

# Nuclear ribosomal DNA and karyotypes indicate a NW African origin of South American *Hypochoeris* (Asteraceae, Cichorieae)

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## Abstract

*Hypochoeris* has a disjunct distribution, with more than 15 species in the Mediterranean region, the Canary Islands, Europe, and Asia, and more than 40 species in South America. Previous studies have suggested that the New World taxa have evolved from ancestors similar to the central European *H. maculata*. Based on internal transcribed spacer (ITS) sequences and fluorescence in situ hybridization (FISH) with 5S and 18S–25S rDNA of the previously overlooked *Hypochoeris angustifolia* from Moyén Atlas, Morocco, we show that it is sister to the entire South American group. A biogeographic analysis supports the hypothesis of long-distance dispersal from NW Africa across the Atlantic Ocean for the origin of the South American taxa rather than migration from North America, through the Panamian land bridge, followed by subsequent extinction in North America. With the assumption of a molecular clock, the trans-Atlantic dispersal from NW Africa to South America is roughly estimated to have taken place during Pliocene or Pleistocene.

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## 1. Introduction

The genus *Hypochoeris* (Asteraceae, Cichorieae) is distributed in North Africa, the Canary Islands, Europe, Asia, and South America. The co-occurrence with its sister genus *Leontodon* in the Mediterranean region (North Africa and S Europe) and the abundance of Old World species in this region suggest a Mediterranean origin of *Hypochoeris* (Samuel et al., 2003; Stebbins, 1971). The Hypochaeridinae are distributed in Eurasia and North Africa (Bremer, 1994). There are no other Hypochaeridinae in South America (Bremer, 1994). Old World *Hypochoeris* (c. 15 species) also contain greater karyotypic (chromosome numbers  $x = 3, 4, 5$ , and 6 and all symmet-

ric karyotypes; Cerbah et al., 1998a, 1999; see Figs. 1 and 2) and genetic diversity (Cerbah et al., 1998b; Samuel et al., 2003) than the South American group (c. 40 species; Samuel et al., 2003; Weiss-Schneeweiss et al., 2003). Old World *Hypochoeris* have been divided among four well defined sections on the basis of pappus characters (Hoffmann, 1893). This classification has been supported by chromosome numbers (Cerbah et al., 1998a) and DNA sequence data (Samuel et al., 2003). The sequence data suggest that Hoffmann's (1893) fifth section *Robertia* does not belong within *Hypochoeris*, but rather within *Leontodon* (Cerbah et al., 1998b; Samuel et al., 2003). The monophyletic South American species (Samuel et al., 2003) all have asymmetrical, bimodal karyotypes with  $n = 4$  (Weiss et al., 2003; Weiss-Schneeweiss et al., 2003), but differ from each other both morphologically and ecologically (e.g., Bortiri, 1999). They have

