

THE ORIGIN OF *DENDROSENECIO* WITHIN THE SENECIONEAE (ASTERACEAE) BASED ON CHLOROPLAST DNA EVIDENCE¹

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Chloroplast DNA restriction-site variation was surveyed using 15 enzymes for 37 accessions from the tribe Senecioneae (Asteraceae), plus two outgroup species, in order to determine the placement within the tribe of the giant senecios (*Dendrosenecio*). The survey revealed 176 phylogenetically informative mutations and 121 autapomorphic mutations. *Dendrosenecio* is diagnosed by a minimum of 15 mutations, which suggests that the giant senecios evolved from a relatively isolated lineage within the Senecioneae, and this conclusion is supported by earlier evidence from chromosome counts and phytochemistry. Among the taxa sampled, the closest relatives of *Dendrosenecio* are *Cineraria deltoidea* and two species of *Euryops*. Support was not found for suggestions in the literature that the closest relatives of *Dendrosenecio* are species in *Solanecio* or *Senecio* subgen. '*Crociseris*.' The position of the *Dendrosenecio/CinerarialEuryops* clade is weakly supported as basal to the majority of other senecionoid genera. The tussilaginoide genera sampled (*Ligularia*, *Petasites*, *Roldana*, and *Tussilago*) are monophyletic in our analysis, with the surprising inclusion of *Pericallis hybrida* as the sister-taxon to *Roldana suffulta*. The sister-group to the *Dendrosenecio/CinerarialEuryops* clade includes all species of *Delairea*, *Gynura*, *Kleinia*, *Packera*, *Senecio*, and *Solanecio* sampled. Within *Senecio*, subgenera *Senecio* and '*Crociseris*' form a monophyletic core, with subgenus '*Kleinioidei*' being broadly paraphyletic or possibly polyphyletic.

Since the discovery of *Dendrosenecio johnstonii* (Oliv.) B. Nord. (Asteraceae) on Mt. Kilimanjaro, Tanzania, by H. H. Johnston (1886), the giant senecios have attracted considerable interest and discussion by taxonomists and evolutionary biologists. These plants typically have large leaf-rosettes borne on thick, woody stems that branch after flowering to produce candalabra-like growth forms the size of telephone poles. They have diversified on ten mountains in eastern Africa (Knox, 1993a; Knox and Palmer, 1995) to form 17 taxa (11 species and six nonautonymic infraspecific taxa; Knox, 1993b), and the adaptive radiation of this group involved much convergent or parallel evolution, resulting in a "mosaic of variation" in morphological features (Mabberley, 1973) that confounded earlier attempts to reconstruct their evolutionary history. The giant senecios were initially treated as *Senecio* (Oliver, 1887), a placement explicitly supported by several workers (Cotton, 1932, 1944; Hedberg, 1957; Mabberley, 1973, 1974) until Nordenstam (1978) recognized *Dendrosenecio* as a genus distinct from a more narrowly delimited *Senecio* (Knox, 1993b).

A recurrent question in the literature concerns the clos-

est relatives of the giant senecios. Several species in *Senecio* subgen. '*Crociseris*' (see Table 1 for authors) and the segregate genus *Solanecio* have been suggested. Within *Senecio*, these include *S. subsessilis* (Engler, 1892) and other coarse herbs from upland eastern Africa in sect. *Plantaginei* (*S. ochrocarpus* and *S. karaguensis* O. Hoffm.; Mabberley, 1974; Nordenstam, 1978), the coarse European herbs *S. umbrosus* and *S. doronicum* in sect. *Crociseris* (Mabberley, 1974), and the South American *S. hualtata* DC. in sect. *Hualtatini* (DC.) Bak. (Hauman, 1935). The two *Solanecio* species are robust shrubs from tropical Africa (*S. mannii*; Carlquist, 1974, p.554) and Ethiopia, (*S. gigas*; Nordenstam, 1978). With the exception of *Senecio karaguensis* and *S. hualtata*, the remaining species were included in a preliminary survey (Knox, 1993c) of restriction-site variation, which included the North American herb *Packera aurea* and used the cultivar *Pericallis hybrida* (formerly treated as *Cineraria*; Jansen et al., 1990; Jansen, Michaels, and Palmer, 1991) as the outgroup species. This survey found that these putative close relatives to *Dendrosenecio* shared a more recent common ancestry with each other, and that *Pericallis*, *Dendrosenecio*, and the clade comprising all other taxa sampled were separated by long basal branches. In the present study, this preliminary survey of the tribe Senecioneae was therefore expanded using readily available material (Table 1) in order to determine the placement of *Dendrosenecio* within the tribe and to identify potential close relatives.

