

## The melding of systematics and biogeography through investigations at the populational level: examples from the genus *Hypochoeris* (Asteraceae)

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### Abstract

In recent years molecular data, especially from DNA, have provided more precise estimates of relationships among vascular plants. Different types of data have been used efficaciously at different levels of the taxonomic hierarchy from ordinal and familial classifications to genetic variation within populations. The impact on systematics has been enormous, often confirming previous hypotheses established through morphological or other data, but sometimes offering novel and surprising insights. Although it is far from clear which genes or intergenic regions will eventually be known to contain the most helpful phylogenetic information for general and special classification, it is abundantly clear that a genetic yardstick will be used routinely. The impact of molecular data on plant systematics is now having a similar import in biogeography. Sequence data, as well as DNA fingerprinting of various types, are now being employed to assess patterns of isolation and speciation, timing of changes of distributions and speciation events, routes of migration and/or dispersal, population-level divergence, and hybridization. Systematics and biogeography, therefore, are melding together more closely than ever before, because the same kinds of data can be used to address questions regarding evolutionary relationships as well as patterns of distribution in space and time. Data at the populational level are especially helpful in a multidisciplinary context for answering questions regarding infraspecific affinities and for explaining distributions resulting from recent historical and ecological factors. Examples from the genus *Hypochoeris* (Asteraceae) from southern South America, using DNA sequence and AFLP data, are used to illustrate these points. The genus appears to have originated in Eurasia, dispersed to South America during the past several million years, and radiated into more than 45 species that are adapted to many different ecological regimes.

In den letzten Jahren haben molekulare Daten, besonders DNA-Daten, präzisere Einblicke in die Verwandtschaftsbeziehungen zwischen Höheren Pflanzen ermöglicht. Unterschiedliche Datentypen wurden erfolgreich auf verschiedenen taxonomischen Rangstufen verwendet, von Ordnungs- und Familien-Klassifikationen bis hin zu genetischer Variation innerhalb von Populationen. Der Einfluss auf die Systematik war enorm, wobei frühere, von morphologischen oder anderen Daten abgeleitete Hypothesen oft bestätigt wurden, manchmal jedoch neue und überraschende Einblicke resultierten. Obwohl bei weitem noch nicht geklärt ist, welche DNA-Regionen den höchsten phylogenetischen

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Informationsgehalt für die Klassifikation von Gattungen und Arten enthalten, ist vollkommen klar, dass man in Zukunft einen genetischen Maßstab routinemäßig verwenden wird. Der Einfluss, den molekulare Daten bis jetzt auf die Pflanzensystematik ausgeübt haben, trägt nun in gleicher Weise zur Klärung biogeographischer Fragestellungen bei. So werden Sequenzdaten und verschiedene DNA Fingerprinting-Methoden dazu verwendet, Isolations- und Artbildungsmuster, Migrationsrouten, Verbreitung durch Pollen und Samen, Differenzierung von Populationen und Hybridisierung zu erforschen. Systematik und Biogeographie verschmelzen enger als je zuvor, weil dieselben Daten verwendet werden, um evolutionäre Verwandtschaftsverhältnisse und Verteilungsmuster in Raum und Zeit zu untersuchen. Daten auf dem Populationsniveau sind in einem multidisziplinären Zusammenhang besonders hilfreich, um zwischenartliche Verwandtschaftsverhältnisse zu untersuchen und Verteilungen zu erklären, die aus historischen und ökologischen Faktoren resultieren. Um diese Punkte zu illustrieren, verwenden wir DNA Sequenz- und AFLP-Daten anhand des Beispiels der Gattung *Hypochaeris* (Asteraceae) aus dem südlichen Südamerika. Es scheint, dass diese Gattung in Eurasien entstanden ist, innerhalb der letzten Millionen Jahre nach Südamerika vorgedrungen ist und dort eine Radiation in mehr als 45 Arten durchgemacht hat, die an viele verschiedene ökologische Nischen adaptiert sind.

**Key words:** AFLP – Compositae – DNA – *Hypochaeris* – phylogeny – South America – speciation

## Introduction

Plant systematics as a discipline has a long and independent history. Beginning with attempts by Theophrastus during classical Greek times to understand the plant world, through the age of the herbalists (1460–1660), to early classifiers such as Caesalpino, Bauhin, Ray, and Tournefort, and finally to Linnaeus in the mid 18<sup>th</sup> century, systematics has been a central focus of the botanical sciences (Morton 1981). Linnaeus provided encyclopedic assessments of different aspects of plant systematics (e.g., generic, specific, bibliographic, nomenclatural, biogeographic), creating a strong foundation for all future work (Stafleu 1971). Since that time, plant systematics has continued to develop actively and flourish.

