Phylogeny and evolutionary diversification of Adenocarpus DC. (Leguminosae)

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Abstract Phylogenetic relationships of Adenocarpus species were assessed by sequence analyses of the ITS and 3′ end of ETS (nrDNA) regions and the trnL-trnF intergenic spacer (cpDNA). The nrDNA analysis recovered four main clades within Adenocarpus. Clades 1–3 comprise morphological and molecularly well-differentiated species that occur in the western Mediterranean realm. Clade 4 comprises three distinctive endemic species from the Canary Islands, an endangered Algerian endemic, and a set of species close to A. complicatus with distinct geographical areas but with little molecular variation between taxa. The latter species are centred in the Iberian Peninsula but also distributed along the Mediterranean basin (from the Iberian Peninsula to Turkey). The phylogenetic position of A. mannii, a morphologically distinctive species with a unique afro-tropical distribution, is not unequivocally resolved, being sister to clade 3 in the ETS tree but to clade 4 in the ITS tree. Rates of evolution and ages of divergence of major groups were estimated using nonparametric rate smoothing with a fixed calibration point of 41.2 Ma and constraining the node of the separation of Anarthrophyllum and Mediterranean Genisteae at a minimum age of 13.6 and a maximum of 25.8 Ma. The estimated ages indicate that the diversification of Adenocarpus and first separation of two lineages may have occurred during the onset and the wake of the profound Middle Miocene cooling episode. One of the lineages separated rapidly into two groups (clades 1 and 2) while the second one led to clade 3, A. mannii and clade 4. Clades 1, 2 and 3 differentiated into the present species soon after these major events whereas clade 4 radiated much later, during the Pliocene.

Keywords Adenocarpus; dating analyses; Genisteae; molecular phylogeny

INTRODUCTION

Genisteae (Adans.) Benth. are a monophyletic tribe of Fabaceae, predominantly distributed in the Northern Hemisphere and with centres of diversity in the Western Mediterranean area (west Morocco to Spain and surrounding countries) and the Eastern Mediterranean area (Balkan region) (Cristofolini, 1991). The tribe also extends to the Canary Islands, northern Europe, and America (Lupinus L.). The most recent rearrangement of the tribe includes several geographically distant genera that nevertheless share secondary metabolites and morphological characteristics: Anarthrophyllum Benth. in South America, and Melolobium Eckl. & Zeyh., Dichilus DC., Polhillia C.H. Stirt. and Argyrolobium Eckl. & Zeyh. in southern Africa (Polhill, 1994; Polhill & Van Wyk, 2005). Within the tribe, Adenocarpus DC. is morphologically well characterised by the presence of glandular papillae on the legumes of all the species (Polhill, 1976). Other features that are common but by no means uniform in the genus are glandular papillae on the calyx, leaves fasciculate on very short shoots and corolla yellow-orange (Bisby, 1981). Adenocarpus has been regarded as part of a basal grade within Genisteae together with the other African genera. In particular, Adenocarpus has been linked to Melolobium because of the presence of glandular trichomes in the legumes in both genera. However, glands in the two genera are most probably non-homologous, being multicellular in Adenocarpus and unicellular in Melolobium (Moteetee & al., 2002). Molecular phylogenetic analyses (Käss & Wink, 1997) indicate that Adenocarpus forms a monophyletic clade close to the mainly Mediterranean Cytisus and Genista groups (Polhill, 1976), and is not directly related to the African Genisteae.

The total area of distribution of Adenocarpus includes Macaronesia, northern and tropical Africa, southwestern Europe, and more locally, Central and South Italy, Greece, West Turkey, Libya and Syria. However, the maximum species density of Adenocarpus occurs in the western Mediterranean area, with several endemics restricted to northern Africa (Rif and Atlas Mountains of Morocco) and the Iberian Peninsula. Remarkably, one species (Adenocarpus mannii (Hook. f) Hook. f.) occurs at tropical latitudes, whereas the rest are circum-Mediterranean.

Several species of Adenocarpus are clearly differentiated on morphological grounds (e.g., A. bacquei Batt. & Pitard, A. artemisiifolius Jahandiez, Maire & Weiller, A. boudyi Battand. & Maire, A. decorticans Boiss., A. foliolosus DC., A. viscosus (Willd.) Webb & Berthel.). In contrast, a set of morphologically close forms distributed along the Mediterranean basin, and especially on the Iberian Peninsula, are not easy to identify and taxonomically troublesome. Gibbs (1967) includes all these forms in a large circum-Mediterranean polymorphic taxon (A. complicatus (L.) J. Gay subsp. complicatus). However, recent revisions (Castroviejo, 1999a,b; Brullo & al., 2001) split these forms into the following species, some of them with...