



A systematic classification of Ephedraceae: living and fossil

YONG YANG

State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, the Chinese Academy of Sciences, 20 Nanxincun, Xiangshan, Beijing 100093, China. Email: ephedra@ibcas.ac.cn

Abstract

A number of Ephedroid macrofossils have been described from the Early Cretaceous in the last decade, indicating huge diversity of early Ephedraceae. However, relationships among these fossils and modern *Ephedra* remain ambiguous. This study proposes a new systematic classification of the family at the generic level based on the reduction and sterilization evolutionary hypothesis of female reproductive organs. Two subfamilies and two tribes are described as new to science. In this new classification, the family Ephedraceae consists of two subfamilies: Siphonospermoideae Y. Yang *subfam. nov.* and Ephedroideae Y. Yang *subfam. nov.*, and the latter subfamily is divided again into two tribes: Liaoxieae Y. Yang *trib. nov.* and Ephedreae Y. Yang *trib. nov.* Ten genera are included in the new classification, and two genera are listed as doubtful due to their taxonomic characters being insufficient to place them in Ephedraceae.

Key words: Classification, Ephedraceae, female cone, morphology, reduction and sterilization hypothesis, systematics

Background

The modern Ephedraceae of the Gnetales consist of only 1 living genus *Ephedra* L. (1753: 1040) and ca. 55 species that are widely distributed through the North Temperate Zone and high mountains of S America (Stapf 1889; Florin 1933; Gifford & Foster 1989; Stevenson 1993; Price 1996; Caveney *et al.* 2001; Yang 2007a).

Due to extensive extinction in the geological past, modern Ephedraceae possess a set of morphological characters disjunct from the other two monotypic families of the Gnetales (Gnetaceae and Welwitschiaceae) as well as from other living seed plants including cycads, *Ginkgo*, conifers, and angiosperms (Pearson 1929; Cutler 1939; Martens 1971; Fu *et al.* 1999). Plants of this family have branches/twigs including nodes and internodes, the node is enlarged, and the internode is longitudinally furrowed. Leaves usually bear 2 (-4) parallel veins, and are opposite and decussate or ternately whorled; they are free and linear in Early Cretaceous fossils and a few extant species, but fused into a sheath at a node in most living species. Female cones of extant *Ephedra* are compound, and have a few pairs/whorls of bracts, but only the uppermost pair/whorl of bracts enclose 1-3 seeds. The bracts are fleshy, coriaceous, or membranous when the cone is mature. The characteristic female reproductive unit bears an outer envelope and an inner integument, the integument is elongated into a micropylar tube passing through the apical opening of the outer envelope. Male cones have many whorls/pairs of bracts, each bract usually subtends an axillary male reproductive unit; the male reproductive unit consists of a pair of bracteoles enclosing an inner antherophore; each antherophore has 3-12 stalked or sessile bilocular synangia at the tip.

Evolutionary inference of such an ancient family based on molecular systematic studies is not convincing by sampling only the living representatives. The relationships of modern *Ephedra* show strong geographical structure, and molecular clock analysis dates the origin of *Ephedra* at ca. 32 Mya (e.g. Huang *et al.* 2005; Ickert-Bond *et al.* 2004; Ickert-Bond *et al.* 2009). This age is far more recent than an Early Cretaceous origin as evidenced by macrofossils (Yang *et al.* 2005; Rydin *et al.* 2006a; Wang & Zheng 2010; Yang & Wang 2013).

Palaeobotanical evidence has been providing past links for living groups of plants. Fortunately, many Ephedroid macrofossil taxa bearing evolutionary significance were described from the Early Cretaceous worldwide in the last two decades, e.g. Asia (Guo & Wu 2000; Sun *et al.* 2001; Tao & Yang 2003; Yang *et al.* 2005; Rydin *et al.* 2006b; Liu *et al.* 2008; Krassilov 2009; Rydin & Friis 2010; Wang & Zheng 2010; Yang 2010; Yang &

Wang 2013; Yang *et al.* 2013), Australia (Krassilov *et al.* 1998), Europe (Rydin *et al.* 2006a), N America (Rydin *et al.* 2006a), and S America (Cladera *et al.* 2007; Kunzmann *et al.* 2009). These include mesofossils of seeds, and macrofossils of vegetative shoots and reproductive shoots. The concept of the family is according to Yang *et al.* (2013). Twenty seven species of 10 genera were confirmed here to belong to Ephedraceae. Two genera were listed as doubtful/excluded due to their characters not being comparable to the family Ephedraceae. Among the 27 species, 1 is described from Australia, 1 from South America, 1 from North America, 2 from Europe, and 22 from northeastern Asia.

