

A cone-like flower from the Lower Cretaceous of China

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Angiosperms are by far the most diversified plant group in the current world, and their great diversity was a prerequisite for the radiation of mammals — including human beings. Understanding the evolutionary history of angiosperms is one of the key tasks for palaeobotanists. In the past decades numerous fossils of early angiosperms have been documented worldwide ¹⁻¹⁴. However, these fossils usually lack anatomical details. Theoretically, angiosperms must have evolved from their ancient gymnospermous ancestors ¹⁵, but most of the currently known early angiosperms have well-defined angiosperm features that are lacking in known gymnosperms. Such a gap between gymnosperms and angiosperms leaves a lacuna in the evidence chain for evolutionary hypotheses. Thus searching for an angiosperm flower especially with enough anatomical details to appear chimeric between gymnosperms and angiosperms becomes an ultimate task for systematic botanists. Here we report a female flower (*Xilinia shengliensis* gen. et sp. nov) that demonstrates the feature characteristic of angiosperms, angio-ovuly, as well as cone-like morphology that is unusual in angiosperms. Its chimeric character assemblage makes *Xilinia* unique and interesting in terms of angiosperm origin. In addition, *Xilinia*'s anatomic details open a rare window to observe early angiosperms in detail and provide raw materials for deciphering the evolution of flowers.

MATERIALS AND METHODS

The Lower Cretaceous of Inner Mongolia, China is famous for its coal production, and many coal mines are exploited by stripping the covering sediments. One of them, Shengli Coal Mine, is located near Xilinhot, Inner Mongolia, about 460 km north of Beijing. Several coal layers of economic interest in the Shengli Formation are exploited in the Shengli Coal Mine (44°0'20"N, 116°1'10"E, Fig. S1a). Associated with these coal layers are intercalating layers of siltstones. Our present specimen is uncovered from one of such layers overlying Coal Layer 5 (Fig. S1b), which was dated as the Albian (late Early Cretaceous)¹⁶.

Geologically, this area belongs to the Erlian Basin (also called Eren Basin). The coal-bearing strata in the mine belong to the Baiyanhua Group (the Lower Cretaceous) ¹⁷⁻²¹. The group includes the overlying Shengli Formation and underlying Xilin Formation ¹⁷⁻²¹. Some authors also call the Shengli Formation as the Saihantala (Saihan Tal) Formation ²²⁻²⁴. Stratigraphically, the Shengli Formation (Saihantala Formation) was comparable to the Fuxin Formation, Chengzihe Formation ^{17-21,23-25}. Recent dating indicated that the coal in the formation was formed around 107-109 Ma (the Albian, the late Early Cretaceous), setting an upper limit for the age of the specimen studied here ²⁶.

Our specimen was collected from an indurated siltstone layer overlying Coal Layer 5 in June, 1994 (Fig. S1b). The three-dimensionally preserved coalified material made detailed anatomical study possible. Lithological analysis of the sediments performed in the School of Geological Sciences and Engineering, Nanjing University, Nanjing, China indicated that the dark brown fossiliferous layer was composed of siderite and hematite. The hardness of siderite and hematite allowed faithful three-dimensional preservation of the fossil material.

The specimen in the present study was preserved as a coalified compression, and it was exposed by physically breaking the sediment bulk. The specimen was photographed with a Nikon 300s camera. Due to apparent desiccation and shrinking after burial, the coalified plant parts could be easily dislocated from the sediment. These parts were removed and cleaned with HF for later observation. The axis and connected carpels were photographed using a Zeiss stereomicroscope and a Nikon SMZ1500 microscope, then coated with gold and observed using a Hitachi S800 SEM at the Institute of Botany, CAS or a Leo 1530 VP SEM at the Nanjing Institute of Geology and Palaeontology, CAS, and their images were recorded either on black-white negatives or digitally. Nitric acid was applied to soften the coalified plant parts before paraffin sectioning. This processing made some of the epidermis more or less transparent and elastic. The softened plant parts were dehydrated, put in alcohol, embedded in paraffin, and sectioned following the routine applicable for extant plant materials, except without staining²⁷⁻²⁹. The thin sections were then observed and photographed using a Nikon light microscope. A small piece of a carpel including ovule membrane was embedded in SPI-Pon, ultrathin cut for TEM according to the procedure described previously³⁰. The TEM observation was performed using a Hitachi 7650 TEM at the Nanjing Normal University, Nanjing, China, and the results were recorded digitally in JPEG format. The printed pictures were digitalized and saved in TIFF format. All photographs were organized for publication using a Photoshop 7.0.

RESULTS

Xilinia gen. nov

(Figure S2-8)

Generic diagnosis: Flower female, pedicellate, with perianth. Perianth elements and carpels helically arranged along the flower axis. Perianth elements linear. Each carpel composed of an ovarian wall and an ovule within. Ovarian wall composed of longitudinally oriented cells, covered with isodiametric epidermal cells. Ovule including an integument and a nucellus. Integument composed of radially arranged parenchymatous cells. Ovule anatropous, with its micropyle close to the flower axis. Ovule membrane sac-like, with longitudinally oriented straight-walled cells, with clear stratification including layers similar to nexine, columella, and tectum.

Etymology: *Xilin-* for Xilinhot, where the fossil was collected.

Type species: *Xilinia shengliensis* gen. et sp. nov.

Remark: The fossil flower is distinguished from all known fossil plants by its unique character assemblage of linear perianth elements, helically arranged carpels, and each carpel enclosing an anatropous ovule with ovule membrane.

