



## Higher substitution rates and lower $dN/dS$ for the plastid genes in Gnetales than other gymnosperms



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### ABSTRACT

Previous studies have shown that Gnetales exhibit an increase in the rates of substitution in plastid genes. However, the relative roles of selection and drift in driving the observed increase in substitution rate remain unclear. Here we estimated the nonsynonymous ( $dN$ ) and synonymous ( $dS$ ) substitution rates and the  $dN/dS$  ratios for 59 plastid protein-coding genes conserved across Gnetales and other gymnosperms with maximum likelihood methods. Our results show that: (1) values of  $dN$  and  $dS$  for 48 and 50 genes, respectively, are significantly higher in Gnetales relative to the other sampled gymnosperms; (2) the acceleration of  $dN$  is of lower magnitude than that of  $dS$ ; (3)  $dN/dS$  is significantly reduced for 22 of the 59 plastid genes in Gnetales; and (4)  $dN/dS$  is extremely heterogeneous among the Gnetalean genes, varying by up to a factor of 40. We propose that while biological characteristics such as generation time and plant height may contribute to the rate increase in Gnetales, the special habitats that they occupy are linked to the gene-specific reduction of  $dN/dS$ .

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## 1. Introduction

Although rates of nucleotide substitutions in plastid genomes are generally low, reports are accumulating that the plastid genes of certain land plant groups have experienced rate acceleration. Wolf et al. (2011) found that both synonymous ( $dS$ ) and nonsynonymous ( $dN$ ) substitution rates for plastid genes are significantly higher in ferns than in seed plants. In angiosperms, aside from non-photosynthetic plants, extensive increase of  $dN$  has been reported in the plastid ribosomal protein and RNA polymerase genes in Geraniaceae (Guisinger et al., 2008), a single gene, *clpP*, in *Oenothera* and lineages within Caryophyllaceae (Erixon and Oxelman, 2008), and the genes for components of the ATPase complex, photosystem I, photosystem II, and the cytochrome b6/f complex in pea (Wolfe et al., 1987). Elevated substitution rates have also been detected in ribosomal protein, RNA polymerase, and the ATPase complex genes in maize and rice (Gaut et al., 1993). In gymnosperms, accelerated substitution

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rates have been observed in the concatenated sequences of plastid protein-coding genes of the three gnetophytes, *Ephedra equisetina*, *Gnetum parvifolium*, and *Welwitschia mirabilis* (Wu et al., 2007; McCoy et al., 2008; Wu et al., 2009). Around 75% of the plastid protein-coding genes have been shown to display elevated rates of substitution in *Welwitschia mirabilis* based on the comparison of relative divergence factors (McCoy et al., 2008). These rate elevations may be attributed to one or more of the following mechanisms: higher mutation rates, changes in selective pressure, increased fixation of mutations by genetic drift, and species' biological characteristics (Fry and Wernegreen, 2005; Lanfear et al., 2010). However, the relative importance of these different evolutionary forces in driving differential rates of molecular evolution remains unclear.

The Gnetales comprise three genera, *Gnetum*, *Welwitschia*, and *Ephedra*, and approximately 66 species (Doyle and Donoghue, 1986; Friedman, 1998). They are unique among extant gymnosperms in their possession of characters that are similar to key angiosperm synapomorphies. These characters include special water-conducting vessels in the wood, reproductive structures organized into compound strobili, seeds with a micropylar tube, and a variant of the angiosperm process of double fertilization (Doyle and Donoghue, 1986; Friedman, 1998; Doyle, 1998). While sharing these angiosperm-like traits, the three genera are also extremely distinct in their morphology and ecology. *Gnetum* are tropical rainforest vines and trees, with broad leaves striking similar to those of certain dicotyledonous angiosperms (Doyle, 1998). *Ephedra* are shrubs adapted to arid lands with reduced, pointed leaves borne on broom-like photosynthetic stems (Doyle, 1998; Ickert-Bond and Wojciechowski, 2004). *Welwitschia* grows in the deserts of southwest Africa, producing only one pair of strap-shaped leaves (Doyle, 1998). Gnetalean plants are highly specialized to their respective habitats, and theory predicts that such specialization can impact the rate and pattern of molecular evolution (Lanfear et al., 2010).

