

A Left-Handed, Stem-Twining Plant from the Miocene Shanwang Formation of Eastern China

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ABSTRACT

Twining stems of plants are very common in extant tropical and subtropical forests, and the climbing growth habit of plants may be an evolutionary innovation and ecological adaptation to either closed, shady or open, edge environments. However, the origin of handedness in climbing plants remains unclear. Here we report a Miocene (ca. 16 million years ago) macrofossil from the Shanwang Formation of Shandong Province, Eastern China, unequivocally exhibiting the first direct fossil evidence for a left-handed, stem-twining growth habit in plants. This fossil plant bears a thicker, slightly curved supporting stem (2 - 3.5 mm wide), which is loosely, spirally twined by a thinner stem (1.5 - 2 mm wide), possibly representing part of distal branches from a liana or vine.

Keywords: Climbing Growth Habit; Handedness; Liana; Miocene; Shanwang Formation; Stem-Twining Plants; Vine

1. Introduction

Climbing plants (lianas and vines) are abundant and diverse in tropical and subtropical forests [1-7], and some (e.g., pumpkins, cucumbers, grapes, and wisterias) have been widely cultivated by humans (**Figure 1**). They are mechanically dependent climbers and differ from self-supporting plants (trees and shrubs) in possessing a wealth of climbing mechanisms such as twining stems, clasping tendrils, modified leaves, hooks and spines, retrorse barbs, and adhesive, adventitious roots [3], by which climbers attach themselves to supporting media and ascend towards higher light exposure levels. Interestingly, the twining stems of living climbers have left-handedness and right-handedness as well as a global tendency towards right-handedness [5]. As displayed on many levels from microscopic elementary particles, atoms, amino acids, proteins, DNA (*i.e.*, Deoxyribose Nucleic Acid), and bacteria to macroscopic galaxies, planets, cyclones, plants, animals, and human beings, the phenomenon of left-handedness and right-handedness has attracted extensive attention [8-12]. However, it has remained enigmatic for the origin and preference of handedness in climbing plants since Darwin's time [5,13,14].

The fossil record of climbing plants provides a historical perspective for their early evolution. So far, plants

with tendril-, leaf-, hook- and root-twining mechanisms have been confirmed in Carboniferous—Permian (ca. 359 - 252 million years ago) coal swamp forests of Euramerica, but stem-twining climbers very common in extant tropical and subtropical forest ecosystems previously have not been directly observed in the fossil record [15, 16]. Here we describe a Miocene (ca. 16 million years ago) fossil from diatomaceous shales of the Shanwang Formation at Linqu County, Shandong Province in eastern China, unequivocally exhibiting the first direct macrofossil evidence of twining stems.

2. Material and Methods

The fossil presented here was collected from diatomaceous shales of the Shanwang Formation at Shanwang (lat. 36°54'N, long. 118°20'E), 22 km east of Linqu County, Shandong Province, eastern China (**Figure 2**). Shanwang is famous for exquisitely preserved fossil insects, ostracodes, spiders, fish, amphibians, reptiles, birds, mammals, and plants in lacustrine deposits that have been studied since the 1930s [17-20]. This locality has yielded abundant plant macrofossils that have been assigned to 50 families, 104 genera, and 155 species, which are predominated by dicotyledonous angiosperms [21]. The age of this formation is correlated as late Early Miocene—early Middle Miocene (ca. 16 million years ago

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Figure 1. Distal branches of four extant, stem-twining plants cultivated at the Institute of Botany, CAS, Beijing. (a) *Wisteria sinensis* (Sims) Sweet, showing a right-handed twining and alternate leaves; (b) *Wisteria floribunda* (Willd.) DC., showing a left-handed twining and alternate leaves; (c) *Pueraria montana* (Lour.) Merr., showing a right-handed twining and alternate leaves; (d) *Lonicera japonica* Thunb., showing a left-handed twining and opposite leaves. Bars, 2 cm.

[22]) on the basis of mammalian faunas and radiometric data [23].

This specimen was preserved as branch compressions with a little organic material remaining on a diatomaceous slab (**Figure 3(a)**), which was prepared with sharp needles to reveal morphological features. An attempt to obtain cuticles was unsuccessful. Photographs were taken with a digital camera (Panasonic DMC-FZ30). The illustration (**Figure 3(d)**) was drawn using CorelDraw 10.0 program. Distal branches (**Figures 1(a)-(d)**) of four extant stem-twining plants cultivated at the Institute of Botany, Chinese Academy of Sciences (CAS) were collected to compare with the fossil presented here. The fossil specimen (PE-20120314) was deposited at the Chinese Na-

tional Herbarium (PE), Institute of Botany, CAS, Beijing, China.

3. Results

Being devoid of cuticles, laterally attached leaves, and other useful characters, the identity of this fossil specimen can not exactly be determined, and open nomenclature is adopted here. Hence, this fossil is classified into “*Plantae Incertae sedis*” with a description as follows.