Xilinia shengliensis gen. et sp. nov

Description: The flower is coalified, embedded in a block about 12.5 cm x 11 cm x 4 cm, collected from the Shengli Formation (the Lower Cretaceous) at Shengli Coal Mine (Figs. S1a-b, S2a-b). The flower is female, pedicellate, with perianth, up to 23 mm long and 14 mm wide (Figs. S2a-b). The pedicel is about 3.5 mm in diameter, 11 mm long (Figs. S2a-b, e-f). The perianth is composed of numerous linear perianth elements, rectangular in cross-view, leaving rhomboidal scars on the axis, 1 mm wide, at least 22 mm long, with simple pits on the wall of tracheids (Figs. S2a-g, S4a). The gynoecium is ovoid, about 8 mm wide and 9 mm long, with numerous carpels helically arranged on the flower axis (Figs. S2a-b, S3a). The axis is about 2.6 mm wide in the bottom, tapering to the distal, with numerous stubs left by fallen carpels on it (Figs. S4e,h, S6a-b). Anatomically, the axis is composed of a central pith surrounded by secondary xylem, phloem, and epidermis (Figs. S6a,f-g). The pith is of parenchyma, about 1.1 mm in diameter (Figs. S6a,f). Cells in the pith are more or less isodiametric in cross-view, 17-25×19-39 μm, elongated longitudinally, 49-100 μm long, some with simple pits on their cell walls and organic infillings in the lumina (Figs. S5i, S6a-g). There are two types of organic infillings, solid or spongy, in the cell lumina of the pith (Figs. S6c-d). The xylem includes isolated primary xylem bundles and secondary xylem

cylinder (Figs. S6f-h). The primary xylem is endarch and distributed along the margin of the pith (Figs. S6f-h). The secondary xylem forms a ring around the pith, is about 0.7 mm thick, composed of tracheids, cavities, and rays, penetrated by carpel traces (Figs. S6a-b,f). The tracheids are about 18 μm wide, with simple and bordered pits (Figs. S5i-j, S6c-d,g-h). The cavities are frequently seen in the early secondary xylem, up to 265 μm long and 115 μm in diameter, probably lysigenous (Figs. S6a,b,d-f,i). Rays are uniseriate, 3-8 cells high, and up to 72 μm high (Figs. S5i, 6e). The phloem and epidermis of the flower axis are hardly discernible in the paraffin sections, probably due to the nitric acid processing, although the epidermis can be seen using SEM (Figs. S4e,h). There is no trace of androecium in the flower (Figs. S2a-b). More than 60 carpels are helically arranged along the flower axis, with their traces penetrating the xylem cylinder in the flower axis (Figs. S2a,b, S3a, S6b,f,g). Carpel size and shape vary depending on their positions in the gynoecium, inverted triangular in adaxial and abaxial views, wedge-shaped in side view, 1.7-2.3 mm long, 0.7-1.06 mm wide, and 0.56-0.85 mm thick (Figs. S3b-c, S4c-d,f-g, S5a,f). A carpel is composed of an ovarian wall and an anatropous ovule within (Figs. S3c, S4c, S5f-h). The ovarian wall is composed of longitudinally oriented hypodermis and epidermis (Figs. S5d-h, S6j). The epidermal cells are isodiametric in surface view, about 7-12 $\times$ 11-22 μm in surface view (Figs. S6j). The ovarian wall may be up to 35 μm thick, with longitudinal striations on its inner surface (Figs. S5d-h). There is no style, and the papillae are restricted to the distal portion of the carpel (Figs. S4c-d,f-g, S5a-c). The ovule is anatropous, with its micropyle close to the flower axis (Figs. S5f-h). The integument encloses nucellus, up to 83 μm thick, composed of radially arranged parenchymatous cells, easy to dissolve in nitric acid (Figs. S5f-h). Ovule membrane is about 1.8 mm long, 1 mm wide, thin, smooth-surfaced, amber in color, in sac form, tapering distally, of longitudinally oriented cells, becoming thicker distally due to additional cuticle layer of the integument, enclosed by the integument (Figs. S3b-e, S5f,h, S6k-m, S7a-d). No content is seen within the ovule membrane, and therefore two layers of the membrane are frequently tightly compressed against each other (Figs. S5f, S6k-m, S7b,e). Each membrane is about 1.7 μm thick, including three distinct layers, namely, a 0.36 μm thick nexine, a 0.86 μm thick columella layer, and a 0.66 μm thick tectum layer (Figs. S7a-g). The columella layer includes sparse rod-formed vertical structures separated by wide space (Figs. S7e-g). The tectum layer covers the columella layer, with some stratification (Figs. S7e-g).

Etymology: *shengliensis* for the Shengli Coal Mine, from where the fossil was collected.

Holotype specimen: 9222.

Depository: the Herbarium, Institute of Botany, Chinese Academy of Sciences, Beijing, China.

Horizon: the Shengli Formation, Baiyanhua Group (the Lower Cretaceous).

Age: the late Early Cretaceous (<107 Ma).

Locality: Xilinhot, Inner Mongolia, China (44°0'20"N, 116°1'10"E).

Remarks:

The ovule membrane of *Xilinia* is the origin from which we start to identify all other parts in this fossil plant. The presence and dimension of the ovule membrane in this fossil indicates that it is female, the layer immediately surrounding the ovule membrane is an integument, the layer outside the integument is an ovarian wall, the proximal surrounding parts constitute the perianth, and the whole organ is a female flower.

There is no subtending bract below each carpel in *Xilinia* (different from conifers) as the carpel stubs is smoothly connected to the central axis in the surface view (Figs. S4e,h) and the anatomical observation shows no trace of such subtending bract (Figs. S6a-b). No ovule/seed on the adaxial surface of the lateral appendage in *Xilinia* further alienates *Xilinia* from Coniferales.

Some Mesozoic fossils may appear similar to *Xilinia*, but their similarity is only superficial. For example, *Karkenian* (Ginkgoales) from the Jurassic appears similar to the female part of *Xilinia*, but each of its lateral seeds is inverted on a slender stalk and exposed^{31,32}, unlike ovules enclosed in the ovary in *Xilinia*.

For *Xilinia*, the terms “nexine”, “columella”, and “tectum” are “borrowed” from angiosperm pollen because of

their remarkable resemblance to the stratification of angiosperm pollen wall. However, the significant difference between microspore (pollen) and megaspore (ovule) should be borne in mind.

