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Male spike strobiles with *Gnetum* affinity from the Early Cretaceous in western Liaoning, Northeast China

[1,2]Shuang-Xing GUO* [3]Jin-Geng SHA [4]Li-Zeng BIAN [5]Yin-Long QIU

[1](*Department of Palaeobotany and Palynology, Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences,* Nanjing 210008, China)

[2](*Laboratory of Biodiversity and Biogeography, Kunming Institute of Botany, Chinese Academy of Sciences,* Kunming 650204, China)

[3](*State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences,* Nanjing 210008, China)

[4](*College of Earth Sciences, Nanjing University,* Nanjing 210093, China)

[5](*Department of Ecology & Evolutionary Biology, The University Herbarium, University of Michigan,* Ann Arbor, MI 48109-1048, USA)

Abstract A fossil with *Gnetum* affinity was found in the Jianshangou Member (Barremian Age) of the Yixian Formation (Lower Cretaceous Epoch) of the Jehol Group in western Liaoning, northeastern China. The single fossil specimen is represented by both elongate-cylindrical male spike strobiles which borne within a nodal bract of cauliflorous branch. The spike strobiles have apparent nodes, invisible internodes, and numerous verticillate involucral collars. The microsporangiate units within involucral collars are not seen. The male spike strobiles with verticillate involucral collars occur exclusively in *Gnetum*; hence, the fossil strobiles are attributed to a new taxon, *Khitania columnispicata* gen. & sp. nov., being closely related to *Gnetum*. The general isotopic dating suggests an age of Barremian, ca. 125–122 million years (Myr) ago for the Jianshangou Member. The palaeoecological and palaeoclimatic inference based on the compositions of flora and fauna, and lithological characters of the fossil locality suggests that the fossil plants grew in a subtropical mesophytic forest and under a warmer climate. The remains of male spike strobiles are the first record of gnetalean macrofossil. It documents the evolution of the distinct gnetoid morphology and indicates a wider range of distribution of Gnetaceae in the Early Cretaceous than present day.

Key words biogeography, Early Cretaceous, *Gnetum* affinity, male spike strobiles, northeastern China.

Gnetales represent one of the four extant gymnospermous lineages (Kramer & Green, 1990) and have become critical in the recent debate on relationships between gymnosperms and angiosperms (Donoghue & Doyle, 1999). In contrast, they have a very poor fossil record in comparison with other lineages of seed plants (Crane, 1996). While earlier classic studies and cladistic analyses of morphology suggested that they might be related to angiosperms (Arber & Parkin, 1908; Crane, 1985; Doyle & Donoghue, 1986; Nixon et al., 1994), recent molecular phylogenetic studies often placed them with conifers (Goremykin et al., 1996; Winter et al., 1999; Bowe et al., 2000; Chaw et al., 2000; Frohlich & Parker, 2000; Gugerli et al., 2001; Magallon & Sanderson, 2002; Burleigh & Mathews, 2004), although it could not be completely ruled out that they may be sister to all other extant seed plants (Rydin et al., 2002). To move out of the current dilemma of debate on the seed plant phylogeny, which mostly stems from a large amount of divergence among the five extant lineages (cycads, *Ginkgo*, conifers, Gnetales, angiosperms) at both morphological and molecular levels, one solution would be to search for fossil evidence to reconstruct the evolutionary course of divergent morphology of these lineages (Doyle & Donoghue, 1987). Some close morphological affinity to *Ephedra* and *Welwitschia* pollen grains were ever found from the Katrol Formation (Upper Jurassic) of Kutch, India (Mathur & Mathur, 1965). Since then till a few years ago, reports of gnetalean fossils, particularly of macrofossils, were still extremely scarce (Crane & Upchurch, 1987; Osborn et al., 1993; Crane, 1996; Won & Renner, 2006). Over the last several years, however, several papers have been published on macrofossils of Ephedraceae (Guo & Wu, 2000; Rydin et al., 2004, 2006; Yang et al., 2005), Welwitschiaceae (Rydin et al., 2003; Dilcher et al., 2005), and Gnetales (Wang, 2004). To date, no macrofossil of *Gnetum* has been reported.

In this study, we report a gnetalean fossil that has two male spike strobiles, from the Jianshangou Member of the Yixian Formation in Liaoning Province, northeastern China in the Lower Cretaceous Series. The fossil specimen consists of two male strobiles that have microsporangiate axes with nodes, invisible

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* Author for correspondence. E-mail: <guosx2006@yahoo.com.cn>.

internodes, and nodal whorled bracts on spike to form fused verticillate involucral collars. Such male strobiles are similar to those of extant *Gnetum*, and they occur only in *Gnetum* and not in any other living or extinct plants. The fossil strobiles probably belong to an extinct species in relation to *Gnetum*. The locality of the fossil occurrence is situated in the mid-latitude (lat. 41º12′N), whereas all modern *Gnetum* species are growing in the low latitude (Kramer & Green, 1990) in both of the Northern and Southern Hemispheres. Discovery of this *Gnetum*-related fossil hence suggests that gnetoid plants had more extensive distribution in the Early Cretaceous than today.

1 Material and methods

The fossil material is a single specimen with two male spike strobiles in light brown-yellowish impression, which was collected from the section of eastern hillside of Huangbanjigou to western hillside of Jianshangou Villages (41º12′ N, 119º22′ E) in the Jianshangou Member of the Yixian Formation of the Jehol Group in Beipiao County, Liaoning Province, northeastern China. The Jianshangou Member is the lower part of the Yixian Formation, which is divided into 11 beds with a total thickness of 34.4 m. Occurrence of fossil plants is very abundant and they are mostly concentrated in the beds # 6 and 8 (3.5 and 2.5 m thick, respectively). The lithological characters of the Jianshangou Member consist of grayish-white/ grayish-yellow/black thick-bedded muddy siltstone, volcanic rocks, and volcaniclastic sedimentary rocks (Sun et al., 2001). The fossil specimen described here was preserved in the bed # 8.

