Proc. Natl. Acad. Sci. USA
Vol. 92, pp. 10349–10353, October 1995
Evolution

Chloroplast DNA variation and the recent radiation of the giant senecios (Asteraceae) on the tall mountains of eastern Africa

(adaptive radiation/*Dendrosenecio*/biogeography/phylogenetics)

ERIC B. KNOX*† AND JEFFREY D. PALMER‡

*Herbarium and Department of Biology, University of Michigan, Ann Arbor, MI 48109-1048; and ‡Department of Biology, Indiana University, Bloomington, IN 47405

Communicated by Charles B. Heiser, Indiana University, Bloomington, IN, July 28, 1995 (received for review December 21, 1994)

ABSTRACT **Chloroplast DNA restriction-site variation was surveyed among 40 accessions representing all 11 species of giant senecios (*Dendrosenecio*, Asteraceae) at all but one known location, plus three outgroup species. Remarkably little variation (only 9 variable sites out of roughly 1000 sites examined) was found among the 40 giant senecio accessions, yet as a group they differ significantly (at 18 sites) from *Cineraria deltoidea*, the closest known relative. This pattern indicates that the giant senecios underwent a recent dramatic radiation in eastern Africa and evolved from a relatively isolated lineage within the Senecioneae. Biogeographic interpretation of the molecular phylogeny suggests that the giant senecios originated high on Mt. Kilimanjaro, with subsequent dispersion to the Aberdares, Mt. Kenya, and the Cherangani Hills, followed by dispersion westward to the Ruwenzori Mountains, and then south to the Virunga Mountains, Mt. Kahuzi, and Mt. Muhi, but with dispersion back to Mt. Elgon. Geographic radiation was an important antecedent to the diversification in eastern Africa, which primarily involved repeated altitudinal radiation, both up and down the mountains, leading to morphological parallelism in both directions. In general, the plants on a given mountain are more closely related to each other than they are to plants on other mountains, and plants on nearby mountains are more closely related to each other than they are to plants on more distant mountains. The individual steps of the geographic radiation have occurred at various altitudes, some clearly the result of intermountain dispersal. The molecular evidence suggests that two species are extant ancestors to other species on the same or nearby mountains.**

The giant senecios are an unusual group of plants that have diversified to occupy a range of habitats, from 2500 to 4600 m, on 10 mountains >3300 m tall within 4° of the equator in Zaire, Rwanda, Uganda, Kenya, and Tanzania (1). Now segregated as the genus *Dendrosenecio* (Hauman ex Hedberg) Nordenstam, the giant senecios comprise 11 species and 6 nonautonymic subspecific taxa (2). Their habitats range from upper montane forest (mist-forest) through the giant heather zone and high-altitude wet meadows and extend almost to the upper limit of the unusual afro-alpine zone, whose climate has been characterized as "summer every day and winter every night" because strong diurnal fluctuations exceed seasonal variation (3). These plants typically have a giant-rosette growth form with a massive terminal leaf rosette borne atop a thick woody stem. During reproduction, a large terminal inflorescence is produced, and two to four lateral branches are usually initiated. Old plants appear as candelabras the size of telephone poles, with each branch bearing a leaf rosette (Fig. 1). The giant-rosette growth form, large pith volume, marcescent foliage, and nyctinasty have evolved independently in the montane east African giant lobelias (Lobeliaceae; ref. 4) and the Andean genus *Espeletia* (Asteraceae; ref. 5), which suggests that these features are adaptations to the high-altitude tropical environment. The giant senecios show an unusual trend of massive plants occurring at high elevations, with smaller plants found at lower altitude. Numerous vegetative and floral characters also show altitudinal patterns, and the combined effects of inheritance and adaptation on these and other features have created a "mosaic of variation" (6) that has confounded earlier attempts to reconstruct the evolutionary history of this genus by using morphological traits.

