

# REPEAT INTERCONTINENTAL DISPERSAL AND PLEISTOCENE SPECIATION IN DISJUNCT MEDITERRANEAN AND DESERT *SENECIO* (ASTERACEAE)<sup>1</sup>

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To explore the biogeographic history of Mediterranean/arid plant disjunctions, Old and New World *Senecio* sect. *Senecio* were analyzed phylogenetically using nuclear ribosomal DNA sequences (ITS). A clade corresponding to sect. *Senecio* was strongly supported. Area optimization indicated this clade to be of southern African origin. The Mediterranean and southern African floras were not distinguishable as sources of the main New World lineage, estimated to have become established during the middle Pliocene. Another previously suspected recent dispersal to the New World from the Mediterranean was confirmed for the recently recognized disjunction in *S. mohavensis*. The loss of suitable land connections by the Miocene means that both New World lineages must represent long-distance dispersal, providing the first evidence of repeat intercontinental dispersal in a Mediterranean group. In contrast, migration within Africa may have utilized an East African arid corridor. Recent dispersal to northern Africa is supported for *S. flavus*, which formed part of a distinct southern African lineage. Novel pappus modifications in both disjunct species may have enabled dispersal by birds. An estimated early Pliocene origin of sect. *Senecio* coincides with the appearance of summer-dry climate. However, diversification from 1.6 BP highlights the importance of Pleistocene climate fluctuations for speciation.

**Key words:** Asteraceae; biogeography; Compositae; ITS; Mediterranean flora; molecular clock; phylogeny; plant disjunction; *Senecio*.

The five Mediterranean floras (central Chile, southwest North America, southwest Australia, southern Africa, and the Mediterranean basin) are associated with a characteristic summer-dry climate and high species diversity and endemism (Raven, 1971). Southern Africa displays exceptional diversity, with endemics comprising ~80% of the species and 29% of the genera (Goldblatt, 1978). Across all five floras, at least 40% of species and perhaps 10% of genera are estimated to be endemic (Raven, 1971). These floras are thought to have evolved from a combination of tropical and temperate ancestors in isolation of each other in response to a drying trend throughout the Tertiary (Raven, 1971; Axelrod and Raven, 1978; Quézel, 1978; Raven and Axelrod, 1978). The development of summer-dry conditions, largely since the beginning of the Pliocene (5.2 BP), is thought to have been of central importance (Raven, 1971; Axelrod, 1975, 1977; Spect, 1979). Summer-dry conditions combined with climate fluctuations during the Pleistocene probably eliminated Tertiary mesophytic taxa, allowing the emergence of modern Mediterranean floras. Here we define “Mediterranean” broadly to include adjacent arid areas.

The biogeographic history of plant taxa disjunct between Mediterranean regions is complex and incompletely understood (Thulin, 1994; Fritsch, 1996, 2001; Liston, 1997; Cau-

japé-Castells et al., 2001; Hileman et al., 2001). The possibility of arid corridors connecting Mediterranean regions has been rejected by some (Raven, 1971, 1973) because global ocean and air circulation patterns restrict Mediterranean climates to the tropical/temperate boundary between 30° to 40° north and south of the equator at the western margin of continents. In addition, the post-Tertiary origin of these floras means that ecologically suitable land bridges between the Old and New World are absent (Tiffney and Manchester, 2001), and so long-distance dispersal has been invoked to explain Mediterranean disjuncts (Raven, 1971, 1973; Thorne, 1972).

Nevertheless, continuous arid habitat links have been suggested between southwest and northeast Africa, through the mountains of East Africa, based on animal and plant disjunctions (Balinsky, 1962; Verdcourt, 1969; Jurgens, 1997). Balinsky (1962) called this the “arid track,” which is thought to have reached its greatest development during glacial periods of the Pleistocene (Verdcourt, 1969; van Zinderen Bakker, 1975; Goldblatt, 1978). Support for this comes from the many plant species and genera disjunct between southern and northern Africa (Verdcourt, 1969; de Winter, 1971; Thulin, 1994; Jurgens, 1997), some of which occur within the arid track (e.g., *Androcymbium* [Colchicaceae], *Cephalaria* [Dipsacaceae], *Erica* [Ericaceae], *Gladiolus* [Iridaceae], *Lotonotis* [Fabaceae], *Olea* [Oleaceae], and *Scabiosa* sect. *Scabiosa* [Dipsacaceae]). In addition, a three-way disjunction involving the New World is also seen in a few taxa (Thulin, 1994) (e.g., *Fagonia* [Zygophyllaceae], *Oligomeris* [Resedaceae], *Parkinsonia* [Fabaceae], and *Thamnosma* [Rutaceae]).

Stebbins and Day (1967) have postulated a link between the Mediterranean basin and southwest North America via arid pockets in the Bering Strait land bridge (between eastern Asia

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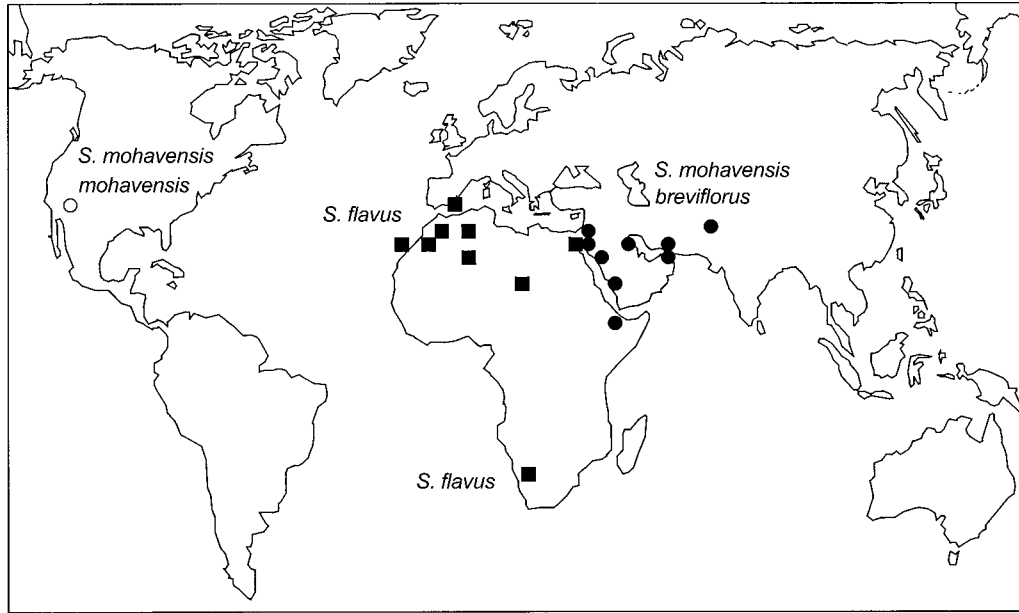


