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A Review on Gnetalean Megafossils: Problems and Perspectives

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ABSTRACT: Gnetalean megafossils were accumulated in the last decade. Taxonomic positions of several of Ephedran megafossil species are, however, controversial, resulting in a complicated nomenclature. *Liaoxia* Z.Y. Cao & S.Q. Wu, "*Eragrostis* Z.Y. Cao & S.Q. Wu", "*Chaoyangia* Duan", and their type species "*Liaoxia cheniae* Z.Y. Cao & S.Q. Wu", "*Eragrostis changii* Z.Y. Cao & S.Q. Wu", "*Chaoyangia liangii* S.Y. Duan", were not validly published in the original publication under the Vienna Code. The species "*Liaoxia cheniae* Z.Y. Cao & S.Q. Wu" was validly published as *Ephedrites cheniae* S.X. Guo & X.W. Wu but later combined into *Liaoxia cheniae* (S.X. Guo & X.W. Wu) Z.Y. Cao & S.Q. Wu and further into *Ephedra cheniae* (S.X. Guo & X.W. Wu) H.M. Liu et al. Some uncertain morphological characters are fundamental to elucidate the taxonomic position of *Ephedrites cheniae* S.X. Guo & X.W. Wu and "*Chaoyangia liangii* S.Y. Duan", e.g. bract number, position, and connation in female cones, seed number and position in a female cone, and morphology of the furcated appendages of reproductive organs of "*Chaoyangia liangii* S.Y. Duan".

KEY WORDS: Cretaceous, Ephedraceae, Gnetales, megafossil, nomenclature, taxonomy.

INTRODUCTION

The Gnetales, containing Ephedraceae, Welwitschiaceae, and Gnetaceae, have been the most controversial group of plants within the five extant lineages of seed plants including cycads, ginkgo, conifers, Gnetales, and angiosperms in phylogenetic studies since the beginning of the 20 century (Arber and Parkin, 1908; Crane, 1985; Doyle and Donoghue, 1986; Nixon et al., 1994; Chaw et al., 2000; Rydin et al., 2002; Hajibabaei et al., 2006). They have frequently been considered to be related to the origin of angiosperms because they bear a unique set of characters, e.g. presence of vessels, archegonia present in *Ephedra* L. but lack in *Gnetum* L. and *Welwitschia* Hook. f., broad leaves with pinnate venation in *Gnetum* but parallel-veined in *Ephedra* and *Welwitschia*, bisexual reproductive organs, and double fertilization etc (Crane, 1985; Doyle and Donoghue, 1986; Friedman, 1990, 1992; Nixon et al., 1994; Rydin et al., 2002; Friis et al., 2007). Though most recent molecular phylogenies indicate that the Gnetales are most close to Pinaceae making conifers paraphyletic since 2000 (Chaw et al., 2000; Bowe et al., 2000; Gugerli et al., 2001; Burleigh and Mathews, 2004; Hajibabaei et al., 2006), the anthophyte hypothesis can not be ultimately excluded because the numerous resemblances occur between the Gnetales and angiosperms and the newly recorded seeds from Early Cretaceous bear intermediate characters of the Gnetales and Bennettitales (Friis et al., 2007, 2009). Fossils are important in elucidating evolutionary questions, but the Gnetales were badly known in strata before 1996 excepting microfossils (Crane, 1996).

This situation, however, was markedly changed in the last decade. The earliest known megafossil Gnetales was dated back to *Palaeognetaleana auspicia* Wang et al., a bisexual cone from Permian of Taiyuan, China, which bears *in situ* Ephedroid pollens and enveloped ovules but can not compared with the extant Gnetales in details (Wang, 2004). The most diverse megafossils of the Gnetales had continuously been reported from the Early Cretaceous worldwide, e.g. Asia (Wu, 1999; Guo and Wu, 2000; Sun et al., 2001; Zhang, 2001; Wu, 2002; Tao and Yang, 2003; Zhou et al., 2003; Yang et al., 2005; Rydin et al., 2006a; Guo et al., 2009), Europe (Rydin et al., 2004, 2006b), Australia (Krassilov et al., 1998), S America (Mohr et al., 2004; Dilcher et al., 2005; Cladera et al., 2007), and N America (Rydin et al., 2006b), these include well preserved seeds, vegetative shoots, and reproductive shoots bearing important evolutionary information. This mini-review is to discuss the known megafossils of Ephedraceae with a focus on their nomenclature and taxonomy.