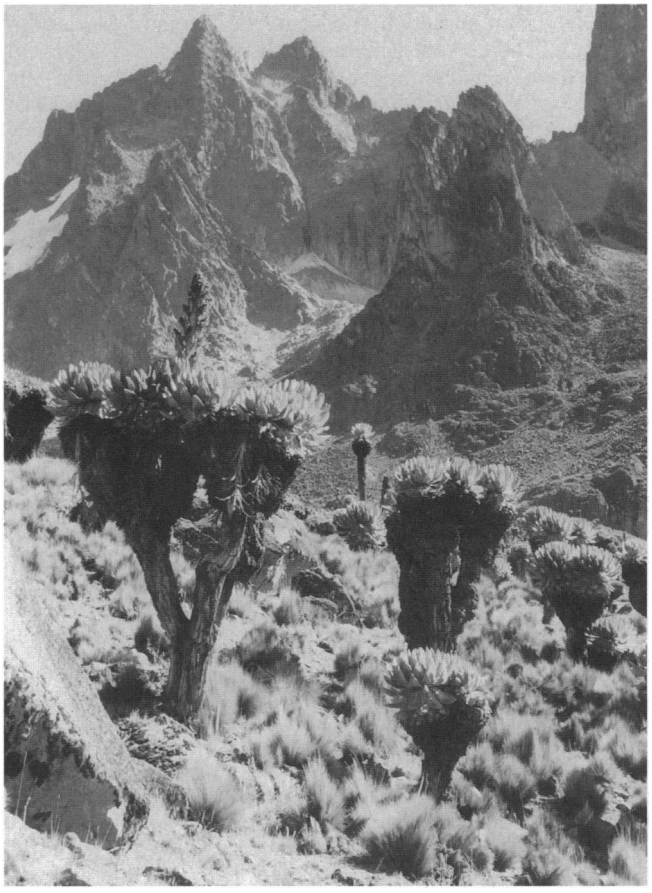

FIG. 1. *Dendrosenecio keniodendron* at 4200 m in the Teleki Valley, Mt. Kenya. A developing inflorescence is emerging from one of the leaf rosettes of the large individual in the foreground.

The giant senecios from the mountains of the Eastern Rift Zone in Kenya and Tanzania show a high degree of morpho-

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

Abbreviation: cpDNA, chloroplast DNA.

†To whom reprint requests should be sent at the present address: Department of Biological Sciences, Rutgers University, Newark, NJ 07102.

logical differentiation, whereas those from the mountains of the Western Rift Zone in Zaire, Rwanda, and Uganda show more intergrading variation (6, 7). Speculation as to which pattern indicates the site of origin (ref. 8; cf. refs. 6 and 9–11) has been inconclusive because of uncertainties regarding biogeographic and genetic processes.

It has been argued that the ancestors of the giant senecios lived at altitudes low enough to permit migration in the region and that the extant species were derived from parallel evolution up each mountain (6, 12–14). Perhaps because humans are obliged to live at lower altitudes and climb mountains one-by-one, it seems only fair that plants should do the same. Less attention has been paid to the fact that, regardless of the mode of origin, once the first species was established in any habitat on any mountain within the current distributional range, the observed radiation could have occurred through a variety of processes. The current geographic distribution is insular and would have remained almost entirely so, even given the response of the vegetation to the estimated extremes of past climates (15). In this case, long-distance dispersal is more likely than migration, and there is no reason why colonists could not start near the top and evolve their way down a mountain.

In this paper, we report a phylogenetic analysis of chloroplast DNA (cpDNA) data from the giant senecios. The molecular phylogeny allows us to reconstruct the geographic and altitudinal radiation of the giant senecios throughout eastern Africa. The altitudinal zonation of vegetation on the tall isolated mountains of eastern Africa creates a stratified system (or two-dimensional array) of habitat islands (see ref. 4). The DNA-based phylogeny provides an estimate of the pattern of descent, even among isolated (and morphologically invariant) populations within species. This phylogeny can then be "superimposed" on a model landscape by using a parsimony criterion to reconstruct the origin and historical delimitation of each species, as well as broader patterns of geographic and altitudinal radiation. As might be expected in cases of adaptive radiation, the pattern of descent among geographically and altitudinally isolated populations/species shows evidence in some cases that one extant species was derived from another extant ancestral species.