The fossil exhibits a clockwise (left-handed) twining direction (**Figures 3(a)-(c)**). The twining stem is thinner, ca. 128 mm long and 1.5 - 2 mm wide, which twines a thicker supporting stem in a loose spiral. The supporting

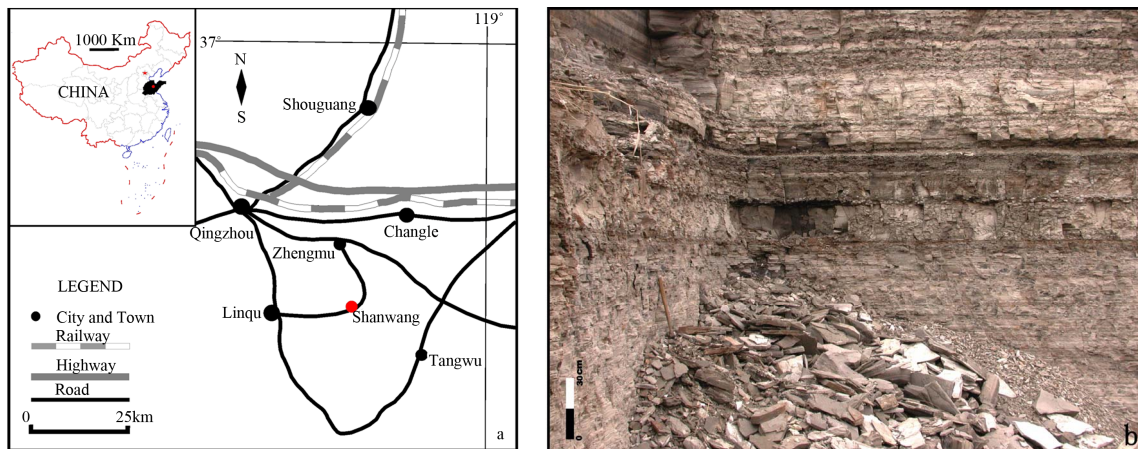


Figure 2. Location and stratigraphy of the Shanwang Formation of Eastern China. (a) Red dot refers to the fossil locality; (b) Showing diatomaceous shales of the Shanwang Formation.

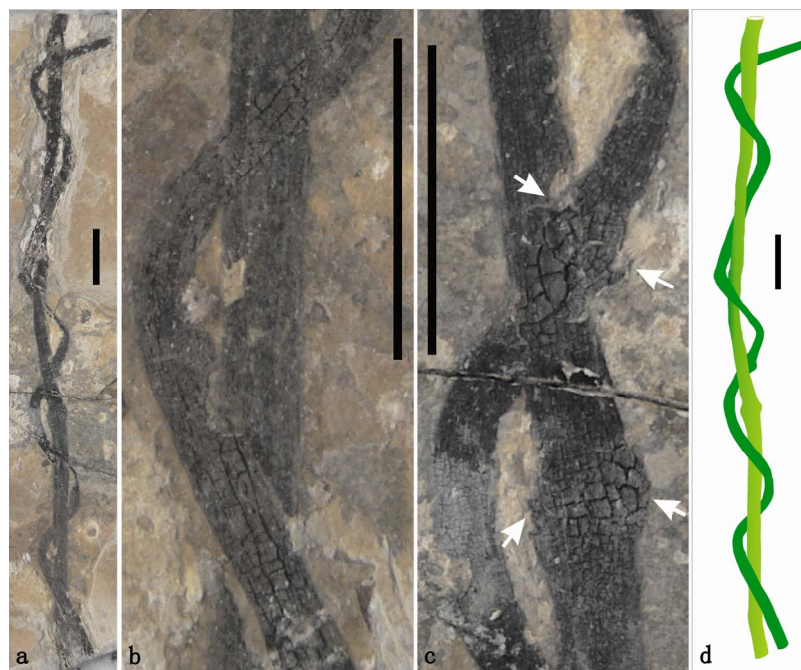


Figure 3. A left-handed, stem-twining fossil from the Miocene Shanwang Formation of Eastern China. (a) Two stems, showing a clockwise (left-handed) twining growth habit. PE-20120314; (b) Enlarged view near the base of stems, showing a left-handed twining direction; (c) Enlarged view near the middle of stems, showing longitudinal striations, carbonized cracks on the surface, and slightly, bilaterally-bulged node (arrowheads); (d) A schematic reconstruction of this fossil plant. Bars, 1 cm.

stem is slightly curved, ca. 115 mm long and 2 - 3.5 mm wide. Both stems appear to have long internodes and a slightly, bilaterally-bulged node (**Figure 3(c)**), implying that there may have borne opposite appendages (e.g., leaves) in life. There are similar, longitudinal striations on the surface of two stems. Cuticles are unavailable. The texture appears to be woody.

In light of the loose spirals and bilaterally bulged nodes, the twining stem presented here is not a tendril around the supporting stem. Both the supporting stem and twining stem have similar longitudinal striations on the sur-

face and slightly bulged nodes possibly with opposite appendages, so this fossil is far more likely to be detached from the same parent plant, representing a part of distal branches from a liana or vine. A schematic reconstruction of this fossil plant is given here (**Figure 3(d)**).

Prior to this study, the existence of stem-twining plants at Shanwang has been inferred by leaf or/and fruit fossils that were classified into living vine or liana genera such as *Wisteria* Nutt., *Pueraria* DC., and *Lonicera* L. [17, 19-21,24,25]. In this study, we provide the first direct macrofossil evidence for a stem-twining habit in plants.

4. Discussion

The climbing growth habit of plants may be an evolutionary innovation and ecological adaptation to either closed, shady or open, edge environments [2-4,7,15,16]. As land plants began to form the earliest forests in the Middle Devonian (ca. 393 - 383 million years ago) [26], climbing habits might have occurred, for example *Leclercqia uncinata* Xu *et al.*, a herbaceous lycopsid with hooked leaves [27]. Today twining stems of climbing plants are very common in tropical and subtropical forests, but prior to this study little is known about their direct macrofossils through time, even in the Mesozoic and Cenozoic. To a large extent, much fewer quantities available for fossilization of twigs and stems than other detached organs (pollen, flowers, seeds, and leaves) [28] may have resulted in an extremely low probability for the twining stems preserved in rocks. As evidenced here from the subtropical Shanwang flora, therefore, the diversity of climbing plants may have been underestimated in subtropical and tropical evergreen forests during the Mesozoic and Cenozoic.

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