DIVERSITY AND DISTRIBUTION OF THE CRETACEOUS GNETALES

The living Gnetales are represented by 3 monotypic families, viz. Ephedraceae, Gnetaceae, and Welwitschiaceae, with Ephedraceae occupying a basal position and sister to a clade including the other two families (Chaw et al., 2000). The Ephedraceae are widely distributed in the N temperate zone and temperate S America. The family includes *ca.* 50 species according to Price (1996) and Yang (2007b) but details of modern diversity of the family remain

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ambiguous especially in the Old World. The Gnetaceae comprise *ca.* 35 tropical species, and the Welwitschiaceae is represented by one single species in Nambia of SW Africa. During the last decade, a number of megafossils were found belonging to the Ephedraceae, the Gnetaceae, and the Welwitschiaceae.

Welwitschiaceae

Fossil seedlings, leaves, and reproductive structures related to the Welwitschiaceae were recorded from Early Cretaceous of Crato Formation, S America (Rydin et al., 2003; Dilcher et al., 2005). *Cratonia cotyledon* Rydin et al. and *Priscowelwitschia austroamericana* (Dilcher et al.) Dilcher et al. are seedlings bearing axis and cotyledons, *Welwitschiostrobus murili* Dilcher et al. is based on reproductive organs while *Welwitschiophyllum brasiliense* Dilcher et al. is leaf remains. These megafossils together with their modern relic species *Welwitschia mirabilis* Hook. f. clearly imply that the family was once much more diversified in history than they are today, and widely distributed in N Gondwana in Early Cretaceous.

Gnetaceae

Megafossils having affinity with Gnetaceae were rarely recorded. *Khitania columnispicata* S. X. Guo et al., a newly recorded megafossil from Early Cretaceous of W Liaoning, China, is considered to have affinity to living *Gnetum* (Guo et al., 2009). This fossil species is preserved with a bifurcate reproductive structure including two elongate-cylindrical spikelike strobiles, and each of the strobiles bears numerous verticillate annular involucral collars. This fossil species is not well preserved, though it shows certain resemblance with *Gnetum*, no structural details available can be compared with its extant counterparts.

Ephedraceae

The Ephedraceae have a much higher diversity than the other two families of the Gnetales in geological history as they are today, about 17 megafossil species were recorded worldwide from Early Cretaceous of Australia, Europe, Asia, N America, and S America.

Ephedrispermum lusitanicum Rydin et al., *Ephedra portugallica* Rydin et al., and *E. drewriensis* Rydin et al. are seeds with *in situ* pollens similar to living *Ephedra* from Europe and N America (Rydin et al., 2006b). These seeds are either from Europe (e.g. *Ephedrispermum lusitanicum* Rydin et al., and *Ephedra portugallica* Rydin et al.) or from U.S.A. (e.g. *Ephedra drewriensis* Rydin et al.).

Ephedra verticillata Cladera et al. is a reproductive shoot from Early Cretaceous of S America but bears no detailed characters comparable to living species (Cladera et al., 2007).

Leongathia elegans Krassilov et al. is vegetative bearing anatomical characters from Australia (Krassilov et al., 1998). The most species-rich locality for megafossil Ephedraceae is from Yixian Formation of Jianshangou Bed, NE China, Asia, 14 species were recorded. Eight of the 14 species have no clear reproductive details and were ascribed either to *Liaoxia* Z.Y. Cao & S.Q. Wu or to *Ephedrites* Goeppert & Berendt.

Ephedra archaeorhytidosperma Y. Yang et al. includes not only reproductive shoots but also ornamented seeds and became the first megafossil species earlier than Tertiary ascribed into the extant genus *Ephedra* (Yang et al., 2005).

Alloephedra xingxuei J.R. Tao & Y. Yang is from Dalazi Formation, NE China, bearing reproductive details and vegetative characters (Tao and Yang, 2003).

