhesive pads are depicted from the Cathaysian flora of the Early Permian Taiyuan Formation of Wuda Coal-field in Inner Mongolia China. Specimens contain elliptical or rounded pads situating at the swollen tip of pinnule lobe tendrils which are highly comparable to those of the extant Parthenocissus tricuspidata in the way that both of them are similar in form and function. Specifically, information we have gained suggested that pteridosperms from the Permian might have performed a similar type of physiological process by producing some chemical substances which assisted them in climbing. The Wuda pteridosperm likely to climbed on Cordaites or Sigillaria trees. Moreover, physical principles such as the pressure difference between inside and outside of the pads also seems to play an important role in assisting climbing. The new finding indicates that some pteridosperms in the Permian Cathaysian flora possessed climbing growth habit as well as those in the Late Carboniferous Euramerica Flora, where climbing/scrambling growth habit is well known in the coal swamp forests. This finding shows one of the several earliest climbing habits in Cathaysia Flora and thus remarkably promotes our understanding of the growth habit of pteridosperm and the change in plant community structure in that area.*

Key Words: *Parthenocissus*, pteridosperms, Permian, sucker-like structure, liana

INTRODUCTION

Plants have evolved various morphological adaptations from the Paleozoic to present day. Adaptations for scrambling/climbing are numerous in extant angiosperms. The larger lianas are typically found in tropical rain forests while smaller ones are usually seen from temperate regions (Kerp *et al*. 2000). Despite the fact that it is relatively easy to find lianas in recent forests, this growth form is hard to recognize in the fossil record, due to their preservation as adpressions of the original plant. Some characteristics of liana such as slender stems, small fronds, and presence of special tendrils are observable in fossils. These adaptations are known both from pteridosperms and Paleozoic ferns (e.g. Krings & Kerp. 1997, Kerp & Krings 1998, Krings & Kerp 1999, Kerp *at al*. 2000, Krings *et al*. 2003, Sun & Deng 2006, Pšenička *et al*. 2020). The highly specialized liana-like plants are tendril-climbers (Kerp *et al*. 2000). These features have been recognized in two Paleozoic pteridosperm species; *Lescuropteris genuine* (Grand'Eury) Remy & Remy (1975) and *Blanzyopteris praedentata* (Gothan) Krings & Kerp (1999) from Euramerican paleoprovince (Krings & Kerp 1997, 1999). Herein I particularly focus on describing another microscopic adaptation of liana-like Paleozoic pteridosperm *Wudaeophyton wangii* Pšenička & Wang (2020) in addition to work by Pšenička *et al*. (2020). This fossil tendril-climber is compared with liana-like angiosperm plant *Parthenocissus tricuspidata* Sieb (Member of the grape family, Vitaceae).

MATERIAL AND METHOD

The author participated in the field collection in the Wuda Coalfield, Inner Mongolia in 2011 during which specimens of *W. wangii* were first collected. Later that same year, a Czech and Chinese paleobotanical team collected better material from the same locality. The Wuda plant remains are pre-

served in volcanic ash. They represent a T^0 assemblage (Wang *et al.* 2012). This volcanic tuff is in the uppermost part of Taiyuan Formation, specifically above Coal No. 7 and below Coal No. 6 (Pfefferkorn & Wang 2007). The age of the volcanic tuff was determined biostratigraphically to be from the latest Carboniferous or earliest Permian (Wang & Pfefferkorn 2013). Some parts of *W. wangii*, such as axes and reproductive organs, are carbonized and anatomically preserved in 3D. Uncoated anatomically preserved specimens were examined in an SEM for this study. All specimens are housed in the paleobotanical collections of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

