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***Senecio* × *saundersii* SAUER & BECK (Asteraceae), an Intermediate Hybrid Between *S. keniodendron* and *S. keniensis* of Mt. Kenya**

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With 8 Figures

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Summary

BECK E., SCHEIBE R., SCHLÜTTER I. & SAUER W. 1992. *Senecio* × *saundersii* SAUER & BECK (Asteraceae), an intermediate hybrid between *S. keniodendron* and *S. keniensis* of Mt. Kenya. – *Phyton* (Horn, Austria) 31 (2): 9-37, 8 figures. – English with German summary.

The most conspicuous representatives of the afroalpine vegetation are the arborescent *Senecios* (tribe *Senecioneae*, *S. ser. Arborei* (O. HOFFM.) C. JEFFREY), the so-called giant groundsels. Their systematic classification and phylogeny is still contested. Due to the restricted habitat and its extreme climatic conditions, ecotypes or hybrids can rapidly produce significant populations. This paper reports on *Senecio* × *saundersii*, a hybrid between *S. keniodendron* and *S. keniensis* (= *S. brassica*), groundsels which are endemic to Mt. Kenya. The population of this hybrid has substantially increased during the last 4 decades. Most of its morphological and anatomical characters are strikingly intermediate between those of the parents. The hybrid is capable of producing intact seeds which, however, could not be germinated

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under controlled condition. Since the germinative capability of one of the parents (*S. keniensis*, which occurs abundantly on Mt. Kenya) is also very small (<2%) the failure to germinate the hybrid's seeds is not a strong counter-evidence against its sexual reproductivity. Parents and hybrids were examined karyologically and the high degree of polyploidy described for two groundsel species could be confirmed and extended (52–54 bivalents), respectively. Unpaired meiotic chromosomes were found frequently with one of the parents (*S. keniensis*), rarely with the other, and not at all with the hybrid. Considering population biology, the extant hybrids must be interpreted as genuine F₁ individuals. The karyological data suggest that *S. keniodendron* may be the obligatory mother. The seeds produced by the hybrids are presumably the results of fertilization by the pollen of one of the parents, i. e. of back crossings. Further increase of the population will presumably result in the formation of introgression complexes (sensu ANDERSON 1968) which will accelerate spreading of the hybrids.

Zusammenfassung

BECK E., SCHEIBE R., SCHLÜTTER I. & SAUER W. 1992. *Senecio* × *saundersii* SAUER & BECK (*Asteraceae*), eine intermediäre Hybride zwischen *S. keniodendron* und *S. keniensis* des Mt. Kenya. – *Phyton* (Horn, Austria) 31 (2): 9–37, 8 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Baumsenecionen (*Senecioneae*, *S. ser. Arborei* (O. HOFFM.) C. JEFFREY, „giant groundsels“) sind die auffälligsten Vertreter der afroalpinen Vegetation. Ihre systematische Gliederung sowie ihre phylogenetische Einbindung in die *Senecioneae* sind noch umstritten. In ihrem jeweils kleinräumigen und von extremem Klima geprägten Habitat können sich Populationen von Ökotypen oder Hybriden schnell etablieren. Über *Senecio* × *saundersii*, eine Hybride zwischen den am Mt. Kenya endemischen *S. keniodendron* und *S. keniensis*, wird hier ausführlich berichtet, da ihre Population in den letzten Jahrzehnten erheblich angewachsen ist. Die Hybride zeigt die meisten morphologischen und anatomischen Merkmale der Eltern in frappanter Intermedarität und ist zur Samenbildung befähigt. Bisher konnte unter kontrollierten Gewächshausbedingungen jedoch kein Keimerfolg erzielt werden, was allerdings angesichts einer Keimrate von ca. 2% der Samen eines Elters (*S. keniensis*) noch kein Beweis gegen die Reproduktionsfähigkeit der Hybride ist. Eltern und Hybride wurden karyologisch untersucht, wobei sich der hohe Polyploidiegrad der Baumsenecionen weiter bestätigte (52–54 Bivalente). Ungepaarte Meiose-Chromosomen treten bei einem Elter (*S. keniensis*) gehäuft, beim anderen selten und bei der Hybride gar nicht auf. Aufgrund populationsbiologischer Überlegungen wird angenommen, daß die derzeitigen Hybriden hauptsächlich originale F₁-Hybriden sind. Aus den karyologischen Befunden ist eine gewisse Wahrscheinlichkeit für *S. keniodendron* als obligate Mutter abzuleiten. Die von der Hybride gebildeten Samen dürften nach Bestäubung durch Pollen eines der Eltern, also durch Rückkreuzung, entstanden sein. Es ist zu erwarten, daß bei einem weiteren Anwachsen der Population(en) Introgressionskomplexe (sensu ANDERSON 1968) aufgebaut werden, die sich dann rasch ausbreiten.

1. Introduction

Representatives of the arborescent *Senecios* (genus *Dendrosenecio* [HAUMAN ex HEDB.] B. NORDENSTAM), the “giant groundsels”, by their

unique megaphytic habit (COTTON 1944) above all other angiosperms contribute to the peculiarity of the so-called afroalpine vegetation of the East African high mountains. In spite of exhibiting various original characters, such as a pseudodi-(3–8)chotomously branched woody axis, each branch of which is terminated by a rosette of numerous huge leaves (“giant rosette” plants), these plants have been interpreted as derivatives of woody (MABBERLEY 1973) or herbaceous (NORDENSTAM 1978) ancestors having inhabited tropical African forests. Since the afroalpine environment strongly favours several adaptational trends of ecophysiological characters, e. g. pachycauly, special designs for cryoprotection (BECK 1987), or pollination by wind (as obvious from nodding capitula e. g. of *Senecio keniodendron*), a considerable controversy about the classification of the different taxa has accompanied the history of discovery and description. The facts that the grounds are too big for proper collection (HEDBERG 1957), that the leaves of young rosettes or from the base of an inflorescence, which could be mounted on a herbarium sheet, have proved to be atypical (HAUMAN 1935) and that flowering events are unpredictable and irregular, may have contributed to the debates as well as the difficulties of collection due to the uncomfortable access of their habitats between 3000 and 4650 m altitude a. s. l. On the basis of his own observations, as well as of the former literature, HEDBERG 1957 grouped the tree-Senecios of Mts. Kenya, Aberdare, Elgon (all Kenya), Kilimanjaro (Tanzania) and Ruwenzori (Uganda) into 11 species and 5 subspecies and later on added 6 further species (1969) which at least in part, have been recorded from other afro-alpine areas (Mt. Kahuzi, Zaire; Cherangani Hills, Kenya). In spite of that narrow-screened classification HEDBERG 1957 pointed to the large intraspecific variability “even of such characters, as are regarded as reliable criteria for specific distinction”, e. g. presence or absence of ray florets, size of capitula, size of ray florets a. s. o. MABBERLEY 1973 by referring many of the interspecific differences applied by HEDBERG 1957 and former authors to the intraspecific classification level of one species, drastically reduced the number of species to 3, viz. *S. johnstonii* OLIVER (including 10 subspecies and 2 varieties), *S. keniodendron* R. E. & T. C. E. FRIES and *S. brassica* R. E. & T. C. E. FRIES (including 2 subspecies).

However, he still maintained *Dendrosenecio* in the rank of a subgenus of *Senecio*, as did HAUMAN 1935 and HEDBERG 1957. NORDENSTAM 1978 providing a new concept of the tribe *Senecioneae*, elevated this group into the rank of a genus (*Dendrosenecio*), but apart from this followed the classification proposed by MABBERLEY 1973.

More recently, in a concept of an account of the tribe *Senecioneae* for the Flora of Tropical East Africa, JEFFREY 1986 has presented a renaissance of the nomenclature of the tree-Senecios, which, following the revision of MABBERLEY 1973 were treated as 3 species of *Senecio* (*S. johnstonii*,

S. keniodendron and *S. keniensis*) and combined into the Ser. *Arborei* (O. HOFFM.) C. JEFFREY.

Apart from some modifications of the subspecies (4) and variety (13) concepts of *S. johnstonii* OLIV., the most incisive change was the renomination of the well introduced *Senecio brassica* R. E. & T. C. E. FRIES (more recently *Dendrosenecio brassica* [R. E. & T. C. E. FRIES] B. NORD.) as *Senecio keniensis* BAKER. As avowed by JEFFREY 1986 a phyletic interpretation of the system of the arborescent *Senecios* is impossible at the present state of knowledge.

While the origin of some of the subspecies may be attributable to an antagonism of evolutionary differentiation and ecophysiological adaptation, hybridization may be responsible for another portion of closely related taxa. Thus three hybrids have been encountered in the overview of *S.* subgen. *Dendrosenecio* provided by HEDBERG 1969, namely *S. elgonensis* × *S. barbatipes*, *S. brassica* × *S. keniodendron* and *S. erici-rosenii* × *S. adnivalis* var. *alticola*. The latter, occurring quite frequently on the Virunga volcanoes may have expanded its area to Mt. Kahuzi (Zaire) where it forms the only representative of the tree *Senecios*, which has been designated *S. kahuzicus* HUMB. (now termed *S. johnstonii* subsp. *adnivalis* (STAPF) var. *erici-rosenii* (R. E. & T. C. E. FRIES) C. JEFFREY). From the other two hybrids, only single specimens have been observed (HEDBERG 1957, 1969) which by strikingly intermediate characters have been recognized as hybrids. While in the case of the former *S. kahuzicus* sexual reproduction of the hybrid is unquestionable, nothing is known in that respect of the other two.