"*Chaoyangia liangii* Duan" comprises reproductive shoots with seed cones enclosing 2 to 3 seeds and surrounded by many furcate hairlike structures. Relationships of this species are not clear, Tao and Yang (2003) believed this an extinct species of *Ephedra* but Sun et al. (1998) thought an affinity with *Welwitschia*.

Ephedra hongtaoi X. Wang & S.L. Zheng from Early Cretaceous of W Liaoning of China is not a valid name thus far, which preserved a whole individual plant comparable to modern *E. sinica* Stapf (Wang and Zheng, 2010).

Moreover, some other megafossils might have an affinity with the Ephedraceae, e.g. *Cyperacites* sp. (Krassilov, 1982, Figs. 240-243) might belong to *Ephedries cheniae* S.X. Guo & X.W. Wu or *Liaoxia cheniae* (S.X. Guo & X.Y. Wu) Z.Y. Cao & S.Q. Wu (published as "*Liaoxia chenii*" in Rydin et al., 2006a). *Carpolithus multiseminalis* G. Sun & S.L. Zheng and *Carpolithus pachythelis* G. Sun & S.L. Zheng are seeds from the same Formation and were described as "*plantae incertae sedes*" (Sun et al., 2001), they might be the ovules of *Ephedra*.

Despite the evolutionary importance of these megafossil Gnetales, several fundamental questions need answer. First, origin of furcated appendages of the female cones and male structures below the female cones of the "*Chaoyangia liangii* Duan" remain unclear, e.g. whether the furcated appendages originated from furcation of the two vascular bundles of bracts or not and whether "*C. liangii*" has bisexual reproductive organs or not are ambiguous? Second, what is the habit of the early Ephedraceae? The genus *Ephedra* mostly lives in dry places today and people used it as an indicator to deduce an arid place if *Ephedra* occurred, this doctrine is dubitable because it is suggested that the early members of *Ephedra* once lived in moist places (Fanton et al., 2006; Sun et al., 2001). Third, bract

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number, position, and connation of female cones are important in classification of the genus *Ephedra* but these characters are not clear in the fossils. Fourth, how many seeds are there in a female cone? It is well known that only the uppermost whorl/pair of bracts are fertile in a female cone, and 1, 2, or 3 seeds are enclosed in a female cone in living species of *Ephedra*. Whether this situation is same in early members of the genus in early Cretaceous is uncertain. Otherwise, taxonomic position of "*Ephedrites cheniae* S.X. Guo & X. W. Wu" and "*Chaoyangia liangii* Duan" can not be elucidated.

Recently, one more species, *Ephedra verticillata* Cladera et al., was recorded from Early Cretaceous of the Anfiteatro de Tico Formation (Baquero Group), Argentina (Cladera et al., 2007). This species preserved not only vegetative but also reproductive features, e.g. stems with verticillate branches, and seed bearing structures single or in clusters of three to five, sessile, rounded to oval in outline, each such structure with two oval-acuminate seeds 0.8 mm wide and 1.8 mm long (Cladera et al., 2007). These features can not be compared with extant species, and differs clearly from other fossil species such as *E. archaeorhytidosperma*, *Dinophyton spinosum*, and *Drewria potomacensis* (Cladera et al., 2007).

