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A TAXONOMIC STUDY OF COMPOSITAE WITH SPECIAL

REFERENCE TO SENECIO

by

David Geoffrey Drury

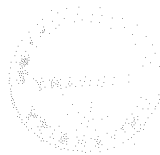
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SECTION I

INTRODUCTION



## SENECIO AND THE CLASSIFICATION OF COMPOSITAE

Senecio is the largest angiosperm genus, taking in about  $1/7$  of all Compositae and exhibiting nearly the whole range of vegetative diversity encompassed by the family. There is no satisfactory definition of the genus, and the oft-quoted 'diagnostic' features are commonly lacking, especially among extra-european species. In fact, in the Genera Plantarum of Bentham and Hooker, the diagnosis of Senecio is essentially the same as that of the tribe Senecionideae. It is a commentary on taxonomic progress that the only comprehensive account is that of De Candolle (1837), although since his time the number of named Senecio species has increased fourfold. Clearly a reappraisal of the taxonomy of Senecio and of its relationships with other Compositae is long overdue.

Regarding the classification of Compositae, one finds that despite name changes the tribes have altered very little since their delimitation and establishment by Cassini (1816-34). This is remarkable because the largest angiosperm family, taking in about  $1/10$  of the flowering plants, would seem to provide plenty of scope for discordant taxonomic opinion. Nevertheless Table 1 shows that of the 13 tribes recognised by Bentham (1873A), seven (i.e. 2, 3, 6, 7, 9, 10 and 13) are identical with or practically the same as Cassini's; and four (i.e. 5, 8, 11 and 12) incorporate or are merely fusion products of short sequences of Cassini's tribes with his groups adopted as subtribes. Only



2 of Cassini's tribes (i.e. 12 and 20) had suffered significant changes.

TABLE 1: Tribes of Bentham compared with those of Cassini.

The fractions in parenthesis are the number of genera in which the schemes correspond / the number of genera (known to both authors) in Cassini's tribe.

Coincidence of Bentham's subtribes with Cassini's tribes is indicated by asterisks.

Tribes (Bentham 1873)	Tribes (Cassini 1826-34)
1. Vernoniaceae	<u>20</u> (28/50)
2. Eupatoriaceae	<u>19</u> (18/19)
3. Asteroideae	<u>13</u> (59/61)
4. Inuloideae	<u>12</u> (85/96), <u>20</u> (10/50)
5. Helianthoideae	<u>9</u> (116/134), <u>10</u> (4/4)*
6. Helenioideae	<u>8</u> (14/14)
7. Anthemideae	<u>11</u> (41/47)
8. Senecionideae	<u>14</u> (34/34)*, <u>17</u> (3/3)*, <u>18</u> (5/6)*
9. Calendulaceae	<u>7</u> (8/9)
10. Arctotideae	<u>6</u> (18/19)
11. Cynaroideae	<u>2</u> (21/36)*, <u>3</u> (41/41), <u>4</u> (31/31), <u>5</u> (1/1)*
12. Mutisieae	<u>15</u> (20/20)*, <u>16</u> (19/19), <u>2</u> (13/36)
13. Cichoriaceae	<u>1</u> (complete agreement)



The classification in current usage is that of Hoffmann (1894); but apart from relatively trivial (usually deleterious) changes it differs from Bentham's scheme only in nomenclature, and the original has proved better for purposes of reference.

Cassini's evolutionary speculation (he designated one section of each tribe the 'prototype or archetype' and produced a map of intertribal relationships not far removed from recent 'phylogenetic' schemes!) reveals that he was well ahead of his time; but his approach to plant classification is primitive and bizarre when viewed from the twentieth century. In any case he accepted the dictum that floral characters are the only reliable indicators of taxonomic affinity, and classified not Compositae, but florets.

His successors appear to have accepted the main outlines of his classification without bringing much original thinking to bear on them. Thus, Bentham's scheme (i.e. the current one) took in more genera but few additional characters. Since the nineteenth century taxonomists have considered Compositae mainly from the floristic standpoint, allowing geographical and political considerations, coupled with the accepted taxonomic system, to govern their choice of material. The test of time, which Cassini's taxonomy has withstood, has not been very stringent.

It is possible that Cassini laid a sound foundation for the taxonomy of Compositae, although in view of his philosophy this would seem unlikely. Furthermore where comparative observations



are available across accepted groupings (e.g. palynology, Stix 1960; cytology, Ornduff et al 1963; anatomy, Dormer 1962B and Carlquist 1957-64), they are generally inconsistent with them; but the authors concerned have rarely investigated fully the taxonomic implications of their work and few (with the exception of Dormer; see also Drury and Watson 1966) have drawn this conclusion.

#### THE PRESENT INVESTIGATION

In investigating the taxonomy of Senecio in the context of Compositae as a whole, the need is for comparative observations recorded for a large cosmopolitan sample. My sample is inevitably small relative to the size of the problem; but it cuts across the artificial boundaries referable to political geography and 'established' taxonomic groups.

Taxonomic 'characters' are difficult if not impossible to define satisfactorily. The fundamental problem is that we have no means of judging to what extent the occurrence of a single observed feature is likely to provide a measure of overall similarity or phylogenetic relationship. The recent attempt (Sokal and Sneath 1963) to introduce the unit character as "one of two or more states which within the study at hand cannot be subdivided logically, except for subdivision brought about by changes in the method of coding", is impractical since organisms are essentially integrated systems. In practice one can only



record comparative observations on various parts of plants, look for correlations to define groups and test these in the light of additional information. In view of the crudity of the method, it seems desirable to use the largest possible number of 'characters' in the hope of masking errors. It is reasonable to seek features which are: (i) conveniently delimited, so that independent observers using the same definitions should recognise the same pattern of variation in the same range of plants, and (ii) easily observable without elaborate preparation of the material. In practice I have recorded comprehensively only those 'characters' where preliminary observations suggested that they might prove profitable.

From a nomenclatural point of view my work leaves much to be desired. However, a less cavalier approach to the use of names would have involved tedious and time consuming exercises having no direct bearing on the present problem. Identifications have been made using appropriate floristic works where available; for the rest I have fallen back on the only monograph, i.e. that of De Candolle. Most species in the sample are relatively well-known and specimens which proved difficult to identify were discarded.



SECTION II

MATERIALS AND METHODS



PLANT MATERIAL

In examining a world sample of any group as large as Compositae, it is necessary to use herbarium material. However dried specimens, despite their limitations, can provide an adequate source of taxonomic information; for it is not the discovery of variations which is the major problem, but the task of recording them for a sufficiently wide range of material. It is not possible to obtain material for anatomical studies from most of the major herbaria, and for this reason Compositae from the southern hemisphere (especially South America) are less well represented in my lists than I would have liked. Nevertheless the sample is a cosmopolitan one, and I stress my indebtedness to the Keepers of the Herbaria at Cambridge, Manchester and Oxford who loaned me specimens.

METHODS

Few anatomists make comparative observations on a sufficiently large scale to impress taxonomists; and for some reason most taxonomists make no attempt to record anatomical observations. Thus numerous readily observable variations have escaped taxonomic use. The fact is that with the aid of dissecting instruments, a razor and a good microscope, it is often easier to elucidate the structure of, say, the pith than to discover the ovary-locule number. By employing the simple techniques outlined below, I have been able to make large numbers of comparative anatomical observations in a relatively short time.



### Stem sections

Samples including nodes were removed from mature aerial parts of specimens, surgery being carried out in such a way as to cause minimal damage to specimens. The samples were resuscitated by boiling in water with 'Teepol' for 20 minutes. Some use was made of temporary preparations using phloroglucinol and HCl, and occasionally it was necessary to resort to the sledge microtome; but sections were mostly cut by hand in water and permanently double stained in the following way:

1. Transfer sections to 50% alcohol.
2. Stain in 1% safranin in alcohol (5-10 minutes depending on material).
3. Rinse in 50% alcohol to remove excess safranin.
4. Transfer to 1% picro-aniline blue, 'drown' and return to 50% alcohol (picro-aniline blue has the advantage of rapidly removing any remaining excess of safranin).
5. Dehydrate in absolute alcohol.
6. Clear in clove oil.
7. Return to absolute alcohol and mount in 'Euparal'.

### Floral parts and leaves

Here lactic acid proved to be a most useful general reagent because: (i) it leaves plant crystals whole, (ii) it remains liquid at room temperature and (iii) semi-permanent preparations can be made by ringing the coverslip with rubber solution.



### Floral parts

Resuscitated florets, opened by splitting down one side, were mounted in lactic acid. After warming to accelerate clearing, the preparations were covered with glass slips. Achenes (complete with pappus) were also mounted in lactic acid and crushed by putting pressure on the coverslip. Florets and achenes demanding more drastic treatment were first bleached with chloral hydrate or nascent chlorine before mounting in the lactic acid.

### Leaves

These were best treated with lactic acid without prior resuscitation, since that process led to difficulties in interpreting stomatal structure. Where leaf hairs formed a dense mat, it was found more convenient to examine them in a detached state; but where a leaf was merely pubescent or seemingly glabrous, an epidermal preparation was examined for hairs.

### Pollen preparations

Semi-permanent pollen slides were prepared in the following way:

1. Place 2-3 young florets, with achenes and pappus removed, on a slide together with 1 drop of 5% KOH.
2. Warm gently over a spirit lamp and macerate the softened florets.



3. Remove the larger fragments and excess KOH.
4. Add 1-2 drops of melted glycerine jelly to the pollen remaining on the slide.
5. To stain, stir the suspension with a needle freshly dipped in aqueous safranin.
6. Cover pollen suspension with a warm glass slip.



SECTION III

OBSERVATIONS



### STOMATA

Regarding the arrangement of subsidiary cells associated with stomata on the abaxial leaf surface, only two of the angiosperm variants described by Metcalfe and Chalk (1950), anomocytic and anisocytic, occur in my sample of Compositae. The anomocytic state is the ~~most~~<sup>more</sup> widespread; but it seems likely that this condition could be further subdivided, for the precise number of cells and associated wall patterns vary greatly. Anisocytic stomata (not previously recorded for the family) seem to be restricted to African succulents (e.g. Kleinia, Othonna and certain Senecio species).

### FOLIAR TRICHOMES

It was probably the apparent uniformity of the floral parts which led early workers (e.g. Archer 1860 and Hayek 1915) to employ variation in foliar trichomes to help them classify Compositae. However such studies were limited to a very few genera (e.g. Olearia and Senecio section Tephroseris). Although a number of catalogues of hair types for Compositae have appeared (Solereider 1899, Metcalfe and Chalk 1950 and Ramayya 1962), I know of only one attempt (Stebbins 1953) to assimilate information of this kind into wider aspects of the taxonomy of the family.

In most Compositae, hairs vary in form from one region of the leaf to another and it seemed that the only way of obtaining



comparative information for a range of species in the time available was to confine my attentions to one part. I chose, arbitrarily, the mid-laminar region of the abaxial surface. Leaves were recorded as glabrous only when hairs could not be found after an intensive microscopic examination. By comparing drawings of hairs, 3 glandular and 15 eglandular types were characterised. Some plants (e.g. Aster tataricus) bear leaves with more than one hair type in the abaxial mid-laminar region and here all forms present were recorded. The 18 hair types are conveniently described and distinguished by presenting illustrations (fig. 1A-R) and a dichotomous key.

#### PITH

Pith structure is markedly variable in the family. Some species have lignified pith parenchyma while others do not; and occasionally one encounters sclereids scattered in an unligified medulla. A feature of many north temperate herbaceous Senecionideae is a tendency for the pith to break down, so that the aerial stem may be completely fistulose.

#### SECONDARY XYLEM

There is a striking diversity in the distribution and size of xylem vessel elements and there is further variation in the structure of rays as seen in transverse stem sections.

##### Vessel distribution

The variation in vessel distribution was rationalised by



FIGURE 1. Leaf hairs

1A-O are the 15 eglandular hair types, ABE-O (X 50),

CD (X 55).

1P-R are the 3 glandular hair types, P (X 150),

QR (X 50).

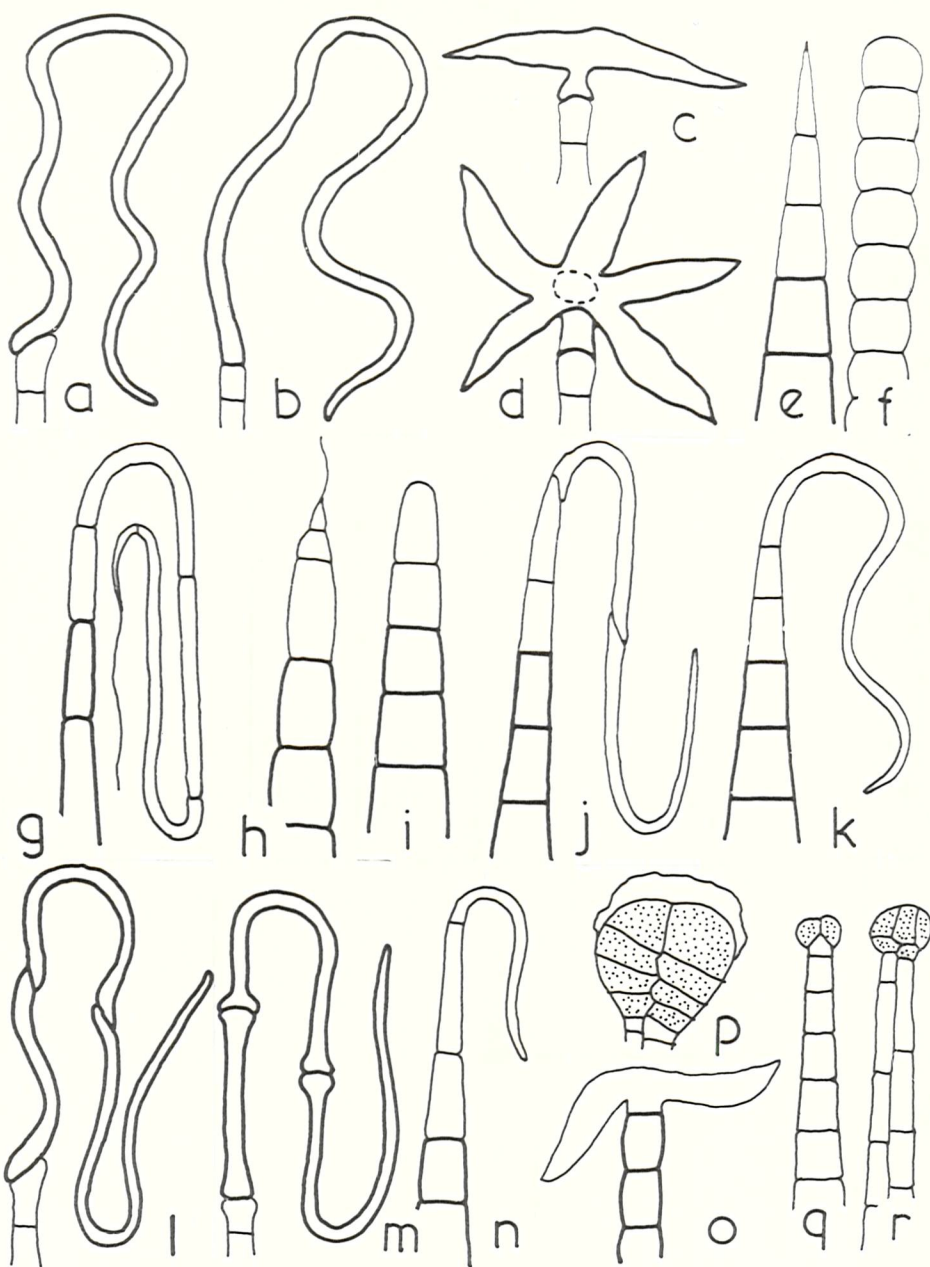


DICHOTOMOUS KEY TO HAIR TYPES

The letters correspond with the illustrations A - R in figure 1.

1. Terminal cells filled with oily contents, hair often capitate. . . . . 2  
Terminal cells vacuous, hair never capitate . . . . . 3
2. Hair uniseriate. . . . . Q  
Hair biseriate. . . . . 4
3. Hair with (1)-2-3(-4) small basal cells surmounted by a uni- or multicellular appendage. . . . . 5  
Hair without distinct basal cells, often tapering into uni- or multicellular flagellum. . . . . 6
4. Glandular head sub-sessile, with a membranous envelope containing oil. . . . . P  
Glandular head borne on a column of cells, without a membranous envelope containing oil. . . . . R
5. Appendage unicellular. . . . . 7  
Appendage multicellular. . . . . 8
6. Cells increasing in length and tapering towards the apex to form a flagellum. . . . . 9  
Cells all approximately the same length (occasionally with an abortive terminal cell), i.e. hairs non-flagellate. . . . . 10
7. Appendage attached to basal cells obliquely. . . . . A  
Appendage attached to basal cells horizontally. . . . . 11
8. Cells of appendage joined to one another obliquely. . . . . L  
Cells of appendage joined to one another horizontally. . . . . M
9. Distal 2 or 3 cells attached to each other obliquely. . . . . J  
Distal 2 or 3 cells attached to each other horizontally. . . . . 12
10. Hair tapering towards the apex, usually relatively thick-walled. . . . . 13  
Hair not tapering towards the apex, usually thin-walled. . . . . F
11. Appendage unbranched. . . . . B  
Appendage branched. . . . . 14
12. Hair tapering gradually towards the apex, tipped by a thread representing an abortive cell. . . . . G  
Hair tapering gradually towards the apex, tipped by 1-2(-3) greatly elongated cells. . . . . 15
13. Terminal cell abortive and thread-like. . . . . H  
Terminal cell complete and prominent. . . . . 16
14. Hair T-shaped. . . . . 17  
Hair stellate. . . . . D
15. Terminal only cell markedly elongate. . . . . K  
Distal 2-3 cells markedly elongate. . . . . N
16. Apical cell rounded. . . . . I  
Apical cell sharply pointed. . . . . E
17. Basal cells thin-walled; arms of appendage thick-walled and at right-angles to basal cells. . . . . C  
Basal cells thick-walled; arms of appendage thin-walled and not at right angles to basal cells. . . . . O







trial and error into the following 10 recognisable classes. A given species usually falls unambiguously into one or other of these classes; but species exhibiting intermediate conditions were scored for both.

1. Many of the vessels arranged radially in groups of 2 and 3, rarely solitary (fig. 2A).
2. Vessels usually solitary, scattered  $\pm$  evenly throughout the wood; occasionally in radial pairs (fig. 2B).
3. Vessels commonly in long radial rows of 5 or more elements (fig. 2C).
4. Vessels in dense concentric bands (i.e. ring porous, fig. 2D).
5. Vessels in radial rows of 3 or more cells long, interspersed with diagonal pairs and clusters of 3-5 elements (fig. 2E).
6. Vessels in narrow radial blocks of 2-3 cells wide, the rows within the blocks interrupted and the blocks themselves separated by wide bands of fibres (fig. 2F). This condition is distinguished from 9 by the absence of segmentation of the xylem cylinder.
7. Vessels in small clusters of up to 6 cells, interspersed with solitary elements and diagonally orientated pairs (fig. 2G).



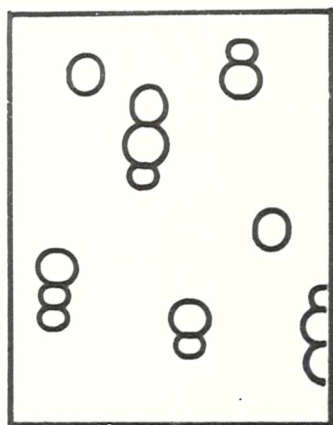
FIGURE 2: Vessel distribution patterns in transverse stem  
sections (not to scale)

Figures 2A - H represent vessel patterns 1 - 8  
respectively.

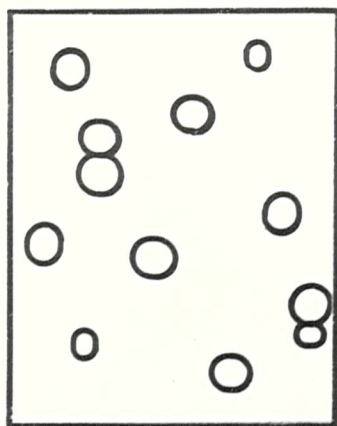
Figure 2I represents vessel pattern 9 and shows  
one segment of xylem cylinder containing  
vessel elements.

(see text for details)

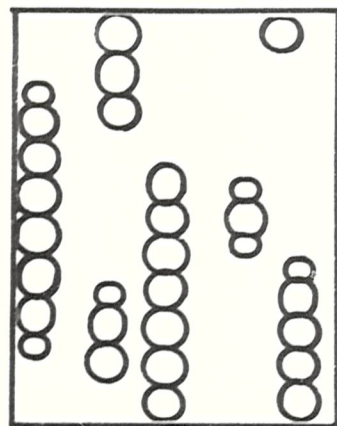




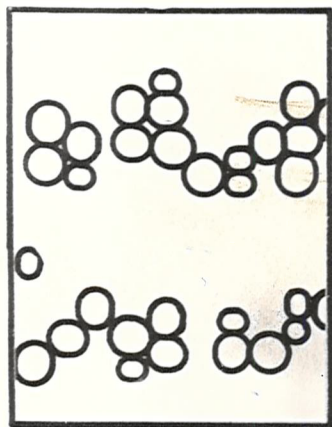
a



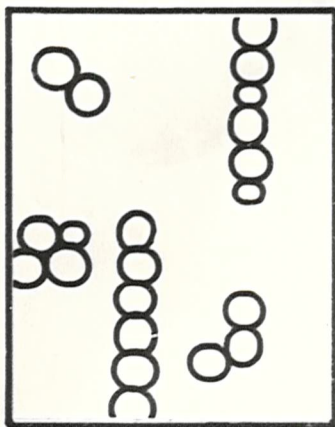
b



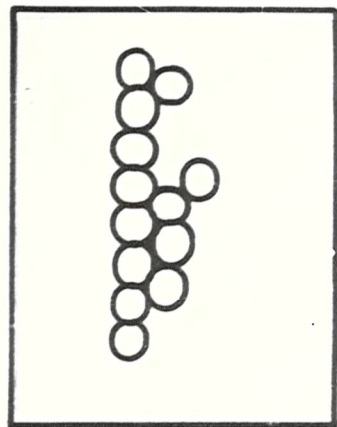
c



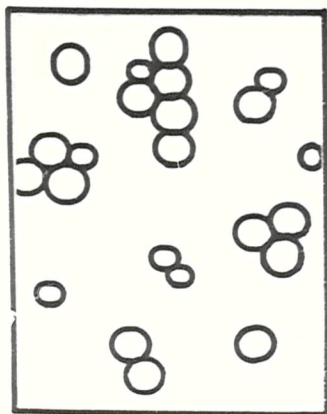
d



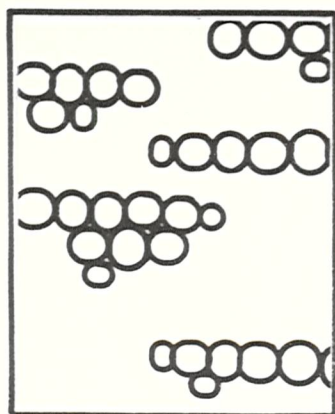
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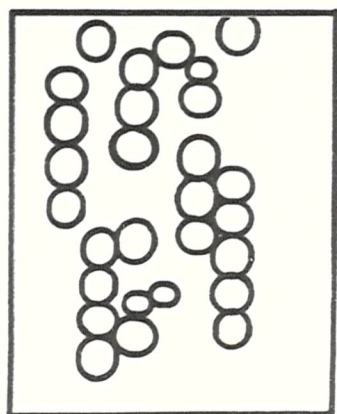
f



g



h



i



8. Vessels in scattered tangential bands, 4-8 cells wide and 1-3 cells deep (fig. 2H).
9. Xylem cylinder segmented, with alternate segments containing fibres only. Within the vessel segments, vessels arranged as in 6 but the radial rows closer (fig. 2I).
10. Vessels indistinguishable from the fibres in transverse section.

#### Vessel size

Since some of the species are ring porous, it would have been misleading to employ the means of diameters of vessels for taxonomic purposes. It seemed more reasonable to allow variation in the maximum vessel diameter to represent this aspect of the diversity among the species. The widest element was selected, for each species, from a random low power view (X 100) of a transverse stem section. Micrometer values were ordered and recorded under six arbitrary groups; for comparative purposes there was no need to convert them to an absolute scale.

#### Ray width

Variation in the width of the xylem rays was also ordered, this time into three states: (1) rays 1-3 cells wide, (2) rays 4-6 cells wide, (3) rays 6+ cells wide. Sometimes (e.g. in the leathery leaved Senecio species of New Zealand) rays fall between these arbitrary limits and here both states have been



recorded. In general, narrow rays are characteristic of Bentham's Microchaete, Euryops and some ericoid Senecio species, while wide rays are a feature of suffrutescent succulents and many herbaceous Senecio species with auricled sessile leaves.

#### INTERFASCICULAR CAMBIUM

Habit details such as overall size, presence or absence of rhizomes etc., which constitute some of the most conspicuous features of growing plants, are rarely given on herbarium sheets and cannot be safely deduced from the specimens. However, it is practicable to determine whether or not the aerial parts possess an interfascicular cambium. It is worth pointing out that a distinction based on this feature is not equivalent to the usual arbitrary separation into annuals, biennials and perennials. For example, it results in placing Senecio vulgaris (an annual with an interfascicular cambium) alongside shrubby plants; but this is not unreasonable in view of the fundamental significance of interfascicular cambium in determining the gross morphological potential of the plant.

#### PHLOEM

In cases where fibres occur in association with the phloem, one of two variants may occur in any given species. The fibres may be scattered throughout the phloem region (in extreme cases the pockets of active phloem occurring within a fibre matrix); or the active phloem and fibres may be present in discrete,



homogeneous regions with the fibres confined to the periphery of the vascular cylinder.

Certain frutescent Compositae have the fibre blocks linked one with another by slender uniseriate bridges of sclereids. These are readily distinguished from phloem fibres by their elongated-rectangular transverse section as well as their simple pitting and brighter red coloration when stained in safranin. Such 'joining sclereids' may occur associated with either of the two fibre patterns.