Fig. 1. Disjunction at the species level in *Senecio flavus* and *S. mohavensis*.

and western North America) during the early Miocene (~20 BP). This is controversial in relation to Mediterranean taxa because it considerably predates the emergence of summer-dry conditions (Raven, 1971; Axelrod, 1975; Spect, 1979; Suc, 1984). In addition, it is thought that by the later Tertiary this land bridge was restricted to cool-tolerant and deciduous taxa and ultimately boreal taxa (Tiffney and Manchester, 2001). Axelrod (1973, 1975) has proposed that a generalist dry-adapted flora—the “Madrean–Tethyan” flora—formed a nearly continuous belt of sclerophyllous vegetation from North America to central Asia from the late Eocene to the end of the Oligocene (38–25 BP). Subsequent climatic cooling and continued continental drift fragmented this flora, which may have represented an important source of xerophytic taxa that later adapted to summer-dry conditions in the Northern Hemisphere. However, the Madrean–Tethyan hypothesis is not universally accepted, and convergence from mesophytic ancestors has been suggested to explain the distribution patterns (Wolfe, 1975).

To further explore the biogeographic history of Mediterranean disjunctions we have focused a molecular phylogenetic approach on *Senecio* sect. *Senecio*. The section contains a group of predominantly annual plants associated with Mediterranean climate in southern Africa, the Mediterranean basin, and southwest North America. *Senecio* is also represented in South America and Australia, but few taxa appear on morphological grounds to be likely members of sect. *Senecio*. This group provides a useful comparison with other studies that have examined Mediterranean disjunction (Fritsch, 1996, 2001; Caujapé-Castells et al., 2001; Hileman et al., 2001) because, unlike taxa already examined, *Senecio* sect. *Senecio* appears to be adapted to long-distance dispersal via its wind-blown pappose fruits (Small, 1919).

Sampling sect. *Senecio* is complicated by considerable taxonomic uncertainty. With ~1250 species, *Senecio* is among the largest genera of angiosperms. Generic and sectional limits are poorly circumscribed (Jeffrey et al., 1977; Jeffrey, 1979; Vincent and Getliffe, 1992) and monophyly of the genus has

not generally been supported in cladistic analyses (Kadereit and Jeffrey, 1996; Pelter et al., 2002).

We have chosen to focus on two particularly striking disjunctions at the species level. *Senecio flavus* is disjunct between Namibia and the Mediterranean basin/northern Africa, while *S. mohavensis* is disjunct between southwest North America and southwest Asia (Fig. 1). The disjunction of *S. mohavensis*, although only recently accepted at the species level (see Coleman et al., 2001), has previously been hypothesized to be of recent origin based on high isozyme similarity of the disjunct taxa (Liston et al., 1989). In addition, evidence from nuclear ribosomal (nr) DNA and chloroplast (cp) DNA (Liston and Kadereit, 1995; Comes and Abbott, 2001) has indicated that *S. mohavensis* is a hybrid derivative of *S. flavus* and a second species, possibly *S. glaucus* subsp. *coronopifolius*, which is a member of a widespread Mediterranean diploid species complex. In *S. mohavensis* two subspecies are now recognized: the type subspecies in southwest North America and the new combination *S. mohavensis* subsp. *breviflorus* in southwest Asia (Coleman et al., 2001). Although some Old World–New World disjunctions appear to result from accidental human introduction (Bassett and Baum, 1969; Raven, 1971; Raven and Axelrod, 1978), morphological differences between the subspecies and reduced fertility in  $F_1$  hybrids indicate that this is not the case in *S. mohavensis* (Coleman et al., 2001).

Following the most recent global taxonomic assessment of *Senecio* (Jeffrey, 1992), three subgroups may be distinguishable within sect. *Senecio*: a “basal austral subgroup,” a “boreal subgroup,” and an “australasian subgroup.” As the australasian subgroup is peripheral to establishing the cause of the two species disjunctions in sect. *Senecio* we have not sampled this group. Instead, we have focused on the other two subgroups, sampling primarily from southern Africa, southwest North America, and the Mediterranean basin.

Phylogenies of Mediterranean taxa also have potential for examining the causes of the high species diversity so characteristic of Mediterranean floras. Enhanced rates of speciation have frequently been linked to the intensification of summer-

dry conditions since the Pliocene (Axelrod, 1977; Axelrod and Raven, 1978; Raven and Axelrod, 1978; Goldblatt, 1978; Suc, 1984). Other suggested causes of diversification include Pleistocene climatic fluctuations, varied and generally poor soils, increasing topographic complexity from mountain formation (Axelrod and Raven, 1978; Goldblatt, 1978; Quézel, 1978; Raven and Axelrod, 1978), pollinator shifts (Johnson, 1995), and alterations to mating system (Thompson, 1999). The few studies of Mediterranean plant groups that have dated diversifications have provided varied results. Pliocene and Pleistocene diversification has been supported in Californian Polemoniaceae (Bell and Patterson, 2000) and southern African *Phyllica* (Rhamnaceae) (Richardson et al., 2001b). In contrast, diversification spread across much of the Tertiary has been supported in northern and southern African *Androcymbium* (Colchicaceae) (Caujapé-Castells et al., 2001), while Pleistocene speciation has been indicated in *Senecio* sect. *Senecio* from the Mediterranean basin (Comes and Abbott, 2001).

