

T A STUDY OF THE INTERRELATIONSHIPS OF  
SOME NATAL SPECIES OF SENECIO  
(ASTERACEAE / COMPOSITAE)

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By

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"You are worthy, our Lord  
and God,  
to receive glory and honour  
and power,  
for you created all things,  
and by your will they were  
created  
and have their being"

(Rev. 4:11 NIV)

## PREFACE

The studies described in this thesis were carried out in the department of Botany, University of Natal, Pietermaritzburg, under the supervision of Dr. F. Getliffe Norris.

I hereby declare that this thesis, submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy, is the result of my own investigation, except where the work of others is acknowledged.

This thesis has not been submitted in any form to another University.



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Leszek Paul Doroszynski Vincent

1984

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## ABSTRACT

This dissertation presents the results of studies of the generic concept of Senecio and the subsequent testing of the hypothesis: that many of the species of Senecio in Natal are congeneric with Senecio L. sensu stricto. The sample of taxa studied consisted of 87 Natal senecios, 5 Cape heterochromous senecios and 10 non-southern African senecios, including the type of the genus, S. vulgaris L. Also included in the study were 5 species from taxonomically closely related genera in the tribe Senecioneae and two senecios of uncertain taxonomic position.

The phenotype of these taxa was investigated with respect to a large number of morphological and micromorphological characters (126) and the data obtained were analysed neurally and numerically.

Aspects of the pollen micromorphology, of all the taxa studied, were also investigated using the scanning electron microscope.

A review of the chemical complement of all the taxa studied, particularly with respect to terpenes and pyrrolizidine alkaloids, was also undertaken.

Six characters were selected as being taxonomically significant with respect to elucidating the generic concept of Senecio. A further 31 characters and the aforementioned 6, were selected as being taxonomically significant with respect to elucidating the interrelationships of the Natal senecios and all the senecios studied.

The generic concept of Senecio has been re-circumscribed and the generic status of each of the senecios studied has been tested according to this concept of Senecio sensu Vincent. In the light of my concept of Senecio, the following species are excluded from Senecio sensu Vincent: S. barbertonicus Klatt, S. cissampelinus (DC.) Schultz Bipontinus, S. fulgens (J.D. Hooker) Nicholson, S. helminthioides (Schultz Bipontinus) Hilliard, S. hockii De Wild. & Muschl., S. medley-woodii Hutchinson, S. radicans (L.f.) Schultz Bipontinus, S. syringifolius O.Hoffm., S. tamoides DC., S. transvaalensis Bolus and S. viminalis BremeKamp. Senecio breviflorus Hilliard, S. seminiveus Wood & Evans and S. tanacetopsis Hilliard are considered to be peripheral to Senecio s. str. sensu Vincent, and are included in Senecio s. lat. sensu Vincent.

The hypothesis regarding the generic status of the Natal senecios has been accepted, subsequent to the circumscription of Senecio s. str. sensu Vincent.

Estimates of the phenetic affinity of all the members of Senecio sensu stricto sensu Vincent, included in this study, have been made. The majority of the Natal senecios, while clearly being members of Senecio s. str. sensu Vincent, are distinct from virtually all the Cape and non-southern African senecios studied. Many of the non-yellow (purple) Natal senecios form clearly allied groups which are distinct from the groups (clusters) composed of yellow senecios. The taxonomic position of several taxa is questioned, in the light of the cluster analyses.

The evidence from the palynological studies neither contradicts nor supports the proposed infrageneric interrelationships, with respect to the Natal members of Senecio s. str. sensu Vincent. The evidence also neither contradicts nor supports the proposed interrelationships between the Natal, the Cape and the non-southern African members of Senecio s. str. sensu Vincent.

The terpene and pyrrolizidine chemistry of many of many of the senecios studied is characterised by the presence of furanoeremophilanes. Eremophilanes also occur and are particularly associated with a number of non-yellow (purple) senecios. Pyrrolizidine alkaloids are not ubiquitous amongst the senecios studied, while some senecios appear to only synthesise pyrrolizidine alkaloids.

The review of the terpene and pyrrolizidine chemistry of the senecios investigated, illustrates how our knowledge at or near the level of analytic characters is far from complete. However, we have definitely progressed from the synthetic level of character use. Nevertheless, the relationships between the members of Senecio s. str. sensu Vincent, could not be evaluated in the light of their individual chemical complement of terpenes and pyrrolizidine alkaloids, because of a lack of information. An hypothesis of the chemical evolution within the Senecioneae is tested within Senecio s. str. sensu Vincent.

Before any taxonomic changes are made to the current composition of Senecio L., the concept of Senecio L. s. str. sensu Vincent, needs to be tested against a far wider sample of the genus.

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## CHAPTER ONE

## INTRODUCTION

The genus Senecio L. (family: Asteraceae/Compositae; tribe: Senecioneae) is a cosmopolitan genus, estimated to comprise between 1 500 species (Nordenstam, 1977) and 3 000 species (Jeffrey et al., 1977). Taxonomically, it is a notoriously difficult group of plants, this difficulty being exacerbated by the extremely large number of species.

The very variable generic and sectional concepts employed by different authors in Senecio have made it virtually impossible to give definitive answers regarding the correct names of many species. While portions of Senecio have been investigated (e.g. Harvey, 1865; Barkley, 1978), these attempts to improve the taxonomy of Senecio have resulted in inconsistent treatments. These inconsistencies are primarily due to the authors confining their studies to plants of particular geographical areas. Consequently, no classification applicable on a world-wide basis has been produced for Senecio.

Jeffrey et al. (1977) responded to this very unsatisfactory situation by developing a universally applicable scheme to stop the perpetuation of the very variable generic and sectional concepts employed by different authors in the Senecio complex. This scheme aimed at providing a "uniform criterion" throughout the Senecio complex and allied genera, against which all available evidence might be evaluated and consistent

systematic conclusions drawn. The scheme was not aimed at producing a definitive classification.

The scheme consisted essentially of investigating selected members of the Senecio complex with respect to characters which are easily and readily observable, this complement of characters being as follows:

"Easily observed characters exhibited by the surfaces of the cypselas, the pappus, the style-arm apices, the anther-collars, the anther-bases, the ray florets and the abaxial surfaces of leaves". Data thus obtained were supplemented, when considered necessary, by study of the "vegetative habit, leaf shape, venation and attachment, flower colour, inflorescence type, involucre type, the endothelial (exothelial) cell thickenings, the pollen grain surface, the pollen grain wall stratification, the configuration of the stigmatic surfaces and, when available, by chromosome numbers, obtained from the compilations of Fedorov (1969), Moore (1973) and occasionally other sources."

The selection of species, of which the above characters were studied by Jeffrey et al. (1977), was made on the basis of existing taxonomic treatments and on the basis of some fifteen years working knowledge of the group.

The results of their application of the aforementioned scheme demonstrated that the extent of the variation within Senecio was far too great to be accommodated within a single genus, and in fact, exceeded

the combined ranges exhibited by species currently referred to several other genera (Jeffrey et al., 1977). However, the existence of discontinuities in character state syndromes has made taxonomic division of the world-wide Senecio complex possible. This is despite the absence of absolute discontinuities in particular characters (Jeffrey et al., 1977).

The application of this "uniform criterion" to the world-wide collections of the Senecio complex at Kew, resulted in the division of this complex into sixteen groups (groups I-XVI) and that the name Senecio should be applied only to species of group IX, within which the type of the genus, S. vulgaris L., falls (Jeffrey et al., 1977). Jeffrey et al. (l.c.) suggested that the remaining groups (groups I-VIII and XVI) might be distinct genera, possibly new or possibly congeneric with other widely recognized genera in the Asteraceae.

While there are problems in the generic delimitation of groups I-VIII and X-XVI, the problems are most acute in group IX, which is the largest in the tribe and which contains the Senecio complex (Jeffrey, 1979)

In 1979, Jeffrey (1979) re-evaluated the aforementioned grouping in the light of further evidence from pappus, numerical, chemical and succulent plant studies, and modified the original concepts. The original group IX was subdivided into the "Eusenecionoids" (group IX [a]), part of which contains Senecio (sensu Jeffrey), and the "Gynuroids" (group IX [b]).



It is clear that the only sound approach to elucidating the generic concept of Senecio L., is to mount a detailed species-by-species comparative study on the members of Senecio (sensu Jeffrey, group IX [a]), working outwards from S. vulgaris, the type of the genus and one of the most specialized members of the tribe.

#### THE SCOPE OF THIS STUDY

This study of the interrelationships of some members of Senecio in Natal necessitated the investigation of the generic concept of Senecio. The approach taken in this aspect of the study was, by implication, to include the type species S. vulgaris. Also included in the study were a number of Cape senecios and a number of non-southern African senecios thought to be closely related to S. vulgaris (Table 1). A number of species from genera closely allied to Senecio were also included in the study, to enable an understanding to be gained of the character variation outside Senecio.

This dissertation presents the results of studies of the generic concept of Senecio and the application of these results to the interrelationships of the senecios investigated, most of which are indigenous to Natal.

The primary hypothesis of this study is as follows:

Many of the species of Senecio in Natal are congeneric with Senecio L. sensu stricto.

To test the primary hypothesis, a large sample of senecios indigenous to Natal, together with some Cape and some non-southern African senecios and a few representatives from taxonomically closely related genera (Table 1), were investigated with respect to a large number of morphological and micromorphological characters (Table 2). The inclusion of a large number of characters enabled data from a wide spectrum of the phenotype to be obtained. This in turn enabled taxonomically significant ("good") characters (Davis & Heywood, 1963) to be selected for subsequent neural and numerical analyses with respect to elucidating the generic concept of Senecio as well as elucidating the interrelationships of the Natal senecios and of the Natal senecios together with the Cape and non-southern African senecios included in the study.

Hilliard (1977) commented that a number of the Natal senecios appear to be clearly allied to varying degrees. These observations are evaluated in the light of the evidence obtained from my study.

Aspects of the pollen micromorphology, of all the taxa investigated (Table 1), were also studied using the scanning electron microscope.

A review of the chemical complement, of all the taxa investigated (Table 1), particularly with respect to terpenes and pyrrolizidine alkaloids, was also undertaken. Included in this review are some very recent findings (Bohlmann et al., 1984a, 1984b) on the chemical complement of some of the senecios investigated whose chemistry has not been previously studied.

The evidence from these further two components of the study has been evaluated with respect to its contribution to the generic concept of Senecio, and the elucidation of the interrelationships of the senecios studied.

In the light of the evidence from the morphological and micromorphological studies, the pollen and phytochemical studies, the generic limits of Senecio L. sensu stricto have been re-circumscribed and estimates of the interrelationships of the Natal senecios and of the Natal senecios together with the Cape and non-southern African senecios studied (Table 1), have been made.

## CHAPTER TWO

## MATERIALS AND METHODS

THE NUMBER AND SELECTION OF TAXA FOR STUDY

Seventy-seven species and six varieties of the approximately one-hundred-and-thirty species of the genus Senecio in Natal were investigated together with five species of Senecio from the Cape, nine species from outside South Africa and eight species from other genera in the tribe Senecioneae (Table 1). The majority of this material came from the NU herbarium, the remainder from BOL, K, NH and PRE.

The species descriptions in Hilliard (1977) were used to select representative specimens of the Natal species for study. Harvey's descriptions in Flora Capensis (Harvey, 1864) were used in the selection of the Cape senecios. While I decided which non-southern African senecios and related genera to include in this study, the selection of the representatives of these taxa was done on my behalf by Mr C. Jeffrey of The Royal Botanic Gardens, Kew (C. Jeffrey, pers. comm.).

The complement of Natal senecios included all the purple senecios described by Hilliard (1977) together with a large number of yellow senecios. In the selection of the yellow senecios, species which are thought to be closely allied and others which are thought to be distantly allied were selected (Hilliard, 1977). Also included in the study were some senecios (S. cissampelinus (DC.) Sch. Bip.,

S. fulgens (J.D.Hooker) Nicholson, S. transvaalensis Bolus & S. viminalis Bremekamp), which have an uncertain taxonomic position in Senecio (Hilliard, 1977, 1978).

The five Cape senecios are termed heterochromous for they have purple ray florets and yellow disc florets.

A complete list of all the taxa investigated is given in Table 1.

#### MORPHOLOGY AND MICROMORPHOLOGY

##### SAMPLE SIZE

A minimum of three representatives of each taxon was studied in detail. This number is not arbitrary but was found to be the minimum number required to achieve acceptable consistency in the data of the representatives of each taxon. Where necessary, more than three representatives were studied to achieve this standard.

##### SELECTION OF REPRESENTATIVES OF EACH TAXON CHOSEN FOR STUDY

In the selection of the representatives of each taxon chosen for study, an attempt was made to select specimens from widely different localities or habitats so as to enable the effect of environmentally induced variation to be encountered.

## PREPARATION OF VEGETATIVE AND FLORAL TISSUE

Samples of leaves, bracts, calyculus bracts and florets were cleared in the following manner. The samples were placed in pyrex glass beakers and covered with lactic acid (c.85%). These samples were heated on an electric hotplate at c.120 °C until the tissues were cleared. This clearing process was carefully monitored to achieve adequate clearing, but at the same time avoiding excessive softening of the tissue.

A portion of cleared leaf tissue (c. 15x15 mm) of each specimen sampled was mounted in lactic acid (c. 85%) and covered with a coverslip.

Some leaf samples discoloured the lactic acid considerably, necessitating several successive changes of the discoloured lactic acid, until adequate clearing was achieved.

At least 4 bracts, 4 calyculus bracts and 6-8 florets of each representative of each taxon were cleared in the above manner.

The cleared bracts, calyculus bracts and florets of each specimen sampled were placed on a separate slide in a small quantity of lactic acid (c. 85%). Before covering these structures with a coverslip the florets were dissected in the following manner: using very fine needles (size 10 embroidery crewel needles) the corollas were slit usually down to the base of the corolla tube. The syngenesious anthers were separated from the corollas by severing the filaments near their point of attachment to the corolla tube. The base of the corolla tube was

separated from the distal end of the cypselas. Some of the freed and slit corollas were displayed with their inner surface uppermost while the remainder were displayed with their outer surface uppermost. The final result being that the corollas, the anthers and attached filaments and the cypselas, usually with the style still attached, were all displayed separated from each other.

Light microscope observations were made using a Reichert compound microscope and a Zeiss dissecting microscope.

#### RECORDING OF CHARACTERS

The term character is used here in the sense of a character being a property or "feature which varies from one kind of organism to another" (Michener and Sokal, 1957) or "anything that can be considered as a variable independent of any other thing considered at the same time" (Cain and Harrison, 1958). Here I assume the "independence" referred to is logical rather than functional or mathematical. Each character consists of one or more states (Michener and Sokal, 1957). The term state usually implies qualitative rather than quantitative subdivision, however, the majority of the quantitative characters investigated in this study, while originally recorded in a continuous form, were finally changed into a qualitative form by subdivision into size classes. Therefore both the qualitative and the quantitative characters in their final form can be considered to consist of character states.

The total number of admissible characters (Sneath & Sokal, 1973) recorded for each species was 122. A list of these characters together with the inadmissible characters (Sneath & Sokal, 1973) is given in Table 2. The details of the character state(s) for each character are given in Appendix A.

Admissible characters are characters which contain information which is a reflection of the inherent nature of the organism. Inadmissible or meaningless characters are those characters which contain information which is not a reflection of the inherent nature of the organism (e.g. collector, herbarium).

The following are inadmissible characters:

SPECIES NUMBER	CHAR 001
COLLECTOR	CHAR 002
COLLECTOR'S NUMBER	CHAR 003
HERBARIUM	CHAR 004
ALTITUDE RANGE	CHAR 005
DISTRIBUTION	CHAR 006
HABITAT(S)	CHAR 007
FLOWERING TIME	CHAR 130

The information on the following characters: SPECIES NUMBER, COLLECTOR, COLLECTOR'S NUMBER and HERBARIUM was recorded on the original record sheets and is provided in *APPENDIX D*.



The characters; ALTITUDE RANGE (CHAR 005), HABITAT(S) (CHAR 007) and FLOWERING TIME (CHAR 130), can be considered to be under the partial influence of genetic factors, in that a plant's preference for specific habitats and a distinct flowering time results in patterns of distribution with respect to altitude. Nevertheless, there are environmental influences upon these preferences which, together with unrepresentative observations, place a restraint on the unreserved inclusion of patterns of altitude range, habitat preference, distribution and flowering time, in the assessment of phenetic relationships amongst the senecios investigated.

While ALTITUDE RANGE (CHAR 005), DISTRIBUTION (CHAR 006), HABITAT(S) (CHAR 007) and FLOWERING TIME (CHAR 130) are meaningless from the point of view of numerical analysis, the information recorded in these three characters has still been of value in assisting me in my neural analysis of the phenetic relationships of the species studied.

The coding of the quantitative character states was achieved using NOMINAL-LEVEL MEASUREMENT (non parametric). The assumption in this measurement procedure is that no assumption with respect to ordering or distances between character states is made. Thus the codes for the character states of the qualitative characters are arbitrary values separating the character states for each respective character.

The maximum value for some of the qualitative characters was recorded rather than the mean because it indicates the maximum genetic potential of each character. Some of these data were obtained from Hilliard (1977).

#### NUMBER OF MEASUREMENTS/OBSERVATIONS OF EACH CHARACTER

At least five measurements/observations were made of each character from each of between three and five representatives of each taxon.

#### MASTER DATA BASE

Using these data, a master data matrix was developed for the entire sample set (Table 1). For the qualitative characters, this was done by noting the variation within each qualitative character between the representatives of each taxon. Where variation was encountered, either the average state was chosen or a new state was described which encompassed the variation encountered. The quantitative characters were incorporated into this master data matrix but the data of the majority of these characters was first subdivided into size classes.

The subdivision of the data of some of the quantitative characters into size classes was achieved by subjecting the original data to frequency analyses, with the aid of the programme; Statistical Package for the Social Sciences (SPSS) by Nie *et al.* (1975). These analyses enabled peaks and troughs to be noted in the distribution of the data for each quantitative character. Size classes for each character were chosen to

accommodate the peaks. This selection was carefully done so as to avoid the danger of dichotomising these peaks into two size classes when one size class is a more accurate representation of the data producing the peak. This careful selection resulted in 'natural' or 'logical' size classes as opposed to arbitrary and hence artificial size classes.

The data in the MASTER DATA MATRIX, for all the taxa studied, are provided in Appendix B.

### NUMERICAL ANALYSES

The techniques used in the analysis of the data of select characters in the aforementioned master data base were those contained in the Numerical Taxonomy System of Multivariate Statistical Programmes (NT-SYS) package (Rohlf et al., 1972). The data were standardized (Sneath & Sokal, 1973) using the STAND subroutine resulting in a mean of zero and a standard deviation of unity. Correlation and distance matrices were computed using SIMINT. Cluster analyses were performed using the TAXON subroutine. Three techniques; single linkage (SINGLE), complete linkage (COMPLETE) and the unweighted pair-group method using arithmetic averages (UPGMA), were used to evaluate both correlation and distance matrices. A cophenetic correlation coefficient was calculated following each clustering routine to determine the amount of distortion the phenogram showed relative to the original master data matrix. In addition to clustering, principal component analysis (PCA) was used to evaluate the data (Harmon, 1967). The subroutine FACTOR was used and both unrotated and rotated components, using the VARIMAX option of the subroutine ROTATE (Kaiser, 1958) were output.

### POLLEN STUDIES

The external morphology of the pollen from each of the taxa investigated in this study (Table 1) was investigated using a scanning electron microscope (SEM) (JEOL JSM - T200) at 15 kV.

A specific sampling strategy was used so as to avoid the possibility of sampling pollen from another unknown species and to enable a large sample of pollen to be obtained from the taxon being sampled. This sampling procedure involved sampling florets just prior to their anthesis. This stage of maturity is indicated by the corolla lobes still being in contact with each other.

Thus, only florets at the correct stage of maturity were removed from the capitulum and the syngenesious anthers dissected out and transferred to a metal stub, one end of which had been prepared with double sided cellotape.

The pollen from these anthers was then spread over the adhesive surface of the stub using a fine brush. These prepared stubs were stored in a desiccator containing dehydrated silica gel, until such time as they were viewed using the SEM. Just prior to viewing, the pollen was sputter-coated with gold/palladium (POLARON SEM coating unit E5100), coating at c. 0,08 torr and c. 2,8 kV for 5 minutes.

Data on the following characters were recorded:

- (i). Shape of pollen grain, using the terminology of Erdtman (1969).
- (ii). Spinule frequency.
- (iii). Length/width (basal) ratio of the spinules.
- (iv). Prominence of the colpi.
- (v). Perforations in the exine.

These aforementioned characters are defined in chapter 7 of this dissertation.

## CHAPTER THREE

## THE CHARACTERS INVESTIGATED

INTRODUCTION

The standard recommendation concerning the number of characters to include in a taxonomic study which employs numerical techniques, for analyses of phenetic relationships, is that no fewer than 60 characters should be employed. However, whenever possible and where it is feasible, considerably more characters should be employed (Sokal & Sneath, 1963; Sneath & Sokal, 1973). This recommendation, it is admitted, is not based on either empirical or theoretical grounds but stems from the attempt at trying to answer the "problem of the congruence of classifications based on sets of characters from different body parts or life history stages" (Sneath & Sokal, 1973).

Further reasoning is that if phenetic similarity is not a single quantity but rather a shifting concept depending on the method of 'measurement' (parametric and non-parametric) as well as the character base, then the employment of a large number of characters should improve the estimate of phenotypic similarity. This is because it is presumed that there is a better chance of securing a larger number of taxonomically significant characters with a large number of characters.

The improvement in the estimate of phenotypic similarity by using a large number of character is also based on an empirical fact that when

large numbers of characters are employed in a numerical analysis the estimate of similarity obeys what has been termed a principle of inertia. The supposed implication of this principle is that as more characters are added to the data base it takes an increasingly large number of characters with quite different phenetic information to alter appreciably a previously derived estimate of phenetic similarity.

This reasoning has been criticized by Clayton (1970), for besides the difficulty in finding 60 or more characters in some plant groups, there are other real problems associated with large numbers of characters which result in "a tendency for the characters themselves to be of diminishing significance and precision."

The answer to much of the controversy surrounding the place of numerical taxonomy perhaps lies in the following direction. Characters should be selected which are judged, in the light of experience, to be of potential taxonomic significance (sensu Davis & Heywood, 1963 - p.116), and then correlation among them should be sought - this being the orthodox approach. Where the characters are too numerous, then numerical methods can be employed as a tool and an extension to the orthodox approach and so develop a visual presentation of more complex situations for taxonomic appraisal (Clayton, 1970).

I fully support Clayton's view (Clayton, 1970) that "numerical methods should be regarded as a valuable aid to current practice, not as a substitute, nor as an excuse for the uncritical processing of ill-considered data" and I have endeavoured to use this philosophy in my

approach and execution of this study.

The large number of characters investigated in this study (126 admissible characters - Table 2 & Appendix A) has assisted me in gaining an appreciation of the range of morphological and micromorphological variation that exist amongst the senecios studied. The large number of characters has also enabled me to feel more confident in selecting characters which are judged to be taxonomically significant both with respect to elucidating the generic concept of Senecio L. and elucidating the interrelationships of the Natal senecios and of all the senecios studied.

Characters investigated in this study have been judged to be taxonomically significant ("good") (Davis & Heywood, 1963) according to the following criteria:

- (i). The character is not subject to wide variation.
- (ii). The character does not appear to be very susceptible to environmental modification.
- (iii). The character appears to have a low intrinsic genetic variability.

While many characters have been selected as being potentially taxonomically significant, with respect to elucidating the interrelationships of the Natal senecios and of all the senecios studied, only some of these potentially significant characters have been used in the elucidation of the generic concept of Senecio.



In the following discussion of all the characters investigated, those selected as being taxonomically significant with respect to elucidating the interrelationships between the senecios studied have an asterisk [\*] placed next to the character title. Those characters selected as being taxonomically significant with respect to elucidating the generic concept of Senecio, have two asterisks [\*\*] placed next to the character title. Note that the latter group of characters is included in the former group of characters.

The order of the characters in this chapter follows that of Table 2.

The following report on the characters investigated is intended to draw attention to some features and/or some statistics of these characters. Wherever possible, comparisons have been made between my observations and those of other researchers.

The character states of the characters studied are provided in Appendix A, while the particular character state codes (for Characters 005-130) for each taxon studied are provided in Appendix B.

### THE CHARACTERS INVESTIGATED

#### VEGETATIVE HABIT (CHAR 008 - Appendix A)

Of the senecios studied, only 6% of those that occur in Natal, have an annual vegetative habit. Another 6% are known or are suspected of

having a biennial vegetative habit, the remaining species being perennials. The perennials are predominantly herbaceous. The Cape heterochromous senecios (nos. 200-204) and the non-southern African senecios (nos. 210-220), all have an annual habit.

The annual vegetative habit of the Cape heterochromous purple and the non-southern African senecios and the 6% of the Natal senecios, is most probably related to reproductive strategy and environmental conditions in the regions where these species are found.

Within the family, the herbaceous (annual) growth form is thought to be relatively advanced while the shrubby (perennial) growth form is thought to be ancestral (Nordenstam, 1977; Jeffrey, 1979). The implications of this theory with respect to the interrelationships of the senecios studied are discussed in chapter 8 of this dissertation.

#### ROOTSTOCK (CHAR 009 - Appendix A)

While I was unable to record details of the rootstock for many (51%) of the species (Table 1) studied it is clear that the rootstock of the remaining taxa is a perrenating organ. This rootstock is generally stout and woody to rhizomatous.

It is unfortunate that often little attention has been given to the collection of the rootstock of senecios collected to date, for the rootstock, especially the crown, can in some instances be of assistance in identifying a specimen. An example of this is S. coronatus (Thunb.)

Harvey (no. 74), which is the only species in the study which has a silky woolly rootstock (char. state 19).

#### PLANT HEIGHT (MAX.) (CHAR 010 - Appendix A)

The distribution of the recorded PLANT HEIGHT (MAX.) for many (76%) of the taxa studied (Table 1) is provided (Fig. 1).

The most common PLANT HEIGHT (MAX.) for all the taxa for which this character was recorded, is c. 600 mm. Many of these taxa, while being perennial, die back each year to a perennial rootstock. Those taxa with a much greater maximum height are predominantly true perennials.

#### LEAF DISTRIBUTION (CHAR 011 - Appendix A)

There are three major trends in leaf distribution amongst the senecios studied (Table 1):

- (i). Only cauline leaves present.
- (ii). Radical and cauline leaves present.
- (iii). Mostly radical leaves present.

There are several variations on a theme for each of these trends as well as some overlap between these trends as indicated in the descriptions of the many states recorded for this character (Appendix A).

**LEAF LENGTH (MAX.): RADICAL (CHAR 012 - Appendix A)**

While only 38% of all the senecios studied (Table 1) possess radical leaves, there is considerable variation in the maximum length of these leaves between species. The distribution of LEAF LENGTH (MAX.): RADICAL (Fig. 2) indicates a range of 40 mm - 600 mm.

**LEAF LENGTH (MAX.): CAULINE (CHAR 013 - Appendix A)**

Again there is considerable variation in the maximum length of these leaves between the senecios for which this character was recorded. The distribution of LEAF LENGTH (MAX.): CAULINE (Fig. 3) indicates a range of 20 mm - 500 mm.

**LEAF WIDTH (MAX.): RADICAL (CHAR 014 - Appendix A)**

The distribution of LEAF WIDTH (MAX.): RADICAL (Fig. 4) amongst the senecios possessing radical leaves, indicates a range of 8 mm - 90 mm.

**LEAF WIDTH (MAX.): CAULINE (CHAR 015 - Appendix A)**

There is a wide range in the width of the cauline leaves amongst the senecios studied. The distribution of this range (5 mm - 110 mm) is provided in Fig. 5.

[\*] LEAF SHAPE: RADICAL (CHAR 016 - Appendix A)

[\*] LEAF SHAPE: CAULINE (CHAR 017 - Appendix A)

The leaf shape of the radical and cauline leaves of most of the senecios studied is highly polymorphic between species and in some senecios the shape of the radical and cauline leaves is moderately polymorphic. This infraspecific polymorphism can occur within and between populations of a single species (e.g. S. gerrardii Harvey). Consequently, leaf shape has been recorded in such a manner so as to encompass the variation encountered within each species and many character 'states' have been described as a consequence of the variation between species (Appendix A). Leaf shape syndromes are often restricted to a single species, but there are a few exceptions as indicated below:

#### LEAF SHAPE: RADICAL

- (i). Character state 03 - Senecio purpureus L.  
S. anomalochrous Hilliard
- (ii). Character state 29 - S. asperulus DC.  
S. affinis DC.

#### LEAF SHAPE: CAULINE

- (i). Character state 03 - S. purpureus  
S. anomalochrous
- (ii). Character state 37 - S. hieracioides DC.  
S. asperulus  
S. affinis  
S. bupleuroides DC.  
S. urophyllus Conrath  
S. scitus Hutch. & Burt Davy

S. scitus Hutch. & Burtt Davy

LEAF APEX: RADICAL (CHAR 018 - Appendix A)

LEAF APEX: CAULINE (CHAR 019 - Appendix A)

There is considerable variation between species and some variation within species with respect to the shape of the leaf apices, especially in those of the cauline leaves.

The most common shape of the leaf apex for both radical and cauline leaves is ACUTE (char. state 06). There are, however, a number of character states which are species specific, especially with respect to the cauline leaf apices. Some examples of these are provided below:

## LEAF APEX: RADICAL

- (i). Character state 02 - S. dregeanus DC.
- (ii). Character state 04 - S. purpureus
- (iii). Character state 08 - S. barbatus DC.

## LEAF APEX: CAULINE

- (i). Character state 07 - S. sp. aff. S. poseideonis
- (ii). Character state 14 - S. mooreanus Hutchinson
- (iii). Character state 15 - S. mauricei Hilliard & Burtt
- (iv). Character state 20 - S. latifolius DC.
- (v). Character state 21 - S. medley-woodii Hutchinson
- (vi). Character state 22 - S. barbertonicus Klatt

LEAF MARGIN: RADICAL (CHAR 020 - Appendix A)

LEAF MARGIN: CAULINE (CHAR 021 - Appendix A)

As with leaf shape, the leaf margin of the radical and cauline leaves of most of the senecios studied (Table 1) is highly polymorphic between species and in some instances within a species. This is reflected in the manner in which observations of this character have been recorded in Appendix A. Leaf margin syndromes are often restricted to a single species, but there are a few exceptions as indicated below:

LEAF MARGIN: RADICAL

- (i). Character state 30 - Senecio paludaffinis Hilliard  
S. affinis  
S. lydenburgensis Hutchinson &  
 Burtt Davy
- (ii). Character state 35 - S. caudatus DC.  
S. heliopsis Hilliard & Burtt

LEAF MARGIN: CAULINE

- (i). Character state 04 - S. purpureus  
S. umgeniensis Thellung
- (ii). Character state 15 - S. tanacetopsis Hilliard  
S. seminiveus Wood & Evans  
S. subcoriaceus Schlechter  
S. arabidifolius O. Hoffmann  
S. viminalis Bremekamp

LEAF BASE: RADICAL (CHAR 022 - Appendix A)

LEAF BASE: CAULINE (CHAR 023 - Appendix A)

Despite there being many species of the southern African senecios which do not have radical leaves (49 spp.), thirty-one character states have been observed amongst those senecios producing radical leaves. Character states 01 and 20 are the commonest but besides these there are very few character states shared by two or more species (e.g. char. states 04, 07 & 19).

Considering the cauline leaves, there are 60 character states on record. Here, the commonest character state is number 14, being shared by 15 senecios. The next commonest state is number 02, being shared by 5 senecios.

This degree of polymorphism in the features of the leaf base of the radical and cauline leaves is akin to that found in the shape of the radical and cauline leaves, but here there are fewer instances of overlapping character states.

[\*] LEAF VENATION: RADICAL (CHAR 024 - Appendix A)

[\*] LEAF VENATION: CAULINE (CHAR 025 - Appendix A)

Although seven states of venation have been recorded in the radical leaves, the dominant state (char. state 01) is that of a distinct midrib and indistinct lateral veins. This character state is shared by 22 species of Senecio. Character state 06, in which distinct lateral veins are found, is the next dominant state. Character state 07 is unique to S. subcoriaceus, and is a diagnostic feature of this species amongst the



Natal senecios.

There are seventeen character states for the venation of the cauline leaves, the dominant state (char. state 01) being the same as that for the radical leaves as is the next dominant character state (char. state 07). However, there are several character states which are possessed by single species. Some of these occurrences are given below:

LEAF VENATION: CAULINE

- (i). Character state 08 - Senecio oxyriifolius
- (ii). Character state 11 - S. latifolius
- (iii). Character state 15 - S. panduriformis Hilliard
- (iv). Character state 17 - S. cissampelinus (DC.) Schultz

Bipontinus

LEAF TEXTURE: RADICAL (CHAR 026 - Appendix A)

LEAF TEXTURE: CAULINE (CHAR 027 - Appendix A)

While there are many states for each of these characters there is some overlap between character states. The major trend in leaf texture is that of leaves being foliaceous with some form of pubescence. However, some of the other character states are: "leathery", "coriaceous", "thick-textured", "succulent and membranous".

LEAF ATTACHMENT: RADICAL (CHAR 028 - Appendix A)

LEAF ATTACHMENT: CAULINE (CHAR 029 - Appendix A)

There is a considerable number of types of attachment of both the radical and cauline leaves (20 and 44 character states respectively), this is despite there being some overlap between some of the character states. The most common form of attachment is "petiolate". The next most common form of attachment is attachment via a petiole-like structure where the base of the petiole-like structure is sometimes broad or expanded and may be half-clasping to clasping.

In many species the attachment of the cauline leaves differs with respect to the position on the stem, the trend being towards sessile attachment with ascent up the stem. This range of leaf attachment up the stem draws attention to the importance of collecting the whole plant, for the presence of the lower stem leaves is essential, in some cases, for the species to be correctly identified.

LEAF PUBESCENCE (ABAXIAL): RADICAL (CHAR 030 - Appendix A)

LEAF PUBESCENCE (ABAXIAL): CAULINE (CHAR 031 - Appendix A)

LEAF PUBESCENCE (ADAXIAL): RADICAL (CHAR 032 - Appendix A)

LEAF PUBESCENCE (ADAXIAL): CAULINE (CHAR 033 - Appendix A)

Each of these characters has a large number of character states (32, 50, 32 & 49 respectively). While there is some overlap between some of the character states of each character, there remains a considerable amount of variation between the senecios studied (Table 1). There are also a large number of character states of each character which have a single

occurrence.

Most of the species possessing radical leaves are pubescent to some degree, there being only one species, S. ngoyanus Hilliard, which is consistently glabrous. There are twenty one senecios bearing cauline leaves which are consistently glabrous (CHAR 031 & 033, state 05 for both).

**[\*] LEAF TRICHOMES: BASE (CHAR 034 - Appendix A)**

This character comprises the region of the leaf trichome between the apex and the proximal end of the trichome.