#### CORTEX

The stem cortex of Compositae is notable for its consistency. Besides the presence or absence of resin canals (see below) the only attribute I found to record was the presence or absence of isolated or grouped sclereids. These can be distinguished from joining sclereids by their more or less isodiametric aspect in transverse section, and in that they are never contiguous with the phloem fibres.

#### RESIN CANALS IN STEMS

Col (1894-1904) demonstrated that resin canals in Compositae originate schizogenously and tabulated data on resin canal position in a range of genera. He recognised three patterns of distribution, defined on the positions relative to the vascular bundles ("adpo~~x~~sé", "latero-dorsal" and "interposé"); but in my much larger sample it is necessary



to distinguish three additional types.

1. Cortical canals, spaced regularly in a ring in the mid-cortical region. Their position bears no obvious relation to that of the vascular bundles (uncommon).
2. Endodermal canals adjacent to the blocks of phloem fibres ("adpo~~X~~sé" of Col, widespread).
3. Endodermal canals between the blocks of phloem fibres (i.e. confined to species with homogeneous blocks of phloem fibres; including both "latero-dorsal" and "interposé" of Col, which seem indistinguishable; infrequent).
4. Canals within the phloem (only in Senecio hartwegii).
5. Pith canals, appearing in one or two concentric rings (uncommon). The canals of the inner ring or the single ring always develop opposite the protoxylem points. The members of the outer ring, if present, usually alternate with the canals of the inner ring.

Col's statement that resin canals are absent from the aerial parts of the Vernoniaceae is incorrect; actually they do occur in some of these plants (e.g. Chresta spp.), in the cortex and associated with the phloem fibres. This fact seriously detracts from 'phylogenetic' schemes for Compositae incorporating Col's data (e.g. Small 1917 et seq., Augier and De Merac 1951).



### NODAL CONFIGURATION

Despite the paucity of records, the complete range of nodal configurations recognised by Sinnott (1914) has already been demonstrated in Compositae (multilacunar, Dormer 1950; trilacunar and unilacunar, Solbrig 1961); but taxonomists have failed to take account of this diversity. I have recorded nodal types under four headings as follows:

1. Unilacunar, characterised by one foliar trace and one gap in the stele. Confined in Compositae to certain shrubby species (e.g. Olearia ramulosa and Senecio cassinioides) having small leaves with recurved margins.
2. Trilacunar, where three leaf traces leave three gaps (a widespread condition in Compositae).
3. Multilacunar, in which many traces leave a corresponding number of gaps; often associated with the scapigerous habit of herbaceous Compositae in the northern hemisphere.
4. 'Quinquelacunar', where there are constantly five stelar gaps associated with five leaf traces. It would appear that this kind of node has never previously been described. In Compositae it is found in certain aborescent species of the southern hemisphere (e.g. Brachyglottis, Albertinia and Olearia species).



## CRYSTALS

There is little information available on the structure, chemical composition and development of crystalline cellular inclusions. In fact Dormer's recent (1961) critical account of calcium oxalate crystals in certain Compositae is a landmark, although Dormer himself made it clear that his investigation was merely preliminary. Anatomists, following Sachs (1875), De Bary (1884) and Haberlandt (1914), generally recognise five crystal categories for calcium oxalate: (i) crystal sand, (ii) druses, (iii) raphides, (iv) individual angular crystals, (v) sphaerocrystals. Dormer's detailed work concerns only two of these categories, namely druses and individual angular crystals; but he found it necessary to subdivide the latter into (a) isodiametric crystals, (b) hexagonal crystals, (c) curvilinear crystals, (d) plate crystals.

### Crystal forms

Seven crystal types are distinguishable in the Compositae of the present sample. Of those listed below, types 5 and 6 are traditional categories, type 4 has already been described by Dormer (1961) and type 7 is new. Types 1, 2 and 3 (elongate, intermediate and isodiametric) represent subdivisions of Dormer's hexagonal crystals, which in the present sample display a considerable range in size. Records for individual species are here based in each case on measurements of five crystals selected as fully developed and typical.



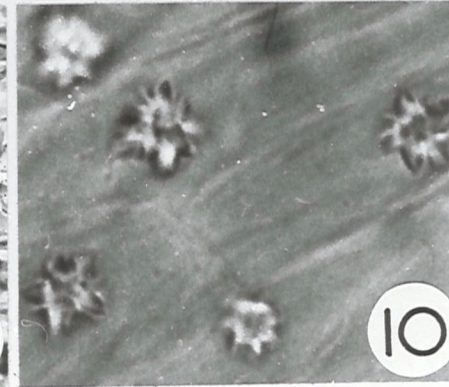
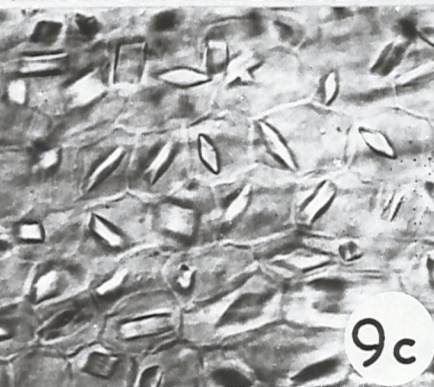
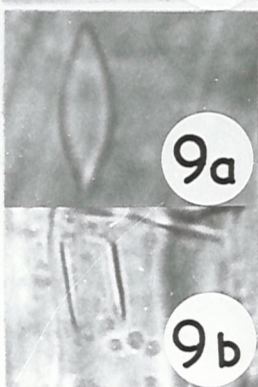
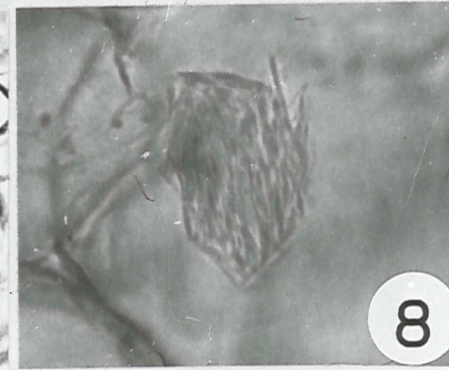
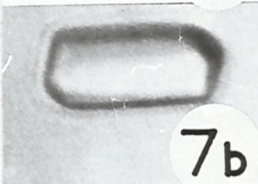
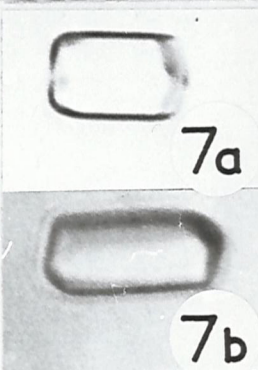
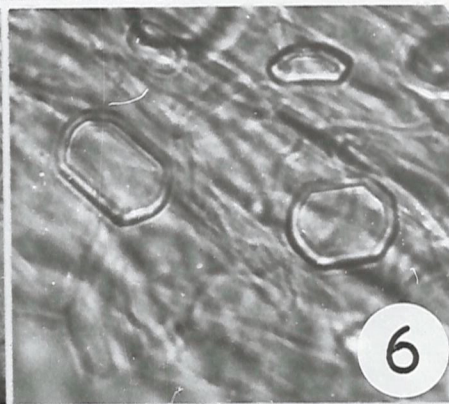
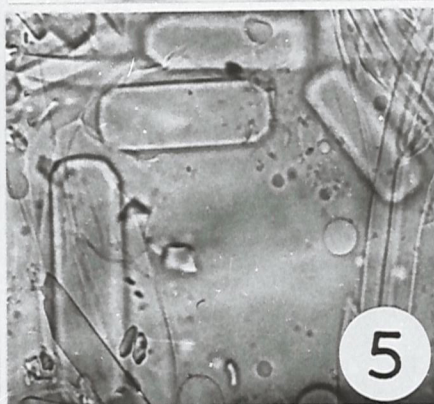
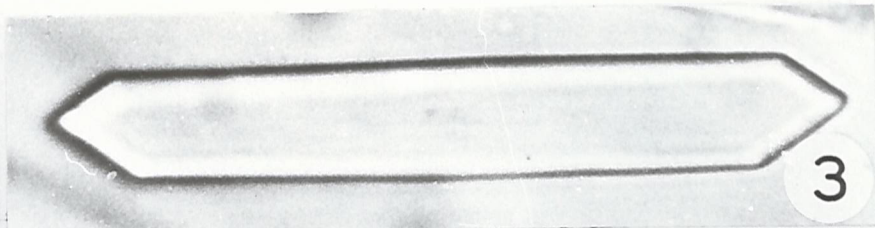
1. Elongate hexagonal crystals with a length/breadth ratio of 6 or more, and flat in side view (fig. 3).
2. Isodiametric crystals, with a length/breadth ratio of between 1-1.5, and flat in side view; not to be confused with the 4-sided isodiametric type described for Onopordon and Arctium by Dormer (fig. 6).
3. Intermediate hexagonal crystals with a length/breadth ratio between types 1 and 2 (fig. 4). In certain species (e.g. Senecio vulgaris) it is not uncommon to find them with truncate or rounded ends (fig. 5).
4. Curvilinear crystals in face view exhibit smoothly curved sides meeting to produce similar apices (fig. 9A and 9C). Forms narrower in face view and with dissimilar apices are described for Centaurea by Dormer (1962A). In side view they vary from square to rectangular (fig. 9B and 9C).
5. Druses, conglomerate or cluster crystals, are  $\pm$  spherical aggregations of small angular crystals (fig. 10), structurally comparable with those of Carthamus (Dormer 1961).
6. Raphides, (fig. 8).
7. Crystal mixture: the achene wall of certain Vernoniaceae contain a characteristic mixture of lozenge-shaped, cuboid and trapezoid crystals (along with **apparent** fusion products) which are relatively



FIGURES 3 - 10. Crystal forms

- Figure 3. Inula helenium, elongate hexagonal crystal from achene wall, X 2525.
- Figure 4. Senecio gregorii, intermediate hexagonal crystal with pointed ends from ovary wall, X 600.
- Figure 5. Senecio vulgaris, intermediate hexagonal crystals with truncate ends from the ovary wall, X 700.
- Figure 6. Senecio cernuus, isodiametric ovarian crystals X 2300.
- Figure 7. Albertinia eleagnus, crystal mixture.
- 7a and 7b. Individual crystals, both X 2800.
- 7c As seen in achene wall, X 1250.
- Figure 8. Solidago sempervirens, raphides in pith cell, X 1300.
- Figure 9. Ligularia stenocephala, curvilinear crystals.
- 9a. In face view, X 1200.
- 9b. In side view, X 1200.
- 9c. As seen in ovary wall, X 650.
- Figure 10. Senecio campestris, druses in achene wall, X 2100.







short in face view and broadly rectangular in side view (fig. 7A, 7B and 7C).

#### Distribution of the types

Crystals abound in the ovary and achene walls and also appear occasionally in stamen filaments, styles, epidermal cells of ray and disc corolla, in the pith and in the stem cortex. One usually finds that in a given species, crystals vary in form from <sup>one</sup> morphological region to another. It was practical to record only those found in ovary, achene and pith.

In the ovary, crystal types 1, 2, 3, 4 and 5 can occur singly, although types 4 and 5 are frequently associated. However it is uncommon to find types 1, 2 and 3 mixed with types 4 and 5. Achenial crystals when present seem to show less variation and are limited to types 1, 4, 5 and 6. Types 1 and 6 always occur singly, while 4 and 5 can be present together. Types 2, 4, 5 and 6 have all been found in the pith parenchyma, but always singly.

#### ACHENIAL HAIRS

Achenes of Compositae are commonly adorned with eglandular hairs of a characteristic form. Their structure was first elucidated in an admirable but neglected paper by Macclowskie (1883), who showed that each hair is duplex with two additional cells associated with its base (fig. 11 and 12). Among hairs of this kind there seem to be two main variants:



FIGURES 11 - 16

Figures 11, 12, 15 and 16. Illustrations of achenial hairs

Figure 11. Arnica montana, thick-walled type with apices of duplex cells diverging and pointed, X 400.

Figure 12. Senecio vulgaris, thin-walled type with apices of duplex cells appressed and rounded, X 900.

Figure 15. Senecio gregorii, tip of hair showing the spiral nature of contents in duplex cells, X 1800.

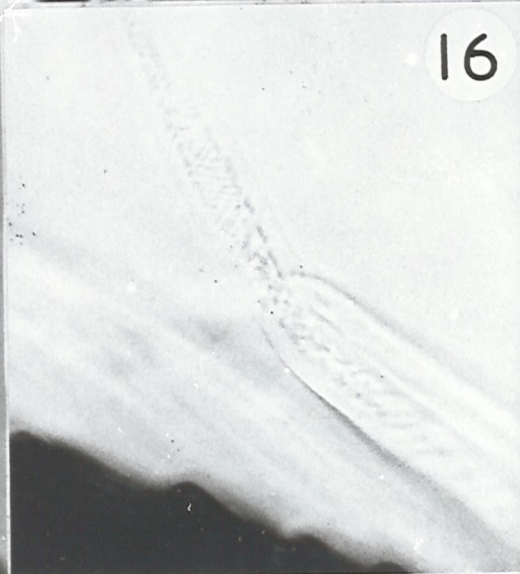
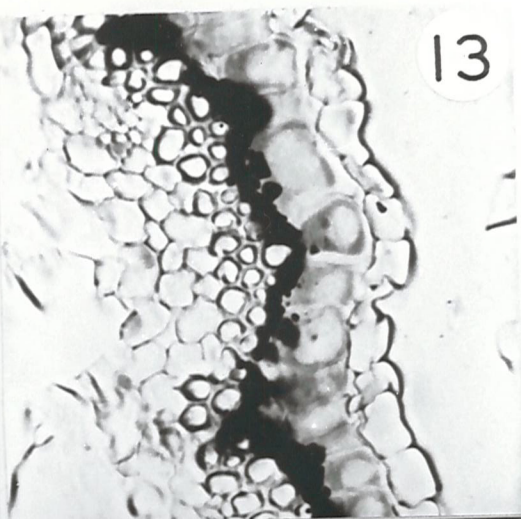
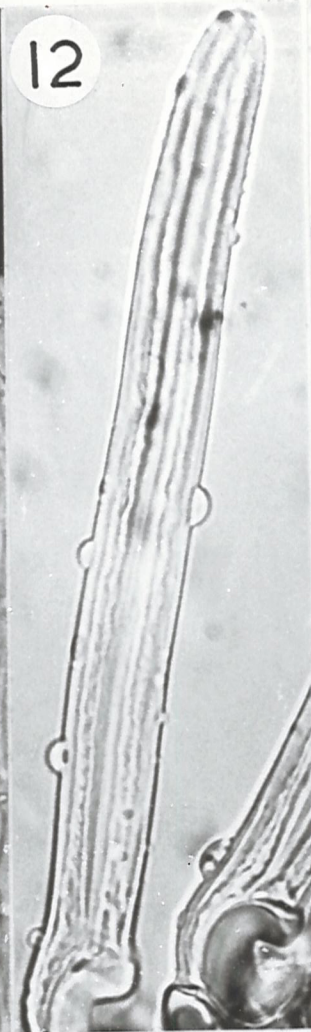
Figure 16. Senecio vulgaris, tip of hair showing exuded spiral, apparently contained in a sheath (only one duplex cell in focus), X 950.

Figures 13 and 14. Illustrations of 'carbonaceous' layer

Figure 13. Arnica montana, transverse section of mature achene showing the sub-epidermal origin of the carbonaceous layer, X 450.

Figure 14. Arnica montana, carbonaceous layer as seen in surface view, X 350.







1. Hairs with duplex cells thick-walled and frequently pitted, their apices sharply pointed and diverging (common in the Asteroideae and Vernoniaceae, fig. 11).
2. Hairs with duplex cells thin-walled, without marked pitting and with rounded appressed apices (common in the Senecionideae, fig. 12 and 15).

To these distinguishing features I tentatively add another. MacIowski showed that in some cases the contents of the duplex cells ultimately assume the form of spirals (fig. 15) which are extruded under wet conditions (fig. 16). There has been some speculation regarding the functional significance of this curious phenomenon (Green 1964). It seems in fact to be confined to those achenial hairs of my type 2; for I have observed it in about 70% of the species under this heading, but never in species with the thick-walled hairs of type 1.

#### 'CARBONACEOUS LAYER'

During the maturation of the achenes of certain species, brown substances appear sub-epidermally (fig. 13) as small amorphous particles distributed irregularly just below the insertion of the pappus. At a later stage the entire achenial surface between the ribs assumes a black-brown mottled appearance (fig. 14). Hanausek (1920) referred to this layer as 'carbogenic' since his chemical analysis of it revealed a great quantity of carbon; but Mayers (personal communication)



suggests that it probably consists of the polyphenol, melanin. This so called 'carbonaceous' layer is manifest throughout the tribes Helianthoideae, Helenioideae and in most of the Eupatoriaceae seen by me as well as in occasional genera of Vernoniaceae and Senecionideae. Here I have simply recorded its presence or absence for every species examined.

#### PAPPUS

Taxonomic descriptions of pappus are invariably crude and empirical. Terms like setose, pilose, paleaceous, coroniform and aristate, stabilized by Cassini (1816-30), are still in use. The species considered here are mostly setose, but nevertheless there is manifest variation among them in pappus construction (Drury and Watson 1965). For the purposes of the present exercise however the distribution of only three very distinct variants (ordinary, clubbed and fluked) has been noted. Their structural characteristics are presented in Fig. 17, 18 and 19 and contrasted in Table 2.



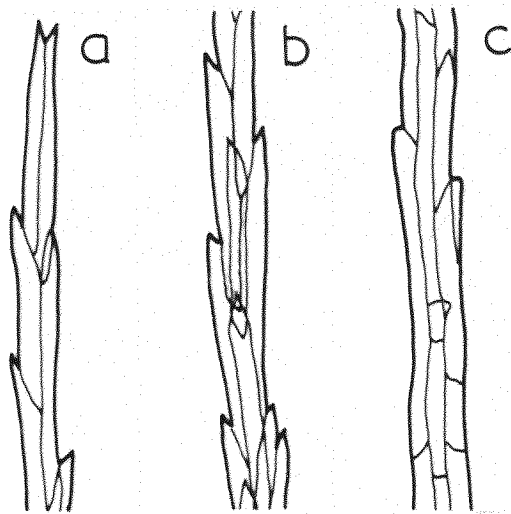
FIGURES 17 - 19. Pappus structure

- Figures 17a-c Senecio bidwillii, clubbed pappus bristle,  
X 30.
- 17a Apical region showing swollen cells crowded  
together.
- 17b Portion of middle region.
- 17c Portion of basal region.
- Figure 17d Microchaete glabrata, apical region of  
clubbed pappus bristle, the swollen cells  
not crowded together, X 30.
- Figures 18a-c Senecio rigidus, ordinary pappus bristle,  
X 40.
- 18a Apical region.
- 18b Portion of middle region.
- 18c Portion of basal region.
- Figures 19a-c Senecio rigidus, fluked pappus hair, X 40.
- 19a Apical region.
- 19b Portion of filamentous middle region.
- 19c Portion of basal region.
- Figure 19d Senecio californicus, apical region of  
fluked pappus hair showing exaggerated  
downward spines, X 40.

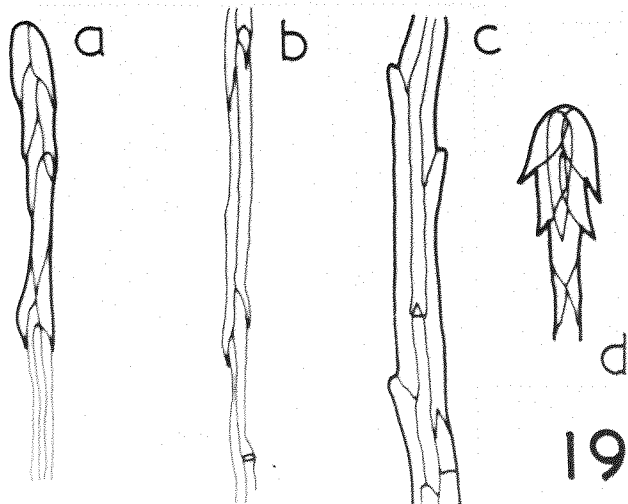




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18



19



TABLE 2: Comparison of pappus types.

CLUBBED	ORDINARY	FLUKED
1. Hairs consisting entirely of thick-walled cells, their lumina relatively wide.	Hairs consisting entirely of thick-walled cells, their lumina relatively wide.	Hairs with cells of the middle region thin-walled and filamentous, their lumina relatively narrow.
2. Hairs <u>not</u> tapering from the middle region to the apex.	Hairs gradually tapering from the middle region to the apex.	Hairs <u>not</u> tapering from the middle region to the apex.
3. Cells in the middle and apical regions having their <u>upper</u> ends produced to form external elongations or spines.	Cells in the middle and apical regions having their <u>upper</u> ends produced to form external elongations or spines.	Cells in the middle and apical regions having their <u>lower</u> ends produced to form external elongations or spines.
4. Cells of the distal region swollen and crowded together to form a head.	Cells of the distal region <u>not</u> swollen and crowded together.	Cells of the distal region swollen and crowded together to form a head.
5. Hairs rigid.	Hairs rigid.	Hairs flexuous.
6. Hairs detaching easily when achene mature.	Hairs detaching easily when achene mature.	Hairs <u>not</u> detaching easily when achene mature.



Pappus bristles in most of the setose species seen by me are of the ordinary type. However, in some members of the genus Senecio (e.g. Senecio vulgaris), the bristles of individual achenes fall into two morphological categories. Here, the majority are of the ordinary kind, but restricted to one region on the outer of the two irregular pappus whorls are 5-10 fluked hairs. Clubbed hairs are not normally found mixed with the other forms, but Senecio quinquelobus is exceptional in having a mixture of both clubbed and fluked hairs. In the present sample of Compositae clubbed bristles are confined to certain representatives of the Asteroideae (e.g. Olearia rani) and Senecionideae (e.g. Senecio bidwillii).

#### ANTHER TAILS

Certain appendages associated with the base of the pollen-sac, the so-called 'tails' (caudae) and the 'auricles', have been considered important characters in classifying Compositae ever since their presence and distribution were brought into prominence by Cassini (1826 et seq.). Lessing (1832) often employed them for diagnostic purposes and De Candolle (1836) used the presence of tails to help characterise the Helianthoideae and the divisions of his Vernonidae. Bentham (1873B) utilised the variation in form and degree of adhesion of the tails to define 11 categories, and Small (1917) added still more; but I have been unable to apply their minor



distinctions using herbarium material and have chosen to ignore them. It is astonishing that during the long history of its usage, there has been no endeavour to define the meaning of the expression "anthers tailed"; and the morphological relationship between tails and auricles has been persistently overlooked. It has been necessary, therefore, to reconsider the gross morphology of the anther.

In Liabum discolor and certain other species, the anthers are dorsifixed so that each pollen-sac is furnished with fertile processes (the auricles of Benthams, fig. 20) below the filament insertion. In contrast the anthers of some species (e.g. Senecio vulgaris, fig. 21) are basifixed, i.e. without auricles. However, many cases occur (e.g. Senecio greyi, fig. 22) where the anthers are 'basifixed', but display sterile cellular appendages emanating from the base of the pollen bearing region. These are the so-called tails, and it seems reasonable to interpret them as sterile auricles. Thus there are three anther types involved:

1. Anthers with fertile auricles (fig. 20), including in practice all those traditionally "auricled".
2. Anthers with sterile auricles (fig. 22), taking in all those traditionally "tailed".
3. Anthers without auricles (fig. 21).

In practice some species (e.g. Senecio bidwillii) in groups long described as "tail-less" do in fact possess sterile



FIGURES 20 - 28

FIGURES 20-22. Illustrations of stamens, showing variation in form of filament collar and bases of pollen-sacs below the filament insertion.

- Figure 20     Liabum discolor with fertile auricles,  
X 200.
- Figure 21     Senecio vulgaris with baluster-form filament  
collar and no auricles, X 300.
- Figure 22     Senecio greyi with a cylindrical filament  
collar and with sterile auricles, X 200.