The aim of this study was to estimate a phylogeny from a representative sample of *Senecio* sect. *Senecio* using sequence data from the internal transcribed spacers (ITS) of nr DNA. The phylogenetic trees were then used to explore (1) the direction and timing of sectional and species disjunction and (2) the timing of diversification of the group. Where possible, pappus morphology was examined to ascertain the distribution of characters such as barbs and hooks, which may be associated with animal dispersal of *Senecio* achenes (fruits).

## MATERIALS AND METHODS

**Plant material**—Leaf material for ITS sequence analysis was obtained from cultivated material and herbarium specimens (see Appendix, available as Supplementary Data accompanying the online version of this article). In addition, seven preexisting sequences were obtained from GenBank (accession nos. AJ400803, AJ400807, AJ400810, AJ400813, AF459943, AF459965, and AF459968). Sampling was focused on southern Africa, the Mediterranean basin, and North America, reflecting the “basal austral” and “boreal” subgroups of Jeffrey (1992). Sampling was necessarily incomplete because of the large size and unclear limits of the section. Single representatives of three other genera in the tribe Senecioneae were included in the ingroup. *Erechtites* and *Crassocephalum* were included as allied genera from the New and Old World, respectively, while the monotypic South African genus *Stilpnogyne* was included because it shares unusual morphological characteristics (petiole leaves and disciform capitula) with *S. flavus*. The predominantly southern African genus *Euryops* was selected as outgroup based upon a cladistic analysis of morphological characters in Senecioneae (Bremer, 1994).

**DNA extraction and sequencing**—Total genomic DNA was isolated using a modified hexadecyltrimethylammonium bromide (CTAB) protocol (Doyle and Doyle, 1990). The entire ITS1–5.8S–ITS2 region was polymerase chain reaction (PCR) amplified using primers ITS4 and ITS5 (White et al., 1990). Reactions were carried out in 25  $\mu$ L volumes containing 1 unit *Taq* polymerase (Bioline, London, UK), 10% volume Biotaq buffer (Bioline, London, UK) [160 mmol/L (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub>, 670 mmol/L Tris-HCl, 0.1% Tween-20], 2 mmol/L MgCl<sub>2</sub>, 0.1 mmol/L dNTPs, 0.2 mmol/L of each primer and approximately 5 ng of template DNA. Denaturation at 94°C for 3 min was followed by a thermal cycle of 1 min denaturation, 94°C; 1 min annealing, 55°C; 1.5 min extension, 72°C; 35 cycles. A final extension step of 4 min at 72°C was carried out. The PCR products were cleaned using Wizard PCR Preps (Promega UK, Southampton, UK) with the specified protocol. Both ITS strands were cycle sequenced using the amplification primers and BigDye (Applied Biosystems, Warrington, UK) with the specified protocol. Denaturation at 94°C for 30 s was followed by a thermal cycle of 10 s denaturation, 96°C; 5 s annealing, 50°C; 4 min extension, 60°C; 30 cycles. Unincorporated dye

terminators were removed using DyeEx Spin Kits (Qiagen, Crawley, UK) with the specified protocol.

Because of the putative hybrid origin of the tetraploid ( $2n = 40$ ) *S. mohavensis* involving progenitors with widely divergent ITS sequences (Comes and Abbott, 2001), cloning of ITS was carried out for this species. The internal transcribed spacer region was cloned using the pGEM-T Easy Vector (Promega UK) with the specified protocol, followed by DNA extraction and purification using Plasmid Midi Kits (Qiagen) with the specified protocol.

Sequences were obtained on an ABI PRISM 377 automated sequencer (Perkin-Elmer, Foster City, California, USA). Forward and reverse sequences were manually assembled using the computer program Chromas version 2.12 (Technelysium, Helensvale, Australia). Alignment was carried out manually using the computer program GeneDoc (Nicholas et al., 1997). Boundaries of the two ITS regions were determined by comparison with published *Senecio* sequences (Bain and Golden, 2000). Aligned sequences are available on request from the corresponding author.

**Phylogenetic analysis**—Phylogenetic analyses were conducted on the combined ITS1 and ITS2 regions (excluding the 5.8S gene) using PAUP\* version 4.0b8 (Swofford, 1998). Maximum-parsimony (MP) analysis was performed with TBR, MULTREES, and COLLAPSE (max) options in effect. The MP trees were generated by Fitch parsimony with a heuristic search that used 500 replicates of random sequence addition. Gaps (insertions/deletions [indels]) were treated as missing data. Confidence in tree topologies was assessed using bootstrap analysis (Felsenstein, 1985) of 1000 replicates with the same settings as used in the searches, but with closest taxon addition. Maximum-likelihood (ML) analysis was performed using parameter estimates for ML obtained by a hierarchical likelihood ratio testing approach using the program MODELTEST version 3.06 (Posada and Crandall, 1998). The substitution model selected, both for the full data set and a subset, was TrN +  $\Gamma$ . This uses a general time-reversible model and gamma-distributed ( $\Gamma$ ) among-site rate variation. Heuristic searches were carried out with TBR, MULTREES, and COLLAPSE options in effect.

The hypothesis of clock-like evolution was tested using the likelihood ratio test (Goldman, 1993). Support for alternative hypothesized topologies was assessed by nonparametric Templeton tests (Templeton, 1983).

## RESULTS

**Sequence analysis**—The total length of aligned ITS1 and ITS2 sequences was 494 base pairs (bp) (ITS1, 263 bp; ITS2, 231 bp), which comprised 263 (53.2%) constant characters and 134 (27.1%) variable and parsimony-informative characters. Sequence divergence (measured as uncorrected *p* distance) ranged from 0.0% (e.g., *S. mohavensis* subsp. *mohavensis*–*S. mohavensis* subsp. *breviflorus*) to 18.8% (*Crassocephalum crepidioides*–*S. californicus*) between ingroup taxa and from 14.8% (*S. flavus*–*Euryops acraeus*) to 20.6% (*Crassocephalum crepidioides*–*Euryops acraeus*) between ingroup and outgroup taxa. The TrN +  $\Gamma$  model of substitution under ML gave a transition/transversion ratio of 1.86 across the whole matrix.

