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Report

A new gnetalean macrofossil from the Lower Cretaceous of the Laiyang Basin, eastern China

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Gnetophytes are a key group of plant for understanding seed plant phylogeny, partly because of their unique and elusive morphology, such as xylem with vessels, phloem with chaperones, reticular veins, and double fertilization (Endress, 1996). In particular, the ovule bears a membranous integument, the upper part of which extends beyond the seed envelope to form a micropylar tube. Therefore, gnetophytes occupy a unique evolutionary position in the phylogeny of seed plants and apparently represent a transition between angiosperms and other gymnosperms (Ran et al., 2018). Modern gnetophytes consist of only three families: Ephedraceae, Gnetaceae, and Welwitschiaceae, and each family contains only one genus. Ephedraceae (*Ephedra* L.) are the earliest diverging group of Gnetales, with a total of 70 extant species, and usually occur in cold and arid places in Asia, Europe, northern Africa, western North America and South America (Price, 1996; Yang et al., 2017b).

The earliest reliable fossil records of gnetophytes can be traced back to at least the Late Permian, but they are mostly preserved as fragmented twigs, leaves, and seed fossils (Wu et al., 1986; Wang, 2004). During the Early Cretaceous, gnetophytes were most abundant, and many gnetalean mega-fossils have been reported in Australia, Europe, North America, South America, Mongolia and particularly in northeastern China (Liaoning). These reported gnetophyte fossils show higher diversity of gnetophytes in Cretaceous than today, providing significant clues for studying the origin, evolution, and geological distribution patterns of this plant group. However, currently, there is no effective hypothesis or evidence on how the unique morphological features of gnetophytes have arisen or on the relationships between living and fossil species. Therefore, any fossil material related to gnetophyte plants is highly valuable and meaningful.

Here, we describe a new macrofossil plant of Ephedraceae from the Lower Cretaceous Laiyang Formation in Shandong Province, eastern China. This new reproductive shoot is well preserved and possesses unusual female spikes that distinguish it from all other known gnetophyte species. The new fossils may improve our understanding of the relationships and evolution of the divergent morphology within the gnetophytes, and help to understand the diversity and biogeography of modern species. The detail of geological setting and fossil preparation and illustration are provided in Appendix A.

1. Systematic description

Order—Gnetales Luerssen, 1879
Family—Ephedraceae Dumortier, 1829
Genus—*Laiyangia* P.H. Jin, gen. nov.
Etymology—The generic name "*Laiyangia*" is derived from the Laiyang localities where the specimens were collected.

Generic diagnosis—Reproductive shoots having swollen nodes and internodes; leaves opposite, triangular, the lower part *ca.* 2/3 fused into a sheath; female spikes compact with no observable nodes and internodes, axillary to leaves or terminal to twigs, shortly pedunculate and narrowly elongate, with 5–8 pairs of fertile bracts; bracts decussately opposite, triangular and incurved, with each subtending 1 axillary sessile seed; seeds ellipsoid and plump with a distal and hollow micropylar tube.

Type Species—*Laiyangia compacta* P.H. Jin, sp. nov.
Species—*L. compacta* P.H. Jin, sp. nov.
Holotype—SDLY–2020–41A, B (Figs. 1A (a, b, d-i) and 1B)
Other illustrated material—SDLY–2021–47A (Fig. 1A (c))
Type locality—Hangyadi Country, Laiyang City, Shandong Province, China (Fig. S1A, B)
Stratigraphy—Laiyang Formation, Lower Cretaceous (Hauterivian–Barremian) (Fig. S1A–C)

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Etymology—The species name '*compacta*' refers to the compactness of the female spikes of the fossil species.

Specific diagnosis—The same as for the genus.

Description—The studied material include several articulated reproductive branches of *L. compacta*, and two were preserved well enough to be described in detail. The most completely preserved specimen is, *ca.* 5.13–9.53 cm long and *ca.* 3.52–4.66 cm wide (Fig. 1A (a, b)). The main shoot is slightly curved, with nodes and internodes. Nodes are swollen; internodes are straight, 2.97–3.27 cm long, *ca.* 0.58–1.72 mm wide, with many fine longitudinal striations (Fig. 1A (h)). The main shoot branches at least 4 times. Lateral branches are spreading upwards at 30–80° and monopodial or dichasially ramifying once to twice. Leaves subtend lateral branches, are triangular, approximately 0.83–0.87 mm long and 0.46–0.51 mm wide at the widest point of the base, 2–3 opposite at nodes and fused into a sheath in the *ca.* 2/3 lower part, but their venation is indiscernible.