The character LEAF TRICHOMES: BASE was recorded separately from the characters LEAF TRICHOMES: APEX (CHAR 035) and LEAF TRICHOMES: APPENDAGES (CHAR 036) because it was noted at the outset of the study that some species had a leaf trichome base common to all of them but several different states of leaf trichome apex were distributed amongst these same species. The opposite situation was also found to occur. A similar situation was found to exist with respect to the appendages of the leaf trichomes. Consequently, I decided that the best means of recording features of the leaf trichomes would be by means of the above three characters.

There is a most interesting range of leaf trichome bases recorded in twenty-nine character states (see Appendix A, character 034 for illustrations). Some of these trichomes can be readily seen with a X10

hand lens but most can only be studied using the compound microscope with a total magnification ranging between X40 and X400.

The frequency distribution of the various character states of the leaf trichome bases is provided in Fig. 6.

There are a number of character states which are common to groups of species, for example:

Character state 03 - 18 Senecio spp. and 1 non Senecio

Character state 09 - 5 Senecio spp. and 1 non Senecio

Character state 19 - 4 Senecio spp.

There are also several character states which have a single occurrence, for example:

Character state 02 - S. anomalochrous

Character state 11 - S. variabilis Schultz Bipontinus

Character state 27 - S. elegans L.

[\*] LEAF TRICHOMES: APEX (CHAR 035 - Appendix A)

There is considerable variation in the appearance of the apices of the leaf trichomes, recorded in forty-one character states.

The frequency distribution of the various character states of the leaf trichome apices (Fig. 7).

As with the previous character there are a number of character states which are common to groups of species, for example:

Character state 22 - 9 Senecio spp. and 1 non Senecio

Character state 02 - 7 Senecio spp. and 1 non Senecio

Character state 28 - 2 Senecio spp.

There are also several character states which have a single occurrence, for example:

Character state 07 - S. rhyncholaenus DC.

Character state 27 - S. hieracioides

Character state 39 - S. viscosus L.

There are several character states which consist of two types of apex (e.g. char. states 03, 09 & 11). Some of these character states have the same two types of apex but differ with respect to the frequency of occurrence of each type of apex (e.g. char. states 12, 13 & 18).

**[\*] LEAF TRICHOMES: APPENDAGES (CHAR 036 - Appendix A)**

This character concerns the occurrence of a terminal appendage which arises from the apex of the trichome.

In those senecios that do produce leaf trichomes with terminal appendages, the appendage usually is in the form of a long (at X400)

thin, unicellular thread-like structure. Besides this common form of terminal appendage there are two other forms. The first of these takes the form of a broad, unicellular thread-like structure (char. state 07). The second of these takes the form of a branched terminal structure (char. state 08).

There are many senecios (38) with leaf trichomes which lack a terminal appendage.

Drury and Watson (1965), in a study of some Eurasian senecios describe eleven trichome types, some of which appear to correspond with some of those found in some of the senecios and species of related genera investigated in this study. The coincidence and occurrence of these trichome types is indicated in Table 3. Five of the eleven 'Drury and Watson' trichome types occur amongst the material investigated in this study: their trichome type 8 has the most frequent occurrence (10 spp.): trichome types 2, 3 and 4 have only a single occurrence, while trichome type 7 which coincides with two of the forms described in this study (CHAR 035, char. states 38 & 40), occurs in four species examined in this study.

While there appears to be some coincidence in trichome type, as mentioned earlier, I must point out that the length of the terminal appendages that have been recorded in this study appear to exceed greatly the length of the terminal appendages illustrated by Drury and Watson (1965).

**LEAF TRICHOMES: GLANDULAR (CHAR 037 - Appendix A)**

There are three major trends in this character:

- (i). Leaf trichomes eglandular.
- (ii). Some leaf trichomes (few to most) glandular.
- (iii). All leaf trichomes glandular.

The first trend is by far the most common in the material studied, occurring in 41 senecios. The second trend occurs in 14 senecios while the third trend occurs in 21 senecios.

These figures indicate that approximately 80% of the pubescent senecios investigated have glandular trichomes of varying frequency of occurrence.

**FLOWERING STEM: APPEARANCE (CHAR 038 - Appendix A)**

While seventy-eight character states record the variation in the appearance of the flowering stem(s) there are many character states which overlap to some degree, often as a result of infraspecific variation. However, this large number of character states indicates the considerable degree of variation that exists both between species and within species of Senecio and species of related genera investigated in this study.

Only the following 5 character states are shared by more than one

## species:

- Character state 01 - Senecio anomalochrous  
S. dregeanus  
S. discodregeanus
- Character state 02 - S. purpureus  
S. gerrardii
- Character state 28 - S. polyanthemoides Schultz Bipontinus  
S. juniperinus L.f.
- Character state 47 - S. caudatus  
S. inornatus DC.
- Character state 49 - S. saniensis Hilliard & Burt  
S. heliopsis
- Character state 55 - S. bupleuroides  
S. urophyllus
- Character state 68 - S. brachypodus DC.  
S. pleistocephalus Spencer Moore

## FLOWERING STEM: PUBESCENCE (CHAR 039 - Appendix A)

Despite the overlap between many of the character states in this character, again often due to considerable infraspecific variation, the degree of variation within this character remains substantial, ranging from glabrous to densely (and sometimes glandular) pubescent to white felted.



**FLOWERING STEM: GLANDULAR (CHAR 040 - Appendix A)**

The majority (50 spp.) of the senecios for which this character was recorded have eglandular flowering stems. The majority (23 spp.) of the remaining species have flowering stems which are consistently glandular either by means of sessile glands on the flowering stem and/or trichomes which have glandular apices. The remaining senecios have flowering stems and/or trichomes which are inconsistently glandular.

The majority of the senecios which have eglandular flowering stems have some form of glandular trichomes on their leaves.

**PEDUNCLES: APPEARANCE (CHAR 041 - Appendix A)**

This character, like several others already discussed, also exhibits considerable variation both within and between species. Consequently, there are many character states which overlap to varying degrees. Nevertheless, the predominant trend is that the majority of the species of Senecio studied have sparsely to densely pubescent and bracteate peduncles.

**LEAF STOMATA (CHAR 042 - Appendix A)**

The character states recorded under this character are derived from observations of the abaxial and adaxial surface of the cauline leaves of each of the taxa investigated in this study (Table 1).

The stomata of all the species investigated lack accessory cells and are

classified as anomocytic (Radford et al., 1974).

There are three senecios (S. madagascariensis Poiret, S. barbatus, S. coronatus) which consistently have four epidermal cells surrounding each stoma on both the abaxial and the adaxial surface of the cauline leaves (char. state 02). However, these cells are not distinguishable as accessory cell.

The major trend is that 94 of the senecios investigated possess anomocytic stomata on both the abaxial and the adaxial surface of the cauline leaves (char. state 01).

Six species have anomocytic stomata, predominantly on the abaxial surface of the cauline leaves, there being only a few anomocytic stomata on the adaxial surface (char. state 04). These species are: Senecio pterophorus DC., S. serratuloides DC., S. brachypodus, S. pleistocephalus, S. tamoides DC. & S. brevilorus Hilliard.

#### INFLORESCENCE BRACTS (CHAR 043 - Appendix A)

This character was included in the list of characters to be studied for I anticipated that the variation between the species that would be recorded might be of assistance in improving my understanding of the affinities between the species of Senecio and related genera studied. However, this turned out not to be the case, for there is a considerable degree of overlap between the thirty-seven character states recorded. There is also a lack of any distinct trend in the appearance of the

inflorescence bracts.

**CAPITULA: LENGTH (CHAR 044 - Appendix A)**

The distribution of all the taxa studied (Table 1) with respect to the seven size classes of this character is illustrated in Figure 7.

As illustrated (Fig. 8) most (80 spp.) of the senecios studied have capitula between 5 mm and 13 mm in length (size classes 1-3). A minority (13 spp.) of these species have noticeably small capitula, the range of length being between 5 mm and 7 mm.

There are 5 senecios which have noticeably long capitula, the length of these capitula ranging between 19 mm and 25 mm.

**CAPITULA: DIAMETER (CHAR 045 - Appendix A)**

This character records the diameter of the disc of the capitula and excludes the length of the limb of the ray florets.

The distribution of all the taxa studied (Table 1) with respect to the six size classes of this character is illustrated in Fig. 9.

While there are five species which have extremely narrow capitula (< 3 mm), the majority of the senecios (81 spp.) have capitula ranging between 4 mm and 10 mm in diameter.

There are 8 senecios which have relatively broad capitula, the diameter of these capitula ranging between 13 mm and 25 mm, the tendency being towards the upper end of this range.

Many senecios exhibit a positive association between the length and diameter of their capitula. Some examples are:

SHORT AND NARROW CAPITULA - (5-7 mm X  $\leq$  3 mm)

Senecio microglossus DC.

S. brachypodus

LONG AND BROAD CAPITULA - (19-25 mm X 13-25 mm)

S. sandersonii Harvey

S. caudatus

**CAPITULA: RADIATE/DISCOID** (CHAR 046 - Appendix A)

While there are many senecios which are consistently either radiate or discoid there are four species of Senecio (S. sp. aff. S. speciosus, S. hypochoerideus DC., S. glaberrimus DC. & S. deltoideus Lessing) which are inconsistent in that they can be frequently found in both the radiate and the discoid state (char. state 3), even within the same population.

Both Senecio poseideonis Hilliard & Burtt and S. paludaffinis are usually radiate but discoid plants are occasionally found.

A large majority (56 spp.) of the senecios investigated consistently

have radiate capitula (char. state 1).

Many (35 spp.) of the remaining species of Senecio consistently have discoid capitula (char. state 2).

#### **CAPITULA: HOMO/HETEROGAMOUS (CHAR 047 - Appendix A)**

While it has transpired that this character is logically correlated (Sneath & Sokal, 1973) with the previous character (CHAR 046), it was originally included so as to permit the recording of differences within the disc and the ray florets. However, no differences of this nature were recorded amongst the taxa studied.

#### **CAPITULA: ARRANGEMENT (CHAR 048 - Appendix A)**

This character, like several others already discussed, exhibits considerable variation both within and between species. Consequently, there are many character states which overlap to varying degrees. Nevertheless, the predominant trend is that the majority of the senecios studied have their capitula arranged in corymbose-panicles, which are frequently but not always spreading.

A number of species have their capitula arranged in a corymb of various forms (e.g. char. states 17, 46 & 57).

There are several character states which occur in more than one species and which are reasonably distinct as 'character states' (Michener &

Sokal, 1957). Some examples of these are provided below:

Character state 03 - Senecio purpureus

S. gerrardii

Character state 39 - S. achilleifolius DC.

S. brevilorus

Character state 50 - S. brachypodus

S. pleistocephalus

[\*] INVOLUCRE SHAPE (CHAR 049 - Appendix A)

The two most common states of this character are; involucre "campanulate" and involucre "turbinate". Fifty-four senecios have campanulate involucre while another 21 senecios have turbinate involucre. A further 9 senecios have narrowly campanulate involucre, while broadly campanulate involucre are found in 3 species.

There are a number of species (9 spp.) which have involucre of an intermediate shape for they exhibit turbinate-campanulate involucre.

The radiate forms of S. poseideonis have intermediate (turbinate-campanulate) involucre while the discoid forms consistently have campanulate involucre.

[\*] INVOLUCRAL BRACTS: NUMBER (CHAR 050 - Appendix A)

The distribution of all the taxa studied (Table 1) with respect to the six size classes of this character is illustrated in Fig. 10.

As illustrated in figure 9, there are two conspicuous trends with respect to this character amongst the senecios studied (Table 1):

- (i). 10-14 Involucral bracts - 38 spp. & 1 var.
- (ii). 20-22 Involucral bracts - 30 spp. & 2 vars.

There are also two minor trends with respect to this character amongst the senecios studied:

- (i). 7-8 Involucral bracts - 13 spp.
- (ii). 16-18 Involucral bracts - 11 spp.

Only a few species (S. pleistocephalus, S. deltoideus & S. viminalis) produce relatively few (5-6) involucral bracts, and only one species, S. caudatus, produces relatively many (26-32) involucral bracts.

It is most interesting to compare the number of involucral bracts occurring in each senecio with the Fibonacci series 1-2-3-5-8-13-21-34. This comparison reveals relatively good congruence with this series with 13 or 21 bract being most common, as illustrated below:

FIBONACCI SERIES	NUMBER OF INVOLUCRAL BRACTS AND SENECIOS	
5	5-6	3 spp. of <u>Senecio</u> .
8	7-8	13 spp. of <u>Senecio</u> .
13	10-14	38 spp. & 1 var. of <u>Senecio</u> .
21	20-22	30 spp. & 2 vars. of <u>Senecio</u> .
34	26-32	1 spp. of <u>Senecio</u> .

Note, however, that 11 senecios produce 16-18 involucre bracts, this number range being a little distant from both 13 and 21 of the Fibonacci series.

Barkley (1978), in his revision of many North American senecios, found a similar congruence between the number of involucre bracts and the Fibonacci series, also with 13 or 21 bracts being most common.

[\*] INVOLUCRAL BRACTS: LENGTH (CHAR 051 - Appendix A)

The distribution of all the taxa studied (Table 1) with respect to the size classes of this character is illustrated in Fig. 11.

The majority of the senecios studied (43 spp. & 1 var.) have relatively short (6-8 mm) involucre bracts. A further 32 senecios have involucre bracts between 9-10 mm in length. There are a few species (6 spp.) that have relatively long (> 14 mm) involucre bracts.



[\*] INVOLUCRAL BRACTS: SHAPE (CHAR 052 - Appendix A)

Many (73 spp.) of the senecios investigated (Table 1) exhibit a lanceolate and keeled form of involucre bract. Besides these common features these involucre bracts may have acute or acuminate apices and the bases of the involucre bracts are swollen in a two species (S. tamoides & S. cissampelinus)

The remaining senecios have some form of oblong involucre bracts. These range from being keeled to being broad (10-15 mm) and flat.

It is interesting to note that there are several senecios (S. bupleuroides, S. glaberrimus, S. latifolius & S. retrorsus DC.) which have relatively broad involucre bracts (char. state 10) associated with relatively few (7-8) involucre bracts (CHAR 050, char. state 2). This association is also associated with relatively narrow capitula (CHAR 045, char. state 2). However, there are exceptions to the above associations in that some senecios (S. rhomboideus Harvey, S. othonniflorus DC. & S. breviflorus), which produce relatively few and broad involucre bracts, have broader capitula (8-10 mm) (CHAR 045, char. state 3).

Character states 13 and 14 are unique to S. fulgens (J.D. Hooker) Nicholson and S. deltoides respectively.

**INVOLUCRAL BRACTS: PUBESCENCE (CHAR 053 - Appendix A)**

This character like several others already discussed also exhibits considerable variation both within and between species. Consequently, there are several character states which overlap to varying degrees.

While 38 senecios and 5 non-senecios consistently have glabrous involucre bracts (char. state 01) the indumentum amongst the remaining species ranges from very sparsely pubescent (char. state 27) to densely glandular-pilose (char. state 08).

The presence of trichomes on the involucre bracts is not always associated with trichomes on the leaves for there are many senecios, with glabrous involucre bracts, which possess some form of pubescence on their leaves (e.g. S. inaequidens DC., S. brevidentatus M.D. Henderson & S. albanensis DC. var. doroniciflorus (DC.) Harvey).

Conversely, there are four senecios (S. cathcartensis O. Hoffmann, S. ngoyanus, S. oxyriifolius DC. & S. radicans (L.f.) Sch. Bip.) which have glabrous leaves but some form of pubescence on their involucre bracts.

There are a number of senecios in which glabrous leaves are associated with glabrous involucre bracts (e.g. S. urophyllus, S. glaberrimus, S. barbertonicus & S. cakilefolius DC.).

**[\*] INVOLUCRAL BRACTS: TRICHOMES** (CHAR 054 - Appendix A)

The large number of character states (43) recorded for this character is indicative of the considerable variation that exists with respect to the type of trichomes found on the involucre bracts of all the taxa investigated in this study (Table 1).

Considering the 44 character states recorded for this character, nine of these character states (char. states: 12 (part), 13, 14, 15, 16, 36, 37, 38 (part) & 44) are different from all those character states recorded for the leaf trichomes (CHARs 034-036). Consequently, it would be incorrect, in the case of some species (e.g. S. harveianus MacOwan, S. tanacetopsis & S. chrysocoma Meerburgh) to extrapolate the type(s) of trichome(s) found on the involucre bracts from the type(s) of trichome(s) found on the leaves and vice versa.

However, there are a number of character states which are the same or very similar to those recorded for the leaf trichomes (CHARs 034-036) and which are common to both the leaves and the involucre bracts in several of the senecios studied (e.g. char. states 06, 07, 09, 33).

The most frequent trichome type (char. state 05) occurs in nine taxa (6 spp. & 3 vars.). The next most frequent trichome type (char. state 22) occurs in six species. The majority of the remaining trichome types (char. states) have a single occurrence.

**INVOLUCRAL BRACTS: APEX VESTITURE (CHAR 055 - Appendix A)**

As with many other characters this character was included in the study to provide the opportunity of using its information should this information be judged to be important in assessing the interrelationships between the species investigated.

Although there was no prior evidence of the appearance of this character, it was included in this study as a logical extension of the general survey of the micromorphology of the taxa studied.

While seven character states were recorded there is considerable overlap between these states. Nevertheless, the dominant trend among the senecios studied is for the apices of the involucre bracts to be finely papillose and sub-apically verrucose (char. state 04). The papillose region often has a few longer uni- or multicellular trichomes and in several species (e.g. S. juniperinus, S. consanguineus DC., S. lydenburgensis Hutch. & Burtt Davy & S. grandiflorus Berg.) these trichomes are quite plentiful and form a dense apical tuft interspersed with papillose cells.

**INVOLUCRAL BRACTS: LENGTH RELATIVE TO DISC FLORETS  
(CHAR 056 - Appendix A)**

There are three major trends, with respect to this character, amongst the species investigated in this study (Table 1):

- (i). Character state 1 - 40 spp. & 2 vars. of Senecio & 5 non-senecios (spp. 223, 226, 228, 229 & 232).
- (ii). Character state 3 - 27 spp. & 2 vars. of Senecio & 1 non-senecio (sp. 225).
- (iii). Character state 4 - 25 spp. & 2 vars. of Senecio.

Only one species (S. dregeanus) has involucre bracts that consistently exceed the length of the disc florets (char. state 02), while three species (S. sandersonii, S. sp. aff. S. speciosus & S. hirsutilobus Hilliard) have involucre bracts that equal or slightly exceed the length of the disc florets (char. state 05).

#### INVOLUCRAL BRACTS: GLANDULAR (CHAR 057 - Appendix A)

Many of the senecios studied (37 spp. & 7 vars.) have some involucre bract trichomes which possess glandular apices, while some of the remaining senecios have a glandular apex on all of their involucre bract trichomes. A further 28 senecios have involucre bracts which are either glabrous or pubescent, these trichomes always being eglandular.

Senecio rhyncholaenus is the only species, to my knowledge, which is distinctly viscid (char. state 4). I thought at first that this viscosity was a product of the particular trichome type occurring on the involucre bracts of this species, however, this trichome type (CHAR 054, char. state 06) also occurs in S. radicans which is not viscid. One possible explanation for the lack of viscosity in S. radicans is

that the contents of its trichomes are biochemically different although the hairs are morphologically similar to those of S. rhyncholaenus.

There are also many senecios (32 spp.) which possess one or more resin-filled canals in their involucre bracts and in S. brevilorus these resin-filled canals are orange, even after the bracts are cleared in lactic acid.

#### INVOLUCRAL BRACTS: COLOUR (CHAR 058 - Appendix A)

The most frequently occurring colour of the involucre bracts is green turning brown with maturation (char. state 3; 40 spp. & 1 var.). There is another group of senecios (38 spp. & 3 vars.) which have green involucre bracts with darkly pigmented (brown) apices. There is yet another group (7 spp. & 2 vars.) which also have green involucre bracts but with purple tinged apices, the purple colour, presumably due to anthocyanin accumulation, remains through to maturity of the bracts (char. state 4). This latter character state is modified in another few species (6 spp. & 2 vars.), in that besides the apices being tinged purple, this colour extends down the keel (char. state 1). The occurrence of the purple colouration is not consistently correlated with purple florets, for while several 'purple senecios' (7 spp. & 3 vars.) exhibit this colouration of their involucre bracts, there are many more 'purple senecios' which do not exhibit this colouration.

The remaining three character states (char. states 5, 7 & 8) have single occurrences in S. inaequidens, S. medley-woodii and S. viminalis respectively.

**CALYCVLUS BRACIS: NUMBER (CHAR 059 - Appendix A)**

The distribution of all the species studied (Table 1) with respect to the six size classes of this character is illustrated in Figure 12.

A large number of species (53 spp.) have 3-5 calyculus bracts (char. state 2). There are relatively few species (8 spp.) which produce relatively few (1-2) calyculus bracts (char. state 1) and similarly relatively few species (5 spp.) which produce relatively many (20-30) calyculus bracts (char. state 6).

There are five species, including two senecios (*S. cissampelinus* & *S. gallicus* Chaix) which lack calyculus bracts (nos. 122, 124, 213, 224 & 226 - Table 1). This is of interest for attention has been drawn to the questionable acceptance of *S. cissampelinus* in Senecio by Hilliard (1977) while *S. gallicus* is regarded as Senecio s. str. by Jeffrey et al. (1977) and Jeffrey (1979). The status of *S. cissampelinus* will be discussed in chapter 5 of this dissertation.

**CALYCVLUS BRACIS: LENGTH (CHAR 060 - Appendix A)**

The distribution of all the species studied (Table 1) with respect to the four size classes of this character is illustrated in Figure 13.

While there are a number of senecios (16 spp.) which have relatively short (1-2 mm, char. state 1) calyculus bracts the majority of the

senecios investigated in this study possess calyculus bracts 3-6 mm long (char. state 2). A further nine species have calyculus bracts 7-9 mm long (char. state 3) while four senecios (*S. macrospermus* DC., *S. dregeanus*, *S. caudatus* & *S. helminthioides* (Sch. Bip.) Hilliard) have noticeably long calyculus bracts (10-17 mm, char. state 4). While these calyculus bracts are noticeably long they do not exceed the length of the involucre bracts in each species, although they are usually not much shorter than the involucre bracts. It is interesting to note that, based on this study, these four species are judged to be relatively distantly related to each other.

#### CALYCLUS BRACCS: POSITION (CHAR 061 - Appendix A)

There are three distinct trends with respect to the position of the calyculus bracts amongst the taxa studied (Table 1):

- (i). Character state 03 - 48 spp. & 2 vars. of Senecio & 1 non-Senecio (no. 229).
- (ii). Character state 01 - 23 spp. & 4 vars. of Senecio & 1 non-Senecio (no. 223).
- (iii). Character state 04 - 11 spp. & 2 non-senecios (nos. 228, 232).

The calyculus bracts of all the species with the above character states are in a uniseriate formation. However, there are a number of species (9 senecios & 2 non-senecios (nos. 228, 232)) which have their calyculus bracts arranged in 1-3 or 4 series (char. states 06 & 07).



The remaining 3 character states (char. states 02, 05 & 08) have a single occurrence in S. dregeanus, S. skirrhodon DC. and S. albanensis var. doroniciflorus respectively.

The position of the calyculus bracts amongst the senecios studied is moderately consistent.

The type species, Senecio vulgaris L. and some of the other european senecios, deemed to be Senecio sensu stricto by Jeffrey et al. (1977) and Jeffrey (1979) and only 5 southern African senecios (S. harveianus, S. chrysocoma, S. grandiflorus Berg., S. arenarius Thunb. & S. multibracteatus Harv.) have their calyculus bracts arranged in 1-3 or 4 series while the remaining senecios studied have their calyculus bracts arranged consistently in a uniseriate manner.

#### CALYCVULUS BRACTS: PUBESCENCE (CHAR 062 - Appendix A)

This character exhibits considerable variation both within and between species. This has resulted in there being several character states which overlap to varying degrees.

While sixteen species of Senecio and one non-Senecio consistently have glabrous involucreal bracts (char. state 05), the pubescence amongst the remaining species ranges from very sparsely pubescent (char. state 42) to densely glandular-pilose (char. state 12).

The following character states are the most frequent:

- (i). Character state 05 - 16 spp. of Senecio.
- (ii). Character state 10 - 7 spp. of Senecio & 1 non-Senecio.
- (iii). Character state 11 - 2 spp. & 4 vars. of Senecio.
- (iv). Character state 12 - 5 spp. & 1 var. of Senecio.
- (v). Character state 41 - 4 spp. & 2 vars. of Senecio.

Many of the remaining character states have a single occurrence.

As the presence of trichomes on the involucre bracts is not always associated with trichomes on the leaves, so too there are several senecios which consistently have trichomes of some sort on their calyculus bracts but have glabrous involucre bracts (e.g. S. polyanthemoides, S. vernalis Waldst. & Kit. & S. inornatus). On the other hand there are also several senecios which do consistently have glabrous calyculus bracts associated with glabrous involucre bracts (e.g. S. microglossus, S. urophyllus & S. vulgaris L.).

[\*] CALYCVLUS BRACIS: TRICHOMES (CHAR 063 - Appendix A)

The large number of character states (52) recorded for this character is indicative of the considerable variation that exists with respect to the trichomes found on the calyculus bracts of all the species studied (Table 1) which possess calyculus bracts.

There are 11 more character states for this character than for the

character - INVOLUCRAL BRACTS: TRICHOMES (CHAR 054). There are trichome types not previously recorded (char. states 17, 18, 19, 24, 27, 42, 50 & 51) and there are also a number of character states which record various new combinations. The remaining character states are identical to those recorded for the involucral bracts (CHAR 054).

The following is a list of the most frequently occurring character states:

- (i). Character state 09 - 13 spp. of Senecio & 1 non-Senecio (no. 225).
- (ii). Character state 29 - 6 spp. of Senecio.
- (iii). Character state 21 - 5 spp. of Senecio.
- (iv). Character state 43 - 4 spp. of Senecio & 1 non-Senecio (no. 229).

Many of the remaining character states have a single occurrence.

There are many species which possess the same trichome type on their calyculus bracts and on the involucral bracts (e.g. S. variabilis, S. glanduloso-pilosus Volkens & Muschler, S. saniensis & S. lautus Willd.). On the other hand there are also several species which possess a different trichome type or combination of trichome types on their calyculus bracts compared with those found on their involucral bracts (e.g. S. rhyncholaenus, S. hieracioides, S. asperulus & S. mauricei).

**CALYCVLVS BRACTS: APEX VESTITURE (CHAR 064 - Appendix A)**

Although there was no prior evidence of the importance of this character, it was included in this study as a logical extension of the general survey of the micromorphology of the taxa studied

There are 3 trends that can be distinguished:

- (i). Character states 2 & 3 - 25 spp. of Senecio & 3 non-senecios (nos. 225, 229, 232) and 8 spp. & 3 vars. of Senecio & 1 non-Senecio (no. 227) respectively.
- (ii). Character state 15 - 19 spp. & 1 var. of Senecio & 1 non-Senecio (no. 223).
- (iii). Character state 09 - 17 spp. of Senecio & 1 non-Senecio (no. 228).

**CALYCVLVS BRACTS: GLANDULAR (CHAR 065 - Appendix A)**

Many of the senecios studied (39 spp. & 6 vars.) have some calyculus bract trichomes which possess glandular apices. The majority of the remaining senecios have eglandular trichomes on their calyculus bracts.

Six senecios (S. polyanthemoides, S. pterophorus, S. rhyncholaenus, S. anomalochrous, S. dregeanus & S. brevilorus) have noticeably resinous calyculus bracts, especially those of S. rhyncholaenus which are viscid, as are its involucrel bracts (see the discussion on this point under CHARACTER 057), while the calyculus bracts of S. brevilorus have 1-3

distinct orange resinous nerves as do its involucre bracts.

**CALYCVLUS BRACIS: COLOUR (CHAR 066 - Appendix A)**

The majority of the senecios studied (75 spp. & 2 vars.) have green calyculus bracts which eventually turn brown. However, many of these species have calyculus bracts which have dark brown pigmented apices, as is the case with the involucre bracts of many species (CHAR 058). This pigmentation is persistent, even after clearing in lactic acid. There are also several species which have purple/red tinges to the apices of their calyculus bracts. This latter colouration, which is presumably due to anthocyanin accumulation, is not associated with purple florets.

There appear to be no significant patterns of occurrence of this character.

**CALYCVLUS BRACIS: SHAPE (CHAR 067 - Appendix A)**

The majority of the senecios studied (72 spp. & 5 vars.) have lanceolate calyculus bracts (char. state 02). Five species have noticeably deltoid calyculus bracts (char. state 06), while S. subcoriaceous has oblong calyculus bracts which have obtuse apices (char. state 07), the majority of remaining species having acute and occasionally acuminate apices. The calyculus bracts of S. helminthioides are unique in that they are broadly elliptic (char. state 09).

**FLORET COLOUR: RAY FLORETS (CHAR 068 - Appendix A)**

Flower colour has been a problematic area in botany for many years because of the lack of a universal and objective scheme to ascribe and describe flower colour.

"Floret colour" is a difficult character to record in the absence of the use of a universal and objective scheme to describe flower (floret) colour.

Consequently, this problem is implicit in the recording of floret colour for all the taxa studied (Table 1). The result is that many of the character states are based on species descriptions of the various species investigated while a number are based on my own observations.

Since there is this difficulty in describing flower colour accurately and objectively, perhaps the most equitable solution would be to divide the flower colour of the species studied into yellow and purple the latter perhaps being more aptly termed non-yellow so as to include the wide range in colour tone within nominal purple. Thus there are the YELLOW senecios and the NON-YELLOW senecios.

Sixty-three of the senecios studied have ray florets and of these, 53 are nominally 'yellow'. The range of colour tone within this nominal 'yellow' ranges from pale (clear) yellow to canary yellow to bright yellow to orange-yellow.

The frequency of the character states amongst the 'yellow' senecios is provided below:

- (i). Character state 10 - 26 spp. of Senecio.
- (ii). Character state 06 - 12 spp. of Senecio (incl. radiate S. vulgaris).
- (iii). Character state 02 - 10 spp. of Senecio.
- (iv). Character state 09 - 4 spp. of Senecio.
- (v). Character states 08 & 11 - 1 sp. of Senecio each.

The remaining 11 radiate senecios are 'non-yellow' (nominally purple), the range of colour tone within this 'non-yellow' ranging from deep pink to mauve to purple.

The frequency of the character states amongst the 'non-yellow' senecios is provided below:

- (i). Character state 01 - 6 spp. of Senecio.
- (ii). Character state 04 - 2 spp. of Senecio.
- (iii). Character states 03 & 05 - 1 var. of Senecio each.

It is important to note that while most of the senecios investigated are homochromous 'yellow' or 'non-yellow', the senecios from the Cape included in this study (Table 1) are heterochromous in that they have 'yellow' disc florets and 'non-yellow' (purple) ray florets.

**FLORET COLOUR: DISC FLORETS (CHAR 069 - Appendix A)**

The problem concerning the subjectiveness of ascribing floret colour, discussed under the previous character, applies equally here too.

The range in colour tone amongst the nominally 'yellow' and nominally 'non-yellow' (purple) senecios with respect to the disc florets is more extensive than that found in the ray florets, especially amongst the 'non-yellow' senecios.

There are three commonly occurring character states amongst the 'yellow' senecios these being:

- (i). Character state 22 - 31 spp. of Senecio.
- (ii). Character state 04 - 15 spp. of Senecio.
- (iii). Character state 05 - 10 spp. of Senecio.

Many of the remaining eight character states associated with the 'yellow' senecios have a single occurrence.

The range in colour tone amongst the 'non-yellow' senecios is represented in 17 character states. The majority of these character states have a single occurrence, there being only 3 which occur in more than one 'non-yellow' Senecio, these being the following:



- (i). Character state 02 - 8 spp. & 2 vars. of Senecio.
- (ii). Character state 09 - 3 spp. of Senecio.
- (iii). Character state 19 - 2 vars. of Senecio.

Several of the 'non-yellow' senecios (nos. 25, 28, 29, 30, 37 & 42 - Table 1) exhibit an interesting phenomenon with respect to disc floret colour in that while the majority of the specimens of a species will be 'non-yellow', specimens are encountered which are 'yellow'. Some examples of this are provided below:

- (i). Senecio subrubriflorus O.Hoffmann - char. state 08.
- (ii). S. sandersonii - char. state 13.
- (iii). S. glanduloso-pilosus - char. state 16.

Whilst the majority of the senecios studied can be allocated to either the 'yellow' or the 'non-yellow' Senecio categories, there are three senecios, S. rhyncholaenus, S. viminalis and S. radicans, which produce white disc florets. However, S. rhyncholaenus can be allocated to the non-yellows on account of it having mauve anthers, while the affinity of the other two species is more than likely to be with the 'yellow' senecios when other characters are taken into consideration.

#### RAY COROLLA: FLORET NUMBER (CHAR 070 - Appendix A)

The distribution of all the radiate senecios studied (Table 1) with respect to the five size classes of this character is illustrated in Figure 14.

There are two major trends amongst the radiate senecios with respect to the number of ray florets per capitulum:

- (i). 5-8 florets (char. state 2) - 20 spp. of Senecio.
- (ii). 12-14 florets (char. state 4) - 30 spp. & 1 var. of Senecio.

There are also two minor trends amongst the radiate senecios with respect to the number of ray florets per capitulum:

- (i). 2-4 florets (char. state 1) - 4 spp. of Senecio.
- (ii). 9-11 florets (char. state 3) - 9 spp. of Senecio.

It is interesting to note that two of the four species which produce 2-4 florets per capitulum (S. retrorsus & S. brachypodus) are consistently radiate while the other two species (S. glaberrimus & S. deltoideus) can be radiate or discoid and are often found in one or other state.

It is also most interesting to compare the number of ray florets produced in each of the rayed senecios with the Fibonacci series (1-2-3-5-8-13-21). This comparison reveals relatively good congruence with this series with 5-8 or 12-14 ray florets being most common, as illustrated below:

FIBONACCI SERIES	NUMBER OF RAY FLORETS AND SENECIOS	
2 & 3	2-4	4 spp. of <u>Senecio</u> .
5	5-8	20 spp. of <u>Senecio</u> .
8	9-11	9 spp. of <u>Senecio</u> .
13	12-14	30 spp. & 1 var. of <u>Senecio</u> .

The Fibonacci series number of the ray florets either equals the Fibonacci series number of the involucre bracts or is one or occasionally two numbers less than the Fibonacci series number of the involucre bracts within a taxon.

Barkley (1978), in his revision of many North American senecios, found a similar congruence between the number of ray florets and the Fibonacci series. He also noted a relationship between the Fibonacci series number of the ray florets and the Fibonacci series number of the involucre bracts within a species.

#### RAY COROLLA: COROLLA LENGTH (CHAR 071 - Appendix A)

This character is measured from the distal end of the limb to the proximal end of the corolla tube of the ray floret.

The distribution of all the radiate senecios studied (Table 1) with respect to the six size classes of this character is illustrated in Figure 15.