MATERIALS AND METHODS

Plant material from all 11 species of *Dendrosenecio* was obtained from the field as seed or fresh or dried leaf tissue as follows (with accession numbers in parentheses): *Dendrosenecio adnivalis* (Stapf) E. B. Knox subsp. *adnivalis* var. *adnivalis* (Knox 283), subsp. *adnivalis* var. *petiolatus* (Hedberg) E. B. Knox (Knox 280), and subsp. *friesiorum* (Mildbr.) E. B. Knox (Knox 273); *Dendrosenecio battiscombei* (R. E. Fr. & T. C. E. Fr.) E. B. Knox (Knox 11, 13, 15, 2049, 2144, 2158; Burd 18); *Dendrosenecio brassiciformis* (R. E. Fr. & T. C. E. Fr.) Mabb. (Knox 17, 2131); *Dendrosenecio cheranganiensis* (Cotton & Blakelock) E. B. Knox subsp. *cheranganiensis* (Knox 3) and subsp. *dalei* (Cotton & Blakelock) E. B. Knox (Knox 712); *Dendrosenecio elgonensis* (T. C. E. Fr.) E. B. Knox subsp. *elgonensis* (Knox 696, 702) and subsp. *barbatipes* (Hedberg) E. B. Knox (Knox 695, 2054); *Dendrosenecio erici-rosenii* (R. E. Fr. & T. C. E. Fr.) E. B. Knox subsp. *erici-rosenii* (Knox 136, 150, 292, 398, 455) and subsp. *alticola* (Mildbr.) E. B. Knox (Knox 158, 381); *Dendrosenecio johnstonii* (Oliv.) B. Nord. (Knox 48, 2434); *Dendrosenecio keniensis* (Baker f.) Mabb. (Knox 26, 2041); *Dendrosenecio keniensis* × *keniodendron* (Knox 31, 2043); *D. keniodendron* (R. E. Fr. & T. C. E. Fr.) B. Nord. (Knox 32, 2042, 2143); *Dendrosenecio kilimanjari* (Mildbr.) E. B. Knox subsp. *kilimanjari* (Knox 814, 2010, 2435) and subsp. *cottonii* (Hutch. & G. Taylor) E. B. Knox (Knox 50); *Dendrosenecio meruensis* (Cotton & Blakelock) E. B. Knox (Knox 45, 1670). *Cineraria deltoidea* Sond. (Knox 2037) and two species of *Euryops, Euryops dacrydioides* Oliv. (Knox 2436) and *Euryops chrysanthemodes* (DC.) B. Nord., were used as outgroups because of their positions as the closest relatives to *Dendrosenecio* within a broader survey of Senecioneae (16). Voucher specimens are deposited in the University of Michigan Herbarium. Within *Dendrosenecio*, plants from all known localities were sampled, except Mt. Muhi, Zaire (due to war in Rwanda).

All molecular methods, including total DNA isolation, agarose gel electrophoresis and blotting, and filter hybridization using 24 lettuce and tobacco cpDNA clones and clones for the entire nuclear ribosomal DNA repeat from pea, were performed as described in ref. 16. DNAs from all samples were digested with each of the following 16 restriction enzymes: *Ase* I, *Bam*HI, *Ban* I, *Ban* II, *Bcl* I, *Bgl* II, *Bst*NI, *Cla* I, *Dde* I, *Dra* I, *Eco*O109I, *Eco*RI, *Eco*RV, *Hin*dIII, *Nci* I, and *Rsa* I. Because of the limited variation detected with these enzymes (see *Results*), four taxa [*D. erici-rosenii* subsp. *erici-rosenii* (Knox 150), *D. elgonensis* subsp. *barbatipes* (Knox 695), *D. battiscombei* (Knox 15), and *D. johnstonii* (Knox 48)] were screened for cpDNA variation by using the following 15 additional restriction enzymes: *Apa* I, *Ava* I, *Ava* II, *Bgl* I, *Bst*EII, *Bst*XI, *Hin*cII, *Kpn* I, *Pst* I, *Pvu* II, *Sal* I, *Sca* I, *Sma* I, *Stu* I, and *Xho* I. Restriction-site maps were constructed for all enzymes except *Dde* I and *Rsa* I. Presence or absence of a restriction site was coded as 1 or 0, respectively, thereby eliminating the need for polarity assignments prior to phylogenetic analysis using outgroup comparison with PAUP 3.1.1 (17) on a Macintosh computer.

RESULTS

The survey of cpDNA restriction-site variation among the giant senecios and three outgroup species identified 60 phylogenetically informative mutations (data matrix available upon request from E.B.K.). A phylogenetic analysis using Wagner parsimony and the TBR option of PAUP resulted in a single most-parsimonious tree of 62 steps with a consistency index of 0.97 (Fig. 2). One of the two homoplastic characters in this data set has an unpolarizable change in the basal segment between the *Euryops* and *Cineraria/Dendrosenecio* clades and a restriction-site gain in the common ancestor of the *D. adnivalis/D. erici-rosenii/D. elgonensis* clade, and the other shows parallel gains in *D. erici-rosenii* and *D. adnivalis* subsp. *friesiorum*. No autapomorphies were detected in the 40 *Dendrosenecio* samples, and a total of only 9 informative cpDNA site changes were found (Fig. 2). Therefore, in an attempt to uncover additional variation, 4 taxa of giant senecios that represent the range of diversity of the genus as revealed by the initial 16 restriction enzymes (Fig. 2) were screened with 15 additional enzymes. No restriction-site mutations were detected, and we therefore decided that additional survey work with these enzymes was not warranted.

Approximately 550 sites were scored for each giant senecio by using the 12 6-bp cutting enzymes, 146 sites were scored with the two 5-bp cutters, and 300 sites were scored with the two 4-bp cutters. A maximum of 6 of the ≈5230 bp of cpDNA sequence sampled at these nearly 1000 sites varied between any two giant senecios (Fig. 2). Levels of cpDNA sequence divergence (calculated as in ref. 18) thus range from 0% to a maximum of only 0.11%.