Female spikes are compact with no observable nodes and internodes, shortly pedunculate and narrowly elongate, axillary to leaves or terminal to twigs, *ca.* 1.36–2.70 cm long and 0.22–0.29 cm wide. Each female spike bears 5–8 pairs of fertile bracts (Fig. 1A (d)). Bracts are decussate and opposite and close to the axis, narrowly triangular with an acute apex, incurved, *ca.* 1.33–3.23 mm long and 0.35–0.52 mm wide. Each bract subtends one seed on the adaxial side, while in one specimen, it was observed that there may be four seeds on the adaxial side of the uppermost bract of the female spike (Fig. 1A (e–g)) (this feature is only an isolated occurrence). Seeds are ellipsoid and plump, approximately 1.73–2.42 mm long and 1.03–1.60 mm wide, and probably have an oval to cuspidate apex, a smooth surface, and fine longitudinal grooves. Each seed bears a thin outer envelope and a distal, hollow micropylar tube, approximately 0.70–0.86 mm long and *ca.* 0.04–0.07 mm in diam. (Fig. 1A (e–g)).

Fortunately, some epidermal features were observed in the outer epidermis of the seed envelope under fluorescence microscopy. Epidermal cells are irregular, polygonal or elongate rectangular with straight anticlinal walls, regularly arranged in longitudinal files, approximately 40–60 μm long and 10–20 μm wide (Fig. 1A (i)). Stomata are sparsely distributed and irregularly arranged in longitudinal files (Fig. 1A (i)). Stomatal complexes are rounded to elliptical in outline, haplocheilic, monocyclic, approximately 60–80 μm long and 40–50 μm wide. The guard cells are slightly sunken and generally surrounded by five to seven subsidiary cells, which form a ring (Fig. 1A (i)).

2. Comparison with other gnetalean plants

Laiyangia compacta bears a reproductive shoot with nodes and internodes, a monopodial or dichasially branching pattern and opposite triangular leaves. Female spikes are narrowly elongate with short pedicels, straight or slightly curved, and relatively compact with no observable nodes or internodes. The female spikes consist of 5–8 pairs of decussate and opposite fertile bracts, each bract usually subtends one axillary sessile seed. All of these characteristics conform to the circumscription of the Ephedraceae. The integument in seeds of *L. compacta* is elongated to form long micropore tubes. This feature appears only in extant and extinct gnetalean plants, and in Bennettitales and some extinct members that are closely related to Gnetales, such as the Erdtmanithecales and some genera for which only scattered seed fossils are preserved that are not clearly classified (Mendes et al., 2008, 2010; Friis et al., 2009). Our new fossils clearly differ from Bennettitales the reproductive structure of which is a bisexual cone. Only dispersed reproductive structures (seeds, male cones, and pollen) are seen in the Erdtmanithecales, and the seeds have a three−valved seed envelope. Other characteristics of the female spikes cannot be further compared.

Over 54 fossil species of Gnetales have been reported from the Mesozoic of southern Europe, Australia, North America, South