There are three major trends amongst the radiate senecios with respect to the length of the ray corolla:

- (i). 8-11 mm (char. state 2) - 23 spp. of Senecio.
- (ii). 12-15 mm (char. state 3) - 11 spp. & 1 var. of Senecio.
- (iii). 16-20 mm (char. state 4) - 17 spp. of Senecio.

The majority of the radiate non-yellow senecios (8 spp.) produce relatively long ray corollas (char. state 4) while the yellow senecios produce ray corollas of very variable (interspecific) length.

There are three radiate senecios (S. microglossus, S. sylvaticus L. & S. erectitoides Bak.) which produce relatively short (5-7 mm, char. state 1) ray corollas while there are seven species (e.g. S. dregeanus, S. hirsutilobus & S. hypochoerideus) which produce moderately long ray corollas and two species (S. macrospermus & S. heliopsis) which produce noticeably long (26-40 mm, char. state 6) ray corollas.

The length of the ray corollas of all the radiate senecios investigated, with the exception of S. brevilorus and S. sylvaticus, exceed the length of the disc florets. The length of the ray corollas of the latter two species equals that of the disc florets, S. brevilorus having ray corollas of 5-7 mm long (char. state 1), while S. sylvaticus has ray corollas of 8-11 mm long (char. state 2).

**RAY COROLLA: COROLLA SHAPE (CHAR 072 - Appendix A)**

While all of the radiate senecios investigated have corolla tubes which are parallel sided there is variation with respect to the shape of the limb.

The majority (59 spp. & 1 var.) of the radiate senecios investigated have oblong limbs which are parallel sided and characteristically c. 3 mm or wider (char. state 01). Of the remaining radiate senecios, three species have limbs of the same shape but characteristically c. 2 mm wide (char. state 03) (*S. viscosus* L., *S. sylvaticus* & *S. erectitoides*) while two species (*S. inornatus* & *S. brevilorus*) have distinctly oblong/elliptic limbs (char. state 03).

**RAY COROLLA: LIMB VENATION (CHAR 073 - Appendix A)**

The most frequent form of limb venation amongst the radiate senecios investigated is character state 02 (52 spp. & 1 var.). This consists of four (or occasionally 5 or more) distinct parallel vascular strands traversing the length of the limb. At the distal end of the limb, the vascular strands fuse in a characteristic pattern as illustrated (char. state 02). Where there are more than four vascular strands these anastomose near the limb apex to form the characteristic pattern of vasculature found in the limb apices of all the taxa studied (e.g. char. state 01).

The second most frequent form of venation amongst the radiate senecios (10 spp.) is similar except that the four parallel vascular strands are

finely branched and are frequently interspersed with thinner vascular strands (char. state 01).

In cleared limbs this venation (char. states 01 & 02) is colourless with the exception of S. brevilorus which has orange vascular strands (char. state 04). This orange colouration also occurs in the vasculature of the involucrel and calyculus bracts of S. brevilorus, as discussed earlier (CHARs 057 & 065).

#### RAY COROLLA: COROLLA TRICHOMES (CHAR 074 - Appendix A)

Eleven distinct trichome types, presenting a broad range of appearance, and two combinations of these trichome types have been recorded for this character. These trichomes may be uniseriate or biseriate, clavate or capitate and they vary considerably in length.

The majority of the radiate senecios studied (46 spp.) possess trichomes on the corolla tubes of their ray florets, while eight senecios (7 spp. & 1 var.) do not have ray corolla trichomes.

Amongst the radiate senecios, the corolla trichomes characteristically occur only on the corolla tube while in Cineraria geifolia L. (no. 232) the trichomes also occur on the proximal end of the lower surface of the limb. In most of the radiate senecios studied there are only a few trichomes scattered up the corolla tube, while in some species the trichomes are densely distributed.

Another noticeable feature is that the apices of most of the trichome types point distally. The majority of the trichome types are microscopic and are frequently quite difficult to find, especially when sparsely distributed.

While the occurrence of corolla trichomes and the type of trichome possessed is consistent in many species, several species frequently, but not invariably, possess corolla trichomes (e.g. S. hypochoerideus, S. praeteritus Killick & S. caudatus).

The following are the most frequently occurring character states:

Character state 03 - 9 spp. of Senecio

Character state 05 - 8 spp. of Senecio

Character state 09 - 8 spp. of Senecio

Character state 02 - 7 spp. of Senecio

Character state 10 - 5 spp. of Senecio

The remaining character states have a single occurrence.

It is interesting to note that, with the exception of one trichome type (char. state 14), none of the trichome types recorded match any of the trichome types found on the leaves (CHARs 034- 036), involucre bracts (CHAR 054) or calyx bracts (CHAR 063). The exception occurs in S. tanacetopsis where the trichome type found on the ray corolla tubes matches the trichome type found on the involucre bracts (CHAR 054, char. state 36) as well as the type found on the calyx bracts (CHAR

063, char. state 47).

All but types 14 and 15 (char. states 14 & 15) are eglandular.

**RAY COROLLA: RESINOUS (CHAR 075 - appendix A)**

The two character states recorded for this character indicate something of the uncertainty of whether or not the limbs of the radiate senecios studied are resinous. This uncertainty is due to the fact that in almost all the radiate species studied, it is difficult to determine, with any degree of certainty, whether the vascular strands in the limbs transport resinous substances. The exception is S. brevilorus where the veins are orange and even in this case the decision that these vascular strands are resinous is an extrapolation from the fact that the orange vascular strands in the involucre bracts are resinous. There certainly are no median resin ducts as found in the disc florets of some senecios (CHAR 085).

**RAY COROLLA: LIMB APEX (CHAR 076 - Appendix A)**

While four character states record the various forms of this character amongst all the senecios investigated, the most commonly occurring form of limb apex is character state 02 (59 spp. & 1 var.). Character state 03 (which lacks verrucae on the three small apical lobes of the limb), occurs in S. pterophorus and S. juniperinus. The limb apex is entire in S. hastatus L. while in S. brevilorus the limb apex is noticeably dissected into three lobes each lobe being finely verrucose.



It is interesting to note that in those senecios where there are more than four main vascular strands running to the apex there is no concomitant increase in the number of apical lobes, for the extra vascular strands anastomose to form the only characteristic pattern of vasculature found in the limb apices (e.g. char. state 02).

#### RAY COROLLA: LIMB SHAPE (CHAR 077 - Appendix A)

This character was originally included in the study so as to provide the opportunity of recording variation between the species with respect to the shape of the limb. However, all the variation that has been encountered has been recorded under CHARACTERS 072 and 076.

#### RAY COROLLA: LIMB EPIDERMAL CELL SHAPE (CHAR 078 - Appendix A)

The epidermis of the upper surface of the limb (ligule) of the ray florets of all the senecios investigated in this study is of the "senecionoid" type described by Baagøe (1977b). This type of epidermis consists of oblong, tabular cells with more or less convex outer walls. The radial and tangential walls are usually straight although they can be slightly undulating. The cuticle has a fine pattern of transverse or longitudinal, more or less rugose stripes (at X400) (Baagøe, 1977b).

Baagøe (1977b) also describes a "senecionoid papillose" type of epidermis which appears to be correlated with white and purple limb colour in some purple- and white-rayed Senecio species, and in some

members of the Calenduleae.

Nordenstam (1978) has also found the "senecionoid papillose" type of epidermis to be correlated with white and purple limb colour, with a few exceptions.

My observations show no correlation between the non-yellow colour of the limb and the presence of a "senecionoid papillose" type of epidermis, for all the non-yellow senecios studied possess the "senecionoid" type of limb epidermis.

Three character states have been recorded for this character, each of these falling within the description of the "senecionoid" type of limb epidermis. The main differences separating the first two character states (char. states 05 & 06) are: cell length and frequency of the fine rugose striations (stripes). The third character state (char. state 11) comprises the combination of the first two character states occurring in the same species.

I must also point out that while the "senecionoid" type of limb epidermis is described as possessing a cuticle with a pattern of transverse or longitudinal, more or less rugose stripes according to Baagøe (1977b), all of the senecios investigated in this study possessed transverse rugose striations in the cuticle of the epidermal cells. However, the occasional representative of a few species did possess longitudinal rugose striations in the cuticle of the epidermal cells of the lower surface of the limb but the upper surface of these

representatives was consistently transversely striated.

**RAY COROLLA: LIMB ORIENTATION (CHAR 079 - Appendix A)**

The ray florets of the majority (55 spp. & 1 var.) of the radiate senecios investigated in this study are orientated in a patent (spreading) manner (char. state 01), while the ray florets of six of the remaining radiate senecios (e.g. S. serratuloides, S. affinis & S. inornatus) are soon recurved (char. state 03).

Senecio brevilorus and S. sylvaticus have the limbs of their ray florets orientated vertically and these rays are often quite difficult to see because they are only as long as the disc florets (char. state 04).

**DISC COROLLA: FLORET NUMBER (CHAR 080 - Appendix A)**

The distribution of all the taxa studied (Table 1) with respect to the five size classes of this character is illustrated in Figure 16.

There are two major trends amongst the senecios studied, with respect to the number of disc florets per capitulum:

- (i). 10-30 florets (char. state 2) - 29 spp. of Senecio.
- (ii). 40-60 florets (char. state 3) - 47 spp. & 5 vars. of  
Senecio.

There are also three minor trends amongst the senecios with respect to the number of disc florets per capitulum:

- (i). 5-8 florets (char. state 1) - 4 spp. of Senecio.
- (ii). 70-90 florets (char. state 4) - 13 spp. & 1 var. of  
Senecio.
- (iii). > 100 florets (char. state 5) - 3 spp. of Senecio.

There are many senecios which exhibit a positive correlation between the number of disc florets and the diameter of the capitulum and there are several species which exhibit a negative correlation between these same two characters. Some examples are provided below:

SPECIES # (Table 1)	DISC FLORET # (char. state)	CAPITULUM DIAMETER (char. state)	CORRELATION
75	5	6	positive
81	5	5	positive
1	4	2	negative
35	4	2	negative

The significance of there being both positive and negative correlations is that they indicate that the diameter of the disc florets varies between species. Senecio macrospermus and S. madaqascariensis illustrate this clearly, for the disc florets of S. madaqascariensis are noticeably narrower than those of S. macrospermus hence a relatively large number of disc florets can be accommodated in the relatively narrow capitulum of S. madaqascariensis.

[\*] DISC COROLLA: COROLLA LENGTH (CHAR 081 - Appendix A)

The distribution of all the taxa studied (Table 1) with respect to the four size classes of this character is illustrated in Figure 17.

The majority of the senecios studied have disc florets in the size range 5-15 mm. This size range is divided into two size classes:

(i). 5- 8 mm (char. state 2) - 57 spp. & 6 vars.

of Senecio.

(ii). 9-15 mm (char. state 3) - 22 spp. of Senecio.

It is interesting to note that of these two size classes the first (5-8 mm) is the most commonly occurring amongst the senecios studied. This indicates that, with respect to many of the senecios, the length of the disc florets is independent of changes in other characters such as capitulum diameter and the number of disc florets.

Of the remaining species, four (S. inaequidens, S. arabidifolius, S. deltoideus & S. lautus) have relatively short (4-4,7 mm) disc florets (char. state 1) while S. viminalis and S. fulgens have relatively long (> 17 mm) disc florets (char. state 4).

[\*] DISC COROLLA: COROLLA SHAPE (CHAR 082 - Appendix A)

The characteristic shape of the corolla of the disc florets of all the senecios studied is a tube, dilated in the upper one third and terminating in 5 lobes.

The only variation that occurs in this character is in the degree to which the lobes are dissected. This variation in the degree of dissection of the lobes is divided into two character states. The disc florets of the majority (69 spp. & 6 vars.) of the senecios have shallowly dissected corolla lobes while the remainder (26 spp.) have

deeply dissected lobes.

**DISC COROLLA: COROLLA VENATION** (CHAR 083 - Appendix A)

The pattern of venation in the disc corollas (char. state 01) is invariant throughout all the taxa studied (Table 1).

The disc corollas of all the taxa studied always have 5 veins from the base of the corolla which bifurcate at each sinus and then anastomose in the corolla lobes to form a "closed venation" (Drury & Watson, 1965).

**DISC COROLLA: COROLLA TRICHOMES** (CHAR 084 - Appendix A)

While the majority (88 spp. & 2 vars.) of the senecios studied do not have any trichomes on the tubes of the disc corollas, five different types of trichome (char. states 02, 03, 04, 05 & 10) have been found amongst the remaining senecios, their occurrence being frequent or occasional. The majority of the character states detailing the occurrence of the various trichome types have a single occurrence.

Two of the trichome types are biseriate the remaining types being uniseriate. Two of the trichome types (char. states 02 & 04) are unique while the remaining types are also found on the corolla tubes of some of the radiate senecios. Only two of the trichome types (char. states 02 & 03) appear to be glandular.

It is interesting to note that more discoid senecios possess trichomes

on the their disc corolla tubes than do radiate senecios. The distribution of the various trichome types amongst these discoid and radiate senecios is provided below:

(i). DISCOID SENECIOS

Character state 02 - S. erubescens Ait. var. erubescens

S. glanduloso-lanosus Thellung

Character state 03 - S. polyodon DC. var. polyodon

S. arabidifolius

Character state 04 - S. poseideonis (discoid form)

Character state 07 - S. erubescens var. dichotomus DC.

Character state 08 - S. subcoriaceus

(ii). RADIATE SENECIOS

Character state 06 - S. madaqascariensis

Character state 07 - S. polyodon var. subglaber

(O.Kuntze) Hilliard

& Burtt.

Character state 11 - S. coronatus

Character state 12 - S. natalicola Hilliard

(iii). RADIATE OR RARELY DISCOID SENECIOS

Character state 07 - S. paludaffinis

Also of interest is the occurrence of two different trichome types amongst the two varieties of S. erubescens and another two trichome types amongst the two varieties of S. polyodon.



[\*] DISC COROLLA: RESINOUS (CHAR 085 - Appendix A)

This character refers to the presence of resin ducts in the corolla lobes and/or corolla tubes of the disc florets. Resin ducts are distinguishable from the vascular strands in that the latter are distinctly helically thickened, while the former are not thickened but appear as a relatively less dense tissue in comparison to the adjacent tissue.

Many (30 spp. & 1 var.) of the senecios studied lack any recognisable form of resin ducts although there is the possibility of the veins in each corolla lobe being a transport system for resinous compounds. Of the remaining senecios, 46 species and 5 varieties have a broad resin duct traversing up the middle of each corolla lobe to the apex (char. state 02). There is a third group of senecios (13 spp.) which have a very short median resin duct in each corolla lobe, this apparently not descending much below the point where the lobes fuse (char. state 03).

While the resin ducts described above (char. state 02) are either colourless or the same colour as the surrounding corolla lobe, a few species have either a median orange (char. states 04 & 06, - 4 spp.) or yellow (char. state 07, - S. barbertonicus) resinous line, descending down each of the corolla lobes. However, in S. brevilorus the orange resinous lines extend all the way down the corolla lobes to the base of the corolla tube (char. state 04).

Senecio brevilorus is the only species which possesses orange resinous lines/ducts in other floral structures (i.e. involucre bracts (CHAR

057), calyculus bracts (CHAR 065 and ray corolla: limb venation (CHAR 073)).

**[\*] DISC COROLLA: LOBE APEX (CHAR 086 - Appendix A)**

The majority (48 spp. & 5 vars.) of the senecios studied have the following characteristics of the lobe apices of the disc corollas: lower and upper surfaces and the margins of the lobe apex - finely and densely verrucose (char. state 02 - e.g. S. madagascariensis, S. umqeniensis & S. cathcartensis). A further fourteen species have a very similar appearance of the lobe apices of their disc corollas, the difference being that the lower and upper surfaces and the margins of the lobe apices are very finely verrucose (char. state 07 - e.g. S. serratuloides, S. panduriformis & S. vulgaris). While this distinction between these two character states may seem to be unwarranted, the difference is quite unmistakable at X400 magnification.

Another group of senecios (6 spp. & 1 var.) have lobe apices of their disc corollas which are similar to those with character state 02 except that the verrucose cells each have a noticeably pointed apex (char. state 06 - e.g. S. ingeliensis Hilliard, S. paludaffinis & S. brevidentatus). A further three senecios (S. sandersonii, S. arabidifolius & S. discodregeanus Hilliard & Burtt) have a noticeably swollen lower surface to each lobe apex of the disc corolla (char. state 04).

A summary of the distribution of these character states is provided below:

- (i). Character state 02 - 47 spp. & 5 var. of Senecio.
- (ii). Character state 04 - 3 spp. of Senecio.
- (iii). Character state 07 - 14 spp. of Senecio.

The following and remaining character states found amongst the remaining senecios have a single occurrence:

- (i). Character state 03 - S. barbatus
- (ii). Character state 08 - S. hirsutilobus
- (iii). Character state 09 - S. fulgens
- (iv). Character state 12 - S. arenarius

It is interesting to note that character state 03 and 08 bear some similarity to each other in that the cells of the lobe apices of the disc corollas are elongated. In S. barbatus these cells produce a papillose appearance while in S. hirsutilobus these cells form multicellular hairs.

#### GYNOECIUM (RAY): STYLE-ARM LENGTH (CHAR 087 - Appendix A)

The distribution of all the taxa studied (Table 1) with respect to the two size classes of this character is illustrated in Figure 18.

The majority (54 spp. & 1 var.) of the radiate senecios studied have

style-arms of their ray corollas in the size range 0,4-1,4 mm (char. state 1), the most frequent length being between 0,8 mm and 1,2 mm.

The style-arms of the remaining radiate senecios (9 spp.) are frequently 1,5-2.5 mm in length (char. state 2).

My early impressions were that style-arm length and the length of the ray corolla were correlated, as in S. medley-woodii, S. hypochoerideus, S. macrospermus and S. dregeanus, all of which have relatively long ray corollas (CHAR 071, char. states 5 & 6) and style-arms (char. state 2). However, this is not the case in a number of other senecios. A negative correlation between these two characters is found in a number of species which produce relatively long ray corollas (CHAR 071, char. states 5 & 6) but relatively short style-arms (char. state 1) (nos. 46, 47, 48, 63 & 85, Table 1). A negative correlation between these two characters is also found in a number of senecios which produce moderately long ray corollas (CHAR 071, char. state 4) but relatively long style-arms (char. state 2) (nos. 35, 43, 83, 86 & 111). Although this negative correlation is less marked than the former.

#### GYNOECIUM (RAY): STYLE-ARM APICES (CHAR 088 - Appendix A)

The majority (56 spp. & 1 var.) of the radiate senecios investigated have a distinctly verrucose and truncate apex to each of the style-arms (char.state 02).

Character states 05 and 06 are very similar but are nevertheless

distinct in that the style-arms recorded as character state 05 are consistently verrucose down the whole outer surface of each style-arm. However the style-arms recorded as character state 06 are consistently verrucose only on the distal portion of the outer surface of each style-arm.

Character state 04 is unique to Senecio brevilorus, the median apical fascicle being composed of a few longer, more or less fused, papillae of variable length, the central papillae being the longest. The remainder of the apex is verrucose.

A summary of the distribution of the character states is provided below:

- (i). Character state 02 - 56 spp. & 1 var. of Senecio.
- (ii). Character state 04 - S. brevilorus
- (iii). Character state 05 - S. achilleifolius  
S. medley-woodii  
S. scitus
- (iv). Character state 06 - S. tanacetopsis  
S. seminiveus  
S. brachypodus

#### GYNOECIUM (RAY): STIGMATIC SURFACE (CHAR 089 - Appendix A)

The appearance of the stigmatic surface of the style-arms of the ray corollas of all the radiate senecios and non-senecios investigated is invariant (char. state 01). The inner surface of each style-arm has two

distinct stigmatic surfaces traversing the length of the arm these being separated by a narrow median region of non-stigmatic tissue. This form of stigmatic surface was termed "banded" by Wetter (1983).

See CHARACTER 096 for further discussion on the stigmatic surface.

**GYNOECIUM (RAY): STYLE BASE (CHAR 090 - Appendix A)**

The style base is part of the composite structure called the stylopodium. The stylopodium consists of the style base, the area of attachment of the style to the cypsela, and an associated nectary located on the distal end of the cypsela (Wetter, 1983).

While there is some variation within some species with respect to the appearance of the style base resulting in 3 character states, the general trend amongst the radiate senecios and non-senecios is for the style base to be parallel sided (char. state 03) ("unenlarged" sensu Wetter (1983)). The style base is also "free" from the nectary (CHAR 091) in that a small projection of nectariferous tissue is attached to the style-base, and supports the style-base atop the nectary (Wetter, 1983).

Since there is little variation in the shape of the style base of the ray corollas of the radiate senecios and non-senecios, this character can be considered to be relatively invariant.

See CHARACTER 097 for further discussion on the style base.

**GYNOECIUM (RAY): NECTARY (CHAR 091 - Appendix A)**

This character is defined under CHARACTER 090.

There are two trends. The first is a nectary which has only a very small projection of nectariferous tissue forming a very small pillar of approximately the same width as the style base (char. state 02). The first impression of this character state is that it is an "immersed" stylopodium in that the style base first appears to be in direct contact with the nectariferous disc atop the cypsela (Wetter, 1983). However, closer inspection will reveal the presence of the exceedingly small projection of nectariferous tissue.

The second trend is a nectary which has a noticeable projection of nectariferous tissue (c. 100  $\mu\text{m}$ ) this projection also being of approximately the same width as the style base (char. state 03).

Both of these nectary types are "free" as described in CHARACTER 090.

A summary of the distribution of these two nectary types amongst the radiate senecios is provided below:

- (i). Character state 02 - 18 spp. of Senecio.
- (ii). Character state 03 - 45 spp. & 1 var. of Senecio.

See CHARACTER 098 for further discussion on the nectary.

#### GYNOECIUM (RAY): OVARY VESTITURE (CHAR 092 - Appendix A)

The vestiture of the immature pericarp of the ray cypselas, was investigated for two reasons. The first was to monitor changes in the vestiture, in particular, to ascertain whether the density decreases with age. The second reason being to enable me to document the pubescence of the ray cypselas as well as noting any differences in pubescence between the immature ray and disc cypselas (see CHAR 099).

In no instance was a change in the density of pubescence recorded as the ray cypselas matured. Thus, when cypselas pubescence is referred to in keys, accurate predictions can be made from immature cypselas of either ray or disc florets.

The various character states recorded for this character are included in the MASTER DATA MATRIX (Appendix B) for completeness and for future reference.



**GYNOECIUM (RAY): OVARY WALL CRYSTALS (CHAR 093 - Appendix A)**

The decision to include this character in this study was stimulated particularly by the work of Nordenstam (1978) on many members of the Senecioneae including some members of Senecio and also by the work of Drury and Watson (1965) and Dormer (1961). Nordenstam (1978) remarks that "ovary crystals of many distinct forms occur throughout the family (Compositae) and while some attention has been paid to the occurrence of ovary wall crystals in the Senecioneae, much more study is needed, especially to get some idea of the range of variation present within the huge genus Senecio s. str." The need to improve our understanding of the occurrence and range of variation of these ovary wall crystals within Senecio is further motivated by the work of Dormer (1961) who showed that the shape of the calcium oxalate crystals found in the ovary wall of some members of the tribe Cynareae (Asteraceae) was taxonomically useful.

Three forms of crystal were found in the ovary wall (inner ovary wall), these being: "homomorphic oblong", "heteromorphic hexagonal plates" and "acerose" (Nordenstam, 1978).

"Homomorphic oblong" crystals were found both on their own (char. state 01) and associated with "heteromorphic hexagonal plate" crystals (char. state 02). Relatively small (c. 5  $\mu$ m) "heteromorphic hexagonal plates" (char. state 03) were also found irregularly in some species (char. state 07). The "acerose" crystals (char. state 05) were only found on their own.

Nordenstam (1978) mentions that there is usually one crystal per cell but that there are instances where each cell may contain many crystals. In this study there was always one crystal per cell despite the variation in size amongst the various crystals that were found.

While some (9 spp.) of the radiate senecios studied did possess ovary wall crystals, many of the senecios (47 spp.) did not and a further group (7 spp. & 1 var.) possessed ovary crystals, but inconsistently. It was initially thought that the cause of the absence and inconsistency in the occurrence of these crystals amongst the radiate senecios was due to the use of the clearing medium - lactic acid, which does digest calcium oxalate. However, to test this possibility, some ovaries were examined after being softened in boiling water. Some of the species which lacked crystals when cleared in lactic acid also lacked them when treated as above. Consequently, it was decided that the absence or inconsistency in the occurrence of these ovary wall crystals was not an artifact resulting from the clearing procedure. This is despite the fact that it was noted that the surface of the crystals was etched by the lactic acid but this was only noticeable after c. 30 min. in hot (c. 100 °C) lactic acid while most clearing of the ovary wall was satisfactory after c. 10 minutes.

The occurrence of calcium oxalate crystals in the ovary wall will be discussed further under CHARACTER 100.

[\*] GYNOCIDIUM (DISC): STYLE-ARM LENGTH (CHAR 094 - Appendix A)

The distribution of all the taxa studied (Table 1) with respect to the four size classes of this character is illustrated in Figure 19.

The majority (84 spp. & 6 vars.) of the senecios studied have style-arms of their disc corollas in the size range 0,6-1,5 mm (char. state 2), the most frequent length being between 0,8 mm and 1,2 mm.

A further seven senecios have style-arms in the size range 1,6-2,5 mm (char. state 3 - e.g. S. asperulus, S. medley-woodii, S. barbertonicus & S. radicans) while only two senecios (S. sylvaticus & S. erectitoides) have style-arms in the size range 0,4-0,5 mm (char. state 1). The remaining two senecios (S. viminalis & S. fulgens) have noticeably long style-arms, these being in the size range 3,0-4,5 mm (char. state 4) the predominant length being 3,0 mm.

Interestingly, there appears to be correlation between disc corolla length and style-arm length. Two species (S. viminalis & S. fulgens) have relatively long disc corollas (CHAR 081, char. state 4) and relatively long style-arms (char. state 4). Another much larger group of senecios have relatively short disc corollas (CHAR 081, char. state 2) and relatively short style-arms (char. state 2).

[\*\*] GYNOECIUM (DISC): STYLE-ARM APICES (CHAR 095 - Appendix A)

The range in appearance of the style-arms of the taxa investigated in this study (Table 1) is quite fascinating and is recorded in twelve distinct character states.

The style-arms of the majority (74 spp. & 6 vars.) of the senecios investigated are truncate with a sub-apical semicircle (incomplete ring) of spreading papillae (char. state 09). There is a small sub-apical region on the inner surface of each style-arm which is devoid of papillae, but appears to be receptive. This "nude" sub-apical region corresponds to the width of the stigmatic surface. Some representatives of some species have convex to conical apices to the style-branches as opposed to truncate apices. The apices in all the specimens examined are distinctly verrucose, this pattern ending abruptly at the semicircle of spreading papillae.

A number (13 spp.) of the remaining senecios have style-arms which are very similar to those described above but they differ in that the outer surface, proximal to the semicircle of spreading papillae, is also verrucose, the verrucae facing distally at c. 45 degrees to the outer surface (char. state 11). The appearance of these style-arms is distinct from those of character state 09.

The majority of the remaining character states have a single occurrence.

A proposed scheme of the possible affinities of these twelve forms of

style-arm is illustrated in Figure 20. Character state 09 is the putative primary form of the style-arm apex with character state 13 being closely related to this form. Character states 11 and 14 (group A) and 10, 15, 17 and 19 (group B) are more distantly related to the primary form, while character states 16 (group C), 22 and 20 and 21 are increasingly distantly related to the primary form (see Figure 20).

A summary of the distribution of the character states amongst all the taxa investigated in this study (Table 1) is provided below:

- (i). Character state 09 - 74 spp. & 6 var. of Senecio.
- (ii). Character state 10 - S. brevilorus
- (iii). Character state 11 - 13 spp. of Senecio.
- (iv). Character state 13 - S. haygarthii Hilliard
- (v). Character state 14 - S. medley-woodii  
S. deltoideus  
S. syringifolius  
Emilia flammea Cass.
- (vi). Character state 15 - S. viminalis
- (vii). Character state 16 - S. fulgens
- (viii). Character state 17 - S. tanacetopsis  
S. seminiveus
- (ix). Character state 19 - S. transvaalensis Bolus  
S. hockii De Wild. & Muschl.
- (x). Character state 20 - Crassocephalum cernuum (L.f.)  
Moench
- (xi). Character state 21 - Gynura auriculata Cass.

(xii). Character state 22 - Kleinia grandiflora DC.

Kleinia neriifolia Haw.

**GYNOECIUM (DISC): STIGMATIC SURFACE (CHAR 096 - Appendix A)**

The appearance of the stigmatic surface of the style-arms of the disc corollas of all the senecios and non-senecios studied is invariant (char. state 01).

The stigmatic surface of the style-arms has a "banded" appearance (Wetter, 1983) as was found on the style-arms of the ray corollas (CHAR 089).

Wetter (1983), in his study of some members of the Senecioneae, describes three basic configurations of the stigmatic surface: "entire", "cleft" and "banded". The "entire" configuration was frequently found amongst the Cacalioid genera investigated but not at all amongst the Senecionoid genera. Amongst the Senecionoid genera both the "cleft" and "banded" configurations were found but not the "entire" configuration. Amongst the five species of Senecio investigated (incl. S. vulgaris) both forms of Senecionoid configuration were found including a "cleft" form of configuration in which the apex has a triangular area of cells which are morphologically distinct from the other cells of the style-arms, this form of configuration being termed "transitional" by Wetter (1983).

[\*] GYNOECIUM (DISC): STYLE BASE (CHAR 097 - Appendix A)

This character is defined under CHARACTER 090.

A large majority (82 spp. & 6 vars.) of the senecios studied produce style bases which are very slightly dilated, there being only a very slight acropetal taper (char. state 05). This character state is clearly distinguishable from the "unenlarged" shape described by Wetter (1983). A number (7 spp. - e.g. S. purpureus, S. hirsutilobus & S. oxyriifolius) of the remaining senecios produce an "enlarged" style base (char. state 04) the "enlarged" shape extending distally in a gradual taper. The remaining senecios (6 spp. - e.g. S. serratuloides, S. medley-woodii & S. anomalochrous), with one exception, also produce "enlarged" style bases but the "enlarged" shape extends distally for only a very short distance (char. state 03) in comparison to the length of the previously described style base (char. state 04). Only S. discodregeanus produces the noticeably long style bases of character state 01. The "enlarged" base is also noticeably broader than the remaining distal portion of the style.

The style bases of all the senecios studied are "free" (Wetter, 1983).

[\*] GYNOECIUM (DISC): NECTARY (CHAR 098 - Appendix A)

For a definition of this character see CHARACTER 090.

There are five distinct forms of the nectary of the discoid florets amongst the senecios studied and there two discernible trends with

respect to these five forms. The first trend (char. state 03) takes the form of a nectary with a noticeable projection of nectariferous tissue, which is attached to the style base (CHAR 097) and is narrower than the style base. The second trend (char. state 06) takes the form of a relatively shorter projection of nectariferous tissue, than that just described, which is attached to and equals the width of the style base.

The remaining forms of nectary are variations on the first of the above two trends. The first of these consists of a relatively long projection of nectariferous tissue attached to a relatively broader style base (char. state 01). The second form is very similar to the previous form except that the projection of nectariferous tissue is strikingly longer and consistently so within the four species in which it occurs (char. state 07). The third form consists of an exceedingly short projection of nectariferous tissue, which has the appearance of a slightly raised pillar of nectariferous tissue of approximately the same width as the style base (char. state 05). The first impression of such a stylopodium is that it appears to lack a nectary, however, closer inspection reveals the presence of an exceedingly small nectary. This latter form of nectary is also found amongst some radiate senecios.

A summary of the distribution of these two nectary types amongst the radiate senecios is provided below:

- (i). Character state 01 - 7 spp. of Senecio.
- (ii). Character state 03 - 55 spp. & 6 vars. of Senecio.
- (iii). Character state 05 - S. tanacetopsis



S. deltoideus

S. tamoides

S. helminthioides

(iv). Character state 06 - 25 spp. of Senecio.

(v). Character state 07 - S. variabilis

S. umoeniensis

S. glanduloso-pilosus

S. oxyriifolius

Only two of these five forms of nectary are found amongst the radiate senecios these being character state 05 ( $\equiv$  CHAR 091, char. state 02) and character state 06 ( $\equiv$  CHAR 091, char. state 03).

While there is some correlation, with respect to the form of the nectary, between the disc and ray florets of many radiate senecios (S. serratuloides, S. seminiveus, S. glaberrimus & S. latifolius), there are several radiate senecios which do not produce a similar or identical nectary in the disc and ray florets (e.g. S. madagascariensis, S. pterophorus & S. grandiflorus).

#### GYNOECIUM (DISC): OVARY VESTITURE (CHAR 099 - Appendix A)

The vestiture of the immature pericarp of the disc floret cypselas was investigated for the same reasons as the vestiture of the immature pericarp of the ray floret cypselas (CHAR 092).

The observations of this character were the same as those described for the vestiture of the pericarp of immature ray cypselas (CHAR 092).

Since the same observations were made for the vestiture of the ray cypselas (CHAR 092) the implications are that accurate predictions can be made regarding the vestiture of mature ray and disc cypselas by observing the vestiture of immature ray or disc cypselas. This could be of use where the vestiture of cypselas is referred to in keys.

It is interesting to note that Wetter (1983) found a similar level of stability in five other microcharacters between immature and mature florets of Digitacalia tridactylis (Rob. & Greenm.) Pippen (Senecioneae).

The various character states recorded for this character are included in the data matrix (Appendix B) for completeness and for future reference.

#### GYNOECIUM (DISC): OVARY WALL CRYSTALS (CHAR 100 - Appendix A)

Please refer to CHARACTER 093 for the initial discussion on this character.

The same three forms of crystal as in CHARACTER 093, were found in the ovary wall of the disc floret cypselas, these being: "homomorphic oblong", "heteromorphic hexagonal plates" and "acerose" (Nordenstam, 1978). However, another shape of crystal was also found, this being distinctly tetragonal (char. state 15).

"Homomorphic oblong" crystals were often associated with "heteromorphic hexagonal plate" crystals (char. state 06) while relatively long (c. 20  $\mu\text{m}$ ) "heteromorphic hexagonal plates" usually occurred with "acerose" crystals (char. state 08). Relatively small (c. 5  $\mu\text{m}$ ) "heteromorphic hexagonal plates" occurring with relatively small "acerose" crystals were also found (char. state 02).

As in similar studies of ray floret ovaries, I was unable to confirm Nordenstam's observations that, while there is usually only one crystal per cell, there are instances where each cell may contain many crystals (Nordenstam, 1978). In this study there was always one crystal per cell, despite the variation in size amongst the various crystals that were found.

Many (59 spp.) of the senecios studied lacked ovary wall crystals, while a further group (13 spp. & 1 var.) sometimes possessed ovary wall crystals. Only 36 species and 6 varieties of Senecio consistently possessed ovary wall crystals.

