A new macrofossil ephedroid plant with unusual bract morphology from the Lower Cretaceous Jiufotang Formation of northeastern China

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Abstract

Background: The evolution of the Jehol Biota of western Liaoning in China includes three phases, initiation in the Dabeigou phase, radiation in the Yixian phase, and decline in the Jiufotang phase. Numerous ephedroid macrofossils were reported from the Lower Cretaceous Yixian Formation. However, so far none has been found in the younger Jiufotang Formation (ca. 120.3 Ma) of western Liaoning.

Results: Here we report a new species Jianchangia verticillata gen. et sp. nov. with unusual morphology from the Lower Cretaceous of the Jiufotang Formation, Lamadong Village, Jianchang County, Liaoning. This species is the first record of gnetophytes from the Jiufotang Formation. It is similar to other ephedroid species from the Yixian Formation in possessing linear leaves with parallel veins, jointed shoots with swollen nodes and longitudinally furrowed internodes, and ovulate cones possessing two whorls of bracts enclosing two chlamydosperms, but differs from all known species by the ovulate cone having multiple fine linear verticillate bracts.

Conclusions: This study expands our knowledge about the diversity of early gnetophytes in the Lower Cretaceous, and demonstrates the lineage continuity of gnetophytes from the Yixian Formation to the younger Jiufotang Formation.

Keywords: China, Diversity, Ecology, Evolution, Ephedraceae, Gnetophytes, Jiufotang Formation, Lower Cretaceous

Background

Modern gnetophytes consist of three monogeneric families: Ephedraceae (Ephedra L., 60 spp.), Gnetaceae (Gnetum L., 44 spp.), and Welwitschiaceae (Welwitschia Hook. f., 1 sp.) [1]. The three living families possess divergent characters: Ephedraceae are usually dichasially branched shrubs, rarely small trees or lianas, possess linear parallel-veined leaves at the swollen nodes, compact ovulate cones with only one distal pair/whorl of fertile bracts, and are distributed in cold and arid places; Gnetaceae are commonly lianas, rarely small trees, possess pinnately veined broad leaves at the swollen nodes, and ovulate spikes with multiple loosely arranged fertile bract collars, and occur in tropical/subtropical evergreen forests; while Welwitschiaceae are short and unbranched plants, have ovulate cones with many pairs of fertile bracts, have two giant persistent leaves with multiple parallel veins connected by crossveins, and are restricted to arid coastal areas of southwestern Africa [1–9].

Despite their divergence, these plants consistently bear a unique chlamydosperm, i.e. one or two outer envelopes enclosing an inner ovule with the integument elongated beyond the envelope into a micropylar tube [10–16]. This unusual structure is different from the naked ovule in cycads, Ginkgo L., conifers, and from the angiospermous ovule completely enclosed within a closed carpel, thus displaying a seemingly transitional morphology between angiosperms and other groups of gymnosperms. Recent phylogenetic/genomic/phylotranscriptomic studies have suggested that the gnetophytes...
are sister to the Pinaceae, i.e. the gnepine hypothesis [17–20], though conflicting results have been reported [21–23].

Palaeobotanical studies are promising because early fossils are filling gaps between these morphologically isolated families. Many gnetalean macrofossil plants have been reported from the Lower Cretaceous in Australia [24], Europe [25, 26], North America [25–28], South America [29–37], and particularly the Yixian Formation of western Liaoning, northeastern China [15, 38–54]. These fossil plants display a wide range of morphological diversity including leaf/bract and cone morphology, and are important in evolutionary studies of the early gnetophytes. Previously reported fossils are mainly from the Jianshangou Bed (ca. 125 Ma) of the Yixian Formation [55, 56], but none from younger strata such as the Jiufotang Formation (ca. 120.3 Ma) [57]. The evolution of the Jehol Biota consists of three phases, i.e. initiation during the Dabeigou phase, radiation in the Yixian phase, and decline in the Jiufotang phase [57]. Almost all known Cretaceous gnetalean fossils in northeastern China were found in the Yixian Formation. Any fossils from the Dabeigou phase and the Jiufotang phase would be interesting because they might provide some clues on the evolution and ecology of early gnetophytes.