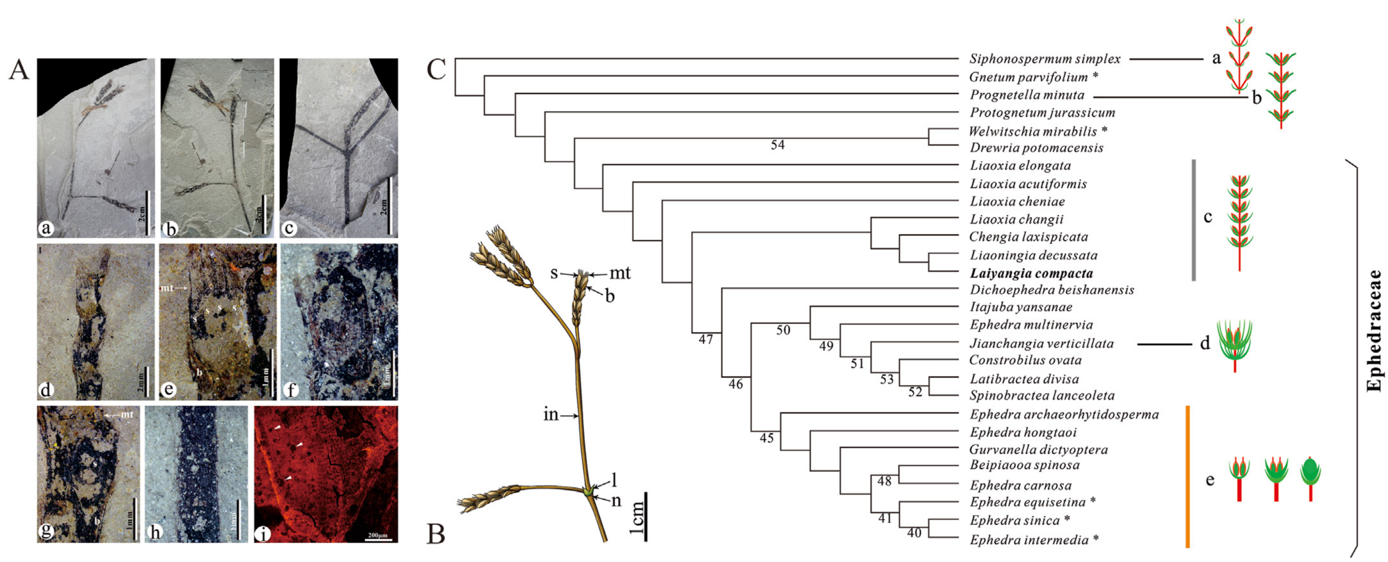

Fig. 1. A, *Laiyangia compacta* gen. et sp. nov. a–c, Part and counterpart displaying the general morphology of the species; scale bars = 2 cm; a, b, Specimen no. SDLY−2020−41A, B; c, Specimen no. SDLY−2021−47A; d-h, Female spikes under stereo microscopy, Specimen no. SDLY−2020−41A, B.; d, Female spikes showing their position and decussately opposite fertile bracts, scale bars = 2 mm; e, the uppermost bract of the female spike displaying 4 seeds in the adaxial part and the hollow and straight micropylar tubes, scale bars = 1 mm; f, g, individual fertile bract displaying one seed in the adaxial part and the hollow and straight micropylar tube, scale bars = 1 mm; h, Straight internode of reproductive shoot displaying longitudinal striations, scale bars = 1 mm; i, Details of epidermal features in the outer epidermis of the seed envelope under fluorescence microscopy, showing epidermal cells and stomatal complexes (white arrow), Specimen no. SDLY−2020−41A; b = bract; s = seed; mt = micropylar tube. B, Reconstruction of *Laiyangia compacta* gen. et sp. nov., abbreviations: in = internode; n = node; l = leaf; b = bract; s = seed; mt = micropylar tube. C, Phylogenetic relationships of *Laiyangia compacta* gen. et sp. nov. (bold type) with illustrations based on constrained Parsimony analysis of morphological characters for extinct species plus living species (*) conducted under TNT v.1.5 software, showing the most parsimonious position of *L. compacta* are within the family Ephedraceae. a, *Siphonospermum*; b, *Prognetella*; c, The compact female spikes type of *Chengia*–*Liaoningia*–*Liaoxia* group and *Laiyangia compacta* gen. et sp. nov.; d, *Jianchangia*; e, Female cone types of fossil and modern *Gurvanella*–*Beipiaoa*–*Ephedra* group.

America, and Asia, especially in the Yixian Formation of northeastern China, which has the richest diversity. However, most of these fossil species can be distinguished from our fossils by morphology of their leaves, bracts and seeds, and a comparison between *Laiyangia compacta* and related fossils is provided in Tables 1 and S2.

Constrobilus ovata Y. Yang et L.B. Lin, *Latibractea divisa* Liu et al., and *Spinobractea lanceolata* Liu et al. are reported from the Lower Cretaceous of the Yixian Formation in Liaoning, northeastern China (Liu et al., 2013). *Laiyangia compacta* differs from all three species in that those three species bear pinnately veined broad leaves and reduced female cones with 2–3 seeds (*C. ovata*) or 1–2 seeds (*S. lanceolata*). *Siphonospermum* Rydin et Friis from the Early Cretaceous of northeastern China bears a loosely organized female shoot with pedunculate ovules and no associated bracts, which is also different from *L. compacta* (Rydin and Friis, 2010). *Daohugoucladus sinensis* Yang et al., recently reported from the Middle-Late Jurassic Daohugou bed, Inner Mongolia, bears decurrent, long and linear leaves with a prominent midvein and reduced female cones with one seed, making it significantly different from our new macrofossils (Yang et al., 2023).