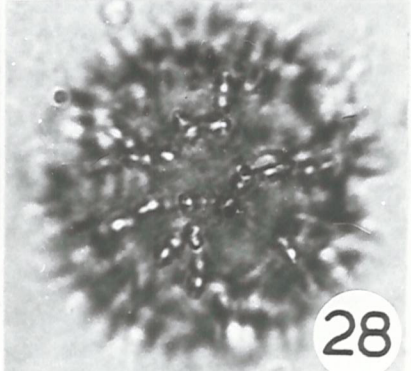
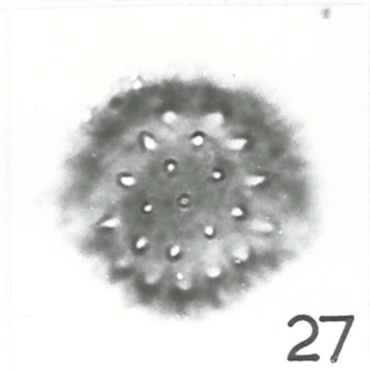
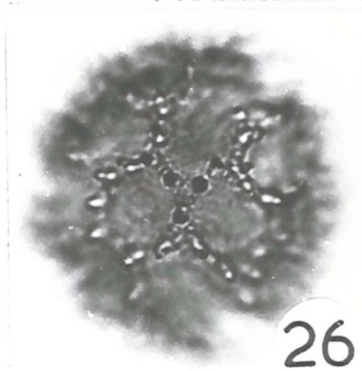
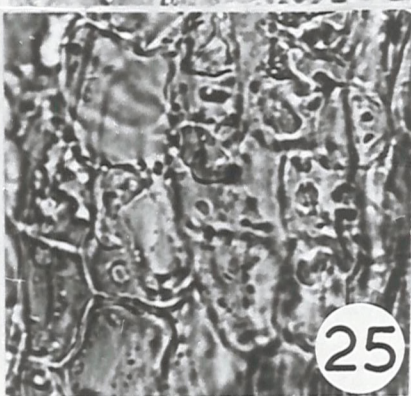
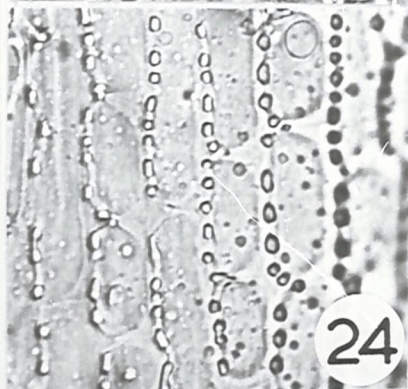
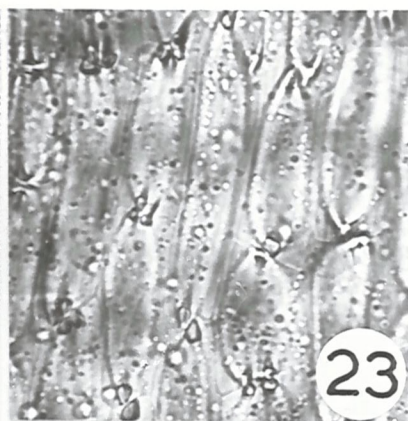
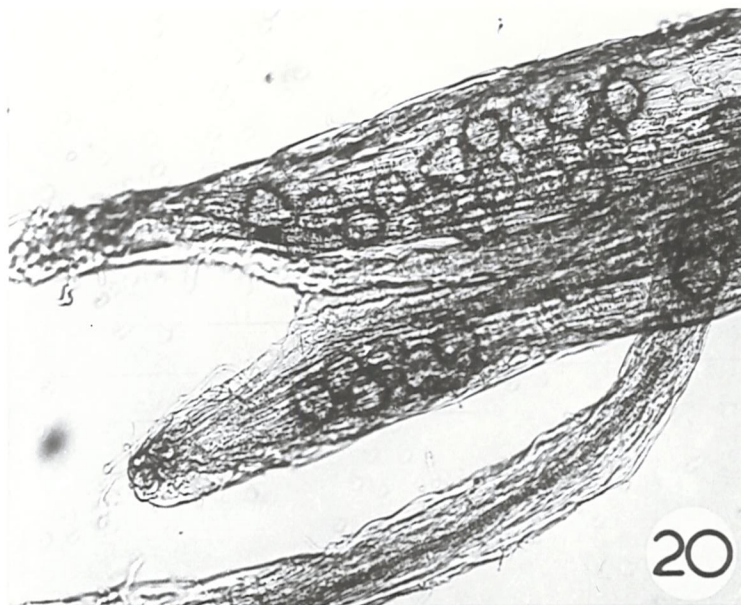
FIGURES 23-25. Fibrous layer of anther wall in surface view; longitudinal axis of the anther vertical.

- Figure 23     Senecio greyi, polarised tissue, X 680.
- Figure 24     Senecio vernalis, radial tissue, X 530.
- Figure 25     Chresta sphaerocephala, transitional tissue,  
X 700.

FIGURES 26-28. Illustrations of pollen types.

- Figure 26     Chresta exsucca, lophate grain with regular  
lacunae, X 850.
- Figure 27     Ligularia stenocephala, echinate grain  
X 740.
- Figure 28     Lychnophora affinis, lophate grain with  
irregular lacunae, X 810.







auricles. This discrepancy may have arisen because previous workers were using different definitions, which they never recorded. Alternatively, it is possible that some recorded 'observations' represent extrapolations of the kind to which taxonomists have been especially prone.

#### FILAMENT COLLAR

The stamens of Compositae are probably unique in possessing a downward extension of connective tissue which forms an incomplete monostromatic collar of thick-walled cells, the incomplete portion lying on the adaxial side of the filament. The functional significance of this region remains unexplored, but the combination of thick and thin-walled cells suggests that it might be concerned with anther movements. It was first noted by Cassini (1826) who knew it as "l'article antherifere", and I refer to it here as the 'filament collar'. In the present sample of Compositae, filament collars are generally referable to one of two previously undescribed forms:

1. Baluster-form. Here the collar is basally distended, reflecting the presence of enlarged cells in its lower part (restricted to certain genera of the tribe Senecionideae, fig. 21).
2. Cylindrical. Here the collar is cylindrical, and there are no enlarged cells. (occurs throughout



the Inuloideae, Helianthoideae, Calendulaceae,  
Asteroideae and Vernoniaceae, fig. 22).

Intermediates between the two forms (i.e. where the collar shows indistinct swelling) are remarkably rare, having been found in only 3/369 species.

#### FIBROUS LAYER

Recently Dormer (1962B) has reported on the taxonomic significance of variations in endothecium (fibrous layer) histology involving the abaxial surface of the anther in Compositae. The three tissue types outlined by him are readily recognised, and new definitions are not required for the present purpose. Their characteristics can be summarised as follows:

1. Polarised tissue consists of endothelial cells (when viewed in optical section) with wall thickenings in the form of ribs strongly concentrated upon their upper and lower ends (fig. 23).
2. Radial tissue has endothelial cells which, when viewed in situ, are seen to be ribbed all round (fig. 24).
3. Transitional tissue consists of endothelial cells, the side walls of which seem to be without special thickening; but the outer faces carry predominately transverse bands or plates of thickening, often with



cross connections (fig. 25).

Dormer mentioned the distribution of fibrous types for a very small sample from 10 of the 13 tribes of Compositae. My more extensive survey, while confirming the usefulness of his tissue types, necessitates some modifications of his taxonomic conclusions. Thus the Cichoriaceae are not unique in having transitional tissue on the abaxial flap of the anther, for Vernoniaceae (which he neglected to examine) also show this condition. Moreover, although Dormer demonstrated the heterogeneity<sup>e</sup> of the Senecionideae by revealing the distinction between Petasites, Tussilago and Doronicum (genera with polarised thickenings) and Senecio (with radial thickenings), the inconsistency in this tribe is, in fact, more serious than he suspected; for there is marked variation in this respect within the genus Senecio itself.

#### POLLEN

Stix (1960), with the aid of electron-micrographs, observed variations in exine stratification and was thus able to distinguish 45 pollen types in 225 species of Compositae. She pointed out that grain size and aperture form and number do not help in the delimitation of pollen types, since size varies within species and tricolporate grains are the rule. However, she did not attempt to correlate her morphological observations with other features; and since for the most part



her species do not coincide with mine, I have been able to make only indirect taxonomic use of her conclusions (see Section VI). The direct observational data on pollen recorded in this thesis are limited to the distribution of two variants, readily detected under the light microscope.

1. Lophate grains have spines forming a reticulum on the surface, often associated with ridges (e.g. Chresta, fig. 26 and Lychnophora, fig. 28). This condition has long been known in the Cichoriaceae (Wodehouse 1935); but it also occurs in certain Vernoniaceae and the genus Liabum.
2. Echinate grains have evenly spaced spines and no ridges (fig. 27). They are found in the Helianthoideae, Asteroideae, Inuloideae, Calendulaceae, Senecionideae and Eupatoriaceae.

Grains of a given species can usually be ascribed to the one condition or the other, although in the lophate state the lacunae are sometimes (e.g. fig. 28) less conspicuous than in fig. 26.

#### RAY FLORETS

Nineteenth-Century taxonomists recognised two kinds of ray floret, namely ligulate and filiform. The terms are still in use, but have never been defined with any precision. In fact, the two floret types seem readily distinguishable as follows:



1. Florets with long, conspicuously vascularised ligules, (ligulate florets).
2. Florets without ligules, or with short ones bearing no vascular traces (filiform florets).

However, since earlier workers neglected to publish definitions for the floret types, it is possible that distributions of the types<sup>as</sup> recorded by me in the present sample of Compositae will not coincide exactly with their descriptions of these same plants.

Investigation of ligulate rays reveals variation in venation pattern, which can conveniently be reduced to three classes:

1. A 4 nerved condition, which is the most common and is usually exhibited by medium sized rays. Here, 4 traces emanate from the tube and approach the tip of the ligule. Usually the inner two bifurcate near the ligule tip, their outer arms joining with the incurving laterals to produce two vascular arches; and the inner arms fuse to form a third (fig. 29). A few species (e.g. Senecio sylvaticus) have florets which are best placed under this heading, but which are exceptional in having 4 free traces falling short of the ligule tip.
2. A 4+ nerved condition, which is less common and is associated with large ligules. This state can best



be pictured as a modification of the 4 nerved type, with supernumerary traces which never contribute to the vascular arches (fig. 30).

3. A 4- nerved condition, which is uncommon, and characterises species with small ligules. The vascular traces number 1-3 and are never joined to form arches.

The recognition of these three venation categories successfully eliminates <sup>intra-</sup>specific variation, which rules out a system based on absolute vein number; and species are usually constant for the venation patterns. In a very few instances, where a plant shows two of the three pattern types, there is never any difficulty in deciding on the typical condition; and in such cases the most frequent expression has been recorded as representative.

De Candolle remarked on the presence of staminodes in certain genera (e.g. in Arnica and Ligularia), and I am able to extend the list considerably. Observations are here confined to a record of the presence or absence for each species of infertile stamen-like structures in the throats of ray florets.

#### GROSS MORPHOLOGY

Some characters customarily mentioned in descriptions and diagnoses have been purposely disregarded. It is impossible

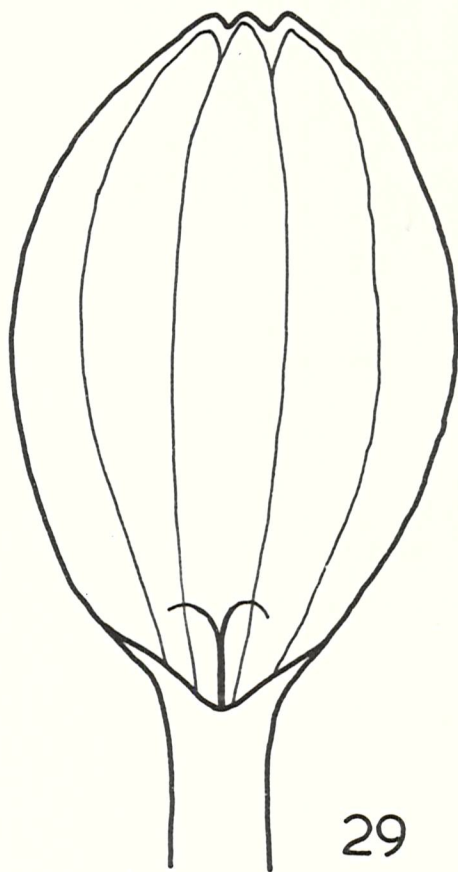


FIGURES 29 and 30. Ligule venation patterns.

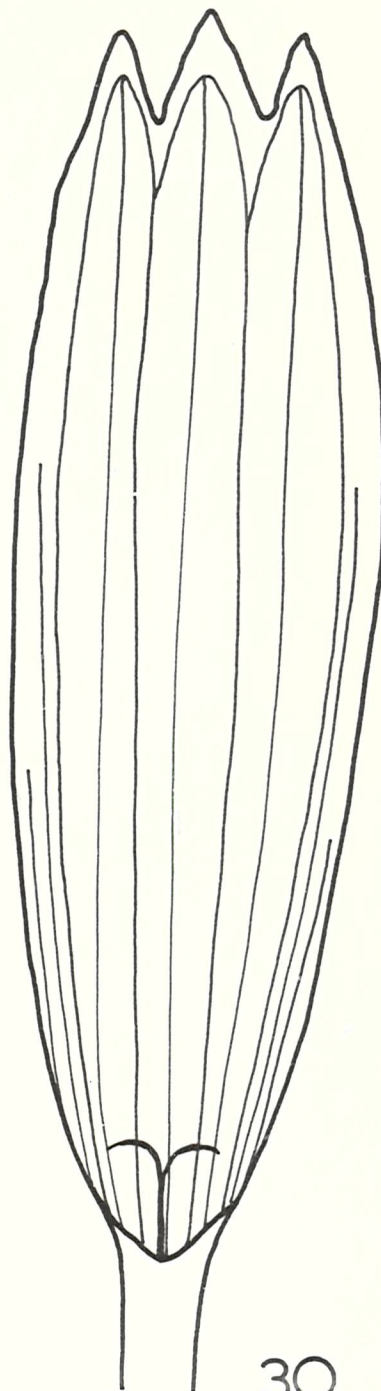
Figure 29 Senecio rigidus, 4 nerved condition, X 23.

Figure 30 Arnica montana, 4+ nerved condition, X 8.





29



30



or impracticable to arrive at reliable comparative data for such features as habit, capitulum size, floret colour, subterranean<sup>e</sup> parts, number and proportion of floret types and styler form using herbarium material. Furthermore, several features commonly mentioned loosely in taxonomic work are still in need of satisfactory definition: e.g. number of rows of involucral bracts, 'inflorescence' and styler construction. However, certain features of gross morphology, although commonly overlooked, readily lend themselves to unambiguous recording:

1. Phyllotaxy: leaves opposite or 'alternate'.
2. Leaves with or without petioles, or having the lamina decurrent on the petiole (i.e. three variants).
3. Regarding leaf venation, the sample includes:
  - (a) Radiate or Palmate (as in Tussilago farfara), where the veins diverge from the base of the lamina.
  - (b) Pinnate (as in Senecio fuchsii), where the laterals diverge from points along a midrib.
  - (c) Arched or parallel (as in Senecio segmentatus, somewhat intermediate between classes (a) and (b) ), where lateral veins diverge from near the base of the lamina and run more or less parallel with the midrib.



SUMMARY OF RECORDED OBSERVATIONS

Each of the 45 characters listed below has been consistently recorded for a sample of 369 species, taken from 7 of the 13 tribes recognised by Benthham (1873): Helianthoideae - 6 spp., Inuloideae - 3 spp., Calendulaceae - 7 spp., Vernoniaceae - 10 spp., Eupatoriaceae - 2 spp., Asteroideae - 28 spp., and Senecionideae - 313 spp. The comparative data are fully recorded in Appendix I. Slides have been deposited with the Curator of the Manchester Museum.

Stomata

1. anisocytic/anomocytic

Foliar trichomes

2. eglandular, present/absent

3. eglandular type, (15 forms)

4. glandular, present/absent

5. glandular type, (3 forms)

Pith

6. collapsed pith, present/absent

7. if not collapsed, then

lignification present/absent

8. sclereids, present/absent

Cambium

9. interfascicular cambium,  
present/absent

Secondary xylem

10. vessel distribution (10 types)

11. size of widest vessel (6  
categories)

12. xylem rays, present/absent

13. width of xylem rays (3 categories)



- |                           |  |
|---------------------------|--|
| <u>Phloem</u>             | 14. phloem fibres, present/absent                                  |
|                           | 15. lignified phloem, present/absent                               |
|                           | 16. joining sclereids, present/absent                              |
| <u>Cortex</u>             | 17. sclereids, present/absent                                      |
| <u>Resin canals</u>       | 18. resin canals, present/absent                                   |
|                           | 19. position of resin canals (5 categories)                        |
| <u>Node</u>               | 20. nodal configuration, (4 categories)                            |
| <u>Crystals</u>           | 21. pith crystals, present/absent                                  |
|                           | 22. pith crystal type, (4 forms)                                   |
|                           | 23. achenial crystals, present/absent                              |
|                           | 24. achenial crystal type, (4 forms)                               |
|                           | 25. ovarian crystals, present/absent                               |
|                           | 26. ovarian crystal type, (5 forms)                                |
| <u>Achenial hairs</u>     | 27. disc floret achenes with duplex hairs present/absent           |
|                           | 28. if duplex hairs present, then thick-walled type present/absent |
| <u>Carbonaceous layer</u> | 29. carbonaceous layer, present/absent                             |
| <u>Pappus</u>             | 30. pappus on disc florets, present/absent                         |
|                           | 31. if pappus present, setose present/absent                       |



32. if pappus present and setose,  
fluked hairs present/absent
33. if pappus present and setose,  
clubbed hairs present/absent
- Anther tails 34. stamen auricles present/absent
35. if present, fertile/sterile
- Filament collar 36. cylindrical/baluster-form
- Fibrous layer 37. fibrous layer type (3 forms)
- Pollen 38. lophate/echinate
- Ray florets 39. ray florets, present/absent
40. if ray florets present, then  
filiform, present/absent
41. if ray florets present, then  
staminodes, present/absent
42. if ray florets present and not  
filiform, venation type, (3  
categories)
- Gross morphology 43. leaves opposite/alternate
44. leaves with/without petioles/  
decurent lamina
45. leaf venation, palmate/pinnate/  
parallel



SECTION IV

PROCESSING THE DATA



### HIERARCHICAL INTERPRETATION OF THE DATA

The most useful system of classification for biological material is one based on overall resemblances; for besides providing a convenient repository for known facts, it offers the hope of successful prediction where information is not yet available. The appended data sheets contain the observational records involving over 100 entries for each of 369 species of Compositae. In order to arrive at a scheme reflecting overall similarities among these plants, it is necessary first to compare every line with every other and then to order the species accordingly: the method is basically the same as in classical taxonomy, but the more numerous observations are fully recorded. The large range of the observational data however, leads to a problem of interpretation. Manifestly the task of simply calculating all possible  $2 \times 2$  comparisons for 369 species would be very laborious, and the subsequent sorting even more so. Some form of mechanical computation is indicated, and fortunately I have had access to computation facilities and a recently developed taxonomic programme at the Computing Research Section, C.S.I.R.O., Canberra, Australia. I am no mathematician and have used the computer merely as a taxonomic tool. However, it is necessary to make some remarks on numerical taxonomy, and to discuss briefly the programme used, before attempting to interpret taxonomically the results



of the analysis.

### COMPUTATIONAL METHODS

Fundamentally there are two methods of classifying individuals using multivariate data: 'hierarchical' and 'non-hierarchical'. Of these only the hierarchical method need concern us here; for it alone enables individuals to be compared with each other at any desired level of similarity - a distinct advantage in taxonomic work where one wishes to relate each organism ultimately with every other.

Hierarchical classifications may be achieved by either 'subdivisive' or 'agglomerative' processes. The former commences the analysis with all the information for the whole population, which is subjected to successive dichotomous divisions. At present, the only operational programme employing this method is 'Association Analysis' (Williams and Lance 1958, Williams and Lambert 1959, 1960 and 1961). The drawback to its full scale application to taxonomic data is that the resulting classification is 'monothetic'; i.e. the membership of a group is dependent on the possession by all its members of a single attribute (comparable with a taxonomic key character). Consequently it misclassifies in cases where an individual fails to exhibit the key character of its group: a situation which is probably commoner in biological material than existing taxonomic schemes, based often on too few



observations, would lead one to believe.

Agglomerative ('polythetic', 'similarity') methods do not suffer from this weakness since they involve progressively fusing most like individuals, until the entire population forms one composite individual. The classificatory process here depends entirely on overall similarities between individuals being compared, and there is no question of 'key characters'. Thus it is possible to employ different kinds of sorting procedure together with a variety of similarity coefficients, and the possible combinations are seemingly unlimited; but there is a growing body of evidence that useful taxonomic groups tend to emerge regardless of the variation in the numerical approach (e.g. Watson, Williams and Lance 1966).

#### THE PROGRAMME 'MULTIST'

The similarity programmes worked out by Sneath (1957), Sneath and Cowan (1958) and Sokal and Sneath (1964) cater exclusively for 'qualitative' data (i.e. expressed simply as +/-). While these may represent the only way of dealing with the empirical characters so often used in classifying bacteria and fungi, the logical inconsistencies and failings inherent in such an approach are readily seen when one considers it in relation to the taxonomy of higher plants. First, these programmes are unable to manipulate satisfactorily numerical (i.e. measured) information. To overcome this limitation such



information has to be ordered and each data class awarded the status of a unit character. In practice this increases the number of characters representing quantitative variation, so that numerical data come to be heavily weighted over other kinds of information.

Secondly and more seriously, difficulties arise with qualitative programmes in connection with 'multistate' and 'inapplicable' characters. These, and the problems they pose, are exemplified in my data by the records concerning eglandular hairs. In comparing any two individuals, the question has to be answered: hairs present or absent? Then, if hairs present, of what type (15 having been described)? If they are absent, the latter question is without meaning, and is logically inapplicable. Using a qualitative similarity method however, the individual must be scored with a negative or a positive for every one of the known types if variation in hair form is to be accounted for at all, regardless of whether the question of hair type is meaningful or not. Consequently, two glabrous species will be awarded 15 'similarities'; *(taking into account negative malitae)* and two species with different hair types will be regarded as having 2 points of difference, not one. In other words, hair characters will be given disproportionate weight, and spurious differences and similarities will be created. The results of this kind of thing can only be taxonomic distortion.

The programme 'Multist' of Williams and Lance, written



for the Control Data 3600 computer at Canberra, is a first attempt to overcome these difficulties. It is an agglomerative polythetic method incorporating 'centroid' sorting. There is strong evidence that this sorting method is most efficient in the delimitation of clear cut groups in ecological data (Lance and Williams in press, Williams, Lambert and Lance in press). Starting with the whole population, most-like individuals fuse to form groups; each group on formation comes to be represented by a hypothetical individual conceived out of its components, and this process continues progressively until all individuals have fused to form a single population. In the case of multistates, similarities are calculated on a proportional basis and numerical characters are assimilated into the analysis directly.

'Multist' has been explored in practice by Ducker, Williams and Lance (1965) and in a very recent article on angiosperm taxonomy by Watson, Williams and Lance (in press). The prototype programme as applied to Ducker's small-scale algal problem carried with it two serious imperfections:

- (i) Unknown or inapplicable qualitative data were treated as applicable and negative.
- (ii) The presence of an unknown or inapplicable record in a multistate character was considered as an additional state, so that artificial similarities and differences were created.



These faults were corrected in the version of the programme used in the analysis of Watson's data for Ericales. The latest version of the programme, as applied to Compositae, incorporates a further refinement to deal with non-exclusive multistate characters (e.g. eglandular hair type and ovarian crystals), where a species can exhibit more than one state of a multistate character.

However, Watson, Williams and Lance have pointed out certain defects which are inherent in any agglomerative method such as 'Multist'. First, the early fusions are made where information content is lowest and the chances of error highest, so there is an inherent likelihood that an occasional individual will later prove to have been misplaced. This danger can be minimised, but not completely eliminated, by using a large number of attributes. It is worth stressing however that both Ducker and Watson obtained meaningful groupings with considerably less information than is available for Compositae, so it was reasonable to hope that the results of the present analysis would be no less meaningful. Secondly, it may be found that early in the analysis an individual X is undoubtedly more like the members of group 1 than group 2; it is therefore added to 1. However as the group grows, individuals may be added to 1 which are increasingly unlike X; later in the analysis therefore, it may become clear that X would, on balance have been better in group 2. This is called the



'migration problem'. The presence of one or more misplaced species within a group will automatically affect the constitution of the hypothetical individual representing that group in the computation. This will in turn influence the future course of the analysis and may lead to further misclassifications. The practical implication of these drawbacks is that, in evaluating a 'Multist' analysis, one should be particularly suspicious of any tiny groups which join large assemblages at high levels of dissimilarity: they may be genuinely isolated, or they may merely represent misclassification or migration.

Despite the optimism of some practitioners, numerical taxonomy is still at a very primitive stage: one cannot yet simply put in the information and extract an ideal classification. There will be errors to correct, and at best one can hope that the computer will have provided the main form of a useful classification.

#### THE 'MULTIST' HIERARCHY OF COMPOSITAE

The main divisions of the hierarchy resulting from the computation of my observations on Compositae are presented in Diagram 1. The subdivisions within each of the major divisions are illustrated separately in Diagrams 2-5.



DIAGRAMS 1 - 5 : Computed hierarchy of Compositae.

Diagram 1: Abridged hierarchy of the main groupings in Compositae. Small assemblages of migrant species are omitted. Crude Subgroups at dissimilarity level 0.2 are numbered and their constituent genera listed.

Diagrams 2 - 5: Divisions within the important Subgroups of Diagram 1. The full hierarchy may be reconstructed from the computer type-out in Appendix III.

Diagram 2: Abridged hierarchy for Subgroup 716 with migrant species omitted. Crude Genera at dissimilarity level 0.145 are numbered and their constituent species listed.

Diagram 3: Full hierarchy for Subgroup 704. Genera at dissimilarity level 0.135 are numbered and their constituent species listed.

Diagram 4: Full hierarchy for Subgroup 714. Genera at dissimilarity level 0.18 are numbered and their constituent species listed.