Here we describe a new macrofossil plant from the Jiufotang Formation, and note that this species possessed certain unusual characters which distinguish it from all other known ephedroid species from the Jianshangou Bed.

Results
Gymnosperms
Subclass – Gnetidae
Order – Ephedrales
Family – Ephedraceae Dumortier
Genus – Jianchangia Y. Yang, Y.W. Wang & D.K. Ferguson, gen. nov.

Diagnosis – Fossil genus showing ephedroid morphology similar to Gurvanella, Callianthus, Beipiaoa, and Ephedra in having an articulated shoot with swollen nodes, longitudinally furrowed internodes, foliar organs having two parallel veins, and a compact ovulate cone having a pair of chlamydomsperms, but distinguished by having linear bracts inserted in whorls.

Etymology – After the county name of the type locality, Jianchang.

Type Species – Jianchangia verticillata Y. Yang, Y.W. Wang & D.K. Ferguson, sp. nov., Figs. 1, 2 and 3

Diagnosis – Ovulate cones sessile or sub-sessile; each possessing two whorls of bracts and two chlamydomsperms; bracts leaf-like, linear-lanceolate, parallel-veined, ascending; chlamydomsperms ca. 1.8 mm long, 1.5 mm wide.

Description – A single impression specimen with no counterpart showing a portion of a reproductive branch, ca. 9.1 cm long, ca. 1 mm thick but thinner distally, and the main branch with four nodes and one lateral branch. Internodes becoming shorter apically, basal internode ca. 3.9 cm long, next internode ca. 2.4 cm long, third internode ca. 2.1 cm long, fourth internode (or peduncle of an ovulate cone) ca. 0.6 cm long, and uppermost internode very short. Basal lateral branch ca. 3.2 cm long, and possessing four nodes, internodes becoming shorter distally, ca. 1.4 cm, 1.1 cm, and 0.5 cm long from the proximal to the distal, uppermost internode very short. Internodes possessing fine longitudinal striations (Figs. 1 and 2a). Ovulate cones sessile or sub-sessile and paired at each node (Figs. 1 and 2b). Each ovulate cone containing two whorls of bracts; four or more bracts at each
node, linear, ascending. Two chlamydosperms enclosed within the uppermost whorl of bracts; obovoid, ca. 1.8 mm long, 1.5 mm wide, and narrowing towards the apex into a short tube (Fig. 2b).

**Distribution** – This species is only known from Lamadong Village, Jianchang County, Huludao Municipality, Liaoning of northeastern China.

**Holotype** – PE2018013101 (Fig. 1), deposited in the National Museum of Plant History of China, Institute of Botany, Chinese Academy of Sciences, Beijing.

**Etymology** – ‘Verticillata’ refers to the whorled linear bracts of the new species.

**Stratigraphic age and horizon** – Early Cretaceous (Aptian, ca. 120.3 Ma), Jiufotang Formation.

**Remarks** – Gnetophytes are common floristic elements in the Lower Cretaceous. They have been found in Europe, North America, South America, Australia, and northeastern Asia including Mongolia and northeastern China [25, 26, 30, 35, 38, 39, 41, 46, 47, 53]. The richest diversity is in the Yixian Formation [16]. Previous findings of ephedroid plants in northeastern China are restricted to Yixian and Lingyuan Counties, Liaoning Province. The new species described here was discovered in Jianchang County, Liaoning Province, China. This locality belongs to the Jiufotang Formation, which is younger than the Yixian Formation [55, 56].

The unique character of our new species lies in the number of foliar organs at the nodes. Though leaves/bracts are linear and possess two parallel veins as in many other gnetophyte species from the Yixian Formation, four or more of them are whorled at the nodes. The ovulate cones possess two whorls of bracts that are ascending and free from one another. There are two chlamydosperms enclosed in the uppermost whorl of

![Fig. 2](https://example.com/fig2.png)

Fig. 2 Morphological details of Jianchangia verticillata gen. et sp. nov. **a** a stem portion displaying the multiple longitudinal striations, **b** ovulate cones displaying the two whorls of linear bracts and the enclosed chlamydosperms; **c** diagram of an ovulate cone in **b** displaying structural details. **Abbreviations:** l, parallel-veined leaves/bracts; mt, micropylar tube; w1, the proximal whorl of bracts; w2, the distal whorl of bracts.
bracts, which shows similarity to Gurvanella, Callianthus, Beipiaoa, and Ephedra [41, 46, 47, 51, 58]. These genera are classified based on their bract morphology (Figs. 4a–c). Our new species shows unusual bract morphology different from these known genera. As a result, we established a new genus here to include the new species based on the current classification of the ephedroid plants.