The Yixian Formation is extensively distributed in four counties of Yixian, Beipiao, Lingyuan and Zhaoyang in western Liaoning. It consists of a set of late Mesozoic terrestrial volcanic lava, volcaniclastic rock and lacustrine sedimentary rock with less fluvial rock. It includes six fossiliferous strata with abundant animal and plant fossils. The protists and animals include dinoflagellates, conchastracans, ostracods, shrimps, insects, spiders, bivalves, gastropods, fishes, reptiles, amphibians, dinosaurs, tortoises, crocodiles, birds, and primitive mammals. The plant taxa include Bryophyte, Lycopodiatae, Equisetatae, Filicatae, Pteridospermae, Bennettitales, Czekanowskiales, Ginkgoales, Coniferae, Gnetales, and Angiospermae. Among the fossil plants, Coniferae are the most abundant in the number of genera and species. Next are Filicatae, Bennettitales, Czekanowskiales, and Ginkgoales. Ephedraceae of Gnetales is also very abundant in the number of specimens (Chen, 1999; Chang, 1999; Guo & Wu, 2000; Sun et al., 2001, 2002; Chang et al., 2003; Ji et al., 2004; Li, 2005; Dilcher et al., 2007).

According to the recent isotopic dating, the geological age of the Yixian Formation is the early Early Cretaceous, between 135–120 million years (Myr) (Zhang et al., 2004) or 127–125 Myr (Zhang et al., 2004). The Jianshangou Member is the lower part of the Yixian Formation attributed to Barremian Age, between 125–122 Myr (Swisher et al., 2002; Zhang et al., 2006; Chen et al., 2006).

Attempts were made to collect more fossil specimens of gnetoid from the same bed of the same locality and from other contemporary strata at different localities, but with no success so far. Effort was also made to extract pollen grains *in situ* from the strobiles, but it failed. The fossil specimen was photographed using a stereo microscope, Nikon SMZ 1500 system.

2 Results

Systematics

Division – *Gnetophyta* Takhtajan 1986

Class – *Gnetopsida* Steward 1983

Order – *Gnetales* Pearson 1929

Family – *Gnetaceae* Lindley 1834

Genus – ***Khitania*** Guo, Sha, Bian & Qiu, gen. nov.

Etymology: Khitan is the name of an ancient ethnic tribe that once inhabited the Liaohe Valley in Liaoning Province, northeastern China.

Generic diagnosis: Two elongate-cylindrical male spikelike strobiles (microsporangiate axes), which with two invisible peduncles borne within a cupular bract of swollen node on cauliflorous branch. Male strobiles with many nodes and invisible internodes, and numerous verticillate annular involucral collars, which formed by the fusion of verticillate bracts on nodes of spike, involucral collars close arrangement, margin entire or somewhat undulation. Microsporangiate units (sessile male "flowers") within involucral collars indiscernible, their number and arrangement unknown (probably one row or two in arrangement).

Khitania columnispicata Guo, Sha, Bian & Qiu, gen. et sp. nov.

Fig. 1: left; 2: A–F

Etymology: Column (from Latin columna) means cylinder; spicata (from Latin spicatus) represents a strobile.

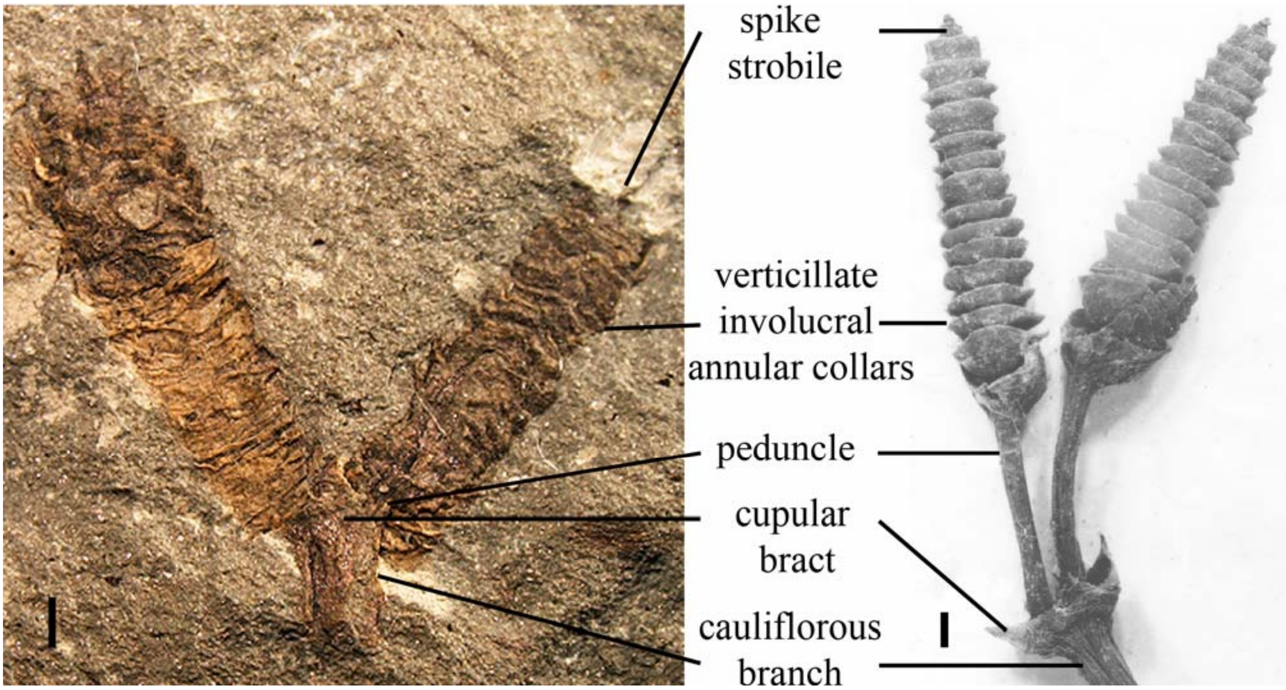

Fig. 1. Comparison of male spike strobiles (microsporangiate axes) between fossil *Khitania columnispicata* (left) and living *Gnetum montanum* Markgraf (right). Scale bars=1 mm.

Holotype: The specimen No. PB 20189 with two male spike strobiles.

Type Locality: Eastern hillside of Huangbanjigou to western hillside of Jianshangou Villages (41º12′ N, 119º22′ E) in Beipiao, Liaoning, northeastern China.