A few studies list the Ephedroid species directly under the order Gnetales (Rydin *et al.* 2006b; Rydin & Friis 2010). Some of the fossils were described as angiosperms but actually belong to the Gnetales/Ephedraceae, e.g. *Gurvanella* Krassilov (1982: 31), *Beipiaoa* Dilcher *et al.* in Sun *et al.* (2001: 151), *Erenia* Krassilov (1982: 33), *Callianthus* Wang et Zheng (2009: 800), and *Baicarpus* Gang Han *et al.* (2013: 917). Taxonomic relationships of these fossils have been discussed (Sun *et al.* 1998; Zhou *et al.* 2003; Krassilov 2009; Wang 2010; Friis *et al.* 2011), but how these plants are related to each other remain ambiguous, which weakens their significance in systematic studies of Ephedraceae.

Krassilov (2009) proposed a classification system of Mesozoic Gnetophytes with 2 subclasses and 9 orders under the Gnetopsida:

Class **Gnetopsida** Eicher ex Kirpotenko (1884: 31) [as “**Gnetopsida** Thomé” (1886: 55)]

Subclass **Gnetidae** Pax (1894: 203) [Syn.: **Eugnetidae** Krassilov (2009: 1275)]

Gnetales Blume in C.F.P. von Martius (1835: 11) [as “**Gnetales** Luerisson” (1879: 79)]

Ephedrales Dumortier (1829: 11)

Welwitschiales Skottsb. ex Reveal (1993: 174)

Fredlindiales Anderson et Anderson (2003: 336)

Heerales Krassilov (2009: 1276)

Cheirolepidiales Anderson et Anderson (2007: 118)

Subclass **Anthognetidae** Krassilov (2009: 1276)

Dinophytonales Krassilov et Ash (2007: 206)

Axelrodiales Anderson et Anderson (2007: 216)

Eoanthales Krassilov *et al.* (2007: 209)

Baisiales Krassilov (2009: 1277)

This is a tentative classification system of living and fossil Gnetalean plants for the first time, thus a nice and thought-provoking try. However, shortcomings are obvious. First, in this classification system, Krassilov (2009) defined the Gnetophytes in a very broad sense, and included lots of Mesozoic fossils not comparable to modern Gnetalean plants in the Gnetophytes, e.g. *Eoantha* Krassilov (1986: 9), *Dinophyton* Ash (1970: 650), *Heerala* Krassilov in Krassilov et Bugdaeva (1988: 361), and did not clarify the evolutionary relationships among those macrofossils. As a result, the system looks inclusive but all subdivisions seem isolated islands and it is not easy to understand the evolutionary history of Gnetalean plants both living and extinct. Secondly, some of the characters by which Krassilov (2009) defined the Gnetopsida are challenged by recent palaeobotanical findings. For an example, Krassilov (2009) thought that the Gnetopsida possess persistent subtending bract(s) and often wing-like in disseminule, but Rydin & Friis (2010) reported a unique Ephedroid plant *Siphonospermum* Rydin et Friis (2010: 5) bearing female reproductive units directly terminal to twigs and lacking subtending bracts. Moreover, Krassilov (2009) thought the Gnetophytes have cupulate ovules formed by decussate bracteoles, but the family Protoephedraceae, a precursor of Ephedraceae, has no characteristic female reproductive units and ovules are not enclosed in cupules formed by bracteoles but attached on megasporophylls of secondary reproductive shoots (Rothwell & Stockey 2013). Thus, a new study on the classification of these macrofossils is necessary for better understanding of the early evolution of the family Ephedraceae.

Those macrofossils from the Early Cretaceous of northeastern Asia preserved female reproductive characters thus allowing a discussion of their evolutionary relationships. Yang *et al.* (2013) proposed a reduction and sterilization evolutionary model suggesting that female reproductive structures of Ephedraceae have experienced a series of aggregation, reduction, modification, and sterilization to make a compact and reduced female cone in adaptation to dispersal: (1) at the beginning, the female reproductive unit (FRU) is terminal to the twigs in

