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A systematic classification of Ephedraceae: living and fossil

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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 &

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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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