Gnetum L. differs from the new genus from Laiyang in possessing broad leaves, female spikes with multiple whorls of seeds, each whorl subtended by a collar of bracts. *Welwitschia* Hook. f. can be distinguished from *Laiyangia compacta* by its giant and strap–shaped leaves and female spikes with multiple pairs of fertile bracts, each subtending an axillary seed. *Drewria potomacensis* Crane et Upchurch (Welwitschiaceae) also differs from our new fossils in these aspects. *Protognetum jurassicum* Y. Yang et al. from the Middle-Late Jurassic of the Inner Mongolian, northeastern China can also be easily distinguished from *L. compacta* by the ovulate spikes, linear and leaf–like bracts, two bracts subtending 4–6 whorled seeds and shorter micropylar tube (Yang et al., 2017c).

Gurvanella Krassilov, *Beipiaoa* Dilcher et al. and some *Ephedra* macrofossil species from the Early Cretaceous of Liaoning, e.g. *Ephedra hongtaoi* Wang et Zheng, *Ephedra archaeorhytidosperma* Yang et al., *Ephedra carnosa* Yang et Wang and *Ephedra multinervia* Yang et Lin, have extremely reduced female spikes with only one (uppermost) pair/whorl of fertile bracts, each subtending an axillary and sessile seed, which are markedly different from those in *Laiyangia compacta* (Wang and Zheng, 2010; Yang et al., 2005, 2013, 2015). *Gurvanella* bear specially shaped bracts possessing an unusual furcate venation. The female spikes of modern *Ephedra* are usually ovate, with multiple pairs/whorls bracts, and only the uppermost pair/whorl is fertile, while the lower bracts are sterile, and each modified fertile bract subtends an axillary and sessile seed with a longer and curved micropylar tube. All of these characteristics are obviously different from those of *L. compacta*.

Similar to *Gurvanella* and *Beipiaoa*, the female spikes of *Jianchangia* Y. Yang, Y.W. Wang & D.K. Ferguson from the Lower Cretaceous Jiufotang Formation of Liaoning, have reduced female spikes with only one (uppermost) pair/whorl of fertile bracts subtending two seeds, but the bracts are linear, ascending and inserted in whorls. In these features *Jianchangia* are different from *Laiyangia compacta* (Yang et al., 2020).

Our new species *Laiyangia compacta* is more similar to *Prognetella* Krassilov, *Chengia* Y. Yang & al., *Liaoningia* Y. Yang & L.B. Lin and *Liaoxia* Cao & Wu (Ephedraceae) from western Liaoning, China, in having multiple pairs of fertile bracts with axillary, sessile seeds (Rydin et al., 2006; Yang et al., 2013, 2015, 2017a). However, the female spikes of *L. compacta* are more compact than those of *Prognetella*, *Chengia* (loosely arranged), *Liaoningia* and *Liaoxia*, with no observable nodes and internodes, and each bract is closer to the axis (Rydin et al., 2006; Yang and Ferguson, 2015;

Table 1
Morphological comparison of *Laiyangia compacta* gen. et sp. nov. with closest extinct gnetalean fossils.

Species	Branch	Leaf shape	Leaf position	Female cone shape	Female cone pedunculate	Bract shape	Bract position	Seed number per cone	Seed number per bract	MT length (cm)	Age
Laiyangia compacta gen. et sp. nov.	monopodial or dichasially	triangular	opposite, 2/3FS	narrowly elongate	yes	long triangular	5–8 pairs, decussately opposite,	multiple, ≥20	4	0.70–0.86, straight	K_1
Siphonospermum simplex	–	linear	opposite	narrowly ovoid	yes	no	no	1	1	2.5–3.5, straight	K_1
Prognetella minuta	–	–	–	deltoid	yes	linear to lanceolate	2–3 whorls	1–3	1	0.2–1, straight	K_1
Jianchangia verticillata	opposite	linear	verticellate	–	no	linear	>2 whorls, verticillate	2	1, UPF	short	K_1
Liaoxia cheniae	opposite-decussate	linear	opposite	obovate, spicate	no	ovoid to triangular-ovoid	2–6 pairs, decussate	multiple	1	–	K_1
Liaoxia changii	opposite-decussate	–	–	obovate to elongate, spicate	no	ovoid to triangular-ovoid	6–10 pairs, decussate	multiple	1	–	K_1
Liaoxia acutiformis	opposite-decussate	linear	opposite	elongate, spicate	no	ovoid to triangular-ovoid	6–12 pairs, decussate	multiple	1	–	K_1
Liaoxia elongata	opposite	–	–	narrowly elongate, spicate	no	ovoid to triangular-ovoid	8–12 pairs, decussate	multiple	1	–	K_1
Liaoxia robusta	opposite	linear	opposite	rounded to ellipsoid, spicate	no	ovoid to triangular-ovoid	4–10 pairs, decussate	multiple	1	–	K_1
Liaoxia longivractea	opposite	–	–	rounded, spicate	no	ovoid to triangular-ovoid	1–2 pairs, decussate	2–4	1	–	K_1
Chengia laxispicata	opposite	linear	opposite	elongate, spicate	–	ovoid	4–8 pairs, opposite- decussate	multiple	1	0.34–0.75, straight	K_1
Liaoningia decussata	dichasial	linear	opposite	elongate, spicate	no	triangular	5–12 pairs, opposite	multiple	1	–	K_1