PROBLEMS AND PERSPECTIVES

Nomenclature

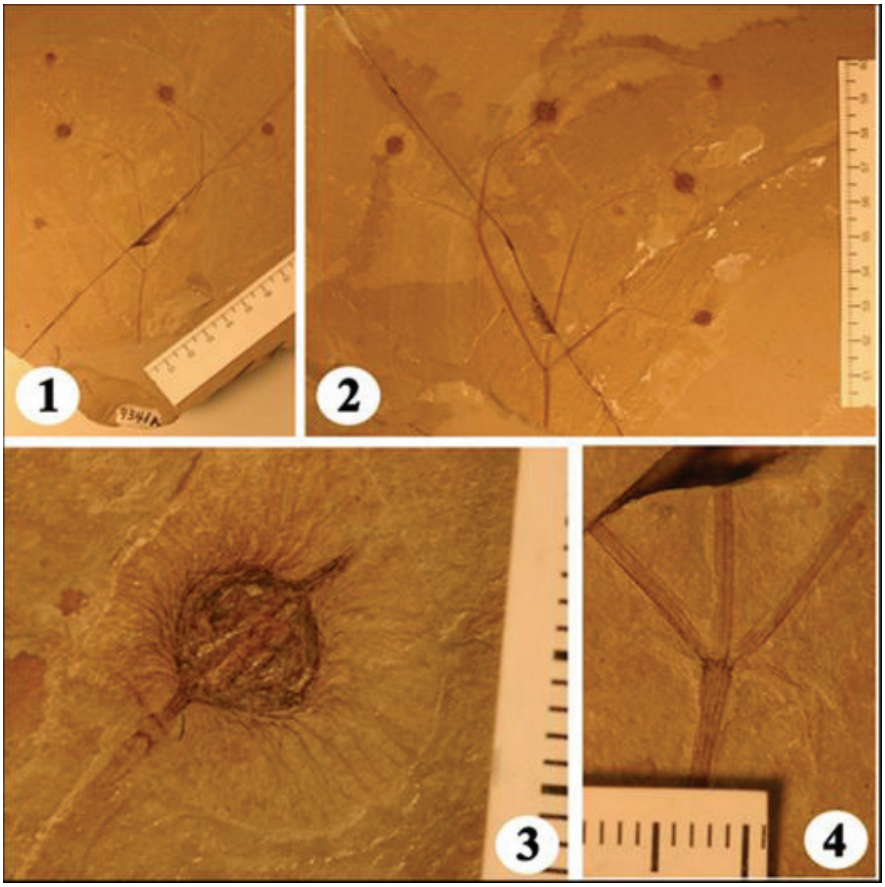
Nomenclature of Asiatic fossils is rather complicated, partly because characters of these fossils remain not clear (see review in Yang, 2006, 2007a, Yang et al., 2005; Rydin et al., 2006a), whether *Ephedrites* Goeppert & Berendt or *Liaoxia* Z.Y. Cao & S.Q. Wu should be applied to those Ephedroid plants depend upon clarification of detailed reproductive features.

Ephedroid megafossils from Tertiary or earlier were used to be ascribed into *Ephedrites* Goeppert & Berendt while those from later were ascribed into the modern genera *Ephedra*. Two points are noteworthy. First, this classification of megafossils of Ephedraceae using fossil age is artificial and should be improved by using fossil characters, actually several megafossil species thus far from Early Cretaceous of Asia, Europe, and N America were already classified into modern genus *Ephedra* because of their characters fell well within the variation range of extant *Ephedra*, which is definitely a good taxonomic practice on the topic (Yang et al., 2005; Rydin et al., 2006a; Liu et al., 2008). Second, the type of *Ephedrites* Goeppert & Berendt was considered to have gnetalean affinity, but later recognized to be a Loranthaceae, thus the name *Ephedrites* Goeppert & Berendt becomes a taxonomic synonym, many noticed the problem, e.g. Wu et al. (1986), Guo and Wu (2000), Yang et al. (2005), and Rydin et al. (2006a).

Yang (2006) proposed to conserve the name *Ephedrites* Goeppert & Berendt with a conserved type for further use of the name as Ephedraceae because of three fundamental reasons. First, several megafossils showing Ephedraceae characters were included in the genus *Ephedrites* Goeppert & Berendt, e.g. *E. armaillensis* Saporta, *E. guozhongiana* G. Sun & S.L. Zheng, *E. elegans* G. Sun & S.L. Zheng, and *E. cheniae* S.X. Guo & X.W. Wu, nomenclatural stability is maintained by conservation of the name *Ephedrites* Goeppert & Berendt with a conserved type. Second, the name has been widely used as Ephedraceae for over a century to indicate fossil Ephedraceae. Third, the name *Ephedrites* Goeppert & Berendt has a straightforward meaning of having *Ephedra* affinity. Rydin et al. (2006a) noticed the problem too but proposed to substitute the name with *Liaoxia* Z.Y. Cao & S.Q. Wu, a name not validly published in Cao and Wu (1998) but in Rydin (2006a), and described 5 fossil species from NE China including *Liaoxia changii* Rydin et al. and *L. cheniae* (S.X. Guo & X. W. Wu) Cao & S.Q. Wu that had been merged into a single species as *Ephedrites cheniae* (2000). Yang (2007) gave a thorough review of the current nomenclatural situation of *Ephedrites* and the problem can not be fundamentally resolved before reproductive details (e.g. bract and seed number of female cones) are clarified.