In the most recent treatment of the Senecioneae, Jeffrey (1992) accepted the two subtribes (Blennospermatinae and Senecioninae) delimited by Nordenstam (1977) and proposed many provisional infrasubtribal groupings that were not formally described. His stated purpose was to provide a list of putative monophyletic genera (and subordinate groups within the still heterogeneous genus

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TABLE 1. Accessions examined for cpDNA restriction-site variation (classification of tribe Senecioneae according to Jeffrey, 1986; 1992).

Classification	Species and author	Accession ^a	Geographic origin
Outgroup species (Asteraceae)	<i>Barnadesia caryophylla</i> (Vell.) S. F. Blake <i>Eupatorium atrorubescens</i> (Lem.) Nicholson	UMMBG (Knox 2439) UMMBG (Knox 2438)	Peru Mexico
Tribe Senecioneae			
Subtribe Biennofermatinae Rydb.	<i>Blennosperma nana</i> (Hook.) S. F. Blake	Ornduff 83739 (UC)	California
Subtribe Senecioninae Dum.	<i>Ligularia stenocephala</i> (Maxim.) Matsum & G. Koidz <i>Petasites japonicus</i> (Siebold & Zucc.) Maxim. <i>Roldana suffulta</i> (Greenm.) H. Rob. & Brettell <i>Tussilago farfara</i> L.	Kowal 3092 Kowal 3093 Kowal et al. 3007 Kowal s.n. 3094	Asia Sachalin Islands Mexico Europe and Asia
Tussilagmoid genera			
Senecionoid genera	<i>Dendrosenecio kilimanjari</i> (Mildbr.) E. B. Knox ssp. <i>cottonii</i> (Hutch. & G. Taylor) E. B. Knox <i>Delairea odorata</i> Lem. <i>Packera aurea</i> (L.) (A. Löve & D. Löve) <i>Cineraria deltoidea</i> Sond. <i>Euryops dacrydioides</i> Oliv. <i>E. pectinatus</i> Cass. <i>Gynura aurantiaca</i> (Blume) DC. <i>Othonna capensis</i> L. H. Bailey <i>Pericallis hybrida</i> B. Nord. <i>Solanecio gigas</i> (Vatke) C. Jeffrey <i>S. manii</i> (Hook. f.) C. Jeffrey <i>Kleinia neriifolia</i> Haw. <i>K. fulgens</i> Hook. f. <i>K. pendula</i> (Forsk.) DC. <i>K. stapeliiformis</i> (Phillips) Stapf	Knox 50 UMMBG (Knox 2422) Knox 880 Knox 2037 Burd s.n. (Knox 2436) MBG 893711 UMMBG (Knox 2424) UMMBG (Knox 2423) Knox 884 Knox 633 Knox 555 UMMBG (Knox 2425) UMMBG (Knox 2426) UMMBG (Knox 2430) UMMBG (Knox 2429)	E. Africa S. Africa N. America S. and E. Africa E. Africa S. Africa Indonesia S. Africa Canary Islands Ethiopia E. Africa Canary Islands S. Africa Arabia and NE. Africa S. Africa
Neotropical group			
Synotoid group			
Packeroid group			
Senecionoid group			
<i>Kleinia</i> Mill. subgen. <i>Kleinia</i>			
Subgen. <i>Notonia</i> (DC.) O. Hoffm.			
<i>Senecio</i> L. subgen. ' <i>Crociseris</i> ' Sect. <i>Crociseris</i> (Reichenb.) Hall. & Wohlf.	<i>Senecio coriaceus</i> <i>S. doronicum</i> L. <i>S. umbrosus</i> Waldst. & Kit. <i>S. inornatus</i> DC. <i>S. ochrocarpus</i> Oliv. & Hiern <i>S. subsessilis</i> Oliv. & Hiern	Kowal 2926 RBG 007.83.60046 Hübl s.n. (Knox 2398) Knox 870 Knox 637 Knox 454, 795	Asia Europe Europe S. and E. Africa Ethiopia E. Africa
Sect. <i>Plantaginei</i> Harv.			
Subgen. ' <i>Jacobaea</i> ' sect. <i>Jacobaea</i> (Mill.) Dumort. ser. <i>Erucifolii</i> (Rouy) Schischk.	<i>S. erucifolius</i> L. <i>S. jacobaea</i> L. <i>S. scaposus</i> DC. <i>S. citrifolius</i> Rowley <i>S. mandraliscae</i> (Tineo) Jacobsen <i>S. rowleyanus</i> M. Jacobs <i>S. stoechadiformis</i> DC. <i>S. madagascariensis</i> Poir. <i>S. sylvaticus</i> L. <i>S. vulgaris</i> L.	RBG 0064875 RBG 0066949 UMMBG (Knox 2431) UMMBG (Knox 2428) UMMBG (Knox 2433) UMMBG (Knox 2427) Kowal 3051 RBG 0020518 RBG 0066994 Knox 2411	Europe Europe and N. Asia S. Africa SW. Africa S. Africa W. Africa Mexico Madagascar Europe and N. Asia Europe (Cosmop.)