**Phylogenetic analysis of ITS sequences**—Fitch parsimony resulted in eight minimum-length trees of 427 steps, with a consistency index (CI) of 0.58 (excluding uninformative characters) and a retention index (RI) of 0.80 (Fig. 2). The single ML tree ( $-\ln = 2929.69$ , not shown) was identical in topology to the MP tree in Fig. 2. Four distinct lineages were resolved. Bootstrap (BS) support was maximal (100%) for three of these and lacking (<50%) for the fourth. Most species thought to represent sect. *Senecio* were placed in the “Groundsel clade” (BS 100%) (Fig. 2). This clade was divided into five subclades—I (BS 82%); North American taxa except *S. brasiliensis* (South American); II (BS 92%); southern African taxa except *S. malacitanus* (Mediterranean); III (BS 78%);

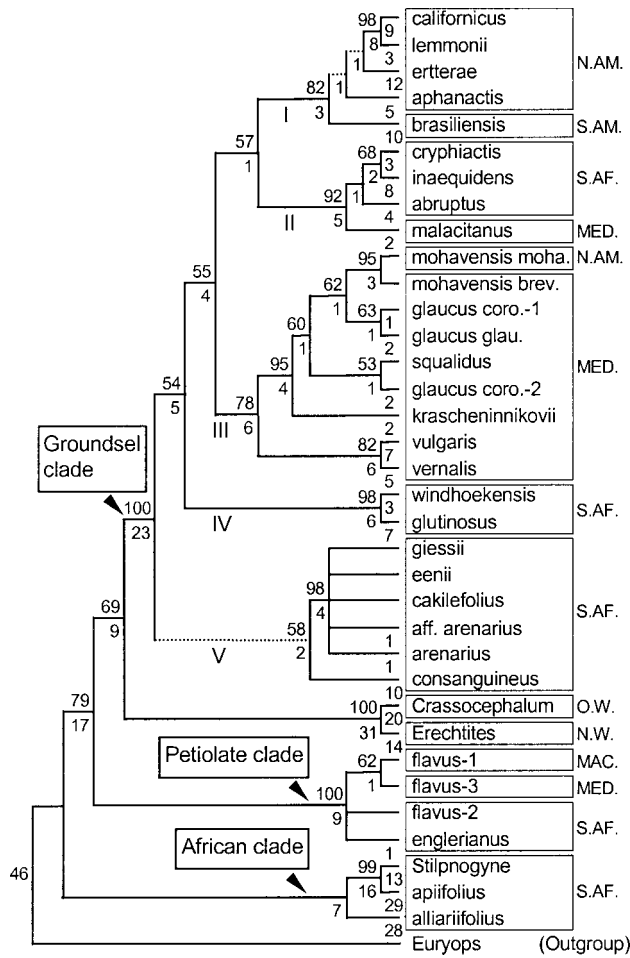


Fig. 2. One of eight maximum-parsimony (MP) ITS trees found for *Senecio* sect. *Senecio* (427 steps; CI = 0.58; RI = 0.80). Tree branch values are number of nucleotide substitutions (below) and bootstrap values from 1000 replicates (above). Dotted lines indicate the three branches that collapse in the strict consensus tree. Roman numerals identify subclades within the Groundsel clade. Area abbreviations: N.A.M., North America; S.A.M., South America; S.A.F., southern Africa; MED., Mediterranean basin; MAC., Macaronesia; O.W., Old World; N.W., New World. Maximum-likelihood (ML) analyses produced a single tree of identical topology.

Mediterranean taxa except *S. mohavensis* subsp. *mohavensis* (North American); and IV and V (BS 98% and 58%): southern African taxa. Subclade V was sister to the remainder of the Groundsel clade. Relationships among the five subclades were poorly supported (<60%). *Senecio flavus*, previously considered part of sect. *Senecio* (Alexander, 1979), was isolated from the Groundsel clade by a well-supported clade (BS 100%) composed of the Old World *Crassocephalum* and the New World *Erechtites*. A strongly supported (BS 100%) clade called the “Petiolate clade” (Fig. 2) was composed of two petiolate-leaved species, *S. flavus* and *S. englerianus*. *Stilpnogyne* also has petiolate leaves, but no link to the Petiolate clade was found. This leaf characteristic was not represented in the Groundsel clade. Finally, sister to the rest of the ingroup was an unsupported clade composed of *S. apiifolius*, *S. alliariifolius*, and *Stilpnogyne bellidioides* called the “African clade” (Fig. 2).

The failure of *Senecio* to form a monophyletic group was supported by a significant increase in tree length of 16 steps

TABLE 1. Estimated age (BP) and standard deviation (SD) of nodes in a maximum-likelihood (ML) clock-constrained ITS tree found for *Senecio* sect. *Senecio* (see Fig. 3). Age estimates are based on two published rates of ITS substitution— $7.83 \times 10^{-9}$  (Sang et al., 1995) and  $6.06 \times 10^{-9}$  (Sang et al., 1994)—and their average.

Node	TrN + $\Gamma$ (distance to tip $\pm$ SD)	Fast clock (BP $\pm$ SD)	Slow clock (BP $\pm$ SD)	Average clock (BP $\pm$ SD)
A	0.03633 $\pm$ 0.0084	4.64 $\pm$ 1.07	6.00 $\pm$ 1.39	5.23 $\pm$ 1.21
B	0.02987 $\pm$ 0.0077	3.81 $\pm$ 0.98	4.93 $\pm$ 1.27	4.30 $\pm$ 1.11
C	0.02259 $\pm$ 0.0067	2.89 $\pm$ 0.86	3.73 $\pm$ 1.11	3.25 $\pm$ 0.96
D	0.01160 $\pm$ 0.0048	1.48 $\pm$ 0.61	1.91 $\pm$ 0.79	1.67 $\pm$ 0.69
E	0.00712 $\pm$ 0.0038	0.91 $\pm$ 0.49	1.17 $\pm$ 0.63	1.02 $\pm$ 0.55
F	0.00165 $\pm$ 0.0018	0.21 $\pm$ 0.23	0.27 $\pm$ 0.30	0.24 $\pm$ 0.26
G	0.00106 $\pm$ 0.0015	0.14 $\pm$ 0.19	0.17 $\pm$ 0.25	0.15 $\pm$ 0.22