Patterns of restriction fragment variation in nuclear ribosomal DNA were too complex, perhaps due to the putatively decaploid status (19) of the giant senecios, to allow unambiguous inference of any phylogenetically informative mutations. However, the putative (based on morphology) F_1 hybrids of *D. keniensis* and *D. keniodendron* showed the predicted additive patterns in ribosomal DNA variation, which allowed *D. keniensis* to be identified as the maternal parent based on cpDNA (Fig. 2).

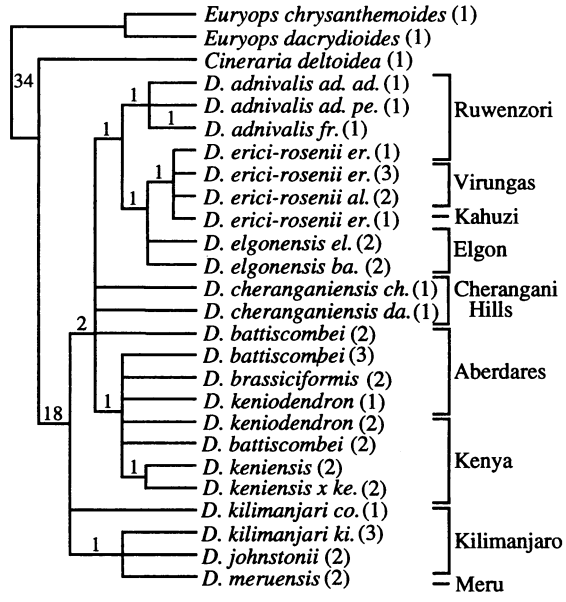

FIG. 2. Wagner parsimony tree for *Dendrosenecio* with *Euryops* and *Cineraria* species used as outgroups. The data set of 60 phylogenetically informative restriction-site mutations yielded a single most-parsimonious tree of 62 steps with a consistency index of 0.97. The unresolved nodes within *Dendrosenecio* are due to insufficient variation; unmarked terminal segments arising from a common node have identical cpDNAs based on our restriction-site sampling. The branch length is indicated above the line at each node. No autapomorphies were detected within the samples of *Dendrosenecio*; the terminal segment leading to *D. adnivalis* subsp. *friesiorum* has a single homoplastic change. Autapomorphies in the outgroups are not shown. The number of populations examined from each taxon is indicated in parentheses. D, *Dendrosenecio*; ad., *adnivalis*; pe., *petiolatus*; fr., *friesiorum*; er., *erici-rosenii*; al., *alticola*; el., *elgonensis*; ba., *barbatipes*; ch., *cheranganiensis*; da., *dalei*; ke., *keniensis*; co., *cottonii*; ki., *kilimanjari*

DISCUSSION

The Origin of *Dendrosenecio*. cpDNA evidence indicates that *Dendrosenecio* is a relatively isolated lineage within the Senecioneae, with no affinities to the putatively close relatives suggested in the literature (16). The giant senecios, apparently decaploid ($n = 50$), show virtually no meiotic irregularities that might suggest a recent origin from a tetraploid ($n = 20$) ancestor (19), and the phytochemistry of *Dendrosenecio* is also distinctive within the Senecioneae (16, 20). Although *Euryops* and *Cineraria* provide suitable outgroup species for polarizing the cpDNA restriction-site data, it is possible that other high-altitude tropical Senecioneae from outside Africa may be more closely related, and the 18 diagnostic restriction-site mutations for *Dendrosenecio* provide a good basis for screening potential relatives (16). In comparison with other groups of giant-rosette plants in the Asteraceae, only six cpDNA restriction-site mutations separate the endemic Hawaiian silversword alliance (Heliantheae) from the North American tarweeds (21, 22), only three mutations separate the Juan Fernandez endemic *Dendroseris* (Lactuceae) from three *Sonchus* species (23), and no mutations were found that separate the Juan Fernandez endemic *Robinsonia* (Senecioneae) from four South American *Senecio* species (24). A consistent feature in the evolution of these groups is the dramatic morphological divergence from their closest known relatives. In contrast, the tetraploid giant lobelias from Africa, Asia, Hawaii and other Pacific islands, and South America represent local radiations that are part of a larger pantropical radiation (25) with comparatively minor divergence in basic growth form, rather than independent evolutionary derivations from small herbaceous ancestors (E.B.K., unpublished data).