Plant biogeography in a scientific sense had its origins with Alexander von Humboldt in the early decades of the 19<sup>th</sup> century (Humboldt & Bonpland 1807). Based on careful observations in the New World tropics, he clarified that the world was not covered throughout by the same types of plant associations known in Europe, and that the compositions of these associations related to abiotic factors of latitude, climate and substrate. Subsequent interest in biogeography in the 19<sup>th</sup> century focused heavily on explaining plant diversity through vegetation analyses and maps of regions, including the entire world (Brown & Lomolino 1998). Physiological and ecological interpretations of biogeographic patterns became more significant during the late 19<sup>th</sup> and early 20<sup>th</sup> centuries. Modern efforts focus largely on quantitative approaches to seeking phytogeographic patterns, having been influ-

enced by similar attempts from phenetic and cladistic schools in plant classification (e.g., Morrone & Crisci 1995).

Plant population biology has originated more recently than systematics or biogeography. Of obvious importance to its development have been concepts of plant populations, especially in an evolutionary context (e.g., Harper 1967, 1977). Emphasis on population genetics by Wright, Fisher, and Haldane in the early decades of the 20<sup>th</sup> century yielded a shift toward viewing populations as important, indeed essential, units of phytodiversity and the evolutionary process (Dobzhansky et al. 1977). Numerous aspects of populations are now being routinely examined including genetics, demography, migration, dispersal, pollination, etc. (e.g., Begon et al. 1996, Falinska 1998).

The modern convergence between plant systematics, biogeography and population biology was greatly stimulated by "The New Systematics" (Huxley 1940). This perspective emphasized that plant species must be treated as populational systems and not just museum types. This healthy outlook has had a beneficial and lasting impact on plant systematics by aiding more biological interpretations of patterns of variation and in studying the evolutionary process itself. More emphasis was placed on understanding infraspecific taxa. This same perspective has stimulated population-level multidisciplinary interest in biogeographic phenomena, population divergence, migration, or life-strategies.

New tools of analyzing relationships with more precise molecular methods have resulted in a stronger interdisciplinary melding between plant systematics and biogeography at the populational level. Molecular ap-

proaches in systematics began with comparisons among taxa based upon cpDNA restriction site data (Palmer 1987), followed by direct gene sequence comparisons as techniques became easier and more automated. Further developments have resulted in detailed measurements of genetic variation among individuals and between populations via overall genetic fingerprint techniques such as RAPDs and AFLPs (Bachmann 2001, Schaal & Leverich 2001). These techniques have now also been used in biogeography to more precisely assess relationships among areas and better understand population dynamics (Brown & Lomolino 1998, Avise 2000).

In our laboratory we have begun systematic and biogeographic studies on the genus *Hypochoeris* (Asteraceae, Lactuceae) to determine a predictive taxonomical sectional structure within the group, to help interpret broad intercontinental biogeographic patterns, and to suggest modes of speciation. The initial focus of these studies has been on molecular phylogenetic reconstructions. Results of these analyses have revealed a rapidly evolving complex of species in southern South America, which has led to more detailed investigations of patterns and processes of evolution and biogeography at the populational level. It is appropriate, therefore, to review briefly some of these results in *Hypochoeris* to indicate how questions of plant systematics and biogeography are now converging at the populational level, especially through use of molecular methods.

*Hypochoeris* contains approximately 60 species, of which ten are known from Europe (DeFilippis 1976), three from Asia, and more than 45 from South America (Bortiri 1999). Morphological differentiation among European species of the genus is great, reflected earlier by the recognition of several genera (Schultz-Bipontinus 1845), now relegated to sections (e.g., Hoffmann 1890). These taxa not only have morphological distinctions, but they also differ karyologically (Cerbah et al. 1995, 1998a, 1999). Recent ITS sequence studies emphasizing European taxa (Cerbah et al. 1998b) reinforce these morphological and cytological differentiations. The c. 45 species of *Hypochoeris* from South America have all been placed in sect. *Achyrophorus* along with the European *H. illyrica*, *H. maculata*, and *H. uniflora*. The picture, therefore, is for two major geographic clusters of the genus, one in Eurasia with few species showing large amounts of character differentiation, and another in South America with many species revealing smaller total amounts of diagnostic character variation. Further, a large ecological diversification exists among South American species of *Hypochoeris* (Bortiri 1999, pers. observ.). They differ in elevation, ranging from