This communication reports on that groundsel which appears to represent HEDBERG's *S. brassica* R. E. FRIES & Th. FRIES jr. × *S. keniodendron* R. E. FRIES & Th. FRIES jr. and has been recorded in JEFFREY's notes as *Senecio keniensis* BAKER subsp. *keniensis* × *S. keniodendron* R. E. & T. C. E. FRIES. The identification was established from a photograph (HEDBERG 1957), from some characters listed later on by the same author in a table (HEDBERG 1969) and by a note on the herbarium voucher. From HEDBERG's note (1957) that it is only known from three collections one might assume that this potential hybrid occurs but rarely. However, since 1979 it has been observed by two of the authors in relative high numbers at all locations of

Fig. 1. a The oldest specimen of the hybrid *Senecio keniodendron* × *S. keniensis* (= *S. × saundersii*) in the Teleki valley of Mt. Kenya near the former Teleki Hut. Note the insulation of the stem by the dense mantle of dead leaves. The stem fork indicates that the groundsel has been flowering once. Originally 4 branches were produced, 3 of which were still intact in 1985. In 1986 the left one died. In 1991, this specimen had collapsed totally. Photo E. BECK, February 1985. – b Flowering specimen of the hybrid groundsel, Mt. Kenya, Teleki valley. – Photo E. BECK, March 1979. – c Achenes of the hybrid as selected into 3 categories: Intact/mature (right), interrupted development (middle) and incomplete/damaged (left). Photo I. SCHLÜTTER.

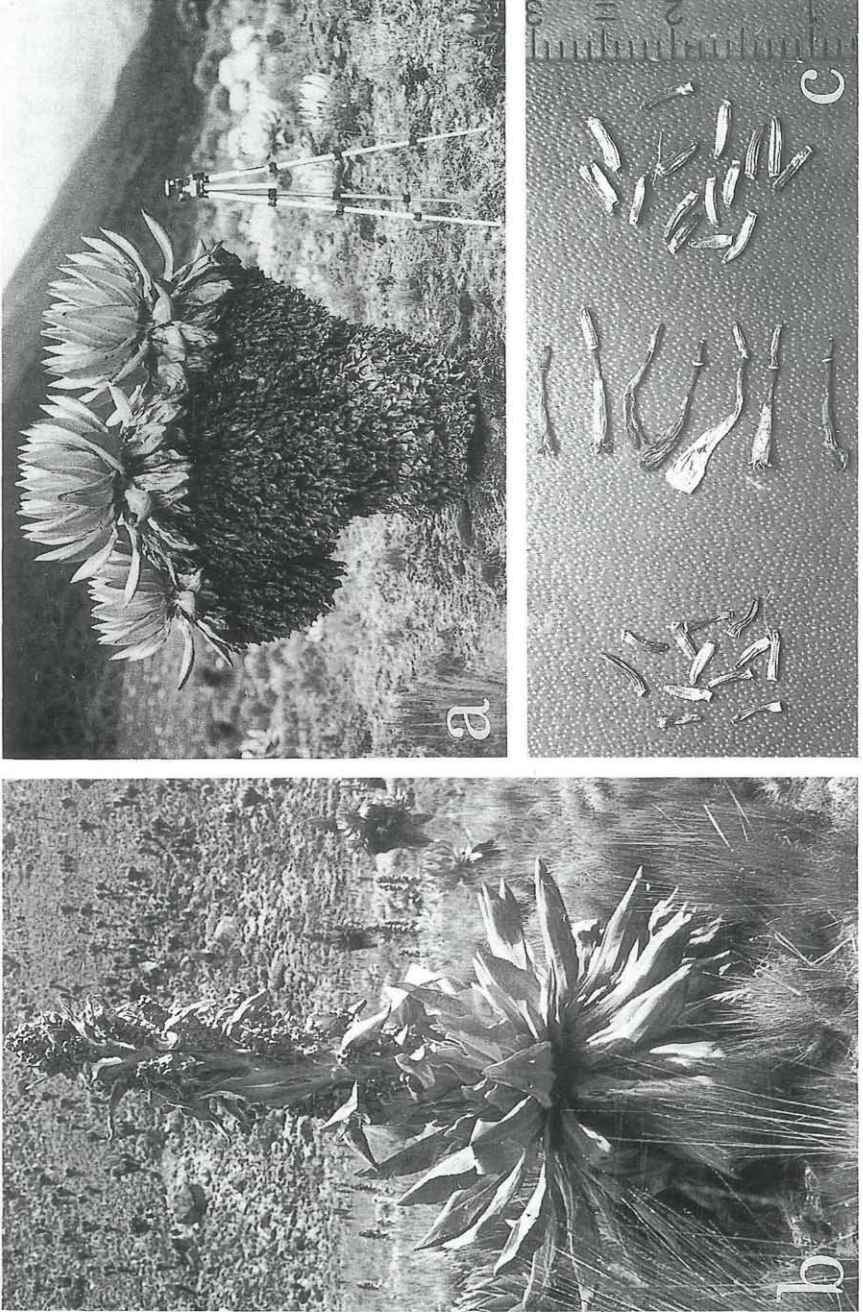


Fig. 1.

Mt. Kenya where the presumptive parent populations intermingle. Unlike *S. kahuzicus*, it has never been found in other places than Mt. Kenya, a fact which might be attributable to the endemism of the parents to this mountain as well as to a very recent origin of the hybrid. It should be mentioned that both presumptive parents represent two of the extant three species of arborescent *Senecios*. *S. keniiodendron* is a monotypic species. The other parent, according to JEFFREY has been granted the rank of a subspecies, namely *S. keniensis* subsp. *keniensis* which is also endemic on Mt. Kenya while the other subsp. *brassiciformis* (R. E. & T. C. E. FRIES) C. JEFFREY is endemic to the Aberdare mountains (for the rank of these taxa see chapter 4). Thus, both parent species are well separated from the Formenswarm of *S. johnstonii*, which are found on the other East and Central African high mountains. Highly polyploid chromosome numbers seem to be characteristic at least of some of the species and subspecies of the Ser. *Arborei* (HEDBERG & HEDBERG 1977). For a satisfactory solution of the taxonomic problems also the less known species should be reinvestigated morphologically as well as karyologically. Not alone the knowledge of chromosome numbers is required, but rather detailed analysis of the whole karyological syndrome, especially the occurrence and the probable effects of additional chromosomes, and the special behaviour of the chromosomes during the meiosis, perhaps, will bring essential insights.

In this communication we present three aspects which are essential for the understanding of the hybrid of *S. keniiodendron* and *S. keniensis* (nothospecies name *S. × saundersii*), namely a detailed morphological and where meaningful anatomical comparison with the parents, a karyological study and finally a compilation of observations pertinent for the population biology of the three groundsels.

2. Material and Methods

The investigations in the field were performed during a series of research expeditions to Mt. Kenya from 1979 until 1986. For counting of the individuals the same areas were inspected in the subsequent years.

Achenes were collected by Mr. Christopher CHESENY CHEBEL, Voi, in the last year 1979. Fig. 1c shows the 3 categories of achenes, into which the seeds were selected.

For the examination of the embryos 50 achenes of each category were soaked in water and then treated under the dissecting microscope.

2.1. Karyologically Investigated Plants

Senecio keniiodendron

Kenya, Mt. Kenya, Teleki valley; 100 m west of the former Klarwill Hut; 4200 m; 4. 3. 1985; leg. E. BECK.
 n = 50; n = 52_{II}, 52_{II} + 1 fragment; n = 52_{II} + 1_I or 5_I; n = 54_{II}.

Senecio keniensis

Kenya, Mt. Kenya, Teleki valley, appr. 300 m NE of the former Teleki Hut; 4150 m; 4. 3. 1985; leg. E. BECK. n = 52_{II}, 52_{II} + 3_I-6_I.

Senecio × saundersii

Kenya, Mt. Kenya, Teleki valley;

“Hybrid 1”: appr. 300 m east of the former Teleki Hut; 4160 m; 18. 2. 1985; leg. E. BECK. 2n = 101-105, 110-114; n = 52_{II}, 54_{II}.

“Hybrid 2”:—; leg. E. BECK: n = 52_{II}.

“Hybrid 3”: appr. 400 m east of former Teleki valley Hut; 4150 m; 10. 2. 1985; leg. E. BECK: n = 52_{II}, 54_{II}.

2.2. Germination Test

For the germination tests a soil was prepared from mould, sand, pumice and peat (1 : 1 : 1 : 1). 100 seeds of one category were sown 6 to 7 times within a period of a year into pots, carefully watered and the germination success was recorded weekly. The pots were kept in the greenhouse of the Botanical Garden Bayreuth at 18–26° C during the day and 12–18° C during the night. 3 pots, sown with *S. keniensis* for stratification were maintained for several weeks in a refrigerator at +3° C, however without increase of the germination rate.

2.3. Karyological Studies

Flower buds of different size and age were fixed in the field (about at 6 p.m.) parallelly in mixture A (96% ethanol: glacial acetic acid = 3 : 1) and mixture B (ethanol: chloroform: glac. a. a. = 6 : 3 : 1 or 2).

After three weeks the fixation fluid was substituted by 70% ethanol and after the samples were brought into the laboratory, the material was stored for 3–5 months at –20° C. For the preparation of pollen mother cells (PMC) the anthers were collected from 4–4,5 mm long flower buds. After staining with hot carmino acetic acid (DARLINGTON & LACOUR 1963) the PMCs were squashed (SAUER 1975). After incubation in isopropanol for 24 h the coverglasses of the slides were sealed with Euparal.