Limitations of the Data. The small number of restriction-site mutations detected among the giant senecios recommends a cautious approach to interpreting these data. From a phylogenetic standpoint, however, the key issue is not the mere number of characters that support a clade, but whether these characters are homologs that accurately record phylogenetic history. Cladistic analysis relies solely on shared derived characters (synapomorphies) for inferring phylogenetic relationships, but from a maximum likelihood perspective, the large number of invariant restriction sites, the lack of autapomorphies, and the high consistency index support our phylogenetic interpretation because the chance of restriction-site change in any segment of the topology relative to the rate of speciation is evidently low. Hence it is likely that the observed synapomorphies are phylogenetically accurate homologies (ref. 26; J. Felsenstein, personal communication). A larger number of restriction-site mutations would have provided a more robust phylogenetic estimate, but our interpretation of a recent and rapid evolutionary history is based on this very paucity of restriction-site variation relative to the geographic, altitudinal, and concomitant morphological radiation.

A second issue concerns the use of cpDNA to infer organismal phylogeny. Doyle (27) discusses the potential effects of introgression and lineage sorting, which may cause a cpDNA-based phylogenetic estimate to be incongruent with the true "species tree." To detect historical introgression events (which make phylogenies reticulate rather than strictly hierarchical), multiple nuclear markers are required to obtain the data needed to reconstruct the reticulations. No unusual relationships (based on previous morphological considerations) were indicated by our cpDNA data that would suggest that introgressive hybridization played an important role in the radiation of *Dendrosenecio*, nor is there any evidence of interspecific hybridization accompanied by chromosome doubling within the genus, as all giant senecios have the same high ploidy level (19). Therefore, although nuclear DNA-based studies of *Dendrosenecio* should be conducted, there is no reason to reject the results of the cpDNA-based work at this time. Comparative studies with other sources of data are also required to detect lineage sorting. The limited population sampling included in the present study revealed "paraphyletic" population structures for *D. battiscombei* and *D. kilimanjari* (Fig. 2, see below). It is possible that future sampling may reveal more complex patterns of cpDNA lineages relative to contemporary taxonomic delimitation, but the stratified system of habitat islands on the mountains of eastern Africa is expected to have involved enough population bottlenecks during the geographic and altitudinal steps of the radiation (relative to vicariant speciation) such that the transmission of ancestral polymorphisms would have been relatively restricted. Although the present study does not disprove more complex scenarios concerning the evolution of the giant senecios, the available data support only a single most-parsimonious phylogenetic interpretation.

The biogeographic interpretation presented below obviously depends on the accuracy of the phylogenetic hypothesis. Although the cpDNA-based phylogeny does not provide complete resolution of all taxa/populations sampled, the phylogeny does provide sufficient evidence for a testable biogeographic reconstruction. As discussed above, future research may demonstrate a more complex evolutionary history, but our current reconstruction (Fig. 3) represents the most parsimonious interpretation of our data.

The Radiation of *Dendrosenecio*. The base of the *Dendrosenecio* clade comprises an unresolved trichotomy of *D. kilimanjari* subsp. *cottonii*, a clade consisting of the remaining Tanzanian giant senecios (including *D. kilimanjari* subsp. *kilimanjari*), and a clade consisting of the non-Tanzanian species (Fig. 2). The "paraphyletic" pattern observed within *D. kilimanjari* suggests that *Dendrosenecio* originated in eastern Africa at a

