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Review

Evolution and biogeography of gymnosperms

Xiao-Quan Wang *, Jin-Hua Ran

State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China

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ABSTRACT

Living gymnosperms comprise only a little more than 1000 species, but represent four of the five main lineages of seed plants, including cycads, ginkgos, gnetophytes and conifers. This group has huge ecological and economic value, and has drawn great interest from the scientific community. Here we review recent advances in our understanding of gymnosperm evolution and biogeography, including phylogenetic relationships at different taxonomic levels, patterns of species diversification, roles of vicariance and dispersal in development of intercontinental disjunctions, modes of molecular evolution in different genomes and lineages, and mechanisms underlying the formation of large nuclear genomes. It is particularly interesting that increasing evidence supports a sister relationship between Gnetales and Pinaceae (the Gnepine hypothesis) and the contribution of recent radiations to present species diversity, and that expansion of retrotransposons is responsible for the large and complex nuclear genome of gymnosperms. In addition, multiple coniferous genera such as *Picea* very likely originated in North America and migrated into the Old World, further indicating that the center of diversity is not necessarily the place of origin. The Bering Land Bridge acted as an important pathway for dispersal of gymnosperms in the Northern Hemisphere. Moreover, the genome sequences of conifers provide an unprecedented opportunity and an important platform for the evolutionary studies of gymnosperms, and will also shed new light on evolution of many important gene families and biological pathways in seed plants.

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* Corresponding author. Address: State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, 20 Nanxincun, Xiangshan, Beijing 100093, China. Fax: +86 10 62590843.

E-mail address: xiaoq_wang@ibcas.ac.cn (X.-Q. Wang).

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1. Introduction

Gymnosperms are of great ecological and economic importance, although this ancient and widespread plant lineage currently comprises only a little more than 1000 species that are two to three orders of magnitude lower than the approximately 300,000 species of extant angiosperms. Also, from the evolutionary perspective, studies of angiosperms depend a lot on our knowledge of gymnosperms given the sister relationship between the two groups. However, the evolutionary study of gymnosperms is still facing great difficulties in the genomic era due to the large genome size, high heterozygosity and long generation time of this group, although a draft assembly of the Norway spruce (*Picea abies*) genome was generated by Nystedt et al. (2013) and several comparative genomics projects involving gymnosperms are being carried out, such as the 1000 Plants (oneKP or 1KP) Initiative (http://www.onekp.com/), the Plant Genomics Consortium (http://sciweb.nybg.org/science2/GenomicsLab.asp), and the Conifer Genome Network (http://www.pinegenome.org/index.php). Nevertheless, in recent years, fascinating progress has been made in our understanding of evolution and biogeography of gymnosperms, which inspires us to write this review. For a better understanding of the content, we first give a brief introduction of the diversity and classification of gymnosperms. Then, we focus on: (1) Phylogeny and evolution of gymnosperms, including evolutionary history, phylogenetic relationships, and molecular and genome evolution; (2) Historical biogeography of gymnosperms.

2. Diversity and classification of gymnosperms

Living gymnosperms are distributed in all continents except Antarctica, of which two-thirds are conifers, a group that constitutes over 39% of the world's forests (Armenise et al., 2012). The gymnosperms play major roles in global carbon cycles, provide important sources of timber, resins and even drugs and foods (Zonneveld, 2012c; Murray, 2013), and are crucial to preventing soil erosion. Additionally, they are a mainstay of gardening.

Gymnosperms represent four of the five main lineages of seed plants, i.e., cycads, ginkgos, gnetophytes and conifers (including cupressophytes and Pinaceae), and were recently classified into four subclasses (Ginkgoidae, Cycadidae, Pinidae and Gnetidae) under the class Equisetopsida (Chase and Reveal, 2009). They comprise 12 families, 83 genera (Christenhusz et al., 2011), and about 1000 species (Table 1), including ca 297–331 species of cycads in 10 genera, one extant ginkgophyte, 80–100 gnetophytes in three genera, and ca 614 species of conifers in 69 genera (Farjón, 2010; Christenhusz et al., 2011). Among these genera, 34 (40.96%) are monotypic, 22 (26.5%) have only two to five species, and only three (*Cycas*, *Pinus* and *Podocarpus*) harbor near or more than 100 species (Table 1, and Fig. 1). It is interesting that half (45) of the genera occur in Asia and 31 in Australia (continent), and the vast majority of the monotypic genera are found in these two continents (Fig. 2).