The occurrence of ovary wall crystals in both ray and disc cypselas appears to be related to the age of the cypselas, for relatively immature cypselas showed more inconsistency in the occurrence of the various crystal types in comparison to relatively mature cypselas. This was also frequently true of the proportions of the various crystal forms, for the size of the crystals was far more variable in relatively immature cypselas than in mature crystals.

As already discussed under CHARACTER 093, I do not think that the absence and inconsistencies of occurrence of ovary wall crystals is a product of the preparative procedures but rather that these findings are representative of the natural occurrence of these crystals.

The majority of the character states recorded for this character, other than character state 01, occur singly, the remaining character states each occurring amongst relatively few senecios.

DISC COROLLA: DISTAL EPIDERMAL CELL SHAPE (CHAR 101 - Appendix A)

DISC COROLLA: PROXIMAL EPIDERMAL CELL SHAPE (CHAR 102 - Appendix A)

These two characters were included in this study to ascertain whether patterns were present in the upper epidermis of the disc corollas, as have been found in the adaxial epidermis of the limbs (ligules) of many radiate members of the Asteraceae (Baagøe, 1977a, 1977b; Nordenstam, 1978).

The distal epidermal cells are those found within the corolla lobes while the proximal epidermal cells are those found lower down the disc corolla but prior to the region where the 'campanulate' portion of the corolla becomes more readily distinguishable as the corolla tube.

The most common pattern on the surface of the epidermal cells in these two regions of the disc corolla is similar to that found on the limbs of the radiate senecios (CHAR 078), in that these cells are predominantly

oblong and tabular with a more or less convex outer wall. The radial and tangential walls are either straight or slightly undulating. The cuticle usually has a pattern of transverse more or less rugose striations and there is no systematic connection between the patterns of adjacent cell. This is the typical "senecionoid" type of limb epidermis as described by Baagøe (1977b)

However, there is a considerable amount of variation within some senecios (CHAR 101, 13 spp. & 1 var.; CHAR 102, 10 spp. & 1 var.) and there are also several trends within this "senecionoid" type of epidermis, together resulting in a several (8) character states for each character. The nett result is that these two micro characters are of little or no value in elucidating the phenetic relationships amongst the senecios investigated.

Nevertheless, despite the considerable amount of variation in several of senecios there are some discernible trends amongst some of the senecios with respect to some of the character states of these two characters. A summary of some of these trends is provided below:

#### DISTAL EPIDERMAL CELL SHAPE

- (i). Character state 03 - 46 spp. & 2 vars. of Senecio.
- (ii). Character state 04 - 21 spp. & 2 vars. of Senecio.
- (iii). Character state 02 - 12 spp. of Senecio.
- (iv). Character state 07 - 6 spp. of Senecio.
- (v). Character state 01 - 4 spp. of Senecio.

#### PROXIMAL EPIDERMAL CELL SHAPE

- (i). Character state 05 - 20 spp. & 1 var. of Senecio.
- (ii). Character state 04 - 16 spp. & 1 var. of Senecio.
- (iii). Character state 07 - 12 spp. of Senecio.
- (iv). Character state 08 - 9 spp. of Senecio.
- (v). Character state 02 - 6 spp. & 2 vars. of Senecio.
- (vi). Character state 03 - 7 spp. of Senecio.
- (vii). Character state 01 - 6 spp. of Senecio.

An examination of the character states (Appendix A) possessed by the senecios studied reveals that there are some senecios which produce similarly shaped distal and proximal epidermal cells (e.g. CHAR 101, char. state 03 & CHAR 102, char. state 06 - e.g. S. chrysocoma, S. othonniflorus & S. grandiflorus). However, this examination also reveals that there are many senecios which do not produce similarly shaped distal and proximal epidermal cells (e.g. CHAR 101, char. state 03 & CHAR 102, char. state 05 - e.g. S. panduriformis, S. hayqarthii & S. umgeniensis).

#### [\*\*] ANDROECIUM (DISC): ANther APEX (CHAR 103 - Appendix A)

This character refers to the shape of the apical appendage (the sterile connective extension) of each anther.

There are four quite distinct character states for this character, three of these being found amongst the senecios studied.

The majority (85 spp. & 6 vars.) of the senecios produce relatively short anther apices (char. state 01). A further 10 senecios produce anther apices which are very similar to those of character state 01 but differ in that their length and breadth are twice that of the apices of character state 01. A summary of the distribution of these four character states is provided below:

- (i). Character state 01 - 85 spp. & 6 vars. of Senecio.
- (ii). Character state 03 - 10 spp. of Senecio.
  - S. syringifolius O.Hoffm.
  - S. hockii
  - Kleinia grandiflora
  - Kleinia neriifolia
- (iii). Character state 04 - S. transvaalensis
  - Crassocephalum cernuum
  - Emilia flammea
- (iv). Character state 05 - Gynura auriculata

[\*] ANDROECIUM (DISC): ANther BASE APPEARANCE (CHAR 104 - Appendix A)

The shape of the anther base varies in the tribe Senecioneae from rounded to acute or acuminate (sagittate) or caudate (Nordenstam, 1978) and a warning has been issued against "relying too heavily on the presence of anther tails in this part of the family" (Nordenstam, 1978). This warning is based on the polytopic occurrence of caudate anthers in many distantly related groups in the tribe, suggesting that anther tails have developed independantly several times (Nordenstam, 1977, 1978).

Five character states have been recorded for this character, three of these being distinct morphological forms, the remaining two being combinations of these three distinct forms

There are two distinct trends amongst the senecios studied. The first comprises obtuse anther bases (char. state 02), while in the second trend comprises shortly tailed and acuminate (sagittate) anther bases (char. state 04). The third distinct morphological form of anther base (char. state 03) is conspicuously tailed and acuminate (sagittate). The remaining two character states (char. states 05 & 06) are combinations of character states 02 and 04. A summary of the distribution of these five character states amongst all the taxa studied (Table 1) is provided below:

(i). Character state 02 - 76 spp. & 6 vars. of Senecio.

S. hockii

Crassocephalum cernuum

Emilia flammea

Gynura divaricata

Kleinia grandiflora

Kleinia neriifolia

Cineraria geifolia L.

(ii). Character state 04 - 17 spp. of Senecio.

S. syringifolius

(iii). Character state 03 - S. othonniflorus

S. cissampelinus



(iv). Character state 05 - S. bupleuroides

(v). Character state 06 - S. urophyllus

It is quite clear from the above summary that the type of anther base possessed is consistent for virtually all the taxa studied, the two exceptions being S. bupleuroides and S. urophyllus, both of which exhibit variation in the form of their anther bases.

While there appears to be relatively little variation between the senecios studied, with respect to this character, several of the species of the related genera, included in this study, also possess some of these character states, notably character state 02 (obtuse anther bases). While this situation does not directly support the warning mentioned earlier concerning the excessive reliance on the possession of anther tails for taxonomic delimitation, it appears that the lack of anther tails is equally suspect.

**[\*] ANDROECIUM (DISC): ANTHOR LENGTH (CHAR 105 - Appendix A)**

The distribution of all the taxa studied (Table 1) with respect to the four size classes of this character is illustrated in Figure 21. "Anther length" includes the apical and basal appendages (CHAR 103 & 104).

There are two major trends amongst the senecios studied:

- (i). Character state 02 - 28 spp. & 5 vars. of Senecio.  
(1,8-2,2 mm)
- (ii). Character state 03 - 40 spp. & 1 var. of Senecio.  
(2,3-2,9 mm)

There are also two minor trends amongst the senecios studied:

- (i). Character state 01 - 16 spp. of Senecio.  
( < 1,7 mm)
- (ii). Character state 04 - 12 spp. of Senecio.  
(3,0-4,0 mm)

Considering those species of Senecio with relatively long (3,0-4,0 mm) anthers (char. state 04), only two of these species (S. viminalis & S. fulgens), have relatively long anthers correlated with relatively long disc corollas (CHAR 081, char. state 4) and style-arms (CHAR 094, char. state 4). Several of the remaining species (S. medley-woodii, S. asperulus, S. hypochoerideus, S. helminthioides, S. barbertonicus & S. radicans) with relatively long anthers have these correlated with moderately long disc corollas (CHAR 081, char. state 3) and style-arms (CHAR 094, char. state 3), while four species (S. affinis, S. macrospermus DC., S. dregeanus & S. heliopsis) with relatively long anthers have these associated with moderately long disc corollas but with relatively short style-arms (CHAR 094, char. state 2). The style-arms are exerted out of the corolla tube in all instances.

**ENDOTHELIAL TISSUE: CELL SHAPE (CHAR 106 - Appendix A)**

The endothecium or fibrous layer (Dormer, 1962) also termed "exothelial tissue" by Robinson and Brettel (1973) and also called the "hypodermal fibrous layer" (Noel, 1983) of the anthers is usually composed of tabular cells, but variation in the shape of these cells in some members of the Compositae has been documented (Dormer, 1962). Nordenstam (1978) in his study of the Senecioneae notes that the endothelial cells are usually more or less elongate.

Elongate endothelial cells (char. state 01) are found in all the taxa investigated in this study (Table 1), with the exception of two species (Kleinia grandiflora & Kleinia neriiifolia). In the latter two species the cells are noticeably square (isodiametric) to slightly elongate (char. state 02).

It is interesting to note that unusually short cells (almost isodiametric) have also been found in Dendrosenecio johnstonii (Oliv.) B.Nord., another member of the tribe Senecioneae (Nordenstam, 1978).

**[\*\*] ENDOTHELIAL TISSUE: CELL WALL CONFIGURATION (CHAR 107 - Appendix A)**

Attention has been drawn to the value of the endothecium in taxonomy by Noel (1983) and by Dormer (1962) and Nordenstam (1978), with reference to the Asteraceae, by Arora and Tiagi (1977) in the Apiaceae and by Eyde

(1977) in the Onagraceae. Noel (1983) mentions that "there are indications of constancy at the generic level, or even through larger groups such as the Asteraceae."

Dorner (1962), in his study of the "fibrous layer" or endothecium of some members of the Asteraceae, describes the cells of this tissue as having a series of moniliform ribs or thickenings in the cell walls (Fig. 22). Dorner (1962), Nordenstam (1976, 1978) and Wetter (1983) have described three configurations of these ribs, differing in the alignment of the ribs with respect to the vertical or long axis of the pollen sac or anther. When the ribs are restricted to the transverse or horizontal walls the configuration of the endothecial tissue is said to be "polarized" (Dorner, 1962; Nordenstam, 1976, 1978; Wetter, 1983). When the cells are ribbed all around the configuration of the endothecial tissue is said to be "radial" (Dorner, 1962; Nordenstam, 1976, 1978; Wetter, 1983). Robinson and Brettell (1973) restrict the definition of the "radial" configuration to include only those cells with ribs on the "vertical" or "radial walls". When the endothecial cells are more or less uniformly thickened and without distinct ribs, the configuration of the endothecial tissue is called "transitional" (Dorner, 1962; Nordenstam, 1978; Wetter, 1983). In many members of the Asteraceae, except in the tribe Lactuceae (Nordenstam, 1978), the "transitional" form of configuration of the endothecial tissue is restricted to a narrow zone near the connective.

De Vaal (1978) mentions that the wall thickenings attain their final form only late in the development of the anther. Consequently, in this

study only anthers that were partially exerted from the disc corolla were sampled, so as to avoid the possibility of studying immature endothelial tissue.

The determination of the type of configuration was made in approximately the same location for each anther examined.

The endothecium of all the taxa studied (Table 1), with two exceptions (*S. cissampelinus* & *Gynura auriculata*), possess a configuration that is similar to the "radial" configuration as described by Dormer (1962), Nordenstam (1978) and Wetter (1983). The difference being that the "radial" configuration produced by the thickenings of the cell walls of the endothecium is restricted to the longitudinal wall nearest the connective of each cell ("radial anticlinal wall" - Esau, 1976) (Figs. 22a, 22b), frequently including the transverse (or horizontal) walls, and not all around the cell wall as described by Dormer (1962), Nordenstam (1978) and Wetter (1983). However, I judge that the "radial" configuration illustrated by Wetter (1983, Fig. 30) is identical to the configuration that I observed which I have called radial anticlinal (char. state 06), and although it is not clear from Nordenstam's illustrations (Nordenstam, 1978, Fig. 2), I think that the "radial" configuration that he observed is probably also radial anticlinal.

There was some variation between species and occasionally within some species with respect to the appearance of the moniliform ribs forming the radial anticlinal configuration. This ranged from the ribs appearing as very short peg-like projections to being conspicuous

peg-like projections, this latter form of projection often having a small to large transverse bar giving the peg-like structure a 'T' shape.

Numerous observations of this radial anticlinal configuration have revealed the peg-like projections forming the moniliform ribs of the endothelial cells to be slightly convex bars spanning the width of the longitudinal wall nearest the connective (radial anticlinal wall) and the 'T' shaped projections to be projections from either side of these slightly curved bars and which seem to be arranged in a median plane relative to the curved bars (Fig. 23).

Dorner (1962) describes a progression in the endothecium from one type of configuration to another, "The rule is that if we start from the edge of the connective and move around the anther to the adaxial side the tissue types, in so far as they are present at all, appear in the invariable order transitional, radial, polarized." In this study, however, the "transitional" type of configuration was seldom found, instead the order of progression starting from the connective, was usually, radial anticlinal, "polarized".

The two taxa (*S. cissampelinus* & *Gynura auriculata*) referred to earlier which do not possess the configuration have the following endothelial cell wall configuration.

In the one aberrant species, *S. cissampelinus*, the configuration is intermediate in that it is predominantly "polarized" but irregularly

distributed peg-like projections are also found, distributed as in the radial anticlinal configuration (char. state 10). The configuration in G. auriculata is conspicuously different from those already described, in that each cell has a distinct imperforate "base plate" with riblike extensions from the edge of the base plate (char. state 11), similar to that described by Noel (1983) of Valeriana capensis Thunb.

**[\*\*] FILAMENT COLLARS: LENGTH (CHAR 108 - Appendix A)**

The distribution of all the taxa studied (Table 1) with respect to the five size classes of this character is illustrated in Figure 30.

The filament collar (Koyama, 1967; Drury, 1973, 1975; Nordenstam, 1978) or anther collar (Robinson & Brettell, 1973; Jeffrey et al., 1977) is a "downward extension of connective tissue which forms an incomplete monostromatic collar of thick-walled cells" (Drury, 1975).

The majority of the senecios investigated have filament collars in the size range 0,3-0,6 mm, the second most frequent size range being 0,7-0,9 mm.

A summary of the distribution of the five character states amongst the senecios studied is provided below:

- (i). Character state 01 - S. polyanthemoides
- (ii). Character state 02 - 79 spp. & 6 vars. of Senecio.
- (iii). Character state 03 - 9 spp. of Senecio.
- (iv). Character state 04 - S. helminthioides  
S. viminalis  
S. radicans  
S. fulgens  
S. pterophorus
- (v). Character state 05 - S. tamoides  
S. barbertonicus

Nordenstam (1978) has drawn attention to the occurrence of "very elongated" filament collars in Notonia DC., Notoniopsis B.Nord. and Kleinia Mill. These "very elongated" filament collars are quite possibly in the size range 1,0-1,4 mm, for the two species, Kleinia grandiflora and Kleinia neriifolia, included in this study both have filament collars in this size range (char. state 4). However, both S. tamoides and S. barbertonicus have filament collars which exceed considerably the length of the aforementioned genera referred to as having "very elongated" filament collars.

[\*] FILAMENT COLLARS: BASAL WIDTH (CHAR 109 - Appendix A)

The distribution of all the taxa studied (Table 1) with respect to the two size classes of this character is illustrated in Figure 31.



This character is a measure of the width of the basal portion of the filament collar just prior to the region where it becomes the filament proper.

The majority of the senecios studied have filament collars with a basal width in the size range 0,2-0,4 mm (char. state 02) while the remainder of the senecios have filament collars with a narrower (<0,1 mm) basal width.

A summary of the distribution of the two character states recorded for this character is provided below:

- (i). Character state 01 - 9 spp. & 2 vars. of Senecio.
- (ii). Character state 02 - 86 spp. & 4 vars. of Senecio.

While there are many senecios which show a correlation between the length and the basal width of the filament collar (length range 0,3-0,6 mm, width range 0,2-0,4 mm) there are a number of senecios which do not show any correlation between these two characters. This is illustrated in several senecios which produce filament collars of varying lengths but with no proportional change in the basal width of the filament collar (e.g. S. glanduloso-lanosus, S. macrospermus, S. tamoides, S. helminthioides & S. radicans).

[\*\*] FILAMENT COLLARS: SHAPE (CHAR 110 - Appendix A)

The fine structure of the filament collar has only recently attracted the attention of synantherologists. Koyama (1966, 1967), drawing upon some earlier observations by Kitamura (1937), cited differences in filament collar shape found between senecioid genera and between sections of Senecio itself. Drury (1973, 1975) has described two types of filament collar. The filament collar is defined as "cylindrical" when the diameter of the filament collar and the filament proper are the same and when the cells of the collar are all the same size (Fig. 24). The filament collar is defined as "balusterform" when "the basal cells of the filament collar are enlarged so that the diameter of the collar at the swollen portion is greater than the filament proper" (Drury, 1975) (Fig. 25).

Nordenstam (1978) mentions that "cylindrical" filament collars generally characterize cacalioid genera, but that they are also found in several genera traditionally associated with Senecio (e.g. Brachyglottis J.R. & G. Forst., Nemosenecio (Kitam.) B.Nord., Sinosenecio B.Nord., Tephrosenis Reichenb. & Urostemon B.Nord.). Nordenstam (1978) also draws attention to the term "cylindrical" pointing out that "cylindrical" filament collars are, "strictly speaking, not cylindrical since they are neither hollow nor circular in transect. Instead they tend to be somewhat flattened, often with adaxially involute margins, and more or less reniform in transect." Since there is a strong correlation between the "cylindrical" filament collar and several other characters typical of cacalioid genera, this shape of filament collar is called "cacalioid" (Nordenstam, 1978) and is the term adopted in this

dissertation.

Basally dilated filament collars "are found in Senecio s. str. and in many more or less senecioid genera, such as Crassocephalum Moench, Culcitium Humb. & Bonpl., Dendrosenecio (Hauman ex Hedb.) B.Nord., Dorobaea Cass., Emilia Cass., Euryops Cass., Jacmaia B.Nord., Odontocline B.Nord., Othonna L., Stilpnoogyne DC. and Xyridopsis B.Nord." (Nordenstam, 1978). Since the variation in the degree of dilation of these filament collars amongst members of the Senecioneae, falls under the descriptive term "balusterform" the non-descriptive term "senecioid" is used for all filament collars which are basally distended (Nordenstam, 1978). While the term "senecioid" is used in this dissertation the term "balusterform" will also be used since this is the shape of the basally dilated filament collars which are produced by many of the senecios investigated in this study.

"Senecioid" and "cacalioid" filament collars are produced by the taxa investigated in this study (Table 1). All the "senecioid" filament collars have a "balusterform" shape (char. states 01-06, 09). However, within this "balusterform" shape, both narrow and conspicuously broad "balusterform" shapes are found.

Two distinct narrow "balusterform" filament collars also occur (char. state 02 & 09), their distinctness lying in the different size and shape of the cells comprising these two forms of filament collar. In the first form (char. state 02) the cells of the monostromatic collar are virtually cubic (isodiametric) and the increase in the size of these

cells, proximally, is quite marked for the cells of the proximal end of the filament collar are three to five times the size of the cells in the uppermost distal region of the filament collar. In the second form (char. state 09), the cells of the monostromatic collar are noticeably elongate and somewhat irregularly shaped and the increase in the size of these cells, proximally, is not marked, being approximately twice the size of the cells of the in the uppermost distal region of the filament collar.

In the conspicuously broad "balusterform" shape of filament collar, the basal region of the filament collar is conspicuously distended forming a distinct basal bulge (char. state 03).

The two "cacalioid" forms of filament collar recorded (char. states 07 & 08), differ only in that in the one form (char. state 07), the width of the filament collar and the filament proper are the same, while in the second form (char. state 08), the width of the filament collar is consistently slightly greater than that of the filament proper. Other than this difference these two forms of filament collar are unquestionably "cacalioid".

While most of the taxa investigated produce one of the several forms of filament collar in a consistent manner, a few senecios have infraspecific variation with respect to the shape of the filament collar in that they produce "senecioid" filament collars varying between narrowly "balusterform" and noticeably broadly "balusterform". This infraspecific variation is recorded in character states 04-06.

Nordenstam (1978) notes that the "cacalioid" form of filament collar is "nearly always associated with a "polarized" endothelial tissue and the "senecioid" form with a "radial endothecium" ( $\equiv$  radial anticlinal configuration? - for defn. see CHAR 107). A notable exception being the genus Graphistylis B.Nord. (Nordenstam, 1978).

The association between the "senecioid" form of filament collar and radial anticlinal endothelial tissue is also evident in this study in that the majority of the taxa studied possess this association. However, there are nine exceptions (S. medley-woodii, S. tamoides, S. viminalis, S. cissampelinus, S. fulgens, S. sylvaticus, Gynura auriculata, Kleinia grandiflora & Kleinia neriifolia). Eight of these nine taxa possess "cacalioid" filament collars associated with radial anticlinal endothelial tissue. The remaining exception, S. cissampelinus, has "senecioid" filament collars associated with an intermediate form of endothelial tissue which is predominantly "polarized" with a limited amount of radial anticlinal endothelial tissue. Thus there are further exceptions to the two associations noted by Nordenstam (1978).

A summary of the distribution of these nine character states amongst the taxa investigated in this study (Table 1) is provided below:

"SENECIOID" FILAMENT COLLARS

- (i). Character state 01 - 55 spp. & 5 vars. of Senecio.
- (ii). Character state 02 - 26 spp. of Senecio.
- (iii). Character state 03 - S. microglossus  
S. transvaalensis
- (iv). Character state 04 - S. sandersonii  
S. umgeniensis  
S. heliopsis
- (v). Character state 05 - S. cathcartensis  
S. polyodon var. polyodon  
S. subrubriflorus  
S. dregeanus  
S. othonniflorus
- (vi). Character state 06 - S. pterophorus
- (vii). Character state 09 - Crassocephalum cernuum

"CACALIOID" FILAMENT COLLARS

- (i). Character state 07 - S. medley-woodii
- (ii). Character state 08 - S. tamoides  
S. viminalis  
S. fulgens  
S. sylvaticus  
Gynura auriculata  
Kleinia grandiflora  
Kleinia neriifolia

CYPSELA (RAY): LENGTH (CHAR 111 - Appendix A)

CYPSELA (RAY): SHAPE (CHAR 112 - Appendix A)

CYPSELA (RAY): RIBBING (CHAR 113 - Appendix A)

CYPSELA (RAY): VESTITURE (CHAR 114 - Appendix A)

CYPSELA (RAY): PERICARP CELLS - SHAPE (CHAR 115 - Appendix A)

The cypselas are small, hard, dry indehiscent fruits with two carpels and an adnate calyx (Jackson, 1949). It is derived from an inferior syncarpous ovary, but is invariably one-seeded as a result of one carpel failing to develop. The term cypselas is considered more strictly correct than the term achene, which has a more general application (Pope, 1983).

These characters of the cypselas were included in this study so as to provide the opportunity to record differences between the ray and disc cypselas with respect to these characters in those taxa which produce ray and disc florets.

However, despite a number of character states being recorded for each of these characters, no distinct infraspecific differences between the ray and disc cypselas with respect to each of these characters were noted. Thus, where reference is made to these characters in keys, either ray or disc florets can be used.

The various character states recorded for these characters are included in the data matrix (Appendix B) for completeness and for future reference.

[\*] CYPSELA (DISC): LENGTH (CHAR 116 - Appendix A)

The distribution of all the taxa studied (Table 1) with respect to the six size classes of this character is illustrated in Figure 32.

The majority (75 spp. & 6 vars.) of the senecios studied produce disc cypselas in the size range 1,8-4,3 mm (char. states 2-4). A further fourteen senecios produce cypselas in the size range 4,5-7,0 mm (char. state 5). There are a few (5 spp.) senecios which produce noticeably short cypselas (1,0-1,7 mm, char. state 1) (S. madagascariensis, S. inaequidens, S. polyanthemoides, S. pterophorus & S. juniperinus) while only S. macrospermus and S. caudatus produce noticeably long cypselas (8,0-10,0 mm, char. state 6).

While many senecios with cypselas in the size range 1,8-4,3 mm produce disc corollas in the size range 5-15 mm (CHAR 81, char. states 2 & 3) this correlation between cypselas length and disc corolla length does not extend to those species with relatively short cypselas (< 1,7 mm) or to those species with relatively long cypselas (8,0-10,0 mm), with a few exceptions. The species lacking this correlation as well as the exceptions are listed below:

SENECIOS WITH RELATIVELY SHORT CYPSELAS

[short cypselas correlated with short disc corollas]

S. madagascariensis

[short cypselas not correlated with short disc corollas]

S. inaequidens

S. polyanthemoides



S. pterophorusS. juniperinus

## SENECIOS WITH RELATIVELY LONG CYPSELAS

[long cypselas correlated with long disc corollas]

S. medley-woodiiS. hastatusS. hirsutilobusS. ingeliensisS. paludaffinisS. saniensisS. helminthioides

[long cypselas not correlated with long disc corollas]

S. umqeniensisS. macrospermusS. discodregeanusS. rhomboideusS. caudatusS. latifoliusS. othonniflorusS. viminalisS. fulgens

## [\*\*] CYPSELA (DISC): SHAPE (CHAR 117 - Appendix A)

Although four character states represent the variation in the shape of the disc cypselas amongst the senecios studied, there is infraspecific variation amongst many of these senecios with respect to character states 01 and 02. Where either of these two character states are used they represent the more common of the two shapes. However, despite the infraspecific variation, the predominant shape of the cypselas of the disc florets amongst all the senecios investigated, is 'fusiform and cylindrical' (char. state 02).

A summary of the distribution of the six character states recorded for this character amongst all the taxa (Table 1) is provided below:

- (i). Character state 01 - 13 spp. & 3 vars. of Senecio.
  - Kleinia grandiflora
  - Kleinia neriifolia
- (ii). Character state 02 - 80 spp. & 3 vars. of Senecio.
  - S. syringifolius
  - S. hockii
  - Crassocephalum cernuum
  - Emilia flammea
  - Gynura auriculata
- (iv). Character state 04 - S. hayqarthii
- (v). Character state 05 - S. transvaalensis
- (vi). Character state 06 - Cineraria geifolia

[\*] CYPSELA (DISC): RIBBING (CHAR 118 - Appendix A)

The majority (79 spp. & 6 vars.) of the senecios studied have ribbed cypselas. This ribbing is composed of between five and ten ribs with a distinct non-ribbed portion between each rib (char. state 07). A further twelve senecios have closely ribbed cypselas (char. state 11), the non-ribbed portion between each rib being much narrower than in the cypselas previously described, while S. qerrardii also has very closely spaced ribs but there appears to be virtually no space between each rib (char. state 01).

The ribbing in S. juniperinus and S. macrocephalus DC. is hardly noticeable or absent (char. state 06) while S. serratuloides has cypselas which are finely striate (char. state 09). The ribbing in S. transvaalensis is quite distinct in that the cypselas are distinctly 5-angled (char. state 15), while in S. hayqarthii the cypselas each have five noticeably robust and prominent ribs (char. state 14).

A summary of the distribution of the eight character states recorded for this character amongst all the taxa (Table 1) is provided below:

- (i). Character state 01 - S. gerrardii
- (ii). Character state 06 - S. juniperinus  
S. macrocephalus  
S. syringifolius
- (iii). Character state 07 - 79 spp. & 6 vars. of Senecio.  
Crassocephalum cernuum  
Emilia flammea  
Gynura auriculata  
Kleinia grandiflora  
Kleinia neriifolia
- (iv). Character state 09 - S. polyanthemoides
- (v). Character state 11 - 12 spp. of Senecio.
- (vi). Character state 14 - S. hayqarthii
- (vii). Character state 15 - S. transvaalensis  
S. hockii
- (viii). Character state 16 - Cineraria geifolia

CYPSELA (DISC): VESTITURE (CHAR 119 - Appendix A)

While there is some overlap between some of the character states recorded for this character, the considerable number of character states (39) indicates the considerable range of vestiture that is possessed by the taxa studied.

The trichomes found on the cypselas of many species are all similar in overall structure, for they are superficially "duplex" but closer examination will reveal a third small, thin-walled cell associated with the base of each "duplex" trichome (Drury & Watson, 1965).

The trichomes were always found to point towards the distal end of the cypselas. The overall length of these trichomes varies amongst the taxa, principally because of differing lengths of the two, usually long, duplex cells which form the bulk of each trichome.

The duplex cells are usually connate to the apex but in some senecios (e.g. S. hastatus, S. vulgaris & S. desfontainei) the apices can be free for up to a quarter of the distal end of the trichome (char. state 24). When the apices are 'free' the apex of each 'distal cell' is noticeably tapered acropetally. Where the apices of the distal cells are not 'free' the overall apex of the trichome is obtuse and occasionally cleft or the apex may appear truncate.

In a few senecios (e.g. S. glanduloso-pilosus, S. barbatus & S. cakilefolius) the inside surface of the cell wall of the duplex cells

is transversely or helically striated (char. state 09) but the majority of the taxa investigated lack this wall sculpturing. The occurrence of sculpturing or "wall thickenings" is alluded to by Drury and Watson (1965) and by Jeffrey et al. (1977).

While I have described some aspects of the appearance of the trichomes and of their variation in the appearance, more important is the variation in the distribution of the trichomes and the form of pubescence which the trichomes attribute to the cypselas. The trichomes are either restricted to the surface area between the ribs on the cypselas or they are found both on and between the ribs, the former form of distribution being the more frequent. The form of pubescence ranges from 'sparsely hispidulous' to 'villous' with 'hispid' being the most frequent form of pubescence.

While glabrous cypselas have frequently been used as a "key character" in the taxonomy of Senecio (Drury & Watson, 1965) only twenty-seven of the senecios investigated in this study have consistently glabrous cypselas (char. state 01) while a further few senecios sometimes have glabrous cypselas. I think that the 'glabrous condition' leading to the use of this character as a 'key character' in earlier taxonomy of Senecio is possibly a result of inadequate observation in many instances. This is borne out by my experience, for a few of the character states (e.g. char. states 31 & 33) are extremely difficult to observe under any magnification other than X400.

[\*] CYPSELA (DISC): PERICARP CELLS - SHAPE (CHAR 120 - Appendix A)

This character refers to the appearance of the cells forming the outer wall of the pericarp also called the "superficial cells" by Jeffrey et al. (1977).

The fact that nine character states have been recorded for this character, indicates something of the variation in the appearance of the outer cells of the pericarp, this is despite there being some character states which consist of combinations of other character states (e.g. char. states 11 & 14).

Despite the variation in this character, two distinct trends can be discerned:

- (i). The outer cells are imbricate and/or possess tubercles (67 spp. & 6 vars. of Senecio).
- (ii). The outer cells are not imbricate and do not possess tubercles (29 spp. of Senecio).

Where the cells of the pericarp are imbricate, the imbrication is always in an incubous pattern. The imbrication may be slight (char. state 05) or pronounced (char. state 13) and as intimated above, tuberculate cells may also be found amongst the outer cells of the pericarp. These tuberculate cells may be either associated with an imbricate pattern of surrounding cells (char. state 07), or they may form the imbricate pattern (char. state 13).

These imbricate and/or tuberculate cells are usually approximately square when observed from above, but noticeably rectangular cells are also present in some senecios.

In those senecios which lack tuberculate cells and/or an imbricate pattern, the outer pericarp cells are rectangular (char. state 01) when viewed from above.

While some of the character states only occur in one or two senecios, the remaining character states are common to groups of senecios and some species of related genera as indicated below:

(i). Character state 01 - 28 spp. of Senecio.

S. hockii

Gynura auriculata

Kleinia grandiflora

Kleinia neriifolia

Cineraria geifolia

(ii). Character state 04 - S. breviflorus

(iii). Character state 05 - 38 spp. & 3 vars. of Senecio.

S. syringifolius

Crassocephalum cernuum

(iv). Character state 07 - 13 spp. of Senecio.

Emilia flammea

(v). Character state 09 - S. chrysocoma

(vi). Character state 10 - S. discodregeanus

S. caudatus

S. saniensis

(vii). Character state 11 - 8 spp. & 3 vars. of Senecio.

(viii). Character state 13 - S. hastatus

S. sylvaticus

(ix). Character state 14 - S. hypochoerideus

S. mooreanus

## [\*] PAPPUS: UNIFORM/DIMORPHIC (CHAR 121 - Appendix A)

In earlier studies on the Senecioneae (Drury, 1967 - in Jeffrey et al., 1977; Jeffrey et al., 1977) both "uniform" and "dimorphic" pappus setae have been encountered. The pappus is described as "uniform" when all the setae are either tapered, with divergent teeth, or, less often, clavate with subconnivent teeth. While the pappus is described as "dimorphic" when there are numerous tapered setae together with numerous fluked setae with retrorsely directed apical teeth, or, rarely, tapered setae with merely reduced teeth.

In this study both "uniform" (char. state 1) and the 'rare' "dimorphic" pappus setae (char. state 2) were encountered. The setae of a "uniform" pappus were all of a very similar width, were tapered and possessed divergent barbs ('teeth' or 'flukes') (CHAR 127) and the apices (CHAR 129) were all very similar in appearance. The "dimorphic" pappi consisted of two forms of setae, both of these forms of setae being tapered, the difference between these two forms of setae in a dimorphic pappus being that there were many setae which were considerably narrower and possessed fewer divergent barbs. The narrow setae were also very



much in the minority.

The majority of the senecios studied have the aforementioned "dimorphic" pappi. There appears to be no correlation between the possession of a "uniform" or "dimorphic" pappus and any other character investigated in this study.

The distribution of the two character states for this character amongst all the taxa investigated (Table 1) is provided below:

(i). Character state 01 - 29 spp. & 1 var. of Senecio.

S. syringifolius

S. hockii

Emilia flammea

Kleinia grandiflora

Kleinia neriifolia

Cineraria geifolia

(ii). Character state 02 - 68 spp. & 5 vars. of Senecio.

Crassocephalum cernuum

Gynura auriculata

PAPPUS SETAE (RAY): LENGTH (CHAR 122 - Appendix A)

PAPPUS SETAE (RAY): APPEARANCE (CHAR 123 - Appendix A)

PAPPUS SETAE (RAY): APICAL CELL NUMBER (CHAR 124 - Appendix A)

PAPPUS SETAE (RAY): APEX (CHAR 125 - Appendix A)

These characters of the pappus were included in this study so as to

provide the opportunity to record differences between the ray and disc cypselas with respect to these characters in those taxa which produce ray and disc florets.

However, despite a number of character states being recorded for each of these characters, no distinct infraspecific differences between the ray and disc pappus with respect to each of these characters were noted. Thus, where reference is made to these characters in keys, either ray or disc florets can be used.

The various character states recorded for these characters are included in the MASTER DATA MATRIX (Appendix B) for completeness and for future reference.

[\*] PAPPUS SETAE (DISC): LENGTH (CHAR 126 - Appendix A)

The distribution of all the taxa studied (Table 1) with respect to the five size classes of this character is illustrated in Figure 33.

