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The genus *Artemisia* (Asteraceae: Anthemideae) at a continental crossroads: Molecular insights into migrations, disjunctions, and reticulations among Old and New World species from a Beringian perspective

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ABSTRACT

Artemisia is the largest genus (ca. 350–500+ spp.) in the tribe Anthemideae and is composed of ecologically, morphologically, and chemically diverse species that are found primarily throughout the Northern Hemisphere. Two major centers of diversity for the genus are located in Eurasia and western North America, but phytogeographic links connecting these two regions are observed all across the North Pacific Rim and adjacent areas in the Arctic, including many islands and archipelagos. Previous phylogenetic studies have helped to clarify major lineages and identify likely sister relationships, but many questions remain unanswered regarding the relationships and migration history of New and Old World species. Here we investigate the phylogenetics of *Artemisia* within a biogeographic context centered in the Beringian Region and offer new hypotheses concerning species relationships, migration history, and the likely role of reticulate evolution in the genus. Our sampling included many new taxa and emphasized multiple accessions of widespread species, species from proposed refugia, and species with disjunct/vicariant distributions. The ITS phylogeny contained 173 accessions (94 new and 79 from GenBank) and indicated that *Artemisia* is paraphyletic by the exclusion of several small Asian genera and the North American genus *Sphaeromeria*. Following a survey of thirteen chloroplast loci, phylogenies based on two plastid markers (*psbA–trnH* and *rpl32–trnL* spacers) were constructed with a reduced data set, and though largely consistent with the ITS topology, revealed several cases of possible introgression among New World and Beringian species. Our analysis reveals that North American *Artemisia* species have multiple origins, and that western North America has served as a source for some colonizing elements in eastern Asia and South America.

1. Introduction

The Beringian Region, which includes present day Alaska, Yukon Territory, and Eastern Siberia, has long been recognized as a biogeographically important refugium and crossroads for the exchange of biota between the New and Old Worlds (Hultén, 1937; Murray, 1981, 1995; Sanmartin et al., 2001). At various times during the Mid–Late Cretaceous (100–80 mya) to the Late Pleistocene (ca. 10,000 ya), a land connection existed across the Bering Strait that allowed floristic exchange between North America and Eurasia. This exchange, however, was not uniform in direction or composition, but varied considerably over time with changing climatic and ecological conditions (Sanmartin et al., 2001). Oscillations of glacial advance and retreat further impacted the distributions of many taxa throughout the region by fragmenting ranges and opening and closing migration routes to southern and eastern ice-free zones in North America. Consequently, the extant flora found in Beringia today contains elements derived from two continents, as well as autochthonous taxa that evolved in situ. In addition to the phytogeographical puzzles, there are phylogenetic questions that remain unanswered concerning relationships of the North American and Eurasian taxa that exhibit vicariant or disjunct patterns (Peng and Wang, 2008; Xiang et al., 1998). Phylogenetic reconstructions of Beringian plants are relatively scarce (Carlsen et al., 2010; O'Quinn and Hufford, 2005), especially with genera that contain both regional endemics and shared species on both continents. Moreover, data on intraspecific genetic variation for Beringian and Arctic species are rather limited (Holderegger and Abbott, 2003), as are studies that address the relationships of these plants to their more southern congeners on both continents.

The genus *Artemisia* L. (Asteraceae, Anthemideae) is an excellent candidate for investigating these subjects and other questions related to long-distance dispersal, island biogeography, migration routes across the North Pacific, and the diversification and evolution of the Arctic flora. *Artemisia* is a large genus (ca. 350–500+

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spp.) and contains many Eurasian and North American endemics, as well as Beringian/Arctic endemics and species with widespread trans-continental distributions. Beringia was evidently an important area for the evolution and bi-directional migration of *Artemisia* between the two continents (Tkach et al., 2008a, 2008b; Watson et al., 2002). Further evidence for the long history of *Artemisia* in Beringia comes from fossil pollen profiles that commonly feature high percentages of *Artemisia* pollen (Colinvaux, 1996; Murray, 1981). In fact, the abundance of *Artemisia* pollen throughout Beringia was once interpreted as evidence for a vast steppe biome that spread across the entire region (Elias et al., 1996).

In a broad sense, *Artemisia* exhibits the well-known pattern of intercontinental disjunction between Eastern Asia and western North America, presumably having migrated at different times via the Bering Land Bridge (Tkach et al., 2008a, 2008b). Another broad disjunct pattern is observed between North America and western South America, where only five endemic *Artemisia* species are found in highly localized habitats in the cordilleran regions of Ecuador, Chile, and Argentina (Pellicer et al., 2010). Additional Old–New World phytogeographical links are seen all across the North Pacific Rim and Arctic areas, including many islands and archipelagos, where *Artemisia* species are found as local and regional endemics or adventive weeds. Species of *Artemisia* occur from the Philippines, Micronesia, Taiwan, Japan, Sakhalin Island, and the Kuril Archipelago to most islands of the Bering Sea Region, including the Aleutian Chain, with extensions southwards along the western coastlines of North America, including the Queen Charlotte Islands and the Channel Islands of California. *Artemisia* species also occur in the Hawaiian Islands, Greenland, and various islands in the Canadian Arctic Archipelago. At present, there are few, if any, comparative data available for these taxa with disjunct intercontinental and/or continental-insular distributions.