A one to one relationship between chlamydosperm and its subtending bract is relatively stable in ephedroid plants excepting Siphonospermum, in which chlamydospersms are pedicelled and have no associated bracts [45]. A chlamydosperm is axillary to a subtending bract and a pair of fertile bracts usually enclose two chlamydospersms in an ovulate cone. Sometimes, the paired bracts enclose only a single chlamydosperm because of abortion, e.g. E. monosperma and E. nebrodensis. The unusual feature of our new genus is that the multiple verticellate bracts enclose only two chlamydospersms in an ovulate cone, which fundamentally breaks the rule of chlamydosperm-bract relationship in Ephedraceae. There are two explanations for this pattern: the first is that the multiple bracts in a whorl are derived by division of two bracts, so there are only two chlamydospersms; the second is that the bracts are primary, but the original multiple chlamydospersms are reduced to only two due to loss. We are inclined to

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**Fig. 3** Reconstruction of Jianchangia verticillata gen. et sp. nov., displaying important characters. **Abbreviations**: c, chlamydosperms; f, ovulate cone; in, internode; n, node; w1, the proximal whorl of bracts; w2, the distal whorl of bracts.

**Fig. 4** Ovulate cones displaying variation of bracts in genera related to Jianchangia gen. nov. a Beipiaoa spinosa Dilcher & al. displaying spinose bracts; b Gurvanella dicyoptera Krassilov displaying a bract having many furcate veins, c Ephedra torreyana S. Watson displaying obtuse bracts.
the first explanation, and believe that the multiple bracts of the same whorl may have been divided/multiplied from two bracts, since opposite phyllotaxis is predominant and presumably ancestral in the gnetophytes.

Discussion
Variation of leaves of early ephedroid plants
Ephedroid plants from the Yixian Formation display a great diversity of leaf morphology. Many of them possess linear and opposite leaves with parallel veins, e.g. Liaoxia cheniae (Wu & Guo) Rydin & al. [46], Ephedra hongtaoi Wang & Zheng [49], Siphonospermum simplex Rydin & Friis [45], Chengia laxispicata Y. Yang & al. [16], Protognetella minuta Krassilov [15], Liaoningia decussata Y. Yang & al. [59], but variation does occur. In Spinobractea lanceolata H.M. Liu & al. [43] and Constrobilus ovata H.M. Liu & al. [43], the leaves are broad and petiolate and have furcate-pinnate venation. In Latiobractea divisa H.M. Liu & al. [43], the leaves are petiolate and divided and seem to be compound. In Ephedra multinervia Y. Yang & al., the leaves are strap-shaped and elongate and have multiple parallel veins connected by cross-veins, similar to those of Welwitschiaceae [52]. Jianchangia verticillata possesses normal ephedroid leaf shape, i.e. linear and parallel-veined, but is distinct from all known gnetalean fossils in that the foliar organs are verticillate.

Morphological diversification of bracts of early ephedroid plants
Representative types of ephedroid ovulate cones are illustrated in Fig. 5; a comparison between Jianchangia and related fossils from northeastern China is provided in Tables 1 and 2. Jianchangia shows similarities to other known early ephedroid plants from northeastern China in the linear and parallel-veined leaves and the articulate reproductive shoots with swollen nodes and fine longitudinal striations. Siphonospermum simplex differs from all known ephedroid plants [16] in having no typical ovulate cones or spikes, the chlamydosperms being pedicelled and lacking subtending bracts/leaves [45]. Pseudoephedra was reported as incertae sedis [44], but may be related to Siphonospermum in that it shows general ephedroid morphology, and the chlamydosperms are pedicelled and not closely associated with any foliar organs. Jianchangia differs from Siphonospermum and Pseudoephedra in the presence of ovulate cones and the whorled bracts subtending the inner paired chlamydosperms.