"*Liaoxia* Z.Y. Cao & S.Q. Wu" and its including species "*Liaoxia cheniae* Z.Y. Cao & S.Q. Wu", "*Eragrostis* Z.Y. Cao & S.Q. Wu" and its including species "*Eragrostis changii* Z.Y. Cao & S.Q. Wu", were not validly published in Cao et al. (1998) because the type deposit is not designated. Guo and Wu (2000) first validly published the former species as *Ephedrites cheniae* when they intended to make a new combination "*Ephedrites cheniae* (Z.Y. Cao & S.Q. Wu) S.X. Guo & X.W. Wu" from "*Liaoxia cheniae* Z.Y. Cao & S.Q. Wu". Later, Rydin et al. (2006a) published a new name *Liaoxia cheniae* (S.X. Guo & X.W. Wu) Z.Y. Cao & S.Q. Wu (as "*Liaoxia chenii* Cao & S. Q. Wu"). Liu et al. (2008) made another new combination, viz. *Ephedra cheniae*, but they clearly made a mistake in the author citation of "*Ephedrites cheniae* (Z.Y. Cao & S.Q. Wu) H.M. Liu et al.", it is S.X. Guo and X.W. Wu (2000) who first validly published the specific epithet *cheniae* (as "*chenii*") based on PB17800 (NPA) while *Liaoxia cheniae* (S.X. Guo & X.W. Wu) Z.Y. Cao & S.Q. Wu is another combination based on *Ephedrites cheniae* S.X. Guo & X.W. Wu in Rydin et al. (2006a) as Yang (2007a) stated "S.Q. Wu is one of the authors both of the paper by Cao et al. and that by Rydin et al. (2006a)

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Figs. 1-4. *Chaoyangia liangii* S.Y. Duan. 1-2: Part and counterpart of type specimens of *C. liangii* showing basic morphology. 3: Female cones of *C. liangii* showing furcated appendages. 4: Nodes showing linear leaves.

under the final sentence of Art. 46.2, the generic name is to be attributed to Z.Y. Cao & S.Q. Wu, whereas the specific name is to be cited as *Liaoxia cheniae* (S.X. Guo & X.W. Wu) Z.Y. Cao & S.Q. Wu, because it must be treated as a new combination based on *Ephredites cheniae* S.X. Guo & X.W. Wu". Cao and Wu (1998) did not validly publish the name "*Liaoxia cheniae* Z.Y. Cao & S.Q. Wu". As a result, the correct citation of authors for *Ephedra cheniae* is "(S.X. Guo & X.W. Wu) H.M. Liu et al." but not "(Z.Y. Cao & S.Q. Wu) H.M. Liu et al."

"*Chaoyangia* Duan" and its type species "*Chaoyangia liangii* Duan" were not validly published because the type (Unknown Coll. 9341) deposit was not clearly designated (Duan, 1998). It turned out to be that the type specimen belongs to Mr. Shikuan Liang, a personal collection. In summer of 2007, I had the opportunity to visit Liang's home in Beijing and check the type specimen (Figs. 1-4). Though Mr. Liang do not intend to transfer the specimen into a public herbarium for the time being, the "*Chaoyangia liangii* Duan" can be validly published based on the specimen under Art. 37.7, the collection may be a private one when it says "For the name of a new species or infraspecific taxon published on or after 1 January 1990 of which the type is a specimen or unpublished illustration, the single herbarium or collection or institution in which the type is conserved must be specified." This is also evident from Rec. 7A.1: "It is strongly recommended that the material on which the name of a taxon is based, especially the holotype, be deposited in a public herbarium or other public collection with a policy of giving bona fide researchers access to deposited material, and that it be scrupulously conserved." A lot of separate female cones of "*Chaoyangia liangii* S.Y. Duan" have been recorded since 1998 (Wu, 1999; Sun et al., 2001, Wu, 2002; Zhang, 2001), and a new name was given to one of these separate reproductive organs, viz. *Gurvenalla exquisita* G. Sun et al. because of resemblances of furcated appendages of female cones of "*Chaoyangia* S.Y. Duan" and *Gurvenalla* Krassilov (Sun et al., 2001). Relationships of this plant are in dispute. Tao and Yang (2003) believed it a genus belonging to Ephedraceae or even a species to *Ephedra*

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L., while others think it more closely related to *Welwitschia* (e.g. Sun et al., 1998; Zhou et al., 2003; Won and Renner, 2006). To resolve this problem, 3-dimensional structure of female cones should be figured out, origin of the furcated appendages and male organs below the female cone should be elucidated.