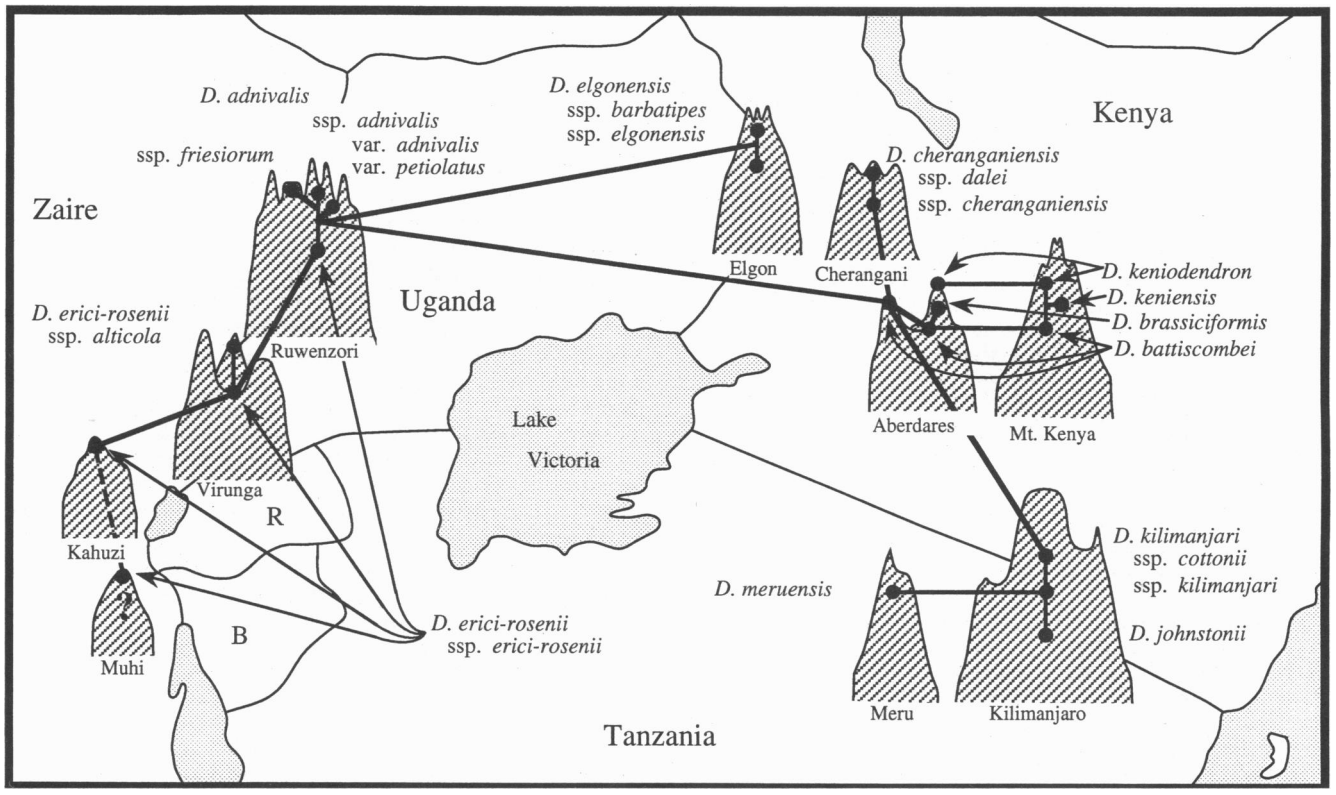

FIG. 3. Biogeographic reconstruction of the radiation of *Dendrosenecio* in eastern Africa. The question mark indicates the uncertain source for colonization of Mt. Muhi by *D. erici-rosenii* subsp. *erici-rosenii*. The map is not drawn to scale (it is stretched horizontally). R, Rwanda; B, Burundi.

high-altitude site on Mt. Kilimanjaro and that *D. kilimanjari* subsp. *kilimanjari* and *D. johnstonii* were derived through downward altitudinal radiation, with an inter-mountain dispersal event giving rise to *D. meruensis* (Fig. 3). The recent ages of Mt. Kilimanjaro and Mt. Meru (28) indicate that the radiation of *Dendrosenecio* occurred within the past million years and that *D. meruensis* was derived within the past 200,000 years. This result is congruent with the observed paucity of restriction-site variation among the giant sencios. With this time frame, only the effects of Pleistocene climatic fluctuations on the altitudinal distribution of montane vegetation need be considered in the historical reconstruction of *Dendrosenecio*.

The delimitation of *Dendrosenecio* species is based on morphological and ecological evidence (1). *Dendrosenecio kilimanjari* is one of two species suggested to be "nonmonophyletic" by these molecular data, but as argued elsewhere (4), all species evolve from other species, and these molecular data permit tentative resolution of the so-called paraphyletic species needed to establish ancestor–descendant relationships. On Mt. Kilimanjaro, the gain of a restriction site diagnoses the putative evolution of subsp. *kilimanjari* from subsp. *cottonii*. The morphological and ecological differentiation, and in the case of *D. meruensis*, the geographic separation, diagnoses the evolution of *D. johnstonii* and *D. meruensis* from *D. kilimanjari*. This reconstruction is conservative with respect to the hypothesized number of intermountain dispersal events. Future evidence may indicate, for example, that *D. johnstonii* is derived from *D. meruensis*, so the number of dispersal events is a minimum estimate. This does not change the general trend of evolution down Mt. Kilimanjaro; it merely leaves in question the relative efficacy of speciation through the exploitation of a new habitat on a single mountain vs. the genetic isolation that might accompany repeated geographic isolation via multiple dispersal events. The insular habitats force a comparison of dispersalist, allopatric explanation vs. nondispersalist peripatric modes of speciation. Although our cpDNA evidence does not provide sufficient resolution to decide between these alternatives in this case, the testable hypotheses are clearly framed so that future research might yield an answer.