when monophyly was enforced ( $Z = -2.51$ ,  $P < 0.05$ , Templeton test). In contrast, a nonsignificant increase in tree length of four steps was found on enforcing the Petiolate clade as sister to the Groundsel clade ( $Z = -0.90$ ,  $P = 0.37$ , Templeton test), indicating that a sister relationship to the Groundsel clade cannot be excluded. Enforcing the monophyly of the southern African members of the Groundsel clade (subclades II, IV, and V, Fig. 2) produced a nonsignificant increase of seven steps ( $Z = -1.36$ ,  $P = 0.17$ , Templeton test).

**Rate constant evolution**—The number of taxa in the full data set meant that clock-constrained ML searches did not run to completion. Consequently, a clock-constrained ML score was estimated from the unconstrained ML tree using the lscores option in PAUP\*. Using the likelihood ratio test, the assumption of a molecular clock was strongly rejected for the complete data set [ $-\ln L = 2(2969.12 - 2929.69) = 78.86$ ,  $df = 34$ ,  $P < 0.001$ ]. The Groundsel clade was also tested for clock-like evolution using *S. flavus* as outgroup. The smaller size of this data set meant that completion of clock-constrained ML heuristic searches was possible. The likelihood ratio test failed to reject a molecular clock in this reduced data set [ $-\ln L = 2(1859.51 - 1842.22) = 34.58$ ,  $df = 26$ ,  $P > 0.05$ ]. Using MP with the reduced data set generated two minimum-length trees of 204 steps, a consistency index of 0.67 and a retention index of 0.83 (not shown).

In the absence of a reliable fossil record or dated geological events, the molecular clock in the Groundsel clade was calibrated using two ITS divergence rates from other Asteraceae (Sang et al., 1994, 1995). The relatively fast rate of  $7.83 \times 10^{-9}$  substitutions per site per year, estimated for *Robinsonia* from the Juan Fernández Islands (Sang et al., 1995), was used to give a “fast clock.” A “slow clock” was calibrated using a rate of  $6.06 \times 10^{-9}$  substitutions per site per year estimated for *Dendroseris* (Sang et al., 1994), also from the Juan Fernández Islands. Calibrating the molecular clock in this way is not ideal, but both of the calibration rates used fall within the range of published ITS substitution rates (Richardson et al., 2001a). *Robinsonia*, like *Senecio*, is in tribe Senecioneae, while *Dendroseris* is in Lactuceae. Consequently, the *Robinsonia* rate may be more appropriate for calibrating a clock in *Senecio*. In addition to using both rates separately (Table 1), an average of the two was used to locate the boundaries of the Pliocene on the clock-constrained tree (Fig. 3). Because nucleotide substitution is not normally distributed, standard deviations (SDs) rather than confidence intervals are reported following the approach of Renner and Meyer (2001) (Table

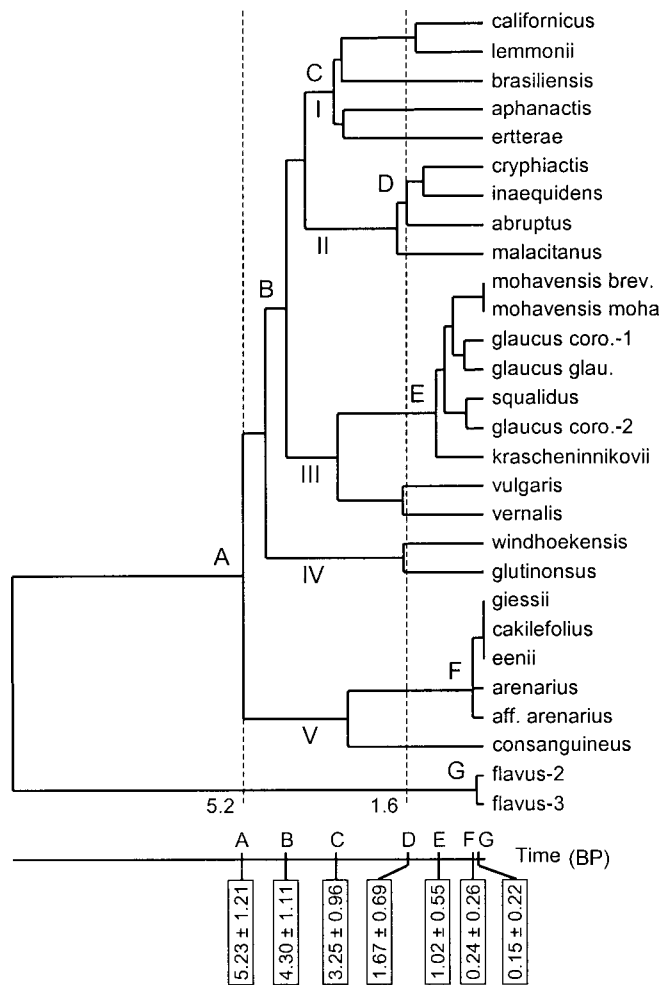


Fig. 3. Maximum-likelihood (ML) clock-constrained ITS tree found for *Senecio* sect. *Senecio* under the TrN +  $\Gamma$  model of substitution ( $-\ln L = 1859.51$ ). Dashed lines mark the limits of the Pliocene as defined by calibration using an average of two published rates of ITS divergence in other Asteraceae (see Results: Rate Constant Evolution). Letters identify dated nodes (see Table 1) and roman numerals identify subclades within the Groundsel clade.

1). All dates quoted in the discussion are based on the average rate (Table 1).