Also somatic chromosome numbers could be determined either in archesporial cells of younger/smaller anthers or in elements of the ovules (integuments, nucellus). Full staining of both, somatic chromosomes and bivalents, was attained after some days. Thereafter also the cytoplasm irreversibly accumulated higher concentrations of the dye.

A troublesome tendency to stickiness of the chromosomes/bivalents complicated the microscopical analysis (cf. AFZELIUS 1924, 1949, Fig. 7).

2.4. Vauchers

Vauchers of the collected plants were deposited in the Herbarium of the Ökologisch-Botanischer Garten der Universität Bayreuth (UBT). Further material could be checked from the collections K = Herbarium of the Royal Botanic Gardens, Kew, NAIROBI = East African Herbarium, Nairobi, Kenya, M = Botanische Staatssammlung, München, UPS = Herbarium of the Institute of Systematic Botany of the University, Uppsala, Sweden, and the private collection Sa = Herbarium W. SAUER, Tübingen, Germany.

3. Results

3.1. Morphology and Anatomy

3.1.1. Stem

Whereas *S. keniensis* is a plant with a creeping, rhizomatous stem, both *S. keni dendron* and the hybrid produce an erect stem. The tallest giant groundsels grow about 10 m high (BECK & al. 1984). The biggest non-flowering stem of the hybrid was approximately 1,2 m high (Fig. 1 a). The erect stems are usually covered by a dense mantle of marcescent leaves which insulates the living stem tissue against the nocturnal frost. Each axis and branch is crowned by a huge leaf rosette ("giant rosette plants") which under suitable conditions produces a terminal 1.0 to several meters tall inflorescence (Fig. 1 b). After flowering the vegetation point of the leaf rosette is exhausted and the leaves die concomitantly with the maturation of the achenes. During this process lateral buds appear around the base of the inflorescence from which new leaf rosettes develop and thereby initiate branching of the axis. Hence, each stem fork or branch story testifies a former flowering event. The degree of stem branching as a result of the number of lateral buds appears to be characteristic of the various species: While *S. keniensis*, presumably as an adaption to its rhizomatous stem, produces a comparably high number of lateral branches, *S. keni dendron* has been described as a sparsely branched tree (HEDBERG 1957). From a series of countings an average number of 4.8 (± 0.83) stem branches per inflorescence was calculated for *S. keniensis* and of 3.3 (± 0.75) for *S. keni dendron* while the hybrid was intermediate (4.2 ± 1.3). This means that 5 branches per storey were most frequently counted on *S. keniensis* and that the respective figures were 4 for the hybrid and 3 for the giant groundsel.

3.1.2. Leaves

Apart from venation, the anatomy of the dorsiventral leaves of the three groundsels shows identical features such as a multiple upper epidermis and several layers of palisade parenchyma. The only anatomical character which is useful for the differentiation is the distribution of the stomata. The leaves of *S. keniensis* and of the hybrid are hypostomatous while those of *S. keni dendron* are amphistomatous though with a numerical preponderance of the stomata on the lower leaf surface.

The morphological characters of the leaves vary significantly and some are effective in the identification of the species. Leaves of a comparable developmental stage must be used for the purpose because, at least with the giant groundsel and the hybrid, broadening of the petiole into its extremely wide and phylloid wings lags considerably behind the growth of the lamina (Fig. 2 a). This is a typical feature of the leaves of the groundsels which has

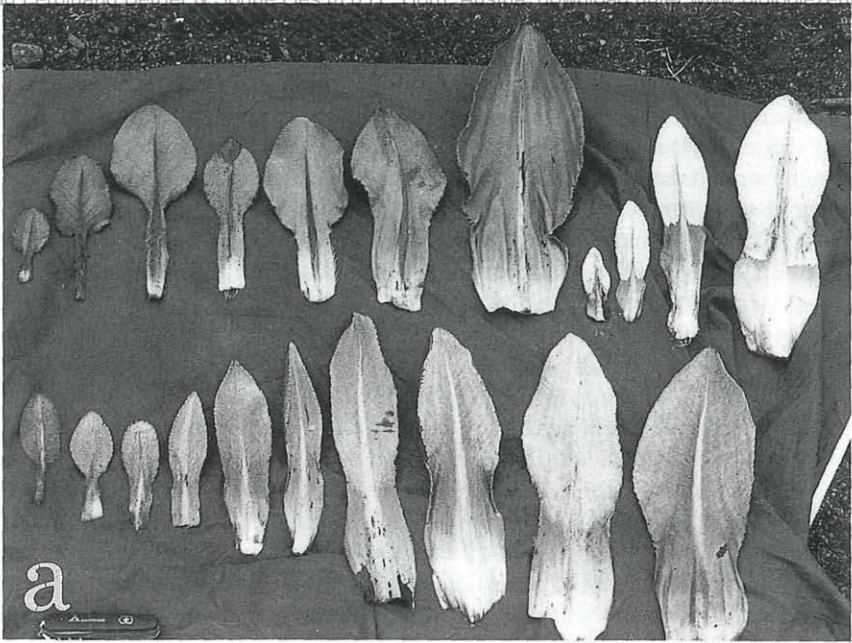


Fig. 2. a Sequence of development stages of leaves of *Senecio kenioidendron* (upper series, Nos. 1–7), of *S. keniensis* (upper series, Nos. 8–11) and of the hybrid (lower series, Nos. 1–10). The lower (abaxial) leaf sides are shown. Photo R. SCHEIBE, March 1979. – b Adult leaves and segments of the respective inflorescences of *S. kenioidendron* (Nos. 1 and 2 from left), *S. kenioidendron* \times *S. keniensis* (No. 3) and *S. keniensis* (No 4). The upper (adaxial) leaf sides are shown. Photo R. SCHEIBE, March 1979.

been investigated with respect to growth zones and venation by MABBERLEY 1973. The sequential development of the lamina and the phylloid wings is impressively shown by the delineation of the indumentum on the abaxial leaf side of *S. keniensis* and of the hybrid. Only the lamina is covered by a tomentum of unbranched multicellular hairs which is sharply set off against the glabrous wings, and, with *S. keniensis*, the lower part of the midrib (Fig. 2 a and 8 d). In *S. keniensis* the development of the indumentum starts very early and finally produces a 1–2 mm thick felt. With the hybrid it commences concomitantly with the development of the wings and its final density is significantly lower than in *S. keniensis*. The abaxial leaf side of *S. keniodendron* is glabrous except the original petiole which produces long, curled, yellow hairs (Fig. 2 a and 8 a). On a first glance, the abaxial leaf side of *S. keniodendron* is green and shiny, while that of the hybrid appears greyish and that of *S. keniensis* is snow-white.

On the contrary, the upper leaf sides of *S. keniodendron* and the hybrid are faintly pubescent and therefore appear dull yellowgreen. The upper lamina of *S. keniensis* is leathery and dark green but sporadically at the edges and on some veins remnants of a cobwebby white indumentum are to be seen. The upper sides of the wings of all 3 groundrels carry long silk brown (*S. keniodendron* and the hybrid) or white (*S. keniensis*) hairs (Fig. 2 b and 8 a–b, d–f).

3.1.3. Roots

S. keniensis which inhabits the moorlands and the wet valley floors produces two types of roots on its rhizomatous stem, namely: I) ordinary adventitious roots with secondary growth and a brownish cork layer on the surface of the older parts, and II) whitish roots which frequently appear to react negatively geotropically. Both types of roots exhibit a multi-layered cortex with conspicuous intercellular spaces. The whitish roots are of a spongy consistence due to the fact that the main intercellular spaces com-

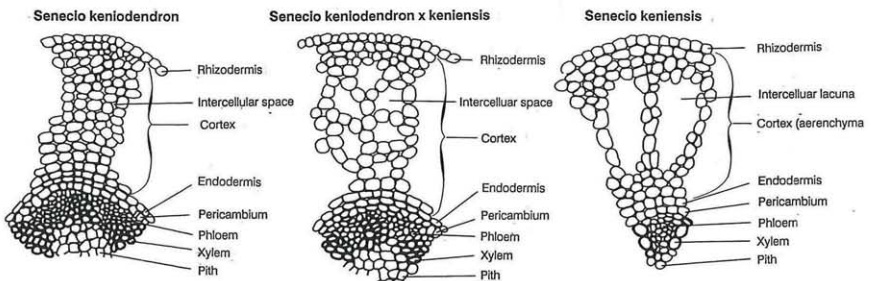


Fig. 3. Segments of cross-sections of roots of *Senecio keniodendron* (a), *S. × saundersii* (b) and of the pneumatophore-like root of *S. keniensis* (c). – Drawings from authentic material by W. SÖLLNER (Bayreuth) and E. BECK.

bine to form channels and thereby give rise to a typical aerenchyma (Fig. 3c). The ordinary roots show pentarch, the pneumatophore-like roots heptarch vascular bundles. *S. keniendendron*, inhabiting the well-drained valley slopes produces a normal tap root system with substantial secondary growth. The cortex of its roots does not show extraordinary intercellular spaces. The vascular bundle is pentarch (Fig. 3a). The hybrid, which frequently grows in moist areas, has a tap-root system, too. Special pneumatophore-like roots, as with *S. keniensis* could not be detected. However, the cortex parenchyma, like the cortex of the ordinary roots of *S. keniensis* is rich in large intercellular spaces which, although not forming an aerenchyma, enable the root to inhabit poorly aerated soils. The vascular bundles were heptarch to polyarch (Fig. 3b).

3.1.4. Inflorescence

The branches of the woody paniculoid thyrses (JEFFREY 1986) of the three groundsels are covered by a creamy white indumentum the density of which corresponds closely to the indumentum of the lower side of the adult leaves. Thus, in the case of *S. keniensis*, it densely covers all branches and branchlets and also the peduncles of capitula. The inflorescence of *S. keniendendron* is scarcely pilose, the indumentum being very incomplete. The hybrid shows a complete indumentum which, however, is significantly less compact than in the inflorescence of *S. keniensis*.