^a Burd = M. C. Burd; Hübl = E. Hübl; Kowal = R. R. Kowal; MBG = Missouri Botanical Garden; Ornduff = R. Ornduff; RBG = Royal Botanic Gardens, Kew; UMMBG = University of Michigan Matthaei Botanical Garden.

Senecio) for the selection of representative species in future systematic studies. We have used Jeffrey's informal classification for the species included in our survey (Table 1), but our sampling represents only a small part of the 112 genera, comprising an estimated 3,400 species, in the tribe. It was not our intention to evaluate Jeffrey's treatment, but our results provide some preliminary insight into infratribal relationships.

MATERIALS AND METHODS

Plant material was obtained from various sources (Table 1) either as seed or fresh or dried leaf tissue. Within the subtribe Senecioninae, we included 32 accessions representing 11 senecionoid genera (*Cineraria*, *Delairea*, *Dendrosenecio*, *Euryops*, *Gynura*, *Kleinia*, *Othonna*, *Packera*, *Pericallis*, *Senecio*, and *Solanecio*) and one accession from each of four tussilaginoide genera (*Ligularia*, *Petasites*, *Roldana*, and *Tussilago*). *Blennosperma nana* was used to represent the subtribe Blennospermatinae, and *Barnadesia caryophylla* and *Eupatorium atrorubescens* were used as ultimate outgroup species (Jansen and Palmer, 1987; Jansen et al., 1990; Jansen, Michaels, and Palmer, 1991). Voucher specimens are deposited in the University of Michigan Herbarium (MICH) or the University of Wisconsin Herbarium (WIS; Kowal Collections). *Dendrosenecio kilimanjari* subsp. *cottonii* was used as a single placeholder to represent the *Dendrosenecio* clade for the reasons given in the Results.