As the largest lineage of gymnosperms, conifers were divided into seven families by Pilger (1926), including Taxaceae, Podocarpaceae, Araucariaceae, Cephalotaxaceae, Pinaceae, Taxodiaceae and Cupressaceae. However, Eckenwalder (1976) proposed a merger of Taxodiaceae and Cupressaceae based on the phenetic analysis and Hayata (1931) proposed to place *Sciadopitys* in a separate family (Sciadopityaceae), and these views have been adopted in most of the following classification schemes of gymnosperms (e.g., Farjón, 2001, 2005; Christenhusz et al., 2011) and supported by most non-molecular and molecular phylogenetic studies (e.g., Hart, 1987; Price and Lowenstein, 1989; Brunsfeld et al., 1994; Gadek et al., 2000; Yang et al., 2012). Currently, it is still controversial whether Taxaceae and Cephalotaxaceae should be merged into a single family (e.g., Quinn et al., 2002; Hao et al., 2008; Christenhusz et al., 2011; Ghimire and Heo, 2014). Recently, Eckenwalder (2009) and Farjón (2010) published two very valuable books on all conifers, recognizing 546 and 615 species, respectively. Although both books provided an identification guide to each species, Farjón incorporated more recent advances in the systematics of conifers and recognized more species, genera, and even families than Eckenwalder. For example, Cephalotaxaceae and Phyllocladaceae were recognized by Farjón (2010), but were put into Taxaceae and Podocarpaceae, respectively, by Eckenwalder (2009). In addition, Farjón (2010) recognized three extra genera, *Pilgerodendron* and *Xanthocyparis* in Cupressaceae and *Sundacarpus* in Podocarpaceae. At the family level, Farjón (1990, 2005) published two excellent monographs on Pinaceae and Cupressaceae *s.l.*, respectively. An interesting thing is that recent phenotypic and molecular phylogenetic studies do not support the monophyly of *Cupressus* (Cupressaceae). Adams et al. (2009) divided this genus into two lineages, including *Cupressus s.s.* comprising the Old World species and a new genus (*Hesperocyparis*) comprising the New World species that are closely related to two small controversial genera, i.e., *Callitropsis* from northwestern North America and *Xanthocyparis* from northern Vietnam (Little, 2006; Yang et al., 2012). However, except that *Xanthocyparis* was accepted by Farjón (2010), the other three genera (*Callitropsis*, *Hesperocyparis* and *Xanthocyparis*) were not accepted by Eckenwalder (2009), Farjón (2010) and Christenhusz et al. (2011). At present, it is widely accepted that conifers comprise two major clades, Pinaceae and the remaining non-Pinaceae conifers (Conifer II or Cupressophytes) (see Section 3.2, phylogenetic reconstruction), with Pinaceae and Podocarpaceae representing the first and second largest families (Farjón, 2001; Knopf et al., 2012).

The gnetophytes comprise three families (Ephedraceae, Gnetaceae and Welwitschiaceae), each containing a single genus (Table 1). Compared to gnetophytes and conifers, there were more debates on the classification of cycads. Initially, all living species of cycads were placed in a single family, the Cycadaceae (see reviews by Stevenson, 1990 and Jones, 2002). However, afterwards, three to four families, including Cycadaceae, Stangeriaceae, Zamiaceae and Boweniaceae, were recognized by different authors (Johnson, 1959; Stevenson, 1981, 1990, 1992). The Boweniaceae was erected by Stevenson (1981), but was mergered into Stangeriaceae by Stevenson (1992). Recently, molecular phylogenetic studies support a division of the 10 cycad genera into two families (Cycadaceae and Zamiaceae) (Treutlein and Wink, 2002; Hill et al., 2003; Chaw et al., 2005; Zgurski et al., 2008; Nagalingum et al., 2011; Salas-Leiva et al., 2013), although the genus status of *Chigua* is still accepted by some researches (http://plantnet.rbgsyd.nsw.gov.au/PlantNet/cycad/) (see review by Osborne et al., 2012).

3. Phylogeny and evolution of gymnosperms

3.1. Origin and diversification

Based on fossil evidence and molecular clock calibration, the divergence between gymnosperms and angiosperms could be dated to about 300–350 million years ago (Mya) in the