



Phylogeographic history of the woodwardioid ferns, including species from the Himalayas

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Abstract

The woodwardioid ferns are well-represented in the Northern Hemisphere, where they are disjunctly distributed throughout the warm temperate and subtropical regions of North America, Europe, and Asia. To infer the biogeographic history of the woodwardioid ferns, the phylogeny of *Woodwardia* was estimated using *rbcL* and *rps4* sequences from divergent distribution regions including the Himalayas. Phylogenetic results support *Woodwardia* as a monophyletic group with *Woodwardia areolatae* and *W. virginica* as basal, these two species from eastern North America diverged early, which are sister clades to the remaining species from America, Europe, and Asia. Based on analyses of the fossil records of these species for divergence times, *Woodwardia* species were estimated to have diverged initially in the Paleogene of North America. After its New World origin, a greater diversification and expansion of *Woodwardia* occurred in eastern Eurasia, with the European arrival of *Woodwardia radicans* during the Middle Miocene. Compared to earlier reports, a migration back into North America via the Bering land bridge is consistent with these data.

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1. Introduction

The woodwardioid ferns, the genus *Woodwardia* Smith, as described in the most recent familial classification (Smith et al., 2006), includes *Anchistea* C. Presl, *Chieniopteris* Ching, and *Lorinseria* C. Presl. This group is characterized by anastomosing veins and indusiate sori borne on the outer arc of areolae. These three segregate genera have been interpreted to represent diversification within *Woodwardia* rather than major evolutionary divergence (Tryon and Tryon, 1982).

Woodwardia species are distributed disjunctly throughout the warm temperate and subtropical regions of the Northern Hemisphere in a classic Arcto-Tertiary distribution pattern, a unique circumboreal distribution within the Family Blechnaceae, which otherwise exhibits a Gondwanan distribution in the temperate and montane tropical regions of the Southern Hemisphere

(Cranfill, 2001; Cranfill and Kato, 2003). At present the genus includes 14 species (Cranfill and Kato, 2003): *W. radicans* (L.) Sm. is endemic to Mediterranean Europe and Macronesia, six species are endemic to North and Central America and the remaining seven species are endemic to eastern and southeastern Asia with extension to Philippines, Indonesia, and New Guinea (Fig. 1).

The genus has been variously revised since its establishment in 1793 (see Cranfill and Kato, 2003 for a detailed review). Although the studies of Cranfill and Kato (2003) supported the monophyly of *Woodwardia* and three subunits of related species using both morphological and chloroplast nucleotide sequence data (*rps4* and *rbcL*), the phylogeny of these ferns received limited attention to date. For example, the Himalayan species were not included in the analysis reported by Cranfill and Kato (2003). Also, the number of taxa sampled in that study was insufficient to determine the relationships of the three subunits of *Woodwardia*. The evolutionary history of *Woodwardia* has been reviewed by Collinson (2001) and Cranfill and Kato (2003), who suggested that this group first arose sometime in

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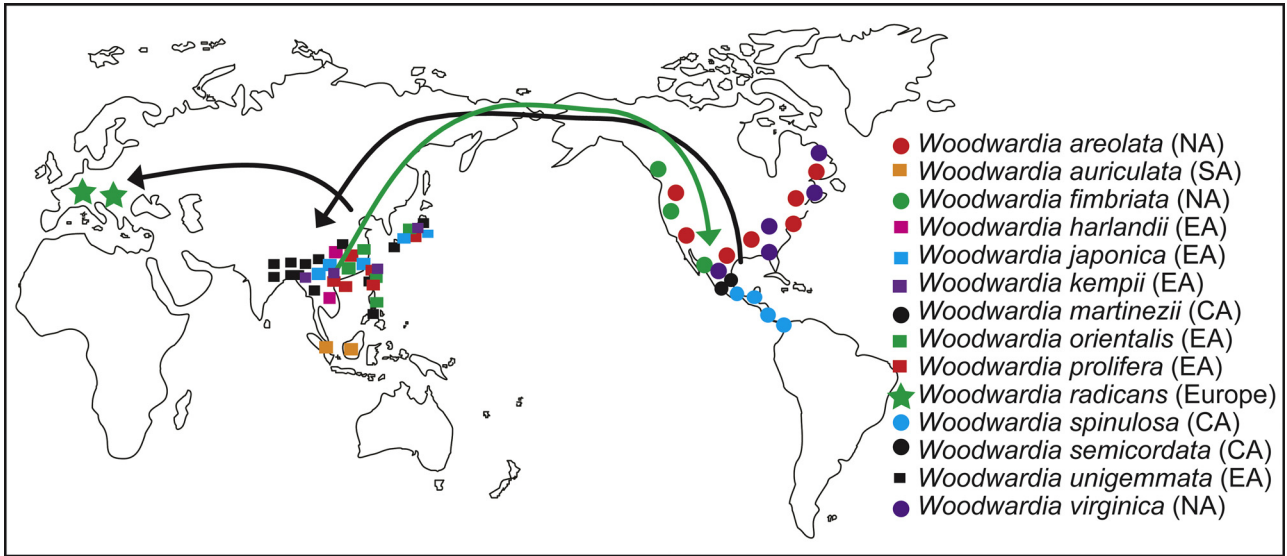


