

Research article

Protognetales: A new gnetoid macrofossil family from the Jurassic of northeastern China

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ABSTRACT

The divergence of the gnetophytes has been controversial due to the lack of appropriate fossils to calibrate the phylogenetic trees. Here we describe a new macrofossil family, Protognetales Y. Yang, L. Xie et D.K. Ferguson, fam. nov., from the Middle Jurassic, consisting of only *Protognetales jurassicum* Y. Yang, L. Xie et D.K. Ferguson, gen. et sp. nov. This monotypic family displays transitional morphology between Ephedraceae and Gnetaceae. It is similar to the Ephedraceae in the longitudinally striated twigs, the linear parallel-veined leaves decussate at the swollen nodes, and to the Gnetaceae in the lax female spikes and a few sessile female reproductive units (FRUs) verticillately arranged at the nodes. These FRUs are subtended by leaf-like linear bracts, and have an apical short and straight tube. The Protognetales provide new evidence to understand the early evolution of the gnetophytes. We reconstructed a phylogeny of gymnosperms based on six DNA markers, and dated the divergence of the gnetophytes with calibration using our new macrofossil. We found that the crown age of the gnetophytes is in the Middle Triassic, the age of modern *Ephedra* is in the Neogene, and modern *Gnetum* is dated back to the K/T boundary.

1. Introduction

The Gnetaceae are exceptional among living gymnosperms, consisting of species that are often woody lianas (rarely trees) bearing dicot-like pinnately-veined broad leaves decussate at swollen nodes (Maheshwari and Vasil, 1961; Martens, 1971; Gifford and Foster, 1989; Biswas and Jori, 1997). The pantropical Gnetaceae together with the temperate Ephedraceae and the southwestern African coastal Welwitschiaceae constitute the living gnetophytes. Though phylogenetic relationships of the gnetophytes to other seed plants remain poorly resolved (e.g. Gugerli et al., 2001; Rydin et al., 2002; Zhong et al., 2010; Xi et al., 2013; Lu et al., 2014), recent molecular phylogenetic studies consistently suggested that the gnetophytes are monophyletic, the Ephedraceae are basal and sister to a clade including the Gnetaceae and Welwitschiaceae (e.g. Bowe et al., 2000; Chaw et al., 2000; Ran et al., 2010). These families were classified into their own order within the Gnetidae (Christenhusz et al., 2011).

The monotypic Gnetaceae include only *Gnetum* L. The genus *Gnetum* contains 39–43 pantropical species, four of which are native to Africa, seven to South America, and 28–32 species to Asia (Ickert-Bond and Renner, 2015; World Checklist of Selected Plant Families: <http://apps.kew.org/wcsp/advanced.do>).

Taxonomy of the genus has been controversial, recent molecular systematic studies suggested that *Gnetum* in Asia needs revision (Kim and Won, 2016; Hou et al., 2016). The Welwitschiaceae consist of one single living species endemic to southwestern Africa, viz. *Welwitschia mirabilis* Hook. f. The Ephedraceae comprise one extant genus ranging through the temperate arid zones and high mountains in Eurasia, N America and S America. The genus *Ephedra* L. encompasses ca. 55 species.

Molecular systematic studies resulted in phylogenetic trees with a similar topography for both *Ephedra* and *Gnetum*, and species relationships show a strong geographic pattern. In *Ephedra*, the Mediterranean species are basal, followed by a split between the Asian species and the New World species, with the South American clade nested within the paraphyletic North American species (Fig. 1, Huang et al., 2005; Ickert-Bond and Wojciechowski, 2004; Ickert-Bond et al., 2009; Rydin and Korall, 2009; Bolinder et al., 2016). In *Gnetum*, the South American clade is basal, followed by a split between the African clade and the Asian clade, the Asian clade includes a Southeast Asian clade and an Indochinese clade, or the Indochinese clade is nested within a paraphyletic Southeast Asian clade (Fig. 1, Won and Renner, 2006; Hou et al., 2015).

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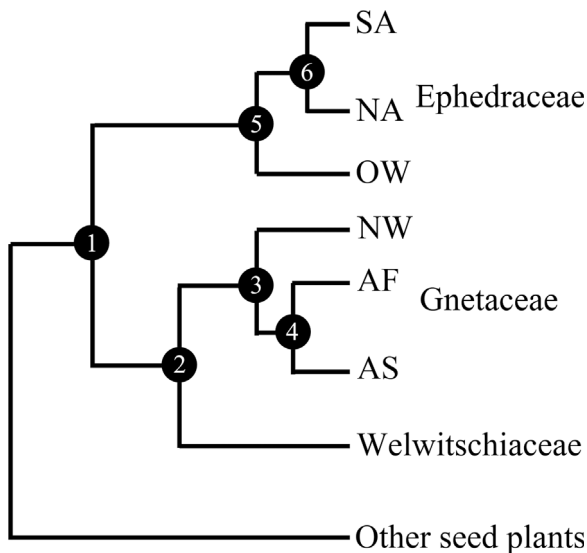


Fig. 1. Divergence of the gnetophytes. NA, North America; SA, South America; OW, Old World; NW, New World; AS, Asia; AF, Africa. Numbers indicate the divergence corresponding to Table 1.