Most (88 spp. & 6 vars.) of the senecios studied produce disc pappus setae in the size range 4,0-9,5 mm (char. states 2-3). Only S. deltoideus produces noticeably short setae (3,0-3,6 mm - char. state 1). Five species of Senecio produce moderately long setae (10,0-14,0 mm - char. state 4) while S. sandersonii and S. viminalis produce noticeably long setae (16,0-18,0 mm - char. state 5).

In most species, the length of the pappus setae is very similar to the

length of the disc corolla. Two exceptions to this correlation occur in S. sandersonii and S. fulgens. Senecio sandersonii has a copious pappus which characteristically exceeds the length of the disc corollas. In S. fulgens the pappus is usually a little shorter than the disc corollas.

[\*] PAPPUS SETAE (DISC): APPEARANCE (CHAR 127 - Appendix A)

The observations of this character were standardised by using X10 eye pieces and objectives.

This character records three distinct aspects of the appearance of the pappus setae, these being:

- (i). Whether or not the setae are noticeably barbellate.
- (ii). Whether the frequency of the barbs increases or decreases up the setae.
- (iii). The differences in appearance between the two forms of setae in "dimorphic" pappi.

Three character states occur relatively frequently among the senecios investigated, these being:

- (i). Character state 04 - 13 spp. of Senecio.
- (ii). Character state 06 - 31 spp. & 4 vars. of Senecio.
- (iii). Character state 09 - 10 spp. of Senecio.

The remaining Character states occur either singly or amongst a maximum of five senecios.

While there are no correlations between any of these three aspects of the appearance of the pappus setae, three distinct trends can be discerned.

The first is that forty-five of the senecios studied have setae which are not noticeably barbellate (char. states 02, 03 & 06) (Fig. 26) while the remaining senecios are noticeably barbellate (char. states 01, 04, 08 & 09) (Fig. 27). The second is that in the majority (85 spp. & 5 vars.) of the senecios studied, the frequency of the barbs decreases towards the apex (char. states 02, 04, 06, 08, 09, 10, 12, 13 (part) & 14). A further seven senecios (6 spp. & 1 var.) have barbs that are reasonably equally distributed up the setae (char. states 03 & 07) while in another five species of Senecio the barbs increase in frequency towards the apex of the setae (char. state 01).

The third trend concerns only those senecios which produce "dimorphic" pappi. Both forms of the pappus setae are noticeably barbellate in twelve species of Senecio which produce "dimorphic" setae (char. states 07, 08 & 09) (Fig. 28). In a further twenty-four species of Senecio with "dimorphic" pappi, only the 'broad' setae are noticeably barbellate (char. state 10). While in a further large group of senecios (31 spp. & 4 vars.) neither of the two forms of pappus setae is noticeably barbellate (char. state 06).

The occurrence of the barb frequency either increasing or decreasing towards the apex, as mentioned earlier in the second trend, is inversely related to the length of the individual cells which produce the barbs.

A synthesis of these trends reveals the following:

- (i). Many of the senecios investigated are not noticeably barbellate.
- (ii). In most of the senecios studied, the frequency of the barbs decreases towards the apex of the setae.
- (iii). In the majority of the senecios which produce "dimorphic" pappi, neither of the two forms of setae is noticeably barbellate.

All the barbs in the senecios studied each had a distinctly pointed apex, with one exception, S. sandersonii, in which the barbs are distinctly deltoid in shape and are noticeably large (Fig. 29).

Jeffrey et al., (1977) mention that variation occurs in the "colour", "texture", "stoutness", "number of cells in cross-section" (about 5 cells below the apex) and "cell length/breadth ratio" of the pappus setae. My observations of some of the above features are as follows: the "colour" of the pappus of all the taxa investigated was consistently 'silver-white' and the "texture" of the pappi was 'silky'; the "number of cells in cross-section" was usually 2-3.

The "number of cells in cross-section" and the "cell length/breadth

ratio" both contribute to the "stoutness" of the pappus setae but they are not necessarily correlated. In the senecios studied the "stoutness" of the pappus setae was frequently observed to be due only to a "cell length/breadth ratio approaching 1, but in a few other senecios both of the aforementioned characters contributed to the stoutness of the pappus setae. In another few senecios the stoutness was observed to be due only to the "number of cells in cross-section". While there were a few senecios which produced what might be termed relatively stout pappus setae, the majority of the senecios produced relatively slender pappus setae, these setae having 2-3 cells in cross-section and a "cell length/breadth ratio" of between 5 and 10 (also about 5 cells below the apex).

[\*] PAPPUS SETAE (DISC): APICAL CELL NUMBER (CHAR 128 - Appendix A)

All of the taxa investigated (Table 1), with the exception of S. medley-woodii and S. discodregeanus, consistently have a two-celled apex. While S. medley-woodii and S. discodregeanus are recorded as commonly producing three-celled apices, two-celled apices also occur, but infrequently.

It is interesting to note that Drury and Watson (1965), in their study of some Eurasian species of Senecio, found the two-celled condition to occur in thirty-nine of the forty-five species they investigated while the three-celled condition occurred in the remaining six species.

The appearance of these two- and three-celled apices will be discussed under CHARACTER 129.

[\*] PAPPUS SETAE (DISC): APEX (CHAR 129 - Appendix A)

Twelve character states have been recorded for this character indicating that considerable variation occurs in this character.

There are four distinct aspects of the appearance of the apex of the setae recorded under this character, these being:

- (i). The length of the apical cells.
- (ii). The degree to which the two (or three) apical cells are connate.
- (iii). The degree of divergence of the apical cells.
- (iv). The stoutness of the apical cells (cell length/breadth ratio).

The only correlation that was found to exist was between the length of the apical cells and the stoutness of the apical cells (positively correlated).

Three character states occur relatively frequently amongst the senecios investigated, these being:

- (i). Character state 04 - 58 spp. & 6 vars. of Senecio.
- (ii). Character state 08 - 13 spp. of Senecio.
- (iii). Character state 02 - 7 spp. of Senecio.

The remaining character states occur either singly or amongst a maximum of four senecios.

As mentioned in CHARACTER 128, most of the taxa studied have two-celled apices with the exception of S. medley-woodii and S. discodregeaus both of which have predominantly three-celled apices (CHAR 128).

Four distinct trends can be discerned amongst the senecios investigated. The first concerns the length of the apical cells relative to the cells immediately proximal to the apical cells. The majority of the senecios (83 spp. & 6 vars.) produce relatively long apical cells (cell length/breadth ratio c. 10), these two cells being appreciably longer than the cells just proximal to the two apical cells (char. states 04, 06, 07, 08, 09, 10, 11 & 13). The remaining senecios produce relatively short apical cells, in this case the two apical cell are virtually equal in length to the two cells just proximal to the two apical cells (char. states 01, 02, 03 & 13).

The second trend concerns the degree to which the apical cells are connate. Only in S. sandersonii are the two apical cells connate right



to the apex (char. state 06). In most of the senecios studied (62 spp. & 6 vars.) the apical cells are connate for approximately three quarters of their length (char. state 03, 04 & 07), while in a further group (29 spp.) the apical cells are connate for only approximately one quarter to a third of their length (char. state 01, 02, 08, 09, 10, 11 & 12).

The third trend concerns the degree of divergence of the apical cells. In the majority of the senecios which produce incompletely connate apical cells, the apices of the apical cells do not diverge (char. states 01, 02, 03, 04, 08 & 11). However, there are a number of senecios (8 spp.) which produce apical cells with diverging apices (char. states 07, 09 & 13). This condition is especially noticeable in S. achilleifolius, S. tanacetopsis, S. seminiveus and S. radicans, all of which have distinctly free apices (char. state 13).

The fourth trend refers to the occurrence of stout and noticeably stout apical cells. Both S. medley-woodii and S. discodregeanus, which frequently produce three-celled apices, have somewhat stout apical cells (cell length/breadth ratio c. 5) (char. state 01). Similar stout apical cells occur in a further group of senecios (7 spp. - e.g. S. dregeanus, S. bupleuroides, S. urophyllus & S. brevilorus; char. state 02). However, these apices are all two-celled. Noticeably stout apical cells (cell length/breadth ratio c. 2-3) are produced by S. othonniflorus and S. helminthioides (char. state 12). The dimensions of the stout and noticeably stout apical cells are appreciably greater than the dimensions of the non-stout apical cells (e.g. char. state 03), despite any similarity in the cell length/breadth ratio.

The apices of all the apical cells of the pappus setae of all the senecios, except S. sandersonii, were acute, while in S. sandersonii the apices are noticeably obtuse (char. state 06).

Another interesting feature is that the apices of the apical cells are frequently situated in an oblique manner (e.g. char. state 04), although apical cells of equal length also occur as the predominant appearance (e.g. char. state 03).

Drury and Watson (1965), in their study of some Eurasian species of Senecio, found that twenty-nine of the forty-five species they studied, produced pappus setae with "divergent" apices while the remainder (16 spp.) had "appressed" ( $\equiv$  connate?) apical cells. In this study something of the opposite situation was observed in that only eight species of all the senecios studied produced pappus setae with divergent apical cells.

ALTITUDE RANGE (CHAR 005 - Appendix A)

DISTRIBUTION (CHAR 006 - Appendix A)

HABITAT(S) (CHAR 007 - Appendix A)

FLOWERING TIME (CHAR 130 - Appendix A)

While the following characters; ALTITUDE RANGE (CHAR 005), DISTRIBUTION (CHAR 006), HABITAT(S) (CHAR 007) and FLOWERING TIME (CHAR 130) are meaningless characters from the point of view of numerical analysis (Sneath & Sokal, 1973), the information recorded in these four

characters has still been of value in assisting me in my neural analysis of the phenetic relationships of the senecios studied.

#### ALTITUDE RANGE (CHAR 005 - Appendix A)

While there are many character states recorded for this character (61) there are overlaps between many of the them. However, a scan through the character states reveals that there are many senecios which are restricted to higher altitudes and there are also many species which are distributed in an altitude continuum from the coast to relatively high altitudes. Similarly there are many senecios which are restricted to relatively low altitude habitats these being coastal and near coastal.

#### DISTRIBUTION (CHAR 006 - appendix A)

As in the character ALTITUDE RANGE there are many character states for this character recording the extensive distribution for some senecios and the restricted and/or sometimes disjunct distribution for other senecios studied.

The distribution patterns of the senecios studied is discussed further in chapter 9 of this dissertation.

#### HABITAT(S) (CHAR 007 - Appendix A)

The senecios studied exhibit a phenomenal capacity to occupy almost any type of habitat, hence the considerable number of character states recorded for this character.

These habitats range from poor, stony or sandy dry soils to marshy stream-sides, from grassland to forest margins and from coastal dunes to high altitude montane grassland.

#### FLOWERING TIME (CHAR 130 - Appendix A)

There is considerable overlap between the fifty-two character states recorded for this character. This is indicative of the considerable degree of overlap in flowering time that exists between many of the senecios studied.

A brief perusal of the character states clearly indicates that the majority of the senecios flower in the summer months and that some of these senecios flower for a considerable period during the summer months (e.g. char. states 03 & 18 - e.g. S. glanduloso-pilosus, S. barbatus & S. anomalochrous) while others flower for a relatively short period during the summer months (e.g. char. state 20 - e.g. S. cathcartensis, S. inornatus & S. rhomboideus).

A few senecios have been observed to flower in any month (e.g. char. state 06 - e.g. S. madaqascariensis, S. skirrhodon & S. consanguineus) while S. radicans and S. cissampelinus only flower in the Autumn and Winter months (char. states 49 & 52).

This chapter has drawn attention to various features and statistics of the characters investigated and where possible, comparisons have been made between my observations and those of other researchers.

Six of the characters (designated [\*\*]) have been selected as being taxonomically significant ("good") characters (Davis & Heywood, 1963) with respect to elucidating the generic concept of Senecio L. A further 31 characters (designated [\*], and the aforementioned 6, have been selected as being taxonomically significant with respect to elucidating the interrelationships of the Natal senecios and of all the senecios studied.

In the following chapters, the generic concept of Senecio L. and the interrelationships of the Natal senecios and of all the senecios studied, will be investigated in the light of the evidence contained in these characters of taxonomic significance.

## CHAPTER FOUR

EVOLUTION OF THE GENERIC CONCEPT OF  
SENECIO

The genus Senecio was formally circumscribed by Linnaeus in *Genera Plantarum* (Linnaeus, 1754) although a number of taxa with this name appeared in *Species Plantarum* (Linnaeus, 1753). The type of this genus is Senecio vulgaris L. (Farr *et al.*, 1979), this being one of the original species described by Linnaeus (Linnaeus, 1753). Copies of the generic description of Senecio L. and of the type species, S. vulgaris L. are reproduced in Figures 34 and 35.

Jeffrey *et al.* (1977) point out that different generic concepts of Senecio are held both in different parts of the world and in treatments of different groups of species within the Senecio complex. This has resulted in the range in character variation amongst species currently referred to Senecio being so great that it overlaps and even exceeds the combined ranges exhibited by species currently referred to several other genera (Jeffrey, *et al.*, 1977).

The philosophy of "The New Synantherology" (King & Robinson, 1970) which includes amongst other things "a rejection of bad characters, elucidation of numerous new characters at an anatomical level, and the application of techniques that make these characters available in the routine taxonomic study of Compositae" (King & Robinson, 1970) is doing

much to help improve the taxonomic concepts in many members of the Asteraceae (e.g. King & Robinson, 1968; Jeffrey et al., 1977; Nordenstam, 1978 & Wetter, 1983)

Studies in the Senecio complex (Jeffrey, et al., 1977; Jeffrey, 1979), using a "uniform criterion" of characters throughout the Senecio complex, against which all available evidence might be evaluated and, subsequently, from which systematic conclusions might be drawn, aimed at elucidating the generic and sectional limits in Senecio. These studies, which coincide with the the philosophy of "The New Synantherology" (King & Robinson, 1970), resulted in the following suggestions based on the material studied by Jeffrey et al. (1977):

- (i). The species can be subdivided into a number of groups only one of which (group IX) should be called Senecio, since the type species, S. vulgaris L. is contained in this group.
- (ii). The remaining groups (groups I-VIII and X-XVI) might be distinct genera, possibly new or possibly congeneric with other widely recognised genera in the Asteraceae.

Thus, Jeffrey et al. (1977) circumscribed the Senecio complex more clearly, as follows:

Herbaceous, perennial or annual, often subscapose, suffrutescent or frutescent, sometimes succulent, sometimes scandent, rarely pachycaul arborescent; leaves pinnately, pinnatopalmately or palmately veined; inflorescences usually

terminal corymbose cymes, sometimes thyrsoid or capitula solitary, terminal; capitula radiate, subradiate or discoid, rays yellow, orange-yellow, purplish or rarely white, disc yellow, orange-red, purplish or brownish; rays 3-10-veined, glabrous or with uniseriate or biseriate hairs; cypselas glabrous or with usually spirally thickened obtuse hairs; cells short to long, smooth or striate, often papillose; pappus uniform or dimorphic, hairs stout to very slender, tapered or tapered and fluked; style-arm papillae medium, median fascicle usually absent; anther-collars nearly always balusterform with clearly differentiated basal cells; anther-bases short, rarely as long as the anther-collars, obtuse to acute.

It is important to note that the above circumscription was not intended to be a definitive classification.

The suggestions of Jeffrey *et al.* (1977) have been re-evaluated in the light of further evidence from pappus, numerical, chemical and succulent plant studies (Drury, 1967; Bohlmann *et al.*, 1979; Jeffrey, 1979; Robins, 1977a, 1977b). This resulted in the original group IX, being subdivided into the "Eusenecionoids" (group IX [a]), part of which contains Senecio s. str. sensu Jeffrey, and the "Gynuroids" (group IX [b]). However, group IX has remained the largest in the tribe and the problems of generic delimitation remain most acute in this group. While the eclectic approach was initially reasonably successful in subdividing the very variable contents of Senecio into groups I-XVI, this eclectic



approach has proved of little value in elucidating the interrelationships and affinities within the large complex of group IX [a], which contains the type species of Senecio L., S. vulgaris L., and all the species putatively most closely allied to it.

Jeffrey (1979) suggested that all the species of group IX are probably more closely related phylogenetically to S. vulgaris than is any species of any other group, yet group IX contains approximately 20 recognised genera. This should be contrasted with the very variable contents of Senecio, prior to its subdivision, which represents Senecio as being grossly paraphyletic.

In an attempt to gain further insight into the Senecio complex, Jeffrey and Chen (1984) investigated the Senecio flora of eastern Asia, using the "uniform criterion" of characters for the Senecio complex (Jeffrey et al., 1977). This study formed part of a larger study on the tribe Senecioneae. In this treatment of Senecio in eastern Asia, where S. vulgaris is widely distributed, sixty species are recognised and a number of species (13 spp.) are excluded from the genus.

In the light of the studies of Jeffrey and Chen (1984), it is estimated that Senecio world-wide, consists of "perhaps 1 000 species." This is considerably fewer than earlier estimates - c. 1 500 species (Nordenstam, 1978) and c. 3 000 species (Jeffrey et al., 1977). This recent estimate of Jeffrey and Chen (1984) perhaps indicates the success of the establishment of a "uniform criterion" for Senecio although they draw attention to the fact that "generic limits in many areas are still

uncertain." No comment has been made in this study on their ideas on the concept of Senecio L. sensu stricto, which I think is unfortunate.

However, Nordenstam (1978) in his studies on the tribe Senecioneae, which were aimed at revising the constituents of the tribe and not specifically aimed at elucidating the generic concept of Senecio s. str., does mention characteristics which he perceives as being characteristic of Senecio s. str. These characteristics being:

- (i). 'Senecioid' filament collars (for details see CHARACTER 110)
- (ii). 'Radial' endothelial tissue (= radial anticlinal) (for details see CHARACTER 107)
- (iii). Discrete stigmatic areas (= banded configuration) (for details see CHARACTER 096)
- (iv). Truncate style-branches (for details see CHARACTER 095)
- (v).  $n = 10$

#### THE DEVELOPMENT OF MY CONCEPT OF SENECIO SENSU STRICTO

It has been stressed by Jeffrey (1979) that to elucidate the taxonomy of the Senecio complex, studies need to be based on S. vulgaris and establish progressively more comprehensive sister-groupings and then the limits of what should be Senecio L. sensu stricto should be decided.

The suggestions by Nordenstam (1978) on the characteristics of Senecio s. str. and the aforementioned exhortation by Jeffrey (1979), are what partially initiated this study on predominantly the Natal members of

Senecio. However, while the implication of Jeffrey's (Jeffrey, 1979) exhortation is that the decision on the limits of Senecio s. str. should only be made after Senecio and related genera world-wide have been investigated (Jeffrey, 1979), it was decided to attempt a decision on what the limits of Senecio s. str. should be, during this study, this being attempted, despite the limitations imposed on the study by the nature and size of the sample.

The strategy used to facilitate this decision was to include in the study the type of the genus, S. vulgaris and several other senecios (spp. 212-220, Table 1) which are thought to be very closely related to Senecio. These latter senecios being suggested by Jeffrey et al. (1977) and Jeffrey (1979) to be representative of the sensu stricto generic concept of Senecio. Also included in the study were some species of related genera (spp. 225-232, Table 1) and two senecios of uncertain taxonomic position (S. syringifolius & S. hockii). All of these taxa were included so as to provide a further frame of reference in my attempt to elucidate what should be the limits of Senecio s. str. and what relationship exists between the Natal senecios and this concept of Senecio sensu stricto. Five species of heterochromous non-yellow senecios (purple ray & yellow disc florets), peculiar to the Cape flora, were also included in the study to assess their phenetic affinity to my concept of Senecio L. sensu stricto.

As mentioned elsewhere in this dissertation (Chapter 3) more than one-hundred morphological and micromorphological 'characters' (Michener & Sokal, 1957) were investigated (Table 2) so as to expose me to as much

of the phenotype of the taxa investigated (Table 1) as possible.

The external micromorphology of the pollen of all the taxa studied (Table 1) using scanning electron microscopy, as well as the organic chemistry of as many taxa as possible have also been investigated. The work on the organic chemistry being performed predominantly by Bohlmann (F.Bohlmann, pers. comm.).

The information from the pollen and the organic chemistry studies will be enlarged upon in Chapter 7 and Chapter 8 respectively, of this dissertation.

#### THE CHARACTERS USED TO DELIMIT MY CONCEPT OF *SENECIO* SENSU STRICTO

As a result of my studies, I suggest the following characters are important in defining the limits of Senecio L. sensu stricto:

- (i). GYNOECEIUM (DISC): STYLE-ARM APICES - CHAR 095
- (ii). ANDROECIUM (DISC): ANTHER APEX - CHAR 103
- (iii). ENDOTHECIAL TISSUE: CELL WALL CONFIGURATION - CHAR 107
- (iv). FILAMENT COLLARS: LENGTH - CHAR 108
- (v). FILAMENT COLLARS: SHAPE - CHAR 110
- (vi). CYPSELA (DISC): SHAPE - CHAR 117

The six aforementioned characters are all "good" taxonomic characters (Davis & Heywood, 1963) for most of the senecios investigated (Table 1), for the following reasons:

- (i). They are not subject to wide variation.
- (ii). They do not appear to be susceptible to environmental modification.
- (iii). They appear to have a low intrinsic genetic variability.

The character states of the above characters which circumscribe Senecio s. str. sensu Vincent, also exhibit moderate to considerable positive correlation with each other. Similarly, the character states which are used to identify senecios which are peripheral to Senecio s. str. also show moderate to considerable positive correlation with each other. It is this correlation amongst these characters that I have used to assign them generic importance.

Each of the above characters comprise a number of character states (see Appendix A). A summary of which character states circumscribe Senecio s. str. and those which are used to identify senecios which are peripheral to Senecio s. str. is provided in Table 4.

Important features of these characters and their character states as well as the occurrence of the character states amongst the taxa investigated are described in Chapter 3 of this dissertation.

The relationship of the Natal senecios (nos. 1-124, Table 1), the Cape heterochromous non-yellow senecios (nos. 200-204, Table 1) and the

non-southern African senecios (nos. 210-220, Table 1), to the aforementioned concept of Senecio s. str. sensu Vincent, together with an indication of which senecios should be considered peripheral (satellites) to Senecio s. str., will now be investigated. The possibility of excluding some of the senecios studied from Senecio s. str. sensu Vincent, on the basis of my circumscription of the generic concept of Senecio, will also be investigated.

## CHAPTER FIVE

A REAPPRAISAL OF THE STATUS OF THE  
NATAL SENECIOS

The application of my concept of Senecio s. str. to the Natal senecios, the Cape heterochromous non-yellow senecios and the non-southern African senecios results in the majority of these senecios, including the type, S. vulgaris, being congeneric with this new concept of Senecio s. str.; the remaining senecios, with two exceptions, only being included in Senecio as peripheral senecios. The two exceptions, S. cissampelinus and S. transvaalensis fall outside the limits of Senecio s. lat. and should be excluded from Senecio (Table 5).

Senecio transvaalensis shows considerable affinity with the tropical African genus Emilia Cassini, for it has lilac florets, style-branch apices with a median fascicle of fused papillae and distinctly 5-angled cypselas. These characteristics suggest that it is best placed in Emilia. The same suggestion has been made by Hilliard (1977, 1978). Senecio cissampelinus shows considerable affinity with the tropical African genus Mikaniopsis Milne-Redhead, its prehensile petioles with their thickened bases being a notable feature of the vegetative habit of this genus. However, the genus Mikaniopsis and the Asiatic genus Cissampelopsis (DC.) Miq., have been under study by Jeffrey (C. Jeffrey, pers. comm.) with the view to elucidating the relationship between these two genera. The result of this study is that Mikaniopsis has been

reduced to synonymy (ined.) under Cissampelopsis (C. Jeffrey, pers. comm.). Consequently, S. cissampelinus would become a member of Cissampelopsis and indeed a comparison of S. cissampelinus with the generic description of Cissampelopsis (Jeffrey & Chen, 1984) confirmed that S. cissampelinus is clearly a member of this genus.

The application of my concept of Senecio to the two senecios of uncertain taxonomic position, S. syringifolius and S. hockii, indicates that these two species also fall outside the limits of Senecio s. lat. (Table 5). The affinity of S. syringifolius seems to lie with Crassocephalum Moench, while the affinity of S. hockii seems to lie with Emilia Cass., as suggested by Jeffrey *et al.* (1977).

The species of Senecio s. str., according to this new concept (Table 5), can be subdivided into eleven homogeneous groups (groups I-XI, Table 5) and a number of ungrouped species.

The peripheral senecios, according to this new concept of Senecio s. str. sensu Vincent (Table 5), show some affinity with some of the aforementioned groups and ungrouped species of Senecio s. str., indicating that the concept of Senecio s. lat. develops from only some of the character states which circumscribe Senecio s. str. sensu Vincent (Table 6), which I have termed a dendritic development.



### NUMERICAL ANALYSIS

A principal components analysis (PCA) (Figs. 36 & 37) of these six characters helps to illustrate how these six characters discriminate Senecio s. str. from the peripheral senecios and the related genera. The PCA also indicates which senecios should be excluded from Senecio (Figs. 36 & 37).

Both rotated and unrotated components of the PCA were produced. However, the rotated components resulted in essentially the same relationships in space and therefore are not presented.

The principal components analysis of the six characters yielded three components with eigenvalues greater than one (80,5% of trace, Table 7). The fact that the first three factors accounted for 80,5% of the trace (Table 8) indicates that the three components (Figs. 36 & 37) are a reasonably accurate representation of the six characters analysed. Component I has correlations greater than 0.4 for: STYLE-ARM APICES (CHAR 095), ANTHER APEX (CHAR 103), ENDOTHECIAL TISSUE: CELL WALL CONFIGURATION (CHAR 107), FILAMENT COLLARS: LENGTH (CHAR 108) and FILAMENT COLLARS: SHAPE (CHAR 110) (Table 9). Component II has correlations greater than 0.4 for FILAMENT COLLARS: LENGTH (CHAR 108) (Table 9), while Component III has correlations greater than 0.4 for CYPSELA (DISC): SHAPE (CHAR 117) (Table 9). Since the components of a PCA are arranged in numerical order of importance, the composition of the three components of this PCA indicates, to a degree, the relative importance of each of the six characters with respect to each other.

A COMPARISON OF MY CONCEPT OF SENECIO SENSU STRICTO WITH THAT OF JEFFREY et al. (1977) AND JEFFREY (1979)

My concept of Senecio s. str. coincides considerably with that of Jeffrey et al. (1977) and Jeffrey (1979) with a few exceptions.

Jeffrey (1979) places S. panduriformis and S. bupleuroides in his group 45 and S. coronatus in his group 44, both of which are outside his concept of Senecio sensu stricto, which consists of groups 40 and 41 (Jeffrey, 1979). However, in my study these species are included in my concept of Senecio s. str. (groups III and VI, Table 5).

In a recent communication (C.Jeffrey, pers. comm.), further suggestions have been made on the contents of Senecio, based on earlier work (Jeffrey, et al., 1977; Jeffrey, 1979) and recent work (C.Jeffrey, pers. comm.). To quote " It looks as if, even when split up, Senecio will still remain a large genus, including probably Senecio 43 p.p., 44, 45, 46 p.p., 47(1), 26-32, 14 p.p., in the broader sense and 14 p.p., 15, 16, 17, 18, 19, 20, 21, 23, 24, 25, 33, 34, 35, 36, 37, 38, 40, 41 & 46 p.p. in the narrower sense". This recent suggestion still places S. panduriformis, S. bupleuroides and S. coronatus in Senecio "in the broader sense". I disagree with this placement of the aforementioned three species, for each satisfies the requirements of the concept of Senecio s. str. sensu Vincent, and are thus clearly members of Senecio sensu stricto.

THE APPLICATION OF MY CONCEPT OF SENECIO SENSU STRICTO TO SOME RECENT  
WORK ON THE SENECIOS OF EASTERN ASIA

The application of my concept of Senecio s. str. to the senecios of eastern Asia (Jeffrey and Chen, 1984) results in the majority of the species of Senecio they recognise, being designated Senecio s. lat., with only the following species falling within my concept of Senecio s. str.:

- S. pseudo-arnica Less. (sp. 2)
- S. lijianqensis C. Jeffrey & Y.L. Chen (sp. 13)
- S. lingianus C. Jeffrey & Y.L. Chen (sp. 20)
- S. ihasaensis Ling ex Y.L. Chen et al. (sp. 26)
- S. kongboensis Ludlow (sp. 27)
- S. actinotus Hand.-Mazz. (sp. 31)
- S. wightii (DC. ex Wight) Benth. ex C.B.Cl. (sp. 50)
- S. desfontainei Druce (sp. 55)
- S. krascheninnikovii Schischk. (sp. 56)
- S. vulgaris L. (sp. 58)
- S. oryzetorum Diels (sp. 60)
- S. yunqinensis Hand.-Mazz. (sp. 61)

The above delimitation of the senecios of eastern Asia into Senecio s. str. and Senecio s. lat., is based on the occurrence of the characteristics of my concept of Senecio s. str. (Table 4), in the species descriptions.

The following assumptions were made in judging the status of the anther

appendages and the length of the filament ("anther-") collars: "ovate-lanceolate" anther appendages (assumed to be in the length/width range of "more than 6:1 - 3:1, Radford et al., 1974) and filament collars "rather long"/"elongate" were accredited the status of Senecio s. lat. according to my concept of Senecio s. str. (Table 4, character 103, character state 03 and character 108, character states 04 and 05).

#### THE APPLICATION OF MY CONCEPT OF SENECIO SENSU STRICTO TO SOME SENECIOS OF NORTH AMERICA

Four senecios occurring in north America (Barkley, 1978) were included in this study, namely: S. californicus DC., S. sylvaticus, S. viscosus and S. vulgaris (Table 1).

The application of my concept of Senecio s. str. to these four senecios results in them being clearly recognised as members of Senecio sensu stricto.

Unfortunately I was unable to apply my concept of Senecio s. str. to the remaining senecios described in the account of Senecio of north America by Barkley (1978), because of the lack of information in his species descriptions on the characters of my generic concept (Table 4).

Now that all the taxa included in this study (Table 1) have been subjected to my concept of Senecio, the interrelationships amongst all the resulting members of Senecio sensu Vincent (Table 5) will now be investigated in the following chapter.

## CHAPTER SIX

THE INTERRELATIONSHIPS OF ALL THE  
SENECIOS STUDIED

THE INTERRELATIONSHIPS OF THE NATAL SENECIOS AND OF THE NATAL SENECIOS  
TOGETHER WITH THE CAPE AND NON-SOUTHERN AFRICAN SENECIOS INVESTIGATED -  
IN THE LIGHT OF EVIDENCE FROM GROSS AND MICROMORPHOLOGICAL STUDIES

INTRODUCTION

The interrelationships amongst the senecios resulting from the application of my concept of Senecio to all the taxa studied, excluding the species recommended for exclusion from Senecio (Table 5), will now be described.

In chapter 3 a number of characters were labelled with an asterisk [\*] to indicate that they are taxonomically significant ("good") (Davis & Heywood, 1963) with respect to elucidating the interrelationships between the senecios investigated. There are thirty-seven of these taxonomically significant characters (Table 10). Two of these thirty-seven characters are invariant. Character 107 is invariant among the Natal members of Senecio (Table 5) while characters 103 and 107 are invariant among all the members of Senecio s. str. (Table 5).

The interrelationships of the following groups of senecios were investigated with respect to the characters which were not invariant (Table 10):

- Group 1. The relationships between the Natal members of Senecio (Table 11).
- Group 2. The interrelationships of the Natal members of Senecio s. str. together with the Cape senecios and the non-southern African senecios (Table 12).

The purpose behind investigating the aforementioned relationships and interrelationships is as follows:

- Group 1. The relationships between the Natal members of Senecio s. str. and the peripheral senecios (Table 11) were investigated with a view to evaluating the relationships that appear to exist at the generic level, as mentioned in chapter 4, in the light of this larger group of characters (36 characters - Table 10). Members of Senecio s. lat. only occur amongst the Natal senecios (Table 11).
- Group 2. The interrelationships of all the members of Senecio s. str. (Table 12), were investigated with a view to testing whether or not these senecios form groups of related species associated with their distribution (i.e. Natal, Cape and non-southern Africa) (35 characters - Table 10).

## THE RELATIONSHIPS BETWEEN THE NATAL MEMBERS OF SENECIO

### CLUSTER ANALYSIS

The relationships between the Natal members of Senecio s. str. and the peripheral senecios (Table 11), with respect to the thirty-six characters (Table 10), were investigated using numerical cluster analysis. A correlation phenogram (Fig. 38) was constructed using the UPGMA technique, this technique producing the highest cophenetic correlation coefficient (0,77). This cophenetic correlation coefficient indicates that there was some distortion from the original matrix in the production of the phenogram.

This cluster analysis (Fig. 38), indicates that there are two reasonably distinct groups (groups A & B), these two groups being slightly negatively correlated (corr. = -0,18). The majority of the Natal members of Senecio s. str. are placed in group A, while all the peripheral senecios are placed in group B, together with a few members of Senecio s. str.. Group B can also be further subdivided into groups B1 and B2, the senecios of group B2 having a very low correlation (corr. = 0,03) with the senecios of group B1 (Fig. 38).

A comparison of the relationships amongst these Natal members of Senecio (Table 11), in the light of these thirty-six characters (Table 10), with their relationships at the generic level is most revealing. The proposed relationships at the generic level (Table 6) between the

members of Senecio s. str. and the peripheral senecios are only partially supported while the proposal that Senecio s. lat. be represented by a dendritic pattern is supported in that the peripheral senecios still appear to be related to only some members of Senecio s. str., to varying degrees (Fig. 38).

A new set of relationships between the Natal members of Senecio s. str. and the peripheral senecios (Table 11) is proposed, in the light of the above numerical analysis. This proposal does not replace the earlier proposal of chapter 5 (Table 6) but rather builds on that proposal, since the above numerical analysis includes the characters upon which the earlier proposal is based.

According to this new proposal, S. tanacetopsis (no. 16) and S. seminiveus (no. 17), which are highly correlated with each other (Fig. 38), are relatively closely related to S. achilleifolius and S. haygarthii (no. 18) and less so with S. serratuloides (no. 9), S. microglossus (no. 10), S. bupleuroides (no. 97), S. mikanioides (no. 109) and S. deltoideus (no. 110) at the 0,3 level of correlation. Senecio medley-woodii (no. 20), S. tamoides (no. 111), S. helminthioides (no. 116), S. barbertonicus (no. 117), S. viminalis (no. 119), S. radicans (no. 120) and S. fulgens (no. 122), have a relatively low correlation with all the remaining Natal senecios (corr. = 0,03) and collectively form group B2 (Fig. 38). All these species, with the exception of S. medley-woodii, are correlated with each other to varying degrees (Fig. 38). Senecio breviflorus (no. 118) shows some correlation with S. scitus (no. 99) in particular and with S. urophyllus (no. 98),



S. scitus (no. 99), S. glaberrimus (no. 101), S. latifolius (no. 102), S. retrorsus (no. 103), S. brachypodus (no. 107) and S. pleistocephalus (no. 108) in general, while S. medley-woodii has an extremely low correlation with all the Natal members of Senecio (corr. = 0,03) (Fig. 38). Senecio barbertonicus and S. radicans are moderately correlated with each other (corr. = 0,57), while S. viminalis and S. fulgens are noticeably correlated (corr. = 0,84) (Fig. 38). Senecio tamoides is moderately correlated with S. viminalis and S. fulgens (corr. = 0,51) (Fig. 38).