Stratigraphic horizon: The Jianshangou Member of the Yixian Formation of the Jehol Group. Barremian Age, early Early Cretaceous.

Repository: The specimen is housed at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Specific description: A cauliflorous branch with both male spikelike strobiles (microsporangiate axes) which with both invisible peduncles borne within a cupular bract of swollen node, upper portion of bract broken, about1.8 mm high, 4.2 mm wide, cauliflorous branch 2.3 mm long and 0.9 mm wide, spikes with numerous verticillate annular involucral collars, apex conical point. Large strobile (Fig. 1: left; Fig. 2: A–C) with about 23 whorls of involucral collars in preservation, base slightly narrow and slightly broadish upward, apex somewhat broken, 6.8 mm long and 2.4 mm wide in widest part, margin entire and somewhat undulate. Microsporangiate units (male "flowers") indiscernible within involucral collars, their number and arrangement unknown. Small strobile (Fig. 1: right; Fig. 2: D–F) with about 17 whorls of involucral collars in preservation, base obtuse and apex partially broken, 5.5 mm long and 1.5 mm wide in preservation, margin entire and slightly undulate. Microsporangiate units within involucral collars indiscernible, their number and arrangement unknown.

3 Discussion

3.1 Systematic implications

This fossil specimen with both male spike strobiles is like a "biforked branch" of Y form at first glance. In fact it is not a "biforked branch" but a lower cupular bract on cauliflorous branch coming out both upper male spike strobiles. Supposing it is a "biforked branch" and that the lower branch should be thick old-branch which must be thicker than two upper young biforked branches in natural order in plants. However, this so called biforked branch of the fossil specimen is just reversed. The lower branch is actually thinner than two upper young "biforked branches". Such phenomenon is not existent and not normal rule in plants. It should indicate that the so called biforked branch bearing lower branch and two upper branches is obviously distinct. The lower branch is smooth and two upper ones have numerous stereoscopically whorled structures (Fig. 1: left; Fig. 2) though they are

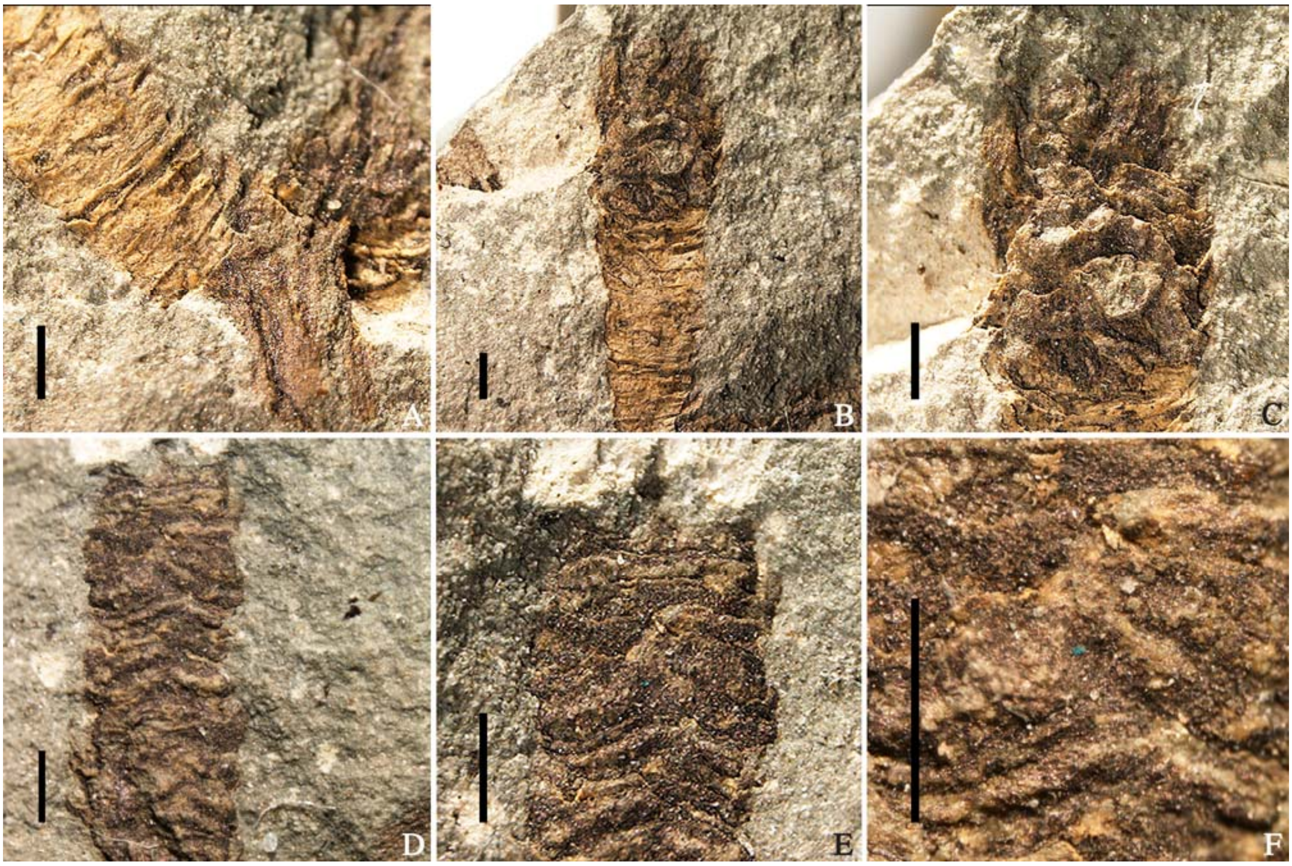

Fig. 2. Morphology and structure of verticillate involucral collars on two male spike strobiles. The involucral collars are the stereoscopical structure and stratification, rugged and jagged in abrasion. **A.** Showing the lower portion of fossil strobiles, two strobiles borne within a cupular bract of swollen node on the top of cauliflorous branch, bract broken at upper portion, the base of two strobiles covered by the cupular bract, invisible peduncles, cauliflorous branch in lower part. **B.** The left strobile with many verticillate involucral collars were distorted and abraded in appearance. The bright rings are the fused whorls of involucral collars. The black rings are grooved gaps among involucral collars where the microsporangiate units (male "flowers") borne inside, but they can be invisible. **C.** Enlarged part of Fig. B, showing the stereoscopical structure and stratification of involucral collars, they are terrace arrangement. Some upper margins of them broken and a siltstone grain affixed to strobile. **D.** The right strobile with deformed and distorted whorls of involucral collars, but regular arrangement and stratification can be recognizable. **E.** Enlarged partly of Fig. D, showing morphological structure of verticillate involucral collars. **F.** Partial enlargement in detail of Fig. E. Scale bars=1 mm

incomplete preservation. Therefore the fossil specimen is impossible to be any vegetative branch system of extinct and extant plants but a specialized reproductive branch system.