Protognetum is a Jurassic macrofossil that also possesses ephedroid vegetative morphology and ovulate spikes; the bracts are linear and leaf-like, but at each node there are only two bracts subtending a whorl of chlamydosperms; these characters indicate its relationship to the Gnetaceae clade [1]. Our new fossil genus Jianchangia can be easily distinguished from Protognetum by the fact that the whorled bracts subtend only two chlamydosperms. Spinobractea has

Fig. 5 Illustrations of representative types of ovulate cones of ephedroid plants. A, Siphonospermum, reproductive shoot with pedicelled chlamydosperms; B, Protognetella, reproductive shoot with axillary and sessile chlamydosperms subtended by elongate leaf-like bracts; C, loosely arranged ovulate spike of Chengia and Liaoningia with shortened internodes and modified bracts; D, ovulate cone of Ephedra with a few pairs of proximal modified sterile bracts and a distal pair of modified fertile bracts, each modified fertile bract subtending an axillary and sessile chlamydosperm; E, ovulate cone of Gurvanella and Beipiaoa with one apical pair of modified fertile bracts, each subtending an axillary and sessile chlamydosperm; F, Jianchangia, ovulate cone with two whorls of leaf-like bracts enclosing two sessile chlamydosperms.
| Taxon          | Locality                                           | Formation                                      | Leaves                                   | Bract present | Bract whorls | Bract position          | Bract shape                                | Literature            |
|---------------|----------------------------------------------------|-----------------------------------------------|------------------------------------------|---------------|--------------|-------------------------|--------------------------------------------|-----------------------|
| *Alloephedra* | Yanji Basin, Jilin Province, China                 | Dalazi Formation, Aptian-Albian, Lower Cretaceous | ovate-triangular                        | yes           | 2            | paired                  | modified                                   | Tao & Yang 2003 [48] |
| *Beipiao*     | Huangbanjigou, Shangyuan, Beipiao, Liaoning, China | Yixian Formation, equivalent to the Barremian, Lower Cretaceous | -                                        | yes           | 1            | paired                  | modified, spinose or acute                 | Sun & al. 2001 [47]  |
| *Chengia*     | Dawangzhangzi, Lingyuan, Liaoning, China          | Yixian Formation, equivalent to the Barremian, Lower Cretaceous | linear                                   | yes           | 4-8          | paired                  | modified                                   | Yang & al. 2013 [16] |
| *Constrobilus*| Beipiao, Liaoning Province                         | Jianshangou Bed, Barremian, Lower Cretaceous | petiolate, broad ovate, pinnately veined | yes           | 1            | paired                  | modified                                   | Liu & al. 2013 [43]  |
| *Ephedra*     | Huangbanjigou, Shangyuan, Beipiao, Liaoning, China | Yixian Formation, equivalent to the Barremian, Lower Cretaceous | acute, triangular?                      | yes           | 1(-2?)       | paired                  | modified, acute                           | Yang & al. 2005 [51] |
| *E. carnosa*  | Huangbanjigou, Shangyuan, Beipiao, Liaoning, China | Yixian Formation, equivalent to the Barremian, Lower Cretaceous | -                                        | yes           | 1            | paired or ternately whorled | modified, fleshy                        | Yang & Wang 2013 [54]|
| *E. hongtaoi* | Dawangzhangzi, Lingyuan, Liaoning, China          | Yixian Formation, equivalent to the Barremian, Lower Cretaceous | -                                        | yes           | 1            | paired                  | modified                                  | Wang & Zheng          |