#### PRINCIPAL COMPONENTS ANALYSIS

Principal components analysis (PCA) of the thirty-six characters (Table 10) of the Natal members of Senecio (Table 11) was also performed. Both rotated and unrotated components of the PCA were produced. However, the rotated components resulted in essentially the same relationships in space and therefore are not presented. The PCA results (Figs. 39 & 40) were quite similar to those obtained in the cluster analysis (Fig. 38). The PCA yielded eleven components with eigenvalues greater than one (77,0% of trace - Table 14), indicating that the characters are not highly correlated. The first two components had eigenvalues greater than 5 and accounted for 41,2% of the variance (Table 15). Component I has correlations greater than 0,5 for the following characters (in decreasing order of importance): LEAF TRICHOMES: APEX (CHAR 035), LEAF SHAPE: CAULINE (CHAR 017), CALYCVULUS BRACCTS: TRICHOMES (CHAR 063), LEAF TRICHOMES: BASE (CHAR 034), LEAF TRICHOMES: APPENDAGES (CHAR 036), DISC COROLLA: COROLLA SHAPE (CHAR 082), LEAF SHAPE: RADICAL (CHAR 016), LEAF VENATION: RADICAL (CHAR 024), GYNODECIUM (DISC): STYLE-ARM APICES (CHAR

095), ANDROECIUM (DISC): ANTHER APEX (CHAR 103), INVOLUCRAL BRACTS: TRICHOMES (CHAR 054), INVOLUCRAL BRACTS: SHAPE (CHAR 052), ANDROECIUM (DISC): ANTHER BASE APPEARANCE (CHAR 104), LEAF VENATION: CAULINE (CHAR 025), DISC COROLLA: LOBE APEX (CHAR 086), FILAMENT COLLARS: LENGTH (CHAR 108), GYNOECIUM (DISC): STYLE-ARM LENGTH (CHAR 094) and INVOLUCRE SHAPE (CHAR 049) (Table 16). Component II has correlations greater than 0,5 for the following characters (in decreasing order of importance): DISC COROLLA: COROLLA LENGTH (CHAR 081), PAPPUS SETAE (DISC): LENGTH (CHAR 126), INVOLUCRAL BRACTS: LENGTH (CHAR 051), ANDROECIUM (DISC): ANTHER LENGTH (CHAR 105), GYNOECIUM (DISC): STYLE-ARM LENGTH (CHAR 094), FILAMENT COLLARS: LENGTH (CHAR 108) and CYPSELA (DISC): LENGTH (CHAR 116) (Table 16). Component III has no correlations greater than 0,5 and only two correlations above 0,3, these being for the following characters (in decreasing order of importance): PAPPUS SETAE (DISC): APEX (CHAR 129) and GYNOECIUM (DISC): STYLE-ARM APICES (CHAR 095) (Table 16).

Components I and II (Fig. 39) are especially helpful in illustrating the two reasonably distinct groups mentioned earlier (groups A & B - Fig. 38) as well as illustrating that the senecios in group B2, namely: S. medley-woodii (no. 20), S. tamoides (no. 111), S. helminthioides (no. 116), S. barbertonicus (no. 117), S. viminalis (no. 119), S. radicans (no. 120) and S. fulgens (no. 122) are correlated with each other to varying degrees while collectively having a low correlation (corr. = 0,03), with all the remaining Natal senecios (groups A & B1) as illustrated in Figure 38. The plots of the PCA (Figs. 39 & 40) also illustrate that group A is far more compact than group B, indicating

that the relationships amongst the senecios of group A are considerably closer than those amongst the senecios of group B. A further important observation is that S. tanacetopsis (no. 16), S. seminiveus (no. 17) and S. brevilorus (no. 118), all of which are peripheral senecios (Table 11), are clearly poorly associated with the senecios of group B2 but are more associated with the members of Senecio s. str. of group B1 (Fig. 39).

### PROPOSALS

In the light of the above numerical analysis and keeping in mind the particular character states (Table 5) of the generic characters (Table 4) possessed by the peripheral senecios (Table 11), I propose that S. tanacetopsis, S. seminiveus and S. brevilorus be retained in Senecio s. lat. and that the remaining peripheral senecios (S. medley-woodii, S. tamoides, S. helminthioides, S. barbertonicus, S. viminalis, S. radicans & S. fulgens - Table 11) be excluded from Senecio s. lat..

Consequently, the list of Natal species recognised as members of Senecio s. str. (Table 11) has been amended according to the above proposals (Table 13).

The excluded species will need to be investigated further so as to decide on whether they can be included into other existing genera or whether new genera need to be erected to accommodate them.

It is interesting to note that a comparison of these excluded species with the representatives of the related genera included in this study

(Table 1), with the assistance of some numerical cluster analysis (UPGMA), using the previously mentioned thirty-seven characters (Table 10), indicates the following: S. tamoides (no. 111) and S. helminthioides (no. 116) show some affinity with Kleinia grandiflora (no. 228) and K. neriifolia (no. 229) (corr. = 0,31); S. barbertonicus (no. 117) and S. radicans (no. 120) also show some affinity with K. grandiflora and K. neriifolia (corr. = 0,42); S. viminalis and K. neriifolia show considerable affinity (corr. = 0,90), while S. fulgens (no. 122) and K. grandiflora also show considerable affinity (corr. = 0,79). Senecio medley-woodii (no. 20) shows a negative correlation with these representatives of the related genera.

It is also interesting to note that Jeffrey (C. Jeffrey, pers. comm.), in his studies of the tropical east African Senecioneae, also excludes S. barbertonicus from Senecio and places it on its own with generic status, "its affinity with the remaining members of the tropical east African Senecioneae being uncertain."

#### THE INTERRELATIONSHIPS OF ALL THE MEMBERS OF SENECIO SENSU STRICTO

##### CLUSTER ANALYSIS

The interrelationships of all the Natal members of Senecio s. str. together with the Cape and non-southern African senecios (Table 12), with respect to the thirty-five characters (Table 10), were investigated using numerical cluster analysis. A correlation phenogram (Fig. 41) was constructed using the UPGMA technique, this technique producing the highest cophenetic correlation coefficient (0,74).

This cluster analysis indicates that there are three reasonably distinct groups (groups A, B & C) amongst these members of Senecio s. str. (Fig. 41). These three groups are slightly negatively correlated with each other, with group B being more negatively correlated with group C than group A (group A with groups B & C, corr. = -0.05; group B with group C, corr. = -0,15). Each of these three groups can be further divided as illustrated in Figure 41. The subdivision of each of these three groups is based on the correlation of the senecios within each subgroup being equal to or greater than 0,3. Group A has been subdivided into eight smaller groups (groups A1-A8). Group B has been subdivided into five smaller groups (groups B1-B5). Group C has been subdivided into twelve smaller groups (groups C1-C12). In many instances the groups within each of the three large groups (groups A, B & C) can be further subdivided into even smaller groups on the basis of the senecios within each of these smaller groups having a correlation with each other equal to or greater than 0,5 (e.g. groups A1a, A1b, B1a, B1b). This latter subdivision, in some instances, results in one or more ungrouped senecios at this level of correlation (corr. > 0,5) (e.g. group B1, no. 18 & group B2, no. 201).

#### THE RELATIONSHIPS BETWEEN GROUPS A, B AND C

The division of the senecios into groups A, B & C (Fig. 41) shows only moderate correlation with their geographic distribution on a continent basis. Evidence of this is seen in groups B and C which contain the majority of the Natal senecios.

However, while the senecios of group A show some correlation with their geographic distribution in that groups A1, A2, A7 and A8 all consist of senecios indigenous to Natal, each of the remaining groups consists of senecios from more than one continent (Table 12).

The composition of group A illustrates clearly how Senecio s. str. has a genotype which is distributed over several major and widely separated continents represented in this study (Table 12).

#### THE INTERRELATIONSHIPS OF THE SENECIOS OF GROUP A

##### CLUSTER ANALYSIS

##### Group A1

Group A1a (Fig. 41), consisting of S. madagascariensis (no. 1), S. skirrhodon (no. 2) and S. inaequidens (no. 3) and group A1b, consisting of S. harveianus (no. 4), S. chrysocoma (no. 53) and S. juniperinus (no. 7) form two distinct groups. These two groups also show moderate affinity with each other (corr. = 0,42).

The senecios of group A1a are thought to form a distinct complex referred to as the S. madagascariensis complex (O.M. Hilliard, pers. comm.) and the cluster analysis of these three species (Fig. 41), with respect to the thirty-five characters of taxonomic significance (Table 10), provides considerable support for this view.

Hilliard (1977) suggested that S. skirrhodon is "possibly no more than a maritime form of S. madaqascariensis" and may be better "placed as a variety of that species." However, the correlation between these two species (corr. = 0,65) suggests that they are better kept as two species (Fig. 41).

Senecio harveianus and S. chrysocoma show considerable affinity with each other (corr. = 0,80) and moderate affinity with S. juniperinus (corr. = 0,69), strongly suggesting that these three species are closely allied despite some of their dissimilarities in facies.

#### Group A2

The two senecios of group A2 (Fig. 41), S. polyanthemoides (no. 5) and S. pterophorus (no. 6) appear only moderately allied (corr. = 0,56) despite their similar facies.

It is interesting to note that the senecios of groups A1 and A2 are clearly allied (corr. = 0,36) this level of affinity perhaps being expressed in their lifestyle in that they are all regarded as weeds.

The senecios of groups A3 to A6 are clearly allied to varying degrees (corr. = 0,38; 0,32 & 0,28 respectively) despite them being distributed over several continents (Table 12).

#### Group A3

All the senecios of group A3 (Fig. 41) are moderately to highly correlated (corr. > 0,52), especially S. californicus

(no. 214) and S. vernalis (no. 215) (corr. = 0,91), indicating that they are clearly allied to varying degrees. It is most interesting that three Cape heterochromous non-yellow senecios; S. grandiflorus (no. 200), S. multibracteatus (no. 203) and S. elegans (no. 204) are allied to S. californicus and S. vernalis both of which are homochromous yellow species. This allied relationship is especially noticeable between S. grandiflorus and S. californicus and S. vernalis (corr. = 0,77). Also noteworthy is that while S. multibracteatus and S. elegans (both heterochromous non-yellow) are allied to the remaining senecios of group A3 (corr. = 0,52), they are clearly allied to each other (corr. = 0,65).

#### Group A4

The senecios of group A4 (Fig. 41) are all distributed in the northern hemisphere (Table 12) and are moderately to highly correlated (corr. > 0,61), indicating that they are clearly allied to varying degrees despite their collective distribution spanning two widely separated continents. Senecio vulgaris (no. 210) and S. gallicus (no. 213) are highly correlated (corr. = 0,96) indicating that these two species are closely allied. The extreme closeness of relationship between S. vulgaris and S. gallicus together with the distribution of S. gallicus with respect to S. vulgaris, possibly reflects the degree of the cladistic relationship between these two species. Senecio viscosus (no. 212) and S. desfontainei (no. 217) show a moderately high level of correlation (corr. = 0,73), indicating that they are allied, although their distribution (Table 12) is disjunct.



Group A5

Senecio sylvaticus (no. 216) and S. erectitoides (no. 219) of group A5 (Fig. 41) show a moderately high level of correlation (corr. = 0,70) suggesting that these two species are allied despite their distribution being disjunct, S. sylvaticus being found in the United Kingdom and the United States of America while S. erectitoides is endemic to Madagascar.

Group A6

The two senecios of group A6 (Fig. 41), the Cape heterochromous non-yellow species, S. arenarius (no. 202) and the yellow-flowered S. lautus (no. 220) of Australia, are not closely allied (corr. = 0,43). Nevertheless, their clustering together indicates that these two species are more closely allied to each other than to any of the other members of Senecio s. str. investigated in this study. The highest correlation which these two species have with the remaining senecios of group A is 0,28, which is in fact with the senecios of groups A3 to A5, which are predominantly non-southern African senecios. The correlation which these two species have with the senecios of groups A1 and A2, which are predominantly Natal senecios, is even lower (corr. = 0,24).

Group A7

Groups A7 and A8 are quite distinct and have a relatively low correlation with each other (corr. = 0,22). However, a similarity between these two groups is that they are both composed entirely of homochromous non-yellow senecios.

It is quite significant that the two varieties of S. polyodon DC. (nos. 33A & 33B) comprising group A7 (Fig. 41) are only moderately correlated (corr. = 0,59). This correlation, which is not based on any ray floret characters (Table 10), suggests that these two senecios are less closely allied than their present taxonomic status suggests. Based on my observations of these two senecios, I suggest that a more appropriate taxonomic status might be at the subspecific or perhaps even the specific level.

#### Group A8

The two senecios of group A8 (Fig. 41), S. poseideonis (discoid plants - 38B) and S. sp. aff. S. poseideonis (no. 39), although not highly correlated (corr. = 0,41), are clearly more allied to each other than to any other members of Senecio s. str. investigated in this study. Note too that the discoid and radiate plants of S. poseideonis (no. 38) are placed in different groups - groups A and B respectively which are slightly negatively correlated (corr. = -0,05). This occurs despite the clustering of these two forms of S. poseideonis being derived from a character set which excludes all features of the ray florets (Table 10). Hilliard (1977) mentions that the two forms of S. poseideonis occurred within the same population which complicates the matter of their relationship in the light of them occurring in the two separate groups. The significance of the occurrence of radiate and discoid taxa within the same species will be discussed further in chapter 9.

## THE INTERRELATIONSHIPS OF THE SENECIOS OF GROUP B

### CLUSTER ANALYSIS

#### Group B1

Group B1a (Fig. 41), consisting of S. serratuloides (no. 9) and S. microglossus (no. 10) and group B1b, consisting of S. bupleuroides (no. 97), S. mikanioides (no. 109) and S. deltoideus (no. 110) form two distinct groups (corr.  $> 0,5$ ). Senecio haygarthii (no. 18), while being a member of group B1, appears to be only relatively distantly allied (corr.  $< 0,4$ ) to the remaining members of group B1.

Senecio serratuloides and S. microglossus of group B1a are clearly allied (corr. = 0,77), this affinity being supported by Hilliard (1977). These two species also appear to be relatively distantly allied to the remaining members of group B1 (corr. = 0,34).

The affinity of S. bupleuroides, S. mikanioides and S. deltoideus for each other is quite surprising for their individual facies are quite distinct. However, keeping in mind that this moderate affinity (corr. = 0,54) is based on a select group of characters (Table 10), which excludes some characters of the facies, it is possibly significant that these three species are more allied to each other than to any of the other senecios investigated in this study (Table 12), for it possibly reflects their degree of cladistic relationship. Hilliard (1977) suggests that S. bupleuroides, S. urophyllus (no. 98), S. scitus (no. 99) and S. glaberrimus (no. 101) are closely allied.

Group B2

Senecio cathcartensis (no. 31) and S. ngoyanus (no. 32) of group B2a (Fig. 41) appear to be moderately closely related (corr. = 0,67). These two species can be confused (Hilliard, 1977) but their species descriptions (Hilliard, 1977), and this analysis, renders them clearly separable. The affinity of these two species with S. cakilefolius (no. 201), albeit moderately low (corr. = 0,39), is most interesting for these are the only two species of groups B and C which have an affinity with one of the five Cape heterochromous senecios investigated in this study (Table 12). Note that S. cathcartensis and S. ngoyanus are non-yellow senecios while S. cakilefolius has non-yellow ray florets and yellow disc florets.

Group B3

Group B3 (Fig. 41) consists of two groups, group B3a and group B3b. Senecio oxyriifolius (no. 89), S. rhomboideus (no. 90) and S. othonniflorus (no. 104) of group B3a are moderately allied (corr. = 0,53). A close relationship between S. oxyriifolius and S. rhomboideus has already been suggested by Hilliard (1977), and is partially supported by this study (corr. = 0,65), with the addition of the relationship between these two senecios and S. othonniflorus.

Group B3b is composed of nine moderately to highly correlated species. Senecio urophyllus (no. 98), S. latifolius (no. 102) and S. retrorsus (no. 103) appear to be closely allied (corr. = 0,84), especially S. urophyllus and S. latifolius (corr. = 0,93). Hilliard (1977) also suggests that S. latifolius and S. retrorsus are allied. Senecio

urophyllus, S. latifolius and S. retrorsus appear to be moderately allied to S. glaberrimus (no. 101) (corr. = 0,58). However, Hilliard (1977) suggests that S. urophyllus and S. glaberrimus are allied to S. bupleuroides.

Senecio brachypodus (no. 107) and S. pleistocephalus (no. 108) of group B3b appear to be very closely allied (corr. = 0,93), an affinity which is supported by Hilliard (1977). The moderate affinity between S. brachypodus, S. pleistocephalus and S. scitus (no. 99) (corr. = 0,64), possibly reflects the degree of their cladistic relationship, for the facies of S. scitus is noticeably different from those of S. brachypodus and S. pleistocephalus. Senecio scitus is considered by Hilliard (1977) to be closely allied to S. bupleuroides.

#### Group B4

Senecio panduriformis (no. 14) and S. sp. aff. S. speciosus (no. 34) of group B4 (Fig. 41) are not closely allied (corr. = 0,40). Nevertheless, their clustering together in this group indicates that these two species are more closely allied to each other than to any of the other members of Senecio s. str. investigated in this study (Table 12). These two species, while having some affinity with S. achilleifolius (no. 15), S. gerrardii (no. 23) and S. poseideonis (radiate plants - no. 38A) of group B5, are only distantly allied to these latter species (corr. = 0,27). It is interesting to note that S. panduriformis is a yellow senecio while S. sp. aff. S. speciosus is a non-yellow senecio.

Group B5

Senecio achilleifolius (no. 15), S. gerrardii (no. 23) and S. poseideonis (radiate plants - 38A) of group B5 (Fig. 41), are also not closely allied (corr. = 0,22). However, their clustering together in this group indicates that these three species are more closely allied to each other than to any of the other members of Senecio s. str. investigated in this study (Table 12). The species of group B5 have their closest affinity with the species of group B4. However, this affinity is extremely low (corr. = 0,27). Note that S. achilleifolius is a yellow senecio while S. gerrardii and S. poseideonis (radiate plants) are both non-yellow senecios.

THE INTERRELATIONSHIPS OF THE SENECIOS OF GROUP C

## CLUSTER ANALYSIS

This group contains five smaller groups which are composed entirely of non-yellow senecios. This correlation exists in groups C3, C4, C6, C7 and C8.

Group C1

Group C1 (Fig. 41), consists of three moderately closely allied senecios (corr. = 0,57): S. purpureus (no. 22), S. natalicola (no. 48) and S. hieracioides (no. 50). Within this group S. natalicola and S. hieracioides are more closely allied to each other (corr. = 0,68) than they are to S. purpureus (corr. = 0,57). Note that S. purpureus is a non-yellow senecio while S. natalicola and S. hieracioides are both

yellow senecios. Hilliard (1977) mentions that S. natalicola has a strong resemblance to S. ingeliensis (no. 47) of group C2. This study lends some support to this view, for while these two species are not closely allied, they do have a distinct affinity to each other for they are clustered in adjacent groups which are allied (corr. = 0,40).

### Group C2

The six species of group C2 (Fig. 41) are moderately closely allied and they form three distinct allied pairs, these being: S. hastatus (no. 43) and S. mooreanus (no. 57) (corr. = 0,72), S. hirsutilobus (no. 46) and S. ingeliensis (no. 47) (corr. = 0,71) and S. asperulus (no. 55) and S. hypochoerideus (no. 56) (corr. = 0,76). Hilliard (1977) suggests that S. mooreanus and S. hypochoerideus are closely allied. This study supports this view although I think their affinity is less close than suggested by Hilliard (1977), as indicated by their correlation (corr. = 0,50). Hilliard (1977) also suggests that S. asperulus and S. hypochoerideus are closely allied, this relationship being supported by this study as their correlation suggests (corr. = 0,76).

### Group C3

Group C3 (Fig. 41), contains S. erubescens var. crepidifolius (no. 24B), S. erubescens var. dichotomus (no. 24D) and S. macrocephalus (no. 36) all of which exhibit a moderately close affinity for each other (corr. = 0,72). The composition of this group is most interesting for it contains only two of the four varieties of S. erubescens (no. 24), the remaining two varieties, S. erubescens var. erubescens (no. 24A) and

S. erubescens var. incisus (no. 24C) are clustered in group C10 and C6 respectively. Senecio erubescens var. crepidifolius and S. erubescens var. dichotomus appear to be only moderately closely allied (corr. = 0,79) although their taxonomic position suggests otherwise. The moderate affinity between these two varieties and S. macrocephalus (corr. = 0,72) possibly indicates their degree of cladistic relationship.

The occurrence of the aforementioned varieties in more than one group suggests that these taxa may be more distinct than their current taxonomic position implies. Note too that groups C3, C6 and C10 are only distantly allied (corr. = 0,21 & 0,12 respectively). However, considerably more material of S. erubescens needs to be investigated to enable this suggestion to be tested.

#### Group C4

Senecio sandersonii (no. 25), S. dregeanus (no. 76) and S. glanduloso-lanosus (no. 26) of group C4 (Fig. 41) are moderately allied (corr. = 0,50). The affinity between these three species is interesting since S. sandersonii is thought to have a distribution restricted to northern Natal, while S. glanduloso-lanosus appears to be restricted to southern Natal. Senecio dregeanus appears to have a distribution which is partially sympatric with the distribution patterns of S. sandersonii and S. glanduloso-lanosus. Thus, the affinity between these three species possibly reflects their degree of cladistic relationship.



It is interesting to note that the senecios of group C3 and C4 are clearly allied (corr. = 0,38), for some members of these groups (vars. 24B & 24D; spp. 25 & 26) are often named "Senecio erubescens", apparently because of their similar facies (Hilliard, 1977). However, the species descriptions of the above senecios (Hilliard, 1977), and the results of this study, indicate that "Senecio erubescens" consists of more or less clearly defined entities (spp. 24-34, Hilliard, 1977).

#### Group C5

Group C5 (Fig. 41) consists of S. barbatus (no. 37), S. caudatus (no. 81) and S. heliopsis (no. 85), all of which exhibit a moderately close affinity for each other (corr. = 0,55). Hilliard (1977), suggests that S. barbatus is allied to S. macrocephalus (no. 36). However, this study suggests that S. barbatus is more closely allied to S. caudatus and S. heliopsis although the senecios in group C5 are distantly allied (corr. = 0,30) to the senecios of group C3 which contains S. macrocephalus. Senecio caudatus and S. heliopsis are frequently confused (Hilliard, 1977), however, these two species appear to be only moderately allied (corr. = 0,55), despite some apparent similarities in their facies. Their habitat preferences are also quite distinct (Hilliard, 1977). It is interesting to note that S. barbatus is a non-yellow discoid senecio while the other two species are yellow and radiate.

#### Group C6

Senecio erubescens var. incisus (no. 24C), S. rhyncholaenus (no. 41), S. arabidifolius (no. 40) and S. subrubriflorus (no. 42) of group C6

(Fig. 41), are moderately to closely allied. These four senecios are also all non-yellow and discoid. The occurrence of S. erubescens var. incisus in this group is most interesting and the possible significance of this occurrence has been commented on earlier. The high affinity between S. erubescens var. incisus and S. rhyncholaenus (corr. = 0,85) is also significant for specimens of these two taxa have been confused (Hilliard, 1977). This high affinity possibly reflects the degree of cladistic relationship between these two senecios. Senecio subrubriflorus is reported to be frequently confused with S. rhyncholaenus (Hilliard, 1977) due to a similarity in facies. However, the descriptions of these two species (Hilliard, 1977) and the results of this study render them clearly separable but still moderately allied (corr. = 0,47). Note that S. arabidifolius is also allied to S. subrubriflorus (corr. = 0,47) and exhibits greater sympatry with S. subrubriflorus than with S. rhyncholaenus (Hilliard, 1977).

#### Group C7

Group C7 (Fig. 41), which contains four non-yellow discoid senecios and one non-yellow radiate senecio, is subdivided into groups C7a and C7b. Group C7a consists of S. variabilis (no. 27), S. glanduloso-pilosus (no. 29) and S. umgeniensis (no. 28), while group C7b consists of S. subcoriaceus (no. 30) and S. speciosus (no. 35). Senecio variabilis and S. glanduloso-pilosus appear to be closely allied (corr. = 0,78), while these two species appear to be moderately allied to S. umgeniensis (corr. = 0,57). Senecio subcoriaceus and S. speciosus appear to be moderately allied (corr. = 0,62). Hilliard (1977) suggested that S. speciosus is allied to S. macrocephalus, but I think that the

affinity between S. speciosus and S. subcoriaceus, as suggested in this study, is more appropriate.

Senecio variabilis has been confused with S. erubescens and S. variabilis, S. umgeniensis, S. glanduloso-pilosus and S. cathcartensis have been termed "Senecio erubescens" by various collectors due to their difficulty in distinguishing distinct entities in the "Senecio erubescens" group (Hilliard, 1977). However, the descriptions of these species (Hilliard, 1977) and the results of this study indicate that while some of the species in the "Senecio erubescens" group (spp. 24-34) are moderately allied they are nevertheless clearly distinct. This study also suggests that the species in the "Senecio erubescens" group (spp. 24-34) are less polymorphic than has been suggested (Hilliard, 1977), for they are clustered in several groups which, collectively, are distantly allied.

#### Group C8

Senecio anomalochrous and S. discodregeanus of group C8 (Fig. 41) appear to be only moderately allied (corr. = 0,51), despite the confusion that can occur when trying to discriminate between these two species on the basis of facies (Hilliard, 1977 & personal observation). The relationship between these two species suggests that their cladistic relationship is more distant than their facies suggest.

#### Group C9

Group C9 (Fig. 41), consists of S. consanguineus (no. 51), S. affinis (no. 64) and S. lydenburgensis (no. 65). Senecio affinis and

S. lydenburgensis of group C9a, appear to be fairly closely allied (corr. = 0,71), but are relatively distantly allied to S. consanguineus (corr. = 0,32). The relationship between these three species is rather interesting for, while the facies of S. consanguineus are dissimilar to those of S. affinis and S. lydenburgensis, these species do appear to be distantly allied (corr. = 0,32). The occurrence of these three species in this group possibly reflects their degree of cladistic relationship and also possibly indicates the degree of cladistic relationship between these species and the remaining species investigated. It is also interesting to note that these three species show some sympatry (Hilliard, 1977).

The affinity between S. affinis and S. lydenburgensis is possibly an example of moderately similar genotypes expressing themselves in similar phenotypes, since the facies of these two species closely resemble each other. This possibly relatively direct relationship between phenotype and genotype does not appear to be very common among the senecios investigated in this study.

#### Group C10

Senecio paludaffinis (no. 63), S. coronatus (no. 74) and S. praeteritus (no. 73) of group C10a (Fig. 41) appear to be clearly allied (corr. = 0,55) but appear to be somewhat distantly allied to the remaining member of group C10, S. erubescens var. erubescens (no. 24A). Senecio paludaffinis appears to be clearly allied to S. coronatus (corr. = 0,70), while the two aforementioned species appear to be moderately allied to S. praeteritus (corr. = 0,55). Hilliard (1977)

mentions that S. praeteritus can be confused with S. brevidentatus (no. 72). However, this study indicates that S. praeteritus and S. brevidentatus (group C11) are only distantly allied (corr. = 0,20).

The occurrence of S. erubescens var. erubescens in group C10 is most interesting for it is far removed from the other varieties of S. erubescens and the other species comprising "Senecio erubescens" (Hilliard, 1977). I suggest that the occurrence of S. erubescens var. erubescens in this group is possibly a more accurate indication of its affinities as well as indicating that its taxonomic position needs to be reviewed.

#### Group C11

Senecio brevidentatus (no. 72) and S. mauricei (no. 82) of group C11 appear to be somewhat distantly allied (corr. = 0,40). These two species, while being allied to the remaining species of group C11, only appear to be distantly allied to these species (corr. = 0,36). Hilliard (1977) suggests that S. mauricei is allied to S. caudatus (no. 81). However, according to this study, S. caudatus (group C5) appears to be only remotely allied to S. mauricei (corr. = 0,13). This is possibly another example of similar facies falsely indicating affinity.

Senecio macrospermus (no. 75), S. saniensis (no. 83) and S. albanensis var. doroniciflorus (no. 86) of group C11a, appear to be moderately allied (corr. = 0,51), while S. macrospermus and S. saniensis appear to be clearly allied (corr. = 0,72). The relationship between S. macrospermus and S. saniensis is most interesting. Senecio

macrospermus occupies habitats between c. 2 500 m and 3 000 m above sea level (Hilliard, 1977) and it occurs between these altitudes on Sani Pass (Natal), while S. saniensis is known only from the summit of Sani Pass (c. 3 000 m) (Hilliard, 1977 & personal observation). Thus the distribution of S. saniensis coincides partially with the distribution of S. macrospermus on Sani Pass. Perhaps the apparent limited distribution of S. saniensis and the affinity between S. macrospermus and S. saniensis, reflects the degree of the cladistic relationship between these two species.

The moderate affinity between S. macrospermus, S. saniensis and S. albanensis var. doroniciflorus (corr. = 0,51) is also interesting for the two former species occupy montane habitats while S. albanensis var. doroniciflorus occupies predominantly coastal and near coastal habitats. The occurrence of these three senecios in this group possibly reflects their degree of cladistic relationship and also possibly indicates the degree of cladistic relationship between these senecios and the remaining senecios investigated.

#### 'Group C12'

'Group C12' consists of a solitary member, S. inornatus s. str. (no. 88). The very distant relationship of S. inornatus to the remaining members of group C is most interesting (corr. = 0,05), for it is a very widespread species occurring from the eastern Cape to Zambia, Malawi and Tanzania (Hilliard, 1977). Perhaps its distant affinity with the remaining senecios of group C indicates that its affinity may lie with some senecios of tropical east Africa.

In conclusion, it is interesting to note that the majority of the homochromous non-yellow senecios recorded in the Natal flora (Hilliard, 1977) are clearly allied with most of the senecios of group C but that they are nevertheless, in many instances, apparently only distantly allied to each other. The majority of the heterochromous non-yellow senecios, which are predominantly restricted to the Cape, are clearly allied to the senecios of group A, many of these senecios having affinities with the non-southern African senecios investigated. This suggests that the Cape heterochromous senecios are only distantly related to the homochromous non-yellow senecios which are most common in Natal. Similarly, the majority of the yellow senecios of Natal appear to be distantly related to the non-southern African senecios, as indicated by their distribution over groups A, B and C (Fig. 41). The majority of these Natal yellow senecios being clustered in groups B and C, while group A contains all the non-southern African senecios and only a few (8) Natal yellow senecios.

#### PRINCIPAL COMPONENTS ANALYSIS OF THE SENECIOS IN GROUPS A, B AND C

Principal component analysis (PCA) of the thirty-five characters (Table 10) of all the members of Senecio s. str. (Table 12) was also performed. Both rotated and unrotated components of the PCA were produced. However, the rotated components resulted in essentially the same relationships in space and therefore are not presented. The PCA results (Figs. 42 & 43) were quite similar to those obtained in the cluster



analysis (Fig. 41). The PCA yielded eleven components with eigenvalues greater than one (74,3% of trace - Table 17), indicating that the characters are not highly correlated. Only the first component had an eigenvalue greater than 5 and accounted for 23,0% of the variance (Table 18). Component I has correlations greater than 0,5 for the following characters (in decreasing order of importance): ANDROECIUM (DISC): ANTHER BASE APPEARANCE (CHAR 104), LEAF TRICHOMES: APEX (CHAR 035), CALYCVULUS BRACTS: TRICHOMES (CHAR 063), LEAF TRICHOMES: BASE (CHAR 034), LEAF SHAPE: RADICAL (CHAR 016), LEAF VENATION: RADICAL (CHAR 024), LEAF TRICHOMES: APPENDAGES (CHAR 036), GYNOCICIUM (DISC): STYLE-ARM APICES (CHAR 095), INVOLUCRAL BRACTS: TRICHOMES (CHAR 054), DISC COROLLA: COROLLA SHAPE (CHAR 082), LEAF VENATION: CAULINE (CHAR 025), INVOLUCRAL BRACTS: SHAPE (CHAR 052) and LEAF SHAPE: CAULINE (CHAR 017) (Table 19). Component II has correlations greater than 0,5 for the following characters (in decreasing order of importance): ANDROECIUM (DISC): ANTHER LENGTH (CHAR 105), CYPSELA (DISC): LENGTH (CHAR 116), DISC COROLLA: COROLLA LENGTH (CHAR 081), FILAMENT COLLARS: BASAL WIDTH (CHAR 109) and PAPPUS SETAE (DISC): LENGTH (CHAR 126) (Table 19). Component III has no correlations greater than 0,5 and only five correlations above 0,3, these being for the following characters (in decreasing order of importance): PAPPUS SETAE (DISC): APEX (CHAR 129), LEAF SHAPE: CAULINE (CHAR 017), DISC COROLLA: LOBE APEX (CHAR 086), GYNOCICIUM (DISC): STYLE BASE (CHAR 097), FILAMENT COLLARS: LENGTH (CHAR 108) (Table 19).

Components I and II (Fig. 42) are especially helpful in illustrating the three reasonably distinct groups mentioned earlier (groups A, B & C -



Fig. 41). Component III does not show any clear grouping with respect to groups A, B and C. Some of the groups within groups A, B and C (Fig. 41), can also be distinguished in the PCA plots (Figs. 42 & 43), although in some cases they are not as clear as in the cluster analysis (Fig. 41) due to the 'compression' of the data into three components.

The plots of the PCA (Figs. 42 & 43) also illustrate that groups A and C are more compact than group B, indicating that the relationships amongst the senecios of groups A and C are moderately closer than those amongst the senecios of group B. This variation in the affinity between the senecios of each group is also illustrated in the cluster analysis (Fig. 41).

The spread of the senecios with respect to components I, II and III (Figs. 42 & 43) is considerable, illustrating that despite Senecio s. str. sensu Vincent, being a reasonably well circumscribed group (Figs. 36 & 37; chapter 5), it remains a very diverse group at the infrageneric level.

While a considerable amount of the phenotype of the senecios included in this study (Table 1), has been investigated (Table 10), two further aspects of the phenotype have also been investigated, namely; pollen morphology and chemical constituents (organic). The following chapter will review the interrelationships of all the taxa investigated (Table 1), as well as the proposed infrageneric interrelationships of the Natal, Cape and the non-southern African senecios (Table 12), in the light of the evidence from the palynological studies, while chapter 8 will review the aforementioned interrelationships in the light of the evidence from the chemical studies.