In 122 Myr ago, the fern and gymnosperm plants were absolutely predominant. The fossil specimen is impossibly related to a fern. The stubby Cycadophyta, Bennettitales and grand Ginkgophyta, and Coniferae are hardly to grow such tiny and fine branch system. The male and female strobiles of gymnosperm in helical arrangement are obviously different from the fossil plant in whorled. It is most important that the upper branches of the remains are characteristic of numerous verticillate-collar structures in regular arrangement. Such distinct characters just occur in extant male strobiles of *Gnetum*.

In extant angiosperm plants, some dicotyledons (*Ficus, Platanus*, *Diospyros*, Magnoliaceae, Polygonaceae, etc.) with whorled structures on branches are formed by stipular traces and some monocotyledons (Cannaceae, Gramineae, Musaceae, Zingiberaceae, etc.) with ring structures on stems and/or branches are formed by sheathing stipules. Their whorled and ring structures on stems and/or branches are loose, rough and irregular arrangement and are far different from those of the fossil strobiles. However, it must still be indicated that these flowering plants are not occurrence yet owing to angiosperm in dawning age at that time.

The fossil specimen is mainly characterized by both male spike strobiles with many verticillate involucral collars in close arrangement which borne within a cupular bract of swollen node on cauliflorous branch. These typical characters of fossil strobiles are quite similar to those of extant *Gnetum*. However, the fossil strobiles have invisible peduncles which are noticeably different from those of extant *Gnetum*. The strobiles of extant *Gnetum* are always measurable peduncles though some species with unconspicuous peduncles.

Among the extant *Gnetum*, some involucral collars have both male and female “flowers” in the same inflorescence (Endress, 1996; Hufford, 1996; Fu et al., 1999), but it is not clear that whether the fossil strobiles have also both male and sterile female “flowers” or only male “flowers” inside involucral collars. Some characters of extant *Gnetum* can not be observed on the fossil strobiles. Such as it is not known whether the fossil strobiles are terminal or lateral, or they are cyme or dichasium and the arrangement of male “flowers” in one row or two. Notwithstanding these above characters (male “flowers”) of fossil strobiles can not be visible owing to the imperfect in preservation of the fossil specimen. The whorled involucral collars of fossil strobiles are still clearly recognizable.

The verticillate involucral collars on strobiles are some distortion and anamorphosis of their natural appearance in the process of transportation, attrition, compression of sedimentation and geological function, and the microsporangiate units (male “flowers”) have also invisible from the involucral collars. Even so the involucral collars may still be comparable with those of extant *Gnetum*. These verticillate structure and arrangement of involucral collars are only shared by both *Khitania* and *Gnetum*. So *Khitania* should be closely related to *Gnetum*.

The fossil pollen grains *in situ* could not be obtained from involucral collars. However, we know from both palynologists Li Wen-Ben and Liu Zhao-Sheng of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Science that both of them have ever studied the dispersed fossil pollen grains in the same beds and the same locality in western Liaoning. These fossil pollen grains are much similar to extant *Gnetum* ones in ornamentation. They are not published owing to these pollen grains not so well in preservation.

In comparison with extant *Gnetum* species, the fossil male strobiles resemble those of *G. pendulum* C. Y. Cheng in size (10–15 mm long, 3–4 mm wide) and in the number of involucral collars (9–25 whorls). However, the fossil strobiles are merely smaller than those of the living taxon. This living species grows in mesophytic forests of 600–1800 m in hillsides and middle mountains in provinces of Yunnan, Guangxi, and Guizhou, southwestern China (Cheng, 1978; Fu et al., 1999). The fossil strobiles are also near to those of *Gnetum montanum* Markgraf in size (20–30 mm long and 2–3.5 mm wide) and in the number of verticillate involucral collars (13–17 whorls). The living species is larger in size and fewer in the number of involucral collars. It grows in mesophytic forests of 500–2200 m in hillsides and mountainous slopes in provinces of Guangdong, Guangxi, Hunan and Yunnan of southern and southwestern China, and also ranging in India, Sikkim, Burma, Thailand, Laos and Vietnam. The northernmost distributional limit of extant *Gnetum* species in the Northern Hemisphere is *G. parvifolium* (Warburg) W. C. Cheng which grows now in Fujian (26º36′ N), southeastern China and reaching southward from provinces of Jiangxi, Hunan, Guangdong, Guangxi, Guizhou and Hainan, southern China to Laos and Vietnam (Cheng, 1978; Fu et al., 1999).

The modern Gnetaceae includes a unique genus with 39 species (Price, 1996), which can be divided into two Sections: *Gnetum* Markgraf and *Scandentia* Griffith. The two sections can be differentiated each other in that the former one represents the easily visible internodes among the nodal involucral collars, while the latter one represents closely successive involucral collars one another of male strobile. A recent molecular phylogenetic study shows that this morphological difference between the two sections is phylogenetically informative (Won & Renner, 2006). The fossil strobiles resemble the two species *G. pendulum* and *G. montanum* of the Section *Scandentia* in which the male spike strobiles have invisible or compact internodes. The Section *Scandentia*, with more than two dozens of species, is a strictly Asian clade, and the section *Gnetum* contains about ten species in northern South America, western Africa, and Southeastern Asia (Price, 1996; Won & Renner, 2006). Hence, besides morphological similarities described above, there also seems to be biogeographic coincidence between the fossil species and the above mentioned extant taxa.