DESCRIPTION OF FOSSIL SPECIMEN

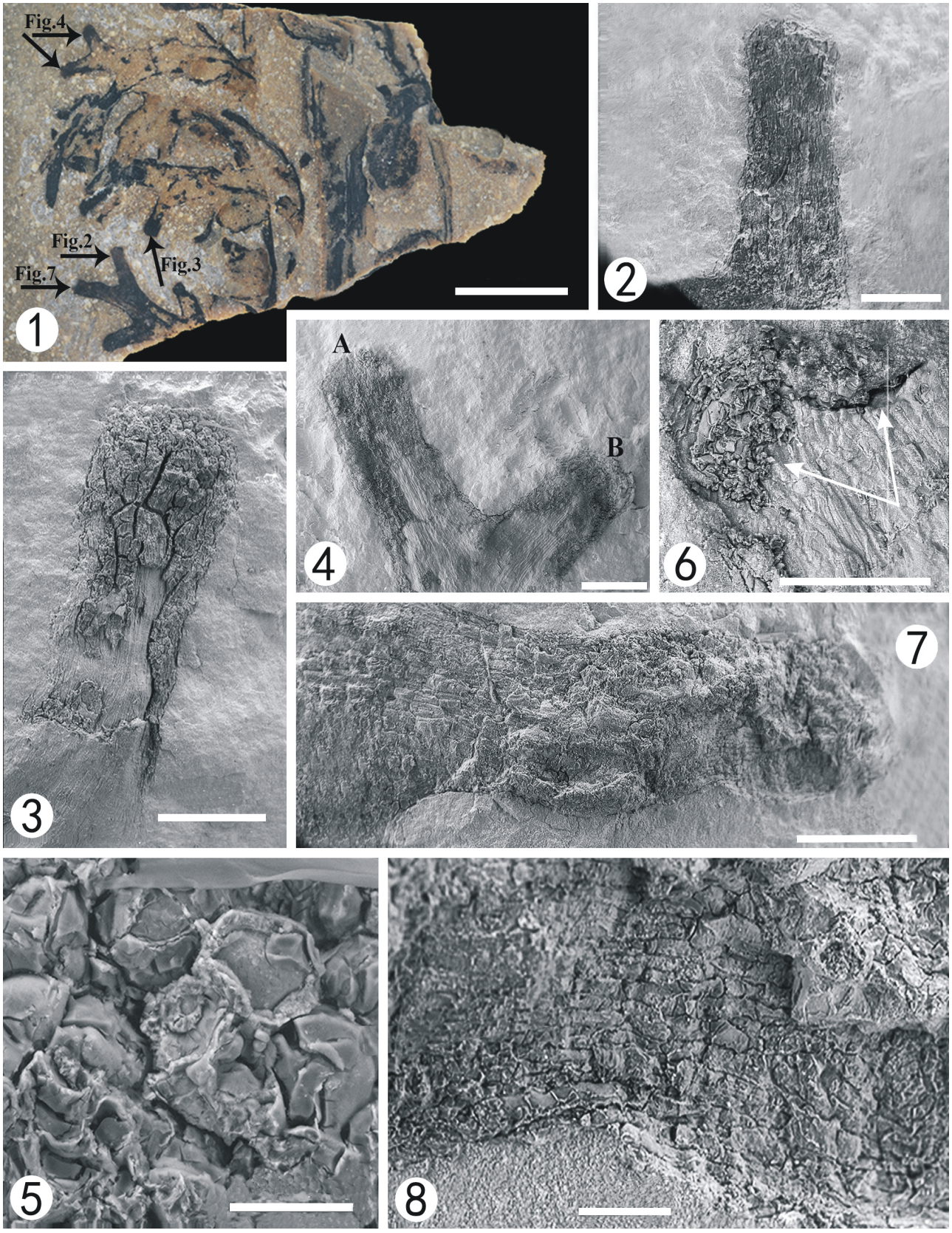
Specimen shows the fragment of ultimate pinna with two complete pinnules. Ultimate rachis is 1.1mm wide, smooth with sporadically distributed hairs. Pinnules grow alternatively despite the fact that they appear to be only on one side of the rachis. In reality, it is the taphonomic effect that makes pinnules from the right side bend to the left (Plate I, Fig. 1). Lobate oblong pinnules, 8mm long and 4mm wide, are attached to the ultimate rachis by the whole pinnule base. Pinnules seem to be thick and coriaceous. The number of lobes per pinnule range from 5 to 7 per pinnule. Lobes are linear and have distinct tips (Plate I, Fig. 1 arrows). The pinnules have two terminal lobes (Plate I, Fig. 4) here identified as tendrils based morphology (Plate I, Fig. 3). Lobe tendrils are linear, (Plate I, Figs 1, 2) probably cylindrical-conical, 1.5–2.2 mm long and 0.5mm wide. Some lobe tendrils are terminated in simple swollen tips which represent immature state of the attachment pads (Plate I, Figs 3, 4A, 7). One tendril tip from the specimen (specimen PB23043) shows a pair of terminal pads (Plate I, Fig. 6 arrows). Immature pads may originally have round shape (500–600 μm in diameter). Some lobe tendrils pads appear to be detached (Plate I, Figs 2, 4B). The sizes of cells in tendrils and pads are not uniform; there is no well-defined boundary between tendrils and pads (Plate I, Figs 2, 3, 7). The cells which form a tendril are tetragonal-polygonal, elongate, 60–210 μm long, 20–25 μm wide and parallel to the longitudinal axis of the lobe tendril (Plate I, Fig. 8). Despite the polygonal shape, slightly sinusoid anticlinal walls cells 70–130 μm long and 55 μm wide are situated in lower and middle parts of pads (Plate I, Fig. 7). Cells at the distal end are polygonal lentiform, about 55 μm across (Plate I, Fig. 5)