## CHAPTER SEVEN

## PALYNOLOGICAL STUDIES

INTRODUCTION

The light microscope studies of Stix (1960) and particularly the transmission electron microscope (TEM) studies of Skvarla and Turner (1966a, 1966b) and Skvarla et al. (1977), indicate that the pollen morphology of the Asteraceae appears to be reasonably consistent at the tribal level.

Considering the pollen morphology within the tribe Senecioneae, Stix (1960), described two pollen types, the Senecio-type and the Arnica-type. Skvarla et al. (1977), in a TEM study of pollen of 25 taxa of the Senecioneae, as circumscribed by Bentham (1873), noted the occurrence of the "Senecioid" structural pattern (Skvarla & Turner, 1966a) and the "Helianthoid" structural pattern (Skvarla & Turner, 1966a). In a study on Senecio, Skvarla et al. (1977) noted that the majority of the species investigated possess the "Senecioid" pattern but that a few species (e.g. S. heritieri DC.) are decidedly "Helianthoid".

Included in the taxonomic scheme for investigating the Senecio complex on a world-wide basis (Jeffrey et al., 1977), is the appearance of "the pollen grain surface and the pollen grain wall stratification". Initial scanning electron microscope (SEM) studies (Jeffrey et al., 1977) of material of Senecio, have revealed that the pollen grains of Senecio are

"uniformly tricolporate and echinate and vary only in the number, density and length/breadth ratio of the spines, and in the degree of prominence of the colpi." Further studies, using the TEM, have shown that the pollen grain walls "vary in thickness and structure, particularly in development and length of the collumellae and in the thickness and degree of elaboration of the foot layer of the ectoexine." (Jeffrey et al., 1977).

Some potential trends in the appearance of the pollen grain surface of several Senecio species have already been noted, with the comment that some fascinating data may have been obtained had this study been combined with TEM studies (J.J. Skvarla, pers. comm.).

This scanning electron microscope (SEM) study aimed at investigating the morphology of the pollen grains of all the taxa investigated (Table 1), with the view to reviewing the proposed relationships between these taxa in the light of the evidence derived from this study. A literature search revealed that pollen of none of the taxa had been investigated, with SEM. A very similar situation exists at the transmission electron microscope (TEM) level, for only one TEM study, which is unpublished (J.J. Skvarla, pers. comm.), included S. desfontainei (no. 217).

It is interesting to note that our knowledge of the pollen of the Asteraceae is predominantly restricted to TEM studies, for there is considerable TEM data but relatively little SEM data. The situation is usually reversed in other families.

### THE POLLEN MORPHOLOGY OF ALL THE TAXA INVESTIGATED

The data of the five pollen characters (Table 20), recorded for each of the taxa investigated (Table 1), are provided in Appendix C.

#### SHAPE OF POLLEN GRAINS

All the taxa studied (Table 1), have spheroidal pollen grains (Fig. 44) (Erdtman, 1969).

#### SPINULE FREQUENCY

The conical shaped spines forming the echinate appearance of the intercolpoid regions of the exine of the pollen grains are here termed spinules, since they are always shorter than 3  $\mu\text{m}$  (Erdtman, 1969).

The frequency of the spinules is referred to as being relatively high when there is very little space between the spinules (Fig. 44), while the frequency of the spinules is referred to as being relatively low when there is a noticeable amount of space between the spinules (Fig. 45).

The majority of the taxa studied (Table 1), have a relatively high frequency of spinules, while the following ten taxa have a relatively low spinule frequency: S. polyanthemoides (no. 5), S. hastatus (no. 43), S. lydenburgensis (no. 65), S. brevilorus (no. 118), S. viminalis (no. 119), S. fulgens (no. 122), S. lautus (no. 220), S. syringifolius (no. 223), Gynura auriculata (no. 227) and

Kleinia grandiflora (no. 228).

#### LENGTH/WIDTH (basal) RATIO OF THE SPINULES

The length/width (basal) ratio of the spinules ranged from 0,60 to 1,50 with the majority of the taxa having ratios in the range 0,80 to 1,00, indicating that, in the majority of the taxa, the spinules are very broad-based (Fig. 48) to moderately broad-based (Fig. 46). Note that the data of this character are not statistically derived.

#### PROMINENCE OF THE COLPI

All the pollen grains of all the taxa studied had three noticeably wide colpi (Fig. 44), these colpi traversing almost the entire polar length of the pollen grain. Each colpus also had a pore in the equatorial plane. These pollen grains are termed tri-colp-orate (Erdtman, 1969).

#### PERFORATIONS IN THE EXINE

Perforations are small circular holes piercing the exine surface (Fig. 47), and are only visible above X 2 500 using SEM (Salgado-Labouriau, 1982). Perforations are distinct from "cavities" (Felippe & Salgado-Labouriau, 1964) in that cavities can be observed in the spines in optical section using light microscopy. In this study, two

distribution patterns of the perforations were noted:

- (i). perforations frequent - [perforations around base of spinules and in between spinules].
- (ii). perforations not frequent - [perforations appear restricted to bases of spinules].

The observation that some taxa appear to have perforations restricted to the bases of the spinules is possibly incorrect, for unacetolysed pollen grains were viewed in all instances. Consequently, it is quite possible that sporopollinin could be obscuring the perforations between the bases of the spinules, particularly if they are smaller than the perforations around the bases of the spinules (Fig. 47). This distinction was observed in most taxa.

An example of this inaccuracy is seen in the observations of S. desfontainei with SEM and TEM. The SEM observations of unacetolysed pollen show an absence of perforations between the majority of the spinules in view, except between those on the edge of the colpus (Fig. 48). On the other hand the TEM observations (J.J.Skvarla, pers. comm.), of an intercolpoid region of the exine of acetolysed pollen, clearly shows the presence of perforations between the spinules (Fig. 49).

#### OTHER OBSERVATIONS

The exine, of the pollen grains of all the taxa studied, has a rough relief between the spinules (Fig. 47) and in the colpi (Fig. 44). This rough relief usually stops at the bases of the spinules but in some

instances extends a little distance above the bases of the spinules. The distal ends of the spinules are entire and smooth and their apices are obtuse (Fig. 47).

### CONCLUSIONS

The pollen grains of all the taxa investigated in this study (Table 1), are spheroidal, uniformly tri-colp-orate ( $\equiv$  tricolporate) and echinate, the echinate appearance being formed by spinules. The exine between the spinules is perforate and the perforations around the bases of the spinules are appreciably wider than those between the bases of the spinules. The surface of the exine between the spinules has a rough relief while the surface of the spinules is smooth. The distal ends of the spinules are entire and their apices are obtuse. The external morphology of the pollen of these taxa varies only in the frequency of the spinules and the length/width (basal) of the spinules. No trends are evident amongst the characters observed, with respect to the taxa studied.

These observations concur with most of those of Jeffrey et al. (1977) and lend support to the view that the pollen morphology of the Asteraceae appears to be reasonably consistent at the tribal level (Stix, 1960; Skvarla and Turner, 1966a, 1966b; Skvarla et al., 1977).

The evidence from this study indicates that the pollen morphology of the taxa studied (Table 1), is reasonably consistent at the tribal level (Senecioneae), with very little infratribal variation. Consequently, the evidence from this study neither contradicts nor supports the

proposed infrageneric interrelationships, with respect to the Natal members of Senecio s. str. sensu Vincent (Table 12). The evidence also neither contradicts nor supports the proposed interrelationships between the Natal, the Cape and the non-southern African members of Senecio s. str. sensu Vincent (Table 12), which were detailed earlier in this dissertation.



## CHAPTER EIGHT

## PHYTOCHEMICAL REVIEW

[Terpenes and Pyrrolizidine alkaloids]

INTRODUCTION

Our understanding of the chemical pattern of the tribe Senecioneae is relatively well known with respect to two classes of compounds; sesquiterpenes (Robins, 1977a; Seaman, 1982), and pyrrolizidine alkaloids (Robins, 1977b; Robins, 1982). However, there is a paucity of information on the occurrence and distribution of terpenes (other than sesquiterpenes), flavonoids and macromolecular constituents (Robins, 1977b).

While some of the genera of the Senecioneae synthesize sesquiterpene lactones, the continuing extensive survey of Bohlmann and associates (e.g. Bohlmann *et al.*, 1979), reveals that the furanoterpenes and biogenetically related skeletal types are the dominant class of terpenes in the Senecioneae (Seaman, 1982). The pyrrolizidine alkaloids together with these furanosesquiterpenes set the tribe apart chemically from the other tribes in the Asteraceae (Seaman, 1982).

The recent revisionary treatment by Nordenstam (1977), of the Senecioneae paid attention to the generic and subtribal boundaries. On the basis of anatomical and cytological evidence, this treatment resulted in the genera of the tribe being grouped into the "Cacalioid"

complex of genera and the "Senecionoid" complex of genera (Nordenstam, 1977).

A comparison of the chemistries of the Cacalioids and the Senecionoids reveals that, although the two groups of genera are linked by the presence of furanoeremophilanes, the Cacalioids produce a greater proportion of sesquiterpene lactones (eremophilanolides and bakkenolides) and fewer aromatic furanoeremophilane compounds than is found in the Senecionoids (Seaman, 1982). The Senecionoids tend to produce, almost exclusively, furanoeremophilanes which is in sharp contrast to the Cacalioid pattern (Seaman, 1982). Bohlmann *et al.* (1979) found large groups of taxa of the "Senecionoid" complex which lack furanoeremophilane chemistries.

#### TERPENES AND PYRROLIZIDINE ALKALOIDS IN SENECIO

Senecio L. appears to be a chemically homogenous assemblage of taxa, almost exclusively producing furanoeremophilane compounds, there being only occasional reports of eremophilanolides (Seaman, 1982). Patterns of chemical variation within Senecio are not readily apparent (Seaman, 1982). However, a number of the South African species of Senecio (*sensu* Jeffrey *et al.*, 1977; Jeffrey, 1979) produce almost exclusively aromatic furanoeremophilanes in contrast to other groups of Senecio which produce mostly non-aromatic furanoeremophilanes (Bohlmann *et al.*, 1979).

While the occurrence of pyrrolizidine alkaloids in the tribe Senecioneae sets this tribe apart from the remaining tribes of the Asteraceae, pyrrolizidine alkaloids occur most frequently in Senecio (Robins, 1982).

The continuing chemical survey of Senecio, principally by Bohlmann and his associates, is continuing to improve our understanding of the chemical constituents of the members of Senecio (sensu Jeffrey et al., 1977; Jeffrey, 1979).

#### TERPENES AND PYRROLIZIDINE ALKALOIDS IN THE SENECIOS INVESTIGATED IN THIS STUDY

A summary of the known distribution of the sesquiterpene and pyrrolizidine constituents of the senecios investigated in this study, is given in Table 21. This includes the most recent work of Bohlmann et al. (1984a) and Bohlmann et al. (1984b).

Our knowledge of the terpene and pyrrolizidine chemistry of Senecio, has increased considerably since the reviews by Robins (1982) and Seaman (1982). This is particularly true of the senecios of southern Africa. The chemistry of many of the senecios investigated in this study is characterised by the presence of furanoeremophilanes, while eremophilanes, the precursors to furanoeremophilanes, are also found in a number of the senecios. The occurrence of eremophilanes is particularly associated with a number of non-yellow senecios. Various pyrrolizidine alkaloids are also found in many of the senecios, while

some senecios, which were specifically tested for the presence of pyrrolizidine alkaloids, did not contain any. Note too that some senecios appear to only synthesise pyrrolizidine alkaloids (Table 21).

#### AN EVALUATION OF THE PROPOSED INTERRELATIONSHIPS OF THE SENECIOS INVESTIGATED

To utilise the information on the terpene and pyrrolizidine constituents of the senecios investigated in assessing phenetic relationships, this information must be in the form of analytic characters (Davis & Heywood, 1963). This approach has been used by Seaman (1982), with respect to sesquiterpene lactones of Ambrosia L., with varying degrees of success. Analytic characters are used for the identification, characterization and delimitation of taxa, while synthetic characters are used to group elements into higher taxa and are usually characters of a constant, widely-occurring nature (Davis & Heywood, 1963). Major skeletal types of compounds can be considered as synthetic characters, their use being at relatively high levels of the taxonomic hierarchy. Conversely, a taxon-specific chemical complement would be an example of an analytic character (Seaman, 1982). There is no inherent difference between analytic and synthetic characters, the difference between these two characters lies in their particular usage.

This review of the terpene and pyrrolizidine chemistry of the senecios investigated, illustrates how our knowledge at or near the level of analytic characters is far from complete. We have, however, definitely progressed from the synthetic level of character use, which was the

situation when the chemistry of the Asteraceae was reviewed by Hegnauer (1977) and Mabry and Bohlmann (1977) and the chemistry of the tribe was reviewed by Robins (1977b). The chemical survey of the Senecioneae and particularly with respect to Senecio by Bohlmann and his associates, is contributing to our knowledge of the chemical pattern within genera of this tribe and more specifically, to our knowledge of the chemical complement of individual taxa in Senecio. However, because of the lack of information on the chemical complement of quite a large number of taxa of Senecio sensu Vincent, the possibility of using this information at the analytic level is premature. Consequently, the relationships between the members of Senecio sensu Vincent, described in chapter 6 of this dissertation, cannot be evaluated in the light of their individual chemical complement of terpenes and pyrrolizidine alkaloids because of the many instances in which this information is lacking.

#### AN HYPOTHESIS OF THE CHEMICAL EVOLUTION IN THE TRIBE SENECEONEAE

Jeffrey (1979) noted that the most similar species, in his three major series of the tribe Senecioneae, are perennial mesophytic herbs and proposed that this was the ancestral life-form of the tribe, one that is highly vulnerable to grazing and browsing by insects and mammals. The occurrence of furanoterpenes and pyrrolizidine alkaloids in these species, as a chemical defense mechanism, is thought to be a response to this predation (Jeffrey, 1979).

Bohlmann et al. (1979) and Jeffrey (1979) have proposed that chemical evolution has proceeded along two routes within the tribe. The first route leading to an elaboration of more complex structures (e.g. highly oxidised furanoeremophilanes and bakkenolides) by means of extension of synthetic ability. The second route leading to an overall structural simplification through the reduction or loss of the capacity to synthesize such complex eremophilane structures as furanoeremophilanes and eremophilanolides.

The elaboration of more complex structures by means of extension of synthetic ability, may be seen as a selective response to the putative evolution of tolerance by predators which is presumed to be an ongoing process of mutual response which is possibly responsible for; the diversity of substances, the frequent limitation of particular compounds to groups of apparently very closely related species, the frequent diversity within groups of apparently related species, and the abundant independent development of the same substances in different evolutionary lines (Jeffrey, 1979).

Loss of such biosynthetic capacity, on the other hand, may be compensated by increased synthetic activity involving other natural products such as alkaloids and is associated with divergence from the putative ancestral habit (Jeffrey, 1979). The development of growth forms which are possibly less subject to grazing or browsing pressure, such as: annuals, climbers, succulents and tough-leaved perennials, seems to be associated with the reduction or loss of this biosynthetic capacity (Jeffrey, 1979). The loss of pyrrolizidine alkaloid synthesis

has also been noted to be associated with the divergence from the perennial herbaceous habit, the energy saved possibly being used in other ways more selectively advantageous in the environment occupied (Jeffrey, 1979).

#### THE APPLICATION OF THE HYPOTHESIS OF THE CHEMICAL EVOLUTION IN THE TRIBE TO SENECIO SENSU VINCENT

The hypothesis of Bohlmann et al. (1979) and Jeffrey (1979) concerning the chemical evolution in the tribe, appears to have some support within Senecio sensu Vincent.

In those senecios whose terpene and pyrrolizidine chemistry has been investigated (Table 21), there is a distinct association between the occurrence of elaborated sesquiterpene structures and pyrrolizidine alkaloids and a perennial habit (Character 008, Appendix A & B). However, there are a number of senecios which are annuals, which also synthesise elaborated sesquiterpene structures and pyrrolizidine alkaloids (e.g. S. polyanthemoides (no. 5), S. pterophorus (no. 6), S. elegans (no. 204) and S. viscosus (no. 212)). This association is in conflict with the aforementioned hypothesis. On the other hand S. vulgaris (no. 210) and S. desfontainei (no. 217), which are both annuals, do not appear to synthesise elaborated sesquiterpenes but have maintained the ability to synthesise pyrrolizidine alkaloids. This association does support the hypothesis. Note too that S. brachypodus (no. 107) and S. pleistocephalus (no. 108), which are both succulent, synthesise germacrenes and eudesmanes respectively. This association

between a succulent habit and apparent decrease in synthetic ability also supports the hypothesis. Senecio mikanioides (no. 109), which is also more or less succulent, appears to have lost much of its ability to synthesise elaborated sesquiterpenes, but has retained the ability to synthesise pyrrolizidine alkaloids, these alkaloids being rather special in configuration (Robins, 1982; Bohlmann, pers. comm.). This association also supports the hypothesis. It is also interesting to note that S. deltoideus (no. 110), which I accept as being a member of Senecio s. str. sensu Vincent, is a scrambler and associated with this habit is the synthesis of acetylenes and cholinesters. This association supports the aforementioned hypothesis. Senecio bupleuroides (no. 97), S. glaberrimus (no. 101), S. latifolius (no. 102) and S. retrorsus (no. 103), which are all perennials, produce pyrrolizidine alkaloids of various configurations and do not appear to synthesise any sesquiterpenes (Bohlmann, pers. comm.). According to the hypothesis, this loss of sesquiterpene synthesis is often associated with tough-leaved perennials. However, none of the aforementioned senecios are tough-leaved.

The hypothesis of Bohlmann et al. (1979) and Jeffrey (1979) concerning the chemical evolution in the tribe Senecioneae, has considerable support within Senecio sensu Vincent, however, there are a number of instances which do not support the hypothesis.

The continued production of pyrrolizidine alkaloids in some herbaceous perennial senecios (S. bupleuroides, S. glaberrimus), despite the apparent loss of their biosynthetic capacity to synthesise complex



structures (e.g. highly oxidised furanoeremophilanes), possibly indicates another defence strategy. This defence strategy, which is possibly peculiar to the southern African senecios, could be in response to a possibly more severe predatory environment, than is found in other environments inhabited by senecios. Seeing that pyrrolizidine alkaloids are potentially more lethal than sesquiterpenes, perhaps the maintenance of the capacity to produce pyrrolizidine alkaloids is of primary importance to these senecios, the loss of the capacity to synthesise complex structures being incidental.

The elucidation of the chemical complement of the remaining southern African members of Senecio s. str. sensu Vincent, will indicate whether or not the finer details of the aforementioned hypothesis will require modification so as to accommodate this possibility.

#### PHYTOCHEMISTRY AND PHYLOGENY/DISTRIBUTION OF SENECIO

Glennie et al. (1971) described correlations between flavonoid chemistry and plant geography which occur in the Senecio radicans complex. These correlations, while they contributed little to solving the taxonomic problems in the Senecio radicans complex, were used to study the origins and distribution patterns of members of this complex. No obvious correlations were found between flavonoid chemistry and cytological and morphological patterns.

It is unfortunate that the chemical pattern, with respect to terpenes and pyrrolizidine alkaloids, is unknown for so many of the senecios

investigated in this study, for correlations between chemical constituents (particularly flavonoid chemistry) and plant geography occur in many plant groups (Moore et al., 1970).

While the flavonoid pattern is unknown amongst the senecios investigated, except amongst the Senecio radicans complex, the long-term possibility of the chemical pattern within Senecio being used to elucidate its origins and distribution patterns of its members is most stimulating.

## CHAPTER NINE

## DISCUSSION

The very variable generic and sectional concepts employed by different authors in Senecio, have made it virtually impossible to give definitive answers regarding the correct names of many species. While portions of Senecio have been investigated (e.g. Harvey, 1865; Barkley, 1978), these attempts to improve the taxonomy of Senecio have resulted in inconsistent treatments. These inconsistencies are primarily due to the authors confining their studies to plants of particular geographical areas. Consequently, no classification applicable on a world-wide basis has been produced for Senecio.

Jeffrey et al. (1977) responded to this very unsatisfactory situation by developing a universally applicable scheme to stop the perpetuation of the very variable generic and sectional concepts employed by different authors in the Senecio complex. This scheme aimed at providing a "uniform criterion" throughout the Senecio complex, against which all available evidence might be evaluated and consistent systematic conclusions drawn. The scheme was not aimed at producing a definitive classification.

The scheme consisted essentially of investigating selected members of the Senecio complex with respect to characters which are easily and readily observable, this complement of characters being as follows:

"Easily observed characters exhibited by the surfaces of the cypselas, the pappus, the style-arm apices, the anther-collars, the anther-bases, the ray florets and the abaxial surfaces of leaves". Data thus obtained were supplemented, when considered necessary, by study of the "vegetative habit, leaf shape, venation and attachment, flower colour, inflorescence type, involucre type, the endothelial (exothelial) cell thickenings, the pollen grain surface, the pollen grain wall stratification, the configuration of the stigmatic surfaces and, when available, by chromosome numbers, obtained from the compilations of Fedorov (1969), Moore (1973) and occasionally other sources."

The selection of species, of which the above characters were studied, was made on the basis of existing taxonomic treatments and on the basis of some fifteen years working knowledge of the group.

The results of the application of the aforementioned scheme demonstrated that the extent of the variation within Senecio was far too great to be accommodated within a single genus and in fact, exceeded the combined ranges exhibited by species currently referred to several other genera (Jeffrey et al., 1977). However, the existence of discontinuities in character state syndromes has made taxonomic division of the world-wide Senecio complex possible. This is despite the absence of absolute

discontinuities in particular characters (Jeffrey et al., 1977).

The application of this "uniform criterion" to the world-wide collections of the Senecio complex at Kew, resulted in the division of this complex into sixteen groups (groups I-XVI) and indicated that the name Senecio should be applied only to species of group IX, within which the type of the genus, S. vulgaris L., falls (Jeffrey et al., 1977). Jeffrey et al. (l.c.) suggested that the remaining groups (groups I-VIII and XVI) might be distinct genera, possibly new or possibly congeneric with other widely recognized genera in the Asteraceae.

While there are problems in the generic delimitation of groups I-VIII and X-XVI, the problems are most acute in group IX, which is the largest in the tribe and which contains the Senecio complex (Jeffrey, 1979)

In 1979, Jeffrey (1979) re-evaluated the aforementioned grouping in the light of further evidence from pappus, numerical, chemical and succulent plant studies, and modified the original concepts. The original group IX was subdivided into the "Eusenecionoids" (group IX [a]), part of which contains Senecio (sensu Jeffrey), and the "Gynuroids" (group IX [b]).

It is clear that the only sound approach to elucidating the generic concept of Senecio L., is to mount a detailed species-by-species comparative study on the members of Senecio (sensu Jeffrey, group IX [a]), working outwards from S. vulgaris, the type of the genus and one of the most specialized members of the tribe.

This study of the interrelationships of some members of Senecio in Natal necessitated the investigation of the generic concept of Senecio. The approach taken in this aspect of the study was, by implication, to include the type species S. vulgaris. Also included in the study were a number of Cape heterochromous senecios and a number of non-southern African senecios thought to be closely related to S. vulgaris (Table 1). A number of species from genera closely allied to Senecio were also included in the study, to enable an understanding to be gained of the character variation outside Senecio.

The data obtained from each of the taxa investigated, for a large number of characters (Table 2), enabled a large proportion of the phenotype to be evaluated with respect to the selection of taxonomically significant ("good") characters (Davis & Heywood, 1963) for the evaluation of the generic concept of Senecio.

This evaluation resulted in the following six characters being selected for the elucidation of the generic concept of Senecio (see Table 4):

- (i). The appearance of the style-arm apices of the disc florets (CHARACTER 095).
- (ii). The appearance of the anther apex (CHARACTER 103).
- (iii). The cell wall configuration of the endothelial tissue (CHARACTER 107)
- (iv). The length of the filament collars (CHARACTER 108).
- (v). The shape of the filament collars (CHARACTER 110).
- (vi). The shape of the disc cypselas (CHARACTER 117).

The circumscription of Senecio according to these six characters results in the majority of the senecios studied being congeneric with Senecio sensu Vincent, with 10 senecios being regarded as peripheral (satellite) senecios while 4 senecios are excluded from Senecio sensu Vincent (Table 5).

My generic concept of Senecio described in chapter 4 of this dissertation, delimits a natural assemblage within Senecio sensu stricto. While this concept also supports many of the suggestions of Jeffrey et al. (1977) and Jeffrey (1979) regarding the limits of Senecio s. str. (sensu Jeffrey), it also indicates that the concept of Senecio held by Jeffrey et al. (1977) and Jeffrey (1979) could still be too broad. The concept also supports some of the suggestions by Nordenstam (1978) on characters he has perceived as being characteristic of Senecio s. str.

Jeffrey and Chen (1984) have recently described the Senecio flora of eastern Asia and on the basis of their improved understanding of the generic limits of Senecio, they suggest that Senecio perhaps comprises approximately 1 000 species world-wide. This is a noticeable decrease from the estimates of Nordenstam (1977) [1 500 spp.] and Jeffrey et al. (1977) [3 000 spp.]. However, Jeffrey and Chen (1984) do mention that the "generic limits in many areas are still uncertain". Jeffrey and Chen (1984) also point out that, according to their circumscription, "Senecio is undoubtedly a basic, paraphyletic group in the subtribe, but it has not yet been sufficiently well-studied for its splitting into

firmly-based, probably monophyletic entities to be possible."

The application of my concept to the Senecio flora of eastern Asia, as recently described by Jeffrey and Chen (1984), suggests that here too it is able to circumscribe this assemblage of senecios into a more homogenous group than is currently contained in the Senecio flora of eastern Asia. However, I must emphasise that this judgement is based solely on their comprehensive descriptions, which contain information on the characters pertinent to my generic concept.

It is obvious that my concept needs to be tested on further representatives of Senecio from many more areas of its cosmopolitan distribution, before any of the consequences resulting from the application of this concept are put forward in new taxonomic delimitations. Nevertheless, it is encouraging to see that the application of this concept appears to be meeting the need of circumscribing the currently heterogeneous assemblage of Senecio in Natal into a more homogenous group.

Perhaps the application of my concept of Senecio to further representatives of Senecio from many more areas of its cosmopolitan distribution, will suggest that Senecio sensu Vincent is monophyletic. However, it must be remembered that a taxonomic system in practice will always remain a hypothetical reflection of phylogeny.

Note too that my concept of Senecio clearly indicates that the Cape heterochromous non-yellow senecios and the non-southern African senecios



(nos. 200-220, Table 1) are all members of Senecio s. str., according to my circumscription of Senecio. The concept also unequivocally indicates that S. cissampelinus, S. transvaalensis, S. syringifolius and S. hockii should be excluded from Senecio sensu Vincent (Table 5). These exclusions have considerable support from Hilliard (1977, 1978), Jeffrey (1979) and Jeffrey (C. Jeffrey, pers. comm.).

The inclusion of an additional thirty-one taxonomically significant characters to the six characters of generic importance, made it possible to define the limits of Senecio sensu lato sensu Vincent. The analysis of the senecios subsequent to the application of my generic concept (Table 11), with respect to this larger set of characters (Table 10), resulted in the number of peripheral senecios (Table 11) being reduced from 10 to 3, the remaining senecios being excluded from Senecio sensu Vincent (Table 13).

Attention was drawn, in chapter 5, to the apparent dendritic shape of the concept of Senecio sensu lato sensu Vincent. This dendritic shape accommodated 10 senecios which were judged to be peripheral senecios according my concept of Senecio sensu stricto (Table 6). However, I have mentioned that the number of peripheral senecios is reduced to 3 when the analysis includes many more characters. Consequently, the dendritic shape is altered but the peripheral senecios (S. tanacetopsis, S. seminiveus & S. breviflorus) still appear to be allied to varying degrees to the groups of Senecio s. str., as indicated in Table 6.

An analysis of the relationship of these 3 peripheral senecios to the

members of Senecio s. str., using the larger number of characters (Table 10), indicates that S. tanacetopsis and S. seminiveus, which are clearly allied to each other, are also clearly allied to S. achilleifolius. However, S. breviflorus, which originally showed affinity to the senecios of groups X and XI (Table 6) appears to have more affinity with S. urophyllus, S. scitus, S. latifolius and S. retrorsus, when compared with these latter senecios with respect to the 37 characters (Table 10). Nevertheless, this affinity appears relatively distant.

Subsequent to my circumscription of the generic concept of Senecio sensu stricto and sensu lato, estimates were made of the phenetic affinities between the Natal members of Senecio s. str. sensu Vincent (Table 12) and of the phenetic affinities between all the members of Senecio s. str. sensu Vincent (Table 12). These estimates were with respect to the thirty-seven taxonomically significant characters (Table 10).

Numerical cluster analyses of these members of Senecio s. str. sensu Vincent (Table 12), with respect to these 37 characters, indicates that the majority of the Natal senecios, while being clearly members of Senecio s. str. sensu Vincent, are distinct from virtually all the Cape and non-southern African senecios investigated. Furthermore, many of the non-yellow senecios form clearly allied groups which are distinct from the groups (clusters) composed of yellow senecios (Fig. 41).

In chapter 6 of this dissertation, comparisons were made between my estimate of phenetic similarity between certain senecios and those of Hilliard (1977). An example of this is seen in my estimate of phenetic

similarity between S. bupleuroides, S. urophyllus, S. scitus and S. glaberrimus (Fig. 41) and Hilliard's estimate of phenetic similarity between these aforementioned species. Hilliard (1977) estimates that these senecios are clearly allied. However, my estimate of their phenetic similarity suggests that these senecios are more clearly allied to other senecios than to each other (see chapter 6 & Fig. 41).

The hypothesis of nonspecificity states that there are no distinct large classes of genes affecting exclusively one class of characters, such as morphological, physiological, or affecting special regions of the organisms, such as leaves (Sneath & Sokal, 1973). However, the hypothesis of nonspecificity has been shown to be only partially correct. Identical classifications are not produced from different sets of characters for the same species. I suggest that the aforementioned differences in the estimate of phenetic similarity are due to different character sets, these being samples of phenotypic expression derived from different genome complements. These two estimates of phenetic similarity will need to be tested in the light of further evidence of the genotype produced in the phenetic of the senecios concerned, such as evaluating the chemical pattern in each species. Unfortunately this information is still unavailable for most of these senecios.

While some of my estimates of phenetic similarity between the senecios investigated differ from those of Hilliard (1977) I hasten to point out that many of my estimates are supported by Hilliard (1977). I have drawn attention to these in chapter 6 of this dissertation. It should also be noted that the qualitative estimates of phenetic similarity made

by Hilliard (1977) were made in the light of evidence from many more senecios while my quantitative estimates are restricted to the sample investigated (Table 1). Consequently, changes in these quantitative estimates may occur when more senecios are investigated. An example of a good candidate for a possible change in the estimate of phenetic similarity is S. erubescens (no. 24), which comprises 4 varieties. The analyses of these 4 varieties in this study suggest that they are more distant than their taxonomic status suggests (see chapter 6 & Fig. 41).

#### CONSTRAINTS ON THE PROJECT

In a study in which interrelationships between species is being investigated, it is important to have a clear understanding of the generic limits of the group in question. The generic concept of Senecio is very variable, as pointed out by Jeffrey et al. (1977). Consequently, the task of investigating the interrelationships of many of the Natal senecios, necessitated that the generic concept of Senecio be investigated. Subsequent to the attempt to clarify the generic concept of Senecio, the relationships of the Natal senecios to this clarified concept needed to be assessed, to decide which species are congeneric with Senecio s. str. sensu Vincent and which senecios should be excluded from any further analyses of interrelationships of members of Senecio L.

This necessitated detailed observations of representatives of the type of the genus, S. vulgaris, and of many other senecios, as well of some species from other taxonomically closely related genera in the

Senecioneae (Table 1). The necessity of investigating relatively many senecios, placed a constraint on the number of representatives of each taxon, this usually being a minimum of three representatives. While I judge that this sample size is, in most instances, large enough to represent accurately the qualitative characters of the taxa investigated, it is possibly inadequate for a reasonably accurate representation of the variation in the quantitative characters to be obtained. This view is based on my observations of larger samples ( $n = 10$ ), where it was observed that the quantitative characters were variable (not statistically significant), in comparison to the often observed consistency of the qualitative characters. Consequently, the original measurements recorded from the minimum of three representatives may, in some instances, not be an adequate reflection of the actual variation that would be encountered in a larger sample. To try to minimise the accrual of unrepresentative data on both quantitative and qualitative characters, an attempt was made, in the selection of the specimens of each taxon to be studied, to select specimens from noticeably different localities and/or habitats so as to enable the effect of environmentally induced variation to be encountered. Nevertheless, the sample size used, necessitated by the magnitude of this project, placed a constraint on the efficacy of this selection procedure

A second constraint on the number of representatives of each taxon that could be investigated, was the large number of characters investigated. However, the majority of the characters investigated are those, suggested by Jeffrey *et al.* (1977), that should be used in investigating

Senecio s. lat. and related genera together with many additional characters that I judged to be important in enabling me to obtain a relatively good understanding of the phenotype of the taxa investigated. I judged the observation of a large number of characters to be crucial to the selection of the characters of generic importance as well as to the selection of those characters of importance with respect to elucidating the interrelationships of the taxa investigated. Indeed it has been stated that good systematics revolves around the use of a multiplicity of characters out of which the critical or "key" characters are selected (Cronquist, 1968).

While a large number of characters were investigated in this study (Table 2), not all of these were used in the numerical analyses. This is due to there being a number of characters which have character states which overlap to varying degrees (e.g. Characters 019, 020 & 021). These characters are unsuitable for numerical analysis, as the apparent differences resulting from numerical treatment of data containing such characters will not be a true reflection of the actual relationship being assessed. However, the information contained in these 'unsuitable' characters was kept in mind when assessing the numerical analyses and in some cases assisted in elucidating some of the interpreted relationships.

## DISCUSSION OF THE NUMERICAL TECHNIQUES USED

The concept of numerical taxonomy has progressed from simple comparisons of similarities and differences to more sophisticated multivariate techniques (for a review, see Sneath & Sokal, 1973). Numerical techniques can be useful in understanding the distribution and amount of variation of morphological characteristics (McNeil, 1979). Methods such as clustering or principal components analysis (PCA) can assist in developing taxonomic concepts, but they do not themselves define the taxonomic boundaries. Each analysis must be carefully interpreted, and can only serve as a guideline in taxonomic delimitations.

The UPGMA clustering routine used in this study, which clusters by the unweighted pair group method, using arithmetic averages, was chosen because it produces the best phenograms, as measured by the cophenetic correlation coefficient (Sneath & Sokal, 1973; Duncan & Baum, 1981). During this study other clustering techniques were tested for their suitability, this being judged on the same basis as the selection of the UPGMA technique.

In the study by Jeffrey *et al.* (1977) on the generic and sectional limits in Senecio, a very important fact emerged, this being that intermediate states were always found between the various character states of the characters which they studied. Thus they mention that it is ... "impossible meaningfully to allocate character states to classes, such as might be necessary for their scoring for use in numerical analyses." While the allocation of character states to classes is frequently performed in numerical analyses, this technique was avoided

in this study, with the exception of some of the quantitative characters (e.g. CHARs 044, 045, 050), because of the occurrence of intermediate states between many of the characters investigated (Table 2). This avoidance enabled a large number of taxonomically significant and suitable characters to be selected for numerical analysis (Table 10), despite there still being many characters which were unsuitable for numerical analysis, because of the lack of discontinuities between their character states.