| *E. multinervia* | Dawangzhangzi Village, Songzhangzi Town, Lingyuan City, Chaoyang District, Liaoning Province, China | Daxinfangzi Bed, Yixian Formation, Barremian, Lower Cretaceous | long, strap-shaped, having multiple parallel veins | yes           | 1            | paired                  | modified                                  | Yang & al. 2015 [52] |
| *Gurvanella*  | Chaoyang, Liaoning, China; Mongolia                | Yixian Formation, equivalent to the Barremian, Lower Cretaceous | linear, having 2(?) parallel veins        | yes           | 1            | ternately whorled       | modified with profusely branched veins     | Sun & al. 2001 [47]  |
| *Jianchangia* | Lamadong Village, Jianchang County, Liaoning Province, northeastern China | Jiuotang Formation, Aptian, Lower Cretaceous | linear, parallel-veined                  | yes           | 2            | verticillate            | linear, leaf-like                         | This study            |
| *Latibractea* | near Beipiao, Liaoning Province                   | Jianshangou Bed, Barremian, Lower Cretaceous | leaves petiolate, divided, parallel-veined | yes           | 3 or 4       | paired                  | modified                                  | Liu & al. 2013 [43]  |
| *Liaoxia cheniae* | Shangyuan Village of Beipiao, Liaoning, China   | Yixian Formation, equivalent to the Barremian, Lower Cretaceous | linear, parallel-veined                  | yes           | 2-6          | paired                  | modified                                  | Rydin & al. 2006 [26, 46] |
| Taxon          | Locality                                           | Formation                                      | Leaves                                      | Bract present | Bract whorls | Bract position | Bract shape | Literature        |
|---------------|----------------------------------------------------|-----------------------------------------------|---------------------------------------------|---------------|--------------|----------------|-------------|------------------|
| *Prognetella* | Huangbanjigou, Shangyuan, Beipiao, Liaoning, China | Yixian Formation, equivalent to the Barremian, Lower Cretaceous | linear, having 2-4 parallel veins | yes, in reproductive shoots but not in typical cone | -             | paired          | leaf-like      | Yang & Ferguson 2015 [15] |
| *Protognetum jurassicum* | Daohugou, Ningcheng County, Chifeng City, Inner Mongolia Autonomous Region, China | Yixian Formation, equivalent to the Barremian, Lower Cretaceous | linear                                      | yes           | 2            | paired          | linear, leaf-like | Yang & al. 2017 [1, 59] |
| *Pseudoephedra* | Dawangzhangzi Village, Lingyuan City, Liaoning Province, China | Yixian Formation, Barremian–Aptian, Lower Cretaceous | linear                                      | probably no   | -            | -              | -            | Liu & Wang 2016 [44] |
| *Siphonospermum simplex* | Jianshangou, Beipiao, Chaoyang City, west Liaoning, China | Yixian Formation, equivalent to the Barremian, Lower Cretaceous | linear, having 3 parallel veined | no            | -            | -              | -            | Rydin & Friis 2010 [45] |
| *Spinobractea* | near Beipiao, Liaoning Province                     | Jianshangou Bed, Barremian, Early Cretaceous | broadly lanceolate, forked venation | yes           | 2-4          | paired          | lanceolate    | Liu & al. 2013 [43] |
ovulate spikes with multiple pairs of bracts that appear to be elongate and strap-shaped [43], characters which are different from the whorled linear bracts enclosing only two chlamydospersms in Jianchangia. Gnetum possesses ovulate spikes with multiple whorls of chlamydospersms, with each whorl subtended by a collar of bracts, while Welwitschia has ovulate cones with multiple pairs of fertile bracts each subtending an axillary chlamydosperm. The circular and paired bracts in Gnetum and Welwitschia distinguish them from our new genus.