Table 1
Former dating of the gnetophytes.

L\N	N1	N2	N3	N4	N5	N6
L1	–	–	–	–	8–32	–
L2	125*	115*	6–11	–	–	–
L3	125*	110*	26	22	–	–
L4	166.61	111.35	–	–	30.39	24.78
L5	173	110*	81	73	20	–

N1–N6 correspond to the node number in Fig. 1. L1, Huang and Price, 2003; L2, Won and Renner, 2003; L3, Won and Renner, 2006; L4, Ickert-Bond et al., 2009; L5, Hou et al., 2015. The asterisk indicates the date of the calibration point.

Despite the similar phylogenies, molecular dating on divergence of the gnetophytes gave different results (Table 1). Ickert-Bond et al. (2009) suggested the crown age of the gnetophytes to be in the Middle Jurassic (~167 Myr), while Lu et al. (2014) indicated a younger age (~146 Myr). The wide Gondwana distribution of modern *Gnetum* was considered to be the result of a recent radiation, either in the Upper Oligocene to mid-Miocene (Won and Renner, 2006), or Eocene and thereafter (Ickert-Bond et al., 2009). However, Hou et al. (2015) dated *Gnetum* back to the Late Cretaceous (ca. 81 Myr), and suggested that the early divergence within *Gnetum* was correlated with the breakup of Gondwana.

Fossil evidence is important in calibrating the time tree in dating analyses. Numerous macrofossils of gnetophytes have been reported (e.g. Crane and Upchurch, 1987; Krassilov and Bugdaeva, 1999; Guo and Wu, 2000; Sun et al., 2001; Tao and Yang, 2003; Yang et al., 2005, 2013, 2015; Dilcher et al., 2005; Rydin et al., 2006a, 2006b; Cladera et al., 2007; Mohr et al., 2007; Guo et al., 2009; Krassilov, 2009; Kunzmann et al., 2009, 2011; Wang and Zheng, 2010; Rydin and Friis, 2010; Ricardi-Branco et al., 2013; Liu et al., 2013; Yang and Wang, 2013; Löwe et al., 2013; Rothwell and Stockey, 2013; Friis et al., 2014; Yang, 2014; Yang and Ferguson, 2015). Most of them are related to the Ephedraceae (e.g. Guo and Wu, 2000; Sun et al., 2001; Yang et al., 2005, 2013, 2015; Rydin et al., 2003, 2006a, 2006b; Cladera et al., 2007; Wang and Zheng, 2010; Rydin and Friis, 2010; Liu et al., 2013; Yang and Wang, 2013; Yang, 2014; Yang and Ferguson, 2015), a few to the Welwitschiaceae (Crane and Upchurch, 1987; Rydin et al., 2003; Dilcher et al., 2005; Friis et al., 2014), but only one to the Gnetaceae (Guo et al., 2009). Compared to the stem age of the gnetophytes, these fossils are relatively young. The discrepancy of origin and



Fig. 2. A female spike of *Gnetum gnemon* showing the verticillate female reproductive units (FRUs).

diversification of the gnetophytes is largely attributable to the poor knowledge of early gnetoid fossils in the past. New Gnetaceae macrofossils should be helpful in determining the diversification and biogeography of the modern species.

New macrofossils may shed light on the evolution of the divergent morphology within the gnetophytes as well. The genus *Gnetum* shows distant similarity to the other two genera within the gnetophytes as well as to the other seed plant groups, e.g. cycads, *Ginkgo*, conifers, and angiosperms (Gifford and Foster, 1989), but it remains unclear how the modern morphology was derived. *Gnetum* species are usually lianas, rarely small trees, possessing opposite broad leaves bearing pinnate venation, and female spikes consisting of verticillate female reproductive units (FRUs) (Fig. 2, Maheshwari and Vasil, 1961; Martens, 1971). *Welwitschia* is a dwarf plant having two giant strap-like leaves with many parallel veins, and compact strobili with multiple whorls of fertile units (Martens, 1971; Gifford and Foster, 1989; Biswas and Jori, 1997). *Ephedra* has an extremely reduced morphology, with linear leaves or rudimentary dry scale leaves free or fused at the basal portion sheathing the nodes and taking no longer part in the photosynthesis which is then restricted to the green shoots, compact strobili having only the uppermost pair/whorl of fertile bracts which enclose 1–3 seeds (Martens, 1971; Gifford and Foster, 1989; Biswas and Jori, 1997). There is no working hypothesis and evidence on how the unique morphological characters of *Gnetum* were derived.

Here we describe a new macrofossil from the Jurassic of northeastern China which shows a combination of key morphological characters of both *Gnetum* and *Ephedra*. We also have reconstructed a phylogenetic tree using six genes and conducted dating analyses based on the new fossil.

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