Discovery of the gnetoid fossil in Early Cretaceous demonstrates that the distinct morphology of *Gnetum* can indeed be traced to at least 122 Myr ago. Recently, several studies have shown that the highly divergent morphology of *Ephedra* and *Welwitschia* also likely evolved at least by the beginning of the Cretaceous (Rydin et al., 2003, 2004, 2006; Dilcher et al., 2005; Yang et al., 2005; Friis et al., 2007). Further, a fossil attributed to a general gnetalean affinity, with some conifer characteristics, was reported from Upper Permian in northern China (Wang, 2004). Together with the extensive pollen record and the few macrofossils reported earlier (Crane & Upchurch, 1987; Osborn et al., 1993; Crane, 1996 and references therein; Diéguez, 1996), we now seem to be at a much better position than merely a few years ago to understand the evolutionary history of this enigmatic group of seed plants. The increasingly rich fossil record of Gnetales as revealed by excavations in Brazil, China, and Portugal thus may help to evaluate the conifer affinity of extant Gnetales as suggested by recent molecular phylogenetic studies (Goremykin et al., 1996; Winter et al., 1999; Bowe et al., 2000; Chaw et al., 2000; Frohlich & Parker, 2000; Gugerli et al., 2001; Magallon & Sanderson, 2002; Burleigh & Mathews, 2004; Friis et al., 2007) as well as classic morphological studies (Coulter & Chamberlain, 1910; Carlquist, 1996).

3.2 Palaeoclimatic, ecological and biogeographic implications

The site where *Khitania* was excavated is situated at 41º12′N. It is 14º36’ north of where *G. parvifolium*, the species that has the most-northerly distribution, grows today in Fujian Province, southeastern China, 26º36′N (Cheng, 1978; Fu et al., 1999). Supposing the growing climate of *Khitania* is similar to that of extant *Gnetum*, and then the site where *Khitania* was excavated also should indicate a subtropical or tropical climate in Early Cretaceous. The fossil locality is consistent with palaeogeographic map in Barremian Age (Smith et al., 1994).

Today, all extant *Gnetum* species are distributed on both sides of the equator, between 15º S to 27º N (Fig. 3). They mostly grow in tropical lowland, low mountain forests, humid forests, forest edges, and savannahs. Some species are also well adapted to sub-arid and sub-humid climate (Van Steenis, 1948–1954).

A recent palaeogeographic and palaeoclimatic study of this region indeed provides some evidence to support this hypothesis (Haggart et al., 2006). In Early Cretaceous, there was a temperate and moderately humid climate existing along the eastern part of the Inner Zone of Japan, as well as in the inland of northeastern Russia. An oceanic climate also prevailed along the coastal regions of the Russian Far East and the Outer Zone of Japan due to influence by circulation from the equatorial regions. The subtropical-tropical conditions with frequent desiccation existed along the western end of the Inner Zone of Japan and on the Korean Peninsula. The central East Asia area was dominated by temperate and humid or subtropical to tropical and arid climates, whereas the coastal regions were influenced by warm waters flowing northward from the equatorial regions that mixed with cooler waters coming from the north. Both Jianshangou flora and the coeval Tetori flora from Honshu of Japan are quite similar to each other in composition and habitation. They indicate a tropical to subtropical and humid climate with sometimes dry climate at that time (Ding et al., 2003; Chen & Komatsu, 2005; Matsukawa et al., 2006). The Cretaceous Period was ever the warmest period of the Mesozoic Era and had a greenhouse climate. The fossils and oxygen isotope data reveal that the global mean annual temperature was generally 3–10 ºC higher than today, and that the mean latitudinal temperature gradient of the ocean is estimated at only 0.15–0.3 ºC per one latitude during Cretaceous. The temperature change could result from the transformation of global

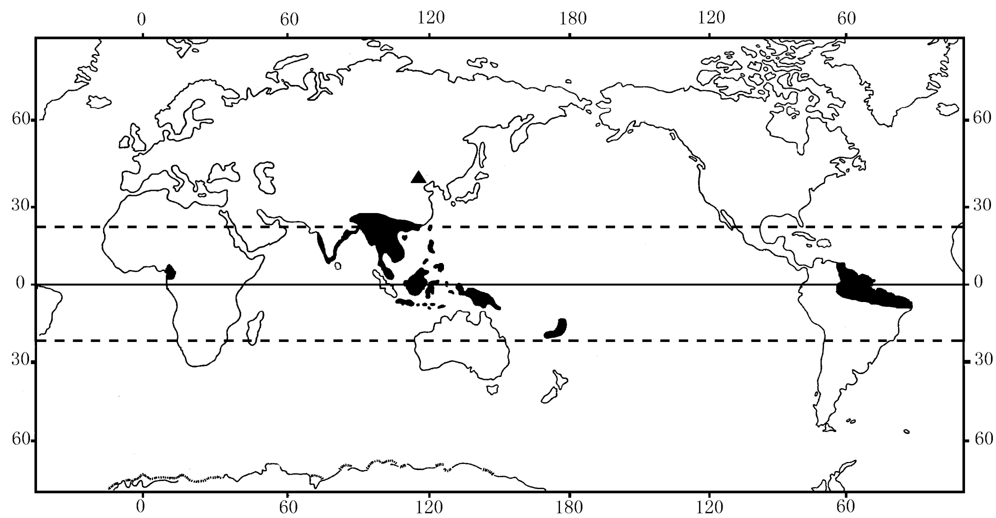

Fig. 3. Map showing the distribution of living *Gnetum* (black ranges) and fossil locality (black delta). (After Foster & Gifford, 1974, modification)

ocean structure and ocean current (Wilson & Norris, 2001; Norris et al., 2002; Hu, 2004; Wang & Hu, 2005). Based on the compositions of belemnites of Barremian (127–121 Myr) in eastern England, the seawater palaeotemperature was also fluctuant from 11 ºC in early Barremian to a peak of 20 ºC in Late Barremian (McArthur et al., 2004). All above mention shows that Barremian Age is a quite warm age. The mean temperature of seawater surface in warm season in northern European is now below 8 ºC. Hence it is not surprise that the gnetoid plants were able to grow at that time in northeastern China.