DISCUSSIONS

Literally, angiosperms are defined by their enclosed seeds. The exceptions to this rule (i.e., gymnosperms with enclosed seeds) include Caytoniales and some Coniferales³³⁻³⁶. Caytoniales have their seeds enclosed by their cupule walls but have their ovules pollinated in a gymnospermous way, namely, their pollen grains enter the cupule, approach and then fertilize the ovules. In the meantime, some Coniferales may have their seeds enclosed and protected after pollination³⁶. Therefore a strict and sufficient criterion for angiosperms is angio-ovuly before pollination, that is, the ovules are enclosed before pollination (Tomlinson and Takaso, 2002; Wang, 2010, 2018). All plants with their ovules enclosed before pollination are unexceptionally angiosperms. The presence of ovule membrane with little content in *Xilinia* suggests that the original content lacks fossilizable materials before fossilization. Considering the very delicate parenchyma of the integument has been preserved perfectly in the same fossil (Figs. S5f-h), such a lack of preserved material within the ovule membrane sac implies that the ovules of *Xilinia* were still premature, lacking cellularized content when fossilized. Therefore *Xilinia* is very likely preserved in its pre-pollination stage. The integument encloses the nucellus almost completely except at the micropyle (Fig. S5g). The ovule is inside the ovarian wall that is integral, except for physical cracks caused by desiccation (Figs. S4c-d,f-g, S5a,f-g), suggesting that ovules of *Xilinia* are fully enclosed by its ovarian wall. This enclosure of the ovule before pollination is in line with the occurrence of papillae on the carpel tip (Figs. S5b-c), which may function as a stigma during the pollination. Furthermore, the female portion of *Xilinia* is surrounded by the lower helically arranged perianth elements (Figs. S1a-f). All the above information collectively points to *Xilinia* being an angiosperm.

Although an angiosperm, *Xilinia* has several features frequently seen in gymnosperms and unexpected for typical angiosperms, including ovule membrane with columellate stratification, lack of typical perianth, unisexuality, and bordered pits. Following we will discuss these characters and their implications.

The occurrence of ovule membranes are rare in angiosperms³⁷, and only poorly developed in Magnoliaceae³, so the presence of ovule membrane in *Xilinia* is at odds with an angiosperm affinity. Furthermore, the ovule membrane stratification present in *Xilinia* is never seen in any known seed plants^{3,32,38-51}. An ovule membrane has been reported in various fossil taxa, but only limited number of them have been examined using TEM, making our comparison here incomplete. Among those observed using TEM, neither of Cladoxylopsids⁵⁰, Lycopodales^{40,41,52-54}, Isoetales⁵⁵, Marsileales⁴⁴, nor those of Pteridospermales^{38,54}, Cordaitales⁵⁴, Ginkgoales^{32,42,48}, Coniferales^{45,56} has a wall stratification like that seen in *Xilinia*. Among them, only some Pteridospermales, Cordaitales, and Lycopodales^{38,54}, Cordaitales⁵⁴, Ginkgoales^{32,42,48}, Coniferales^{45,56} have a three-layered ovule/megaspore membrane stratification (Table 1). However, their spongy layer is composed of anastomosing bacula, thus distinct from the vertically oriented, distantly-spaced rod-like structures seen in the columella-like layer of *Xilinia* (Figs. S7e-g). *Xilinia* is unique among seed plants in terms of its ovule membrane organization. It is noteworthy that such stratification is comparable to that of a typical angiosperm pollen wall. The occurrence of similar stratification in the megaspore (ovule) of *Xilinia* and typical angiosperm pollen may be taken as an example of parallel evolution occurring in two genders.

The helical arrangement of the carpels in *Xilinia* is not only like that of carpels in Magnoliales⁵⁷ but also like that of lateral cone appendages in Cycadales and Coniferales⁵⁸⁻⁶⁰. Such a feature has been taken as plesiomorphic for angiosperms⁶¹.

The perianth elements of *Xilinia* are linear or needle-like rather than typical petaloid, implying that these elements may not play as much protective or attractive roles as their counterparts do in typical extant flowers. This

observation agrees with the implications given by *Chaoyangia*^{5,12} and *Archaeofructus*^{6-8,10,62,63}, *Baicarpus*⁶⁴, *Neofructus*⁶⁵, *Eofructus*⁶⁶, *Nothodichocarpum*⁶⁷, from the Barremian-Aptian, which have no perianth at all. Also it agrees with the result of outgroup comparison: the outgroup of angiosperms, gymnosperms, have no perianth, either. However, a perianth-like structure has been interpreted at least in *Callianthus* from the Barremian-Aptian^{11,12}, suggesting that early angiosperms had diversified in terms of perianth morphology by the Albian.

Dioecism is a feature frequently seen in gymnosperms but only relatively rarely seen in angiosperms. Classical theories proposed that the flowers were ancestrally bisexual, and unisexual flowers were derived from bisexual ones through reduction^{11,12}. However, these theories cannot satisfactorily explain how the monoecism in angiosperms is derived from dioecism in gymnosperms, specifically, how the formerly separated male and female parts got aggregated into an individual plant organ, flower. *Xilinia* seems more similar to a female cone in conifers, rather than a typical bisexual flower. The organization and morphology of *Xilinia* are not alone in their mystery, and they are coupled with the chimeric anatomic details.

The presence of simple pits (frequently seen in angiosperms) in the vascular bundle of the perianth element and bordered pits (frequently seen in gymnosperms but rarely seen in Monocots, *e.g.* *Dracaena*⁶⁸) in the flower axis of *Xilinia* appears to point to its chimeric affinity between angiosperms and gymnosperms. This is further reinforced by the cone-like morphology and organization of *Xilinia*. Such an unusual chimeric character combination suggests that *Xilinia* may not have fully completed its transition from gymnosperms to angiosperms, bridging these otherwise distinctly separated groups.

