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Reticulate evolution in the *Acrolophus* subgroup (*Centaurea* L., Compositae) from the western Mediterranean: Origin and diversification of section *Willkommia* Blanca

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Abstract

Section *Willkommia* (*Centaurea*, Compositae) is endemic to the east-central portion of the Iberian Peninsula and northwestern Africa. The section has been included with sections *Acrolophus* and *Phalolepis* in the informal subgroup *Acrolophus*. We have used a molecular phylogenetic approach to test the hypothesis proposed by earlier authors that the diversification of section *Willkommia* involved a schizoendemic process from an ancestral syngameon. Comparative analysis of the transcribed spacer sequences of the nuclear ribosomal DNA (ITS and 3′ETS) regions reveals the presence of three different types of ribosomal sequences in the *Acrolophus* subgroup (referred to here as the *Willkommia*, *Acrolophus–Phalolepis* and *Simulans* ribotypes) which show a sectional-independent geographic structure. This evidence, together with the presence of additive polymorphic sites in the *Willkommia* sequences which agree with the geographic distribution of the taxa, suggests that members of section *Willkommia* and the western Mediterranean taxa of sections *Acrolophus* and *Phalolepis* fit a reticulate evolution model.

Keywords: Reticulate evolution; Concerted evolution; Nuclear ribosomal DNA; ITS; ETS; Syngameon; *Willkommia* section; *Centaurea*; Compositae

1. Introduction

Following Heywood (1960), "micro-endemic vicariants" is a term used for those groups of endemic plants whose parentage is obvious and which are spatially rather than genetically (reproductively) isolated. In these plants, morphological differentiation is usually weak and the groups are not widely separated geographically. Populations have been fragmented into discrete units (e.g., on separate mountain peaks or mountain ranges), and often the morphological differences between taxa, although small, are constant. Heywood (1960) proposed that species included in section *Willkommia* Blanca of the genus *Centaurea* L. are examples of micro-endemic vicariants. Based on the patterns of morphological and karyological differentiation together with geographical distribution, Blanca (1981a) more recently suggested that species of section *Willkommia* represented schizoendemics (terminology proposed by Favarger and Contandriopoulos, 1961); that is, an ancestral syngameon gave rise to the present taxa principally by spatial isolation and genetic drift, although different degrees of genetic isolation could have occurred between the taxa, which would explain the high taxonomic complexity.

Section *Willkommia* includes 22 species, 17 subspecies and 9 varieties (Table 1) distributed from the middle-east of the Iberian Peninsula to North Africa (from Morocco to

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Table 1
Sampled *Acrolophus* subgroup taxa and outgroups