The non-Tanzanian *Dendrosenecio* clade (Fig. 2) consists of an unresolved basal polytomy that comprises three molecularly undifferentiated lineages (the high-altitude Aberdare populations of *D. battiscombei* and the two subspecies of the Cherangani Hills endemic, *D. cheranganiensis*), a Western Rift Zone/Mt. Elgon subclade, and a Mt. Kenya/Aberdare subclade (excluding the high-altitude Aberdare populations of *D. battiscombei*). The paraphyletic structure of *D. battiscombei* relative to *D. brassiciformis, D. keniodendron*, and *D. keniensis* suggests that *D. battiscombei* originated at a high-altitude site on the Aberdares and that *D. battiscombei* is ancestral to these other three species (Fig. 3). This putatively high-altitude origin of *D. battiscombei* is consistent with the hypothesis that it was derived from *D. kilimanjari* subsp. *cottonii* via long-distance dispersal from Mt. Kilimanjaro. The lack of molecular resolution within the Mt. Kenya/Aberdare clade does not provide a phylogenetic hypothesis for the three derived species, but a biogeographically parsimonious interpretation of the distribution pattern suggests that *D. brassiciformis* (a wet-site Aberdare endemic) evolved from *D. battiscombei* on the Aberdares and that *D. keniensis* (a wet-site Mt. Kenya endemic) and the alpine *D. keniodendron* (Fig. 1) evolved from *D. battiscombei* on Mt. Kenya. Although a few plants of *D. keniodendron* grow on the summit of Sattima Peak of the Aberdares, these are most likely colonizers that dispersed from the large populations of *D. keniodendron* on Mt. Kenya.

Dendrosenecio cheranganiensis consists of two subspecies that show no cpDNA variation but are very distinctive morphologically and ecologically, with the dwarf subsp. *dalei* restricted to a few high-altitude wet sites. In growth form and ecology, subsp. *cheranganiensis* is similar to the low-altitude form of *D. battiscombei*, but our molecular data provide no basis for inferring the evolutionary relationship between *D.*

cheranganiensis and *D. battiscombei*. It seems likely that subsp. *dalei* was derived from subsp. *cheranganiensis* (6, 29).

The Western Rift Zone/Mt. Elgon clade (*D. adnivalis*/*D. erici-rosenii*/*D. elgonensis*; Fig. 2) consists of a monophyletic *D. adnivalis* and a subclade consisting of *D. erici-rosenii* and *D. elgonensis*. *Dendrosenecio erici-rosenii* is diagnostically monophyletic with no molecular differentiation (within this study) among the subspecies or populations, and the two *D. elgonensis* subspecies show no molecular differentiation but are not diagnostically monophyletic. The most conservative interpretation of these data is that *Dendrosenecio* reached the Ruwenzori Mountains at a moderately high-altitude site, with one lineage diversifying into the subspecies and varieties of *D. adnivalis*, a second lineage giving rise to *D. elgonensis* through long-distance dispersal to Mt. Elgon, and a third lineage evolving into *D. erici-rosenii* with subsequent dispersal to the Virunga Mountains, Mt. Kahuzi, and Mt. Muhi, and with subsp. *alticola* derived from subsp. *erici-rosenii* in the Virunga Mountains (Fig. 3).

The Generalized Pattern of Speciation. The molecular data indicate that the diversification of the giant senecios in eastern Africa primarily involved repeated altitudinal radiation. There are instances in which the possibility of additional geographic events is not refuted by the available cpDNA evidence (e.g., the origin of *D. johnstonii* or *D. erici-rosenii*), but there is no general pattern of basal relationships among the montane-forest species, from which the alpine species were derived, as suggested (6, 12–14).

We hypothesize that the early diversification involved geographic movement at high altitudes among the tallest mountains (Mt. Kilimanjaro, the Aberdares/Mt. Kenya, Mt. Elgon, and the Ruwenzori Mountains). This may seem surprising given the inhospitable climate of the alpine zone for botanists and other animals, but it is the alpine zone that supports the largest populations of giant senecios. Subsequent diversification seems to have involved altitudinal movement into lower habitats, and this provided opportunities for colonization of mountains that are too small (e.g., Mt. Kahuzi) or too recent (e.g., Mt. Meru) to support alpine vegetation. In some cases, these midaltitude geographic events were possibly followed by subsequent altitudinal events (e.g., *D. cheranganiensis* subsp. *dalei* and *D. erici-rosenii* subsp. *alticola*), but these speculations require morphological interpretations to supplement our cpDNA evidence.

The biogeography shows the expected pattern of close relationship among species on nearby mountains, with one exception (Fig. 3). *Dendrosenecio elgonensis* is more closely related to species from the Western Rift Zone than it is to *D. cheranganiensis* or other species from the Eastern Rift Zone. Biogeography was used as a framework for constraining interpretation of the cpDNA data, so our reconstruction cannot be used to test a formal biogeographic model. Of ecological interest is the fact that no evidence was discovered during the fieldwork of recent establishment of a species on a mountain in a habitat already occupied by another species. Are successful geographic events contingent upon available habitats being unoccupied by congeners, and if so, what are the implications of such historical contingencies for our expectations and interpretations of historical evolutionary pattern?