GROWTH HABIT AND TAPHONOMY

According to Pšenička *et al.* (2020), the growth habit of *W. wangii* suggests that it is likely to be a liana with 4mm wide stems and Calystophytalean-type growth anatomy, small fronds (less than 40mm) with three order of branching, and highly variable pinnule shape. All specimens of *W. wangii* are all recovered from the upper part of volcanic ash bed; this flora is interpreted as allochthonous. None have been recovered from the base of the ash bed, in floras interpreted as autochthonous. Large fronds of tree ferns and cordaitalean branches are buried with the remains of this species. I conclude that some pteridosperms from the upper ash were lianas of reaching to the crowns of the tallest trees in forest such as Cordaitalean (in *Cordaites-Psaronius* forests) or sigillarian (in *Sigillaria-Paraingia-Psaronius* forests). That the fossil

Plate I Specimen of *Wudaeophyton wangii* from the early Permian Taiyuan Formation in Wuda Coalfield, Inner Mongolia, China. 1. An overview of the current studied specimen. Arrows indicate pinnule lobes to be magnified and illustrated further. Scale bar = 5 mm. 2. SEM magnification of a pinnule lobe from the lower most pinnule as marked in Fig. 1. Scale bar = 0.5 mm. 3–4. Swollen tips at the end of tendrils; 3. Pinnule lobe tendril with an adhesive pad, magnified from the second lower most pinnule (as indicated in Fig. 1). Scale bar = 0.5 mm; 4. Magnification of distal parts of pinnules (as indicated in Fig. 1) ended with two terminal lobes marked as A and B. Scale bar = 0.5 mm. 5. Cells of the terminal pad of Fig. 3 are polygonal lentiform; some also have blebs after exudation. Scale bar = 50 μm. 6. Tendril tip with two terminal pads indicated by arrows. Scale bar = 0.5 mm. 7. SEM of a pinnule lobe (as indicated in Fig. 1) showing its morphology. Scale bar = 0.5 mm. 8. Magnification of the apical part of the tendril of Fig. 7, showing the cells appear to be tetragonal-polygonal, elongated. Scale bar = 100 μm.

Plate I



remains of *W. wangii* rarely occurred in autochthonous plant assemblage at Wuda supports this conclusion. Individual plants that were attached to the standing necrotized stems were knocked off during the volcanic eruption and preserved in the volcanic ash. Only small fragmentary specimens of *W. wangii* were sticking on tree limbs. The majority of the biomass consists of plant debris that decayed before fossilization.