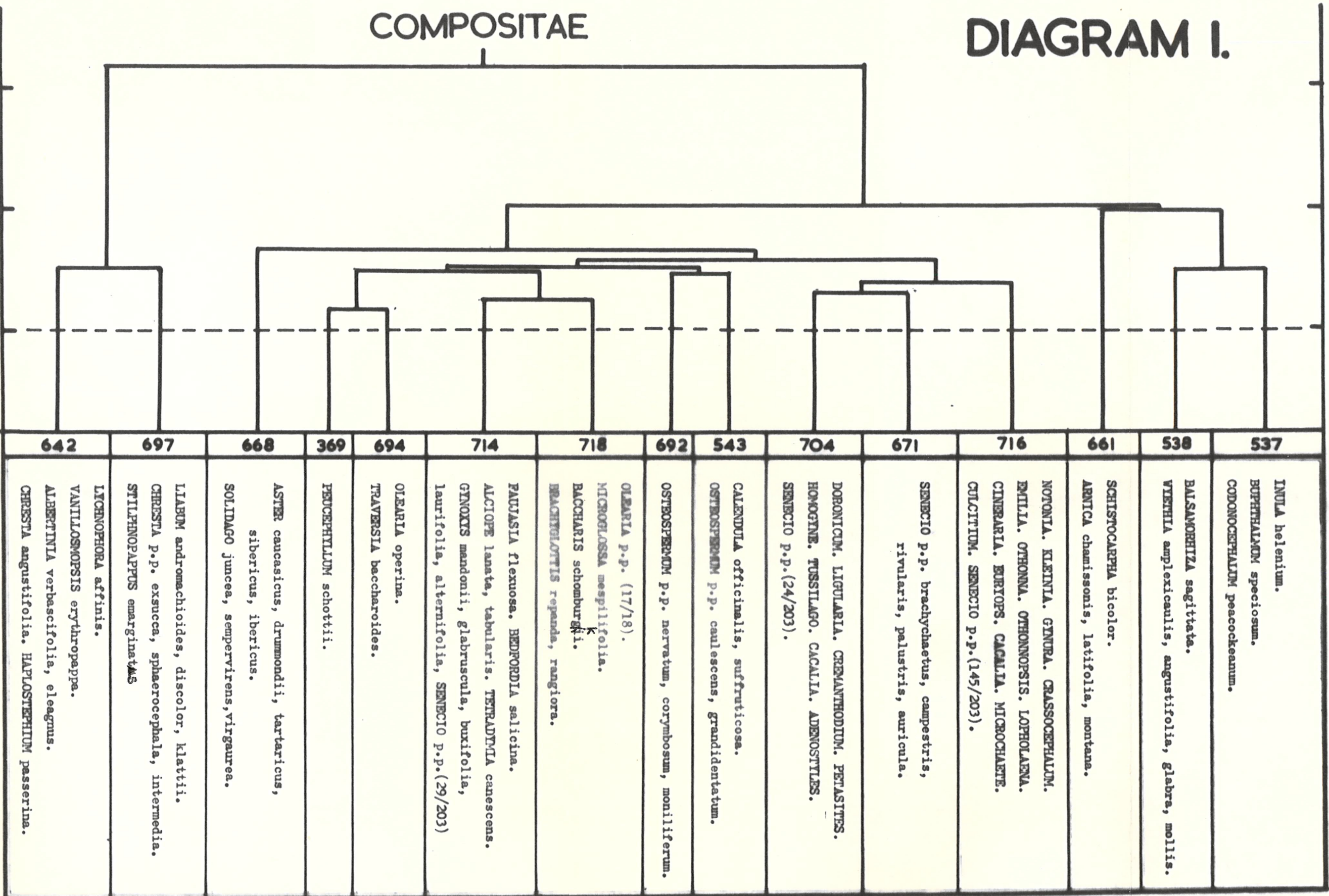
Diagram 5: Full hierarchy for Subgroup 718. Genera at dissimilarity level 0.17 are numbered and their constituent species listed.



## COMPOSITAE

## DIAGRAM I.

MEASURE OF DISSIMILARITY.

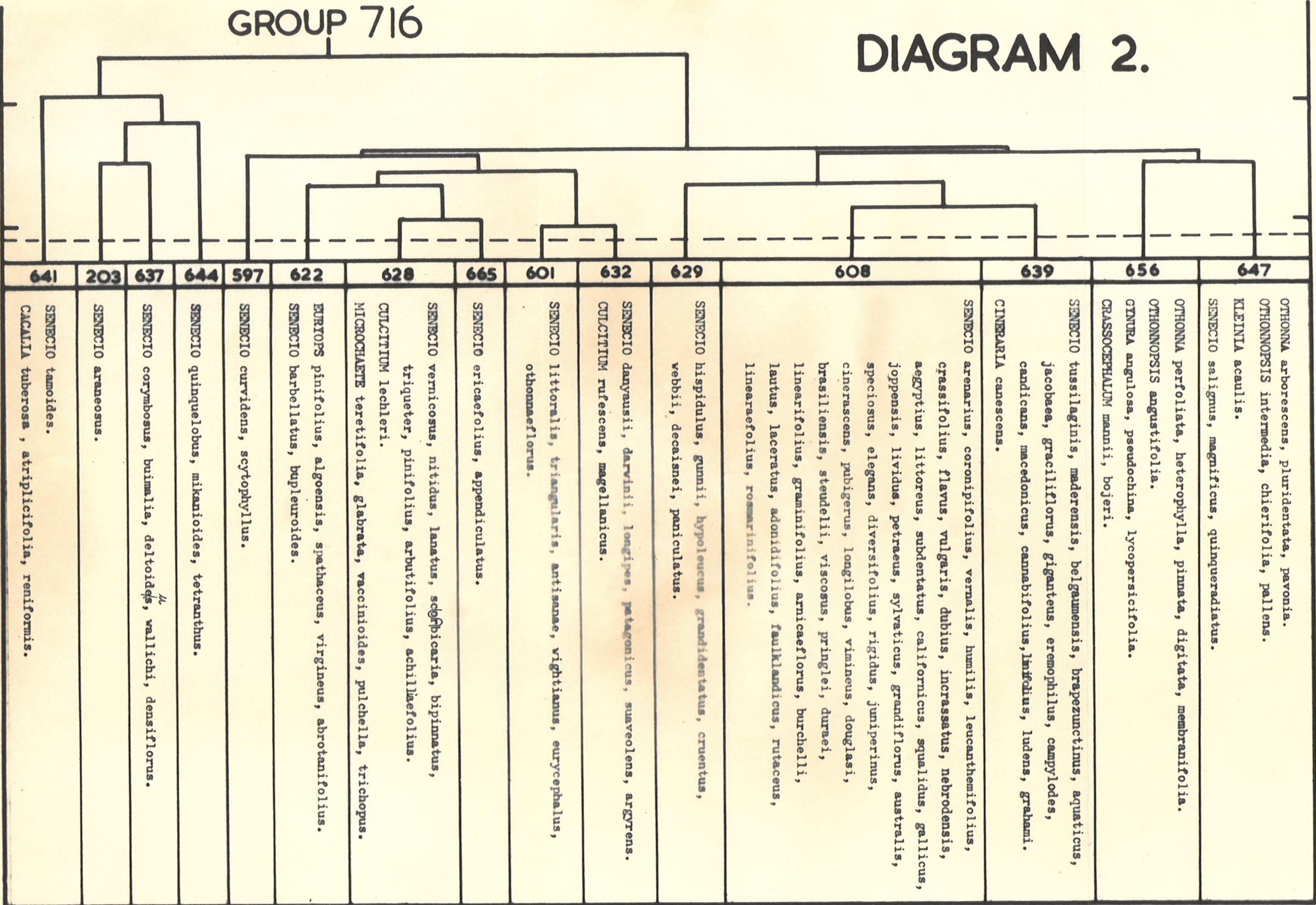




# DIAGRAM 2.

GROUP 716

MEASURE OF DISSIMILARITY.





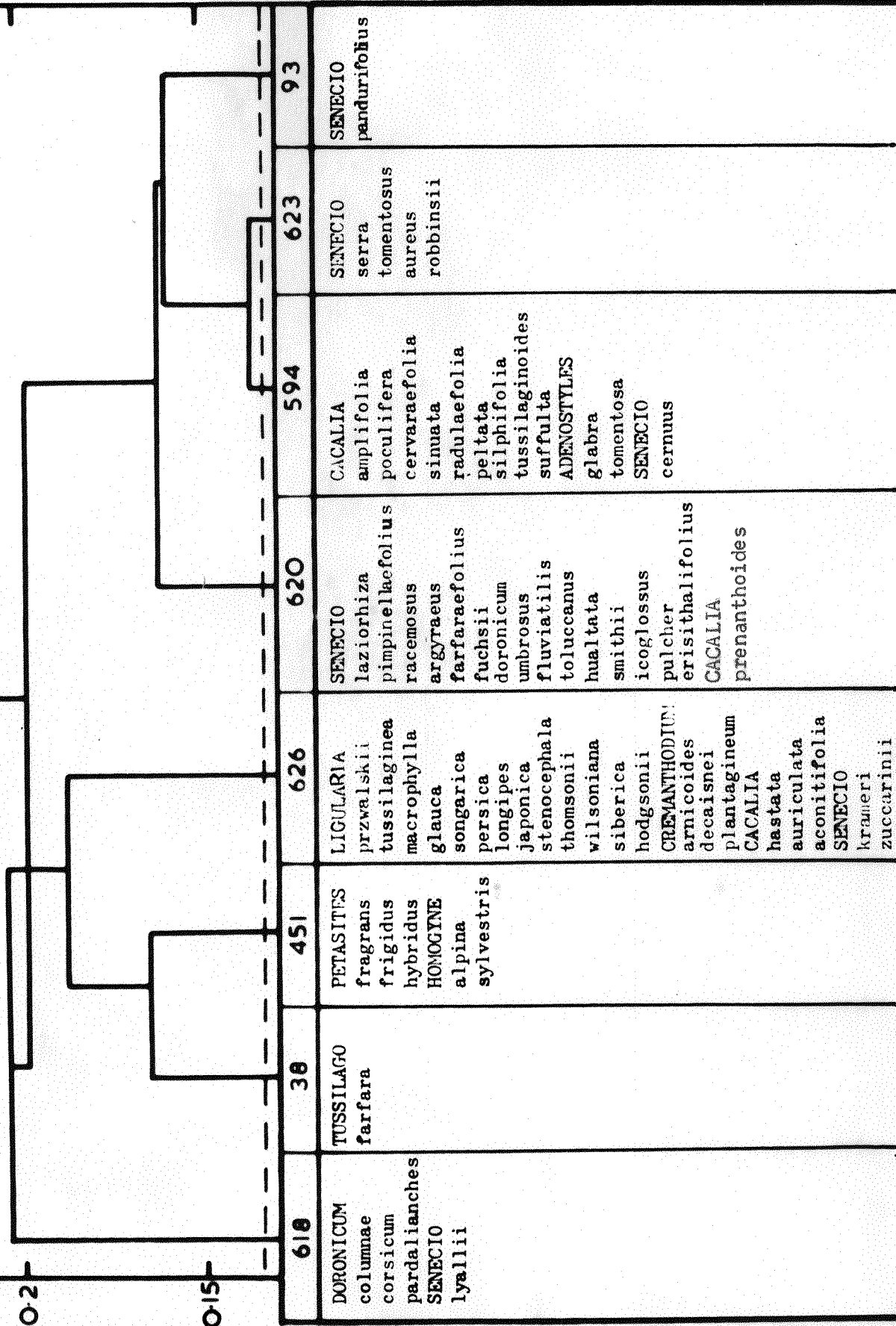
# GROUP 704

## DIAGRAM 3.

DISSIMILARITY

0.2

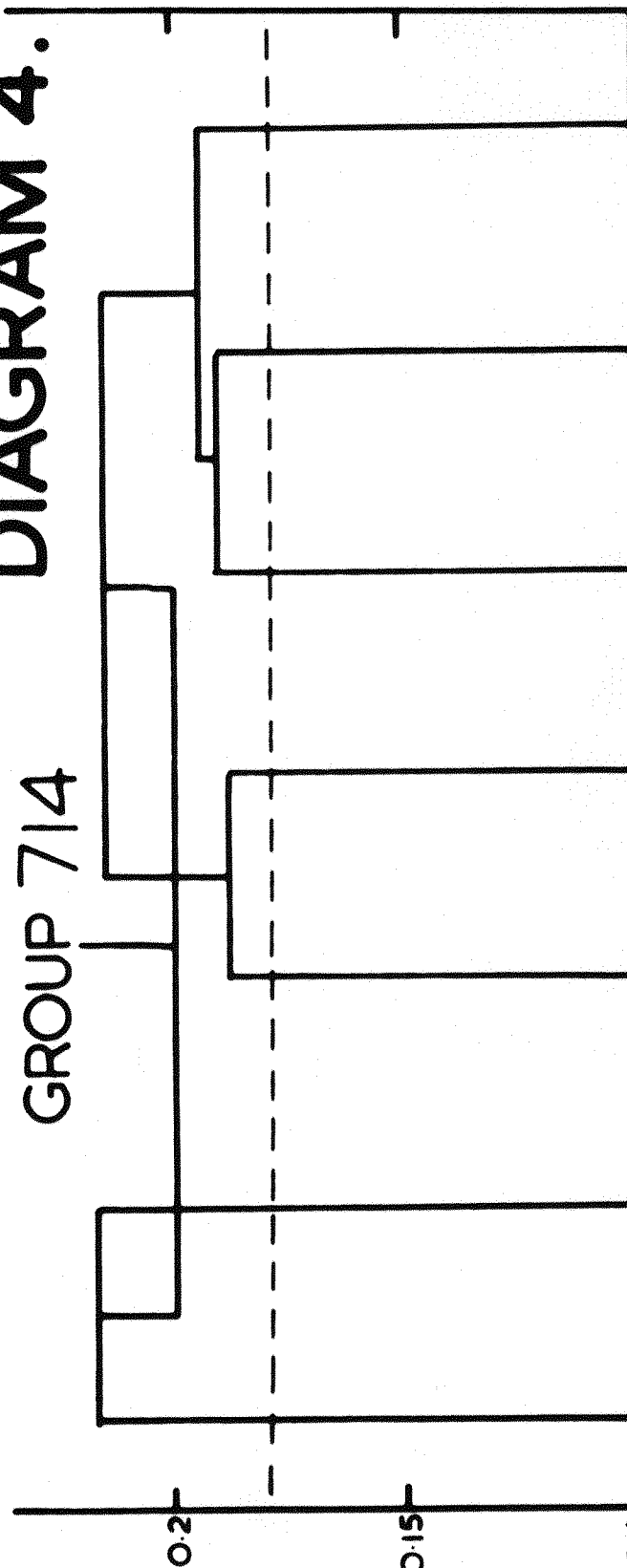
0.15





# DIAGRAM 4.

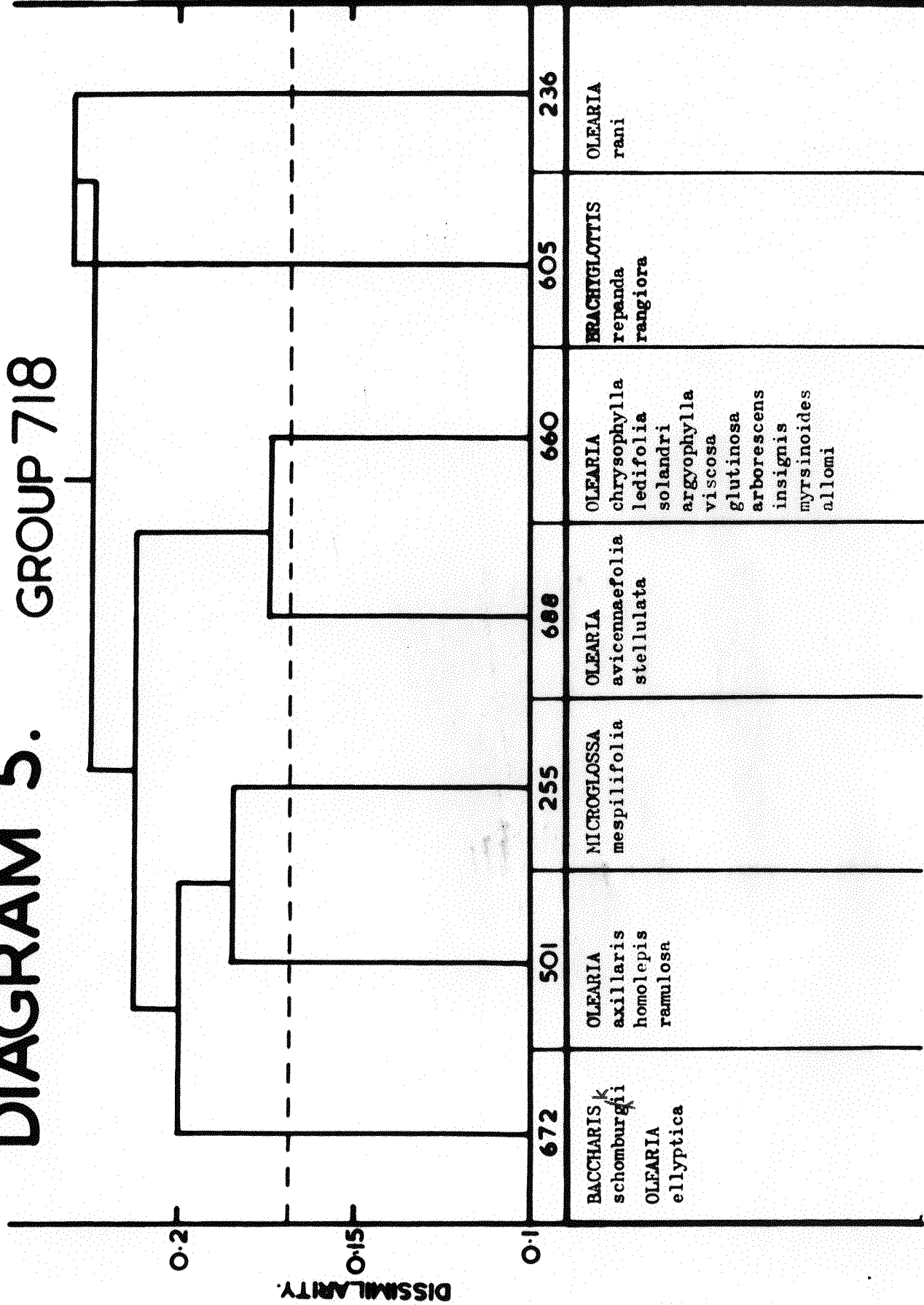
GROUP 714



160	636	367	185	635	685	674
SENECIO hectori	SENECIO petasites albonervius hartwegii	TETRADYMIA canescens	PAUJASIA flexuosa	SENECIO huntii centropappus elaeagnifolius rotundifolius greyi laxifolius compactus bidwillii monroi stewartiae cassiniioides BEDFORDIA salicina	SENECIO sciadophilus denticulatus bellidioides lagopus saxifragoides robustus grandifolius cymosus haastii hypochioneus	SENECIO perdicoides hypargyreaus kirkii roldana ALCIOPE tabularis lanata GYNOXYS mandonii glabruscula buxifolia laurifolia alternifolia



# DIAGRAM 5. GROUP 718





SECTION V

INTERPRETING THE HIERARCHY IN THE FORM OF A  
CLASSIFICATION



EXTRACTING A CLASSIFICATION

The interpretation of computed hierarchies in taxonomic terms is likely to remain an arbitrary procedure. In Diagram 1 for example, one might recognise 2 main groups above dissimilarity level 0.3, 3 groups at 0.299, or 4 groups at level 0.28. However the final classification should fulfil two practical requirements: (i) since taxonomy aims at making generalisations possible, most 'groups' should include more than one individual and preferably several; and (ii) although it is desirable to be reasonably consistent regarding the levels at which the various taxonomic categories (i.e. tribe, subtribe and genus) are recognised, it is in practice undesirable to disrupt the accepted nomenclature in so far as this is scientifically meaningful. This is especially important in connection with generic names, where nomenclatural changes can be grossly inconvenient. Clearly expediency should be a very important consideration in fixing the dissimilarity levels at which groups are to be recognised.

In interpreting the hierarchy of Compositae shown in Diagrams 1-5 with these criteria in mind, it seems reasonable to bring out three main units (here termed Group, Subgroup and Genus), coinciding roughly with the orthodox categories of tribe, subtribe and genus. As it happens the dissimilarity level of 0.2 in Diagram 1 is a reasonable level at which to



define Subgroups. This leads to the recognition of 15 Subgroups, which are numbered and their constituent genera recorded in Diagram 1. The 15 Subgroups could be arranged under a number of different Groups; but it is plain from the Diagram that 642 and 697 fuse together and are very different from the rest of the Compositae sampled. Therefore 642 and 697 conveniently form the two Subgroups of one Group; by the same argument 661, 538 and 537 are recognisable as another Group and 668 as a third. There remains a complex of 9 Subgroups (i.e. 369, 694, 714, 718, 692, 543, 704, 671 and 716) which nevertheless fuse at relatively high levels to give 3 pairs and 1 trio; and these might reasonably be regarded as 4 further Groups. The expected difficulty arises in fixing a level at which to pick out Genera; for some Subgroups are more homogeneous than others (contrast 704, Diagram 3 with 714, Diagram 4). Therefore in order to extract 'generic' groupings coinciding so far as possible with recognised genera and at the same time to arrive at reasonably sized species groups in those cases where recognised genera have broken down, it is necessary to terminate the hierarchies within Subgroups at different levels. Groupings which seem to me to represent suitable 'generic' units for larger Subgroups 716, 704, 714 and 718 are numbered and their constituent species recorded in Diagrams 2-5 respectively. The large Subgroup 716 lends itself to further taxonomic manipulation, and it is convenient to recognise several Series



of genera within it. Thus 641, 203, 637 and 644 (fusing together in Diagram 2) are very different from the other Genera of this Subgroup and are conveniently regarded as a series; likewise 656 and 647 constitute another series, and so on.

### DETECTING ERRORS

In view of what is currently known about agglomerative methods and their defects, the classification thus obtained had to be scrutinised for errors; and there are two ways of approaching this problem. The first involves comparing every individual with every other in the form of a 2 X 2 table for all of the 369 species. This would be impracticable, the computer having been employed in the first place to eliminate the laborious tasks of comparison and sorting. However it seemed worthwhile to undertake this exercise on a small scale; so I calculated (on the same basis as the computer analysis) the percentage similarities for every pair of 35 species, some suspected of being misplaced, others selected to represent the large groups (Table 3 ). The pattern of similarity values thus displayed demonstrates the general validity of the computer hierarchy and shows that there have been no serious coding or procedural errors; but two examples serve to show that the expected misclassifications have occurred: i.e. that species constituting minor groups may be either wrongly placed or truly taxonomically isolated. The species involved in these examples







are asterisked in Table 3 for ease of reference.

Example 1. Senecio pygmaeus, having fused early in the analysis with two Emilia species, joined another small group at a fairly high level before merging with an assemblage containing 185 species. Table 3 shows that although Senecio pygmaeus is 90% similar to Emilia sonchifolia, it is 92% similar to Senecio vulgaris with which, therefore, it ought to have become associated at a lower level. In addition Senecio pygmaeus and Senecio vulgaris have, on the evidence of the comparison table, much the same set of affinities with other species. Senecio pygmaeus evidently belongs in the group which includes Senecio vulgaris, and has been badly misclassified.

Example 2. Peucephyllum schottii formed a small group with Traversia baccharoides and Olearia oporina (fusing with them at a high level) which in turn fused at a still higher level with a major assemblage containing well over 300 species of Compositae. Table 3 reveals that Peucephyllum is 80% and 70% similar to Traversia baccharoides and Olearia oporina respectively, but differs markedly from them and any of the other 32



species in the table in its overall pattern of relationship. Peucephyllum schottii seems therefore to be truly taxonomically isolated.

It is one thing to know that misclassification has occurred, and quite another to identify all the species involved. Apart from the construction of a 2 X 2 table, there is at present no alternative but to call on intuitive assessments (i.e. a taxonomists' judgement!), based on experience gained while working closely with the plants concerned. In places where I suspected an error the original data lists were placed side by side and manifest inconsistencies were corrected. This procedure is somewhat subjective and seems at first sight highly unsatisfactory, but the amended groupings were to be tested later against additional, independent, information.

The extent to which misclassification had occurred, in terms of species, seems to be in the region of <sup>-20%</sup>10%. The most serious cases (i.e. those above dissimilarity level 0.2 involving genera and subgroups) are 714 and 694 (Diagram 1), 641 (Diagram 2) and 605 (Diagram 5). There follows a suggested classification for this sample of Compositae, in which the various necessary corrections are incorporated. Migrant species and species groups (bracketed) are asterisked.

In many cases the computer hierarchy fails to reveal with ideal precision the exact affinity of one group with another.



For example in Diagram 1, 668 fuses with a hypothetical individual representing 369, 694, 714, 718, 692, 543, 704, 671 and 716; but the diagram gives no clue as to which of these 668 is most closely related . Here again I have relied partly on the small 2 X 2 comparison table, and partly on a re-examination of the original observations in the light of the hierarchy, in deciding on a reasonable linear arrangement. However from a taxonomic point of view, the actual sequence of groupings is less important than the contents of the groupings themselves.



TABLE 4: Classification of the sample of 369 species of Compositae  
into Groups, Sub-groups, Series and Genera. Suggested  
generic groupings are headed by underlined names which  
are not intended as nomenclatural proposals. Species  
whose precise taxonomic position remains uncertain are  
listed after the classification, with their general  
affinities in parenthesis.

---

GROUP I

SUB-GROUP 1

<u>Balsamorhiza</u>	sagittata Nutt.
<u>Wyethia</u>	amplexicaulis Nutt., angustifolia Nutt., glabra Gray, mollis Gray.

SUB-GROUP 2

<u>Inula</u>	helenium L.
<u>Bupthalmum</u>	speciosum L.
<u>Codonocephalum</u>	peacockeanum Aitch. et Hemsley.

SUB-GROUP 3

<u>Schistocarpha</u>	bicolor Less.
<u>Arnica</u>	chamissonis Less., latifolia Bong., montana L.

GROUP II

<u>Aster</u>	caucasicus Willd., drummondii Lindl., tataricus L.f., sibiricus L., ibericus Stev.
<u>Solidago</u>	junceae Ait., sempervirens L., virgaurea L.



GROUP III

SUB-GROUP 1

Calendula officinalis L., suffruticosa Vahl.  
Osteospermum p.p.1. caulescens Harv., grandidentatum DC.

SUB-GROUP 2

Osteospermum p.p.2. nervatum DC., corymbosum L.,  
moniliferum L.

GROUP IV

SUB-GROUP 1A

Doronicum columnae Ten., corsicum Poir.,  
pardalianches L.  
Senecio p.p.1. lyallii Hk.f.

SUB-GROUP 1B

Ligularia hodgsonii Hk., persica Boiss.,  
macrophylla (Ldb.)DC., sibirica (L.)  
Cass., japonica DC., tussilaginea  
(B.f.)M., stenocephala (Max)Mts.et K.,  
przewalskii (Max)Diels., wilsoniana  
(Hemsl.)Grnm., thomsonii (Clke.)Poj.,  
songarica (Fisch.)Ling., glauca (L)Hoff.,  
longipes Poj.  
Cremanthodium arnicoides (Wall.)Good., plantagineum  
var. ellisii Max., decaisnei Clke.  
Cacalia p.p.1. hastata L., auriculata DC., aconitifolia  
Bunge.  
Senecio p.p.2. krameri F. et S., zuccarinii Max.  
Petasites fragrans Presl., frigidus Fries.,  
hybridus (L.)Gaertn.  
Homogyne alpina (L.)Cass., sylvestris Cass.  
Tussilago farfara L.  
Cacalia p.p.2. amplifolia DC., poculifera (Wats.)Rob.,  
peltata H.B.K., cervariaefolia DC.,  
sinuata Llav. et Lex., radulaefolia  
H.B.K., silphifolia Rob. et Grnm.,  
tussilaginoides H.B.K., suffulta Grnm.