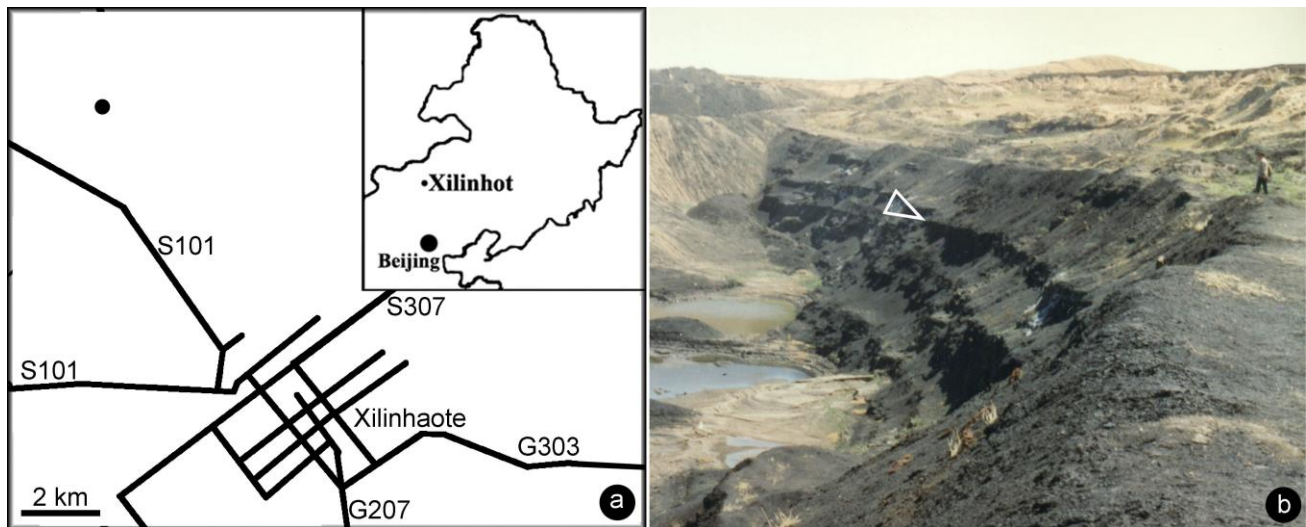


Figure S1. General information of the fossil locality.

- a. Geographical position of the fossil locality. The inset shows northeastern China and the fossil locality (Xilinhot) is north to Beijing. The main map shows the fossil locality (black dot) in the northwest of Xilinhot City.
- b. Outcrop at the Shengli Coal Mine, Xilinhot, Inner Mongolia, China (44°0'20"N, 116°1'10"E) in 1994. The fossil specimen is collected from the layer arrowed.

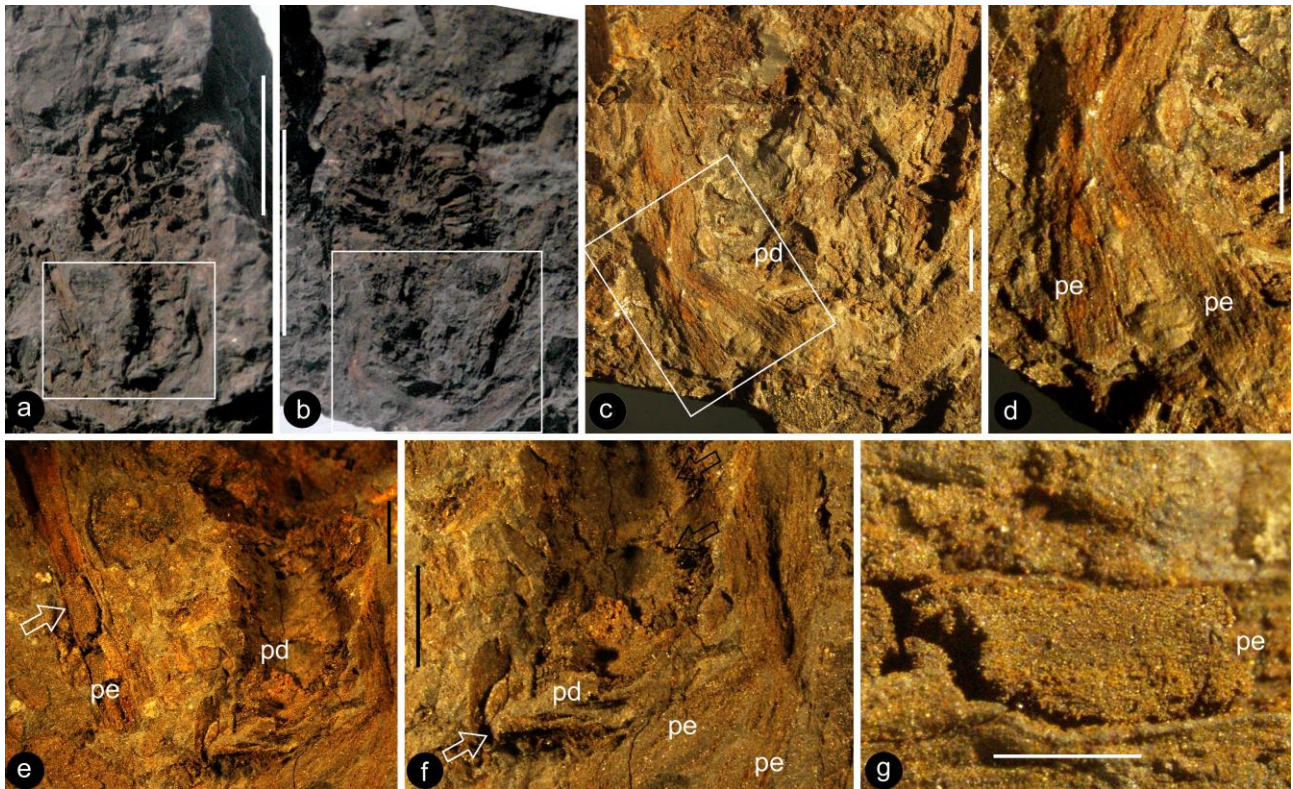


Figure S2 *Xilinia* and its details. Light microscopy. Specimen number 9222.

- a, b. Two facing parts showing the general morphology of the cone-like flower. Note the helical arrangement of the carpels around the axis (missing in the figures). Bar = 1 cm.
- c. A detailed view of the rectangle in Fig. S2b. Note the pedicel (pd) and surrounding perianth elements. Bar = 2 mm.
- d. A detailed view of two perianth elements (pe) in Fig. S2c. Bar = 1 mm.
- e. A detailed view of the rectangle in Fig. S2a. Note the pedicel (pd) and one of the surrounding perianth elements (pe, arrow). Bar = 2 mm.
- f. A detailed view of the bottom-right portion in Fig. S2e. Note the pedicel (arrow, pd) and physically connected surrounding perianth elements (pe) physically connected. Bar = 2 mm.
- g. A detailed view of the perianth element (pe) arrowed in Fig. S2e. Note the organic preserved tissue. Refer to Figs. S4a-b. Bar = 1 mm.