Jianchangia is also similar to a few other macrofossils from the Lower Cretaceous Yixian Formation in its ephedroid vegetative morphology and presence of bracts in ovulate spikes/cones, e.g. Prognetella Krassilov [15], Chengia Y. Yang & al. [16], Liaoningia Y. Yang & L.B. Lin [59], and Liaoxia Cao & Wu [46], but differs from all of them in having unspecialized bracts arranged into whorls. In Beipiaoa and Ephedra, the bracts are modified but only two or three are inserted at each node [47]. This is also the case in Erenia Krassilov and Callianthus, in which the bracts are not leaf-like but specialized and encapsulate a pair of chlamydospersms [58]. Constrobilus and Latibractea probably belong to this complex because both of them have ovulate cones with one pair of chlamydospersms, as in modern Ephedra, but their leaves are unusual, divided in Latibractea and broad and pinnately veined in Constrobilus [43]. The differences between Jianchangia and these two genera are

| Taxon                  | Female cone | Chlamydospersms | Chlamydospersms | Chlamydospersms | Literature |
|-----------------------|-------------|-----------------|-----------------|-----------------|------------|
|                        | present     | pedicled        | in a cone       | sculptured      | Literature |
| Alloephedra            | yes, compact | no              | 2               | no              | Tao & Yang 2003 [48] |
| Beipiaoa               | yes, compact | no              | 2               | no              | Sun & al. 2001 [47] |
| Chengia                | yes, but laxly arranged into spikes | no | Many in multiple whorls | no | Yang & al. 2013 [16] |
| Constrobilus           | yes, compact | no              | 2               | no              | Liu & al. 2013 [43] |
| Ephedra archaeorhytidosperma | yes, compact | no | 1-2 | transversely wrinkled | Yang & al. 2005 [51] |
| E. canosa              | yes, compact | no              | 1-3             | no              | Yang & Wang 2013 [54] |
| E. hongtai             | yes, compact | no              | 2               | no              | Wang & Zheng |
| E. multinervia         | yes, compact | no              | 2               | no              | Yang & al. 2015 [52] |
| Gurvanella             | yes, compact | no              | usually 3      | no              | Sun & al. 2001 [47] |
| Jianchangia            | yes, compact | no              | 2               | no              | This study |
| Latibractea            | yes, compact | no              | -               | -               | Liu & al. 2013 [43] |
| Liaoxia cheniae        | yes, compact | no              | many            | no              | Rydin & al. 2006 [26, 46] |
| Prognetella            | no, in reproductive shoots | no | paired at nodes of reproductive shoots | no | Yang & Ferguson 2015 [15] |
| Protognetum jurassicum | laxly arranged spikes | no | 4-6 whorled at nodes of a reproductive shoot | no | Yang & al. 2017 [1, 59] |
| Pseudophedra           | no          | yes             | not organized into a cone | no | Liu & Wang 2016 [44] |
| Siphonospermum simplex | no          | yes             | pedicled        | no              | Rydin & Friis 2010 [45] |
| Spinobractea           | yes, more or less in lax spikes | no | 1-2 | no              | Liu & al. 2013 [43] |
obvious, the bracts of the latter two genera are specialized and paired, thus differing from the leaf-like and whorled bracts in Jianchangia.

In summary, bracts of these ephedroid macrofossils show intergrading modifications from absence to presence, and from leaf-like to specialized shape. These transformations together with the reduction of the fertile whorls of the ovulate spike may reflect the evolutionary stages and probable relationships among them, but phylogenetic analysis is needed to test the direction of these transformations.

There are a few other reported gnetalean fossils, but unfortunately we cannot compare them with our new fossil genus because these plants are either pollen-producing, e.g. Khitania Guo & al. [38] and Eamesia Y. Yang & al. [53], or they are mesofossil seeds/chlamydosperms with no diagnostic characters of bracts and ovulate cones, e.g. Ephedra drewriensis Rydin & al. [26], E. portugallica Rydin & al. [26], and Bicatia Friis & al. [25].

Ecology

Modern Ephedra usually lives in dry areas, in Gobi-type deserts (e.g. E. rhytidosperma Pachom., Fig. 6a), on cliffs (e.g. E. equisetina Bunge, Fig. 6b), or in stony crevices (e.g. E. monosperma Gmel. ex C.A. Mey., Fig. 6c), and they are distributed from Mediterranean regions eastwards to Siberia and northern China, in southwestern U.S.A. and northwestern Mexico, and Andean South America as well [60]. Early ephedroid plants may have occupied more diverse habitats than they do now, probably also in humid swampy places [15], and even in water [49], and these plants evolved a set of characters adapted to the palaeoenvironment. Prognetella is provided with an unusual set of characters, for instance, the fragmented reproductive shoots and frequent cystiform chlamydosperms may have facilitated the dispersal of diaspores in a lacustrine environment [15]. Our new species displays leaf/bract morphology distinct from other species of the Yixian Formation and extant species, which may represent an ecological adaptation. The numerous fine linear leaves of Jianchangia may be functionally analogous to the finely divided leaves of many living species of aquatic flowering plants, e.g. Myriophyllum spicatum L. and Hippuris vulgaris L. [61, 62].