Total cellular DNA was isolated using the modified CTAB procedure of Doyle and Doyle (1987), and was purified by centrifugation in cesium chloride/ethidium bromide gradients. DNA aliquots from all samples were digested with each of 15 restriction enzymes: *AseI*, *BamHI*, *BanI*, *BanII*, *BclI*, *BglII*, *BstNI*, *Clal*, *DdeI*, *DraI*, *EcoO109*, *EcoRI*, *EcoRV*, *HindIII*, and *NciI*. Twenty-two clones of a lettuce cpDNA library (Jansen and Palmer, 1987, 1988; Knox, Downie, and Palmer, 1993) were used as probes in filter-hybridization experiments to map restriction sites in the cpDNAs. Two subclones from tobacco (Solclones 2 and 3 in Olmstead and Palmer, 1992) were used as probes to represent the one uncloned portion of the lettuce genome. Methods were performed as described in Palmer (1986), Palmer et al. (1988), and Knox, Downie, and Palmer (1993). Gel electrophoresis for DNA digested with *DdeI*, which cuts cpDNA frequently, was conducted using a 2% gel in order to provide better resolution of small fragments.

Restriction-site maps were constructed for all enzymes except *DdeI*. For this enzyme, only two unambiguous, phylogenetically informative restriction sites were included in the data set. All Senecioneae have two derived inversions relative to tobacco (Jansen and Palmer, 1987; Knox, Downie, and Palmer, 1993). *Barnadesia caryophylla* lacks these inversions, and only unambiguous, shared mutations were scored for *B. caryophylla* and the other outgroup species, *Eupatorium atrorubescens*. For the ingroup species, autapomorphies were included in the data set for all enzymes except *DdeI*. Presence or absence of a restriction site was coded as 1 or 0, respectively, thereby eliminating the need for polarity assignments prior to analysis using outgroup comparison (Watrous and Wheeler, 1981). The analyses, which included bootstrap and decay analyses (Felsenstein, 1985; Bremer, 1988; Donoghue et al., 1992), were conducted using PAUP (Swofford, 1993) on a Macintosh computer. An heuristic search with the Random Addition option (100 replicates) was performed to ensure that all islands of shortest trees were found (Madison, 1991).

RESULTS

Our survey of restriction-site variation revealed 176 phylogenetically informative restriction-site mutations and 121 autapomorphic mutations out of a total of ≈ 720 sites surveyed in each genome (excluding the *DdeI* sites that were not mapped; data matrix available from E. B. Knox upon request). A phylogenetic analysis of the 176

shared mutations found a single island of eight shortest trees of 349 steps, with a consistency index (CI; Kluge and Farris, 1969) of 0.50. The eight shortest trees result from alternative topologies for the clade comprising *Senecio* subgen. *Senecio* and subgen. '*Crociseris*.' The strict consensus tree with *Barnadesia* and *Eupatorium* as the outgroup is shown in Fig. 1. We have indicated the minimum number of restriction-site mutations that support each node, which we feel is a more conservative way of reporting the results than the conventional way of selecting either the acctran or deltran optimization of character support. Our analysis of 40 accessions that represent all 11 species of *Dendrosenecio* shows remarkably little cpDNA divergence (only nine variable sites; Knox and Palmer, 1995). In order to limit computational demands for bootstrap and decay analyses, we have used a single placeholder for the genus. Of these nine variable sites, five are unique and one is homoplastic within *Dendrosenecio*, while the remaining three are homoplastic with taxa outside *Dendrosenecio*. Because of the large number of mutations that diagnose *Dendrosenecio* (a minimum of 15, with seven of these unique mutations), our results are unaffected by the choice of a placeholder, and we have accordingly used *D. kilimanjari* subsp. *cottonii*, which is basal within the genus and has no mutations of its own.

Of the 15 unambiguously diagnostic restriction-site mutations for *Dendrosenecio*, seven are unique restriction-site gains and the remaining eight (seven site losses and one gain) are homoplastic within the context of this data set but are consistently optimized as diagnostic for *Dendrosenecio*. Three additional mutations may also be diagnostic, but the pattern of homoplasy does not permit unambiguous character optimization for the *Euryops/CinerarialDendrosenecio* clade. The placement of *Cineraria deltoidea* as the closest relative to *Dendrosenecio* has a moderate level of support (bootstrap = 67%, decay = 2). The placement of the two *Euryops* species as the sister-group of *CinerarialDendrosenecio* is less strongly supported (bootstrap = 49%, decay = 1).