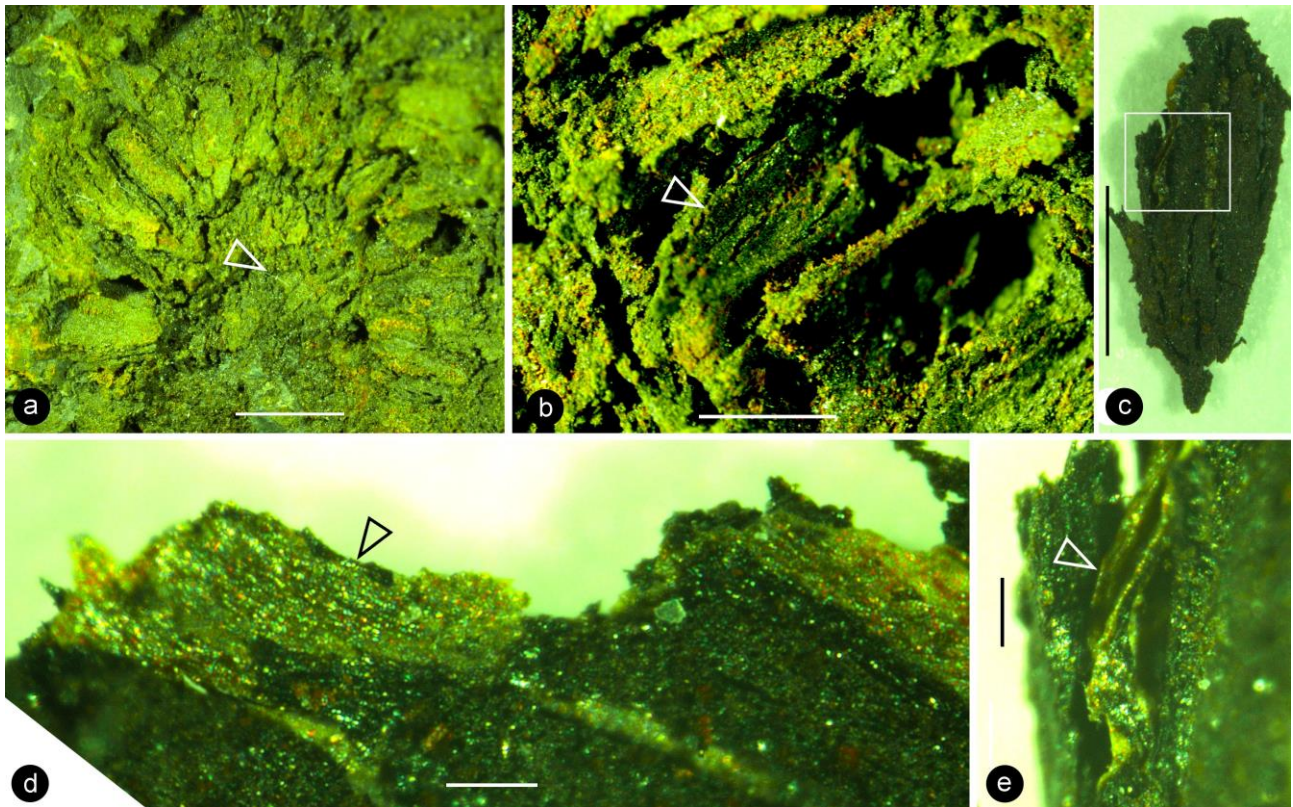


Figure S3. Details of the carpels and ovule membrane. Light microscopy.

a. Multiple carpels helically arranged around the centre (arrow). Bar = 2 mm.

b. One of the carpels (arrow) still embedded in the sediments. Bar = 1 mm.

c. The same carpel as in Fig. S3b, free of sediments. Bar = 1 mm.

d. Amber-colored ovule membrane (arrow) *in situ* in a carpel. Bar = 0.1 mm.

e. Shiny amber-coloured ovule membrane (arrow) embedded in coalified tissues, enlarged from the rectangle in Fig. S3c. Bar = 0.1 mm.