- Adenostyles glabra (Mill.)DC., tomentosa Vill.  
Senecio p.p.3. cernuus Gray.  
Senecio p.p.4. serra Sond., tomentosus Mx., aureus L.,  
robbinsii Oakes.  
Senecio p.p.5. pandurifolius Harv.  
Senecio p.p.6. laziorhiza DC., pimpinellaefolius  
H.B.K., racemosus DC., fuchsii Gmel.,  
doronicum L., umbrosus W.K.,  
fluviatilis Wall., toluccanus DC.,  
hualtata Bert., smithii DC., icoglossus  
DC., pulcher Hk. et Arn., erisithalifolius  
Sch.Bip., (macedonicus\* Gris.,  
eremophilus\* Rich., cannabifolius\* Less.,)  
paucifolius\* Gmel., (lobatus\* Pers.,  
neomexicanus\* Gray), dumentorum\* Gardn.,  
(triangularis\* Hk., eurycephalus\* Tor.  
et Gray).  
Cacalia p.p.3. prenanthoides H.B.K.

SUB-GROUP 1C

- Senecio p.p.7. brachychaetus DC., campestris DC.,  
rivularis (W.K.)DC., palustris DC.,  
auricula Bourg.

SUB-GROUP 1D

- Cacalia p.p.4. (reniformis\* Muhl., atriplicifolia\* L.,  
tuberosa\* Nutt.).

SUB-GROUP 2A

- Notonia (grandiflora\* DC.  
Kleinia p.p.1. neriifolia\* Haw.)  
Othonna p.p.1. arborescens L., pluridentata DC.,  
pavonia E.Mey.  
Othonnopsis intermedia Boiss., chierifolia Benth.  
et Hook., pallens Benth. et Hook.  
Kleinia p.p.2. acaulis DC., (repens\* Haw., articulata\*  
Haw.).  
Emilia (sonchifolia\* DC., flammea\* Cass.)  
Gynura angulosa DC., pseudochina var.  
hispida Twaites, lycopersicifolia DC.



Othonna p.p.2.

perfoliata Jacq., heterophylla L.f.,  
pinnata L.f., digitata L.f.,  
membranifolia DC., triplinervia\* DC.,  
linifolia\* L.f.

## Othonnopsis

angustifolia DC.

Crassocephalum

bojeri (DC.) Robyns., mannii (Hk.f.)  
Milne-Redhead.

Lopholaena

dregeana\* DC.

Senecio p.p.8.

gregorii\* FvM., (paucifolius\* DC.,  
angulatus\* L.), oxyriaefolius\* DC.,  
segmentatus\* Oliv.



Senecio p.p.10.  
(cont'd)

tussilaginis\* Lindl.), glaber\* Less.,  
littoralis Gaud., cruentus DC.,  
webbii Christ, decaisnei DC.

SUB-GROUP 2C

Senecio p.p.11.

linifolius Clke., ludens Clke., grahami  
Hk.f., aquaticus Hill., jacobaea L.,  
graciliflorus DC., giganteus Desf.,  
belgaumensis Clke., diversifolius\* Wall.,  
(palmensis\* Smith., gibbosus\* DC.,  
taygeteus\* Boiss. et Heldr., candidus\*  
DC.), (lineatus\* DC., oliganthus\* DC.),  
(incanus L., leucophyllus\* DC.).

Cineraria

canescens Wendl.

SUB-GROUP 2D

Culcitium

rufescens H.B.K., magellanicum Hom. et  
Jacq., (nivale\* H.B.K., reflexum\* H.B.K.),  
lechleri\* Sch.Bip.

Senecio p.p.12.

danyauii Sch.Bip., darwinii Hk. et Arn.,  
longipes Hk.f., patagonicus Hk. et Arn.,  
argyrens Phil., chiliensis\* Less.

Senecio p.p.13.

ericaefolius Benth., appendiculatus DC.

Microchaete

teretifolia Benth., glabrata Benth.,  
vaccinioides Benth., pulchella Benth.,  
trichopus Benth.

Senecio p.p.14.

vernicosus Sch.Bip., nitidus DC.,  
scombicaria DC., lanatus DC.,  
arbutifolius H.B.K., triqueter Less.,  
pinifolius Lam., bipinnatus Less.,  
achillaeefolius DC.

Euryops

spathaceus DC., virgineus Less.,  
pinifolius A.Rich., algoensis DC.,  
abrotanifolius DC., oligoglossus\* DC.

Senecio p.p.15.

barbellatus DC., bupleuroides DC.,  
abrotanifolius\* L., adonidifolius\* Loisel.

Gamolepis

euryopoides\* DC.

Senecio p.p.16.

curvidens Sch.Bip., scytophyllus H.B.K.

SUB-GROUP 2E

Senecio p.p.17.

araneosus DC., corymbosus Wall.,



Senecio p.p.17.  
(cont'd)

buimalia Buch-Ham., deltoideus Less.,  
wallichii DC., densiflorus Wall.,  
tamoides DC., quinquelobus DC.,  
mikanoides Otto., tetranthus DC.,  
acuminatus\* Wall., wightianus\* DC.,  
(alatus\* Wall., kunthianus\* Wall.),  
(campylodes\* DC., candicans\* Wall.).

SUB-GROUP 3

Senecio p.p.18.

hectori J.Buch.

Senecio p.p.19.

petasitis DC., hartwegii Benth.,  
albonervius Grnm.

Tetradymia

canescens DC.

Luina

hypoleuca\* Benth.

Faujasia

flexuosa Benth. et Hk.f.

Bedfordia

salicina DC.

Senecio p.p.20.

huntii FvM., centropappus FvM.,  
eleagnifolius Hk.f., rotundifolius  
Hk.f., laxifolius J.Buch., compactus  
Kirk, bidwillii Hk.f., monroi Hk.f.,  
stewartiae J.B.Armst., cassinioides  
Hk.f., greyi Hk.f.

Senecio p.p.21.

sciadophilus Raoul, denticulatus DC.,  
bellidioides Hk.f., lagopus Raoul,  
saxifragoides Hk.f., robustus J.Buch.,  
grandifolius Less., cymosus Remy,  
haastii Hk.f., hypochioneus Boiss.

Gynoxys

mandonii Sch.Bip., glabruscula Rusby, *Li*  
buxifolia Cass., laurifolia Cass.,  
alternifolia Sch.Bip.

Brachyglottis

(repanda\* Forst., rangiora\* J.Buch.).

Alciope

tabularis DC., lanata DC.

Senecio p.p.22.

perdicoides Hk.f., hypargyraeus DC.,  
kirkii Hk.f., roldana DC.

Senecio p.p.23.

sandemanii\* Cuatr., barba-johannis\* DC.

Traversia

baccharoides\* Hk.f.



GROUP V

<u>Olearia</u> p.p.1.	rani (A.Cunn.) Druce.
<u>Olearia</u> p.p.2.	chrysophylla Benth., ledifolia Benth., solandri Hk.f., argyophylla FvM., viscosa Benth., glutinosa Benth., arborescens Forst., insignis Hk.f., myrsinoides FvM., allomi Kirk.
<u>Olearia</u> p.p.3.	avicennaefolia Hk.f., stellulata DC.
<u>Microglossa</u>	mespilifolia DC.
<u>Olearia</u> p.p.4.	homolepis FvM., axillaris FvM., ramulosa Benth.
<u>Baccharis</u>	schomburgkii Baker.
<u>Olearia</u> p.p.5.	el <del>ly</del> ptica DC
<u>Olearia</u> p.p.6.	oporina Hk.f.

GROUP VI

SUB-GROUP 1

<u>Lychnophora</u>	affinis Mart.
<u>Haplostephium</u>	passerina Mart.
<u>Vanillosmopsis</u>	erythropappa Sch.Bip.
<u>Albertinia</u>	verbascifolia Mart., elaeagnus Mart.
<u>Chresta</u> p.p.1.	angustifolia Gardn.

SUB-GROUP 2

<u>Liabum</u>	andromachioides Hemsl., discolor Benth. et Hk., Klattii Rob. et Grnm.
<u>Stilphnopappus</u>	emarginatus
<u>Chresta</u> p.p.2.	exsucca DC., sphaerocephala DC., intermedia Gardn.



Species of uncertain position

<i>Peucephyllum schottii</i> Gray	( ? )
<i>Liabum rusbyi</i> Britton	(Group V)
<i>Senecio salignus</i> DC	(Group IV/3)
<i>Cacalia suaveolens</i> L.	(Group IV/1 or 2)
<i>Senecio antisanae</i> Benth.	(Group IV/2)
<i>Senecio prunifolius</i> Wedd. )	(Group IV/2)
<i>Senecio psidiifolius</i> Rusby )	
<i>Senecio quinquerradiatus</i> Boiss.	(Group IV/2)
<i>Senecio farfaraefolius</i> Boiss. et Kotschy	(Group IV/2)
<i>Senecio argaeus</i> Boiss. et Bal.	(Group IV/2)



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SECTION VI

DISCUSSION AND CONCLUSION



COMPARISON WITH BENTHAM'S CLASSIFICATION

The arrangement laid out in Table 4 is very different from all the classifications previously proposed for these Compositae. The numerous points of departure from the orthodox treatment of these plants are best brought out by comparing my scheme with that of Bentham (Table 5), whose system was adopted with only trivial (frequently deleterious) changes by Hoffman<sup>n</sup> (1894). De Candolle's classification (1837), based on Lessings views (1832), has no advantages over Bentham's and since it is now obsolete there is no need to consider it in this context.

Acceptance of the new classification, summarised for convenience of discussion in Table 5, involves acknowledging that of Bentham's 7 tribes examined by me, only 3 (Calendulaceae, Helianthoideae and Inuloideae) gain unqualified support. Even Calendulaceae seem remarkably heterogeneous considering the small size of the sample, for 2 new groups (692 and 543, Diagram 1; Subgroups III/1 and 2, Table 4) have emerged at a high level. The Inuloideae, on the evidence of this small sample, appear as a natural group allied to the two helianthoid genera; a relationship to some extent anticipated by Bentham, who arranged the Helianthoideae and Inuloideae in sequence.

Of the rest, the Asteroideae have fallen into 2 groups (Groups III and V, Table 4; 668 and 718, Diagram 1) standing far apart; and on this evidence the tribe seems worthless.



TABLE 5 : Comparison of Bentham's classification in terms of genera with the arrangement proposed in Table 4 .

Genus	Bentham (1873) tribes and subtribes	Drury (1966) groups and subgroups
Vanillosmopsis	Vernoniaceae-Euvernoniaceae	VI/1
Albertinia	"	VI/1
Stilphnoppappus	"	VI/2
Haplostephium	Vernoniaceae-Lychnophoreae	VI/1
Lychnophora	"	VI/1
Chresta (Eremanthus)	"	VI/1, VI/2
Adenostyles	Eupatoriaceae-Adenostyleae	IV/1B
Solidago	Asteroideae-Homochromeae	II/0
Aster	Asteroideae-Heterochromeae	II/0
Olearia	"	V/0
Microglossa	Asteroideae-Conyzeae	V/0
Baccharis	Asteroideae-Baccharideae	V/0
Codonocephalum	Inuloideae-Euinuleae	I/2
Inula	"	I/2
Bupththalmum	Inuloideae-Bupththalmeae	I/2
Wyethia	Helianthoideae-Verbesineae	I/1
Balsamorhiza	"	I/1
Liabum	Senecionideae-Liabeae	VI/2
Schistocarpha	"	I/3
Peucephyllum	?Senecionideae-Tussilagineae	Position uncertain
Luina	?	IV/3
Tussilago	"	IV/1B
Petasites	"	IV/1B
Homogyne	"	IV/1B
Cremanthodium	"	IV/1B
Alciope	"	IV/3
Arnica	Senecionideae-Eusenecioneae	I/3
Doronicum	"	IV/1A
Lopholaena	"	IV/2A
Faujasia	"	IV/3
Brachyglottis	"	IV/3
Culcitium	"	IV/2D
Gynura	"	IV/2A
(Crassocephalum)	"	IV/2C
Cineraria	"	IV/2A
Emilia	"	IV/2A
Notonia	"	IV/2A
Senecio (Cacalia, Ligularia, Kleinia, Microchaete etc.)	"	IV/1B, IV/1C, IV/2A, IV/2B, IV/2C, IV/2D, IV/2E, IV/3.
Gynoxys	"	IV/3
Bedfordia	"	IV/3
Tetradymia	"	IV/3
Othonnopsis	"	IV/2A
Euryops	Senecionideae-Othonneae	IV/2D
Gamolepis	"	IV/2D
Othonna	"	IV/2A
Calendula	Calendulaceae	III/1
Osteospermum	"	III/1, III/2.



Adenostyles, the solitary representative of Eupatoriaceae has been submerged at a low level in Group IV (Diagram 3, 704), casting doubt on another tribe. The two helianthoid genera, Wyethia and Balsamorhiza, seem to be related; but it appears that they (together with Inuloideae) belong near Schistocarpha and Arnica from Senecionideae (661, Diagram 1). Liabum, conventionally regarded as Senecionideae, has joined Vernoniaceae.

Long-cherished subdivisions within tribes suffer to an even greater extent than the tribes themselves, and in all only 1 subtribe (i.e. Verbesineae) of the 9 where more than one genus has been examined gain support. The liberal mixing of species <sup>within</sup> ~~from~~ the subtribes of Asteroideae and Vernoniaceae can only be interpreted as casting doubts on the usefulness of those groupings. In the Senecionideae, the subtribes (i.e. Liabeae, Tussilagineae, Eusenecioneae and Othonneae) have all failed to emerge in recognisable form and in their places stand three completely new Subgroups. In Inuloideae, representatives of Euinuleae have fused at a very low level with Bupthalmum, which represents the Bupthalmeae in this sample (Group I/2 Table 4). Numerous genera, including four important ones, have not emerged from the computation intact: the species of Senecio and Cacalia are scattered over Groups IV and V/1 respectively, while Osteospermum and Olearia are distributed as fragments across Groups III and V/1 <sup>respectively</sup>.



If the implications of this result are to be taken seriously, one concludes that not only the Senecionideae but the whole structure of the taxonomy of Compositae might require drastic revision. This suggestion is likely to come as a shock to synanthologists; but I intend to show in the discussion which follows that there is ample independent information to support it.

#### EVIDENCE IN SUPPORT OF THE NEW CLASSIFICATION

Although abundant assorted information is available for Compositae, much of it is of relatively little value in taxonomic work, being neither sufficiently comprehensive nor properly comparative. The external criteria which can be brought to bear in testing my scheme are limited to the following:

- i. Geography
- ii. Cytology (chromosome numbers)
- iii. Habit
- iv. Original observations not included in the computer analysis
- v. Mycology (host ranges of rust fungi)
- vi. Palynology
- vii. Embryology

There follows an assessment of the new scheme in the light of the information from these sources. For convenience of discussion, the Groups and Subgroups are considered separately from the Genera.



## Groups and Subgroups

### Geography

If evolution has occurred, one would expect taxonomically related plants to show geographical consistency and the old scheme is manifestly unsatisfactory in this respect. By contrast, Groups I, II, III, V and VI of Table 4 gain some support; for the species of Groups I and II are restricted to the northern hemisphere while the vast majority of those from Groups III, V and VI are confined to the southern hemisphere.

Group IV (corresponding largely with Senecionideae) is cosmopolitan, but here the Subgroups, which are quite new, prove geographically meaningful. Subgroup 1 includes mainly north temperate plants, while Subgroups 3 and 2D are restricted to regions south of the equator. An East Africa-India distribution, which characterises the Subgroups 2A, 2C and 2E is also geographically reasonable, being explicable on the basis of continental drift. (In his recent reconstruction of the palaeozoic land masses using palaeomagnetic data, Creer (1965) shows India and East Africa in close proximity). Only Subgroup 2B seems geographically unlikely, having a crescentic distribution ranging from South America, through New Zealand and Africa to Europe. It is probably significant however, that numerous notorious ruderals (e.g. Senecio vulgaris and Senecio squalidus), fall in this Subgroup.



TABLE 6 : Diploid Chromosome numbers in Compositae.

Classification (Drury 1966)	Genus	Chromosome number (2n)
Group I		
Subgroup 1.	Balsamorhiza	38.
	Wyethia	38.38.38.
Subgroup 2.	Inula	20.(16.18.24.32.)
	Bupthalmum	20.
Subgroup 3.	Schistocarpa	16.
	Arnica	38.38.106-108.
Group II	Aster	18,54.36.
	Solidago	18,36.18.18.
Group III	Calendula	28,32.28,32.
Group IV		
Subgroup 1.	Doronicum	60.
	Senecio - 1.	60.
	Ligularia	58.58.60.60.60.60.60.60.
	Cacalia - 1.	60.52.
	Petasites	52.60.60.
	Homogyne	c.135.
	Tussilago	60.
	Cacalia - 2.	60.60.60.c.50.
	Adenostyles	38.38.
	Senecio - 4.	46.
	Senecio - 5.	40.40.40.40.40.40.40.46.80. c.80.
	Senecio - 7.	46,48,90.48.
	Cacalia - 4.	50.50.
Subgroup 2A.	Notonia	20.
	Kleinia - 1.	20.
	Kleinia - 2.	20,30.20.c.90.100.
	Gynura	20.
	Emilia	10.20.
	Othonna	20.
	Senecio - 8.	40.60.c.92.
Subgroup 2B.	Senecio - 10.	18.20.20.20.20.20.20.20.40. 40.40.40.40.40.40.40.40.60. 60.60.
Subgroup 2C.	Senecio - 11.	40.40.40.
	Cineraria	(40.)
Subgroup 2D.	Culcitium	c.40.
	Senecio - 12.	40.
	Euryops	(20.)
	Senecio - 14.	40.40.
Subgroup 2E.	Senecio - 16.	20.20.
Subgroup 3.	Senecio - 18.	60.
	Tetradymia	(60.124)
	Bedfordia	60.
	Senecio - 19.	60.60.60.60.60.60.60.
	Senecio - 20.	60.60.60.60.60.
	Senecio - 21.	60.60.
	Brachyglottis	60.60.
	Luina	60.
	Traversia	60.
Group V	Olearia	18.c.108.
	Baccharis	(18)
	Microglossa	(18)

Bracketed numbers are for species other than those examined.



## Cytology

Chromosome number is not a simple numerical attribute, for a plant having 20 somatic chromosomes might be cytologically closer to one with 40 chromosomes than to one with 14. For this reason it is not legitimate to incorporate details of chromosome number in a numerical analysis. However, these can conveniently be kept back and used to judge the merits of a classification based on other criteria. In Table 6 are arranged, alongside the proposed classification of these Compositae, all the relevant diploid chromosome counts taken from Darlington and Wylie (1956), Cave et al., (1958-63) and Hair and Beuzenburg (unpublished). It is clear from this that the new arrangement is compatible with cytological knowledge. Multiples of 10 chromosomes are nearly confined to, and are characteristic of the vast Group IV; while so far as the information goes, counts in Group II and V are all multiples of 9. The numbers  $2n = 38$  and  $2n = 16$  are almost unknown outside Group I.

Ornduff, Raven, Kynos and Kruckeberg (1963), in a cytological survey of the Senecionideae, failed to find any relationship between the established subtribes and chromosome numbers; but not only is Group IV (which takes in most of that tribe) characterised by the chromosome range of its constituents (i.e. mostly multiples of 10), but the Subgroups are also partially separable in cytological terms. Diploid values of



20 and 40 are the theme in Subgroup 2, while being entirely absent from Subgroup 3 and confined to 1 out of 11 genera in Subgroup 1; Subgroups 1 and 3, on the other hand, include a markedly high concentration of plants with  $2n = 60$ . Even within Subgroup 2, chromosome numbers are compatible with the suggested layout: for the Subgroups 2A and 2E mostly exhibit diploid counts of 20, in contrast with 2B, 2C and 2D where  $2n = 40$  is the most common condition.

### Habit

Of the 45 characters used in the computation, only 3 are directly associated with gross morphology. Yet 4 of the 6 Groups under consideration are internally consistent for features of habit other than those used in the analysis. The members of Groups I and II are perennial herbs, usually having thin leaves. Many species in Groups V and VI on the other hand, are trees or shrubs and the leaves are generally coriaceous or somewhat fleshy. Group III includes a mixture of life forms, but here the two Subgroups are consistent: for Subgroup 1 consists of perennial herbs with thin leaves, while Subgroup 2 includes shrubby plants with coriaceous or fleshy leaves.

Although Group IV is also heterogeneous in terms of habit 2 out of 3 of its Subgroups are consistent in this respect; for Subgroup 1 consists of rhizomatous herbs with ephemeral radicle leaves, in contrast with Subgroup 3 where shrubby and



arborescent species with leathery leaves predominate. Subgroup 2 embraces a variety of habit forms, but 6 out of 7 Subgroups within it are separable on features of gross morphology. Thus Subgroup 2A takes in all the succulents in the entire sample. It includes Othonna, one of the few genera of Compositae with a single row of fused involucre bracts and no basal calyculatum. Examination of the other species in 2A with this in mind reveals that the bracts of Emilia, Kleinia and Othonnopsis species also show slight tendencies to adhesion and are without a calyculatum; and more spectacularly the bracts of Senecio gregorii, another member of this alliance, are fused to their tips! Fusion of the involucre bracts is not confined to Subgroup 2A, occurring elsewhere in Subgroup 2D; but the high concentration of species showing this peculiarity certainly lends support to Subgroup 2A.

Most of the notorious weedy Senecio species (e.g. Senecio vulgaris and Senecio squalidus) fall in Group IV, Subgroup 2B. These usually have pinnatisect auricled leaves, often with more or less linear segments, and they are also notable for the possession of numerous small, frequently slender capitula. Subgroup 2D consists entirely of ericoid plants commonly displaying a characteristic growth pattern: the apices of the main branches die back after a limited period of growth, their place being taken by a series of lateral branches arising from below the abortive tips. This results in the 'pulvinate'



habit exhibited by many of the species. Growth habit could not be deduced from many of the available specimens; but 50% of the species in Subgroup 2D show this feature and I have never observed it anywhere else in Group IV.

Climbers and scramblers make up the bulk of Group IV, Subgroup 2E. Their capitula are also decidedly small, but differ from those of 2B in having relatively few florets, and in being borne on divergent axillary branches. In many species in Subgroup 2E, 'stipules' are associated with the base of a distinct petiole; and this state of affairs is not found in other Subgroups of Group IV. Finally, although Subgroup 2C includes an assortment of Senecio forms, the species concerned are distinct from the rest of Group IV in having large quantities of resin along the vascular traces of their florets. Furthermore Subgroup 2C brings together Senecio grahami and Cineraria, which have never before been associated, but which are the only members of the entire sample known to have flattened achenes.

#### Eglandular hairs

The data presented to the computer incorporated details on the distribution of 15 forms of eglandular hair. Alternatively however (and exemplifying the arbitrary nature of taxonomic characters), the variation might have been described in terms of two variants: i.e. hairs clearly divided into basal and proximal parts (Fig. 1A - D, L and M), and hairs essentially



columnar in construction with no such clear differentiation (Fig. 1E - K, N and O). Table 7 shows how these different categories of leaf hair, which seem to be quite independent of the 15 classes used in the computer analysis, fall neatly into place in the proposed scheme.

TABLE 7: Distribution of two eglandular hair types within the new classification.

Classification (Drury 1966)	Columnar hair type (%)	Basal cell hair type (%)	Species with leaf hairs	Species in group
GROUP I	100	0	12	13
GROUP II	100	0	7	8
GROUP III	80	20	6	7
GROUP IV/1	86	14	56	70
/2A	100	0	2	32
/2B	80	20	50	67
/2C	44	56	16	18
/2D	13	87	22	40
/2E	57	43	12	16
/3	8	92	38	41
GROUP V	19	81	19	20
GROUP VI	19	81	13	13

In Groups I, II and III hairs are nearly always of the columnar type, while in Groups V and VI they are usually of



TABLE 8 : Records of known hosts for nine rust fungi taken from Cunningham (1931), Gaumann (1959), Hylander et al. (1953), McAlpine (1906), Walker (comprehensive data for *Puccinia lagenophorae*, personal communication) and Wilson et al. (1965).