3.1.5. Floral characters

Apart from the habit and the tomentum on the lower leaf surface, the structure of the capitula of the three groundsels is very characteristic. While *S. keniensis* produces disc and ray florets as well, the latter are completely missing in the capitula of *S. keniendendron* (Fig. 2b and 8b). The hybrid shows several rudimentary ray florets from which maximally one was found to be completely developed.

Table 1 presents a synopsis of the various floral characters of the three groundsels by which the hybrid proved as an almost ideal intermediate between the presumptive parents. As stated by MABBERLEY 1973, the venation of the ligule of *S. keniensis* varies considerably between 2 and 8 with a dominance of 4 veins per ligule; the same figure was given for the ligule of the hybrid.

3.1.6. Achenes

With respect to the question whether the hybrid is capable of reproduction the examination of the achenes is of particular interest. The hybrid as well as both presumptive parents produce numerous achenes per capitulum which correspond to the respective number of florets. When the achenes

Table 1

Floral characters of *Senecio keniensis*, *S. keniodendron* and the hybrid. (M = MAB-BERLEY 1973)

Species	Diameter of capitula (mm) (without ray florets)	Number of disc florets	Number of ray florets	Ligule length (mm)
<i>S. keniensis</i>	13 –14.5	70±1.4 70–75(M)	(4)–7–13	15 13.5–20(M)
<i>S. keniodendron</i>	15.5–21.6	178±4.6 170–240(M)	–	–
<i>S × saundersii</i>	14.4–18	118±5	1 (5)	7–12

Table 2

Quality of the achenes of *Senecio keniensis*, *S. keniodendron* and the hybrid as indicated by the categories 1 (complete, fully developed), 2 (interrupted maturation), and 3 (damaged) – see also Fig. 1c.

Category	<i>S. keniensis</i>	<i>S. keniodendron</i>	<i>S × saundersii</i>
1	66.0±1.6(%)	88.3±0.6(%)	41.0±1.2(%)
2	5.8±0.8(%)	1.9±0.2(%)	27.3±1.3(%)
3	28.2±1.7(%)	9.8±0.6(%)	31.7±1.2(%)
Number of examined achenes	3298	10420	5463

Table 3

Characters of the complete achenes of *Senecio keniensis*, *S. keniodendron* and the hybrid; Number of veins: The number with the highest frequency is given in brackets. * Unfortunately, the exact size of the embryo of *S. keniensis* was not exactly measured as with the others in the scanning electron microscope.

Characters	<i>S. keniensis</i>	<i>S. keniodendron</i>	<i>D. × saundersii</i>
Colour	dark brown	light brown	golden brown
Length of achenes (mm)	4.93±0.2	4.34±0.2	3.61±0.2
Number of veins (ribs)	7.96±0,3(8)	7.34±0.3(7)	8.66±0.3(9)
Proportion (%) of achenes with intact embryo	25±10.9	56±12.5	62±12.95
Length of intact embryo (mm)	not measured*	6.5	3.5

from various capitula were investigated three categories of quality were quite obvious: 1. Completely developed achenes, 2. achenes the maturation of which was interrupted at an early stage and which therefore maintained the corolla, and 3. collapsed or otherwise damaged achenes (Fig. 1 c). Tab. 2 shows the distribution of the achenes from the three investigated groundsels over these 3 categories. From the hybrid, the proportion of intact achenes is strikingly low as compared with those of the parents. In particular, the number of the achenes showing incomplete development is extremely high, indicating a remarkable frequency of disordered fertilization and maturation processes. These achenes never contained embryos. On the other hand the proportion of the (intact) achenes with a complete embryo was comparably high with the hybrid and with *S. keniodendron*, but very low in *S. keniensis*. This and other characters of the achenes are documented in Table 3. With respect to the pappus a difference could not be observed between the three groundsels: The pappus consists of withish unbranched and brittle setae which emerge in two concentric circles from the upper plate of the achene. Similarity of the three groundsels could further be established for the epidermis of the achenes on the one hand and of the embryos on the other. The former consists of long cylindrical cells while that of the latter is formed from isodiametric cells.

However, the size of the complete achenes of the hybrid was strikingly smaller than that of the parents achenes and the same holds true for the embryos.

3.2. Germination tests

Achenes of the first category which had been collected in Teleki valley (Mt. Kenya) in October 1979 were sown in the greenhouse for the first quarter of the year monthly and later on in intervals of 2–3 months between February 1980 and March 1981. The germinative capability of *S. keniensis* and *S. keniodendron* extinguished within that time-span. The maximal extent of germination was approximately 30% with *S. keniodendron* and 2,3% with *S. keniensis*. Although 1600 achenes of the hybrid were examined, germination could not be achieved. Two quite different explanations of this phenomenon are conceivable: I) Incompatibility of the parents' genes which initiate germination. In that case all specimens of the hybrids are genuine F₁ generation. II) The germinative capability is extremely shortlived and was already gone when the germination experiments begun. This explanation is not unlikely, because with *S. keniensis* the maximum germination success (2,3%) was achieved right upon the first sowing, i. e. 5 months after seed maturation and with *S. keniodendron* one month later. In addition, incompatibility of germination-effective genes should also impair the development of the original F₁ seeds what obviously is not the case. Therefore, the explanation of our failure to raise the hybrids from seeds as being due to a

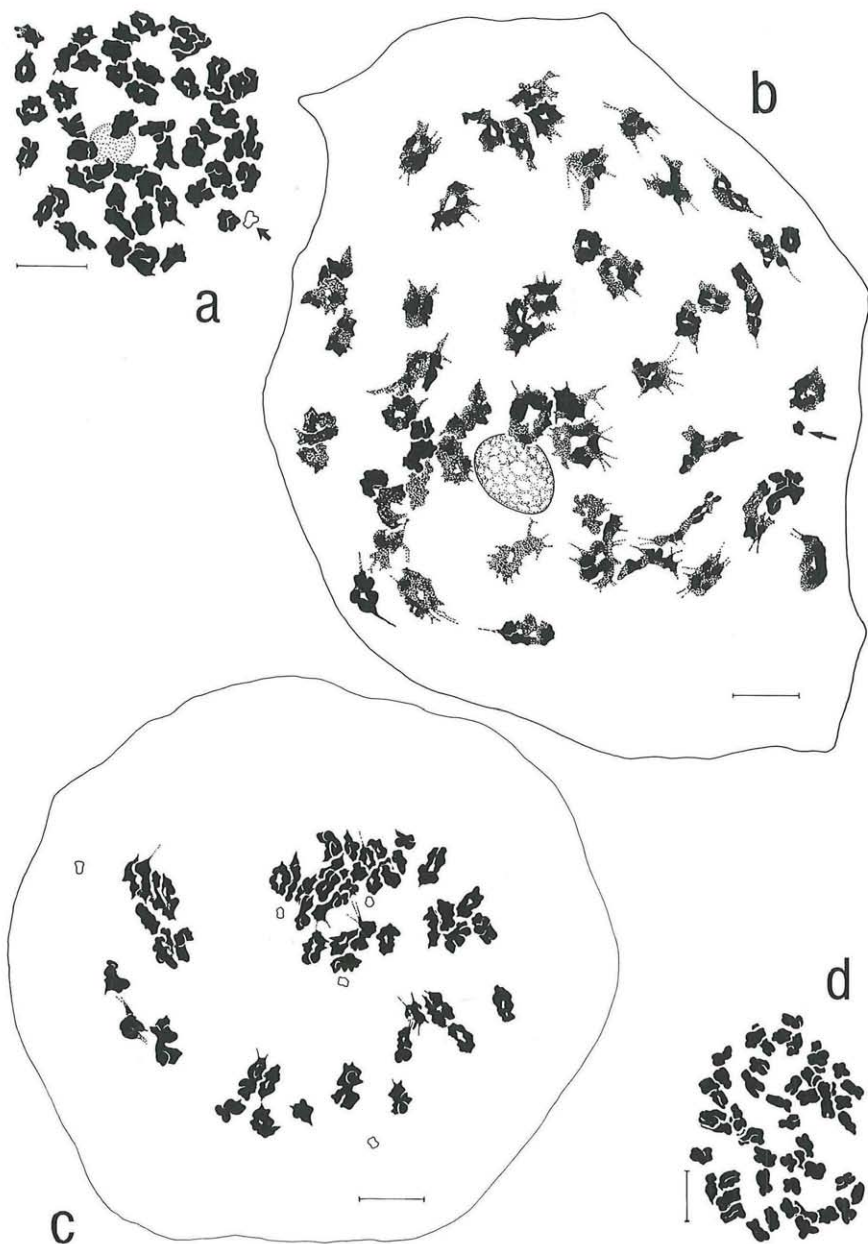


Fig. 4. *Senecio keniodendron*. – a–c Meiosis of PMCs. – a Diplotene ($n = 52_{II} + 1_I$, blank and arrow). – b Diakinesis ($n = 52_{II} + 1$ fragment, arrow). – c Diakinesis/Meta I ($n = 53_{II} + 5_I$, blank). – d Metaphase of the first pollen mitosis ($n = 50$). – Drawings by W. SAUER. – Scale bars = 10 μ m.