the coastal seaside to dry grasslands, forests, and meadows, and into high-Andean habitats. Morphological infraspecific variability is high in these taxa, and unambiguous morphological distinction of closely related species pairs is not easy. Natural hybridization, however, does not appear to be common nor a complicating factor in obscuring species limits (pers. observ.). Cytological differentiation among species is also mostly lacking, with nearly all taxa  $2n = 8$  (except for a few tetraploids; Weiss et al. in press). These characteristics fulfil the requirements of adaptive radiation which is the rapid diversification of species into a wide variety of ecological niches (Schluter 2000). It occurs when a single ancestral species gives rise, through repeated episodes of speciation, to numerous kinds of descendants with different ecological tolerances.

## Phylogenetic systematics

Our initial interest in the systematics and biogeography of *Hypochoeris* has focused on determining phylogenetic relationships across the entire genus and on explaining origins of the intercontinental biogeographic pattern. Our technique of choice for these questions has been DNA sequence analysis. Internal transcribed spacers (ITS) of nuclear ribosomal DNA and chloroplast *trnL* intron and *matK* sequences were used to assess relationships among European and South American species of *Hypochoeris* and outgroups (R. Samuel et al., unpublished data) with ITS showing the most resolution. One of the most parsimonious trees with 456 steps (CI = 0.70, RI = 0.85) is shown in Fig. 1. The spacers ITS1 and ITS2 were included for the analyses, and no multiple rDNA repeat types were observed in the taxa analysed. Monophyly of South American *Hypochoeris* is strongly supported by both ITS (100% bootstrap support) as well as the joint matrix of ITS, *trnL* and *matK* data (not shown; bootstrap 100%). The European species lie basal to the South American taxa, suggesting that species in South America evolved from a single introduction to the continent from a Mediterranean or Macaronesian progenitor such as *H. oligocephala*, *H. cretensis* or the *H. maculata* group.

DNA sequence data support the assumption of adaptive radiation in South American *Hypochoeris* sect. *Achyrophorus*. Total sequence divergence within the South American taxa based on ITS data is 2%, suggesting short divergence times. Only weak resolution within this group is found (Fig. 1). This pattern of genetic variation would be expected with a single introduction of a European progenitor to the South American continent and a fast geographical, ecological, and/or morphological diversification (adaptive radiation) from this new colonist.



derstand sequences of isolation and speciation, (2) infraspecific phylogenies to elucidate the timing of changes in distributions or speciation events, and (3) patterns of genetic variation in colonizing and established populations in a volcanic habitat.

### Historical biogeography

#### Sequences of isolation and speciation

A modern approach to reconstructing biogeographic history is closely interrelated with phylogenetic and molecular systematics (Brown & Lomolino 1998), especially at the populational level. We used Amplified Fragment Length Polymorphism (AFLP) as a DNA fin-

gerprinting method to assess relationships among South American *Hypochaeris* (K. Tremetsberger et al., unpublished data). Three selective primer combinations yielded 241 total fragments in the range from 50 to 310 bp. Within South American taxa, two fragments out of 241 were monomorphic. This suggests that AFLP fragments are still homologous in closely related taxa and that the AFLP method should be useful for the assessment of phylogenetic relationships when sequence divergence is low (as is the case in *Hypochaeris*; see also Hodkinson et al. 2000, Hedrén et al. 2001, Koopman et al. 2001).

Diagnostic grouping among South American taxa, supported by bootstrap values, is obtained by analysis of AFLP fragments (Fig. 2). Two major groups can be