In contrast to the recent primarily high-altitude radiation of the giant senecios, the giant lobelias appear to have initially colonized the ancient upland features in east Africa and then moved onto the tall mountains as they arose (4). The more extensive ecological and geographic ranges and the greater morphological and molecular differentiation of the giant lobelias consistently support this conclusion of vastly different time frames for the evolution of the giant senecios and giant lobelias in eastern Africa. However, both groups show the same general pattern of diversification primarily through repeated altitudinal radiation. Our work contributes to the growing body of molecular systematic studies applied to biogeographic questions (30), whose synthesis should yield important insights into evolutionary processes.

We thank W. R. Anderson, G. R. Smith, and W. H. Wagner for critically reading an early version of this paper; M. C. Burd and the Missouri Botanical Garden for providing live plant material; and the Tanzanian Commission for Science and Technology, the Ugandan National Research Council, the National Museums of Kenya, the Institute Zairois pour la Conservation de la Nature, and the Office Rwandais du Tourisme et des Parcs Nationaux for permission to conduct research in their respective countries. This work was supported by grants from the National Science Foundation and awards from the Rackham School of Graduate Studies, University of Michigan.

1. Knox, E. B. (1993) *Opera Bot.* **121,** 195–216.
2. Knox, E. B. (1993) *Contrib. Univ. Mich. Herb.* **19,** 241–257.
3. Hedberg, O. (1964) *Acta Phytogeogr. Suec.* **49,** 1–144.
4. Knox, E. B. (1993) Ph.D. thesis (Univ. of Michigan, Ann Arbor).
5. Hedberg, I. & Hedberg, O. (1979) *Oikos* **33,** 297–307.
6. Mabberley, D. J. (1973) *Kew Bull.* **28,** 61–96.
7. Mabberley, D. J. (1986) in *High Altitude Tropical Biogeography*, eds. Vuilleumier, F. & Monasterio, M. (Oxford Univ. Press, New York), pp. 81–102.
8. Hauman, L. (1935) *Rev. Zool. Bot. Africaine* **28,** 1–76.
9. Turrill, W. B. (1939) *Bull. Misc. Inform.* **1939,** 208–237.
10. Turrill, W. B. (1964) *Vistas Bot.* **4,** 187–224.
11. White, F. (1971) *Mitt. Bot. Staatssamml. Muench.* **10,** 91–112.
12. Mabberley, D. J. (1974) *New Phytol.* **73,** 967–975.
13. Mabberley, D. J. (1976) *Gard. Bull. Straits Settlem.* **29,** 41–55.
14. Nordenstam, B. (1978) *Opera Bot.* **44,** 1–84.
15. Hedberg, O. (1969) *Biol. J. Linn. Soc.* **1,** 135–148.
16. Knox, E. B. & Palmer, J. D. (1995) *Am. J. Bot.*, in press.
17. Swofford, D. L. (1993) PAUP: Phylogenetic Analysis Using Parsimony, (Smithsonian Institution, Washington, DC) Version 3.1.1.
18. Nei, M. & Li, W.-H. (1979) *Proc. Natl. Acad. Sci. USA* **76,** 5269–5273.
19. Knox, E. B. & Kowal, R. R. (1993) *Am. J. Bot.* **80,** 847–853.
20. Dupré, S., Bohlmann, F. & Knox, E. (1990) *Biochem. Syst. Ecol.* **18,** 149–150.
21. Baldwin, B. G., Kyhos, D. W. & Dvorák, J. (1990) *Ann. Mo. Bot. Gard.* **77,** 96–109.
22. Baldwin, B. G., Kyhos, D. W., Dvorák, J. & Carr, G. D. (1991) *Proc. Natl. Acad. Sci. USA* **88,** 1840–1843.
23. Crawford, D. J., Stuessy, T. F., Cosner, M. B., Haines, D. W., Silva O. M. & Baeza, M. (1992) *Syst. Bot.* **17,** 676–682.
24. Crawford, D. J., Stuessy, T. F., Cosner, M. B., Haines, D. W. & Silva O. M. (1992) *Plant Syst. Evol.* **184,** 233–239.
25. Knox, E. B., Downie, S. R. & Palmer, J. D. (1993) *Mol. Biol. Evol.* **10,** 414–430.
26. Felsenstein, J. (1979) *Syst. Zool.* **28,** 49–62.
27. Doyle, J. J. (1992) *Syst. Bot.* **17,** 144–163.
28. Evans, A. L., Fairhead, J. D. & Mitchell, J. D. (1971) *Nature (London)* **229,** 19–20.
29. Mabberley, D. J. (1971) *Kew Bull.* **26,** 33–36.
30. Sytsma, K. J. & Hahn, W. J. (1994) *Prog. Bot.* **55,** 307–333.