Siphonospermum Rydin et Friis; the FRU is a modified shoot with an ovule included within an outer envelope which is derived from a pair of bracteoles on the secondary shoot; (2) pedicels of the FRU were shortened and thus the FRUs became axillary to leaf-like bracts, e.g. in *Prognatella* Krassilov (1999: 114, including *Baicarpus gracilis* Gang Han et al. (2013: 920) and *B. robusta* Gang Han et al. (2013: 921)); (3) then the linear leaf-like bracts were increasingly shortened and broadened and modified into bracts tightly subtending the axillary female reproductive unit and internode shortening led to more and more compact female cones from *Chengia* Yang et al. (2013: 8) and *Liaoxia* Cao et Wu in Rydin et al. (2006: 241); (4) differentiation of bract structure and fusion and further reduction of female reproductive units of the lower several whorls/pairs of bracts finally gave rise to those female cones bearing only one uppermost pair/whorl of fertile bracts in *Gurvanella* (including *Chaoyangia* Duan (1998: 14)) and *Ephedra*. This morphological hypothesis not only suggests the origin and evolution of female cones of Ephedraceae, but also gives a concrete taxonomic concept to the family Ephedraceae that consists of *Siphonospermum*, *Prognatella*, *Chengia*, *Liaoxia*, *Gurvanella*, *Ephedra* (Yang et al. 2013). Recent finding of Protoephedraceae from the Early Cretaceous of Vancouver, Canada, is important in understanding a more precise pattern of female cones of the precursor of Ephedraceae (Rothwell & Stockey 2013) showing what the secondary reproductive shoot looked like before it was shaped into the characteristic female reproductive unit in Ephedraceae. This corroborated the reduction and sterilization hypothesis and furthered our understanding of the early evolution of the Gnetales. Relationships within the family are outlined based on the reduction and sterilization evolutionary hypothesis (Figure 1). Here a systematic arrangement of the genera of the family has been proposed for the first time as below.