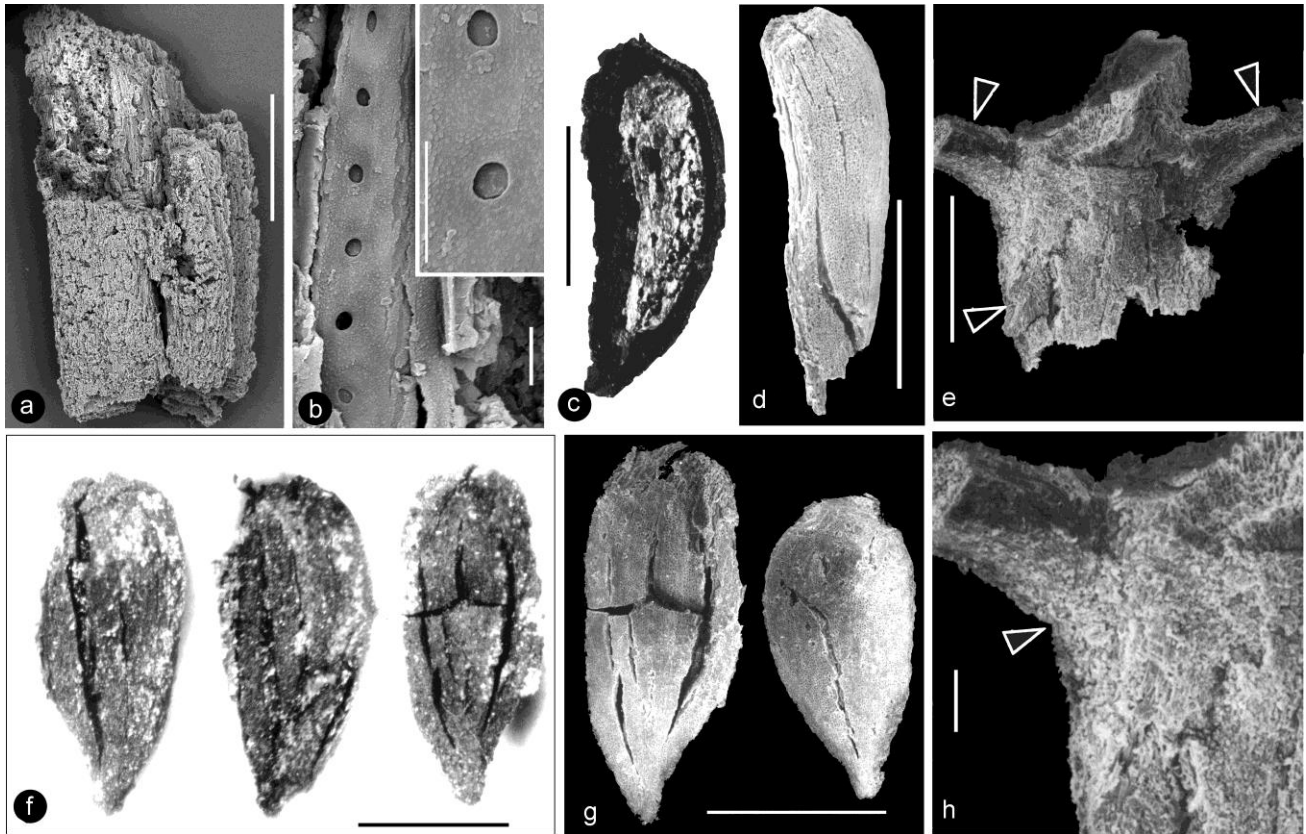


Figure S4 Details of perianth elements, carpels, central axis of *Xilinia* gen. et sp. nov. SEM except 4c and 4f.

- a. The perianth element shown in Fig. S2g. Bar = 5 mm.
- b. Simple pits on the tracheid wall in the perianth element shown in Fig. S4a. Two of them are shown in detail in the inset. Bars are 5 and 1 μ m, respectively.
- c. A side view of a broken carpel, of the same orientation as in Fig. S4d. Note the light-colored ovule membrane inside the carpel. Stereomicroscopy. Bar = 1 mm.
- d. A side view of a wedge-shaped carpel. Bar = 1 mm.
- e. A portion of the axis with helically arranged stubs (arrows) left by the fallen carpels. Bar = 0.5 mm.
- f. Adaxial view of three carpels of triangular shape. Stereomicroscopy. Bar = 1 mm.
- g. Abaxial view of two carpels of triangular shape. The right one is from the distal portion of the gynoecium. Note the cracks due to desiccation. Bar = 1 mm.
- h. Details of the axis shown in Fig. S4e. Note the integral surface (arrow) below the carpel stub, suggestive of lack of subtending bract. Bar = 0.1 mm.

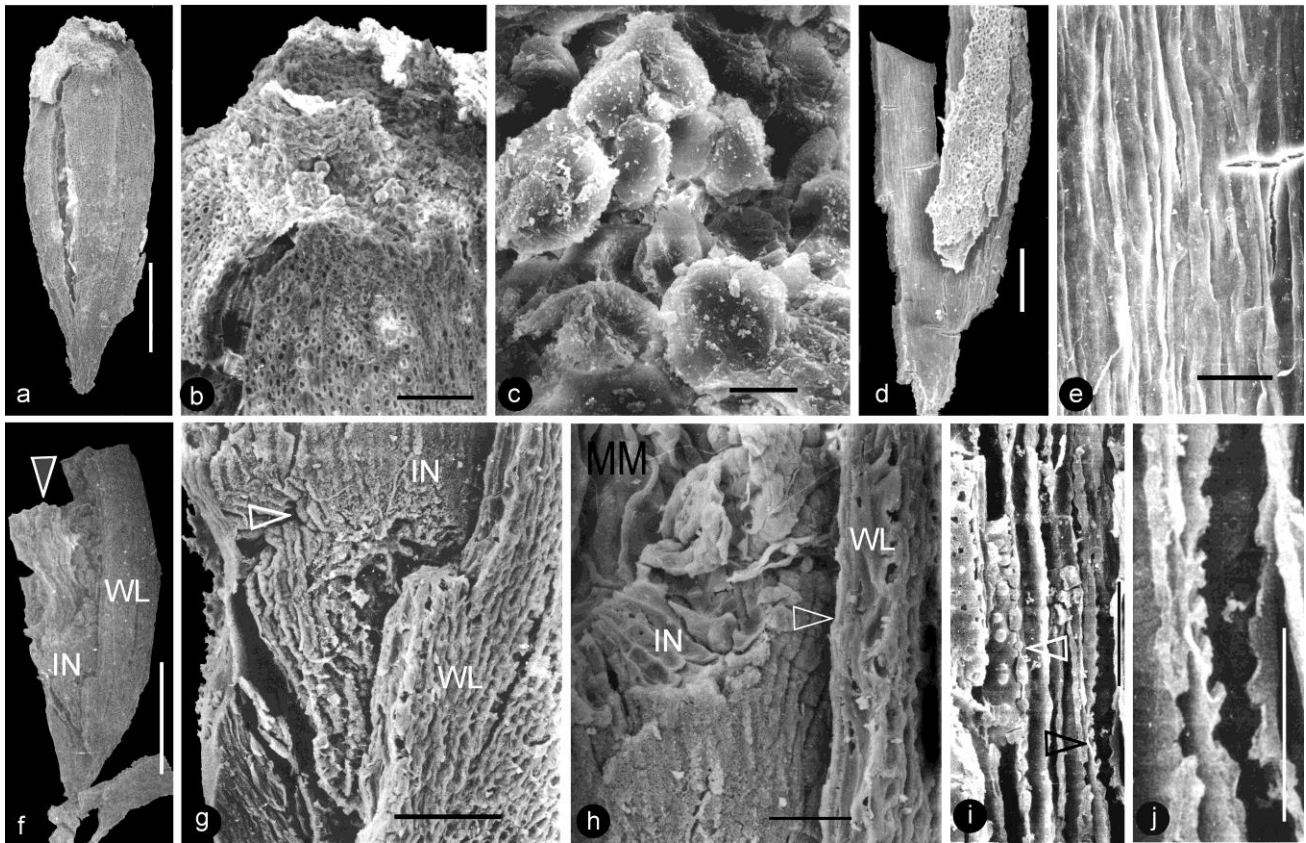


Figure S5. Morphology and anatomy of carpels. SEM.

a. Adaxial view of an integral carpel of triangular shape. Note the cracks due to desiccation. Bar = 0.5 mm.