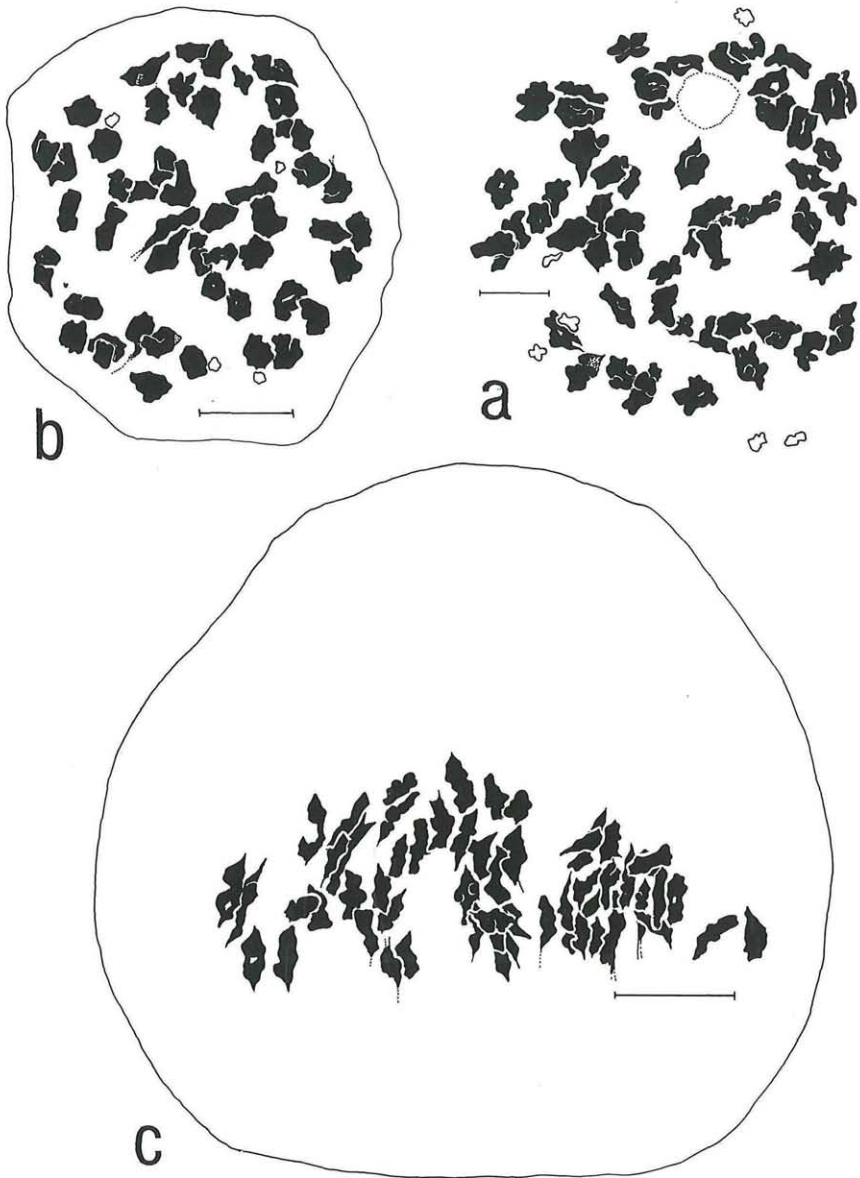


Fig. 5. - a, b *Senecio keniensis*, Meiosis of PMCs. - a Diplotene ($n = 52_{II} + 6_I$). - b early MetaI ($n = 52_{II} + 4_I$). - c *S. x saundersii*, meiosis of PMC, MetaI/AnaI ($n = 54_{II}$). - Drawings by W. SAUER. - Scale bars = 10 μ m.

genetic incompatibility is less probable than the idea that the germinative capability of the seeds was already expired half a year after seed maturation.

3.3. Karyology

First chromosome counts of East/Central African groundsels have been reported by HEDBERG & HEDBERG 1977 for *Senecio keniodendron* ($2n = 10x = 100$), *S. johnstonii* subsp. *elongensis* ($2n = 10x = 100$) and subsp. *cheranganiensis* ($2n = 8x = 80$ and $2n = 2x = 20$).

Following ORNDUFF & al. 1963, 1967 and THULIN 1970, HEDBERG & HEDBERG 1977 attributed the high polyploid chromosome number to the basic chromosome number $x = 10$, which within the tribe *Senecioneae* should be more primitive than the (apparently advanced) basic number $x = 5$ (cf. TURNER & LEWIS 1965, NORDENSTAM 1978).

SCHLÜTTER (unpubl.), however, found aneuploid somatic chromosome numbers in *S. keniodendron*, *S. keniensis*, and within the hybrid complex, namely $2n = 100 \pm 14$. In one of the hybrids investigated in the present work ("Hybrid 1") this number could be corroborated: $2n = 101-105$ or $110-114$.

Although in *S. keniodendron* and *S. keniensis* as well as in the hybrids the bivalent chromosomes apparently have a relatively high tendency of stickiness (Fig. 7b and d), the majority of 53 carefully examined PMCs (Table 4) contained gemini ($n = 52_{II}; = 63\%$), one of which with an additional small fragment (Fig. 7b). Further, 1-5 additional univalent (or "B"?) chromosomes were detected in two of the sixteen examined samples from *S. keniodendron* (Fig. 4a-c) and at least in 90% of *S. keniensis* (Fig. 5a-b), while the plants of the hybrid complex are clearly devoid of "extrachromosomes" (Fig. 5c, 6; Table 4). Apparently the meiosis of the hybrids proceeds in a normal way. Characteristic disturbances of the meiosis were never seen in our material. In the first meiotic prophase the ratio of laggards (Fig. 4-7) and/or of unpaired chromosome - segments was similar in *S. keniodendron*, *S. keniensis* and in their hybrids. The same phenomenon was found in other genera, for instance in West European *Pulmonaria* species. In those cases BOLLIGER 1982 could demonstrate, that the pollen fertility of artificial (F_1) hybrids reached significantly higher proportions than those of the parents. As of yet a satisfactory explanation of the presumed disadvantage of extrachromosomes in a hybrid PMC can not be offered. But it could hint to a regularly loss of additional chromosomes during the PMC meiosis. Further investigations of the EMC meiosis, especially of the parents, would be required in particular with respect to a possible irregular distribution of the extrachromosomes into one of the dyad cells.

It is conceivable to interpret the relatively high number of additional chromosomes in *S. keniensis* in connection with apparent difficulties in the

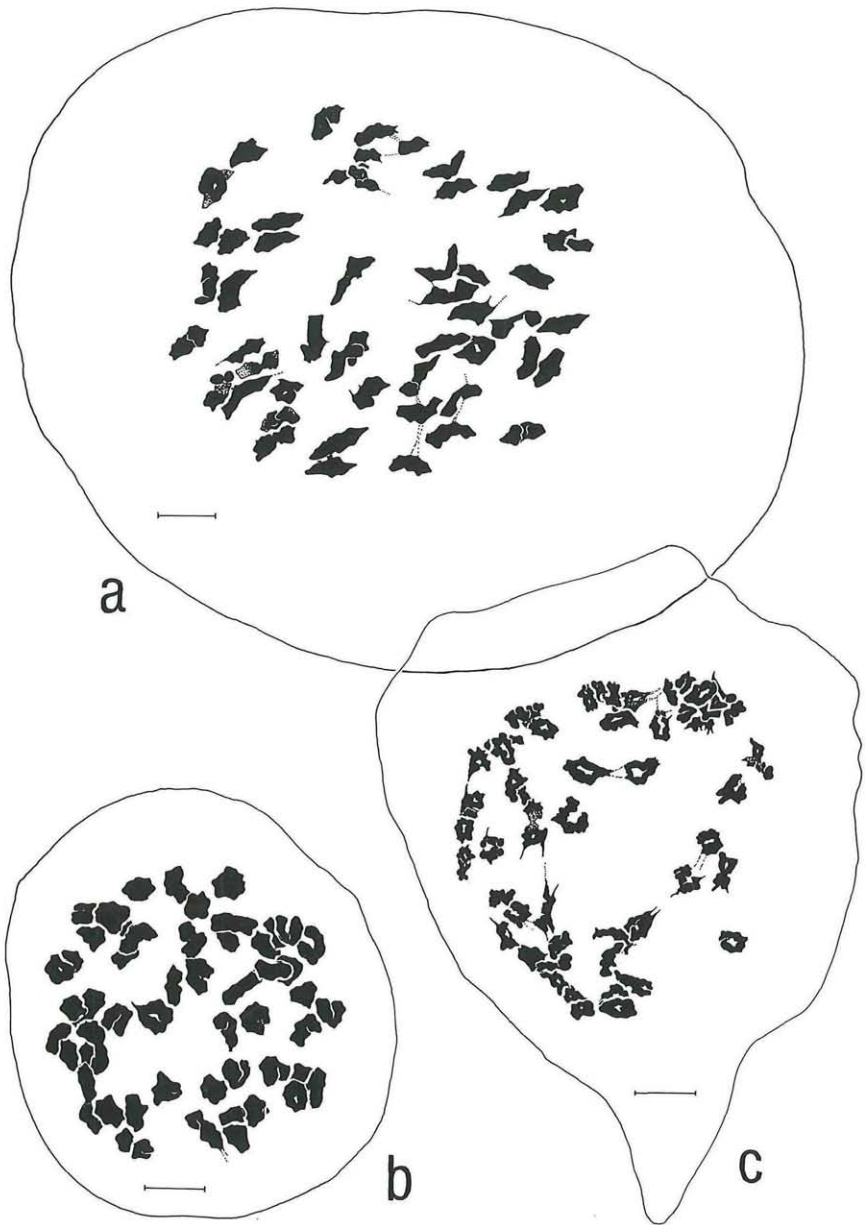


Fig. 6. Hybrids of *Senecio keniodendron* \times *S. keniensis* (= *S. \times saundersii*). – Meiosis of PMCs. – a “Hybrid 1”, MetaI/AnaI ($n = 52_{II}$). – b “Hybrid 2”, Diplotene/Diakinesis ($n = 52_{II}$), c “Hybrid, ältere Fixierung” (= “Hybrid 1”/“Hybrid 2”), Diplotene/MetaI ($n = 52_{II}$). – Drawings by W. SAUER. – Scale bars = 10 μ m.