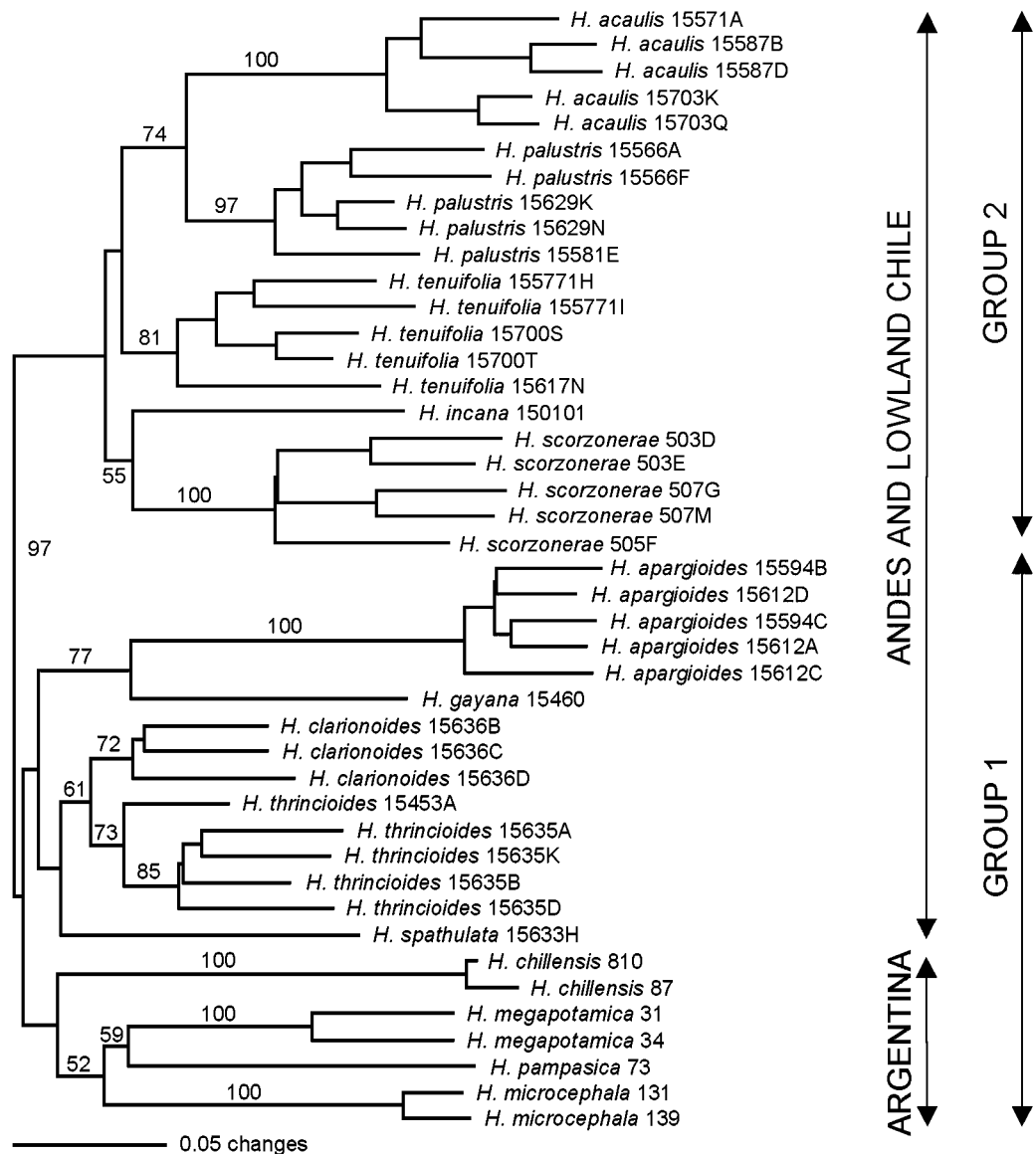


Fig. 2. Phylogram of South American species of *Hypochaeris* obtained from Neighbour Joining analysis of AFLPs. Numbers above branches are bootstrap values (only >50% shown). Numbers after taxon names refer to populations, and capital letters to individual plants. From K. Tremetsberger et al. (unpublished data).

distinguished (97% bootstrap support): (1) Group 1 comprises *H. apargioides*, *H. chillensis*, *H. clarionoides*, *H. gayana*, *H. megapotamica*, *H. microcephala*, *H. pampasica*, *H. spathulata*, and *H. thrincioides*. (2) Group 2 comprises *H. acaulis*, *H. incana*, *H. palustris*, *H. scorzonerae*, and *H. tenuifolia*. Within the two major groups, diagnostic units are obtained, but with less bootstrap support. Within Group 1, the Argentinian *H. megapotamica*, *H. pampasica* and *H. microcephala* form a group, although not well supported (52% bootstrap support). *Hypochaeris clarionoides* forms a group with *H. thrincioides*, and *H. apargioides* with *H. gayana*. Within Group 2, *H. acaulis* and *H. palustris* together form a group.