DISCUSSION

The origin of *Dendrosenecio*—Chloroplast DNA evidence indicates that those robust herbaceous and shrubby species from *Senecio* and *Solanecio* that we have sampled and that were previously suggested as close relatives to *Dendrosenecio* are all more closely related to each other than any are to *Dendrosenecio*. The giant senecios, apparently decaploid ($n = 50$); show virtually no meiotic irregularities that might suggest a recent origin from the predominantly tetraploid ($n = 20$) putatively close relatives suggested in the literature (Knox and Kowal, 1993). *Dendrosenecio* lacks the furoeromphalanes typically found in *Senecio*, *Euryops*, *Ligularia*, and *Othonna*, and contains *p*-hydroxyacetophenone derivatives and scopoletin, which are rare in *Senecio*, and resorcinols that have been isolated in the Asteraceae only from *Baccharis quitenensis* HBK (tribe Astereae; Dupré, Bohlmann, and Knox, 1990). The prenylated *p*-hydroxyphenones are more abundant in the tribes Eupatorieae and Heliantheae, and it is of interest to note that the main constituent (the methyl ether of 2-senecioyl-*p*-hydroxyacetophenone) was

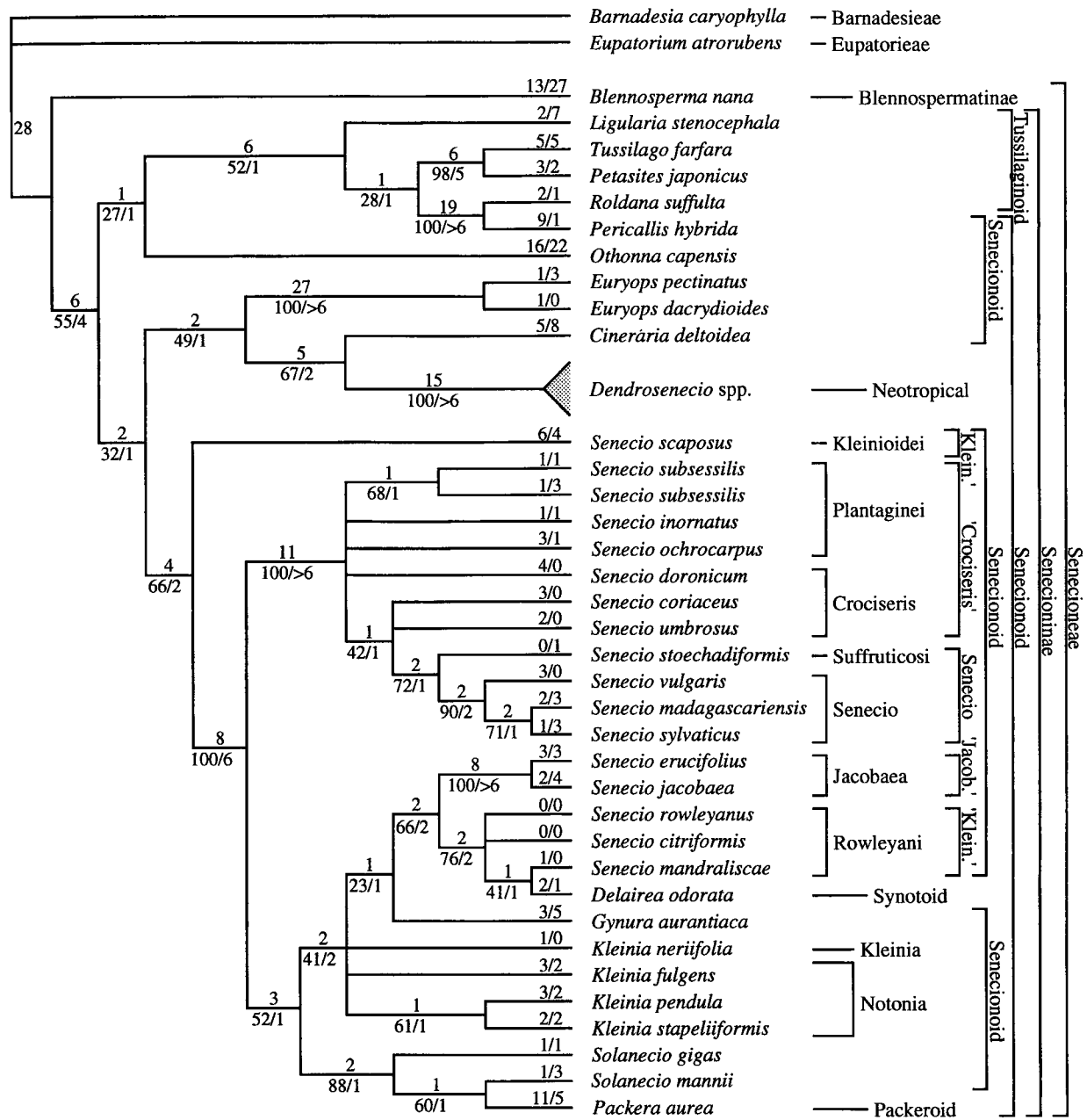


Fig. 1. Wagner parsimony tree for 37 accessions of Senecioneae with *Barnadesia* and *Eupatorium* used as outgroup species. This is a strict consensus of eight equally parsimonious trees generated using 176 synapomorphic restriction-site mutations. Each tree has 349 steps and a CI of 0.50. The numbers above the line at each node indicate the minimum branch length. These values were taken from the table of linkages in the tree description output of PAUP and do not depend on whether ACCTRAN, DELTRAN, or MINF optimization is selected. The reporting of minimum lengths avoids the potentially arbitrary selection of a particular optimization method, but as a consequence, the sum of internal branch lengths and homoplastic changes (289 steps; see tree) will be less than the total tree length (349 steps). The numbers below the branches and preceding the slashes are percentage values that indicate the number of times that a monophyletic group occurred in 100 bootstrap replicates. The numbers after these slashes are decay values that indicate the number of steps needed for a clade to lose resolution. The numbers before and after the slash above the terminal lines indicate the minimum number of homoplastic changes and autapomorphies, respectively. Bootstrap and decay values for the *Dendrosenecio* clade are based on a more detailed study of this group (E. B. Knox and J. D. Palmer, unpublished data).