COMPARISON OF CURRENT FOSSIL SPECIES WITH *PARTHENOCISSUS TRICUSPIDATA*

The polygonal lentiform cells are here in interpreted as secretion cells for producing adhesive fluid. Similar tendril-pads are found in the living angiosperm liana *Parthenocissus tricuspidata* near shoot tips, consisting of a 5–10 axes branched tendril each with its own attachment pad (Steinbrecher *et al*. 2011). *W. Wangii* has specialized pinnules with pads situated on the terminal part of lobes. There are several microscopic analogies between both the living and fossil. Steinbrecher *et al*. (2011), reported that the attachment pads of *P. tricuspidata* transformed from a hemispheric shape to a flattened circle, with age, even if the attachment pad has no substrate contact. Steinbrecher *et al*. (2011) stated that the juvenile attachment structure differentiates into several attachment pads each of which went through several morphological changes; circular pad almost developed, while it was in contact with a substrate. Steinbrecher *et al*. (2011) also assumed that tendrils would die if attachment pads cannot find an appropriate substrate. Nevertheless, I observed only round shaped pads. I suspect that flattened pads are lacking is because most of them were attached on standing necrotized stems. These stems are usually not preserved because I think they decayed prior to fossilization. The pads on some lobe tendrils were lost probably due to damages when they were knocked out of the trees, with the adhesive pads remaining on the branches, by volcanic ash. Junker (1976) and Steinbrecher *et al*. (2011) published SEM photographs of the cell structures of pads, which are like chambers. In *W. wangii* (specimen PB23043), the cells are typically elongated (Plate I, Figs 7, 8). Nevertheless, in contrast to *P. tricuspidata*, where there is a differentiation of the cells; in *W. wangii* a well-defined boundary between tendril and pad cells is not present. *P. tricuspidata* has strong tendrils holding the plant from falling off. According to the results of my test, the shoots of *P. tricuspidata* are

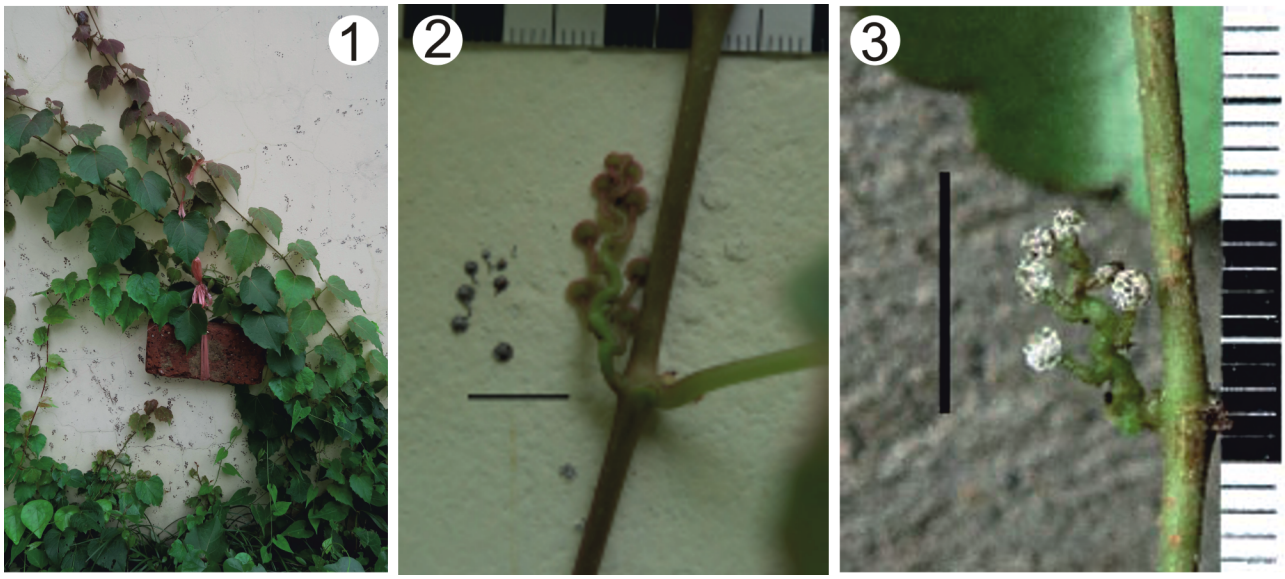


Plate II *Parthenocissus tricuspidata* from a wall of the Jiming Temple of Nanjing, Jiangsu Province, China. 1. Part of the tendrils bearing a two-kilogram red brick. 2–3. Each branch with 5–7 tendrils; 2. Outer surface pads attached to wall; 3. Inner surface of pads after tendril was removed from the wall.