Abbreviations: MT = Micropylar tube, 2/3FS = the lower part *ca.* 2/3 fused into a sheath, UPF = only the uppermost pair/whorl is fertile.
Data from Yang et al. (2013, 2017a, 2020), Rydin et al. (2006), Rydin and Friis (2010), Yang and Ferguson (2015).

Yang et al., 2013, 2017a). *Prognetella* possess linear or strap–like bracts, with 2 or 4 parallel veins on the bract, subtending one axillary seed, with a noticeable gap between the two seeds (Yang and Ferguson, 2015). The leaves of *Chengia, Liaoningia* and *Liaoxia* are opposite, linear and elongated (longer than in *L. compacta*), and each bract subtends one ellipsoid seed with shorter micropylar tube (Yang and Ferguson, 2015; Yang et al., 2013, 2017a). All of these characteristics differ from those of our new species *L. compacta*.

3. Phylogenetic analysis

We conducted a new phylogenetic analysis based on 14 morphological characters for 28 fossil and extant gnetalean species in which morphology was well known, and the characters included branch arrangement, leaf morphology, and reproductive characters. All the morphological characters were coded and recorded in a matrix. The matrix yielded one most parsimonious tree of 36 steps (consistency index [CI] = 0.528, retention index [RI] = 0.785). The detail setting of constrained parsimony analysis is provided in Appendix A.

The phylogenetic results suggested that the most parsimonious position of *Laiyangia compacta* is within the family Ephedraceae (Fig. 1C). *Siphonospermum* is clearly distinct from other gnetalean species possessing very primitive female reproductive organs. *Gurvanella*, *Beipiaoa* and fossil *Ephedra* converged to form a secondary clade with modern *Ephedra*, representing a relatively new reduced female cone form (with the uppermost pair/whorl of bracts are fertile). *Jianchangia* is also closely related to the *Gurvanella–Beipiaoa–Ephedra* group. Our new fossil *L. compacta* is closely related to the *Chengia*, *Liaoningia* and *Liaoxia changii*, all of which possess compact female spikes with multiple pairs of fertile bracts, and possibly represent transitional forms in the evolution of gnetalean plants (Fig. 1C).

4. Evolution of female cones of the gnetophytes

Among the living gnetophytes, the Ephedraceae are more basal group, while the Gnetaceae and Welwitschiaceae are sister (Yang, 2010; Yang et al., 2015). Modern Ephedraceae bear rather reduced female spikes that possess only one apical pair/whorl of fertile bracts and multiple pairs/whorls of sterile bracts (Rydin et al., 2010). Recent palaeobotanical studies generally agree that the reduced female spikes of modern Ephedraceae originated from a spike with multiple pairs/whorls of fertile bracts (Rydin and Korall, 2009; Yang, 2004, 2014; Yang et al., 2013, 2015). *Siphonospermum* seems to represent the primitive form of modern gnetophytes in the evolutionary process. It has loosely organized female shoots with pedunculate ovules and no associated bracts (Rydin and Friis, 2010; Yang and Ferguson, 2015; Yang et al., 2013, 2017b). In the early ephedroid plants *Prognetella*, *Chengia*, *Liaoningia*, and *Liaoxia*, with losses of pedicles of the female reproductive units and shortening of the internodes of the cone axis, the female spike became increasingly compact (Rydin et al., 2006; Yang and Ferguson, 2015; Yang et al., 2013, 2017a). During the evolutionary process, these early female spikes, which had multiple pairs of fertile bracts, eventually became modified into the reduced female spikes of modern Ephedraceae via shortening of the internodes and a reduction in the number of fertile bracts in the lower parts (Yang and Ferguson, 2015; Yang et al., 2013).