The two living species to which *Khitania* most closely resembles, *G. pendulum* and *G. montanum,* both grow in mesophytic forests in southern China (Cheng, 1978; Fu et al., 1999), where the climate ranges from subtropical to tropical zones. It is also known that during Late Jurassic and Cretaceous, particularly the Mid-Cretaceous, there was a relatively stable climate in the Northern Hemisphere and a small range of temporal temperature fluctuations from the equator to the North Pole. It may be safely said that the climate was generally warmer and more equable than today. During the Early Cretaceous, the temperature range between the equator and the pole were presumably 17–26 ºC only (Barron, 1983; Hallam, 1985). The mean annual temperature of Fujian Province is now 15–22 ºC which is still lower than that temperature in Early Cretaceous. Therefore, the temperature may adapt *Khitania* to growth in Early Cretaceous in Liaoning, northeastern China.

The fossil locality represents lacustrine deposit yielding abundant fossil plants. They mostly comprise Charophyte, Bryophyte, Lycopodiatae, Equisetatae, Filicatae, Pteridospermae, Bennettitales, Ginkgoales, Coniferae, Gnetales, Angiospermae, and spore-pollen of unidentified taxa. Among the fossil plants, the preponderant groups are represented by Coniferae, Pteridophyte, Bennettitales, and Ginkgoales in a descending order of abundance. This floristic composition apparently indicates mesophytic to semi-xerophytic forests, reflecting subtropical humid and sub-humid climate sometimes. Some of fossil plants probably grew in lowland or by lakeside at that time (Chang, 1999; Chen, 1999; Sun et al., 2001, 2002; Chang et al., 2003; Ji et al., 2004; Li, 2005; Dilcher et al., 2007). The *Ephedra* fossils have been reported from the same locality (Yang et al., 2005), and all extant *Ephedra* species are xerophytic plants (Kramer & Green, 1991). It might be concluded that the forest in which *Khitania* grew was a mesophytic or semi-xerophytic plants. The smaller size and denser involucral collars of the fossil strobiles in comparison to the extant species are also consistent with a somewhat dry environment in which the plants might have grown in. Both Pteridophyta and Ginkgoales are relatively abundant in Jianshangou flora. These plants are commonly found in subtropical and humid or semi-humid environments. In addition, the xerophytic *Ephedra* plants have also excavated from the Jianshangou site. These data indicate that there was some climatic fluctuation in Cretaceous period (Norris et al., 2002; Fluteau et al., 2004). The lithological characters of the Jianshangou Member also suggest that a climatic fluctuation and alternation between humid and dry climates. There are two layers of black shales in the upper and lower parts and other grayish-green or brown siltstone, mudstone, and shales.

While the climatic and ecological inference is inherently associated with some uncertainties, reconstruction of the historic biogeographic pattern seems to be straightforward. From the fossil evidence presented here, it is clear that Gnetaceae had a more widespread distribution during Early Cretaceous than today. Recently, Won and Renner (2006) suggested that the current distribution pattern of *Gnetum* may be a result of dispersal, which might be true on an intra-continental scale. The inter-continental disjunction the genus exhibits today, on the other hand, is probably better explained by vicariance. Similarly, other two gnetalean genera, *Ephedra* and *Welwitschia*, both showed wider geographic distribution in Early Cretaceous than at present; the fossils were found in South America, Portugal, and northeastern China (Guo & Wu, 2000; Rydin et al., 2003, 2004, 2006; Dilcher et al., 2005; Yang et al., 2005). Furthermore, gnetalean fossils have been discovered in eastern United States (Crane & Upchurch, 1987) and north-central China (Wang, 2004) where these plants no longer grow today. Hence, it seems safe to conclude that the present distribution of Gnetales merely reflects a relic pattern of a once much wider distribution range of a perhaps more diverse group.

3.3 Geological age

The Jianshangou Member of the Yixian Formation of the Jehol Group in western Liaoning contains abundant animal and plant fossils. The different animal and plant fossils have been assessed of different geological ages and no agreement has been reached on the exact age of the Jianshangou Member. The ages of Hauterivian/ Barremian, Barremian/ Aptian, and Aptian/Albian boundaries are 130, 125, and 112 Myr, respectively (Ogg, 2003). Based on the recent measures, the age of the Jianshangou Member is between about 125–122 Myr (Zhu, 2002; Swisher et al., 2002; Zhang et al., 2006; Chen et al., 2006). These lines of evidence suggest that the age of *Khitania columnispicata* is probably between 125–122 Myr (Barremian Age), and that the *Gnetum*-related taxon was existent at least 125 Myr ago.

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References

Arber EAN, Parkin J. 1908. Studies on the evolution of the angiosperms: the relation ship of the angiosperms to the Gnetales. Annols of Botany 22: 489–515.

Barron EJ. 1983. A warm, equable Cretaceous: the nature of the problem. Earth Science Review 19: 305–338.

Bowe LM, Coat G, de Pamphilis CW. 2000. Phylogeny of seed plants based on all three plant genomic compartments: extant gymnosperms are monophyletic and Gnetales are derived conifers. Proceedings of the National Academy of Sciences USA 97: 4092–4097.

Burleigh JG, Mathews S. 2004. Phylogenetic signal in nucleotide data from seed plants: implications for resolving the seed plant tree of life. American Journal of Botany 91: 1599–1613.

Carlquist S. 1996. Wood, bark, and stem anatomy of Gnetales: a summary. International Journal of Plant Sciences 157: S58–S76.

Chang M-M (张弥曼). 1999. Preface. Palaeoworld 11 (Special Issue). Hefei: Press of University of Science and Technology of China. i–ii.

Chang M-M (张弥曼), Chen P-J (陈丕基), Wang Y-Q (王元青), Wang Y (王原). 2003. The Jehol biota. Shanghai: Shanghai Scientific and Technical Publishers. 208.

Chaw S-M, Parkinson CL, Cheng Y, Vincent TM, Palmer JD. 2000. Seed plant phylogeny inferred from all three plant genomes: monophyletic of extant gymnosperms and origin of Gnetales from conifers. Proceeding National Academy of Sciences USA 97: 4086-4091.

Chen J-H (陈金华), Komatsu T (小松俊文). 2005. New advance in researching on the Tetori Group of Japan. Acta Palaeontologica Sinica (古生物学报) 44: 627–635.