Subgroup (Drury 1966)	Host	Rust (species or formenkreis)								
		A	B	C	D	E	F	G	H	I
IV/1	<i>Ligularia tussilaginea</i> (B.f.)M.	+								
	<i>Ligularia macrophylla</i> (Ldb.)DC.	+								
	<i>Ligularia sibirica</i> (L.) Cass.	+							+	
	<i>Cacalia hastata</i> L.					+	+			
	<i>Cacalia auriculata</i> DC.						+			
	<i>Senecio krameri</i> F. et S.					+	+			
	<i>Petasites hybridus</i> (L.) Gaertn.	+								+
	<i>Homogyne alpina</i> (L.) Cass.	+					+			
	<i>Tussilago farfara</i> L.									+
	<i>Adenostyles glabra</i> (Mill.)DC.	+				+	+	+		
	<i>Adenostyles tomentosa</i> Vill.	+				+				
	<i>Senecio doronicum</i> L.	+	+					+		
	<i>Senecio fuchsii</i> Gmel.	+	+	+						
	<i>Senecio fluviatilis</i> Wallr.	+	+							
	<i>Senecio umbrosus</i> W.K.	+	+							
	<i>Senecio cannabifolius</i> Less.	+	+							
	<i>Senecio triangularis</i> Hook.	+								
	<i>Senecio pulcher</i> Hk. et Arn.	+								
	<i>Senecio smithii</i> DC.	+								
	<i>Cacalia atriplicifolia</i> L.	+								
	<i>Senecio brachychaetus</i> DC.									+
	<i>Senecio palustris</i> DC.	+							+	
	<i>Senecio rupestris</i> W.K.	+								
	<i>Kleinia neriifolia</i> Haw.	+								
/2A										
/2B	<i>Senecio sylvaticus</i> L.	+		+						
	<i>Senecio viscosus</i> L.	+		+						
	<i>Senecio vulgaris</i> L.	+		+	+					
	<i>Senecio squalidus</i> L.	+								
	<i>Senecio vernalis</i> W.K.	+								
	<i>Senecio crassifolius</i> Willd.	+								
	<i>Senecio lividus</i> L.	+								
	<i>Senecio leucanthemifolius</i> Poir.	+								
	<i>Senecio gallicus</i> Chaix	+								
	<i>Senecio duriaei</i> Gay	+								
	<i>Senecio cruentus</i> DC.	+				+				
	<i>Senecio heritieri</i> DC.	+								
	<i>Senecio maderensis</i> DC.	+								
	<i>Senecio vimineus</i> DC.	+								
	<i>Senecio brasiliensis</i> Less.	+								
	<i>Senecio burchellii</i> DC.					+				
	<i>Senecio lautus</i> Forst.f.ex Willd.					+				
	<i>Senecio linearifolius</i> A. Rich.					+				
	<i>Senecio quadridentatus</i> Labill.					+				
/2C	<i>Senecio jacobaea</i> L.	+	+	+						
	<i>Senecio aquaticus</i> Hill		+	+	+					
/2D	<i>Senecio chiliensis</i> Less.	+								
/2E	<i>Senecio mikanioides</i> Otto	+								
/3	<i>Senecio campylodes</i> DC.					+				
	<i>Senecio lagopus</i> Raoul					+				
	<i>Senecio bidwillii</i> Hk.f.									+
	<i>Senecio elaeagnifolius</i> Hk.f.									+

- Coleosporium senecionis* (Persoon) Fries.
- Puccinia helianthi* Schweinitz formenkreis.
- Puccinia schoeleriana* Plow. et Magn. formenkreis.
- Puccinia lagenophorae* Cooke.
- Coleosporium cacaliae* (DC.) Otth.
- Uromyces veratri* (DC.) schroeter formenkreis.
- Puccinia eriophori* Thuemen formenkreis.
- Puccinia poarum* Nielsen formenkreis.
- Puccinia pounamu* G.H.Cunn.



the basal cell type. Group IV includes both types, but there some of the Subgroups gain further support; for Subgroup 1, 2A and 2B hairs, when present, are generally columnar, although 2A is notable for its glabrosity. In Subgroup 2D and 3, on the other hand, basal cell- appendage forms predominate. In fact out of 6 Groups and 7 Subgroups in Table 7 , only Subgroups 2C and 2E have roughly equal proportions of the two types.

#### Mycology

Data on host ranges for rust fungi (Uredinales) provide interesting and independent testimony to the taxonomic value of the new Subgroups within Group IV. Remarks are confined to this assemblage because rust information is lacking for the others.

Records of known hosts for 9 relevant rust species and species groups ('formenkreis') from the genera Uromyces, Puccinia and Coleosporium are arranged in Table 8 . It is immediately striking that none of the widely-ranging fungi A, B and C are known to infect plants of Subgroup 3; but that rust I is entirely confined to that Subgroup. The entries for E, F, G and H, on the other hand, certainly lend weight to the taxonomic argument in support of Subgroup 1; for all of the 16 records involved are in that Subgroup, and



each fungus infects plants from at least 3 genera. The absence of entries for rust D in Subgroup 1 lends further support to this alliance.

These results are particularly impressive since fungi are seen to be showing host ranges involving plants which have never before been associated in any taxonomic scheme (e.g. rust G, attacking Ligularia siberica, Adenostyles glabra and Senecio palustris ). There is no question here of mycologists having deliberately restricted their activities to plants they considered closely related. Thus even after allowing for the shortage of mycological information (especially from the southern hemisphere), and despite the tendency of mycologists to define rust species on grounds of host range, it is reasonable to claim some support from plant pathology for my layout of the plants of Group IV. Conversely Table 8 ought to be of interest to mycologists pursuing cross-inneculation experiments.

#### Palynology

The palynological observations of Stix (1960) provide evidence in support of my positions for Liabum and Arnica (universally regarded as Senecionideae ) among Vernoniaceae and Helianthoideae respectively. Stix has shown that the exine stratification pattern of Liabum pollen is distinct



from that of other Senecionideae, and she noted the strong resemblance in this respect between Liabum and her sample of Vernoniaceae. In addition she did not put Arnica in the list of genera displaying her 'Senecio' pollen type, but referred it to the group with 'Helianthus' pollen.

Skvarla and Turner (1966) provide further information on variations in the morphology of pollen-wall layers in Compositae. So far they have recognised 3 pollen types among Senecionideae: 'helianthoid', 'anthemoid' and 'senecionid'. Liabum is again proved peculiar among Senecionideae, since it is the only genus from their sample of 13 where they record 'anthemoid' pollen, implying that it shows some relationship with the Anthemideae. (This suggestion does not invalidate my place for Liabum alongside Vernoniaceae, since the present sample of Compositae does not include genera representing Anthemideae, neither does the sample of Skvarla and Turner take in any Vernoniaceae). Moreover they find that Schistocarpha and Gynoxys both exhibit their 'helianthoid' pollen type, while the remaining genera which coincide with those examined by me ( i.e. Emilia, Euryops, Gynura and Petasites ) display the 'senecionid' pollen type. This confirms my place for Schistocarpha among the Helianthoideae and emphasises that Subgroup IV/3 is worthy of taxonomic



recognition since it is seen to be picking out Senecionideae with 'helianthoid' pollen from among those with 'senecionid' pollen.

### Embryology

The helianthoid nature of Arnica ( conventionally regarded as a member of Senecionideae ) is further confirmed by embryological evidence. Afzelius (1924) found the embryo-sac of Arnica montana to be unique among the wide range of Senecionideae examined by him, in constantly having 2 antipodal cells. This feature is characteristic of certain Helianthoideae, and he anticipated Table 4 in suggesting that Arnica should be transfered to that tribe.

### The genera

My sample of Compositae takes in a host of generic names ( over 70 for Senecio sensu lato alone ), the majority of which are probably redundant. To discuss the merits of each in the light of the proposed classification would be impracticable.



However it is worthwhile to summarise the computer's conclusions with regard to generic names in common usage.

1. Some widely recognised genera where more than one species was examined gain support, in that the species form discrete groups at low levels. They are listed below and the number of species examined out of the total in the genus (Willis 1960) is given to indicate the scope of the sample.

<u>Aster</u> Tourn. ex L. 5/500	<u>Euryops</u> Cass. 6/35
<u>Solidago</u> (Vaill.) L. 3/90	<u>Culcitium</u> Humb. et Bonpl.
<u>Doronicum</u> Tourn. ex L. 3/25	5/20
<u>Wyethia</u> Nutt. 4/12	<u>Arnica</u> Rupp. ex L. 3/50
<u>Petasites</u> (Tourn.) L. 3/15	<u>Calendula</u> L. 2/15

2. Certain small or monotypic genera are indeed very distinct from other Compositae, fusing with their nearest allies only at quite high levels. Their nearest relatives are recorded in parenthesis.

Peucephyllum Gray (position uncertain)  
Traversia Hook.f. (Group IV/3)  
Faujasia Cass. (Tetradymia)  
Tussilago (Tourn.) L. (Petasites)  
Codonocephalum Fenzl. (Inula)  
Schistocarpa Less. (Arnica)  
Lopholaena DC. (Group IV/2A)  
Tetradymia DC (Faujasia)  
Luina Benth. (Group IV/3, ? Tetradymia)

3. In terms of the sample, some well-known 'genera', though



homogeneous, have fused at very low levels with larger genera, implying that their names are superfluous. The genera in which they have been submerged are given in parenthesis.

Cremanthodium Benth. 3/50 (= Ligularia Cass.)

Homogyne Cass. 2/3 (= Petasites (Tourn.) L. )

Adenostyles Cass. 2/6 (= Cacalia - 2)

Bedfordia DC. 1/2 (= Senecio - 20)

Alciope DC. 2/2 (= Gynoxys Cass.)

Brachyglottis Forst. 2/2 (= Gynoxys Cass.)

4. Some 'genera' have proved inseparable, their constituents having been thoroughly mixed. Evidently the present generic boundaries, which mostly depend on a few floral minutiae, here require critical revision.

Othonna L. (10/80); Othonnopsis Jaub. et Spach. (4/8).

Gynura Cass. (3/40); Crassocephalum Moench. (2/30).

Kleinia L. (4/19); Notonia DC. (1/19); Emilia Cass. (2/12).

5. Some genera, sunk in Senecio by Bentham and often ignored, have emerged as homogeneous and remain distinct at relatively high levels, thus gaining support. It should be noted, however, that species from elsewhere have in some cases been added.

Microchaete Benth. 5/7    Tephroseris Reichb. 4/20

(617, Diag. 1)

Ligularia Cass. 13/35    Mesodenia Rafin. 3/6 (641, Diag. 2).

6. Some 'genera' are so drastically fragmented as to imply that they might be worthless as they now stand.



Liabum Adans. 4/60 (2 fragments)  
Chresta Arrab. 4/12 (2 fragments)  
Senecio L. 203/2000 (23 fragments)  
Cacalia L. 16/40 (4 fragments)  
Olearia Moench. 18/90 (6 fragments)  
Osteospermum 5/40 (2 fragments)

The implications regarding the large genera are very serious from a taxonomic point of view, and it is worth discussing these in more detail.

Senecio L.

In the computer hierarchy, Senecio has fragmented into 23 parts (Diagrams 1-4), scattered across the three Subgroups of the vast Group IV (Table 4 ). Evidence supporting the taxonomic value of the Subgroups has already been presented; but it is necessary to consider the fragments individually. It is worth emphasising that the hierarchy is derived from comparative observations of 45 characters (over 100 unit characters) for each species, while the diagnosis of the conventional 'genus' Senecio involves only a very few floral characters which in practice fail to pick out these species from other Senecionideae.

Senecio fragments are of two main types: (i) those which fuse at low levels with well-known genera or fragments thereof, in which they apparently belong; and (ii) those which fuse with groups of well-known genera only at fairly high levels, and which



might ultimately prove to represent 'good' but previously undescribed genera. It seems likely that small isolated fragments, especially South American and African, might represent nuclei of larger groups worthy of generic recognition but to which my sample fails to do justice. Here are relevant phytogeographical and other miscellaneous data which support the fragmentation of Senecio along the lines suggested in Table 4 : unhappily this information is not amenable to tabulation and is simply listed. Fragments which seem to indicate the existence of previously unknown genera are asterisked (see also Table 4 ).

Senecio - 1. (618, Diagram 3) Senecio lyallii Hk.f. fuses at a very low level with all three of the Doronicum species examined. A chromosome count of  $2n=60$  for Senecio lyallii (Hair and Beuzenberg unpublished) and  $2n=60$  for Doronicum pardalianches L. supports the view that they are closely related.

Senecio - 2. (626, Diagram 3). Two species associated by the computer with the ligularias early in the analysis. Like them they are Asian plants.

Senecio - 3. (594, Diagram 3). Senecio cernuus Gray fuses at a very low level with Cacalia - 2 along with Adenostyles and the group remains distinct at a quite high level. These particular cacalias and Senecio cernuus are all American, and Adenostyles is represented



there, so that the group is geographically reasonable.

\*Senecio - 4. (623, Diagram 3). Four species, 3 North American and 1 African, allied to the previous group but sufficiently distinct to suggest the need for a new generic grouping.

\*Senecio - 5. (93, Diagram 3). The African Senecio pandurifolius Harv., an isolated species, standing alone until quite late in the analysis before joining the previous two groups. The computation suggests that this species is as clearly worthy of generic rank as is, say, Tussilago farfara L. (38, Diagram 3).

\*Senecio - 6. (620, Diagram 3 plus migrant species). 23 species, mostly confined to the north temperate regions. Like the other genera in Group VI/1 these are rhizomatous herbs. They prefer damp habitats, in keeping with their suggested place near Ligularia, Tussilago and Petasites.

Senecio - 7. (671, Diagram 1). 5 species which have remained distinct to a high level, their closest relatives being in 704. The suggested isolation of this Senecio fragment is backed up by cytological evidence, the species having chromosome numbers (Table 6) unknown elsewhere in Group IV/1.

\*Senecio - 8. (not shown in Diagrams). Under the computation all five species in this fragment have migrated from Group IV/2A, where they seem to belong. Like them,



they are all succulents and 4 out of 5 are African. E/

Senecio gregorii FvM., from Western Australia, along with Kleinia repens Haw. and Kleinia articulata, other African succulents, also seem to represent a migrated part of Group IV/2A.

\*Senecio - 9. (629, Diagram 2) and \*Senecio - 10. (608, Diagram 2) together constitute the whole of Group IV/2B already discussed in the previous subsection. The division into two parts is to some extent supported by phytogeography; for while Senecio - 10 has a crescentic distribution covering much of the southern hemisphere, Senecio - 9 is confined to Australia and New Zealand.

\*Senecio - 11. (639, Diagram 2). 17 species constituting the Afroasian Group VI/2C discussed earlier.

Senecio - 12. (632, Diagram 2). 7 species, fusing at a low level with Culcitium. Chilean and Patagonian species with a 'pulvinate' habit and pin-cushion-like capitula borne singly on a scape. They share these features with species of Culcitium.

\*Senecio - 13. (665, Diagram 2) consists of 2 species. Senecio ericaefolius Benth., and Senecio appendiculatus DC., apparently allied to Microchaete (628, Diagram 2) but sufficiently distinct to suggest the need for a new genus.

\*Senecio - 14. (628, Diagram 2). 12 species, apparently



indistinguishable from Microchaete. Like the species of that genus these plants are shrubs, often with small ericoid leaves.

Senecio - 15. (622 Diagram 2). 4 species, two of which (Senecio bupleuroides DC. and Senecio barbellatus DC) are African species with entire coriaceous leaves, like some species of the South African Euryops, with which they fuse. The other two species (Senecio adonidifolius L., and Senecio abrotanifolius L.) seem to have migrated from their true place. They are probably merely temperate forms of Euryops: both species exhibit fused involucre bracts and pinnatifid leaves with linear segments, a characteristic of some Euryops species.

\*Senecio - 16. (592, Diagram 2) contains Senecio curvidens Sch. Bip., and Senecio scytophyllus H.B.K. from Peru and Ecuador respectively, which according to the hierarchy are very isolated from other senecios in Groups IV/2D. This Senecio fragment is more distinct than, for example, Euryops and Culcitium, genera whose status has never been in question, suggesting that Senecio - 16. might be a new genus within the ericoid Group IV/2D.

\*Senecio - 17. (203, 637, 644, Diagram 2) embraces the 16 members of Group IV/2E which have already been discussed in previous paragraphs. This is another very distinctive Senecio fragment, and on grounds of consistency it seems



reasonable to recognise it at generic level.

\*Senecio - 18. (168, Diagram 4) is the arborescent Senecio hectori J. Buch., which remains distinct from its nearest ally (Senecio - 19, Table 4 ; 636, Diagram 4) at a very high level.

\*Senecio - 19. (636, Diagram 4) Three species of succulent trees native to Mexico. They form a very distinct alliance and appear to represent a previously unrecognised genus.

Senecio - 20. (635, Diagram 4). 11 shrubby species confined to New Zealand, which fuse low in the hierarchy with Bedfordia salicina DC., from Tasmania. Cytological evidence supports this union, since a chromosome number of  $2n = 60$  is recorded for Bedfordia salicina and all 7 Senecio species so far examined (Hair and Beuzenburg unpublished).

\*Senecio - 21. (685, Diagram 4). 10 species, the majority natives of New Zealand and the rest from South and Central America. The 5 species for which chromosome counts are available are consistent for  $2n = 60$  chromosomes (Hair and Beuzenburg unpublished).

Senecio - 22. (674, Diagram 4). 4 species, (1 Madagascan, 2 New Zealand and 1 Mexican) which according to the computation are allied to the South African genus Alciope and the South American genus Gynoxys. The two New Zealand species (Senecio perdicoides Hk.f. and Senecio kirkii Hk.f.)



are both known to possess 60 somatic chromosomes (Hair and Beuzenburg unpublished).

\*Senecio - 23. Senecio sandemanii Cuatr. with Senecio barba-johannis DC. which remained alone to near the end of the analysis (not shown in Diagram 1). Re-examination suggests that they are migrant outliers from Group IV/3.

Cacalia L.

The computer analysis brings out the heterogeneity of Cacalia (sensu De Candolle) by presenting it as four fragments. These are rather widely separated constituents of Group IV, Subgroup 1 (Table 4 ). Cacalia was considered as a distinct genus by both De Candolle (1837) and Hoffmann (1889), although Bentham (1873) united it with Senecio. Subsequently Rydberg (1924) substituted four separate genera, (Pericalia, Psacalium, Odontotrichum and Mesodenia), all founded on a few ill-defined features of floral morphology. Few botanists have taken Rydberg's genera seriously; and according to the computation only one of them, Mesodenia (Cacalia - 4., Table 4 ) is recognisable in my sample. It is interesting to note that species now included in Mesodenia have long been recognised as distinct from other cacalias, De Candolle having placed them in Cacalia section Conophora because of their characteristic cone-shaped receptacles. Their position in Group IV/1 is confirmed by geographical and cytological information: Cacalia - 4 is a north temperate American assemblage and the two species for



which chromosome counts are available have  $2n = 50$ .

The bulk of the Cacalia species examined (i.e. 9 out of 16) constitute Cacalia - 2. (Table 4 ; 594, Diagram 3), an assemblage cytologically distinct from all other Senecio fragments in the northern hemisphere except Ligularia. However phytogeography emphasises the distinction between the two, for Ligularia is entirely Asian while Cacalia - 2 is restricted to Central America. The three species included under Cacalia - 1 however appear with the ligularias (Diagram 3); an association consistent with their Asian geography and their chromosome numbers. Cacalia - 3 is Cacalia prenanthoides H.B.K., which belongs with Senecio - 6 (Table 4 ; 620, Diagram 3).

Olearia Moench.

a/ It is plain from Diagram 5 that the taxonomy of the Austral~~Asian~~ genus Olearia requires urgent reconsideration. Most of the sectional groups proposed by Archer (1860), which he based on leaf hair type, are substantiated (Table 4 ); but the computation result suggests that the 6 Olearia fragments (Table 4 ; Diagram 5 and 694, Diagram 1) are very different from one another and are more distinct as groups than many sound and widely recognised genera. A deeper investigation of the genus, in the context of a larger sample of Asteroideae, would be rewarding.



Osteospermum L.

Osteospermum, with 40 species, is the largest of the 8 genera traditionally included in Calendulaceae. The 5 species examined are hardly likely to be fully representative and it is startling to find a major inconsistency in so small a sample. Diagram 1 clearly shows that Osteospermum - 1. (543) and Osteospermum - 2. (692) are more distinct than the Subgroups of Group IV, so I have regarded them as Subgroups in Table 4. Osteospermum caulescens Harv. and Osteospermum grandidentatum DC., (i.e. Group III/1) fuse relatively early in the analysis with the two calendulas. Nordlindh (1943), in a recent monograph of the genus Osteospermum, failed to uncover its heterogeneity; but his views were founded entirely on knowledge of variation in gross achene morphology.



### CONCLUSIONS

Doubts concerning the taxonomic worth of Senecio as a genus, and of the current classification of Compositae, seem well founded and the de novo approach of this investigation justified. Senecio has failed to emerge from a computer analysis of numerous comparative observations, constituent species having been scattered over three novel divisions approximating to the tribe Senecionideae. Inconsistencies have emerged in samples from the tribes Asteroideae, Calendulaceae, Vernoniaceae and Eupatoriaceae, suggesting that these would repay comprehensive study. Inuloideae and Helianthoideae, on the limited evidence presented here, are closely related and perhaps ought to be united. No fewer than 9 genera in addition to Senecio have suffered serious fragmentation. The evidence suggests that the current taxonomic system forms no reliable framework for modern work.

My taxonomic suggestions (Table 4 ) are in accord with the extraneous criteria against which they have been tested; and to this extent they represent sound taxonomy. However the sample, although rationally based, is small in relation to Senecio and Compositae. Therefore it is not possible to provide diagnoses, nor to formalise the new groupings. However it is reasonable to hope that they may provide a useful source of ideas for future investigations. Features which characterise major assemblages, in so far as these are known



at present, are listed in Appendix II.

The nomenclatural implications of such an iconoclastic result are beyond my comprehension at the present time. At least 1000 name changes <sup>might</sup> ~~would~~ be required should they ever be implemented with respect to Senecio alone. However pleas for nomenclatural stability (e.g. Walters 1961) seem out of place here in the face of a classification which conveys a minimum of useful information. The whole question demands long and careful deliberation. In the meantime, it appears from the nomenclatural standpoint merely irresponsible to continue describing new species under such 'genera' as Senecio, Cacalia, Osteospermum and Olearia.



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APPENDIX I

COMPARATIVE OBSERVATIONS AS RECORDED FOR COMPUTATION



KEY TO CODED INFORMATION

Qualitative characters: 1 - 31 (1 = present; 0 = absent;  
\* = inapplicable)

1. Eglandular leaf hairs, present/absent
2. Glandular leaf hairs, present/absent
3. Anisocytic stomata, present/absent
4. Resin canals, present/absent
5. Interfascicular cambium, present/absent
6. Phloem fibres, present/absent
7. Cortical sclereids, present/absent
8. Lignified phloem, present/absent
9. Pith sclereids, present/absent
10. Joining sclereids, present/absent
11. Xylem rays, present/absent (if 5 absent, then inapplicable)
12. Collapsed pith present/absent
13. If pith not collapsed, then lignification present/absent
14. Pith crystals, present/absent (if 12 present, then inapplicable)
15. Achenial crystals, present/absent
16. Ovarian crystals, present/absent
17. Ray florets, present/absent
18. If ray florets present, then filiform florets present/absent
19. If ray florets present, staminodes present/absent
20. Cylindrical filament-collar present/absent
21. Anther auricles, present/absent
22. If auricles present, then fertile auricles present/absent
23. Duplex achenial hairs, present/absent
24. If duplex achenial hairs present, then thick-walled type present/absent
25. Pappus on disc florets, present/absent
26. Pappus if present on disc florets, then setose present/absent
27. If pappus present and setose, fluked hairs present/absent
28. If pappus present and setose, clubbed hairs present/absent



- 29. Opposite leaves, present/absent
- 30. Carbonaceous layer in achene wall, present/absent
- 31. Lophate pollen, present/absent

Numerical characters: 32 and 33

(i.e. the two integers before the first stroke; \* = inapplicable)

- 1. Width of xylem rays. Primary categories distributed over 5 divisions: 1 = (1), 1 and 2 = (2), 2 = (3), 2 and 3 = (4), 3 = (5).
- 2. Widest vessel diameter. Micrometer values ordered into 6 divisions: (1) 0.5-1.0, (2) 1.1-1.5, (3) 1.6-2.0, (4) 2.1-2.5, (5) 2.6-3.0, (6) 3.1 + (conversion factor to  $\mu$  X 16.67).