## DISCUSSION

**Ancestral area of the Groundsel clade**—Diverse criteria have been proposed for inferring the geographical origin of a taxon. Among the more useful is the location of the most ancestral forms (Platnick, 1981). A well-supported and appropriately polarized phylogeny provides an objective means of identifying ancestral and derived taxa. Both MP and ML phylogenies suggest a southern African origin of the Groundsel clade. Within this clade, both basal subclades (IV and V, Fig. 2) are exclusively southern African. However, a New World origin should also be considered because the North American *Erechtites hieraciifolius* is part of the sister group to the Groundsel clade (Fig. 2). New World biogeographic links in the Senecioneae have also been indicated for the Macaronesian *Pericallis* (Kadereit and Jeffrey, 1996; Panero et al., 1999) and the Eurasian *Senecio* sect. *Jacobaea* (Pelser et al., 2002).

Manual area optimization under forward and reverse Camin-Sokal parsimony (Bremer, 1992), using the topology of Fig. 2, also identified southern Africa as the ancestral area of the Groundsel clade. This result was further supported by area optimization under PAUP\* using both ACCTRAN and DELTRAN options. In addition, a New World origin seems unlikely based upon the known distribution of sect. *Senecio*. The section is not diverse in North America and may only be represented in South America by *S. brasiliensis*. In contrast, southern Africa is a known center of diversity for *Senecio* (Nordenstam, 1977; Bremer, 1994) and is probably the area of greatest diversity for sect. *Senecio*. Consequently, a southern African ancestral area appears to be most likely, although high diversity by itself does not provide evidence for an ancestral area because of the confounding effects of differential extinction/speciation rates.

**Species disjunction**—Vicariance involves a taxon of formerly wide distribution becoming split by a barrier to migration (Nelson and Platnick, 1981). This needs to be distinguished from long-distance dispersal if the causes of disjunction are to be understood. Phylogenetic trees can be used to evaluate dispersalist and vicariance hypotheses. Vicariance may be inferred by large phylogenetic gaps associated with stable biogeographic barriers. This pattern has been termed “Deep history” (Riddle, 1996). Here, isolation over long periods of time results in geographically distinct clades separated by long branches. In contrast, single or repeated long-distance dispersal events across a barrier will disrupt this pattern leading to a situation in which monophyletic groups contain members on either side of a geographical barrier.

*Senecio mohavensis* subsp. *mohavensis* is the only North American member of the otherwise Mediterranean subclade III. The lineages leading to the North American subclade I and Mediterranean subclade III separated  $4.30 \pm 1.11$  BP (Fig. 3, Table 1). The large phylogenetic gap between *S. mohavensis* subsp. *mohavensis* and the other North American species and its derived position within subclade III indicate dispersal from southwest Asia to North America. The absence of variation in ITS sequence between the disjunct subspecies of *S. mohavensis* provides an estimated divergence during the last 0.15 million years. This confirms the hypothesized recent origin and direction of this disjunction (Liston et al., 1989; Liston and Kadereit, 1995), although it does not limit the disjunction to the Holocene as previously suggested. As no case exists for an arid corridor linking Eurasia with North America during the Quaternary, this disjunction must be the result of long-distance dispersal.

*Senecio flavus* is disjunct between the Mediterranean basin and southern Africa. A southern African origin may be inferred from the restriction of *S. englerianus*, the only other member of the Petiolate clade (Fig. 2), to Namibia. The single nucleotide difference between Mediterranean and southern African *S. flavus* provides an estimated divergence time of  $0.15 \pm 0.22$  BP (Fig. 3, Table 1), consistent with Pleistocene migration along the arid track as previously suggested (Liston et al., 1989; Liston and Kadereit, 1995). However, consideration also needs to be given to the possibility of long-distance dispersal by birds because our examination of pappus morphology has revealed novel characteristics suggestive of epizoochory (adhesive animal dispersal).

As an aside, these results are consistent with the putative hybrid origin of *S. mohavensis* in the Mediterranean basin

(Liston and Kadereit, 1995; Comes and Abbott, 2001). The dispersal of *S. flavus* from southern Africa to the Mediterranean predates the dispersal of *S. mohavensis* to the New World, thereby providing time for the hypothesized hybridization to occur. Failure to recover a *S. flavus*-like ITS sequence from cloned *S. mohavensis* sequences indicates that interlocus concerted evolution has homogenized ITS repeats in the direction of the Mediterranean parent (see Wendel et al., 1995).

**Sectional disjunction**—Although the limits of sect. *Senecio* are unclear, the Groundsel clade represents a part of the section because it includes the type species *S. vulgaris*. Establishing the biogeographic history of disjunction between the five subclades of the Groundsel clade is complicated by poor resolution within subclades I and II. The position of *Senecio brasiliensis* (South America) and *S. malacitanus* (Mediterranean basin), within subclades I and II, respectively, is uncertain because both subclades exhibit little internal support (Fig. 2). Consequently, it is not possible to determine whether these taxa are ancestral or derived within their subclades. With regard to *S. malacitanus*, two possibilities exist. Assuming an ancestral position, the southern African sister taxa represent a return to the south (subclade II, Fig. 2). This would also mean that an earlier dispersal to the New World, which established subclade I (Fig. 2), occurred from the Mediterranean basin. Alternatively, a derived position for *S. malacitanus* would mean that dispersal to North America occurred directly from southern Africa, and that the Mediterranean basin was reached twice by distinct southern African lineages. Similarly, an ancestral position for *S. brasiliensis* would mean colonization of North America via an intermediary step to South America, while a derived position would suggest southward expansion from North America (subclade I, Fig. 2). Further sampling is required to clarify these questions.