Although our present sample does not include all taxa of South America, the AFLP results are exciting because they show clear genetic partitioning of individuals into populations, which gives confidence regarding the interspecific relationships portrayed. Most significantly, subgroups within the two major groups correlate to a large degree with karyotypic differences (H. Weiss, personal communication), which gives phylogenetic underpinning for these clusters of species. Further, the Argentinian species of the lowland pampas fall into one clade (although not well supported; similar to results from ITS, Fig. 1, but in that case *H. pampasica* is the outlier). *Hypochaeris megapotamica*, *H. pampasica*, and *H. microcephala* occur together, with *H. chillensis* (also from lowland Argentina, despite the epithet) not far away. This geographic partitioning suggests that two centers of diversity have occurred in the evolution of the species of the Southern Cone, one centered in lowland Argentina (and perhaps also in adjacent Uruguay and southeastern Brazil) and the other in the high Andean habitats in Chile and Argentina. Development of more specific biogeographic hypotheses must await analysis of more taxa from these, and other, regions of South America. Most importantly, however, the AFLP data clearly provide excellent resolution on interspecific relationships within this rapidly evolving complex.

#### Timing of changes in distributions or speciation events

Two main factors have acted upon, and still are acting upon, the vegetation and speciation processes in southern South America: Pleistocene glaciations that were extensive in the Andean Cordillera, and volcanism that is also prominent in the entire Andean Cordillera. We will exemplify the effects of these factors with two case-studies at the populational level within *Hypochaeris*.

The region south of 42°S in South America was completely glaciated during the last full glacial

(25,000 to 14,000 years B.P.; Villagrán et al. 1995). In this region, the Andes were buried under the Patagonian ice field, but the Patagonian steppe east of the Andes and the southernmost part of the continent, Tierra del Fuego, stayed ice-free (Fig. 3). The Region de los Lagos (Lake District, between 42°S and 39°S) indicates locations of Pleistocene glacial basins and can be used to infer limits of the full glaciations. In central Chile, glaciations were more localized in the Andean Cordillera.

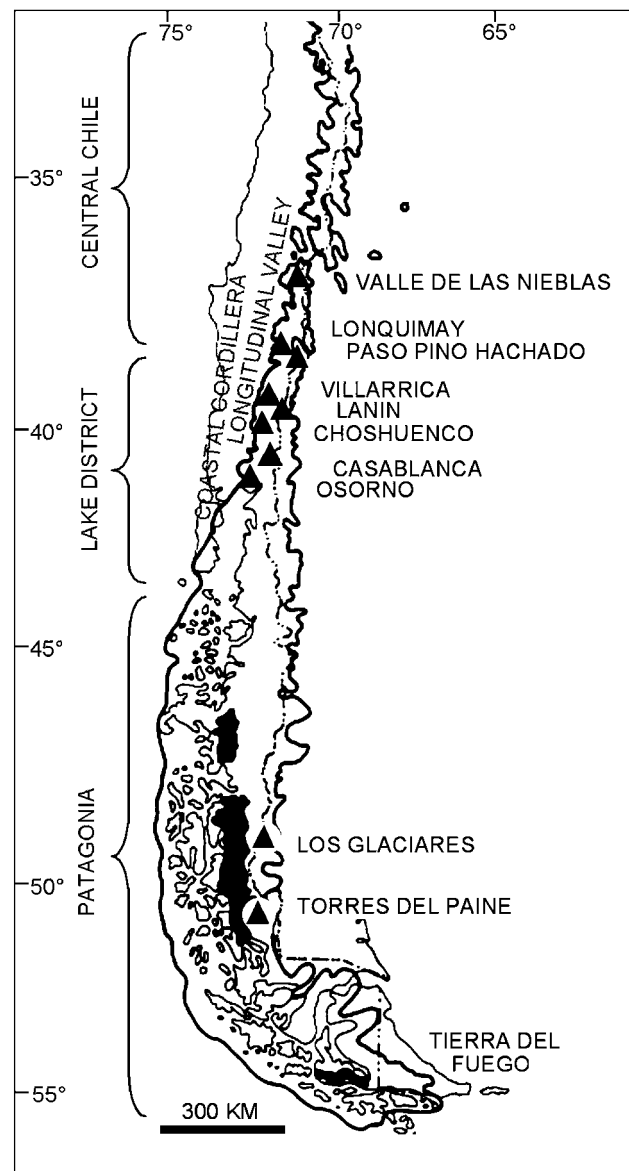


Fig. 3. Map of southern South America showing localities (triangles) of populational samples of *Hypochaeris palustris* within central Chile, the Lake District, and Patagonia. The black line encloses the extent of glaciers during the last full glacial (25,000 to 14,000 years B.P.); the black shading shows the extent of present glaciers. Modified from Villagrán et al. (1995).