b. Apex of the carpel in Fig. S5a. Note the cellular details on the carpel surface (lower) and papillae on the apex (upper). Bar = 0.1 mm.

c. Details of the papillae on the apex of the carpel in Fig. S5b. Bar = 10 μ m.

d. Ovarian wall with cellular details. Bar = 0.2 mm.

e. Longitudinal striations on the inner surface of the ovarian wall, enlarged from Fig. S5d. Bar = 30 μ m.

f. A broken carpel showing ovarian wall (WL), integument (IN), and ovule membrane (arrow). Bar = 0.5 mm.

g. Details of the lower portion of the carpel in Fig. S5f. Note the cellular details of the ovarian wall (WL), integument (IN), and micropyle (arrow). Bar = 0.1 mm.

h. Details of the middle portion of the carpel in Fig. S5f. Note the cellular details of the ovarian wall (arrow, WL), radial files of parenchymatous cells in the integument (IN), and ovule membrane (MM). Bar = 50 μ m.

i. Anatomy of the flower axis. Note the pith parenchyma with organic infilling (white arrow), and bordered pits on the tracheid wall (black arrow). Bar = 30 μ m.

j. Detailed view of bordered pits on the tracheid wall, enlarged from Fig. S5i. Bar = 20 μ m.

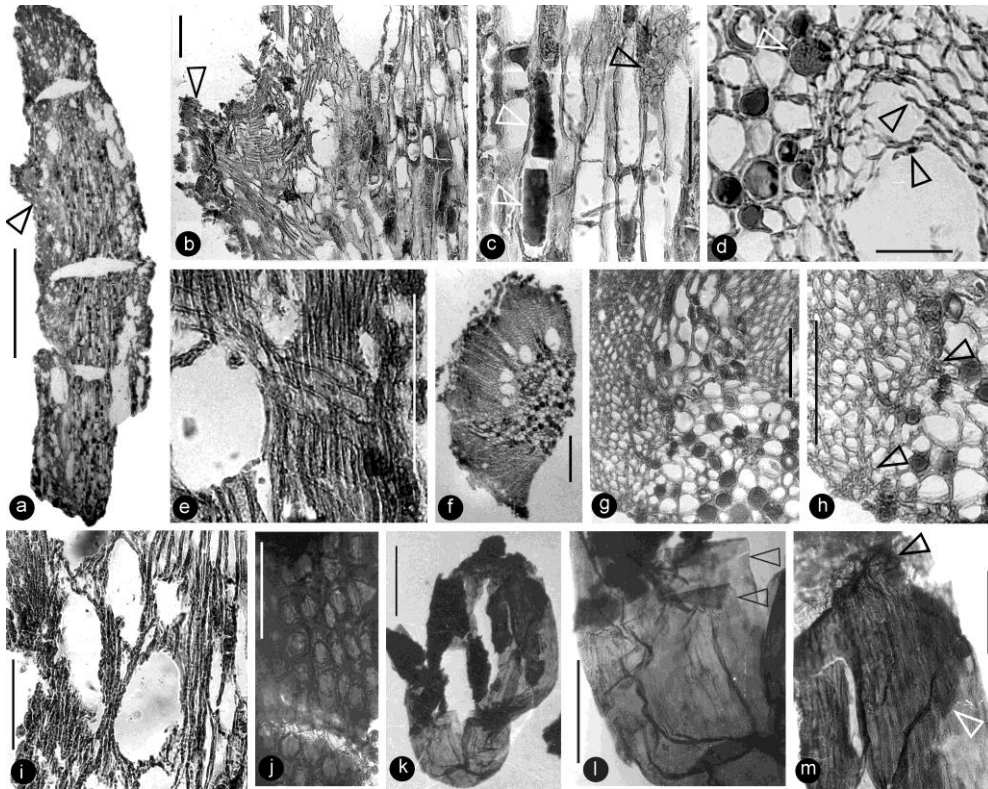


Figure S6. Anatomy of the flower axis and details of the ovule membrane. Light microscopy.

- a. A longitudinal section of the flower axis. Bar = 1 mm.
- b. A detailed view of the axis, enlarged from the arrowed region in Fig. S6a, showing a trace (arrow) to a carpel and pith (right). Bar = 0.1 mm.
- c. A longitudinal detailed view of the pith, enlarged from Fig. S6a. Note the elongate rectangular cells with two types of organic infillings (lower white arrow and black arrow) and simple pit (upper white arrow) on the cell wall. Bar = 0.1 mm.
- d. A close-up of cross-view of the pith (left) and adjacent xylem. Note two types of infillings in the parenchymatous cells in the pith (white arrow) and residual cell walls (black arrows) in the lysigenous cavity in the xylem. Bar = 50 μ m.
- e. A detailed view of the xylem in axis. Note cavity (left) in the xylem and a the formed by a three-cell-high ray and tracheids in the xylem. Bar = 0.1 mm.
- f. A cross-section of a portion of the axis. Note cavities in the inner portion of the xylem. Bar = 0.2 mm.
- g. A detailed view of the axis in cross-section. Note the pith (lower right), xylem (upper left), a trace to a carpel (middle top), and some cells in pith with organic infillings. Bar = 0.1 mm.
- h. Another detailed cross-view of the axis. Note the pith (right), xylem (left), small cells of the protoxylem (arrows), and some cells in pith with organic infillings. Bar = 0.1 mm.
- i. Near longitudinal axis section showing the pith (right) and xylem (left) with cavities. Bar = 0.1 mm.
- j. Elongate or isodiametric epidermal cells of an ovarian wall. Bar = 50 μ m.
- k. Whole ovule membrane, with some coalified materials attached. Bar = 0.5 mm.
- l. A detailed view of the bottom portion of the ovule membrane shown in Fig. S6k. Note the transparent amber-like colour and two layers of the membrane (arrows). Bar = 0.2 mm.
- m. Distal portion of the ovule membrane shown in Fig. S6k. Note the elongate cells on the membrane and an additional layer (arrows), probably due to the presence of an integument. Bar = 0.2 mm.