Chen P-J (陈丕基). 1999. Distribution and spread of the Jehol biota. Palaeoworld 11 (special Issue). Hefei: Press of University of Science and Technology of China. 1–6.

Chen P-J, Li J-J, Matsukawa M, Zhang H-C, Wang Q-F, Lockley MG. 2006. Geological ages of dinosaur-track-bearing formations in China. Cretaceous Research 27: 2–32.

Cheng C-Y (诚静容). 1978. Gnetaceae. In: Flora Reipublicae Popularis Sinicae (中国植物志). Beijing: Science Press. 7: 490–504.

Coulter JM, Chamberlain CJ. 1910. Morphology of Gymnosperms. Chicago: The University of Chicago Press. 458.

Crane PR. 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. Annals of the Missouri Botanical Garden 72: 716–793.

Crane PR. 1996. The fossil history of the Gnetales. International Journal of Plant Sciences 157: S50–S57.

Crane PR, Upchurch GR. 1987. *Drewria potomacensis* gen. et sp. nov., an early Cretaceous member of Gnetales from the Potomac Group of Virginia. American Journal of Botany 74: 1722–1736.

Diéguez C. 1996. Gnetales macrofossil from Late Barremian of las Hoyas (Cuenca, Spain). Fifth International organization of Palaeobotany Conference, Abstracts. 23.

Dilcher DL, Bernardes-De-Oliveira ME, Pons D, Lott TA. 2005. Welwitschiaceae from the Lower Cretaceous of northeastern Brazil. American Journal of Botany 92: 1294–1310.

Dilcher DL, Sun G, Ji Q, Li H-Q. 2007. An early infructescence *Hyrcantha decussate* (comb. nov.) from the Yixian Formation in northeastern China. Proceedings of the National Academy of Sciences USA 104: 9370–9374.

Ding Q-H (丁秋红), Zhang L-D (张立东), Guo S-Z (郭圣哲), Zhang C-J (张长捷), Peng Y-D (彭艳东), Jia B (贾斌), Chen S-W (陈树旺), Xing D-H (邢德和). 2003. Study on the paleoecology of Yixian Formation in Beipiao area, western Liaoning province, China. Geology and Resources (地质和资源) 12 (1): 9–18.

Donoghue MJ, Doyle JA. 1999. Seed plant phylogeny: Demise of the anthophyte hypothesis? Current Biology 10: R106–R109.

Doyle JA, Donoghue MJ. 1986. Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach. Botanical Review 2: 321–431.

Doyle JA, Donoghue MJ. 1987. The importance of fossils in elucidating seed plant phylogeny and macroevolution. Review of Palaeobotany and Palynology 50: 63–95.

Endress PK. 1996. Structure and function of females and bisexual organ complexes in Gnetales. International Journal of Plant Sciences 157: S113–S125.

Fluteau F, Ramstein G, Besse J, Pucéat E, Lécuyer C. 2004. Is mid cretaceous climate equable? Simulations of Aptian and Cenomanian show major climatic differences. Geophysical Research Abstracts 6, p 05263.

Foster AS, Gifford EMJr. 1974. Comparative morphology of vascular plants. 2nd ed. San Francisco: WH Freeman and Company. 751.

Friis EM, Crane PR, Pedersen KR, Bengtson S, Donoghue, Ph CJ, Grimm GW, Stampanoni M. 2007. Phase-contrast

X-ray microtomography links Cretaceous seeds with Gnetales and Bennettitales. Nature 450: 549–552.

Frohlich MW, Parker DS. 2000. The mostly male theory of "flower" evolutionary origins: from genes to fossils. Systematic Botany 25: 155–170.

Fu L-G, Yu Y-F, Gilbert MG. 1999. Gnetaceae. In: Wu Z-Y, Raven PH eds. Flora of China. Beijing: Science Press; St. Louis: Missouri Botanical Garden Press. 4: 102–105.

Goremykin V, Bobrova V, Pahnke J, Troitsky A, Antonov A, Martin W. 1996. Noncoding sequences from the slowly evolving chloroplast inverted repeat in addition to *rbc*L data do not support Gnetalean affinities of angiosperms. Molecular Biological Evolution 13: 383–396.

Gugerli F, Sperisen C, Büchler U, Brunner I, Brodbeck S, Palmer JD, Qiu Y-L. 2001. The evolutionary split of Pinaceae from other conifers: evidence from an intron loss and a multigene phylogeny. Molecular Phylogenetics and Evolution 21: 167–175.

Guo S-X(郭双兴), Wu X-W(吴向午). 2000. *Ephedrites* from Latest Jurassic Yixian Formation in western Liaoning, Northeast China. Acta Palaeontologica Sinica (古生物学报) 39: 81–91.

Haggart JW, Matsukawa M, Ito M. 2006. Paleogeographic and paleoclimatic setting of Lower Cretaceous basins of East Asia and western North America, with reference to the nonmarine strata. Cretaceous Research 27: 149–167.

Hallam A. 1985. A review of Mesozoic climates. Journal of Geological Society in London 142: 433–445.

Hu X-M (胡休棉). 2004. Greenhouse climate and ocean during the Cretaceous. Geology in China (中国地质) 2004: 442–448.

Hufford L. 1996. The morphology and evolution of male reproductive structures of Gnetales. International Journal of Plant Sciences 157: S95–S112.

Ji Q, Li H-Q, Bowe LM, Liu Y-S, Tayler DW. 2004. Early Cretaceous *Archaefructus eoflora* sp. nov. with bisexual flowers from Beipiao, western Liaoning, China. Acta Geologica Sinica 78: 883–896.

Kramer KU, Green P S eds. 1990. Pteridophytes and Gymnosperms. In: Kubitzki K ed. The families and genera of vascular plants. Berlin: Springer-Verlag. 404, with 216 figures.

Li H-Q. 2005. Early Cretaceous sarraceniacean-like pitcher plants from China. Acta Botanica Gallica 152: 227–234.

Magallon S, Sanderson MJ. 2002. Relationships among seed plants inferred from highly conserved genes: sorting conflicting phylogenetic signals among ancient lineages. American Journal of Botany 89: 1991–2006.

Mathur YK, Mathur K. 1965. Occurrence of Gnetalean pollen grains in the Katrol Formation (Upper Jurassic) of Kutch, India. Nature 208: 912–913.