Despite these uncertainties, the timing of dispersal events does allow conclusions to be drawn on the likely causes of sectional disjunction. Each of the five lineages was established before the middle Pliocene (Fig. 3, Table 1). Dispersal from the Old World to the New World occurred before  $3.25 \pm 0.96$  BP (node C, Fig. 3, Table 1). This is not coincident with putative arid pockets on the Bering Strait land bridge during the early Miocene (Stebbins and Day, 1967). During the late Tertiary, the Bering Strait land bridge was restricted to cool-temperate taxa and ultimately boreal taxa (Tiffney and Manchester, 2001) and would therefore represent an unlikely migration route for Mediterranean species. Another land bridge between the Old World and New World existed across the North Atlantic. Geological evidence indicates the North Atlantic land bridge was broken in the early Eocene (Tiffney and Manchester, 2001), at which time it would have been suitable for warm-temperate/tropical taxa. However, some estimates of divergence based on molecular-clock studies imply contact through to the middle or even late Miocene (reviewed in Milne and Abbott, 2002). Regardless of the potentially wide time frame for migration, it is unlikely that the North Atlantic land bridge enabled members of the Groundsel clade to reach the New World. The Groundsel clade emerged at the base of the Pliocene and good post-Miocene evidence for a North Atlantic land bridge does not exist. Consequently, the only plausible explanation is long-distance dispersal. Assuming a southern African origin of the section, the presence of *Senecio* in Australasia represents another example of long-distance dispersal

in the genus, but this requires further examination of evolutionary relationships.

Repeat intercontinental long-distance dispersal appears to be a rare occurrence and we are unaware of any other examples from Mediterranean taxa, although two intercontinental colonizations of the New World have been supported in the predominantly warm temperate and tropical genus *Gossypium* (Malvaceae) (Wendel and Albert, 1992). In studies of southwest North American–Mediterranean disjunctions a vicariant relationship has generally been supported (Fritsch, 1996, 2001; Liston, 1997; Hileman et al., 2001; Davis et al., 2002b). A monophyletic disjunct Mediterranean group within *Styrax* (Styracaceae), dated to a late Miocene divergence, could possibly represent long-distance dispersal, as this is rather late for a North Atlantic land bridge, but its seeds appear to be maladapted for this (Fritsch, 1996, 2001). Although not Mediterranean, a vicariant pattern, probably involving the North Atlantic land bridge, has also been supported in tropical dalbergioid legumes (Fabaceae) (Lavin et al., 2000) and Malpighiaceae (Davis et al., 2002a). Taken together, these studies indicate that intercontinental long-distance dispersal across ocean barriers is rare in Mediterranean and tropical taxa. However, this is not a general pattern as studies of ampho-Atlantic arctic plant species have repeatedly indicated recent trans-Atlantic dispersal (Haraldsen et al., 1991; Haraldsen and Wesenberg, 1993; Hagen et al., 2001). Based on present evidence, it is not possible to determine the direction of the two colonizations of the New World by *Senecio*.

Dispersal north in Africa either occurred once before  $4.30 \pm 1.11$  BP (node B, Fig. 3, Table 1), corresponding to ACCT-RAN area optimization under PAUP\*, or twice in the middle Pliocene and Pleistocene (subclades III and II, respectively, Fig. 3), corresponding to DELTRAN optimization. In the single dispersal scenario, a return to southern Africa occurred within subclade II before  $1.67 \pm 0.69$  BP (node D, Fig. 3, Table 1). Although the arid track is generally thought to have reached its greatest development in the Pleistocene, aridification during the Miocene and Pliocene may have provided an earlier corridor for arid-adapted species. Molecular-clock analysis in the disjunct genus *Androcymbium* (Colchicaceae) (Caujapé-Castells et al., 2001) has indicated that the arid track may have existed by the late Miocene. Therefore, regardless of which of the two scenarios is accepted, a northward expansion along the arid track may have occurred. However, because our results clearly demonstrate the potential for repeated long-distance dispersal in this group, the arid track may be of limited significance. For now, the cause of this disjunction remains uncertain. Some East African *Senecio* species have been assigned to sect. *Senecio* (Jeffrey, 1986), and inclusion of these in future work will be necessary to address this question further.

**Pappus morphology and bird dispersal**—Variation in pappus morphology provides some insight into how *S. flavus*, and possibly *S. mohavensis*, came to be widely disjunct. In most of the species examined, variation was limited and in agreement with previous findings (Drury and Watson, 1966). Typically, almost all pappus hairs are covered with forward-pointing spines and the pappus is largely shed at achenial maturity. Frequently, a small number of pappus hairs (<15 per achene) are of a distinctly different form. Such hairs are flexuous, firmly attached, and largely unornamented. These hairs have been called “fluked hairs” (Drury and Watson, 1966) because of

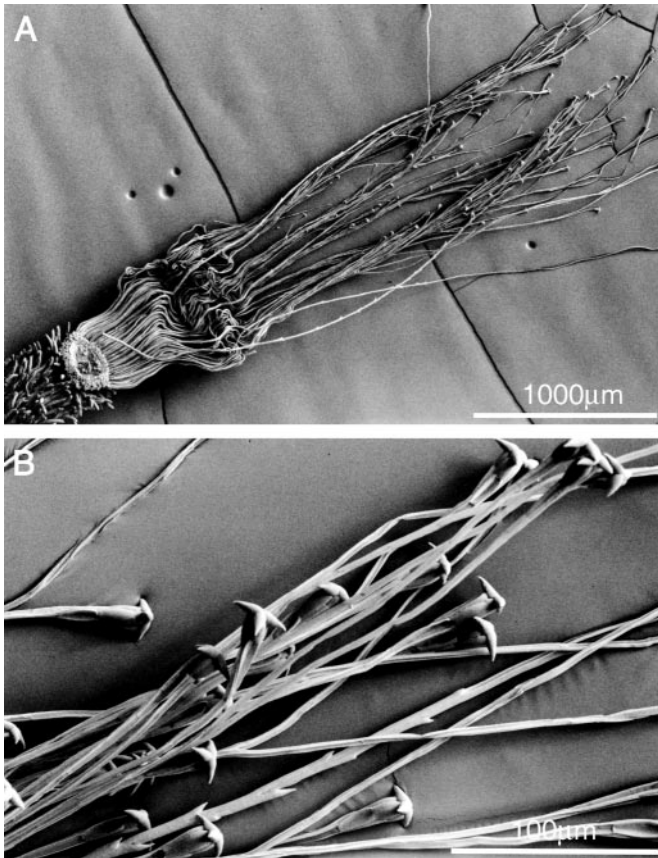


Fig. 4. Connate fluked pappus. (A) Entire structure in *Senecio flavus*, achene apex in bottom left corner; (B) detail of grapple tips in *S. flavus*.

the frequent presence of backward-pointing projections at the swollen tip. *Senecio flavus* departed from this general pattern by having ~100 fluked hairs per achene, accounting for one-third of the pappus. These fluked hairs are fused to each other near the junction with the achene (Fig. 4A). Above this, the hairs separate and have a flexuous form, beyond which the shaft is straight. The hairs, which are of variable length, are each terminated with a regularly three-pronged grapple-like tip (Fig. 4B).