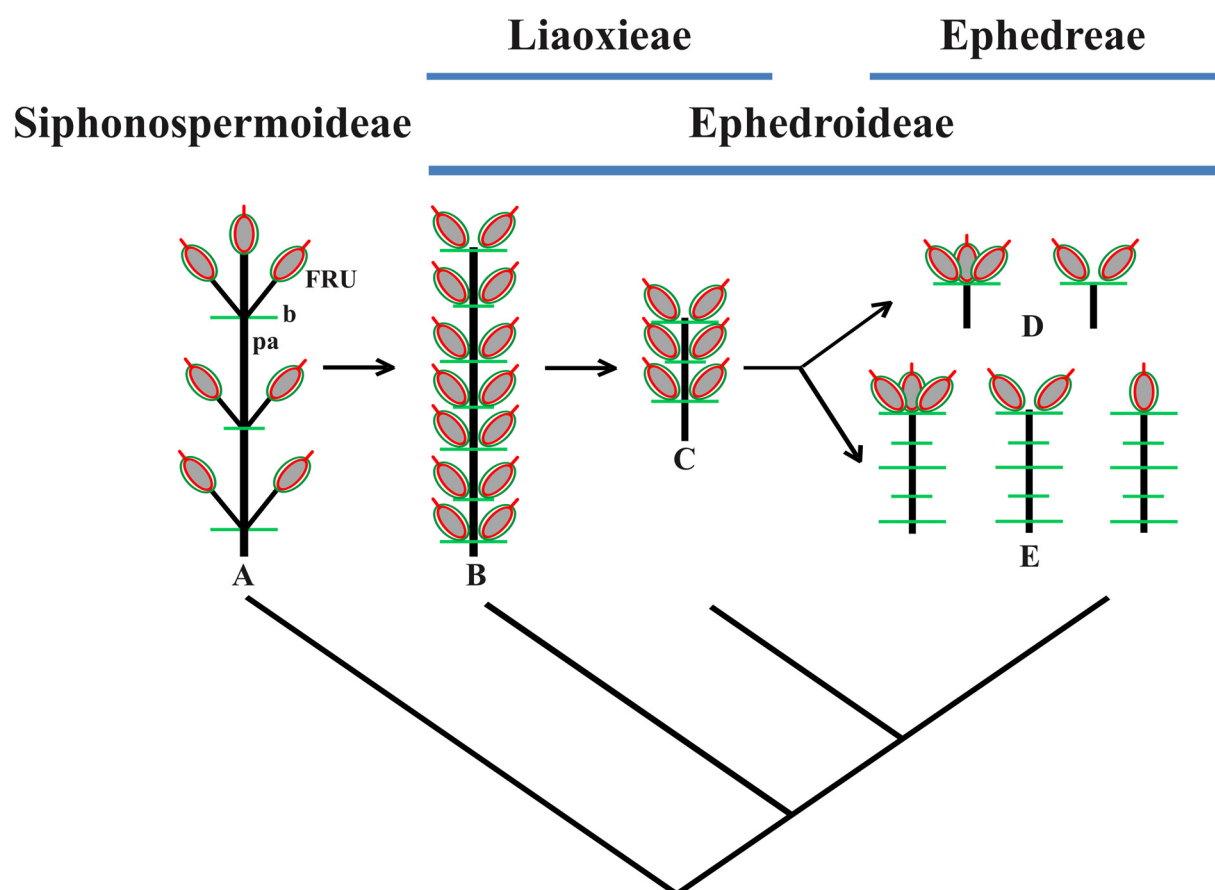


FIGURE 1. Suggested relationships of Ephedraceae based on the reduction and sterilization evolutionary hypothesis. A, showing the loosely arranged female spike of *Siphonospermum* with pedunculate FRUs; B, showing the lax female spike of *Prognatella* and *Chengia* with sessile FRUs and obvious internodes; C, showing the compact female cone of *Liaoxia* with multiple pairs of fertile bracts; D–E, showing the compact female cone of *Gurvanella*, *Erenia*, *Alloephedra*, *Amphiephedra*, *Beipiaoa*, and *Ephedra* having only the uppermost pair of fertile bracts but varying in number of bract whorls and FRUs. FRU, female reproductive unit; b, bract; pa, primary axis.

Systematics

Class Gymnospermae

Order Gnetales

Family Ephedraceae Dumortier, emend. Yang *et al.* (2013: 7)

1. Subfamily **Siphonospermoideae** Y. Yang, *subfam. nov.* Type: *Siphonospermum* Rydin et Friis (2010: 5)

Diagnosis. This subfamily possesses typical ephedroid morphology, the reproductive shoots consist of nodes and internodes, internodes are usually furrowed; leaves are lengthy, linear and parallel-veined; the characteristic female reproductive unit (seed/ovule) present, but terminal to twigs without subtending bracts.

The subfamily is monotypic, with only *Siphonospermum* from the Lower part of the Yixian Formation of western Liaoning, China.

1.1 *Siphonospermum* Rydin et Friis, *BMC Evol. Biol.* 10: 183 (2010) —T.: *S. simplex* C. Rydin et E.M. Friis 1 species from the Early Cretaceous of western Liaoning, China.

2. Subfamily **Ephedroideae** Y. Yang, *subfam. nov.* —T.: *Ephedra* L. (1753: 1040)

Diagnosis. This subfamily possesses typical ephedroid morphology; the reproductive shoots consist of nodes and internodes; leaves are linear and parallel-veined, free or fused; the characteristic female reproductive unit (seed/ovule) is axillary to subtending bracts; the bracts are parallel-veined, its shape varies from linear and leaf-like to modified and bract like, free from each other to fused, its stature ranges from pendulous or spreading to erect or even enclasped, its nature is either herbaceous, fleshy, dry and coriaceous, or dry and membranous.

2.1 Tribe **Liaoxieae** Y. Yang, *trib. nov.* —T.: *Liaoxia* Cao et Wu in Rydin *et al.* (2006: 241)

Diagnosis. This tribe is distinguished by the female cone bearing multiple whorls/pairs of fertile bracts.

This tribe consists only of fossil members from the Lower Cretaceous of both Mongolia and northeastern China.

2.1.1 *Prognotella* Krassilov et Bugdaeva in *Acta Palaeobot. Suppl.* 2: 114 (1999) —T.: *P. minuta* Krassilov et Bugdaeva

1 (-2?) fossil species from the Baisa locality in the upper reaches of the Vitim river, Transbaikalia of Mongolia (Early Cretaceous), and from the Lower part of the Yixian Formation.

2.1.2 *Chengia* Yang *et al.* in *BMC Evol. Biol.* 13: 72 (2013) —T.: *Ch. laxispicata* Y. Yang *et al.*

2 fossil species from the Early Cretaceous of western Liaoning, China.

2.1.3 *Liaoxia* Cao et Wu in Rydin *et al.*, *Pl. Syst. Evol.* 262: 241 (2006) —T.: *L. cheniae* (Guo et Wu) Cao et Wu Syn.: *Ephedrites* Göpp. & Berendt in Berendt, *Bernstein Reste Vorwelt* 1(1): 105. t. 4, f. 8-10; t. 5, f. 1. (1845). pro parte “*Liaoxia*” Cao et Wu in *Chin. Sci. Bull. (Chin. Ed.)* 42: 1765 (1997), et in *Chin. Sci. Bull. (Engl. Ed.)* 43: 231 (1998) *nom. inval.* Type deposit not designated.