originally isolated from *Espeletia schultzii* Wedd. (Bohlmann and Rao, 1973), an Andean alpine species with many convergent adaptations of the giant-rosette growth form seen in *Dendrosenecio* (Hedberg and Hedberg, 1979). The high chromosome number (with no irregularities) and the unusual phytochemistry support the conclu-

sion that the lineage that gave rise to *Dendrosenecio* may be relatively ancient and isolated within the Senecioneae, although *Dendrosenecio* itself seems to have had a relatively recent origin (1 million yr) and rapid radiation in eastern Africa (Knox and Palmer, 1995). A similar pattern of a recent radiation of a lineage separated from its

closest relatives by a long branch length was recently reported in *Aquilegia* (Ranunculaceae; Hodges and Arnold, 1994).

It is important to keep in mind that the molecular phylogenetic basis of our conclusion that *Dendrosenecio* is an isolated lineage within the Senecioneae is a function of our sampling strategy, which was to search among all potential (and also accessible) closest relatives of this genus. The large number of restriction-site mutations (15) separating *Dendrosenecio* from *Cineraria* is significant in ways that the large numbers of mutations separating, for example, *Euryops* (27) or the *Senecio subsessilis-sylvaticus* clade (11) from their closest examined relatives are not. If we had been looking for the closest relatives of *Euryops* or this *Senecio* clade, and our sampling had exhausted all likely possibilities (as it did for *Dendrosenecio*), then we could have drawn similar conclusions about these taxa. In fact, we feel confident that we could locate species that are basal to our pair of *Euryops* species or this *Senecio* clad, and hence start breaking up these long branches, but at this point it is not obvious where we should look for closer relatives of the giant senecios. We are not saying that these other long branches are not *potentially* significant; rather, our sampling (or lack thereof) does not allow us to interpret these branch lengths in the same way that we can interpret the results with respect to *Dendrosenecio*.