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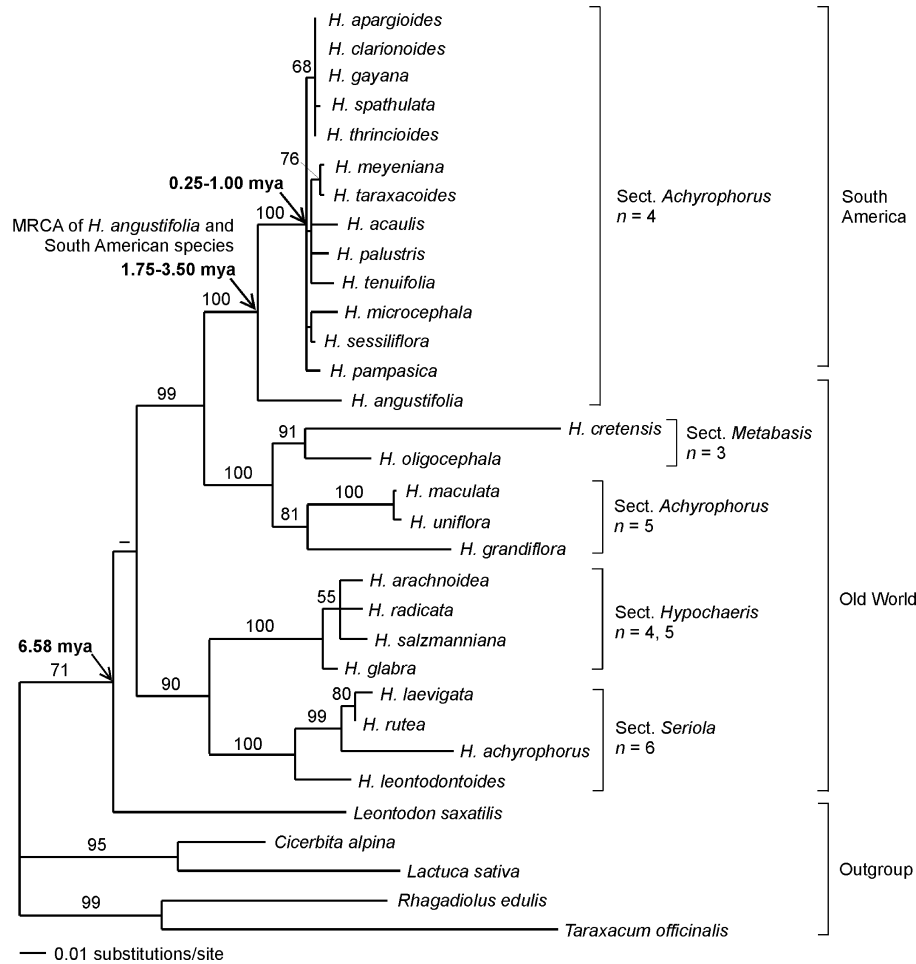


Fig. 1. Single best maximum likelihood phylogram of nuclear rDNA sequences (ITS1, 5.8S rDNA, ITS2; 658 nucleotides) of *Hypochaeris* and outgroups. Model of DNA substitution: SYM + G. Values above branches: bootstrap proportions (500 replicates; hyphen indicates BP < 50%). Node for calibration: 6.58 mya for divergence of *Leontodon saxatilis* and *Hypochaeris uniflora*. Sectional designations according to Hoffmann (1893).

been included within the otherwise Eurasian sect. *Achyrophorus* containing *H. grandiflora*, *H. maculata*, and *H. uniflora* based on the presence of just one row of pappus hairs (Hoffmann, 1893). The Eurasian sect. *Achyrophorus* has  $n=5$  and similar karyotypes, including also localization of rDNA loci (Cerbah, 1997; Weiss-Schnee-weiss et al., unpubl.).

The biogeographic origin of the South American group is still problematic. Two conflicting hypotheses exist to explain how *Hypochaeris* arrived in South America given its absence from North America. (1) Stebbins' (1971) hypothesis is based primarily on the assumption that the asymmetrical, bimodal karyotype is generally a derived genomic character in flowering plants. It is found in the South American group, in contrast to Old World *Hypochaeris*, which have rather symmetrical karyotypes. Stebbins (1971) suggested that *Hypochaeris* may have existed in North America during the Tertiary as small populations in pioneer habitats, a situation which might have favored evolution of asymmetrical, bimodal karyotypes (two large and two small chromo-

some pairs). After entering South America during the Pliocene, perhaps by migration through the Panamanian land bridge, *Hypochaeris* might have diversified into different environments, and the North American populations gone extinct. (2) Samuel et al. (2003) suggested that there might be a simpler and hence more attractive explanation, namely long-distance dispersal directly to South America. DNA sequence evidence of Samuel et al. (2003) showed that two Old World sections (*Achyrophorus* and *Metabasis*) are closely related with the South American group. Based on karyotypic similarity of *H. maculata* and relatives of the Eurasian sect. *Achyrophorus* and the South American species (both possess two 18S–25S rDNA loci, and the intrachromosomal location of the single 5S rDNA locus is the same), Weiss-Schnee-weiss et al. (2003) presented a model of chromosomal changes during evolution from a *H. maculata*-like ancestor, i.e., *H. maculata* or *H. uniflora*, which share similar karyotypes, or their unknown/extinct relative, to the South American species. These detailed karyotypic analyses, including particularly the number and localization

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