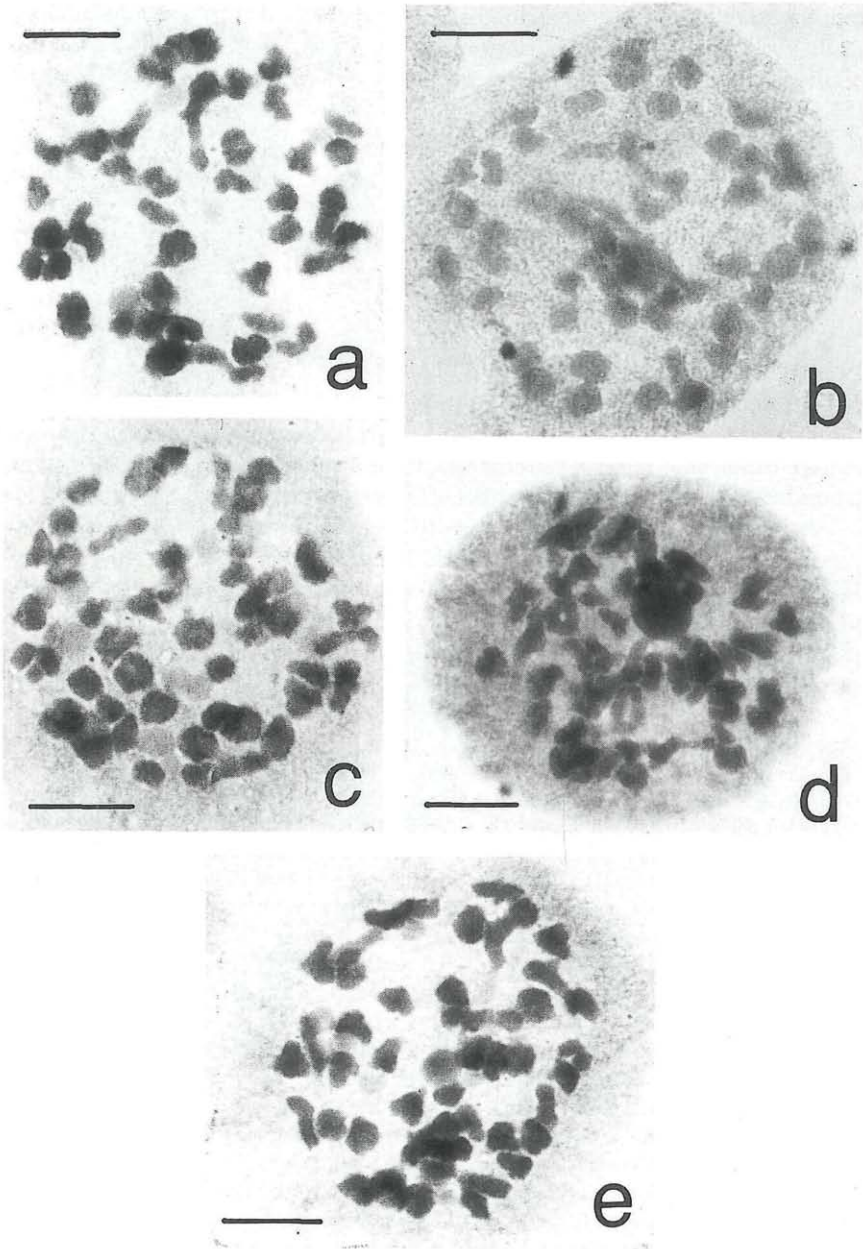


Fig. 7. Microphotographs of the meiosis of PMCs. – a *Senecio keniodendron*, Diakinesis/MetaI. – b *S. keniensis*, Diakinesis. – c *S. keniodendron* × *S. keniensis*, “Hybrid 1”, Diakinesis/MetaI. – d “Hybrid 3”, Diakinesis. – e “Hybrid 2”, Diakinesis/MetaI. – Fig. a by transmission light, Fig. b–e by phase-contrast. – Microphotographs by W. SAUER. – Scale bars = 10 μ m.

- 3 Stem stout, up to 5–6–10 m; length of rosette-leaves up to ± 60 cm, amphistomatous, lower surface of lamina green and shining, petiole and lower part of midrib on the upper (adaxial) surface with long curled yellow hairs; capitula with 170–240 tubular florets nodding. Endemic to alpine belt of Mt. Kenya. 1. *S. keniodendron*
- 3* Stem slender, up to 1.2 m; length of rosette-leaves up to ± 41 cm, hypostomatous, lower surface of lamina with a greyish, \pm less dense indumentum; capitula with many (ca. 120) tubular florets and also with few rather rudimentary ray florets. – Alpine belt of Mt. Kenya, in between the parents (1) and (2). 4. *S. \times saundersii*

4.1. *Senecio keniodendron* R. E. & T. C. E. FRIES

(Fig. 8a–b)

Nomenclature, type, synonyms v. JEFFREY 1986: 892.

Description: Perennial, tree-like giant rosette plant; – stem stout, the upper parts with a dense mantle of marcescent leaves, erect, up to 5–6–10 m, with sparse branching; – tap root system with secondary growth, bundles pentarch; – rosette leaves entire, coriaceous, with glabrous laminae, \pm (28) 38 (44) \times (15) 16 (20) cm (up to 60 cm long), $L_i = \pm 2.19$, amphistomatous; young leaves with a broad triangular-ovate lamina, suddenly tapering into the very narrow winged petiole, petiole $\frac{2}{8}$ – $\frac{1}{2}$ of total leaf length; adult leaves (somewhat) panduriform, lamina (ca $\frac{3}{4}$ of the total length), broad ovate, with 25–35 pairs of veins, apex rounded or broadly acuminate, margin \pm serrate dentate except of the upper $\frac{1}{2}$; petiole (ca $\frac{1}{4}$ of the total leaf length) with phylloid wings, nearly as wide as the lamina (± 13 – 15 cm or more), margins partly \pm dentate-serrate; upper surface dull yellow-green with long brown silky hairs on midrib and lower part of petiole; lower surface green and shiny, sparsely hairy except the petiole, which is covered by long yellow curled hairs; – inflorescence terminal, paniculoid thyrses, 1 m or more, the creamy-white indumentum very patchy, scarcely pilose; – bracts narrow linear-lanceolate; – capitula numerus, nodding, living cup-shaped, 15.5–22 mm (in herbarium specimens [20–] 27 [–34] mm) in diameter, involucrem dark purple, with ± 178 (170–240) tubular florets; – achenes light brown, mostly 7-costate, ± 4.3 mm long; – chromosome numbers: $2n = \pm 100$, 100 ± 14 ; $n = 50$, 52_{II} , $52_{II} + 1$ fragment, 54_{II} . – Endemic to the alpine belt of Mt. Kenya (East Africa), growing on well drained valley slopes between 3800–4500 m.

There do exist three records of *S. keniodendron* from the Aberdare Mts. According to FRIES & FRIES 1948: 79–80 (1) the specimen of DALE no. 2849 (on Sattima, 12500 ft.) may refer to *S. brassiciformis*, while they could not identify the other record (2) of J. G. RAMMELL no. 3063 (Aberdare, Jan. 1933; K). But following K. SCHMITT (recent personal commun.) the last mentioned specimen, just as (3), the record of TAYLOR no. 1334, “Aberdare” (DALE & GREENWAY 1961: 160) might refer to *S. johnstonii* subsp. *battiscombei* var. *battiscombei*, which produces rosette leaves, both with glabrous and/or tomentose lower surface; but both types of leaves with 15–18 pairs of veins.

Herbarium specimens examined: East Africa. Kenya, Central Province, Nanyuki-District: Mt. Kenya, Nanyuki-Chagoria Track, 13.000 ft., 19. 6. 1843, leg. Mr. & Mrs. R. E. MOREAU 151 (K). – Teleki Valley, 100 m west of former Klerwill Hut, 4200 m, 4. 3. 1985, leg. E. BECK (UBT). – Teleki Valley, Südabhänge mit Paramo-Vegetation oberhalb des Mackinder's Camp, 4100–4300 m, 29. 3. 1974, leg. G. & W. SAUER 18.219 (Sa). – Teleki Valley, alpine region, at the edge of Teleki tarn, 4350 m, 28. 7. 1948, leg. O. HEDBERG 1726 (K, UPS). – Mt. Kenya, afroalpine Zone, 4000 m, 9. 9. 1978, leg. J. GRAU 1849 (M). – In alpine belt of Mt. Kenya, 13.000 ft., 31. 1. 1959, leg. E. M. v. ZINDEREN BAKKER 933 (K). – Rocks east of Caesar's Seat, 12.700 ft.; 15. 6. [19]35; leg. C. G. ROGERS (K).

4.2. *Senecio keniensis* BAKER

(= *S. brassica* R. E. & T. C. E. FRIES)

(Fig. 8d)

Nomenclature and type v. JEFFREY 1986: 892.

Synonyms: Hitherto known synonyms v. JEFFREY 1986: 892, furthermore: *Senecio keniensis* BAKER subsp. *keniensis* C. JEFFREY in Kew Bull. 22: 892 (1986).