able to support two kilograms (Plate II, Fig. 1). The pads stick to the supporting substrate no matter how smooth the surface. The overall effectiveness of adhesion is directly proportional to the number of pads. A branch of less than 2 meters can have about 100 tendrils each with 5–7 pods or 250–350 pads/meter of branch (Plate II, Figs 2, 3). Thus W. wangii could have supported a climb to the top of the canopy.

According to He *et al.* (2008), there are three major factors that contribute to the adhesiveness of *P. tricuspidata*. First the adhesive chemical substance the plant secretes. Second, pad morphology with large numbers of sponge-like structures and vessels in each pad. The third factor is the pressure. The air initially inside the pad is depleted in the chemical reaction between the wall and adhesive chemical substances resulting in lower pressure in the pod than the ambient pressure.

MECHANISM PRINCIPLE

Numerous tendrils with pads locating at the end of the *P. tricuspidata*'s branch are the attachment structures of this plant. Ambient air pressure was maintained when the plant is climbing. The *P. tricuspidata* decreases the air pressure between the pad and the attachment surface during photosynthesis (Junker 1976, Steinbrecher *et al.* 2011). These lianas can seal around the pad edges allowing the internal pressure to decrease in comparison with the outside ambient pressure. The low pad pressure aids in keeping the pads attached to the substrate. Figure 1 is a generalized sketch showing the principle of the pad in the air.

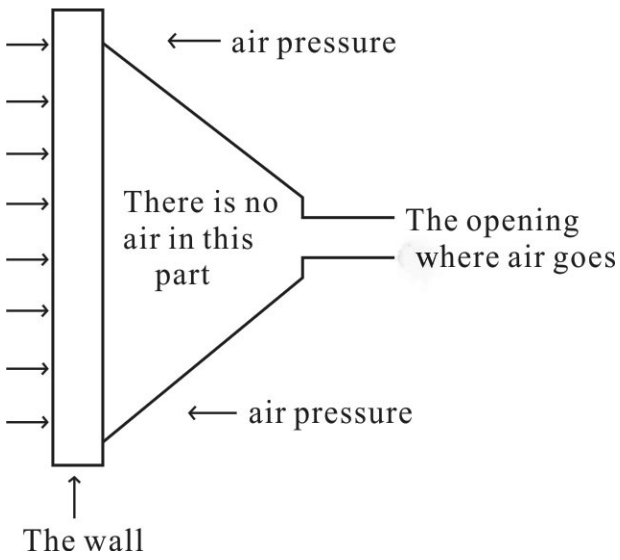


Figure 1. *Sketched graph showing the mechanical principle. As the air inside pad depletes, the pressure outside presses and flattens the pad and thus the pad will be able to stick onto the substrate.*

TENDRILS WITH ADHESIVE PADS CLIMBING ORGAN HAVE EVOLVED OVER 300 MA

Krings *et al.* (2003) showed that tendrils with adhesive pad structures had evolved in the late Carboniferous to early Permian (ca. 300 MYBP). A Carboniferous seed fern *Blanzyopteris pradentata* has climbing tendrils (Krings & Kerp 1999, fig. 7) with numerous apically widened branchlets terminating in adhesive pads. In these features *B. pradentata* is very similar to *W. wangii* illustrating that climbing tendrils can develop from pinnule lobes. Morphologically the adhesive pads in the fossil species are comparable to those of living *P. tricuspidata*.