Multistate characters: 34 - 45

(i.e. the integers between strokes; \* = inapplicable)

- 1. Eglandular leaf hair type: 1-15 are types A - O respectively in figure 1.
- 2. Glandular leaf hair type: 1, 2 and 3 are types Q, R and P respectively in figure 1.
- 3. Nodal configuration: (1) Multilacunar, (2) Trilacunar, (3) Unilacunar, (4) Quinquelacunar.
- 4. Position of resin canals: (1) cortical, (2) Adjacent to phloem fibre blocks, (3) between phloem fibre blocks, (4) in the phloem, (5) in the pith.
- 5. Vessel distribution type: 1-10 are distribution types 1-10 respectively (see text for details).
- 6. Pith crystal type: (1) druses, (2) curvilinear,



- |                              |  |
|------------------------------|--|
| 6. (cont'd)                  | (3) intermediate hexagonal,<br>(4) raphides.   |
| 7. Achenial crystal type:    | (1) druses, (2) curvilinear,<br>(3) elongate hexagonal,<br>(4) crystal mixture.                          |
| 8. Ovarian crystal type:     | (1) druses, (2) curvilinear,<br>(3) isodiametric, (4) intermediate<br>hexagonal, (5) elongate hexagonal. |
| 9. Ray floret venation:      | (1) 4- nerved, (2) 4 nerved,<br>(3) 4+ nerved.   |
| 10. Fibrous layer of anther: | (1) polarised, (2) radial,<br>(3) transitional.  |
| 11. Leaves:                  | (1) petiolate, (2) with decurrent<br>lamina, (3) sessile.  |
| 12. Leaf venation:           | (1) palmate, (2) pinnate,<br>(3) parallel.   |



1. *Aster tataricus* L.f. 1001010100\*1\*\*1110010\*111100000 \*\*/5,8\*/1/2,5\*\*\*/1/1/3/1/1/2/
2. *Aster drummondii* Lindl. 10011010010011110010\*111100000 1.0 3.0/5\*\*\*/1/2/2/2/1/2/2/2/1/2/
3. *Aster sibericus* L. 1001010100\*0011110010\*111100000 \*\*/5\*\*\*/2/2\*/4/1/2/3/2/2/2/
4. *Aster caucasicus* Willd. 1101010000\*0011110110\*111100000 \*\*/5,8/2/2/2\*\*\*/2/1/2/2/2/2/2/
5. *Aster ibericus* Stev. 11011100001001110010\*111100000 1.0 3.0/5,8/2/2/2/2/2,3/1/1/2/2/1/2/
6. *Solidago sempervirens* L. 00011010010011110010\*111100000 1.0 3.0/5,8/2/2/2/2/2,3/1/1/2/2/2/2/
7. *Solidago virgaurea* L. 10011010010011110110\*111100000 1.0 3.0\*\*\*/1/2,5/5/4/1/1,2/3/2/2/2/
8. *Solidago juncea* Ait. 1001101010011110110\*111100000 1.0 2.0/5,8\*\*\*/2/2/2\*\*\*/1/2/3/2/1/2/
9. *Inula helenium* L. 1101010000\*00111001100\*111100000 \*\*/5/3/1/3\*\*\*/3/2,4/2/1/1/2/
10. *Bupthalamum speciosum* L. 1101010000\*000111001100\*0\*\*0000 \*\*/5/3/1/3\*\*\*/3/2,3/2/1/1/2/
11. *Cedonoccephalum peacockeanum* A.et H. 1101010000\*000110\*\*11011100000 \*\*/5/3/1/2,3\*\*\*/3/2\*\*\*/1/1/2/
12. *Balsamorhiza sagittata* Nutt. 1101010000\*1\*\*0110110\*0\*\*0\*\*010 \*\*/5/3/1/2,5\*\*\*/1,2,3/3/1/1/2/
13. *Wyethia angustifolia* Nutt. 1101010000\*0010110110\*0\*10\*\*010 \*\*/5/3/1/2,5\*\*\*/1,3\*\*\*/1,2/3/1/3/2/
14. *Wyethia glabra* Gray 0101010000\*0000110110\*0\*10\*\*010 \*\*/3/3/1/2,5\*\*\*/2,3/3/1/1/2/
15. *Wyethia mollis* Gray 1101010000\*0000110110\*0\*10\*\*010 \*\*/5/3/1/2,5\*\*\*/1,2,3/1/1/2/
16. *Wyethia amplexicaulis* Nutt. 1101010000\*0000110110\*0\*10\*\*010 \*\*/5/3/1/2,5\*\*\*/1,2,3/1/1/2/
17. *Schistocarpus bicolor* Less. 1001110000\*000010010\*0\*1100110 \*\*/5/3/1/2,5\*\*\*/1,2,3/1/1/3/
18. *Ligularia hodgsonii* Hk. 0001010000\*1\*\*1110110\*0\*1100000 \*\*/1/2,5\*\*\*/1/1,2/3/1/1/1/
19. *Ligularia persica* Boiss. 1001010000\*1\*\*11101100\*1100000 \*\*/9\*\*\*/1/2\*\*\*/1/1,2/2/1/1/2/
20. *Ligularia macrophylla* (Ldb.) DC. 0001010000\*1\*\*1110110\*0\*1100000 \*\*/1/2\*\*\*/1/2/2/1/1/2/
21. *Ligularia siberica* (L.) Cass. 1001010000\*1\*\*1110110\*0\*1100000 \*\*/9\*\*\*/1/2,5\*\*\*/1/3/1/1/1/
22. *Ligularia japonica* DC. 1001010000\*1\*\*01101100\*1100000 \*\*/8,9,14\*\*\*/1/2\*\*\*/1,3/3/1/1/1/
23. *Ligularia tussilaginea* (Bm.f.) M. 1001010000\*1\*\*111011011100000 \*\*/12\*\*\*/1/2\*\*\*/1/2/3/1/1/1/
24. *Ligularia stenocephala* (Max.) M.et K. 1001010000\*1\*\*11101100\*1100000 \*\*/8,9\*\*\*/1/2\*\*\*/1/3/1/1/1/
25. *Ligularia przewalskii* (Max.) Diels 1001010000\*000110110\*0\*1100000 \*\*/11\*\*\*/1/2,5\*\*\*/1/2/1/1/1/
26. *Ligularia wilsoniana* (Hemsl.) Grm. 1001010000\*1\*\*1110110\*0\*1100000 \*\*/11\*\*\*/1/2\*\*\*/1/1,2/3/1/1/1/
27. *Ligularia thomsonii* (Clke.) Poj. 1001010000\*0001101100\*1100000 \*\*/2\*\*\*/1/2\*\*\*/1/3/1/1/1/
28. *Ligularia songarica* (Fisch.) Ling 1001010000\*1\*\*1110110\*0\*1100000 \*\*/14\*\*\*/1/2\*\*\*/1/1,2/3/1/1/2/
29. *Ligularia glauca* (L.) Hoff. 0001010000\*1\*\*1110110\*0\*1100000 \*\*/1/2\*\*\*/1/1,2/3/1/1/2/
30. *Ligularia longipes* Poj. 0001010000\*1\*\*11101100\*1100000 \*\*/1/2\*\*\*/1/1,2/3/1/1/2/
31. *Senecio krameri* F.et S. 1001010000\*000110\*\*1100000 \*\*/9\*\*\*/1/2\*\*\*/1/1,2/3/1/1/1/
32. *Senecio zuccarinii* Max. 0001010000\*010110\*\*1100\*1100000 \*\*/1/2\*\*\*/1/2\*\*\*/1/1/1/
33. *Cremanthodium arnicoides* (Wall.) Good. 1001010000\*1\*\*0110110\*0\*1100000 \*\*/9\*\*\*/1/2\*\*\*/1/3/1/1/2/
34. *Cremanthodium plantagineum* Max. 1001010000\*1\*\*0110110\*0\*1100000 \*\*/9\*\*\*/1/2\*\*\*/1/3/1/1/2/
35. *Cremanthodium decalvei* Clke. 1001010000\*1\*\*1110110\*0\*1100000 \*\*/7\*\*\*/1/2\*\*\*/1/2,3/3/1/1/1/
36. *Homogyne alpina* Cass. 1001010000\*1\*\*0110110\*0\*1100000 \*\*/10\*\*\*/1/2\*\*\*/3\*\*\*/1/1/1/
37. *Homogyne sylvestris* Cass. 1001010000\*1\*\*0110110\*0\*1100000 \*\*/10\*\*\*/1/2\*\*\*/3\*\*\*/1/1/1/



38. *Tussilago Farfara* L. 1101010000\*1\*\*00101010\*0\*1100000 \*\*/2/2/1/2/\*\*/\*\*/1/1/1/1/
39. *Petasites fragrans* (Vill.) Presl 1001010000\*1\*\*0110010\*0\*1100000 \*\*/11/\*\*/1/2/\*\*/\*\*/3/3/1/1/1/
40. *Petasites frigidus* Fries 1001010000\*1\*\*0110010\*0\*1100000 \*\*/10/\*\*/1/2/\*\*/\*\*/3/3/1/1/1/
41. *Petasites hybridus* (L.) Gaertn. 1001010000\*1\*\*011010\*0\*1100000 \*\*/2/\*\*/1/2/\*\*/\*\*/3/1/1/1/
42. *Cacalia hastata* L. 1001010000\*000110\*\*1100\*1100000 \*\*/5/\*\*/1/2/\*\*/\*\*/1/1/2/\*\*/1/1/1/
43. *Cacalia auriculata* DC. 1001010000\*000110\*\*1100\*1100000 \*\*/9/\*\*/1/2/\*\*/\*\*/1/2/\*\*/1/1/1/
44. *Cacalia aconitifolia* Bunge 0001010000\*000110\*\*1100\*1100000 \*\*/\*\*/\*\*/1/2/\*\*/\*\*/1/2/\*\*/1/1/1/
45. *Cacalia reniformis* Muhl. 1001100000\*1\*\*010\*\*10\*0\*1100000 \*\*/9/\*\*/2/2/\*\*/\*\*/1/2/1/1/
46. *Cacalia atriplicifolia* L. 0001110000\*000010\*\*10\*0\*1100000 \*\*/\*\*/\*\*/2/2/\*\*/\*\*/1\*\*/2/1/1/
47. *Cacalia tuberosa* Nutt. 0001100000\*1\*\*010\*\*10\*0\*1100000 \*\*/\*\*/\*\*/2/2/\*\*/\*\*/1\*\*/2/1/3/
48. *Cacalia peltata* H.B.K. 1001010000\*001010\*\*10\*0\*1100000 \*\*/5/\*\*/1/2/\*\*/1,2,3\*\*/3\*\*/2/1/1/
49. *Cacalia suffulta* Grmn. 1001010000\*000010\*\*10\*0\*1100000 \*\*/8,10/\*\*/1/2/\*\*/\*\*/2,3\*\*/2/1/1/
50. *Cacalia amplifolia* DC. 1001010000\*000010\*\*10\*0\*1100000 \*\*/14/\*\*/1/2,5/\*\*/\*\*/3\*\*/2/1/2/
51. *Cacalia silphifolia* Rob. et Grmn. 1001010000\*1\*\*010\*\*10\*0\*1100000 \*\*/9/\*\*/1/2,5/\*\*/\*\*/3\*\*/2/1/2/
52. *Cacalia tussilaginoidea* H.B.K. 1001010000\*000010\*\*10\*0\*1100000 \*\*/5/\*\*/1/2,5/\*\*/\*\*/3\*\*/2/1/1/
53. *Cacalia radulaefolia* H.B.K. 0001010000\*000010\*\*10\*0\*1100000 \*\*/\*\*/\*\*/1/2,5/\*\*/\*\*/3\*\*/2/1/2/
54. *Cacalia sinuata* Llav. et Lex. 0001010000\*000010\*\*10\*0\*1100000 \*\*/\*\*/\*\*/1/2,5/\*\*/\*\*/3\*\*/2/1/2/
55. *Cacalia poculifera* (Wats.) Rob. 1001010000\*000010\*\*10\*0\*1100000 \*\*/14/\*\*/1/2,5/\*\*/\*\*/3\*\*/2/1/1/
56. *Cacalia cervariaefolia* DC. 1001010000\*000010\*\*10\*0\*1100000 \*\*/14/\*\*/1/2,5/\*\*/\*\*/1,2\*\*/2/1/2/
57. *Cacalia suaveolens* L. 1001010000\*000010\*\*00\*0\*1100000 \*\*/9/\*\*/2/2/\*\*/\*\*/3\*\*/2/1/2/
58. *Cacalia prenanthoides* H.B.K. 1001010000\*1\*\*010\*\*00\*0\*1100000 \*\*/10/\*\*/1/2/\*\*/\*\*/3,4\*\*/2/1/2/
59. *Adenostyles glabra* (Mill) DC. 1001010000\*1\*\*010\*\*10\*0\*1100000 \*\*/10/\*\*/1/2/\*\*/\*\*/3\*\*/2/1/1/
60. *Adenostyles tomentosa* Vill. 1001010000\*1\*\*010\*\*00\*0\*1100000 \*\*/12/\*\*/1/2/\*\*/\*\*/3\*\*/2/1/1/
61. *Senecio fluviatilis* Wall. 1001100000\*0000110100\*0\*1100000 3.0 3.0/8/\*\*/1/2/\*\*/\*\*/4/3/2/2/2/
62. *Senecio umbrosus* W.K. 1001110000\*0000110100\*0\*1100000 \*\*/7/\*\*/1/2/\*\*/\*\*/4/3/2/3/2/
63. *Senecio macedonicus* Gris. 1001110000\*0000110000\*0\*1100000 \*\*/7/\*\*/2/2/\*\*/\*\*/5/3/2/1/2/
64. *Senecio doricum* L. 1001110000\*0000110100\*0\*1100000 \*\*/7/\*\*/1/2/\*\*/\*\*/4/3/2/1/2/
65. *Senecio fuchsii* Gmel. 1001110000\*0000110100\*0\*1100000 3.0 2.0/8\*\*/2/2/7\*\*/4/2/2/1/2/
66. *Senecio racemosus* DC. 1001010000\*0000110100\*0\*1100000 \*\*/15/\*\*/2/2/\*\*/\*\*/4/3/2/1/2/
67. *Senecio triangularis* Hk. 1001110000\*1\*\*011000\*0\*1100000 \*\*/8\*\*/2/2/\*\*/\*\*/3/2/2/1/2/
68. *Senecio cannabifolius* Less. 1001110000\*00001101010101100000 3.0 3.0/8\*\*/2/2/7\*\*/3/2/2/1/2/
69. *Senecio paucifolius* Gmel. 1001110000\*0000110101011100000 \*\*/9/\*\*/1/2/\*\*/\*\*/3/2/2/3/2/
70. *Senecio brachychaetus* DC. 1001010000\*1\*\*1110010\*0\*1100000 \*\*/10/\*\*/1/2/\*\*/\*\*/1/3/2/2/3/2/
71. *Senecio campestris* DC. 1001010000\*1\*\*1110010\*0\*1100000 \*\*/10/\*\*/1/2/\*\*/\*\*/1/3/2/2/3/2/
72. *Senecio rivularis* (W.K.) DC. 1001010000\*1\*\*1110110\*0\*1100000 \*\*/10/\*\*/1/2/\*\*/\*\*/1/3/2/3/2/
73. *Senecio palustris* DC. 0101010000\*1\*\*0110010\*0\*1100000 \*\*/\*\*/1/1/2/\*\*/\*\*/3/2/2/2/2/
74. *Senecio toluccanus* DC. 1001010000\*1\*\*0110100\*0\*1100000 \*\*/7/\*\*/1/2/\*\*/\*\*/3,4\*\*/3/2/3/2/



75. *Senecio hualtata* Bert. 1001010000\*1\*\*0110100\*0\*1100000 \*\*/7\*\*/1/2\*\*/\*\*/3,4/2/2/1/2/
76. *Senecio smithii* DC. 1001010000\*1\*\*0110100\*0\*1100000 \*\*/7\*\*/1/2\*\*/\*\*/3,4/3/2/1/2/
77. *Senecio icoglossus* DC. 1001010000\*1\*\*0110100\*0\*1100000 \*\*/7\*\*/1/2\*\*/\*\*/3/3/2/3/2/
78. *Senecio pulcher* Hk. et Arn. 1001010000\*1\*\*0110100\*0\*1100000 \*\*/7\*\*/1/2\*\*/\*\*/3,4/2/3/2/
79. *Senecio erisithalifolius* Sch. Bip. 1001010000\*1\*\*0110100\*0\*1100000 \*\*/7\*\*/1/2\*\*/\*\*/3,4/3/2/1/2/
80. *Senecio dumentorum* Gardn. 1001110000\*1001101010101100000 1.0 3.0/11\*\*/2/2/7\*\*/\*\*/1,2/1/2/2/2/
81. *Senecio neomexicanus* Gray 1001010000\*1\*\*0110100\*0\*1100000 \*\*/12\*\*/2/2\*\*/\*\*/5/3/2/1/2/
82. *Senecio pimpinellaefolius* H.B.K. 1001010000\*0000110100\*101100000 \*\*/8\*\*/1/2\*\*/\*\*/4/3/2/1/2/
83. *Senecio grandifolius* Less. 1001100000\*1001101100\*1100000 3.0 3.0/12\*\*/1/1,2/5\*\*/\*\*/3,4,5/2/2/1/2/
84. *Senecio eurycephalus* Torr. et Gray 1001110000\*1\*\*0110000\*0\*1100000 \*\*/12\*\*/2/2\*\*/\*\*/5/3/2/1/2/
85. *Senecio lobatus* Pers. 0001010000\*1\*\*0110000\*101100000 \*\*/2/2\*\*/\*\*/5/2/2/1/2/
86. *Senecio eremophilus* Rich. 1001110000\*0000110000\*101100000 \*\*/9\*\*/2/2\*\*/\*\*/3/2/2/1/2/
87. *Senecio cernuus* Gray 0001010000\*000010\*\*00\*0\*1100000 \*\*/1/2\*\*/\*\*/3\*\*/2/1/2/
88. *Senecio aureus* L. 1001010000\*1\*\*0110000\*0\*1100000 \*\*/14\*\*/1/2\*\*/\*\*/4,5/2/2/1/2/
89. *Senecio robinsonii* Oakes 1001010000\*1\*\*0110000\*0\*1100000 \*\*/14\*\*/1/2,5\*\*/\*\*/5/2/2/1/2/
90. *Senecio tomentosus* Mx. 1001000000\*0000110000\*101100000 \*\*/14\*\*/1/2,5\*\*/\*\*/4,5/2/2/1/2/
91. *Senecio antisanae* Benth. 1001110000\*1\*\*010\*\*00\*0\*1100000 \*\*/12\*\*/2/2\*\*/\*\*/3\*\*/2/1/2/
92. *Senecio salignus* DC. 0001100000\*100110010\*101100000 1.0 2.0\*\*/2/2,4/7/1,2,3\*\*/3/2/2/2/2/
93. *Senecio pandurifolius* Harv. 1001010000\*000010\*\*\*0\*1101000 \*\*/1\*\*/1/2,5\*\*/\*\*/1,3,4\*\*/2/2/2/
94. *Senecio auricula* Bourg. 0001010000\*0100110000\*101100000 \*\*/1/2\*\*/\*\*/3/3/2/3/2/
95. *Senecio serra* Sond. 0011010000\*0000110000\*0\*1100000 \*\*/1/2,5\*\*/\*\*/1,3,5/2/2/1/2/
96. *Senecio lasiorhiza* DC. 1001010000\*0000110100\*101100000 \*\*/5\*\*/1/2\*\*/\*\*/1,4/2/2/1/2/
97. *Senecio othonnaeflorus* DC. 0001110000\*1\*\*010\*\*\*100\*1100000 3.0 2.0\*\*/2/2\*\*/\*\*/1,3\*\*/2/1/2/
98. *Senecio barbellatus* DC. 0001010000\*1\*\*111001100\*1100000 \*\*/2/2\*\*/\*\*/1/3,4/2/2/2/2/
99. *Senecio bupleuroides* DC. 0001010000\*000011001100\*1100000 \*\*/2/2\*\*/\*\*/3,4/2/2/2/2/
100. *Senecio petasitis* DC. 1001110000\*001110110\*0\*1100000 \*\*/5\*\*/2/2\*\*/1/1,2,4/2/2/1/1/
101. *Senecio albonervius* Griseb. 1001110000\*001110110\*0\*1100000 \*\*/1,3\*\*/2/2\*\*/1,2,1,2,4/2/2/1/1/
102. *Senecio hartwegii* Benth. 1001\*10100\*001110110\*101100000 \*\*/12\*\*/2/2,4\*\*/1/1,3/3/2/1/1/
103. *Othonnopsis pallens* Benth. et Hk. 0011110000\*100110000\*101100000 3.0 2.0\*\*/2/2,4/7\*\*/\*\*/1,4/2/2/2/2/
104. *Othonnopsis angustifolia* DC. 0011110000\*1001110010\*101100000 3.0 3.0\*\*/2/2,4/7\*\*/\*\*/1,4,5/3/2/2/2/
105. *Othonnopsis intermedia* Boiss. 0011110000\*100110010\*101100000 3.0 3.0\*\*/2/2,4/7\*\*/\*\*/4/3/2/2/3/
106. *Othonnopsis cheirifolia* Benth. et Hk. 0011110000\*100110010\*101100000 3.0 2.0\*\*/2/2,4/4\*\*/\*\*/3,4/3/2/2/3/
107. *Othonna arborescens* L. 0011100000\*0000110110\*101100000 \*\*/2/2,2\*\*/\*\*/5/3/2/2/3/
108. *Othonna triplinervioides* DC. 0011100000\*1\*\*0110000\*101100000 \*\*/2/2\*\*/\*\*/1,4,5/2/2/1/3/
109. *Othonna pinnata* L.f. 0011010000\*00011100\*0\*101100000 \*\*/2/2\*\*/\*\*/1/4/2/2/1/2/
110. *Othonna perfoliata* Jacq. 0011010000\*1\*\*11110\*0\*101100000 \*\*/2/2\*\*/\*\*/1,4,5\*\*/2/2/3/
111. *Othonna digitata* L.f. 0011110000\*00001110\*0\*101100000 \*\*/2/2\*\*/\*\*/4,5\*\*/2/1/2/
112. *Othonna heterophylla* L.f. 0011010000\*1\*\*11110000\*101100000 \*\*/1/2\*\*/\*\*/1/4/3/2/1/3/











189. *Senecio haastii* Hk.f. 1001010000\*000011011100\*1100000 \*\*/1\*/1/2\*/\*\*/\*4/2/1/1/2/
190. *Senecio hypargyreaus* DC. 1001110000101011001100\*1101000 3.0 2.0/12\*/2/2\*/\*\*/1/1,2,4/3\*/1/2/
191. *Alcioppe tabularis* DC. 1001100001000011011011100000 3.0 2.0/12\*/2/2\*/\*\*/\*1,2/3/1/1/2/
192. *Alcioppe lanata* DC. 1001110000101001101101110101000 3.0 2.0/12\*/2/2\*/\*\*/\*1,2/3/1/1/2/
193. *Senecio sciadophilus* Raoul 1001110000100011001101010101000 3.0 2.0/9\*/2/2/2\*/\*\*/1/4/2/1/1/2/
194. *Senecio deltoideus* Less. 10011100001000010\*\*0101010101000 1.0 4.0/11\*/2/2/7\*/\*\*/1,4\*/2/1/1/
195. *Senecio mikanioides* Otto 1001100000100101010\*\*010101100000 5.0 5.0/9\*/2/2/7/2\*/\*\*4\*/2/1/1/
196. *Senecio tamoides* DC. 000110000011\*\*1110000\*01100000 5.0 6.0/2\*/2/2/7\*/\*\*1/1,4/3/2/1/1/
197. *Senecio cordifolius* L. 0001100000\*00001100010101100000 \*\*/2/2\*/\*\*/\*4/2/2/1/1/
198. *Senecio quinquelobus* DC. 00011000001001110\*\*010101110000 5.0 6.0/2\*/2/2/7/2/1/4\*/2/1/1/
199. *Senecio densiflorus* Wall. 10011100001001011000100\*1100000 3.0 5.0/1,11\*/2/2/7/3/2/2/1/2/
200. *Senecio acuminatus* Wall. 00011100011000001000100\*1100000 3.0 4.0/2\*/2/2/7\*/\*\*/1/2/1/2/
201. *Senecio corymbosus* Wall. 10011100001000010\*\*1100\*1101000 3.0 6.0/1\*/2/2/7\*/\*\*1,2\*/\*\*/1/1/
202. *Senecio buimalia* Buch-Ham. 10011100001000010\*\*1100\*1101000 3.0 3.0/1\*/2/2/7\*/\*\*1,2\*/\*\*/1/1/
203. *Senecio araneosus* DC. 100111000011\*\*010\*\*1100\*1100000 5.0 6.0/1,10\*/2/2/7\*/\*\*4\*/1/1/1/
204. *Senecio campylodes* DC. 000111000011\*\*010\*\*1100\*1100000 3.0 3.0/2\*/2/2/7\*/\*\*4/2/2/1/2/
205. *Senecio kunthianus* Wall. 1001010000\*0000101\*10101100000 \*\*/1\*/2/2\*/\*\*/\*2/2/1/3/
206. *Senecio alatus* Wall. 1001010000\*00001100101101010000 \*\*/5\*/2/2\*/\*\*/\*3\*/\*\*/1/2/
207. *Senecio tetranthus* DC. 1001100000\*0010111001010101000 \*\*/11\*/2/2\*/\*\*/3\*/\*\*/2/1/1/
208. *Senecio wallichi* DC. 1001110000\*00001100100\*1100000 \*\*/9,11\*/2/2\*/\*\*/\*1,2\*/2/1/2/
209. *Senecio wightianus* DC. 100111000010000110000\*0\*1100000 5.0 3.0/9\*/2/2/2\*/\*\*4/2/2/1/2/
210. *Senecio grahami* Hk.f. 100110000010001100\*0\*101100000 5.0 3.0/2,11\*/2/2/7\*/\*\*1/5/2/2/1/1/
211. *Senecio diversifolius* Wall. 100111000010000110000\*101100000 5.0 4.0/11\*/2/2/7\*/\*\*4/2/2/2/2/
212. *Senecio graciliflorus* DC. 100110000010000110000\*101100000 3.0 2.0/11\*/2/2/7\*/\*\*5/2/2/1/2/
213. *Senecio ludens* Clke. 100110000011\*\*0110000\*101100000 5.0 6.0/9,11\*/2/2/7\*/\*\*4/2/2/1/1/
214. *Senecio giganteus* Desf. 1001110000100001100010101100000 1.0 4.0/11\*/2/2/7\*/\*\*5/2/2/1/2/
215. *Senecio jacobaea* L. 100111000010010110000\*101100000 3.0 3.0/11\*/2/2/7/3\*/\*\*5/2/2/1/2/
216. *Senecio aquaticus* Hill. 100111000010000110000\*0\*1100000 3.0 3.0/11\*/2/2/7\*/\*\*5/2/2/1/2/
217. *Senecio belgaumensis* Clke. 1001110000\*0000110000\*101100000 \*\*/2,11\*/2/2\*/\*\*/\*5/3/2/1/1/
218. *Senecio candicans* Wall. 100111000010000110000\*101100000 5.0 3.0/1\*/2/2/7\*/\*\*4/2/2/1/2/
219. *Senecio appendiculatus* DC. 1001110000100011000100\*1100000 1.0 3.0/12\*/4/2/5\*/\*\*1,3,4,5/3/2/1/2/
220. *Senecio incanus* L. 1001100000\*00000101011100000 \*\*/3\*/2/2\*/\*\*/\*3/2/1/2/
221. *Senecio leucophyllus* DC. 1001010000\*1\*\*0010001011100000 \*\*/3\*/2/2\*/\*\*/\*2/2/1/2/
222. *Senecio taygeteus* Boiss.et Heldr. 10011110011010110000\*101100000 1.0 4.0/2\*/2/2/7\*/\*\*5/3/2/1/2/
223. *Senecio candidus* DC. 1001111001101010100\*101100000 3.0 3.0/2\*/2/2/7/3\*/\*\*5/2/2/1/2/
224. *Senecio gibbosus* DC. 100111000110100110000\*101100000 2.0 3.0/2\*/2/2/7\*/\*\*5\*/2/1/2/
225. *Senecio oliganthus* DC. 10011100001010010\*\*0100\*1100000 1.0 2.0/2\*/2/2/2\*/\*\*3,4\*/2/2/3/
226. *Senecio lineatus* DC. 100111100010101010100\*1100000 1.0 4.0/2\*/2/2/7/2/3\*/\*\*3,4/2/2/3/
227. *Cineraria canescens* Wendl. 100111000010000110000\*101100000 5.0 3.0/1,12\*/2/2/6\*/\*\*3,4/2/2/1/1/



