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ScienceDirect
Molecular Phylogenetics and Evolution 41 (2006) 566–578
MOLECULAR PHYLOGENETICS AND EVOLUTION
www.elsevier.com/locate/ympev

Molecular evidence for adaptive radiation of *Micromeria* Benth. (Lamiaceae) on the Canary Islands as inferred from chloroplast and nuclear DNA sequences and ISSR fingerprint data

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Received 26 January 2006; revised 20 May 2006; accepted 26 May 2006
Available online 6 June 2006

Abstract

The Canary Islands have been a focus for phylogeographic studies on the colonization and diversification of endemic angiosperm taxa. Based on phylogeographic patterns, both inter island colonization and adaptive radiation seem to be the driving forces for speciation in most taxa. Here, we investigated the diversification of *Micromeria* on the Canary Islands and Madeira at the inter- and infraspecific level using inter simple sequence repeat PCR (ISSR), the *trn*K-Intron and the *trn*T-*trn*L-spacer of the cpDNA and a low copy nuclear gene. The genus *Micromeria* (Lamiaceae, Mentheae) includes 16 species and 13 subspecies in Macaronesia. Most taxa are restricted endemics, or grow in similar ecological conditions on two islands. An exception is *M. varia*, a widespread species inhabits the lowland scrub on each island of the archipelago and could represent an ancestral taxon from which radiation started on the different islands. Our analyses support a split between the "eastern" islands Fuerteventura, Lanzarote and Gran Canaria and the "western" islands Tenerife, La Palma and El Hierro. The colonization of Madeira started from the western Islands, probably from Tenerife as indicated by the sequence data. We identified two lineages of *Micromeria* on Gomera but all other islands appear to be colonized by a single lineage, supporting adaptive radiation as the major evolutionary force for the diversification of *Micromeria*. We also discuss the possible role of gene flow between lineages of different *Micromeria* species on one island after multiple colonizations.

Keywords: *Micromeria*; Lamiaceae; Canary Islands; *trn*K; *trn*T-F; FPS2; ISSR markers; Adaptive radiation

1. Introduction

The Canary Islands, part of the Macaronesian phytogeographic region, consist of an archipelago of seven major volcanic islands located in the northeastern Atlantic Ocean in close proximity to the western Sahara coast. The geological history of the archipelago is characterized by a temporal sequence of volcanic eruptions over the past 20 million years with the ages of the islands decreasing from east to west (i.e. 20.7 Ma for Fuerteventura to 0.7–0.8 Ma for El Hierro) (Carracedo, 1994; Guillou et al., 2004). The older, eastern islands contain mountain ridges of low altitude (i.e. Lanzarote 671 m, Fuerteventura 807 m), whereas the highest volcanoes in the central and western islands exceed 1400 m with the Teide-peak on Tenerife rising to 3718 m. The Canary Islands are characterized by a subtropical climate that is strongly influenced by the humid trade winds from the northeast and the cold Canaries Current that causes persistent, dense fog at around 1000 m in elevation. South sides of the islands as well as high altitudes

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1055-7903/$ - see front matter © 2006 Elsevier Inc. All rights reserved.
doi:10.1016/j.ympev.2006.05.037

frequently experience desert and semi-desert conditions with very low levels of precipitation. In contrast, the slopes of the mountains are characterized by high to medium humidity and rainfall augmented by condensation and fog. These sharp elevational gradients in climate have resulted in the formation of distinct ecological zones: coastal deserts and arid low land scrub, humid and semi-arid subtropical scrub and woods, humid laurel forest ("laurisilva") in the cloud belt, a heath belt (Fayal-Brezal) as transition vegetation between laurel forest and, at high altitudes, humid to dry temperate pine forests as well as dry subalpine scrub. Local adaptation to these habitats within islands, as well as physical isolation among the islands, are main factors responsible for the rich flora of Macaronesia with at least 831 species and 40 genera endemic in this region (Humphries, 1979; Hansen and Sunding, 1993).

In the last decade, the Canary Islands have been in the focus for phylogeographic studies on the colonization and diversification of endemic angiosperm taxa (e.g. Böhle et al., 1996; Kim et al., 1996; Barber et al., 2000; Francisco-Ortega et al., 2001; Mort et al., 2002; Allan et al., 2004; Fairfield et al., 2004; Trusty et al., 2005). Based on phylogeographic patterns, inter island colonization has been proposed as a driving force for species differentiation within highly diverse genera on the Canary Islands (i.e. Francisco-Ortega et al., 1996, 2001). This mechanism was supported by phylogenies indicating niche conservatism, where taxa with similar ecological preferences comprise a single clade, and suggests that adaptation to specific ecological zones occurred only once within the archipelago (Francisco-Ortega et al., 2001). An alternative explanation is adaptive radiation, where adaptation to the distinct habitats occurs independently on each island. Examples supporting an adaptive radiation on each island are found in several taxa (e.g. Kim et al., 1996; Percy and Cronk, 2002). Both colonization and adaptive radiation seem to be important in most taxa (Panero et al., 1999; Barber et al., 2000; Francisco-Ortega et al., 2002; Mort et al., 2002; Allan et al., 2004; Trusty et al., 2005). Studies of the evolution of plant diversity on the Canary Islands indicate that most of the plant groups of the Canary Islands evolved by adaptation to different ecological zones as well as by inter-island colonization.