It has been suggested that the common ancestor of the Gnetaceae and Welwitschiaceae had an ephedroid morphology (Yang et al., 2015). For example, *Protognetum* has vegetative organs similar to those of Ephedraceae, such as swollen nodes and striated internodes and opposite linear leaves with parallel venation. The female reproductive organs are similar to those of Gnetaceae, such as the lax spikes with verticillate and complicated female reproductive units at the nodes (Yang et al., 2017c). Within the modern gnetophytes, *Laiyangia compacta* is most similar to Ephedraceae in its vegetative organs, such as the dichasially branched shoot with swollen nodes, and the triangular leaves opposite at nodes and normally fused into a sheath. However, the female reproductive organs of *L. compacta* were different from those of modern *Ephedra*, but similar to those of extant Gnetaceae and fossil *Liaoningia*, *Chengia* and *Liaoxia*. The ovulate structure of *L. compacta* organized into increasingly compact spikes having multiple pairs/whorls of bracts and multiple seeds (vs. only the uppermost pair/whorl is fertile in female spikes of Ephedraceae). Thus, the *L. compacta* appears intermediate in between the ephedroid and gnetoid in morphology is very likely one of the early transitional forms between ephedroids and gnetoids.

5. Ecology

Modern *Ephedra* plants generally grow in arid regions, Gobi-type deserts, cliffs, or stony crevices. They are distributed from the Mediterranean region eastwards to Siberia and northern China and in the southwestern United States, northwestern Mexico, and the Andes Mountains in South America (Musaev, 1978). Early *Ephedra* plants may have occupied a broader range of habitats than they do today, possibly including wetlands or swamps and even aquatic environments (Wang and Zheng, 2010; Yang and Ferguson, 2015; Yang et al., 2020). For instance, the frequent presence of cystiform chlamydosperms in *Prognetella* may facilitate the dissemination of diaspores in lacustrine environments (Yang and Ferguson, 2015). *Jianchangia* exhibits a unique morphology of fine linear bracts, different from other fossil species and extant representatives, which may also suggest an ecological adaptation to aquatic environments (Yang et al., 2020). The evolution of plants is closely related to the environment and climate, and their form, structure and function must be able to adapt to the external climate and environmental conditions, which will ultimately be recorded in plant structure. Features of the plant epidermis also vary in similar ways. Anatomical studies of the modern gnetophytes show that stomata are usually absent in the seed envelope. However, in a few species adapted to arid environments, stomata are common but only found in the outer epidermis and in upper parts of the seed envelope, such as in *Ephedra alata* and *Ephedra californica* (Rydin et al., 2010). In this study, multiple stomata were clearly observed in the outer epidermis of the seed envelope from *Laiyangia compacta* under a fluorescence microscope.

Moreover, the sedimentary characteristics of the Laiyang Formation clearly represent a fluvial-lacustrine depositional environment in the Laiyang Basin (Luo et al., 1990). A rich gymnospermous flora is found in the present locality, which included genera of *Pararaucaria*, *Elatides*, *Podozamites*, *Cupressinocladus*, *Pagiophyllum*, *Brachyphyllum* and *Pseudofrenelopsis*, many of which belong to Cheirolepidiaceae, such as the species of the genera *Pseudofrenelopsis, Pagiophyllum*, *Brachyphyllum* and *Pararaucaria*, which indicate relatively arid and water-stressed environments (Jin, 2018). Therefore, we infer that the palaeoclimate of the Laiyang area in the Early Cretaceous may have been drier than previously imagined.

In this study, we describe *Laiyangia compacta* P.H. Jin as a new ephedroid species from the Lower Cretaceous of eastern Shandong in China. This new genus shows transitional morphology between early Ephedraceae and modern Gnetaceae, and potentially signifying an important clade within the ancestor of the Gnetaceae. It may provide clues regarding the relationships of gnetophyte plants with other seed plants. Furthermore, a driver palaeoclimate of the

Laiyang area in the Early Cretaceous is inferred based on the appearance of *L. compacta*.

CRediT authorship contribution statement

Peihong Jin: Writing – original draft, Conceptualization. **Mingzhen Zhang:** Writing – original draft, Resources, Funding acquisition. **Baoxia Du:** Writing – review & editing, Investigation. **Jing Zhang:** Visualization, Software, Data curation. **Bainian Sun:** Writing – review & editing.

Declaration of competing interest

There is no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pld.2024.03.002.

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