During Quaternary glaciations, vegetation is hypothesized to have descended altitudinally and to have moved northwards (Vuilleumier 1971). Pleistocene refugia are hypothesized to have existed in the Longitudinal Valley and/or the Coastal Cordillera that parallel the main Andean Cordillera on its western side. Furthermore, there exist some indications of disjunct refugia in the southeasternmost portion of the continent (Tierra del Fuego; Villagrán et al. 1995).

Our general interest is on the impact that Pleistocene glaciations have had on ongoing speciation processes in the southern Andes. As specific example, we have undertaken a phylogeographic study of *Hypochaeris palustris* (A. Müllner et al., unpublished data), where we tested the hypothesis of isolation by distance versus deep gaps in the infraspecific phylogeny. We relied on the following expectations. Isolation by distance throughout the range of the species would result from migration of plants from a (single) Pleis-

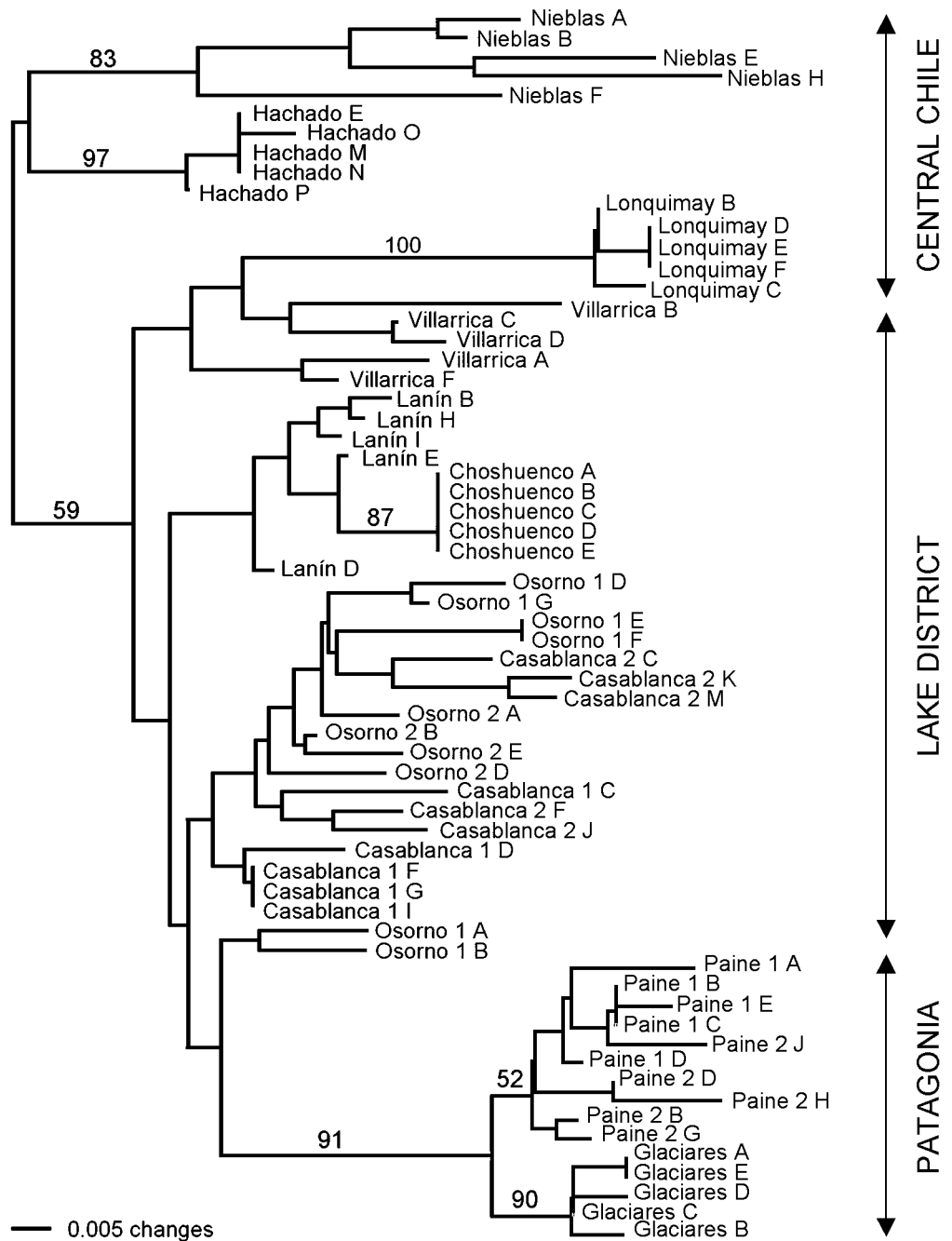


Fig. 4. Intraspecific phylogenetic tree of *Hypochaeris palustris* obtained from Neighbour Joining analysis based on AFLPs, showing bootstrap values (>50%). Numbers after localities refer to different populations, and capital letters to individual plants. From A. Müllner et al. (unpublished data).

tocene refugium to formerly glaciated regions, whereas a deep gap in the infraspecific phylogeny would result from a long-lasting separation in two separate (disjunct) refugia. Gene flow is expected to be low in *H. palustris* due to its predominantly inbreeding reproductive mode (H. Weiss, personal communication). Thus, contemporary gene flow is unlikely to have swamped historical genetic patterns in this species.

We assessed genetic variation with AFLP markers from populational samples of *H. palustris* from three regions (Fig. 3): (1) Patagonia, which was formerly completely glaciated (Los Glaciares and Torres del Paine); (2) the Lake District, which was also completely glaciated (Villarrica, Lanín, Choshuenco, Casablanca, and Osorno); and (3) central Chile, which was only locally glaciated (Valle de las Nieblas, Lonquimay, and Paso Pino Hachado). We analysed 135 fragments from three selective primer combinations in the range of 50 to 480 bp.

The Neighbour Joining analysis (Fig. 4) shows a strong distinction between Patagonia on the one hand, and the Lake District and central Chile on the other. Similarly, of 35.85% genetic variation (AMOVA) among the three geographic regions, 35.20% (i.e., almost the entire amount) is found when central Chile and the Lake District are combined to one group and compared to Patagonia (Table 1). This suggests a long-lasting separation between the two groups and perhaps a Pleistocene refugium in central Chile and a second, disjunct refugium, in high latitudes (Tierra del Fuego).