Description: Perennial dwarf giant rosette plant; – stem subterranean, a relatively thin, creeping, branching, and rooting rhizome; – with 2 types of roots (1) ordinary adventitious roots with secondary growth and brown cortex layer on the surface of elder parts, vascular bundles pentarch, (2) pneumatophore-like, frequently negatively geotropically growing whitish roots of spongy consistence (aerenchyma), vascular bundles heptarch; – rosette leaves entire, leathery, \pm (23–) 35 (–39) \times (11–) 14 (–18) cm, $L_i = 2.50$, hypostomatous; lamina (ca. $\frac{2}{3}$ of total leaf length), broad ovate-lanceolate, \pm acuminate and somewhat contracted to the base, slightly panduriform, margin throughout serrate-dentate, 15–18 pairs of veins, venation non confluent with that of petiole; petiole (ca. $\frac{1}{3}$ of total leaf length), with very broad \pm membranaceous lamina-like wings (\pm 7–11 cm [top] or \pm 6–9 cm [base] wide); upper leaf surface dark green, nearly glabrous or only on margin and some veins with sporadical remnants of a white cobwebby indumentum; lower surface: only lamina snow white, covered by a 1–2 mm thick felty tomentum of unbranched multicellular hairs, sharply setting off against glabrous petiole-wings and lower part of midrib; – inflorescence a terminal paniculoid thyrse up to 2.5 m, axes completely covered by a compact creamy-white tomentum; – lower bracts \pm membranaceous, \pm ovate-lanceolate, with narrow, rounded apex and enlarged base \pm semiamplexicaul, glabrescent; – capitula numerous, 13–15 mm (on herbarium specimens \pm [15–] 18 [–24] mm) in diameter (without ray florets), with 70–75 tubular florets and 7–13–19 bright yellow ligulate flowers; ligulae up to 13–20 mm, (2)–4—(5–8) veined; – achenes dark brown, mostly 8-costate, \pm 5 mm long; – chromosome numbers: $2n = \pm 100$, 100 ± 14 ; $n = 52_{II}$, 54_{II} . – Endemic to alpine belt of Mt. Kenya (East

Africa), between 3000–4300 m growing on moorland or on (very) wet valley floors.

Herbarium specimens examined: East Africa, Kenya, North Nyeri District: Mt. Kenya, 4300–4500 m, 7. 2. 1960, leg. W. RAUH Ke 413 (M). – Mt. Kenya swampy ground, 12.000 ft.; 1. 12. [19]43; leg. J. BALLY 153 or B 3353 (K). – Mt. Kenya, afroalpine Zone, 9. 9. 1978, leg. J. GRAU 1890 (M). – Naro Moru Track, rock outcrops in boggy moorland zone with *Carex* tussocks, 13.000 ft., 8. 9. [19]63, leg. VERDCOURT 3733 (K). – NW slopes in the upper part of Teleki Valley, alpine belt, 4000 m, 25. 7. 1948, leg. O. HEDBERG 1692 (UPS). – Teleki Valley, alpine region, on slightly moist ground in the bottom of the valley, 4000 m, 6. 8. 1948, leg. O. HEDBERG 1842 (UPS); leg. SYNGE 1832 (NAIROBI). – Teleki Valley, 4200 m, 1. 9. 1969, leg. K. MÄGDEFRAU 18 (M). – Teleki Valley appr. 300 m NE of former Teleki Hut, 4500 m; 4. 3. 1985; leg. E. BECK (UBT). – Sirimon track, ± swampy slopes with tussocky grasses, *Alchemilla* etc., 13.000 ft., 9. 11. 1970, leg. D. J. MABBERLEY 407 (K).

4.3. *Senecio saundersii* W. SAUER & E. BECK, nothospec. nov.
(= *S. keniodendron* R. E. & T. C. E. FRIES × *S. keniensis* BAKER)
(Fig. 1, 8 e, f)

Holotypus: Kenya Colony: Mt Kenya, Teleki Valley, alpine region on flat, moist ground in the upper part of valley; 4200 m.s.m; 27. 7. 1948; leg. Olov HEDBERG: 1703 (UPS). Syntypes: K, NAIROBI.

Eponymy: SAUNDERS was the botanist accompanying MACKINDER in the 1899 first successful expedition to Mt. Kenya.

Synonymous Formulae: *Senecio keniodendron* R. E. & T. C. E. FRIES × *S. brassica* R. E. & T. C. E. FRIES: HEDBERG, *Webbia* 11: 482 (1955) – mentioned in the text. – *Senecio brassica* R. E. & T. C. E. FRIES × *S. keniodendron* R. E. & T. C. E. FRIES: HEDBERG, *Symb. Bot. Upsal.* 15 (1): 227 (1957). – *Senecio brassica* R. E. & T. C. E. FRIES subsp. *brassica* × *S. keniodendron* R. E. & T. C. E. FRIES: MABBERLEY, *Kew Bull.* 28 (1): 89 (1973). – *Senecio keniensis* BAKER subsp. *keniensis* × *S. keniodendron* R. E. & T. C. E. FRIES: JEFFREY, *Kew Bull.* 41 (4): 892 (1986).

Descriptio: Inter parentes. – *S.* × *saundersii* differt a *S. keniensis* caule erecto, usque ad 1,2 m alto; cortice radiceis polaris multis spatiis intercellularibus praedito etsi non aerenchyma formante; plerumque foliis rosularibus paululum maioribus ± (32-) 37 (-41) × (11-) 15 (-19) cm, $L_1 = \pm 2,47$, pagina superiore pilis sericeis longis fulvis ornatis atque indumento paginae inferioris (abaxilis) laminae griseo parce densiter obtecto; bracteis ± frondosis, distincte petiolatis, ± anguste ovati-lanceolatis, acuminatis; capitulis paululum maioribus, ca. 14–18 mm (in plantis exsiccatis ± [18-] 24 [-28] mm) diametro, involucri obscuri-fulvi, numero florum tubularium minore ± 120, floribus ligulatis absentibus vel nonnullis ± rudimentariis, ± 7–12 mm longis provisus nec non achaeniis auri-fuscis minoribus, ± 3,6 mm longis, 9 – costatis. – Differt a *S. keniodendrono* plerumque dimensionibus partium vegetabilium dilute minoribus; fascicu-

lis vasorum radice polaris hepta- usque ad polyarchibus; axibus inflorescentiae indumento dilute griseo densissimo oblecto ac bracteis frondosis distincte latioribus, ovati-lanceolatis et perspicue petiolatis; capitulis minoribus, $\pm 14-18$ mm diametro, numero minore florum tubularium ± 120 ac aliquis floribus ligulatis rudimentariis, $\pm 7-12$ mm longis praeditis vel nullis nec non achaeniis auri-fuscis, aliquid minoribus, $\pm 3,6$ mm longis, 9-costatis. – Numerus chromosomatum: $2n = \pm 101-105, 110-114$; $n = 52_{II} + 3_I - 6_I$; $n = 54_{II}$. – Haec nothospecies in regione alpine montis Kenya (Africa Orientalis) endemica; crescit solitarie vel in populationibus \pm magnis collecta, quidem in areis humidis, non autem in locis uliginosis.

Description: Clearly intermediate between the parents. – *Senecio* \times *saundersii* differs from *S. keniensis* by erect stems, up to 1.2 m; by a tap root system with a cortex rich in larger intercellular spaces, but not forming a typical aerenchyma; by somewhat longer rosette leaves, $\pm (32-)$ 37 (-41) \times (11-) 15 (-19) cm, $L_1 = \pm 2.47$, with long brown silky hairs on the upper surface and a less dense greyish indumentum on lower (abaxial) surface; by \pm narrow ovate-lanceolate, petiolate, \pm membranaceous bracts; by somewhat larger capitula, 14–18 mm (on herbarium specimens $\pm [18-] 24 [-28]$ mm) in diameter, dark brownish involucrem, a lower number of tubular florets (± 120) and none to several rudimentary ligulate flowers ($\pm 7-12$ mm long) as well as by golden-brown, somewhat smaller, ± 3.6 mm long, 9-costate achenes, – From *S. keniodendron* by generally smaller dimensions of the vegetative organs; hepta- to polyarch vascular bundles of the tap root system; by a very dense greyish indumentum of the inflorescence axes and distinctly broader bracts; by smaller capitula (14–18 mm in diameter), less tubular florets (± 120), none to several rudimentary, 7–12 mm long ligulate florets as well as by smaller, ± 3.6 mm long, golden-brown, 9-costate achenes. – Chromosome number: $2n = \pm 101-105, 110-114$; $n = 52_{II} + 3_I - 6_I$; $n = 54_{II}$. – Endemic to the alpine belt of Mt. Kenya (East Africa); growing solitarely or in \pm extent populations in between the parents, frequently on moist areas, but not on moorlands.

Herbarium specimens examined: East Africa, Kenya: Mt. Kenya, Teleki [Valley], mesic valley bottom, 4180 m, – 6. 1976, leg. T. P. YOUNG 44 (K). – Teleki Valley, alpine region, on flat, moist ground in the upper part of the valley, 4200 m, 27. 7. 1948, leg. O. HEDBERG 1703 (K, NAIROBI; UPS, holotypus).

4.4. *Senecio brassiciformis* R. E. & T. C. E. FRIES s. str.

(Fig. 8c)

Nomenclature and type v. C. JEFFREY 1986: 892.

Synonyms: Hitherto known synonyms v. C. JEFFREY 1986: 892; furthermore: *Senecio keniensis* BAKER subsp. *brassiciformis* (R. E. & T. C. E. FRIES) C. JEFFREY, Kew Bull. 41 (4): 892.