Matsukawa M, Ito M, Nishida N, Koarai K, Lockley MG, Nichols DJ. 2006. The Cretaceous Tetori biota in Japan and its evolutionary significance for terrestrial ecosystems in Asia. Cretaceous Research 27: 199–225.

McArthur JM, Mutterlose J, Price GD, Rawson PF, Ruffell A, Thirlwall MF. 2004. Belemnites of Valanginian, Hauterivian and Barremian age: Sr-isotope stratigraphy, composition (87Sr/86Sr, δ13C, δ18O, Na, Sr, Mg), and palaeo-oceanography. Palaeogeography, Palaeoclimatology, Palaeoecology 202: 253–272.

Nixon KC, Crepet WL, Stevenson D, Friis EM. 1994. A reevaluation of seed plant phylogeny. Annals of Missouri Botanical Garden 81: 484–533.

Norris RD, Bice KL, Magno EA, Wilson PA. 2002. Jiggling the tropical thermostat in the Cretaceous hothouse. Geology 30: 299–302.

Ogg JG. 2003. Status of divisions of the International Geologic Time Scale. Lethaia 37:183-199.

Osborn JM, Taylor TN, de Lima MR. 1993. The ultrastructure of fossil ephedroid pollen with gnetalean affinities from the Lower Cretaceous of Brazil. Review of Palaeobotany and Palynology 77: 171–184.

Price RA. 1996. Systematics of the Gnetales: a review of morphological and molecular evidence. International Journal of Plant Sciences 157: S40–S49.

Rydin C, Källersjö M, Friis EM. 2002. Seed plant relationships and the systematic position of Gnetales based on nuclear and chloroplast DNA: conflicting data, rooting problems and the monophyly of conifers. International Journal of Plant Sciences 163: 197–214.

Rydin C, Mohr B, Friis EM. 2003. *Cratonia cotyledon* gen. et sp. nov.: a unique Cretaceous seedling related to *Welwitschia*. Proceedings of the Royal Society B: Biological Sciences 270 (Suppl. 1): S29–S32.

Rydin C, Pedersen KR, Crane PR, Friis EM. 2006. Former diversity of *Ephedra* (Gnetales): evidence from Early Cretaceous seeds from Portugal and North America. Annals of Botany 98:123–140.

Rydin C, Pedersen KR, Friis EM. 2004. On the evolutionary history of *Ephedra*: Cretaceous fossils and extant molecules. Proceedings of the National Academy of Sciences USA 101: 16571-16576.

Smith AG, Smith DG, Funnell BM. 1994. Atlas of Mesozoic and Cenozoic coastlines. Cambridge: Cambridge University Press. 55.

Sun G (孙革), Zheng S-L (郑少林), Dilcher DL, Wang Y-D (王永栋), Mei S-W (梅盛吴). 2001. Early angiosperms and their associated plants from western Liaoning, China (辽西早期被子植物及伴生植物群). Shanghai: Shanghai Scientific and Technological Education Publishing House. 227.

Sun Z-M (孙知明), Xu K (许坤), Ma X-H (马醒华), Liang H-D (梁鸿德), Yang T-S (杨天水), Li R-H (李荣辉), Li Y (李瑜), Zhao Y (赵越). 2002. Magnetostratigraphy of the Jurassic-Cretaceous boundary near Bird-bearing Beds in western Liaoning. Acta Geologica Sinica (地质学报) 76: 317–324.

Swisher III CC, Wang X-L, Zhou Z-H, Wang Y-Q, Jin F, Zhang J-Y, Xu X, Zhang F-C, Wang Y. 2002. Further support for a Cretaceous age for the feathered-dinosaur beds of Liaoning, China: New $^{40}Ar/^{39}Ar$ dating of the Yixian and Tuchengzi Formation. Chinese Science Bulletin 47: 135–138.

Van Steenis CGGJ. 1948–1954. Flora Malesiana. Ser. 1 Spermatophyta. P. Noordhoff Ltd. 4: 631.

Wang C-S (王成善), Hu X-M (胡休棉). 2005. Cretaceous world and oceanic red bed. Earth Science Frontier (地学

前缘) 12 (2): 11–21.

Wang Z-Q. 2004. A new Permian gnetalean cone as fossil evidence for supporting current molecular phylogeny. Annals of Botany 94: 281–288.

Wilson PA, Norris RD. 2001. Warm tropical ocean surface and global anoxia during the mid-Cretaceous period. Nature 412: 425–429.

Winter KU, Becker A, Muenster T, Kim JT, Saedler H, Theissen G. 1999. MADS-box genes reveal that gnetophytes are more closely related to conifers than to flowering plants. Proceedings of the National Academy of Sciences USA. 96: 7342–7347.

Won H, Renner SS. 2006. Dating dispersal and radiation in the gymnosperm *Gnetum* (Gnetales)—Clock calibration when outgroup relationships are uncertain. Systematic Biology 55: 610–622.

Yang Y, Geng B-Y, Dilcher DL, Chen Z-D, Lott TA. 2005. Morphology and affinities of an Early Cretaceous Ephedra (Ephedraceae) from China. American Journal of Botany 92: 231–241.

Zhang H (张宏), Liu X-M (刘小明), Yuan H-L (袁洪林), Hu Z-C (胡兆初), Diwu C-R (第五春荣). 2006. U-Pb isotopic age of the Lower Yixian Formation in Lingyuan of Western Liaoning and its significance. Geological Review (地质论评) 52: 63–71.

Zhang L-D (张立东), Guo S-Z (郭胜哲), Zhang C-J (张长捷), Peng Y-D (彭艳东), Chen S-W (陈树旺), Xing D-H (邢德和), Ding Q-H (丁秋红), Zheng Y-J (郑月娟). 2004. The lithostratigraphic characteristics of Yixian Formation in Beipiao-Yixian area, Liaoning Province. Geology and Resoures (地质与资源) 13(2): 65-74.

Zhu R-X, Saho J-A, Pan Y-X, Shi R-P, Shai G-H, Li D-M. 2002. Paleomagnetic data from Early Cretaceous volcanic rocks of west Liaoning: evidence for intracontinental rotation. Chinese Science Bulletin 47: 1832–1837.