The occurrence of private alleles, i.e., fragments confined to one region only, can be used as an indicator of distinctiveness of regions (e.g., Avise 2000). Whereas Patagonia has eight private alleles, central Chile and the Lake District have four private alleles each. The presence of more Patagonian private alleles may suggest that a high-latitude disjunct refugium existed in Patagonia. Furthermore, only Patagonia has private alleles that are constant throughout all individuals analysed in that region (four) which strengthens the conclusion. When regions are combined, central

Chile and the Lake District together have eight private alleles, and the Lake District and Patagonia together have five. This shows that the Lake District region occupies an intermediate position between central Chile and Patagonia. Migration of plants from refugia in central Chile, from the Coastal Cordillera, the Longitudinal Valley, or unglaciated parts of the Andean Cordillera, therefore, may have contributed to the recolonization of the formerly completely glaciated Lake District as well as plants from high-latitude refugia.

To determine the level and timing of impact of glaciation upon species of *Hypochaeris* of the Southern Cone, we quantified the percentage of genetic variation found among the five closely related species, *H. acaulis*, *H. incana*, *H. palustris*, *H. scorzonerae*, and *H. tenuifolia* (Fig. 2). With 48.36% (AMOVA; based on 1 to 10 individuals from 1 to 3 populations from each species; 241 AFLP fragments from three selective primer combinations analysed), this value is higher than the value (35.85%) for infraspecific divisions among geographic regions in *H. palustris*. This suggests that in *H. palustris* the impact of separation in disjunct Pleistocene refugia was strong, but acted at the infraspecific level. Adaptive radiation in species of South American *Hypochaeris*, therefore, may be older than the last full glacial. The most recent (Wisconsin) glacial period may have affected plant evolution at the infraspecific rather than the interspecific level. Recent studies of patterns of diversification in North American terrestrial vertebrates (e.g., Brown & Lomolino 1998) are casting doubt on the old idea that many contemporary species formed as a result of isolation during the most recent glacial-interglacial cycles of the Pleistocene. The analysis of genetic variation within and between species, obviously, gives only a rough estimate of relative timing of changes in distributions or speciation events.