Fig. 1. Distribution of the genus *Woodwardia* and the hypothesized migration routes indicated by arrows based on *rbcl* sequence information from extant species. Line in black: migration route from NA to Eurasia; Line in green: a migration back to America from Asia; NA: North America, CA: Central America, EA: eastern Asia, SA: southeastern Asia.

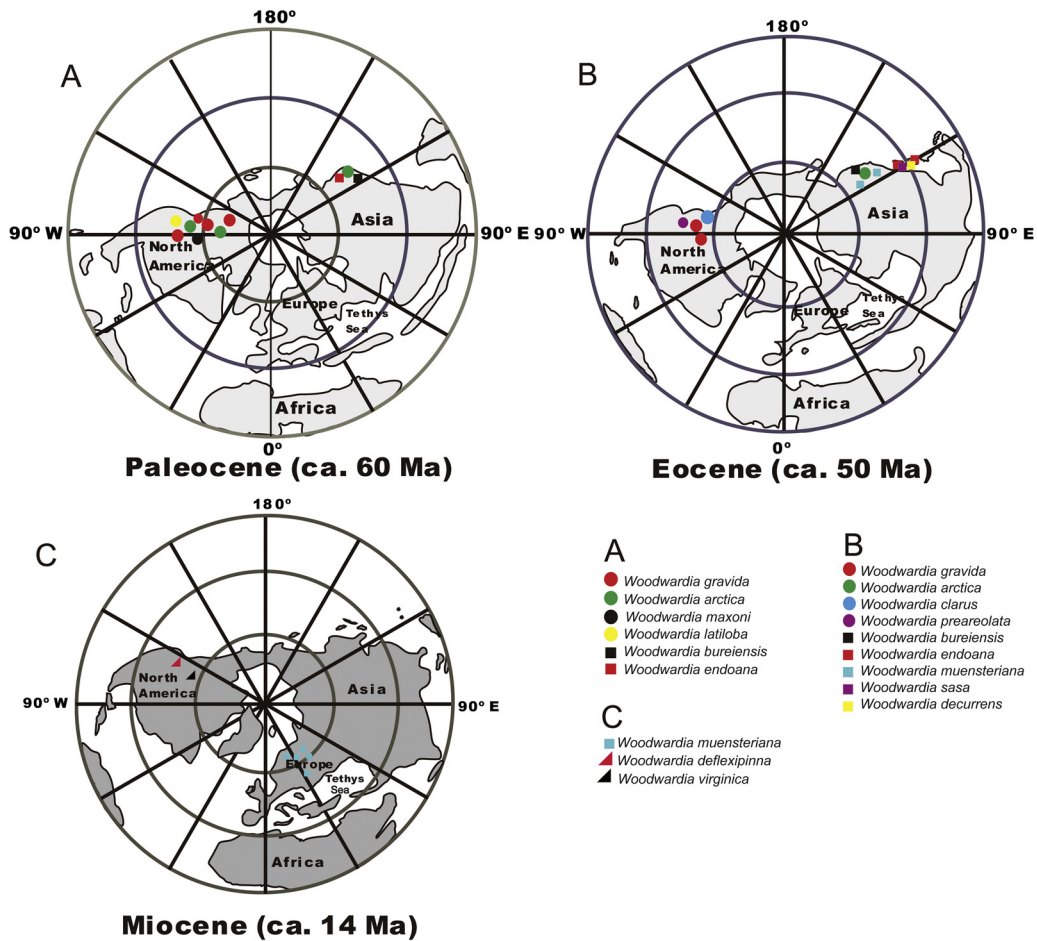


Fig. 2. Paleogeographic maps, showing the distributions of *Woodwardia* fossils using references cited in Collinson (2001). The base maps with paleocoastlines of Paleocene (ca. 60 Ma), Eocene (ca. 50 Ma), and Miocene (ca. 14 Ma) were modified from the paleomaps of Scotese (1997).

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