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The phylogenetic history and biogeography of the frankincense and myrrh family (Burseraceae) based on nuclear and chloroplast sequence data

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Abstract

Generalized hypotheses for the vicariant, Gondwanan origin of pantropically distributed eudicotyledon families must be refined to accommodate recently revised dates that indicate major continental rifting events predate the evolution of many tricolpate angiosperm clades. Here, we use molecular phylogenies of an eudicotyledon family previously hypothesized to have a Gondwanan origin, the Burseraceae, to test this and other alternative biogeographical hypotheses in light of recalibrated geological events. Phylogenies based on nuclear and chloroplast data were reconstructed for 13 of the 18 genera (50 spp. total) of Burseraceae using parsimony, maximum likelihood, and Bayesian methods. Ages of all lineages were estimated using penalized likelihood and semiparametric rate smoothing [Bioinformatics 2003 (19) 301], which allows the user to calibrate phylogenies based on non-clock-like DNA sequence data with fossil information. Biogeographical hypotheses were tested by comparing ages of species and more inclusive lineages with their extant and most parsimonious ancestral distributions. Our data support a North American Paleocene origin for the Burseraceae followed by dispersal of ancestral lineages to eastern Laurasia and Southern Hemisphere continents.

Keywords: Boreotropical land bridge; Burseraceae; Fossil dating; Gondwana; Laurasia

1. Introduction

The Burseraceae are best known for producing fragrant resins of economic, medicinal, and cultural value, such as frankincense, myrrh, and copal (Langenheim, 2003). The family comprises 18 genera (ca. 700 spp.) and is divided into three tribes (Canarieae, Protieae, and Bursereae) each of which is distributed pantropically across a broad range of low-elevation, frost-free habitats including rainforest, dry deciduous forest, and desert. The Burseraceae and the order to which it belongs, the Sapindales, are part of the monophyletic group of flowering plants that bear tricolpate pollen, the eudicotyledons (Doyle and Hotton, 1991). Molecular phylogenetic studies of the Sapindales (APG II, 2003; Gadek et al., 1996) place the Burseraceae sister to the Anacardiaceae, a family that closely resembles the Burseraceae and with which it has been traditionally allied. The Burseraceae are distinguished morphologically from the Anacardiaceae by the presence of fragrant non-allergenic resin (vs. sometimes allergenic), pulvinulate leaflets, induplicate-valvate (vs. usually imbricate) petals, and two epitropous ovules (vs. one apotropous) per carpel.

The pantropical distribution of the tribes and their component genera poses a challenge to interpreting the biogeographical history of the Burseraceae. All tribes are represented in the American, African, and Indo-Asian tropics, and generic diversity is highest in the Southern

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Hemisphere. Additionally, each tribe contains a cosmopolitan genus distributed across all three tropical regions: *Dacryodes* (Canarieae), *Protium* (Protieae), and *Commiphora* (Bursereae). On the basis of this information, and the fact that the Burseraceae cannot survive freezing temperatures at higher latitudes, Raven and Axelrod (1974) proposed that the Burseraceae had a tropical Gondwanan origin followed by vicariance of its ancestral lineages. Yet, one can only hypothesize a scenario involving Gondwanan vicariance if the Burseraceae originated prior to the division of South America from Africa, which is the last division of Gondwanan landmasses at tropical, frost-free latitudes. Recently, published dates indicate that the division of South America and Africa took place between 105 and 119 Ma (McLoughlin, 2001). To place this event in context, the earliest known fossils attributable to the eudicotyledon lineage and the Sapindales date to ca. 125 Ma (Doyle and Hotton, 1991; Magallón et al., 1999) and ca. 65 Ma (Knobloch and Mai, 1986), respectively. The early eudicot fossils are not attributable to any extant family but were found in Gabon, a former Gondwanan terrane. By contrast, the Sapindales fossil attributed to the Rutaceae was found in Germany, which is a former Laurasian terrane. A model in which extant pantropical distributions of the Burseraceae are due solely to strict Gondwanan vicariance requires that the Burseraceae originated either in Gondwana before proto-south east Asia rifted from the supercontinent (300–152 Ma; Hall, 1995; McLoughlin, 2001; Metcalfe, 1995) or originated before the division of Africa and the Madagascar-India subcontinent (165 Ma; McLoughlin, 2001), events that are unlikely to have subdivided any eudicotyledon lineage, much less the Burseraceae.