Chaoyangia liangii S.Y. Duan in Sci. China, Ser. D. 41(1): 14. 1998. Holotype: China, Liaoning, Chaoyang, Yixian Formation of Early Cretaceous, S.K. Liang 9341 (Mr. Shikuan Liang's personal collection in Xiangshan, Beijing).

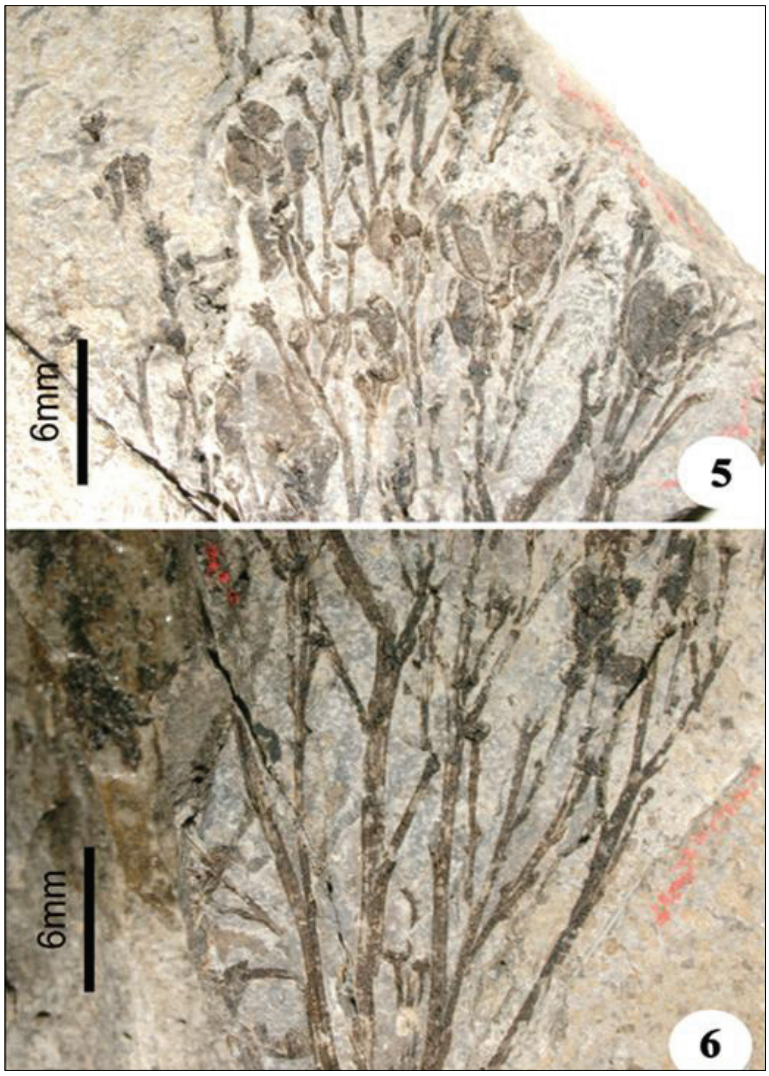
Tao and Yang (2003) described a new genus of the Gnetales with a single species included, viz. *Alloephedra xingxuei* J. Tao & Y. Yang which shows similarities with *Ephedra* L. mainly in reproductive characters (e.g. 2-seeded female cones terminal to twigs, twigs with many fine striations, and reduced leaves), but differs from the latter by vegetative characters (a leaf is singly attached to twigs that are alternate). The singly attached leaf on twigs suggests that the leaf position is alternate in *Alloephedra* (Plate II Fig. 6 in Tao and Yang 2003, and Figs. 5-6 in this study), and the alternate twigs corroborate this suggestion. Liu et al. (2008) did not check the fossil specimens, but questioned the taxonomic ascription of *Alloephedra* only based on a comparison of branching patterns of living *Ephedra* and *Alloephedra*. They mentioned that twigs are not always opposite but opposite proximally and alternate distally in *Ephedra equisetina* Bunge and concluded that the variation pattern of twigs in *Alloephedra* ranges within variation of *Ephedra*. In fact, leaf position is mainly opposite/clustered/whorled at nodes (e.g. *E. saxatilis*, *E. equisetina*, *E. rhytidosperma*, *E. intermedia*, *E. przewalskii*, and *E. sinica* etc). An obvious question to this conclusion is: are there opposite leaves or twigs present in *Alloephedra*? The answer is clearly negative. I check the type specimen again and confirm the observations of Tao and Yang (2003). As a result, observations of Liu et al. (2008) are clearly inadequate, and their conclusion is untenable. It is thus cursory to merge *Alloephedra* J. Tao & Y. Yang into *Ephedra*.