In the Euramerican floras of the Westphalian-Stephanian transition, the dominant tree vegetation changed from large lycopods to large tree ferns with both groups developing closed canopy. During this time of transition increasing numbers of liana climbing/scrambling plant taxa developed (Kerp & Krings 1998). Such complex Cathaysian floral community structure has not been recognized (Wang *et al.* 2012). At this time there is little evidence of plants with apparent climbing habits in Cathaysian flora (Zhou *et al.* 2019) The climbing habits reported herein suggest that the peat-forming community structure, in Cathaysia Flora might have also become more complex.

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REFERENCES

He, T.X., Yang, W.W., Deng, W.L. 2008. A climbing plant with super-adhesive function advances and new results of the most recent study on Parthenocissus tricuspidata. *Progress in Natural Sciences, 18 (11)*, 1220-1225 (in Chinese).

Junker, S. 1976. A scanning electron microscopic study on the development of tendrils of *Parthenocissus tricuspidata* Sieb. & Zucc. *New Phtologists*, 77, 741-746.

Kerp, H, Krings, M. 1998. Climbing and scrambling growth habits: common life strategies among Late Carboniferous seed ferns. *C.R. Académie des Sciences, Paris, Palaeontology, 326*, 583-588.

Kerp, H., Krings, M., Taylor, T.N. 2000. Morphologycal and Biomechanical Diversity among Late Palaeozoic Seed Ferns – Scrambling and Climbing Growth Habits. In book: H.C. Spatz, T. Speck, ed., Plant Biomechanics. Proceedings of the 3rd Plant Biomechanics Conference Freiburg-Badenweiler August 27th to September 2nd 2000, Publisher: Thime Verlag, Stuttgart, pp.117-122.

Krings, M., Kerp, H. 1997. Cuticles of *Lescuropteris genuina* from the Stephanian (Upper Carboniferous) of Central France – evidence for a climbing growth habit. *Botanical Journal of Linnean Society, 123,* 73-89.

Krings, M., Kerp, H. 1999. Morphology, growth habit, and ecology of *Blanzyopteris praedentata* (Gothan) nov. comb., a climbing neuropterid seed fern from the Stephanian of central France. *International Journal of Plant Science, 160,* 603-619.

Krings, M., Kerp, H., Taylor,T. N., Taylor, E. 2003. How Paleozoic Vines and Lianas Got off the Ground: On Scrambling and Climbing Carboniferous–Early Permian Pteridosperms. *The Botanical Review 69(2)*, 204–224.

Pfefferkorn, H.W., Wang, J., 2007. Early Permian coal-forming floras preserved as compressions from the Wuda District (Inner Mongolia, China). International Journal of Coal Geology 69, 90–102.

Pšenička, J., Wang, J., Hilton, J., Zhou, W., Bek, J., Opluštil, S., Votočková Frojdová, J. 2020. A small heterophyllous vine climbing on *Psaronius* and *Cordaites* trees in the earliest Permian forests of North China. *International Journal of Plant Sciences, 181(6)*.

Steinbrecher, Z., Beuchle, G., Melzer, B., Speck, T., Kraft, O., Schwaiger, R. 2011. Structural development and morphology of the attachment system of *Parthenocissus tricuspidata*. *International Journal of Plant Sciences, 172(9)*, 1120–1129.

Sun. K.Q., Deng, S.H. 2006. *Parasphenopteris* Sun & Deng, a new genus from the Lower Permian of Wuda, Nei Mongol, China. *Acta Phytotaxonomica Sinica 44 (2)*, 161-164.

Wang, J., Pfefferkorn, H.W., Zhang, Y., Feng, Z. 2012. Permian vegetational Pompeii from Inner Mongolia and its implications for landscape paleoecology and paleobiogeography of Cathaysia. *PNAS*, 1–6.

Wang, J., Pfefferkorn, H.W., 2013. The Carboniferous–Permian transition on the North China microcontinent—oceanic climate in the tropics. *International Journal of Coal Geology 119*, 106–113.

Zhou, W. M., Li, D. D., Pšenička, J., Boyce, C. K., Wang, J., 2019. A left-handed fern twiner in a Permian swamp forest. *Current Biology*, 29, R1172-R1173.