7 fossil species from the Early Cretaceous of western Liaoning, China.

Nomenclature of *Liaoxia* is quite complicated: the name was not validly published in Cao *et al.* (1998) since the type deposit was not designated, but later validated in Rydin *et al.* (2006b). Yang (2007b) gave a detailed discussion for this problem, but it seems better to use *Liaoxia* because it is a validly published and available name for the genus on the one hand, and both taxonomy and nomenclature of *Ephedrites* were not well resolved.

2.2 Tribe **Ephedreae** Y. Yang, *trib. nov.* —T.: *Ephedra* L. (1753: 1040)

Diagnosis. This tribe is distinguished by the female cone bearing only one whorl/pair of fertile bracts.

This tribe includes both fossil and living members.

2.2.1. *Gurvanella* Krassilov in *Palaeontogr. Abt B* 181: 31 (1982) —T.: *G. dictyoptera* Krassilov

“*Chaoyangia*” Duan in *Sci. China Ser. D.* 27: 519 (1997), et in *Sci. China Ser. D.* 41: 14 (1998) *nom. inval.* Type deposit not designated.

2 fossil species from the Early Cretaceous of both Mongolia and western Liaoning, China (Sun *et al.* 2001).

2.2.2 **Beipiaoa** Dilcher *et al.* in Sun *et al.*, *Early Angiosperms and Associated Plants from Western Liaoning, China*, 151 (2001)—T.: *B. spinosa* Dilcher *et al.*

3 fossil species from the Early Cretaceous of western Liaoning, China. Krassilov (2009) thought reproductive organs of *Beipiaoa spinosa* Dilcher *et al.* are cupules of *Eoantha ornata* Krassilov (1999: 113), but the morphology of the two species looks different each other. There are many collections of *Beipiaoa* in the Yixian Formation and additional studies are still needed.

2.2.3 **Erenia** Krassilov in *Palaeontogr. Abt B* 181: 33 (1982)—T.: *E. stenoptera* Krassilov

Syn.: *Callianthus* Wang *et Zheng* in *J. Int. Pl. Biol.* 51: 800 (2009) syn. nov. —T.: *C. dilae* Wang *et Zheng*

1 fossil species from the Early Cretaceous of Mongolia and western Liaoning, China.

2.2.4 **Amphiephedra** Miki in *Bull. Mukogawa Women's Univ., Nat. Sci.* 12: S21 (1964)—T.: *A. rhamnoides* Miki

1 fossil species from the Early Cretaceous of western Liaoning, China.

2.2.5 **Alloephedra** Tao *et Yang* in *Acta Palaeontol. Sin.* 42: 212 (2003)—T.: *A. xingxueii* J.R. Tao *et Y. Yang*

1 fossil species from the Dalazi Formation (Aptian-Albian, Early Cretaceous) of Jilin Province, China

2.2.6 **Ephedra** L., *Sp. Pl.*: 1040 (1753)—T.: *E. distachya* L.

Syn.: *Baicarpus* Gang Han *et al.*, *Acta Geol. Sin.* 87: 917 (2013) syn. nov.

Ca. 55 living species widely distributed in the North Temperate Zone, and Temperate South America, and 4 fossil species among which 3 species are from the Early Cretaceous of western Liaoning of China, and 1 species from the Baqueró Group, Anfiteatro de Ticó Formation (Aptian, Early Cretaceous) at Estancia Bajo Grande, Santa Cruz Province, Argentina.

Unplaced genera

Leongathia Krassilov *et al.* in *Alcheringa* 22: 127 (1998)—T.: *Leongathia elegans* Krassilov *et al.* (1998: 127)

1 fossil species of a vegetative shoot from the Lower Cretaceous of Koonwarra Fossil Bed, Victoria, Australia.

Ephedrispermum Rydin *et al.* in *Ann. Bot.* 98: 129 (2006)—T.: *Ephedrispermum lusitanicum* Rydin *et al.* (2006: 129)

1 mesofossil species of seeds having *in situ* pollen from Calvaria Member, Figueira da Foz Formation (late Aptian or early Albian) at Buarcos, North of Figueira da Foz of Portugal. Friis *et al.* (2009) ascribed this genus into the BEG clade, but its position in the new system of the family Ephedraceae can not be determined since lacking characters of female cones.

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