Morphology

Morphological evolution of the Welwitschiaceae can not be outlined from the recently reported megafossils but the Ephedraceae are in a different situation, many megafossils bearing important characters that allow a generalization though some important characters still need reconstruct and clarify. First, ovulate cones of those species are all terminal to twigs, which occurs also in some living *Ephedra* species, e.g. *E. sinica* sometimes (Fig. 7), *E. regeliana* Florin, *E. kokanica*, and *E. fragilis*, etc. Second, leaves in megafossils excepting in *E. archaeorhytidosperma* Y. Yang et al. are linear, free, and much longer than the modern triangular and connate forms. Third, these fossils are profusely branched and the reproductive cones are terminal to twigs. Fourth, habits of these fossils are similar and spreading, branches and twigs are not tightly clustered as many of the living species, e.g. *E. gerardiana*, *E. saxatilis*, *E. przewelskii*, and *E. equisetina*. Fifth, bracts of female cones seem not fused as most of the extant species. Sixth, female cones enclosed 1, 2 or 3 seeds bearing straight or slightly curved micropylar tubes are comparable to extant species. In *Gurvenalla exquisita* and "*Chaoyangia liangii* Duan", 2 or 3 seeds were observed in a female cone, but in *E. archaeorhytidosperma*, 1 or 2 seeds are enclosed in a female cone, there are 2 seeds/ovules per cone in *E. hongtaoi*, seed number is ambiguous in other species and need clarify, e.g. *Ephedrites cheniae*, *Liaoxia acutiformis*, and *Liaoxia changii*. In general, seed number per cone in both *E. archaeorhytidosperma* and "*Chaoyangia liangii* Duan" ranged within the variation of extant *Ephedra*. Seventh, micropylar tubes were observed within only 2/3 species, in *Gurvenalla exquisita* and "*Chaoyangia liangii* Duan", the micropylar tube is straight and longer (over 3 mm) but the micropylar tube in *E. archaeorhytidosperma* is shorter (1-2 mm) and slightly curved at the tip which might be caused by the opening shape, in the former species, the opening is truncate but in the later species it is oblique. It is Meyer (1846) who first used morphology of micropylar tubes in classification of *Ephedra* into two sections, viz. *E.* sect. *Discostoma* with truncate openings and *E.* sect. *Plagiostoma* with oblique openings. It suggests that the opening shape of these fossils also ranged within the modern species.

While some characters are clear in these Early Ephedran species, some are not and need clarify in the future. First, "*Chaoyangia liangii* Duan" is unique in the furcated hair like appendages around its female cones, and the possible male structure below the female cones. Though the gross morphology of this species agrees with extant *Ephedra*, e.g. the articulate and dichasial shoots with striate internodes, female cones terminal to twigs, the tri-ovulate cones, ovules/seeds bearing straight micropylar tubes, many believed the female cone is flat but not three-dimensional and associated it with living *Welwitschia*. To resolve this debate, reconstruction of the reproductive organs including the female and male structures next below the female cone is urgent. Second, bract position and number of cones are not clear because of bad status of preservation though sometimes they were described as opposite and decussate or whorled of 3. These questions can not be answered until well- preserved complete

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Figs. 5-6. Type specimen of *Alloephedra xingxuei* J.R. Tao et Y. Yang. 5: Upper portion of the plant showing female cones terminal to twigs, 5018b. 6: Lower portion of the type showing the singly attached leaf and alternate twigs, 5018a.