Cineraria deltoidea is a small, straggling, semiwoody climber, which in eastern Africa grows primarily in open montane forest but occasionally reaches the alpine zone (3,750 m). *Euryops pectinatus* is a fast-growing south African shrub commonly planted as an ornamental that has escaped into disturbed, midaltitude sites (1,750–2,250 m) in Kenya. *Euryops dacrydioides* is an endemic alpine shrub on Mt. Kilimanjaro. The basal positions of *Cineraria* and *Euryops* relative to the *Dendrosenecio* clade suggest that the ancestor of *Dendrosenecio* was at least semiwoody and may have been frost tolerant, but few other conclusions can be drawn because of the length of the branch separating *Dendrosenecio* and *Cineraria* and the numerous morphological differences among *Dendrosenecio*, *Cineraria*, and *Euryops*.

Although the ancestor of the giant senecios remains undetermined, some possibilities can be eliminated. In much the same way that the east African mountains can be thought of as a two-dimensional array of habitat islands (E. B. Knox and J. D. Palmer, unpublished data), the question of ancestral relations for *Dendrosenecio* can be conceptualized using three dimensions, namely, altitude, latitude, and longitude. In the global pattern of vegetation, the latitudinal ecological continua (e.g., Arctic to north temperate alpine to tropical alpine to south temperate alpine to Antarctic) have an obvious altitudinal correlation. Longitude represents a third, idiosyncratic dimension that may facilitate or hinder the geographic movement of plants (e.g., the circumboreal landmasses vs. the oceans, lowlands, and mountains of the tropics).

Because none of the previously suggested east African candidates proved to be close relatives, the recent origin of *Dendrosenecio* via a simple altitudinal event can be eliminated as a likely explanation. Previous arguments against this possibility have stressed the problem of acquiring frost tolerance (Carlquist, 1974, pp. 550, 569). It

seems doubly unlikely that *Dendrosenecio* originated from frost-intolerant plants growing elsewhere in the tropics (i.e., via a combined altitudinal and longitudinal event). The close relationship between the species in *Senecio* subgen. '*Crociseris*' sect. *Crociseris* (Europe) and sect. *Plantaginei* (Africa) suggests that other temperate candidates in subgen. '*Crociseris*' are not likely to be closely related to *Dendrosenecio*. This eliminates a simple north-south latitudinal event as a likely explanation.

The remaining possibilities include: (1) a simple longitudinal event of dispersal from tropical highlands elsewhere in the world; (2) a simple south-to-north latitudinal event from a south African ancestor; and (3) a combined latitudinal/longitudinal event, which merely has a longer dispersal distance than a simple latitudinal event. From an ecological standpoint, the first possibility is most attractive because colonists from an ancestor growing in tropical highlands elsewhere would have the greatest preadaptation for establishment on the mountains in eastern Africa. On the other hand, there are no obvious close relatives to *Dendrosenecio* based on growth form and gross morphology, so either extensive modification occurred during the origin of *Dendrosenecio*, or close relatives with similar modifications have gone extinct. The emerging picture of *Dendrosenecio* as a recent diversification of a relatively old lineage suggests that close relatives should be sought among species that are regarded as relictual. Additional sampling from tropical highland species in the so-called neotropical group of senecionoid genera (Jeffrey, 1992) with a chromosome number of 50 (Knox and Kowal, 1993) may reveal closer relatives of *Dendrosenecio* than *Cineraria*, and the 15 unambiguously diagnostic restriction-site mutations for *Dendrosenecio* provide a firm empirical basis for screening potential relatives (information on genomic location of and restriction enzyme used for each variable site is available from E. B. Knox).