#### DISCUSSION OF SOME OF THE CHARACTERS INVESTIGATED

##### LEAF TRICHOMES

The occurrence of some of the leaf trichome types produced by some Eurasian senecios (Drury & Watson, 1965) amongst some southern African senecios is most interesting (Table 3). Despite this coincidence being relatively low, it does nevertheless cast an interesting perspective on the possible affinity between the southern African and Eurasian senecios concerned.

However, I have not investigated the senecios studied by Drury and Watson (1965) with respect to my concept of Senecio. Consequently, any suggestions regarding affinity between these Eurasian and southern African senecios concerned, are tentative.

The numerical analysis of all the members of Senecio s. str. sensu Vincent, investigated in this study (Table 12), produced three groups



with all of the European senecios and some southern African senecios occurring in group A (Fig. 41), suggesting that these southern African senecios concerned have a cladistic affinity with the European senecios. However, a comparison of the senecios listed in Table 3 with their clustered position in the phenogram (Fig. 41), does not support this view, for none of the southern African senecios investigated, which have trichomes coincident with those described by Drury and Watson (1965), are associated with group A (Fig. 41). On the other hand S. vulgaris, S. gallicus, S. vernalis, S. sylvaticus and S. desfontainei, all of which occur in group A (Fig. 41), have trichome types coincident with "hair" types 7 and 8 of Drury and Watson (1965) (Table 3). This coincidence suggests that the aforementioned European senecios are allied to some of the Eurasian senecios, studied by Drury and Watson (1965). However, it should be noted that S. hockii, which has been excluded from Senecio sensu Vincent and Crassocephalum cernuum, also have trichome types which are coincident with "hair" types 7 and 8 of Drury and Watson (1965) (Table 3).

The apparent coincidences of some of the Drury and Watson (1965) "hair" types amongst some of the taxa studied, rather than suggesting relatively close cladistic affinities, are perhaps indicative of degrees of homoplastic phylogeny.

#### LEAF TRICHOME DIVERSITY

It is interesting to note from the Drury and Watson (1965) study, covering forty-five species of Eurasian senecios, that there appears to be much less diversity of trichome type than is the case in my study. Although many more senecios were investigated in my study.

This situation suggests that the assemblage of southern African species of Senecio s. str. sensu Vincent, is considerably more heterogeneous than their Eurasian counterpart. However, this suggestion needs to be tested on the basis of investigating the character variation of many more characters so as to ascertain whether or not the collective phenotype of the Eurasian senecios is more homogeneous than their southern African counterpart.

It is possible that the southern African senecios, particularly the Natal senecios, are considerably more heterogeneous than their Eurasian counterpart, for studies on the Asteraceae in Natal (Hilliard, 1978) suggest that "The Drakensberg is a rich centre of endemism for the big genera Helichrysum and Senecio". The implication is that this area is a centre of speciation for these two large genera (Hilliard, 1978). Therefore, it is perhaps not surprising to encounter phenotypic heterogeneity amongst the senecios studied, for many of these senecios are distributed in the Drakensberg (Hilliard, 1977, 1978).

#### THE POSSIBLE SIGNIFICANCE OF THE CAPITULUM DIAMETER

The diameter of the capitula of the Compositae is thought to be significant in that it has been found that some insects have a decreased ability to find the centre of a disc above a certain size (Baagøe, 1977). This has been demonstrated in the moth Macroglossa (Sphingidae) where the critical size of a single attraction unit (a square) had a side length of c. 30 mm (Faegri & van der Pijl, 1966). Burtt (1961) has pointed out that "larger capitula because they are more conspicuous and produce more seed, will carry a natural advantage unless, or until, they are exposed to selection pressures which can be evaded by a decrease in size". It is thought that the decreased ability of some insects to find the centre of a disc above a certain size represents such a selection pressure (Baagøe, 1977).

Baagøe (1977) also cites that "many Compositae have capitula which are just about 30 mm in diameter, but many are broader". In those species, which do produce larger capitula, the effect of the aforementioned selection pressure may be diminished or even annihilated by an accentuation of the centre by differently coloured rings (Baagøe, 1977).

The significance of the above information to my study lies in the fact that all the senecios investigated have capitula under 30 mm in diameter. This, according to the above discussion, possibly contributes to the successful reproduction of these senecios, in that they presumably comply with the requirements of their insect pollinators by being relatively narrow in diameter (< 30 mm), so assisting these

insects to find the 'discs' of the capitula. The importance of the relatively narrow capitula to the senecios studied is perhaps accentuated by the fact that because all the radiate senecios in this study possess the "senecionoid" type of limb epidermis (see CHAR 078). The consequence of the possession of this type of limb epidermis is that the light reflected from these ray florets is of a relatively low saturation and the limbs lack a velvety appearance. Thus, these limbs are apparently not as attractive to insect pollinators as is the case when the limbs reflect light of a relatively high saturation and have a velvety appearance (Baagøe, 1977). Perhaps the apparent lack of attractiveness of the ray florets, of the senecios studied, does not counteract the presumed effectiveness of the relatively narrow discs of these radiate senecios in attracting insect pollinators.

#### INCONSISTENCY IN THE RADIATE CONDITION

While the majority of the senecios studied are consistently either radiate or discoid there are four senecios (*S. sp. aff. S. speciosus*, *S. hypochoerideus*, *S. glaberrimus* & *S. deltoideus*) which are inconsistent in that they can be frequently found in both the radiate and the discoid state (char. state 3), even within the same population. A further two senecios (*S. poseideonis* & *S. paludaffinis*) are usually radiate but discoid plants are occasionally found. This phenomenon I regard as being of considerable significance.

Bohlmann et al. (1978) have investigated the terpene chemistry of the radiate and discoid forms of *S. hypochoerideus* and have found two

distinct chemical patterns. Both forms have furanoeremophilane skeletal structures but the range of substitutions on this basic skeletal structure differs significantly between the radiate and discoid forms (Bohlmann et al., 1978; Seaman, 1982). This suggests that consideration should be given to recognising these two forms taxonomically. However, in my detailed observations of radiate and discoid representatives of S. hypochoerideus I was unable to discern any morphological or micromorphological features which supported this suggestion. Perhaps it is premature to anticipate that differences in chemical pattern should also be reflected in the phenotype or perhaps a larger sample size would have revealed significant differences.

Detailed observations of the radiate and discoid forms of S. poseideonis indicate that these two forms are more distinct than just differing with respect to whether or not they are radiate. The numerical analyses of these two forms (Chapter 6) clusters the radiate form (no. 38A) in group B5 while the discoid form (no. 38B) is clustered in group A8 (Fig. 41). This situation strongly suggests that these two forms should receive taxonomic recognition, perhaps at the varietal level. It is unfortunate that the chemical pattern of these two forms of S. poseideonis is unknown, for it may be able to further elucidate the relationship between these two taxa.

A study of the floral biology of the radiate and discoid forms of each of the aforementioned species in isolation, so as to ascertain whether or not this condition is maintained, could be most informative.

It is interesting to note that the peripheral florets of the discoid forms were all morphologically hermaphroditic, but whether they are functionally so is unknown. I mention this point for the ray florets of all the radiate taxa investigated, including the aforementioned radiate forms, are morphologically female, resulting in a capitulum which is functionally protogynous, a phenomenon well established in the Asteraceae (Burtt, 1977). The discoid forms appear to have lost this functional dimorphism and the coincident protogyny.

#### INCONSISTENCY IN FLORET COLOUR

The occurrence of nominally yellow specimens of otherwise non-yellow species as occurs in S. sandersonii, S. umqeniensis, S. glanduloso-pilosus, S. barbatus and S. subrubriflorus, raises an interesting question concerning the significance of floret colour within Senecio. Is floret colour taxonomically significant? My view is that the two categories of YELLOW and NON-YELLOW are of limited value because these two categories are artificial. Nevertheless, these two categories have been used because of the considerable degree of variation in floret colour. This variation is due to both the variable descriptions of floret colour by collectors and the presumed inherited differences in the chemical constituents of the floret colour between representatives of the same species.

The occurrence of differences in the floret colour of representatives of the same species, as can be observed in the field, suggests that the chemical pattern of the florets of these representatives should be

investigated in order to ascertain the degree of the chemical differences. This, I think, need only be done for a limited number of species as the information could be extrapolated to the remaining species. In this manner the question regarding the significance of variable floret colour, could be debated.

#### RAY COROLLA: LIMB EPIDERMAL CELL SHAPE

Baagøe (1977) has described a "senecionoid papillose" type of epidermis which appears to be correlated with white and purple limb colour for she found this type of epidermal pattern in purple- and white-rayed Senecio species and also in Castalis Cass., Dimorphotheca Moench and Osteospermum L. of the Calenduleae.

Nordenstam (1978), in his studies on the Senecioneae, confirms the general validity of Baagøe's findings (Baagøe, 1977), for he also found the "senecionoid papillose" type of epidermis to be correlated with white and purple limb colour, with a few exceptions. Some examples of this correlation are found in the white-rayed genera Pladaroxylon Hook. f. and Stenops B. Nord. and in Pericallis D. Don in Sweet, which comprises white-, pink- and purple-flowered taxa while an example of the exceptions to this correlation is the white-rayed Dolichoqlottis scorzoneroides (Hook. f.) B. Nord., which has a smooth limb ("senecionoid") epidermis.

The fact that I found no correlation between the non-yellow colour of the limb and the presence of "senecionoid papillose" type of epidermis

for all the non-yellow radiate senecios investigated, is most interesting. Perhaps the occurrence of the "senecionoid" type of epidermis amongst these non-yellow taxa should be regarded as further exceptions, as found by Nordenstam (1978). However, it is quite possible that the senecios studied by Baagøe (1977) would not be recognised as senecios according to my concept of Senecio, and perhaps this accounts for Baagøe's findings differing from mine.

#### DISC COROLLA FLORET NUMBER VERSUS HABIT

It is interesting to note that there is a correlation between the number of disc florets and the annual and perennial habit, for while there are many perennial senecios which do have relatively few disc florets (char. state 2), there are several perennial senecios (e.g. S. mooreanus, S. macrospermus & S. caudatus) which produce relatively many disc florets. Similarly, there are several senecios which have an annual vegetative habit but which produce many disc florets (e.g. S. multibracteatus & S. elegans).

While the majority of the perennial senecios have a reproductive strategy which produces relatively few disc florets there are some which produce relatively many disc florets (e.g. S. mooreanus, S. macrospermus & S. caudatus). Similarly, while many senecios with an annual vegetative habit produce a moderate number of disc florets, there are several which produce relatively many disc florets (e.g. S. multibracteatus & S. elegans).



Levin and Turner (1977), in a study of many members of the Heliantheae, found that there was a distinct tendency (statistical) for annuals to have smaller "clutch" sizes than perennials ("clutch" size  $\equiv$  to the number of propagules within an involucre). This feature together with smaller and lighter propagules in comparison to the propagules of perennials, is thought to result in greater dispersability of annuals, many of which are weedy, r-strategy species.

Extrapolating the findings of Levin and Turner (1977) to the correlations (not statistical) that appear to exist between the number of disc florets ("clutch" size) and habit of the senecios studied it appears that, on the whole, the tendency for annuals to have smaller "clutch" sizes is not the strategy that Senecio follows. For while only a few of the senecios studied are true annuals their "clutch" sizes are relatively large (e.g. S. multibracteatus & S. elegans). While on the other hand the "clutch" size of the majority of the perennial senecios is relatively small. The situation regarding the "clutch" size in the senecios studied, while differing from the tendency of some members of the Heliantheae, is nevertheless more than likely also to be significant with respect to their reproductive strategies.

#### DISC COROLLA VENATION

Drury and Watson (1965), in their study of some Eurasian senecios, mention that "The disc florets of Senecio ... exhibit a distinctly limited range of types" (of corolla venation). In their study only two types of disc corolla venation were found. They noted that there were

always five traces (veins) from the base of the corolla which bifurcated at each sinus and then the bifurcated traces continued into the corolla lobes where in some species they anastomosed at the tips of the corolla lobes, a condition which they called "closed venation". While in other species the traces did not anastomose at the tips of the corolla lobes, a condition which they called "open venation". They also noted that while the corolla venation was usually constant for some species, other species exhibited both forms of venation, both between representatives of these species and within the same capitulum.

However, in my study the disc corollas of all the taxa studied always had 5 veins from the base of the corolla which bifurcated at each sinus and then anastomosed in the corolla lobes to form a "closed venation". No infraspecific variation was observed with respect to the type of venation, as encountered by Drury and Watson (1965).

The interspecific and intraspecific variation described by Drury and Watson (1965) is possibly indicative of their study having consisted of a rather heterogeneous group of senecios, many of which are probably not members of Senecio s. str. sensu Vincent, as discussed earlier. However, I must point out that the "closed" condition was found in all the taxa studied (Table 1). Perhaps this indicates something of the degree of the cladistic relationship between the African and non-African members of the Senecioneae included in my study.

#### THE APPEARANCE OF THE STIGMATIC SURFACE

It is interesting to note that while both "cleft" and "banded" configurations were found in the five senecios studied by Wetter (1983), using SEM, only the "banded" configuration was found amongst the taxa investigated in this study.

Nordenstam (1978) has documented that the "banded" configuration occurs "in Senecio s. str. and in a number of related genera ..." but does not refer to the occurrence of a "cleft" or "transitional" configuration amongst the members of the Senecioneae which he has studied.

The taxonomic position of three of the five senecios studied by Wetter (1983) (S. cineraria DC., S. douglasii DC. & S. vulgaris L.) can be commented upon according to the studies of Jeffrey et al. (1977) and Jeffrey (1979). Senecio cineraria is placed in group 15 of the "Eusenecionoids" while S. douglasii is placed in group 25 of the "Eusenecionoids" (Jeffrey, 1979). Senecio vulgaris is placed in group 40 of the "Eusenecionoids". The members of group 40, together with those of group 41, are considered to form Senecio sensu stricto. Consequently, it is quite possible that neither S. cineraria nor S. douglasii are members of Senecio s. str. sensu Jeffrey.

In the light of the above discussion regarding the taxonomic position of the aforementioned three species it should be noted that only S. vulgaris is reported to have a "banded" configuration while S. cineraria is reported to have a "cleft configuration" and S. douglasii a "cleft and apically divided" configuration (Wetter,

1983).

My studies suggest that the "banded" configuration is the typical form of configuration in Senecio s. str. sensu Vincent.

I would like to mention that while the use of cleared tissue has been satisfactory for most of the characters studied, this is one character that was often difficult to observe after this manner of preparation. Some of my own scanning electron microscope (SEM) observations of this character, together with those of Wetter (1983), clearly suggest that the SEM is a more suitable tool for observing the configuration of the stigmatic surface. It enables the configuration of the stigmatic surface to be decided unambiguously. A comparison of the quality of resolution of the SEM and the light microscope, in the study of the configuration of the stigmatic surface, can be readily made from Figures 1-13 of Wetter's study (Wetter, 1983).

#### JUDGING THE MATURITY OF CYPSELAS AND THE TAXONOMIC VALUE OF OVARY WALL CRYSTALS

In chapter 3 (Character 100) of this dissertation I drew attention to the occurrence of ovary wall crystals in ray and disc cypselas appearing to be related to the age of the cypselas. It was found that inconsistencies in both the occurrence and the proportions of the crystals was minimal in mature cypselas while in relatively immature cypselas these inconsistencies were very frequent. Consequently, it appears that it is imperative that the occurrence and appearance of

ovary wall crystals be only observed in mature cypselas.

This raises the question "when is a cypsela mature?" My first criterion for judging the maturity of a cypsela is very much restricted to the field, in that maturity is indicated by the ease with which the cypsela can be removed from its point of attachment to the capitulum - the ease being 'proportional' to the maturity. However, this rule of thumb is not nearly so easy to apply to a herbarium specimen. Here my criterion, based on my experience, has been the ease with which the corolla can be separated from its point of attachment to the cypsela after the clearing procedure in lactic acid - again the ease being 'proportional' to the maturity of the cypsela. Nevertheless, despite applying the latter rule of thumb, inconsistencies still occurred, indicating that it remains extremely difficult to judge the maturity of a cypsela in herbarium material.

The character, 'ovary wall crystals', clearly needs to be observed in as many representatives of a species as are required to obtain a sense of stability in the observations of the appearance of the ovary wall crystals. It would also be a good practice to avoid the use of lactic acid in the preparation of cypselas for the observation of ovary wall crystals, but to rather follow the method of Nordenstam (1978). This would completely avoid the risk of altering the appearance and occurrence of ovary wall crystals, this risk being present when the lactic acid procedure is used for extended periods of time as described in chapter 3 (Character 093).

The study by Dormer (1961) of the ovary wall crystals of some members of the Cyanareae, indicated that the distribution and shape of these crystals appears to be genetically controlled and hence taxonomically useful. Therefore the gathering of information on the shape of the ovary wall crystals and their distribution amongst Senecio, should be pursued with a view to investigating the possibility of this information being taxonomically useful, as is the case in the study by Dormer (1961).

#### THE APPEARANCE OF THE ANTHER APEX

The fact that this character has only been used to a limited extent in the taxonomy of the tribe Senecioneae (Nordenstam, 1978) and of the genus Senecio, is of considerable interest to me for this character has emerged to be of considerable importance with respect to clarifying the generic concept of Senecio. Further investigation into the remaining members of the tribe Senecioneae, with respect to the appearance of the anther apex, may show this character to be important at the tribal level.

#### THE SIGNIFICANCE OF THE ENDOTHECIUM CONFIGURATION

Earlier in this dissertation (chapter 3, Character 107) I described the configuration of the endothecium of the majority of all the taxa studied, with two exceptions (S. cissampelinus & Gynura auriculata), as being radial anticlinal. The endothecium configuration of S. cissampelinus possessed an intermediate endothecium configuration in

that it was predominantly "polarized" but irregularly distributed peg-like projections were also found. While the configuration in G. auriculata consisted of a distinct imperforate "base plate" with rib-like extensions from the edge of the "base plate".

Having found this pattern of distribution of the endothecium configuration, it would be most interesting to examine the endothecium configuration of the remaining members of the tribe Senecioneae so as to ascertain whether there are further types of configuration. This study appears to indicate that the endothecium configuration is not constant at the generic level or at the tribal level within the Senecioneae. Further information on this character from the remaining members of the tribe may reveal constancy in the configuration somewhere between the tribal and generic levels. This information would also enable some assessment to be made of the statement "there are indications of constancy at the generic level, or even through larger groups such as the Asteraceae" (Noel, 1983), with respect to the Senecioneae.

#### DIMORPHIC PAPPUS SETAE

Drury and Watson (1966) described the occurrence of "fluked" pappus setae in forty species of Senecio L. out of a total of 245 senecios studied. These "fluked" setae form a "dimorphic" pappus in that they occur together with non-fluked or so called "ordinary" setae. Of the forty senecios in which these "fluked" pappus setae occur, a number have been included in this study, namely: S. arenarius, S. californicus, S. elegans, S. gallicus, S. grandiflorus, S. speciosus, S. sylvaticus,



S. vernalis, S. viscosus and S. vulgaris.

In my detailed study of the pappi, I have found both "uniform pappi" (Jeffrey et al., 1977) which consist of "ordinary" pappus setae (Drury and Watson, 1966) and "dimorphic" pappi (Jeffrey, 1979) which consist of "ordinary" setae and setae which are considerably more flexuous and have reduced teeth (barbs) in comparison to the "ordinary" setae (Jeffrey, 1979). Some of the senecios included in this study, including some of the aforementioned senecios, have "ordinary" pappi, while others have "dimorphic" pappi, but no specimens have been found to possess the "fluked" pappus setae described by Drury and Watson (1966). This lack of occurrence of "fluked" pappus setae in all of the senecios studied, including the aforementioned senecios, is disconcerting for I have observed at least 15 pappi in each of the taxa that I have studied. I also kept in mind that there are reported to be only 5-10 "fluked" setae in each pappus (Drury & Watson, 1966). The dissimilar appearance of these "fluked" pappus setae, as clearly illustrated by Drury and Watson (1966), together with the tendency of these "fluked" pappus setae to be less easily detached from mature cypselas than are the "ordinary" pappus setae (Drury & Watson, 1966), should both have enabled these pappus setae to be readily observed.

This discrepancy in our findings is unfortunate for it has been suggested that the genotypic basis of the unique and complex morphology of this "fluked" type of pappus setae is perhaps indicative of a close cladistic relationship between the species in which it occurs (Drury & Watson, 1966; Jeffrey, 1979). Jeffrey (1979) noted that the occurrence



of these "fluked" pappus setae occurred in species referable to Senecio clusters 21,33,37,39,40,42 and 43 only, suggesting that this is indicative of a close phylogenetic relationship between these groups of senecios despite, the fact that this character state is not expressed in every species referred to these clusters by Jeffrey et al. (1977).

#### THE DISTRIBUTION OF THE NATAL SENECIOS

Extensive observations of the geographical distribution of Asteraceae native to Natal, by Hilliard (1978), has resulted in the recognition of twelve groups or patterns of distribution, together with 4 subgroups.

These observations indicate that "The Drakensberg is a rich centre of endemism for the big genera Helichrysum and Senecio, and many of these endemic species have little or no affinity outside the area." The phenomenon of many of these endemic species of Senecio having little or no affinity outside Natal is supported by my studies on Senecio. The senecios of groups B and C of Figure 41, are clearly not allied to the senecios of group A, which contains the majority of the Cape and non-southern African senecios and only a few of the senecios native to Natal.

It is interesting to note that there is some correlation between the senecios of the subgroups of groups B and C (Fig. 41) and the distribution of these senecios according to Hilliard (1977, 1978). However, only further collecting and further revisionary work will reveal a clearer picture of this montane centre of speciation with

respect to Senecio L. sensu Vincent.

THE RELATIONSHIPS BETWEEN ALL THE MEMBERS OF SENECEO SENSU STRICTO SENSU VINCENT

FACTORS AFFECTING THE ESTIMATE OF PHENETIC SIMILARITY

While many features of the ray florets were recorded in this study (Table 2), I decided to exclude the characters based on these features from my numerical analyses. This decision was based on the fact that their inclusion resulted in species which appeared otherwise closely related, being clustered in relatively distant relationships. An example of this is the relationship between S. brachypodus and S. pleistocephalus. These two species appear to be closely related when the character states of their morphology and micromorphology are compared (Fig. 41). However, when the characters of the ray florets of S. brachypodus are included in the analyses, these two species become relatively distantly related.

Another example of this distortion of apparent affinity upon the inclusion of characters of the ray florets, occurs between S. polyodon var. polyodon (discoid) and S. polyodon var. subglaber (radiate).

It is also important to note that numerical analyses of a group of taxa, only some of which can be scored for all the characters being investigated, necessitates the use of a "no comparison" routine in the analyses. It is suggested by Sneath and Sokal (1973) that "no comparison" (NC) values be kept to a minimum or preferably avoided in

numerical analyses, as they result in complex difficulties when matrices containing NC values are analysed.

Since this study is primarily involved at estimating phenetic affinity based on some degree of patristic development, one might argue that the presence or absence of ray florets is an important aspect in estimating phenetic affinity. Nevertheless, the fact that the inclusion of characters derived from ray florets appears to distort the presumed affinity based on the comparison of the remaining characters, as mentioned earlier, I think it is important to exclude the characters of the ray florets until such time when we know considerably more about the phenotype (in its broadest sense) and the genotype of Senecio.

#### POLLEN MORPHOLOGY

The transmission electron microscope (TEM) studies of Skvarla et al. (1977) on several members of the Senecioneae, including S. heritieri DC. and S. lyallii Hook. f. have shown the presence of two patterns of wall stratification, "Helianthoid" and "Senecioid". The information to date indicates that the patterns of wall stratification, within the Senecioneae, are only reasonably constant at the tribal level. Senecio heritieri was found to possess the "Helianthoid" pattern while S. lyallii possessed the Senecioid pattern. Jeffrey (1979) places S. heritieri in the "Eusenecionoids" (group 42) and has suggested that it will be excluded from Senecio (C. Jeffrey, pers. comm.). Senecio lyallii on the other hand has been placed in the "Herbaceous Cacalioids" group, which is well removed from Senecio sensu Jeffrey (Jeffrey, 1979).

It will be most interesting to see, if after many more members of the Senecioneae have been studied using the transmission electron microscope, whether there are any other patterns of wall stratification either within these two aforementioned patterns or in addition to these aforementioned patterns. Skvarla et al. (1977) mention that the "Helianthoid" pattern may be too inclusive and that modified "Helianthoid" patterns may need to be recognised. These modified patterns may be established for exines with collumellar bases that are smooth, irregular or with subcolumellae (Skvarla et al., 1977). By drawing attention to the internal foramina still other patterns might be recognised which consider the size and shape of these internal foramina.

While the "Senecioid" pattern is distinguished from the "Helianthoid" pattern by the absence of internal foramina, recent studies indicate that these internal foramina are not always absent, for extremely minute holes have been noted in the columellae, but these foramina are noticeably less clearly outlined than the internal foramina of the 'normal' "Helianthoid" pattern (Skvarla et al., 1977).

The significance of the aforementioned incongruity in the "Senecioid" pattern and the possible recognition of further patterns within the "Helianthoid" pattern and perhaps in addition to the aforementioned patterns, is that the stratification pattern of the pollen wall of Senecio may yet become an integral part of its taxonomic position.

### PHYTOCHEMISTRY

Seaman (1982) illustrated how a biogenetically based methodology for sorting out complex molecules' carbon-skeletal and substitutional features of sesquiterpenes into unit characters (Davis & Heywood, 1963) can be of considerable taxonomic value at the interspecific level and above. Cladistics or Hennigian phylogenetic systematics (Hennig, 1966) has provided an extremely useful framework for this analysis. It should be pointed out that while the proposed steps of sesquiterpene biosynthetic pathways are based on sound mechanisms, they have not been established by the usual labelling or enzyme studies.

However, the lack of biosynthetic information on many sesquiterpene compounds, suggests that caution should be exercised in erecting a biogenetically based methodology for the compounds on which biosynthetic information is available. Nevertheless, the foundation for such a system has been laid and will be improved and tested as further biosynthetic information becomes available.

No such biogenetically based methodology has been proposed for sorting out complex molecules' carbon-skeletal and substitutional features of pyrrolizidine alkaloids. This is unfortunate, for the available biosynthetic information on a number of the pyrrolizidine alkaloids indicates that such a system could also be of taxonomic value at the interspecific level and above.

It hardly needs to be mentioned that the acquisition of the outstanding biosynthetic information on both the sesquiterpenes and the

pyrrolizidine alkaloids prevents any serious taxonomic use, ranging from the synthetic level to the analytic level (Seaman, 1982), being made of much of the existing biosynthetic information. Similarly, the lack of information on many of the senecios with respect to their individual chemical complement, precludes any analytic taxonomic use being made of the existing information on species chemical complements.

#### CYTOLOGY

Jeffrey et al. (1977) have "chromosome number" as one of the characters in their "uniform criterion" for evaluating the systematics of the Senecio complex. When available, either from the compilations of Fedorov (1969), Moore (1974) and occasionally from other sources, the "chromosome number" has been included in the initial subdivision of the Senecio complex into the sixteen groups (groups I-XVI). "Chromosome number" has also been included in the re-evaluation of the original concepts (Jeffrey, 1979). According to this re-evaluation (Jeffrey, 1979) the "Eusenecionoids" (group IX [a]) have a chromosome number ranging from  $n = 10$  to  $n = 30$ , with Senecio s. str. sensu Jeffrey, possessing a chromosome number of  $n = 10$ .

However, it is clear that a basic chromosome number of  $n = 10$  is not unique to Senecio s. str. sensu Jeffrey, for this basic chromosome number also occurs in the "Gynuroids" and the "Othonnoids". The chromosome number of  $n = 10$  is also not characteristic of Senecio s. str. sensu Jeffrey for chromosome numbers ( $n$ ) of 20 and 30 are also found amongst some members of Senecio s. str. sensu Jeffrey.

Nordenstam (1977) notes that the "Senecioid" complex, which is equivalent to much of Jeffrey's "Eusenecionoids" (Jeffrey, 1979), is cytologically characterised by the basic number,  $n = 10$ , or numbers like 20 or 5, derived from this basic number. Within the "basal genus Senecio a wide range of chromosome numbers is known", these being: 5, 10, 20, 23, 30, 40, 45, 46, 50, 60 & 90 (Nordenstam, 1977). Chromosome numbers ( $n$ ) in multiples of 10 are well documented for large portions of the genus Senecio, including more than 15 sections (Nordenstam, 1977). Several of the North and Central American sections of Senecio (Aurei, Bolanderiani, Lobati, Sanquisorboidei and Tomentosi) are cytologically distinguished by  $n = 23$ , this number being remarkably constant throughout this assemblage, with a few exceptions (Nordenstam, 1977). No obvious morphological characteristics have been found to separate this assemblage from Senecio (Nordenstam, 1977).

It is apparent that the chromosome number of  $n = 10$  is more than likely not the only gametic number in Senecio s. str. sensu Vincent, for S. bupleuroides, which is clearly congeneric with Senecio s. str. sensu Vincent, has a gametic number of 20. However, the overall picture remains to be seen, after my concept of Senecio s. str. has been applied to the senecios included in the studies by Jeffrey et al. (1977), Jeffrey (1979) and Nordenstam (1977) as well as the many other senecios currently included in Senecio.

It is interesting to note that there is a statistical correlation between a relatively low (c. 10) chromosome number and an annual habit

in many members of the Asteraceae, although there are some exceptions (Solbrig, 1977). Whether this correlation is found in Senecio sensu Vincent, remains to be seen.

There is a dearth of information on the karyotype of most members of the Asteraceae, partly because karyotype studies are a lot more time consuming than obtaining data on chromosome numbers (Solbrig, 1977). Karyotype analyses can be extremely useful in deriving genetic and evolutionary hypotheses and inferring taxonomic relationships. An example of this is a study of the genus Crepis L. (Lactuceae) in which a reduction in karyotype length was recorded in two phyletic lines, facilitating the verification of the integrity of the species of Crepis studied (Babcock, 1947 in Solbrig, 1977).

It is unfortunate that karyotype analyses are seldom included in cytotaxonomic studies of Senecio, for the data obtained from these analyses could be of considerable value in helping to elucidate the taxonomy (phylogenetic taxonomy) of Senecio.

#### FURTHER MEANS FOR INVESTIGATING PHENETIC AFFINITY AT VARIOUS LEVELS WITHIN SENECIO

The majority of the evidence used in elucidating the taxonomic position of Senecio is derived from studies of the morphology, micromorphology, chemistry, pollen morphology and cytology.

However, the technique of electrophoresis of isoenzymes, which provides



evidence on the protein complement of the tissue examined, has not been suggested as a possible further means of elucidating the taxonomic position of Senecio. This is despite the evidence obtained by electrophoresis of isoenzymes being of considerable value at the species and genus level (Smith, 1976).

Koniuszek and Verkleij (1982) have shown the usefulness of this technique in investigating the two taxonomically closely related species S. sylvaticus (no. 216) and S. viscosus (no. 212) (Table 1). Isoenzyme analysis of 14 different enzymes of these two senecios, which are partly co-occurring annual pioneer species on clearings, has revealed that no genetic variation exists within or between populations of these two species. While this study was partly a test of the hypothesis that these two species are genetically isolated, the evidence from their "fingerprints" (Smith, 1976), is also useful in elucidating their phenetics. Indeed this has been achieved, for the "fingerprint" evidence was used to calculate the genetic identity ( $I = 0,636$ ) and the genetic distance with standard error ( $D = 0,453 \pm 0,099$ ) after Nei (1971, 1972). These two quantitative parameters indicate that S. sylvaticus and S. viscosus are clearly allied and their degree of taxonomic affinity is supported.

The "fingerprinting" technique of electrophoresis of isoenzymes could be of considerable value in elucidating the generic concept of Senecio. The technique could also be of considerable value in elucidating the interrelationships of the members of Senecio, and it should not be overlooked.

Considering sectional limits within the genus, Jeffrey (C. Jeffrey, pers. comm.) has found the anatomy of the cypselas of the eastern Asian members of Senecio (sensu Jeffrey) to be of diagnostic value in the recognition of sectional limits within this portion of the genus. This is an exciting finding which needs testing amongst a geographically larger sample of senecios that fall within my concept of Senecio.

### CONCLUSIONS

1. The study of a large number of senecios and some species from related genera (Table 1) enabled the selection of the following six characters, which are judged to characterise the generic concept of Senecio sensu stricto sensu Vincent:

- (i). The appearance of the style-arm apices of the disc florets - CHARACTER 095 - character states: 9, 11, 13 and 14 (Table 4).
- (ii). The appearance of the anther apices - CHARACTER 103 - character state: 1 (Table 4).
- (iii). The cell wall configuration of the endothelial tissue - CHARACTER 107 - character state 6 (Table 4).
- (iv). The length of the filament collars - CHARACTER 108 - character states: 1, 2 and 3 (Table 4).
- (v). The shape of the filament collars - CHARACTER 110 - character states 1, 2 and 3 (Table 4).
- (vi). The shape of the disc cypselas - CHARACTER 117 -

character states: 1, 2 and 4 (Table 4).

2. The original hypothesis: "Many of the species of Senecio in Natal are congeneric with Senecio L. sensu stricto", has been accepted subsequent to my re-circumscription of Senecio.
3. The majority of the Natal senecios, while clearly being members of Senecio s. str. sensu Vincent, are distinct from virtually all the Cape and non-southern African senecios studied.
4. Many of the non-yellow Natal senecios form clearly allied groups which are distinct from the groups (clusters) composed of yellow senecios.
5. Before any taxonomic changes are made to the current composition of Senecio, the concept of Senecio, as circumscribed in this dissertation, needs to be tested against a far wider sample of the genus. This I see as the first priority. Subsequent to this test, the remaining members of the genus (as presently circumscribed) in southern Africa, need to be revised in the light of the revised concept of Senecio s. str. sensu Vincent. Ultimately, each species currently in Senecio will need to be tested against this revised generic concept of Senecio sensu stricto.
6. Further information on the chemical complement (particularly terpenes and pyrrolizidine alkaloids) of the members of Senecio s. str. sensu Vincent, included in this study and subsequently of all the members of Senecio s. str. sensu Vincent, should enable the generic

concept to be further elucidated or perhaps confirm its present circumscription.

7. While the current knowledge of the pollen morphology suggests that this portion of the phenotype of Senecio is invariant, further studies, particularly with the transmission electron microscope, may yet provide characters of generic importance.

8. Since the chromosome number ( $n$ ) of Senecio is suggested to be 10 (Nordenstam, 1977; Jeffrey, 1979), this aspect of the phenotype of the senecios studied requires further study to enable this suggestion to be tested. These studies should also include karyotype analyses.

9. The possibility of using electrophoresis techniques to elucidate the generic concept of Senecio as well as elucidating the interrelationships of the members of Senecio, should not be overlooked.

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