Fig. 7. *Ephedra sinica* Stapf showing female cones terminal to twigs.

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specimens are found. As a conclusion, a thorough comparative analysis between megafossil species from Asia, Europe, N America, and S America is difficult, because charcoalized seed fossils are from Europe and N America, but compressions are from Asia and S America, they provide different characters and can not compared with each other.

Ecology

The Ephedroid fossils including megafossils and microfossils were used as an indicator of dry and cold living conditions in a certain geological time. However, it is not well known that the living *Ephedra* has very diverse habitats, they usually live in dried places, e.g. *E. sinica* in sandy deserts of China and Mongolia, *E. przewalskii* in the gobi of NW China and nearby countries, *E. rhytidosperma* in stony alluvions of lower mountains of Mt. Helan of N China, *E. monosperma* in crevices of sandy stones from Siberia southwards to Tibet, Yunnan, and Sichuan of SW China, *E. equisetina* and its allies (*E. procera* and *E. major*) in crevices of stones on cliffs from Canary islands eastwards to Shandong of China, but some do inhabit in humid places, e.g. *E. likiangensis* in underforest of pines in NW Yunnan of China, *E. minuta* in humid grasslands of W Sichuan of China. The floristic components where the Early Cretaceous megafossils of Ephedraceae lived gave more details of living conditions of Ephedraceae in history. A prominent difference between the fossil Ephedraceae and their extant counterparts is their living conditions. The Asiatic fossils clearly inhabit in a humid and warm lacustrine or coastal environments so that they were preserved together with fishes (Duan, 1998). Contrary to this, the living *Ephedra* is mostly in dry and cold places. Species like *E. likiangensis* and *E. minuta* in humid habitat are clearly derived but not directly inherited from their Early Cretaceous ancestors because they share a set of derived reproductive characters with other two species in Himalayan regions, viz. *Ephedra gerardiana* and *E. saxatilis*, e.g. female cones bear 2 or 3 pairs of bracts connate for over 2/3 of their length, seeds are oblong ovoid and blackish and much larger than species from N China such as *E. intermedia*, *E. przewalskii*, *E. regeliana*, and *E. monosperma*. The Crato plants lived near of the shallow lacustrine environment, maybe in the stream margins (Fanton et al., 2006). In short, it seems not reasonable to estimate the environments using Ephedroid remains as an indicator of arid environments in a geological age as early as Middle/Early Cretaceous.

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買麻藤類巨化石綜述：問題和展望

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摘要：巨化石在植物起源和演化研究中具有十分重要的價值，但在本世紀之前與現代買麻藤類可比較的巨化石罕有報導。這種狀況在過去十年中得到了很大的改善，東亞、北美洲、南美洲和歐洲等地不斷有買麻藤類的巨化石报道，然而，其中一些麻黃類巨化石除了在分類地位上還有爭議外，在命名上也比較混亂，例如：「*Liaoxia* Z.Y. Cao & S.Q. Wu」、「*Eragrostis* Z.Y. Cao & S.Q. Wu」、「*Chaoyangia* S.Y. Duan」及其模式種「*Liaoxia cheniae* Z.Y. Cao & S.Q. Wu」、「*Eragrostis changii* Z.Y. Cao & S.Q. Wu」和「*Chaoyangia liangii* S.Y. Duan」等名稱均沒有合格發表。「*Liaoxia cheniae* Z.Y. Cao & S.Q. Wu」所代表的種首次被合格發表為：*Ephedrites cheniae* S.X. Guo & X.W. Wu，但後來被組合為 *Liaoxia cheniae* (S.X. Guo & X.W. Wu) Z.Y. Cao & S.Q. Wu 和 *Ephedra cheniae* (S.X. Guo & X.W. Wu) H.M. Liu et al.。表示這些種類的分類關係，尚需要一些識別特徵來證明，例如雌毬果中苞片的數目、苞片的位置、苞片的合生程度及種子數目，和「*Chaoyangia liangii* S.Y. Duan」中毬果周圍分叉狀附屬物的形態特徵等。

關鍵詞：白堊紀、麻黃科、買麻藤目、巨化石、命名、分類。

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