Taxa	Locality/voucher/reference	EMBL No. ITS/ETS
Centaurea sect. *Willkommia* Blanca		
C. avilae Pau	SP: Ávila, Sierra de Gredos/GDAC 6087/García-Jacas et al. (2006)	AM114309/AM114368
C. boissieri DC.		
subsp. *atlantica* (Font Quer) Blanca		
var. *atlantica* Font Quer.	MO: Ifrane/MPU 3275	AM114283 AM114284/ AM114338 AM114339 AM114340 AM114341 AM114342
var. *calvescens* (Maire) Blanca	MO: Between Ar-Rachidia and Midelt/GDA 49717	AM114285 AM114286/ AM114343 AM114344
	MO: Tizi-n-Talrhemt/BC	
	MO: Tizi-n-Taghzelt/MPU	
subsp. *boissieri*	SP: Granada, Sierra de Cázulas/GDAC 6597/García-Jacas et al. (2006)	AM114278/AM114333
subsp. *funkii* (Schultz Bip. ex Willk.) Blanca	SP: Granada, Huétor Santillán/GDAC 6605	AM114280/AM114335
subsp. *mariolensis* (Rouy) Dostál	SP: Alicante, Sierra Mariola/GDAC 6657	AM114281/AM114336
subsp. *prostrata* (Coss.) Dostál	SP: Albacete, Sierra de Alcaraz/GDAC 6656	AM114282/AM114337
subsp. *transmalvana* (Emb. & Maire)Breitw. & Podlech	MO: Debdou, Col between Sellaouit et Lalla Mimouna/MPU	–/AM114345
subsp. *willkommii* (Schultz Bip. ex Willk.) Dostál *C. bombycina* Boiss. in DC.	SP: Granada, Sierra de Arana/GDAC 6628	AM114279/AM114334
subsp. *bombycina*	SP: Granada, Sierra de Cázulas/GDAC 6675	AM114303/AM114362
subsp. *xeranthemoides* (Lange in Willk.& Lange) Blanca, Cueto & M. C. Quesada	SP: Granada, Sierra del Manar/GDAC 16501	AM114304/AM114363
C. carratracensis Lange	SP: Málaga, Carratraca, Sierra Aguas/GDAC 42802/ García-Jacas et al. (2006)	AM114302/AM114361
C. citricolor Font Quer	SP: Jaén, Sierra Morena, Collado de los Jardines/ GDAC 6688	AM114314/AM114373
C. cordubensis Font Quer	SP: Córdoba, Cerro Muriano/Jardín Botánico de Córdoba/wr	AM114312/AM114371
C. debdouensis Breitw. & Podlech	MO: Debdou, Gaada de Debdou/MPU/García-Jacas et al. (2006)	AM114317/AM114376, AM114377
C. delicatula Breitw. & Podlech	TN: Djebel Chambi/MPU	AM114318/AM114378
C. gadorensis Blanca	SP: Almería, Sierra de Gádor/GDAC 44171/García-Jacas et al. (2006)	AM114298/AM114357
C. jaennensis Degen & Debeaux in Degen	SP: Jaén, Pozo Alcón, Embalse de la Bolera/GDAC 6724/García-Jacas et al. (2006)	AM114287/AM114346
C. monticola Boiss. In DC.	SP: Granada, pantano del Cubillas/GDAC 6750/ García-Jacas et al. (2006)	AM114313/AM114372
C. paui Loscos ex Willk.	SP: Castellón, Sierra de Espadán/GDAC 6086	AM114307/AM114366
C. pauneroi Talavera & J. Muñoz	SP: Córdoba, Priego de Córdoba, Sierra de Leares/wr	AM114305/AM114364
C. pinae Pau		
var. *integrifolia* (Willk.) Blanca	SP: Castellón, Peñagolosa/GDAC 6773	AM114311/AM114370
var. *pinae*	SP: Teruel, Pto. Ragudo/GDAC 6768/García-Jacas et al. (2006)	AM114310/AM114369
C. pinnata Pau in Vicioso	SP: Zaragoza, Calatayud/GDAC 6777	AM114306/AM114365
C. pomeliana Batt.		
subsp. *pomeliana*	AL: Oran, Djebel Mzi/MPU	AM114315/AM114374
subsp. *rouxiana* (Maire) Breitw. & Podlech	AL: Oran, Djebel Amour, Aín-Aflou/MPU	AM114316/AM114375
C. pulvinata (Blanca) Blanca	SP: Granada, Sierra Nevada/GDAC 44637	AM114296/AM114355
C. resupinata Coss.		
subsp. *lagascae* (Nyman) Fern. Casas & Susana	SP: Alicante, Orihuela, Cerro Hurchillo/GDAC 6711	AM114289/AM114348
subsp. *resupinata*	SP: Albacete, between Elche de la Sierra and Hellín/ GDAC 6714/García-Jacas et al. (2006)	AM114288/AM114347
subsp. *rifana* (Emb. & Maire) Breitw. & Podlech	MO: Atlas Rifano, Targuist/MPU	AM114293/AM114352
subsp. *simulans* (Emb. & Maire) Breitw. & Podlech	MO: Vallée du haut Rhéres/MPU	AM114292/AM114351
subsp. *spachii* (Schultz Bip. ex Willk.) Fern. Casas & Susana		
var. *humilis* Pau	SP: Alicante, El Maigmó/GDAC 6698	AM114291/AM114350
var. *spachii*	SP: Valencia, Játiva/GDAC 6693	AM114290/AM114349
	SP: Valencia, Enguera/GDAC 6704	
subsp. *vulnerariifolia* (Pomel) Breitw. & Podlech	AL: Oran, Nador de Tiaret, Goudjila/MPU	AM114294/AM114353

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