Description*): Perennial, dwarf sessile giant rosette plant without a stem, or rarely with a stem maximally up to 1 m; – adult leaves laxly rosulate, oblanceolate-obovate, entire, leathery, $\pm (30-)$ 40 (-55) \times (5-) 12

*) We refer to the original description by FRIES & FRIES 1922: 338–340.

(-17) cm, $L_i = 3.33$, maximal width in the upper $\frac{1}{3}$ ($\frac{1}{2}$), distinctly acuminate and gradually tapering into a \pm narrow winged petiole, margin throughout serrate-dentate, laminar venation confluent with that of petiole; upper surface yellow-green, sparsely hairy; upper part of lower surface with patchy, greyish, cobwebby tomentum forming an arrow-shaped coat, lower half \pm glabrous; – inflorescence a terminal, oblong-cylindrical paniculoid thyrse, up to 1 m or more; – bracts leaf-like, \pm broad ovate-lanceolate, distinctly petiolate and long acuminate, indumentum of lower surface whitish to greyish, similar to that of the leaves, upper surface \pm densely covered with long white silky hairs; – capitula on herbarium specimens \pm (16-) 18 (-20) mm in diameter, involucrem \pm purplish, 54–105 tubular florets and \pm 15 ligulate florets, \pm 13–14 mm long. – Endemic to the alpine belt of Aberdare Mts. (East Africa); growing on swampy areas (mostly dominated by *Carex* species) between 3000–3600 (3900)m.

Herbarium specimens examined: East Africa, Kenya: Aberdare Mts., 10.700 ft., 21. 10. 1970, leg. D. J. MABBERLEY 362 (K). – Aberdare Mts., near tourist toad swamp in moorlands above forest line, – 2. 1960; leg. Mrs. TWEEDIE 1955 (K). – Aberdare Mts., SW d. Karimu Brücke, Sumpf, 3060 m, 23. 3. 1986, leg. K. SCHMITT 29 (UBT). – Aberdare Mts., ca. 1,7 km E d. Mutubio West Gates, *Carex*-Sumpf, 3110 m, 18. 1. 1987; leg. K. SCHMITT 706a (UBT).

5. Population Biology

The hybrids – *S.* \times *saundersii* – are to be met everywhere in the upper alpine region of Mt. Kenya on moist or even temporarily flooded soil where both parent species occur in close vicinity. They are to be found as individuals or in small groups, but, due to the lack of the rhizomatous stem system, never in families like the cabbage groundsel. In a short comment on the hybrid, HEDBERG 1957 stated that during his field work on Mt. Kenya, he found “a solitary specimen of a plant that was almost exactly intermediate between *S. brassica* R. E. FRIES & Th. FRIES jr. (*S. keniensis*) and *S. keniodendron* R. E. FRIES & Th. FRIES jr.”. (Two earlier collections of such a plant have been recorded.) In a later paper, HEDBERG 1969 listed some of the characters of this plant which prove that the specimen corresponded to the hybrid described here. Undoubtedly, the number of hybrids has considerably increased since the time of HEDBERG’s field work and populations have established not only in Teleki valley but also in the other high alpine valleys of Mt. Kenya. This raises a series of questions which will be addressed in the following:

1. Are the hybrids genuine F_1 specimens or (also) F_2 heterozygotes or heterozygotes originating from back crossings with the parents?

Since the frequency of simultaneously flowering specimens was low (Table 5) and the groundsel in the high altitudinal habitats are usually pollinated by wind, the probability of cross-pollination is small. On the

contrary, if self-pollination is set aside, pollination by one of the parents, preferentially by *S. keniensis* (Table 5) is very likely. The similarly low frequency of flowering *S. keniodendron* specimens in that area is less relevant because the habitat of the hybrid is, except a few microsites, not suitable for the giant groundsel. A consequence of this line of arguments is that the seeds produced by the hybrids by 50% should correspond to those of the parents and by the other half would represent the true F₁ type. However, as shown in Table 3 the seeds of the hybrid are highly uniform and significantly smaller than those of the parents. Therefore, the intact (category 1, Table 2) seeds of the hybrid cannot be addressed as segregation products

Date	Sept. 1980	March 1983	March 1985	Feb. 1986
<i>Senecio keniensis</i>				
Seedlings	—	1.0	4.0	—
Juveniles	7.6	24.0	—	—
Adults	20.1	48.0	49.8	113.6
Flowering specimens	5.3	n. d.	n. d.	—
Dead specimens	n. d.	n. d.	1.3	0.4
Total	27.7	73.0	55.1	114.0
<i>Senecio keniodendron</i>				
Seedlings	—	64.0	2.2	0.4
Juveniles	41.7	5.0	—	—
Adults	5.0	6.0	2.7	1.7
Flowering specimens	0.8	—	—	—
Dead specimens	n. d.	n. d.	—	1.4
Total	46.7	75.0	4.9	3.5
<i>Senecio × saundersii</i>				
Seedlings	—	11.0	—	—
Juveniles	1.6	4.0	—	—
Adults	2.2	10.0	5.3	3.8
Flowering specimens	1.1	—	—	—
Dead specimens	n. d.	n. d.	—	0.7
Total	3.8	25.0	5.3	4.5
Percent of total groundsels	4.9	14.4	8.1	3.7

Table 5

Stock of groundsels per 100 m² of an area of the bottom of Teleki-Valley (Mt. Kenya) about 400 m above the former Teleki Hut at 4150 m a. s. l. *Senecio keniodendron*, descending from the southern slope penetrates into the moister area at the floor which is occupied by *S. keniensis*. The size of the examined areas varied between 100 and 220 m². For *S. keniensis*, rosettes were counted because the relationship to one specimen or another could not be established without damaging the plants. — n. d. = not determined.

containing the genomes of the parents. Rather, the argument that those seeds which carry the parents' genome would not be able to mature on the hybrid cannot be excluded, especially so with respect to the high proportion of achenes showing incomplete development (Table 2). Indeed, a percentage of 41% of intact seeds would be close to the expected proportion of F_1 individuals resulting from back-crossing. Establishment of the genuine F_1 depends on the simultaneous flowering of both parent groundsels. Whereas *S. keniensis* on Mt. Kenya is capable of producing inflorescences continuously, flowering of *S. keniodendron* apparently takes place at irregular intervals, and, with respect to certain areas, virtually synchronously. The term "mast year" has been coined for such a year, when, e. g. in 1979 more than 50% of the giant groundsels on Mt. Kenya had produced inflorescences. In other years only scattered specimens of *S. keniodendron* or at most a patch of these groundsels on a valley slope may be found flowering.

If the majority of the hybrids growing in the Teleki valley area (which was examined in detail) were genuine F_1 individuals, the dynamics of the numbers of seedlings and juvenils must follow those of *S. keniodendron* as is evidenced by Table 5. Hence, at least for the recent stage of population development, hybridization appears to (still) prevail over propagation by own seeds. This interpretation seems to contradict the above statement that the population of the hybrid has substantially increased since the past 40 years. However, prevalence of one mode of origin does not exclude the other, the effect of which may still be too small to be clearly recognized within the observation period of 7 years.

If the majority of the extant population is genuine F_1 , and if the hybrid's characters are mainly intermediate between those of the parents, the hybrid complex may be understood as being composed of reciprocal hybrids.

2. The second paragraph, therefore, must address the question whether hybridization is reciprocal or whether it depends on one of the two species being the obligatory mother. A review of the hybrids characters as described in the first section of this paper shows that the majority is virtually intermediate between those of both parents. Only the life form itself and some characters of the leaf epidermis, such as the distribution of the stomata, the density of the indumentum and the eventual deposition of anthocyanine in the vacuoles (*S. keniodendron*) can be clearly associated with one of the parents. Hence, the morphological and anatomical characters do not allow a conclusion to be drawn on the progeny of the hybrids from reciprocal hybridizations or via an obligatory parental role of one of the established species. Interpretation of the karyological data contributes a suggestion, however not more, to that discussion. 90% of the counted chromosome sets of pollen mother cells of *S. keniensis* contained between 1 to 6 unpaired chromosomes, while in *S. keniodendron* less than 20% exhibited such irregularities (Table 4). Consequently meiosis should be less problematic in the latter species as compared to *S. keniensis*. This argument

provides an explanation for the unexpectedly small proportion of fully developed embryos in the seeds of the cabbage groundsel (Table 3). Thus the probability of a viable pollen of *S. keniensis* having fertilized a functional ovule of *S. keniodendron* is considerably higher than vice versa. This makes an at random reciprocity of hybridization less likely. On the basis of this suggestion the hybrid should be termed *S. keniodendron* × *keniensis* in order to indicate the higher probability of the giant groundsel being the mother.

3. Provided fertility of the hybrid (which is likely but still has to be proven), a process similar to what supposedly has occurred to the hybrid *S. erici-rosenii* R. E. FRIES & Th. FRIES jr. × *S. adnivalis* var. *alticola* (MILDBR.) HEDB. namely the establishment of a "new species", (*S. kahuzicus* HUMB. [HEDBERG 1969]) could be envisaged. From the increase of the population of *S. keniodendron* × *keniensis* since HEDBERG's (1957) observation in the fifties and from the data presented here, incidence of cross pollination should become more and more probable. According to the karyological data, hinderance of the meiosis is not to be expected for the hybrid, because unpaired chromosomes were not detected. Hence, once the hybrid's population is dense enough, its further increase should become considerably accelerated. Because of the restricted geographical and ecophysiological habitat, speciation could advance much faster than is assumed to proceed under normal conditions (HEDBERG 1969).

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