Incorporating these data, we find the assumptions of the generalized vicariant Gondwanan biogeographic model as proposed by Raven and Axelrod (1974) require reassessment for the Burseraceae, as well as for many other extant eudicotyledon taxa that are distributed among American, African, and south east Asian tropics. McLoughlin (2001) suggested associating vicariant biogeographies of Southern Hemisphere angiosperms with more recent episodes of continental rifting, such as the division of Madagascar and India (88 Ma; Storey et al., 1995) or India's collision with the Asian continent (43 Ma) with subsequent dispersal to other Southern and Northern Hemisphere regions. To understand the evolution and diversification of the Burseraceae and to help explain the development of this pantropical distribution pattern, the biogeography of the family was examined in a three-step process. First, a molecular phylogeny of the family was generated to test the monophyly of the tribes and most of the genera using DNA sequences of the chloroplast *rps* 16 intron and the 3′ end of the external transcribed spacer (ETS) of the nuclear ribosomal DNA repeat region. Second, the ages of all lineages within the family were estimated by calibrating the molecular phylogeny with fossil data using the computer program r8s (Sanderson, 2003). This program applies penalized likelihood and a semiparametric method of rate-smoothing (Sanderson, 2003) to phylogenies derived from DNA sequence data that do not evolve in a clock-like manner and allows the user to estimate the ages of clades in the phylogeny by applying fossil-based calibration points to nodes within the phylogeny. Lastly, possible instances of ancestral continental vicariance or long distance dispersal were determined with respect to the ages of lineages by mapping the extant distributions of species onto the phylogeny using parsimony as a criterion.

1.1. Tribal taxonomy and phylogeny of the Burseraceae

Tribal groups were delimited by Engler (1913) on the basis of pyrene structure and subsequently revised by Lam (1932), who established two subtribes within the most polymorphic tribe of the family, the Bursereae (Table 1). Most recently, Harley and Daly (1995; see for detailed taxonomic history of family) revised the subtribes of the Bursereae, Burserinae, and Boswelliinae, to reflect newly collected morphological data and to

Table 1
List of genera in the Burseraceae, approximate number of species, tribal and subtribal placement, and geographic range

Bursereae
Burserinae
Bursera Jacq. ca. 100 spp. Caribbean, Mexico, Central, and S. America
Commiphora Jacq. ca. 190 spp. Africa, India, S. America
Boswelliinae
Aucoumea Pierre 1 sp. W. Africa
Beiselia Forman 1sp. SW Mexico
Boswellia Roxb. ca. 30 spp. NE Africa, Arabia, India
Triomma Hook. f. 1sp. W Malesian region
Unnamed subtribe
Garuga Roxb. 4 spp. India, SE Asia
Canarieae
Canarium L. ca. 105 spp. SE Asia, Malaysia, Africa
Dacryodes Vahl 66 spp. Caribbean, Mexico, C. and S. America, SE Asia, Africa
Haplolobus H.J. Lam 22 spp. E. Malaysia
Pseudodacryodes R. Pierlot 1 sp. Central Africa
Rosselia Forman 1 sp. Rossel Island, New Guinea
Santiria Blume 24 spp. W. Malesian region, Philipines, Moluccas, New Guinea, Africa
Scutinanthe Thwaites 2 spp. Sri Lanka, S. Myanmar, Celebes, Sumatra, Malay Peninsula, Borneo
Trattinnickia Willd. 13 spp. C. and S. America
Protieae
Crepidospermum Hook. f. 6 spp. S. America
Protium Burm. f. 150 spp. Mexico, C. and S. America, Africa, SE Asia
Tetragastris Gaertn. 9 spp. Central and S. America

Garuga was placed informally within the Bursereae by Harley and Daly (1995).