We believe this entire structure is novel and have called it “connate fluked pappus.” A notable feature of the connate fluked pappus is its very firm attachment to the achene, suggesting a dispersal function. This connate fluked pappus was observed in Mediterranean and southern African material of *S. flavus*, but was found to be absent in two accessions, one from Sinai and one from the Canary Islands. The connate fluked pappus was also observed in both subspecies of *S. mohavensis*. However, in this species, the number of hairs is reduced by about 50%, and the connate fluked pappus is less firmly attached. A further difference with *S. flavus* is that the grapple-like tips are variable in the number of prongs (not illustrated).

Barbs and hooks are typical of seeds adapted for epizoochory (Sorensen, 1986). The structure of the connate fluked pappus in *S. flavus* and the strength of its attachment strongly suggest epizoochory. Bird migration from southern Africa to northern Africa, and beyond, is an annual event in more than 300 bird species (Moreau, 1972; Curry-Lindahl, 1981; Walth-

er, 2002). We believe that ground-feeding migrants in open habitats, such as wagtails (*Motacilla* spp.) and shrikes (*Lanius* spp.), represent possible vectors for dispersal of *S. flavus* from southern Africa. In the case of *S. mohavensis*, bird migrations between southwest Asia and southwest North America are unknown (Alerstam, 1990). However, vagrant birds (migrants widely deviating from their normal route) are a common phenomenon throughout the world, and well-documented examples of vagrants involve distances large enough to explain an Old World–New World disjunction (e.g., Thorup, 1998). Consequently, epizoochory may also explain the disjunction of *S. mohavensis*.

Both *S. flavus* and *S. mohavensis* are autogamous (self-fertile) short-lived annuals. Autogamy is of great value in long-distance dispersal because of single colonist establishment, reduced dependence on pollinators, and reduced inbreeding depression. Baker’s Rule (Baker, 1967) highlights the link between autogamy and long-distance dispersal. A good example is seen in the more than 130 Mediterranean species disjunct between Chile and California (Raven, 1963), all of which are herbs and almost all autogamous. Circumstantial evidence for a dispersal role comes from the fact that *S. englerianus*, a close relative of *S. flavus*, was found to lack any form of fluked pappus and is restricted to Namibia.

Another suggested mechanism for bird dispersal in these species is the mucilage produced by *Senecio* achenes after wetting (Liston et al., 1989; Liston and Kadereit, 1995). This cannot be discounted, although it should be noted that temporary mucilage is generally thought to be associated with germination rather than dispersal (Sorensen, 1986).

It seems unlikely that wind dispersal caused these species disjunctions; in both cases, the typical pappus is shed with extreme ease and the connate fluked pappus is clearly ineffective as a parachute.

The connate fluked pappus was absent in all other members of the Groundsel clade that were examined. Consequently, its presence in *S. mohavensis* does provide additional support for the involvement of *S. flavus* in the evolution of this species.

**Timing of diversification**—The considerable species diversity of Mediterranean floras makes the factors that have driven speciation under these conditions of particular interest. The relative importance of the shift to summer-dry conditions and climatic fluctuations during the Pleistocene remains unclear. The few studies of Mediterranean plant groups that have estimated the timing of diversification from molecular clocks have presented varied results. Diversification in *Androcymbium* (Caujapé-Castells et al., 2001) was found to span the Oligocene and Miocene, while in *Linanthus* (Polemoniaceae) (Bell and Patterson, 2000) and *Phyllica* (Rhamnaceae) (Richardson et al., 2001b) considerable diversification since the Pliocene was supported. An earlier study of *Senecio* sect. *Senecio* restricted to taxa from the Mediterranean basin (Comes and Abbott, 2001) has indicated that, even using the most conservative rate calibration for ITS (Sang et al., 1994), rapid speciation occurred in the Pleistocene.

The position of the common ancestor of the Groundsel clade at the base of the Pliocene (Fig. 3) combined with the establishment of the five subclades before the middle Pliocene is suggestive of a link with the spread of summer-dry climate. However, diversification is spread through the Pliocene and into the Pleistocene. All five lineages show Pleistocene diversification, although the extent of this is variable. In subclades

I, II, and IV diversification occurs at the beginning of the Pleistocene, whereas subclades III and V show rapid diversification in the middle and late Pleistocene, respectively (Fig. 3). The apparent lack of diversification in the *S. consanguineus* lineage of subclade V and the relatively low level of diversification in subclades II and IV may be an artifact of incomplete sampling. Because the North American and Mediterranean floras are relatively well known, we can be confident that the limited Pleistocene diversification seen in subclade I and the *S. vulgaris/S. vernalis* lineage of subclade III (Fig. 3) are not sampling artifacts.

Pleistocene climatic fluctuations were of global impact and conclusions about their effects on diversification in other habitats and groups of organisms are needed to put our results into context. Most work has been carried out on animals and a growing number of studies (Hewitt, 1996; Klicka and Zink, 1997; Avise et al., 1998) have supported a protracted history of speciation spanning the Pliocene and Pleistocene. However, rapid recent speciation has also been recorded (Orr and Smith, 1998). Clearly, rates of evolution are variable. Nevertheless, the importance of the dynamic nature of the Pleistocene for speciation is becoming generally appreciated (Hewitt, 2000). Our data and the results of others (Bell and Patterson, 2000; Comes and Abbott, 2001; Richardson et al., 2001b) lend weight to this view with regard to Mediterranean floras.

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