The tribe Senecioneae—Although this survey was not designed to provide definitive insight into the phylogenetic relationships within the Senecioneae, some provisional conclusions can be drawn. The sister-group relationship between subtribe Senecioninae and our single representative of subtribe Blennospermatinae (*Blennosperma nana*; Fig. 1) supports the earlier conclusions of Bremer (1987) and Jansen, Michaels, and Palmer (1991) concerning the basal division within the Senecioneae. Within the subtribe Senecioninae, the tussilaginoide genera have weak support (bootstrap = 51%, decay = 1) as a monophyletic group, with the surprising inclusion of *Pericallis hybrida*, which is strongly supported as a close relative of *Roldana suffulta*. Nordenstam (1978) regarded *Pericallis* as "a very natural and homogeneous group, which is difficult to relate to any extant portion of *Senecio* s. str. . . ." Both *Pericallis* and *Roldana* have chromosome numbers of $n = 30$ (Nordenstam, 1978; Jeffrey, 1992) and also share the trait of sub-palmately lobed and veined leaves (R. R. Kowal, personal communication), and four of the *Pericallis* species were previously placed in the tussilaginoide genus *Doronicum* (Nordenstam, 1978).

The clearly basal position of the succulent *Senecio scaposus* within the *Delairea/Gynura/Kleinia/Packeria/Senecio/Solanecio* clade (Fig. 1) indicates that the succulent *Senecio* subgen. '*Kleinioidei*' is not a monophyletic

group, but additional sampling is needed in order to determine whether the succulent senecios represent a broadly paraphyletic assemblage or, more likely, are the result of convergent evolution. Our sampling indicates that *Senecio* subgen. *Senecio* is a monophyletic group that is nested within the paraphyletic subgen. 'Crociseris'. These two subgenera probably form the core of a monophyletic *Senecio*.

Our three samples of sect. *Rowleyani* constitute a clade that includes the anomalous *Delairea odorata* (syn. *S. mikanioides* Otto ex Walp.). The deeply nested position of *Delairea* suggests that the features linking it with genera in the synotoid group are the result of convergence, but additional sampling is needed to draw firm conclusions. The sister-group of sect. *Rowleyani* is evidently *Senecio* subgen. 'Jacobaea' sect. *Jacobaea* ser. *Erucifolii*, which is monophyletic based on our sampling. It is likely that subgen. 'Kleinioidei' (excluding *S. scaposus* and its relatives) and subgen. 'Jacobaea' have retained primitive features from the ancestral *Senecio*, and that the lineage giving rise to these subgenera has also spawned the segregate genera *Gynura*, *Kleinia*, *Packera*, and *Solanecio*, but, again, more sampling is needed.

The unresolved topology involving *Kleinia* is due to a lack of variation, and *Kleinia* is possibly monophyletic. The position of *Gynura aurantiaca* is only weakly supported, and may prove to be more basal with additional sampling. The weakly supported position of *Packera aurea* as the sister-species (within our survey) of *Solanecio manni* (which makes *Solanecio* paraphyletic) is unexpected and suggests a need for greater taxonomic and molecular sampling for these two genera.

Although this survey provides a preliminary framework for considering phylogenetic relationships within the Senecioneae, much more work is needed in order to obtain a sufficiently reliable and detailed phylogeny on which to base taxonomic decisions. (More extensive molecular surveys of the Senecioneae are being conducted by J. W. Kadereit [Mainz, Germany; in conjunction with C. Jeffrey], and anyone willing to contribute material for molecular systematic studies in the Senecioneae should contact Dr. Kadereit.) One clear result is that none of the putative close relatives previously suggested in the literature are in fact closely related to *Dendrosenecio*. In order to reconstruct the morphological features of the progenitor of *Dendrosenecio* and to determine whether the features formerly used to place *Dendrosenecio* within *Senecio* are retained primitive features or the result of convergent evolution, closer relatives must be found, and these relatives are not likely to be in *Senecio* sensu stricto or its closely allied genera.

NOTE ADDED IN PROOF: The correct identification of the species listed as "*Euryops pectinatus* Cass." in Table 1 and Fig. 1 is "*Euryops chrysanthemoides* (DC.) B. Nord."

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