Recently, complete plastid genome sequences have become available for at least one species of each Gnetalean genus (McCoy et al., 2008; Wu et al., 2009). These data provide an opportunity to explore the occurrence and causes of changes in substitution rates within Gnetales and between this group and their gymnosperm allies. We use maximum likelihood approaches (Yang, 2007) and intensive sampling to make these comparisons. We report that values of both  $dN$  and  $dS$  are significantly higher, and  $dN/dS$  significantly lower for most of the plastid genes in Gnetales than in other gymnosperms. We then discuss how and why this unique pattern of substitutions may have evolved.

## 2. Materials and methods

### 2.1. Taxon sampling and source of sequence data

We sampled a total of 32 species: four that represent all genera of the Gnetales, ten of Pinaceae, eight Cupressophytes, two cycads, and *Ginkgo biloba* (Table 1). The plastid genome sequences were downloaded from GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>).

**Table 1**  
Plant materials and GenBank accession numbers of their plastid genome sequences.

Taxa	Species	GenBank accession No.	Herbarium/Collection places	Voucher numbers
Gnetales	<i>Ephedra equisetina</i>	NC_011954	Academia Sinica, Taiwan, China	—
	<i>Gnetum montanum</i>	NC_021438	South China Botanical Garden, Guangzhou, China	—
	<i>Gnetum parvifolium</i>	NC_011942	Academia Sinica, Taiwan, China	—
	<i>Welwitschia mirabilis</i>	NC_010654	—	—
Pinaceae	<i>Cathaya argyrophylla</i>	NC_014589	Academia Sinica, Taiwan, China	—
	<i>Cedrus deodara</i>	NC_014575	Academia Sinica, Taiwan, China	—
	<i>Larix decidua</i>	NC_016058	Academia Sinica, Taiwan, China	—
	<i>Keteleeria davidiana</i>	NC_011930	Academia Sinica, Taiwan, China	—
	<i>Picea morrissonicola</i>	NC_016069	Academia Sinica, Taiwan, China	—
	<i>Pinus koraiensis</i>	NC_004677	—	—
	<i>Pinus massoniana</i>	NC_021439	Xinyi Forestry Institute, Xinyi, China	—
	<i>Pinus taeda</i>	NC_021440	Yingde Forestry Institute, Yingde, China	—
	<i>Pinus thunbergii</i>	NC_001631	—	—
	<i>Pseudotsuga sinensis</i>	NC_016064	Academia Sinica, Taiwan, China	—
	<i>var. wilsoniana</i>	—	—	—
Cupressophytes	<i>Cephalotaxus oliveri</i>	NC_021110	Wuhan Botanical Garden, CAS, Wuhan, China	—
	<i>Cephalotaxus wilsoniana</i>	NC_016063	Academia Sinica, Taiwan, China	—
	<i>Cryptomeria japonica</i>	NC_010548	—	—
	<i>Cunninghamia lanceolata</i>	NC_021437	Longshan Forest Farm, Lechang, China	—
	<i>Podocarpus totara</i>	NC_020361	—	—
	<i>Taiwania cryptomerioides</i>	NC_016065	Academia Sinica, Taiwan, China	—
	<i>Taiwania flousiana</i>	NC_021441	Longshan Forest farm, Lechang, China	—
Cycadales	<i>Taxus mairei</i>	NC_020321	The Institute of Medicinal Plant Development, Beijing, China	IMPLAD-CP-SNJ029
	<i>Cycas revoluta</i>	NC_020319	The Institute of Medicinal Plant Development, Beijing, China	IMPLAD-CP-SNJ041
	<i>Cycas taitungensis</i>	NC_009618	Academia Sinica, Taiwan, China	—
Ginkgoales	<i>Ginkgo biloba</i>	NC_016986	The Institute of Medicinal Plant Development, Beijing, China	IMPLAD-CP-SNJ035

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