Three phases of floristic development were recognized for the Jehol Biota, i.e. the early initiation Dabei-gou phase, the middle radiation Yixian phase, and the late declining Jiufotang phase [57]. There are only a few plant fossils of gymnosperms recorded from the Jiufotang Formation, e.g. Ginkgoites truncatus Li, Czekanowskia rigida Heer, and Elatocladus pinnatus Sun & Zheng. All three plants were also recorded from the
Jianshangou Bed, Yixian Formation, suggesting a floras
tic similarity between the Jiufotang Formation and the
Yixian Formation. Though ephedroid macrofossils are
common in the Yixian Formation, they have not been
reported from the younger Jiufotang Formation thus
far. Our new species is thus the first ephedroid species
from the Jiufotang Formation. This finding confirms
the floras similarity and continuity between the Yix-
ian Formation and the Jiufotang Formation.

The Yixian Formation displays an enormous diversity
of ephedroid plants. This early burst of Ephedraceae
may have been driven by the turbulent geological envir-
onment at the time [15]. It is well known that volcanic
activity was frequent in the Yixian Formation [57]. This
radiation was not only observed in the gnetophytes, but
also in other plant groups, insects, mammals, dinosaurs,
and birds [55]. In the younger Jiufotang Formation, the
environment was relatively stable [57]. The declining
species diversity in the Jiufotang Formation may be at-
tributable to local extinction.

Conclusions
Here we describe the first record of gnetophytes from the
Lower Cretaceous Jiufotang Formation, Lamadong Village,
Jianchang County, Liaoning Province, northeastern China.
This finding demonstrates the lineage continuity of
gnetophytes in western Liaoning since the Jiufotang For-
formation is ca. 5 Ma years younger than the Yixian Forma-
tion. This new plant Jianchangia verticillata gen. et sp.
nov. also enhances our knowledge of morphological diver-
sity in early gnetophytes. It has multiple foliar bracts,
whorled at the nodes, and is distinguished from all other
known ephedroid plants.

Methods
Our studied fossil was from Lamadong Village, Jianchang
County, Liaoning Province, northeastern China (Fig. 7).
The fossil bed belongs to the Jiufotang Formation. The
Formation dates back to the Aptian, ca. 120.3 Ma [63],
and is well-known for early birds, e.g. Jianchangornis
microdon Zhou & al. [64], Bohaiornis guoi Hu & al. [65],
Schirooura lii Zhou & al. [66], Jeholornis palmapenis
O’Connor & al. [67], Zhongornis haoae Gao & al. [68, 69],
and the dinosaur Moganopterus zhuiana Lu & al. [70].
Plant fossils were rarely reported, and only a few gym-
nosperms have been recorded, e.g. Ginkgoites truncatus
Li, Czekanowskia rigida Heer, and Elatocladus pinnatus
Sun & Zheng [57]. The new fossil is deposited in the
National Museum of Plant History of China, Institute
of Botany, Chinese Academy of Sciences, Beijing,
China. The plant fossil was preserved as impressions,
and is only fragmentary.
The fossil was observed with a light microscope (Nikon Eclipse E600) and was photographed with digital cameras (Nikon D700 and Olympus TG-3). The figures were manually edited and created using Adobe Photoshop CS2 ver. 9.0 and CorelDRAW X4. The map of the type locality was generated using ArcGIS 9.3 (ESRI, Redlands, CA, USA; http://www.esri.com).

Acknowledgements

We thank Ms. A.L. Li for her kind help on line-drawing reconstruction of the fossil plant, J.A. Doyle and an anonymous reviewer for their valuable suggestions. We are also grateful to Li Wang of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences for his kind help in preparing the diagram in Fig. 2.

Authors’ contributions

YY & YWW studied the fossil plants; YY took photos and prepared figures; YY & DF drafted the manuscript. All authors read and approved the final manuscript.

Funding

This work was supported by the National Natural Science Foundation of China [31470301 & 31770211].

Availability of data and materials

All data and materials used in this study are included in this published article.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Received: 11 April 2019 Accepted: 19 December 2019

Published online: 04 February 2020

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