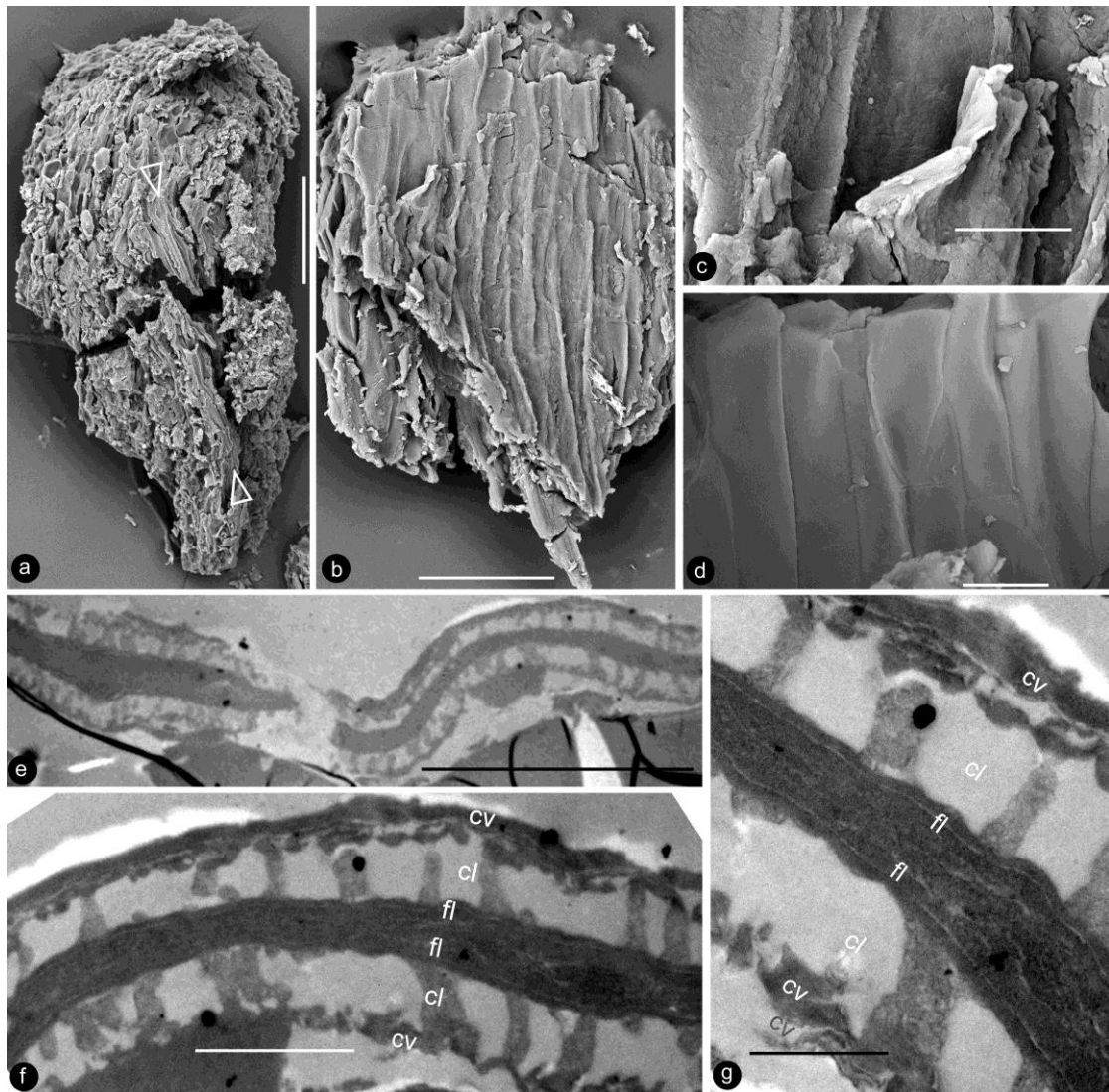


Figure S7. Details of the ovule membrane. Figs. S7a-d are SEM, Figs. S7e-g are TEM.

- a. A longitudinal view of an ovule. Note the ovule membrane (arrows) sandwiched between parenchymatous integument tissues and the integral top surface of the carpel. Bar = 0.1 mm.
- b. A surface view of an ovule membrane. Note the elongate cell outlines on the membrane. Bar = 50 μ m.
- c. Detailed view of Fig. S7b, showing two layers of the membrane appressed each other. Bar = 10 μ m.
- d. A surface view of an ovule membrane showing the elongate cell outline. Bar = 10 μ m.
- e. Two layers of the ovule membrane shown in Fig. S7a, appressed against each other. Bar = 10 μ m.
- f. Detailed view of Fig. S7e, showing two appressed nexine (fl), columella layer (cl), and tectum layer (cv). Bar = 2 μ m.
- g. Detailed view of the ovule membrane enlarged from Fig. S7f, showing two compressed nexines (fl), columella layer (cl), and tectum layer (cv). Note the light-coloured line in the nexine. Bar = 1 μ m.

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Table 1. Megaspore/ovule membrane comparison among *Xilinia* and other taxa.

	Nexine	Spongy layer	Tectum	Sexine	Exine	Affinity	Age
<i>Hexapterospermum delevoryi</i> ⁵⁴	?	granulose	granular	?	?	Pteridospermals	Pennsylvanian
<i>Pachytesta</i> ⁵⁴	0.11-0.22, unlayered	6.3, bacula anastomosing regularly	0.11-0.96	3.68	4.43-6.91	Pteridospermals	Pennsylvanian
<i>Conostoma</i> ⁵⁴	0.11-0.21, no lamellation	3.26-4.23, bacula	0.55-0.84	3.81-5.07	3.94-5.28	Pteridospermals	Pennsylvanian
<i>Mitrospermum compressum</i> ⁵⁴	0.05, no lamellation	spongy, bacula anastomosing irregularly	?	6.08	6.13	Cordaitales	Pennsylvanian
<i>Taxospermum undulatum</i> ⁵⁴	0.11	Spongy, bacula anastomosing regularly	0.4	?	5.22	Cordaitales	Pennsylvanian
<i>Mazocarpon oedipternum</i> ⁵⁴	12-50, anastomosing densely	hollow bacula anastomosing regularly & sparsely	0.56	?	?	Lycopodales	Pennsylvanian
<i>Xilinia</i>	?	rodlet-like	?	?	?	Angiosperms	Early Cretaceous