The genus *Micromeria* Benth. (Lamiaceae, Nepetoideae) as currently understood (Harley et al., 2004) contains about 70 species with a distribution range extending from the Himalayan region to the Macaronesian Archipelago (with Madeira, the Cape Verde and Canary Islands) and from the Mediterranean to South Africa and Madagascar (Doroszenko, 1986; Morales, 1993; Bräuchler et al., 2005). Molecular data suggest the transfer of sect. *Pseudomelissa* to *Clinopodium* (Bräuchler et al., 2005) and the exclusion of sect. *Cymularia* (with *M. cymuligera* Boiss. and Hausskn. an endemit of southeastern Anatolia as the only representative) from *Micromeria* (Bräuchler, unpublished anatomical and preliminary molecular data). From the remaining sections of *Micromeria* s.str., sect. *Micromeria* includes approximately 50 species of perennial suffruticose herbs and shrubs. Centers of diversity are found in the Mediterranean region and the Canary Islands.

Comparative analysis of cpDNA data revealed Macaronesian *Micromeria* (excluding *M. forbesii* from Cape Verde Islands) as monophyletic with a group of taxa from the Western Mediterranean (e.g. *M. inodora* and *M. fontanesii*) as neighbor group (Bräuchler et al., 2005). According to the revision by Pérez de Paz (1978), the genus *Micromeria* includes 16 species and 13 subspecies in Macaronesia, with the highest diversity on Tenerife and Gran Canaria (seven species each). Lower numbers of species are found on La Palma (3), Gomera (2), El Hierro (2), Lanzarote (1) and Fuerteventura (1); (see Fig. 1, Table 1). Only one species, *M. varia* L. colonized the whole archipelago. It occurs mainly in dry to medium dry lowland habitats and is taxonomically split into seven subspecies. *M. hyssopifolia* Webb et Berth. is found in the pine forests of Tenerife and El Hierro while *M. lasiophylla* Webb et Berth. inhabits the high altitude desert of Tenerife and La Palma. The remaining species are narrow endemics. Two of them, *M. leucantha* Svent ex P. Perez and *M. pineolens* Svent., both occurring on Gran Canaria, are forming sect. *Pineolentia* (Pérez de Paz, 1978) because of their morphological distinctness. The most striking features of *M. pineolens* are its shrubby habit (up to 80 cm), leaves exceeding 1 cm in length and large flowers with a corolla size ranging from 10 to

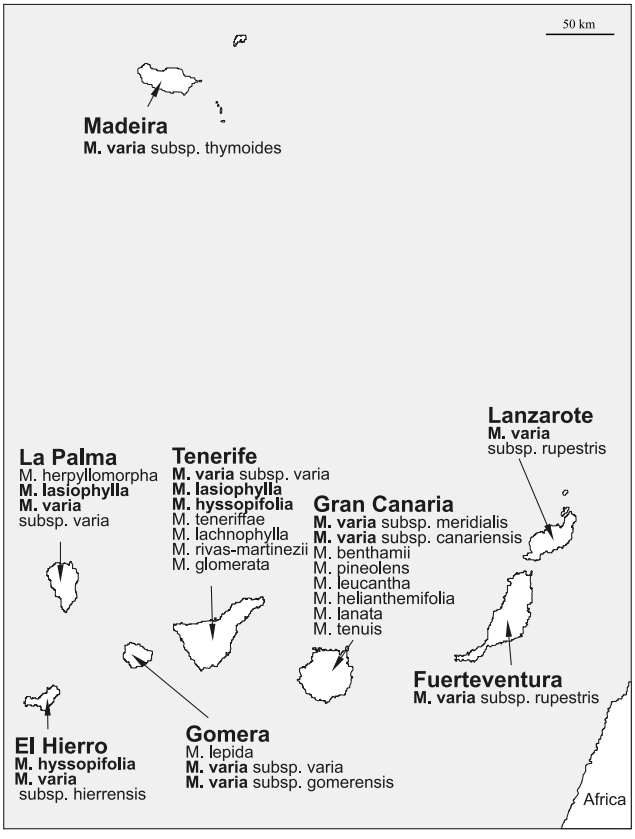

Fig. 1. The Canary Islands and Madeira and the distribution of the species of the genus *Micromeria* on the islands. Species distributed on more than one island are marked bold.