#### Colonization and migration

The analysis of postglacial migration routes is connected with the question of specific colonization and migration capabilities of particular species. These questions relate to metapopulation ecology and genetics where population turnover, i.e., local extinctions and colonizations, are used as hallmarks of true metapopulations (Hanski & Gilpin 1991, Hanski & Simberloff 1997). Colonization represents immigration into an empty habitat patch followed by successful establishment of a new population (Ims & Yoccoz 1997).

In this general context, therefore, we summarize investigations on colonization and migration of the high-Andean *Hypochaeris tenuifolia* (K. Tremetsberg-

**Table 1.** Analysis of molecular variance (AMOVA), based on AFLPs, carried out among three geographic regions defined within the total area of *Hypochaeris palustris* in Chile and Argentina and among combinations of these regions.

Source of variation	Degrees of freedom	Percentage of variation
Among central Chile/Lake District/Patagonia	2	35.85
Among Lake District + Patagonia/central Chile	1	24.38
Among central Chile + Lake District/Patagonia	1	35.20

er et al., unpublished data). This species is one of the first colonizers on dry, volcanic habitats. It is distributed on high volcanic peaks in Chile and Argentina (1750–2400 m) in the southern Andes. A new volcanic eruption occurred in 1988 on Volcán Lonquimay, Chile (Moreno & Gardeweg 1989, Rifo et al. 1989, Gallardo et al. 1995), which created a fresh volcanic ash area. Colonizing populations of *H. tenuifolia* on the fresh ash field created by the volcanic eruption, referred to as “pioneers”, were collected in 1999 and, therefore, were not older than 11 years at most. *Hypochaeris tenuifolia* is a long-lived, chasmogamous, rhizomatous perennial; the plants analysed, therefore, are assumed to be initial arrivals and not their offspring. The colonizer *H. tenuifolia* is well adapted to dispersal based on its long pappus bristles and tall flower scapes (30 cm). Numerous experimental studies have shown that members of Asteraceae have strong potential for long-distance dispersal via light fruits and attached bristles (Sheldon & Burrows 1973, Anderson 1993). The environment of *H. tenuifolia* also supports long-distance dispersal, with its high altitude and exposure to strong winds that exist on these volcanic peaks (Quintanilla 1983).

We assessed the genetic composition of individuals from the pioneer populations on the fresh ash field as well as from undisturbed populations from the same area, referred to as “survivors”, and from populations from other volcanoes. Recorded were 209 AFLP fragments from three selective primer combinations (50 to 480 bp). Pioneer populations do not have significantly different levels of within-populational genetic variation (measured by the Shannon diversity index;  $H_{Sh} = 0.224$ ) than survivor (0.192) or other populations throughout the range of the species (0.203). Genetic differentiation is lower between pioneer populations (measured by  $F_{ST}$  derived from Analysis of Molecular Variance (AMOVA), Schneider et al. 2000;  $F_{ST} = 0.100$ ) compared to survivors (0.244). These results meet expectations of theoretical models of population genetic consequences of extirpation and recolonization when the number of colonists is high and when colonists are drawn from different source populations (Wade & McCauley 1988). The case study on *H. tenuifolia* shows no founder effect (i.e., loss of genetic variation) during recolonization. In contrast to our study, increased genetic differentiation among pioneer populations compared to survivor populations was found in the outbreeding (dioecious) *Silene alba*, growing along roadsides in Giles County, Virginia (McCauley et al. 1995), and in *Silene dioica*, a component of early stages of primary succession on islands in northern Scandinavia (subject to land uplift so that new islands are continuously formed; Giles & Goudet

1997). These observations are compatible with theoretical expectations of the Wade & McCauley model, in which few colonists originate from only a few populations. Differences of genetic structure in the two generic systems may relate to dispersal ability. Fruits of *H. tenuifolia*, equipped with a well-developed pappus, may disperse and establish much more easily than seeds of *S. alba* and *S. dioica*, which lack such efficient particular dispersal mechanisms.

## Conclusions

It is evident, therefore, that AFLP data are extremely helpful in approaching systematic and biogeographic questions in the South American species of *Hypochaeris*. These data are sensitive to populational as well as inter- and intraspecific genetic patterns and can be used to infer closely related species complexes, likely sites of glacial refugia, and patterns of genetic variation in pioneer populations. They provide a good example of the melding of systematics and biogeography at the populational level through the use of new molecular markers.

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