Artemisia has been the focus of numerous investigations over the last several decades (Hayat et al., 2009), and as a result, there exists a substantial body of information concerning the ecology, chemistry, karyology, medicinal uses, and phylogenetic relationships of many species. Despite this attention, taxonomic treatments of this genus continue to differ, and there are still many unresolved issues regarding relationships, character evolution, and migration history. Highly variable morphological traits, intergrading forms, the presence of natural hybrids, polyploidy, and an impressive nomenclatural legacy all make identifications and interpretations of relationships challenging. For example, the Old World genera *Ajania* Polj. (34 spp.) and *Kaschgaria* Polj. (2 spp.), plus the North American endemic *Sphaeromeria* Nutt. (9 spp.), each contain members with transitional characters (e.g., corymbose synflorescences) that are difficult to assess within the subtribe Artemisiinae (Bremer and Humphries, 1993). Traditionally, *Artemisia* s.l. has been organized into four to five infrageneric groups (DeCandolle, 1837; Ling, 1992; Rydberg, 1916; Shultz, 2006) based largely on capitulum morphology (e.g., discoid vs. disciform), floret fertility, and the presence or absence of receptacle hairs. These categories, recognized at subgeneric or sectional ranks, include *Absinthium* (ca. 40 spp.), *Artemisia* (=*Abrotanum*; ca. 280 spp.), *Dracunculus* (ca. 80 spp.), *Seriphidium* (ca. 130 spp. restricted to the Old World), and *Tridentatae* (ca. 10 spp. endemic to western North America). Other morphological features have also been used to establish numerous additional subcategories within *Artemisia* (Ling, 1995a; Poljakov, 1961; Rydberg, 1916) and/or segregate species into other genera (e.g., *Artemisiella* Ghafoor, *Crossostephium* Less., *Delwiensia* W. A. Weber & R. C. Wittmann, *Filifolium* Kitam., *Kaschgaria*, *Mausolea* Bunge, *Neopallasia* Polj., *Picrothamnus* Nutt., *Sphaeromeria*, and *Turaniphytum* Polj.). Recent cladistic analyses (Garcia et al., 2008, 2011a; Pellicer et al., 2011; Tkach et al., 2008a) have revealed multiple patterns of convergence and reversals for particular morphological characters used to make these infra- and intergeneric delimitations, which only underscores the need for continued study.

In this study, we aim to address some of these gaps in our knowledge of *Artemisia* systematics by expanding taxon sampling and conducting molecular analyses specifically within a broad biogeographical context of Old and New World plant disjunctions. Many species have yet to be thoroughly investigated in terms of their phylogenetic relationships, so their inclusion in analyses are crucial to advancing our understanding of the origin, development, and proposed migration history of the genus in the Old and New Worlds. Ancillary goals of this research were to contribute new information to complement other studies of New and Old World disjunctions of Anthemideae and Asteraceae in general (Guo et al., 2004; Himmelreich et al., 2008; Keeley et al., 2007; Zhao et al., 2010), the evolutionary history of Beringian/Arctic plants, for which information is lacking (Abbott and Brochmann, 2003; Carlsen et al., 2010), and the importance of western North America as a source of colonizing elements for eastern Asia and South America (Peng and Wang, 2008). New nuclear ITS sequence data are obtained for many new species and new accessions of previously identified clades that augment the large number of ITS sequences available from GenBank. Phylogenetic relationships are also assessed using sequence data from two chloroplast markers (*psbA–trnH* and *rpl32–trnL*), which were selected based on results from a survey of thirteen chloroplast loci.

2. Materials and methods

2.1. Taxon sampling

All *Artemisia* species with Beringian distributions or ranges in adjacent arctic/subarctic areas of North America and the Russian Far East were targeted for sampling. An emphasis was also placed on sampling multiple populations of widespread species, certain subspecific/varietal taxa, and disjuncts from key biogeographic regions (i.e., centers of speciation, proposed refugial areas, and single islands or archipelagos) from across the North Pacific Rim, North America, and Eurasia. To assess affinities of closely allied genera, additional samples were also obtained from the North American endemic genus *Sphaeromeria* Nutt., the monotypic arctic genus *Hulteniella* Tzvelev, and *Ajania pallasiana* (Fisch. ex Bess.) Polj. *Artemisia mendozana* was the sole representative of the *Artemisia* species endemic to South America. In total, about 4000 specimens (ca. 3800 specimens of 126 species of *Artemisia*, the remaining from allied genera and outgroups) from 22 herbaria (ALA, ALTA, B, CAN, COLO, DAO, GH, ILL, ILLS, MO, NY, OSBU, OSC, RM, S, UBC, UC, US, UT, UTC, WTU, and WU) were examined to assess geographic ranges, morphological diversity, and infraspecific circumscriptions where applicable. This large pool of herbarium material was also supplemented by field collections made during the summer of 2003 and deposited at the University of Illinois Herbarium (ILL). Although specimens for the majority of targeted species were available for study, a few failed to yield viable DNA or were not included due to insufficient herbarium material for DNA extraction.

Because *Artemisia* and some of its allied genera have been the subject of previous phylogenetic studies (cited above), a large number of sequence data (mainly nrITS and ETS) are publically available. Although we took advantage of these data in our preliminary analyses and assessment of outgroups, many taxa were sampled anew as a means for verifying identity and assessing infraspecific variation. For instance, preliminary ITS analyses included a broad selection of outgroups (e.g., *Ajania*, *Arctanthemum*, *Brachanthemum*, members of the former genus *Chrysanthemum* s.l., *Kaschgaria*, *Leucanthemella*, and *Nipponanthemum*) with the dual intent to assess ingroup monophyly and to reevaluate