228. *Senecio argyreaus* Boiss. et Bal. 1001010000\*0000101000\*0\*11000000 \*\*1/\*2/2/\*\*\*/\*4/3/2/1/2/  
229. *Senecio hypochioneus* Boiss. 1001010000\*00001100\*100\*11000000 \*\*1/\*2/2/\*\*\*/\*4/2/2/1/2/  
230. *Senecio farfaraefolius* Boiss. 1001110000\*0000101000\*0\*11000000 \*\*1/\*2/2/\*\*\*/\*4/2/2/1/1/  
231. *Senecio quinquelobus* Boiss. ex DC. 0001110000101001100000\*0\*11000000 1.0 6.0 \*\*2/2/7/\*\*\*4/3/2/2/2/  
232. *Senecio linifolius* Clke. 000110000010000110000\*0\*11000000 5.0 5.0 \*\*2/2/7/\*\*\*4/2/2/2/2/  
233. *Senecio palmensis* Ch. Smith. 00011100001010011000101011000000 4.0 4.0 \*\*2/2/7/\*\*\*4/2/2/2/2/  
234. *Senecio prunifolius* Wedd. 100111010100001100010111000000 1.0 6.0/2/\*2/2/7/\*\*\*3,4/2/2/1/2/  
235. *Senecio psidiifolius* Rusby 1001110000100001100010111010000 1.0 4.0/2/\*2/2/7/\*\*\*3,4/3/2/1/2/  
236. *Olearia rani* (A. Cunn.) Druce 100111111100001100010111010000 1.0 4.0/3/\*4/2,3/7/\*1/1,2,3,4/2/2/1/2/  
237. *Olearia avicennaeifolia* Hk. f. 110111000110100110011011101000 1.0 1.0/4/3/4/2/7/\*\*\*2/2/1/1/2/  
238. *Olearia operina* Hk. f. 1100110000101010111011101000 1.0 3.0/2/3/2/\*2/2,3,4/\*4/3/1/2/3/  
239. *Olearia homolepis* FvM. 110011010010100110010\*111100000 1.0 1.0/2,5/3/2/\*9/\*\*\*2,4/3/2/2/2/  
240. *Olearia ledifolia* Benth. 11001101001010011001100\*1101000 1.0 1.0/3/3/2/\*8/\*\*\*3/2/1/1/2/  
241. *Olearia solandri* Hk. f. 11001101001010110011011101100 1.0 1.0/3/3/2/\*8/\*\*\*1/1,2/3/1/1/2/  
242. *Olearia argyrophylla* FvM. 1100110101010101100110111001000 1.0 3.0/3/4/\*5/\*\*\*1/3,4/3/1/1/2/  
243. *Olearia allomi* Kirk. 10001101001010110011011101000 1.0 1.0/3/\*2/\*8/\*\*\*1/1,2,3/3/1/1/2/  
244. *Olearia viscosa* Benth. 1101110101010110011011101000 1.0 1.0/3/3/2/7/\*\*\*1/3/2/1/1/2/  
245. *Olearia ramulosa* Benth. 11001101001010110010\*111100000 1.0 2.0/2,5/3/3/\*9/\*\*\*1/2,4/2/2/2/2/  
246. *Olearia chrysophylla* Benth. 110011000101011001100\*1101100 1.0 2.0/3/3/2/\*7/\*\*\*1/3/2/1/1/2/  
247. *Olearia stellulata* DC. 10001100001010110010\*111101000 1.0 2.0/4/\*2/\*9/4/\*2/2/2/1/2/  
248. *Olearia glutinosa* Benth. 11011101010010110011011101100 \* 3.0/3/3/2/2,3/7/\*\*\*1/2,4/2/1/1/2/  
249. *Olearia axillaris* FvM. 110011010010100110010\*111100000 1.0 2.0/2/3/3/\*6/\*\*\*2,5/2/2/2/2/  
250. *Olearia arborescens* Forst. f. 1001110101010110011011101000 1.0 1.0/3/\*2/2/7/\*\*\*1/1/2/1/1/2/  
251. *Olearia insignis* Hk. f. 100011000010100110011011101000 1.0 1.0/3/\*4/\*8/\*\*\*2,4/2/1/1/2/  
252. *Olearia myrsinoides* FvM. 100011000010100110011011101000 1.0 1.0/3/\*2/\*6/\*\*\*4/2/1/1/2/  
253. *Olearia elliptica* DC. 010111010010010110010\*1111010005.0 2.0/\*3/2/2/7,4/\*2/2/2/1/2/  
254. *Baccharis schomburgkii* Baker 1100110100100101010\*1111010000 1.0 2.0/8/3/2/\*7,4/\*2/\*\*\*1/2/  
255. *Microglossa mespilifolia* DC. 11011101001011110011011100000 1.0 2.0/5/3/2/2/6,1,3/1/2/2/1/1/  
256. *Chresta angustifolia* Gardn. 11001111111001110\*11111100001 1.0 3.0/4/3/4/\*5/1/4/2,3,4/\*3/1/2/  
257. *Lychnophora affinis* Mart. 10001111111000110\*1110\*1100001 1.0 5.0/4/\*3/\*7/\*\*\*4/2,4/\*3/2/2/  
258. *Haplostephium passerina* Mart. 10001101111010010\*1110\*1100011 1.0 5.0/4/\*3/\*7/\*\*\*1,2,4/\*3/2/2/  
259. *Vanillosmopsis erythroleppa* Sch. Bip. 10001101111000110\*1110\*1100010 1.0 5.0/4/\*2/\*7/\*\*\*4/1,2,3/\*3/2/2/  
260. *Albertinia eleagnus* Mart. 10001111111000110\*1111110010 1.0 4.0/4/\*2/\*7/\*\*\*4/1,2,3/\*3/2/2/  
261. *Chresta exsucca* DC. 100111011001110\*111111100001 1.0 5.0/2,3/\*4/1,2,5/7/1/2,3/1,2/\*3/2/2/  
262. *Stilphnoleppus emarginatus* Gardn. 1100111100101110\*11111100001 1.0 4.0/2,3/3/2/\*7/1/4/2/\*3/2/2/  
263. *Chresta sphaerocephala* DC. 1101110011001110\*11111100001 3.0 4.0/2,3/3/4,1,2,5/7/1/2,3/1,2/\*3/1/2/  
264. *Chresta intermedia* Gardn. 1101110011001110\*11111100001 1.0 5.0/3/3/4,1,2,5/7/1/1,2,4/1,2,3/\*3/1/2/  
265. *Albertinia verbascifolia* Mart. 11001110011000110\*111111100001 1.0 4.0/4/3/4/\*5/\*4/1,2/\*3/1/2/



266. *Senecio ericaefolius* Benth. 10011100001000011000100\*1101000 1.0 1.0/3\*/3/2/3\*/\*/4/2/2/1/2/  
 267. *Senecio arbutifolius* H.B.K. 00011100001010011000100\*1100000 1.0 1.0/0\*/3/2/3\*/\*/3/2/2/1/2/  
 268. *Senecio curvidens* Sch. Bip. 1001110000101001100\*100\*1100000 1.0 3.0/6\*/2/2/2\*/\*/3/2/2/1/2/  
 269. *Senecio scytophyllus* H.B.K. 0001110000101001100000\*0\*1100000 2.0 3.0/0\*/2/2/5\*/\*/2/2/2/1/2/  
 270. *Microchaete glabrata* Benth. 00011100001000010\*\*0100\*1101000 1.0 1.0/0\*/2/2/3\*/\*/3\*/2/2/2/  
 271. *Microchaete vaccinioides* Benth. 00011100101000010\*\*0100\*1100000 1.0 1.0/0\*/2/2/2\*/\*/3\*/2/2/2/  
 272. *Microchaete teretifolia* Benth. 00011100001000010\*\*0100\*1101000 2.0 1.0/0\*/2/2/2\*/\*/3\*/2/2/2/  
 273. *Microchaete pulchella* Benth. 0001110001010010\*\*0100\*1100000 1.0 1.0/0\*/2/2/3\*/\*/3\*/2/2/2/  
 274. *Microchaete trichopus* Benth. 0001110001010010\*\*0100\*1100000 1.0 1.0/0\*/2/2/3\*/\*/3\*/2/2/2/  
 275. *Euryops oligoglossus* DC. 000110001000001100110101100000 \* 1.0/0\*/2/2/2\*/\*/4/2/2/2/2/  
 276. *Euryops spathaceus* DC. 000111000010100110010\*101100000 1.0 1.0/0\*/2/2/2\*/\*/4/2/2/2/2/  
 277. *Euryops virgineus* Less. 00011100000000011001100\*1100000 \* 1.0/0\*/2/2/2\*/\*/4/2/2/2/2/  
 278. *Euryops pinifolius* A.Rich. 0001110000101001100110101101000 1.0 2.0/0\*/2/2/2\*/\*/3,4/2/2/2/2/  
 279. *Euryops algoensis* DC. 0001110000001001100110101101000 \* 1.0/0\*/2/2/2\*/\*/4/2/2/2/2/  
 280. *Euryops abrotanifolius* DC. 0001110000001001101100\*1100000 \* 2.0/0\*/2/2/2\*/\*/4/2/2/2/2/  
 281. *Gamolepis euryopoides* DC. 00011000001010011001100\*0\*\*\*000 1.0 2.0/0\*/2/2/3\*/\*/3/2/2/2/2/  
 282. *Senecio triqueter* Less. 00011100000010010\*\*0100\*1100000 \* 1.0/0\*/3/2/2\*/\*/3\*/2/2/2/  
 283. *Senecio pinifolius* Lam. 00011100000010011000100\*1100000 \* 1.0/0\*/3/2/2\*/\*/3/2/2/2/2/  
 284. *Senecio abrotanifolius* L. 100111000000000110000\*0\*1100000 \* 2.0/6\*/2/2/2\*/\*/3/2/2/2/2/  
 285. *Senecio adonidifolius* Loisel. 100111000010000110000\*0\*1100000 3.0 2.0/6\*/2/2/5\*/\*/4/2/2/2/2/  
 286. *Culcitium reflexum* H.B.K. 1001110100000010\*\*00\*0\*1100000 \* 1.0/12\*/2/2/10\*/\*/3\*/2/2/2/2/  
 287. *Culcitium nivale* H.B.K. 100111010\*000010\*\*00\*0\*1100000 \*\*/3\*/2/2\*/\*/3\*/2/2/2/2/  
 288. *Culcitium megallanicum* Hom.et Jacq. 10011000000000010\*\*00\*0\*1100000 \* 2.0/3\*/2/2/4\*/\*/3,4\*/2/2/2/2/  
 289. *Culcitium lechleri* Sch. Bip. 10011100001010010\*\*00\*0\*1100000 \*\*/3\*/2/2\*/\*/3\*/2/2/2/2/  
 290. *Culcitium rufescens* H.B. 1001110000\*000010\*\*00\*0\*1100000 \*\*/3\*/2/2\*/\*/3\*/2/2/2/2/  
 291. *Senecio lanatus* DC. 10011101001000010\*\*0100\*1101000 1.0 1.0/3\*/2/2/3\*/\*/3\*/2/2/2/2/  
 292. *Senecio argyrea* Phil. 100111000001\*\*0110000\*0\*1100000 \* 1.0/3\*/2/2/4\*/\*/3/2/2/3/2/  
 293. *Senecio chilensis* Less. 100111000111\*\*0110000\*101100000 3.0 3.0/3\*/2/2/4,7\*/\*/3,4/2/2/2/2/  
 294. *Senecio danyauii* var. *intermedia* Sch.Bip. 100111000001\*\*010\*\*\*00\*0\*1100000 \* 2.0/1,2\*/2/2/4\*/\*/4\*/2/2/2/2/  
 295. *Senecio longipes* Hk.f. 000111000001\*\*010\*\*\*00\*0\*1100000 \* 1.0/0\*/2/2/4\*/\*/4\*/2/2/2/2/  
 296. *Seneciodarwinii* Hk.et Arn. 100111000001\*\*0110100\*0\*1100000 \* 2.0/1,2\*/2/2/4\*/\*/4/2/2/2/2/  
 297. *Senecio faulklandicus* Hk.f. 100111000010000110000\*0\*1100000 3.0 2.0/1,2\*/2/2/4\*/\*/4/2/2/2/2/  
 298. *Senecio patagonicus* var. *B.Hk.et Arn.* 10011110000000010\*\*00\*0\*1100000 \* 1.0/1,2\*/2/2/4\*/\*/4\*/2/2/2/2/  
 299. *Senecio littoralis* Gaud. 100111000011\*\*0110100\*0\*1100000 5.0 1.0/12\*/2/2/2\*/\*/3/2/2/2/2/  
 300. *Senecio bipinnatus* Less. 00011100001000010\*\*0100\*1101000 2.0 1.0/0\*/2/2/2\*/\*/1,3,4\*/2/2/2/2/  
 301. *Senecio achilliaefolius* DC. 10011100000000011000100\*1101000 \* 1.0/12\*/2/2/2\*/\*/4,5/2/2/2/2/  
 302. *Senecio rigidus* L. 100111000010000110000\*101110000 3.0 2.0/11\*/2/2/5\*/\*/4/2/2/2/2/  
 303. *Senecio juniperinus* L. 100111000010000110000\*101110000 3.0 2.0/11\*/2/2/5\*/\*/4/2/2/2/2/



304. *Senecio arnicaeflorus* DC. 100111000010100110000\*101110000 1.0 2.0/11/\*2/2/2/\*4/2/2/2/2/
305. *Senecio pubigerus* L. 100111010010000110000\*101110000 3.0 3.0/11/\*2/2/5/\*4/2/2/2/2/
306. *Senecio cinerascens* Ait. 100111000010000110000\*101110000 3.0 2.0/11/\*2/2/5/\*5/3/2/2/2/
307. *Senecio graminifolius* Jacq. 100111010000000110000\*101110000 \* 2.0/11/\*2/2/2/\*4/2/2/2/2/
308. *Senecio vimineus* DC. 00011100000000110000\*101110000 \* 1.0/\*2/2/2/\*4/2/2/2/2/
309. *Senecio rosmarinifolius* L.f. 100111010010000110000\*101110000 3.0 2.0/11/\*2/2/2/\*4/2/2/2/2/
310. *Senecio paniculatus* Berg. 00011110001000010\*\*00\*101110000 3.0 2.0/\*2/2/2/5/\*4/\*2/2/2/
311. *Senecio burchellii* DC. 10011100000000110000\*101110000 \* 1.0/6/\*2/2/2/\*4/2/2/2/2/
312. *Senecio longilobus* Benth. 100111000010000110000\*101110000 1.0 2.0/2/\*2/2/7/\*4/2/2/2/2/
313. *Senecio australis* Willd. 1001110000\*0000110000\*0\*1110000 \*\*/11/\*2/2/\*4/2/2/2/2/
314. *Senecio hypoleucus* FvM. 1001110000100101110000\*101110000 3.0 2.0/2/\*2/2/2/3/\*4/\*2/1/2/
315. *Senecio brasiliensis* Less. 100111000010000110000\*101110000 1.0 2.0/2/\*2/2/1/\*4/2/2/2/2/
316. *Senecio rutaceus* Phil. 000111000010000110000\*0\*1110000 1.0 2.0/\*2/2/2/3/\*4/2/2/2/2/
317. *Senecio glaber* Less. 00011100110100110000\*101110000 1.0 3.0/\*2/2/7/\*4/2/2/2/2/
318. *Senecio iberidifolius* Phil. 000110000011\*\*010\*\*00\*101110000 3.0 3.0/\*2/2/7/\*4/\*2/3/2/
319. *Senecio hispidulus* A.Rich. 1001110000100101110000\*101110000 4.0 2.0/11/\*2/2/2/3/\*4/\*2/2/2/
320. *Senecio gunnii* (Hk.f.)Belch. 1001110000100101110000\*101110000 3.0 3.0/2/\*2/2/2/3/\*4/\*2/1/2/
321. *Senecio magnificus* FvM. 000111000010010110000\*101110000 3.0 3.0/\*2/2/5/3/\*4/3/2/2/2/
322. *Senecio laceratus* (FvM)Belch. 0001110000100101110000\*101110000 2.0 2.0/\*2/2/1/3/\*4/\*2/2/2/
323. *Senecio quadridentatus* Labill. 1001110000100101110000\*101110000 3.0 2.0/2/\*2/2/2/3/\*4/\*2/3/2/
324. *Senecio linearifolius* A.Rich. 0001110000100101110000\*101110000 3.0 2.0/\*2/2/1/3/\*4/2/2/2/2/
325. *Senecio lineariaefolius* Poepp. ex DC. 100111000010010110000\*0\*1110000 1.0 3.0/2/\*2/2/2/3/\*4/2/2/2/2/
326. *Senecio saltensis* Hk.et Arn. 110111000010000110000\*101110000 1.0 1.0/9/1/2/2/2/\*4/2/2/2/2/
327. *Senecio lautus* ssp maritimus Ali 000111000010100110000\*101110000 3.0 2.0/\*2/2/1/\*4/2/2/2/2/
328. *Senecio steudelii* Sch.Bip. 000111000010000110000\*0\*1110000 5.0 3.0/\*2/2/1/\*4/2/2/2/2/
329. *Senecio elegans* L. 110111000010000110000\*101110000 5.0 2.0/11/1/2/2/1/\*4/2/2/2/2/
330. *Senecio grandiflorus* Berg. 100111000010000110000\*101110000 3.0 3.0/11/\*2/2/1/\*4/2/2/2/2/
331. *Senecio pringlei* Gray 010111000010000110000\*101110000 4.0 2.0/\*1/2/2/1/\*4/2/2/2/2/
332. *Senecio petraeus* Boiss. et Reut. 100111000010000110000\*101110000 5.0 2.0/6/\*2/2/1/\*4/2/2/2/2/
333. *Senecio erubescens* Ait. 1101010000\*000011\*\*00\*101110000 \*\*/6,9/1/2/2/\*4/\*2/2/2/2/
334. *Senecio arenarius* Thunb. 1101010000\*0000110000\*101110000 \*\*/6/1/2/2/\*4/2/2/2/2/
335. *Senecio joppensis* Dinsm. 100111000010000110000\*101110000 5.0 3.0/6/\*2/2/1/\*4/2/2/2/2/
336. *Senecio flavus* Sch. Bip. 00011100001000010\*\*00\*101110000 3.0 3.0/\*2/2/1/\*4/\*2/2/2/2/
337. *Senecio brachyuncinus* Boiss. 0001010000\*0000110000\*101110000 \*\*\*/\*2/2/\*4/3/2/1/1/
338. *Senecio duraei* J.Gay 010111000010000110000\*101110000 5.0 2.0/\*1/2/2/1/\*4/3/2/2/2/
339. *Senecio incrassatus* Lowe 000111000010000110000\*101110000 5.0 2.0/\*2/2/1/\*4/2/2/2/2/
340. *Senecio littoreus* Thunb. 100111000010000110000\*101110000 5.0 2.0/6/\*2/2/1/\*4/2/2/2/2/



341. *Senecio coronipifolius* Desf. 1001010000\*000011000000\*\*6/\*2/2/\*/\*4/2/2/2/2/  
 342. *Senecio delphinifolius* Vahl. 1001010000\*0000110100\*1011000000\*\*6,9/\*2/2/\*/\*4/2/2/2/2/  
 343. *Senecio gallicus* Chaix 100111000010000110000\*101110000 3.0 2.0/6/\*2/2/1/\*/\*4/2/2/2/2/  
 344. *Senecio vernalis* W. et K. 100110000010000110000\*101110000 3.0 1.0/6/\*2/2/1/\*/\*4/2/2/2/2/  
 345. *Senecio humilis* Desf. 100111000010000110000\*101110000 5.0 2.0/6/\*2/2/1/\*/\*4/2/2/3/2/  
 346. *Senecio crassifolius* Willd. 100110000010000110000\*101110000 5.0 2.0/6/\*2/2/1/\*/\*4/2/2/3/2/  
 347. *Senecio leucanthemifolius* Poir 1001110000\*0000110000\*1011100000\*\*6/\*2/2/\*/\*4/2/2/3/2/  
 348. *Senecio subdentatus* Ledeb. 100111000010000110000\*101110000 3.0 1.0/6/\*2/2/1/\*/\*4/2/2/2/2/  
 349. *Senecio lividus* L. 1001110000\*0000110000\*101110000\*\*6/\*2/2/\*/\*4/2/2/2/2/  
 350. *Senecio squalidus* L. 100111000010000110000\*101110000 3.0 2.0/6/\*2/2/1/\*/\*4/2/2/2/2/  
 351. *Senecio sylvaticus* L. 10111000010000110000\*101110000 3.0 2.0/9,11/1/2/2/1/\*/\*4/2/2/2/2/  
 352. *Senecio viscosus* L. 010111000010000110000\*0\*1110000 5.0 2.0/\*1/2/2/1/\*/\*4/2/2/2/2/  
 353. *Senecio aegyptius* L. 100111000010000110000\*101110000 4.0 3.0/6/\*2/2/1/\*/\*4/2/2/2/2/  
 354. *Senecio decaisnei* DC. 0001110000\*000010\*\*00\*101110000\*\*/\*2/2/\*/\*4/\*2/1/1/  
 355. *Senecio pygmaeus* DC. 10011000001000010\*\*00\*101110000 4.0 2.0/6/\*2/2/1/\*/\*4/\*2/1/2/  
 356. *Senecio speciosus* Willd. 1001110000\*0000110000\*101110000\*\*11/\*2/2/\*/\*4/2/2/1/2/  
 357. *Senecio dubius* Ldb. 10011100001000010\*\*00\*101110000 3.0 2.0/6/\*2/2/1/\*/\*4/\*2/2/2/  
 358. *Senecio vulgaris* L. 1001110000\*000010\*\*00\*101110000\*\*6/\*2/2/\*/\*4/\*2/2/2/  
 359. *Senecio nebrodensis* L. 0001110000\*0000110000\*101110000\*\*/\*2/2/\*/\*4/2/2/2/2/  
 360. *Senecio californicus* DC. 100111000010000110000\*101110000 4.0 3.0/6/\*2/2/1/\*/\*4/3/2/2/2/  
 361. *Senecio douglasii* DC. 100111000010000110000\*101110000 1.0 2.0/2,6/\*2/2/7/\*/\*4/2/2/2/2/  
 362. *Senecio webbiai* (Sch. Bip.) Christ 1001110000\*0010110000\*101110000\*\*11/\*2/2/2/\*/\*4/2/2/1/1/  
 363. *Senecio heritieri* DC. 10011000000000110000\*101110000\* 1.0/11/\*2/2/2/\*/\*4/3/2/1/1/  
 364. *Senecio cruentus* DC. 1001110000\*0010110000\*101110000\*\*11/\*2/2/2/\*/\*4/2/2/1/1/  
 365. *Senecio maderensis* DC. 100111000010000110100\*101110000 3.0 2.0/2/\*2/2/1/\*/\*4/3/2/1/1/  
 366. *Senecio tussilaginis* Lindl. 1001110000\*0000110100\*101110000\*\*2,11/\*2/2/\*/\*4/3/2/1/1/  
 367. *Tetradymia canescens* DC. 10011101001010110\*\*1100\*1100000 1.0 1.0/1/\*2/2/2/\*1/2/\*1/2/2/  
 368. *Luina hypoleuca* Benth. 1001010000\*001010\*\*110111100000\* 13/\*2/2/\*1/\*1,3/\*1/2/3/  
 369. *Peucephyllum schottii* Gray 010011000011010010\*\*110111100010 3.0 2.0/\*3/2/\*/\*1,2,3/\*1/2/2/



APPENDIX II

SOME FEATURES CHARACTERISTIC OF GROUPS I - VI  
AND SUBGROUPS OF GROUP IV



The information as coded in Appendix I is somewhat inaccessible. Here is a summary of the salient characteristics of the Groups and major Subgroups.

#### GROUP I

Leaves petiolate. Eglandular leaf hairs type E. Glandular leaf hairs present, never type P. Interfascicular cambium usually absent. Nodes multilacunar. Resin canals present, never adjacent to phloem fibres. Carbonaceous layer. Duplex achenial hairs thick-walled. Ovarian crystals curvilinear. Anther fibrous layer polarised. Filament collar cylindrical.

#### GROUP II

Eglandular leaf hairs types E and H. Interfascicular cambium. Vessel distribution pattern 2. Xylem rays narrow. Resin canals adjacent to phloem fibres. Phloem lignified. Pith crystals common, curvilinear type and raphides. Duplex achenial hairs thick-walled. Anther fibrous layer radial. Filament collar cylind~~i~~cal.

#### GROUP III

Leaves rarely petiolate. Resin canals absent. Achenial crystals, druses. Pappus on disc florets absent. Anther fibrous layer polarised. Anther auricles sterile. Filament collar cylindrical. Duplex achenial hairs absent.

#### GROUP IV

Eglandular hairs rarely type E. Interfascicular cambium common. Resin canals adjacent to phloem fibres. Nodes usually trilacunar. Duplex achenial hairs thin-walled. Filament collar frequently baluster-form.



Subgroup 1. Leaves petiolate often with palmate veins. Eglandular leaf hairs rarely type A and B, often G and I. Interfascicular cambium infrequent. Nodes usually multilacunar. Pith commonly collapsed. Duplex achenial hairs rare. Achenial crystals frequent, druses. Ovarian crystals frequently druses, curvilinear or isodiametric. Fibrous layer frequently polarised. Filament collar commonly cylindrical. Ray florets 4+ nerved with staminodes.

Subgroup 2. Interfascicular cambium. Pith usually intact and unlignified. Nodes trilacunar. Duplex achenial hairs thin-walled. Ovarian crystals very rarely druses or curvilinear type. Achenial crystals usually absent. Anther fibrous layer radial. Filament collar baluster-form. Ray florets 4 nerved without staminodes.

Subgroup 2A. Leaves glabrous. Stomata anisocytic. Interfascicular cambium. Vessel diameter medium sized. Vessel distribution frequently pattern 7. Duplex achenial hairs. Achenial crystals frequent, druses. Ovarian crystals commonly intermediate hexagonal. Anther auricles absent.

Subgroup 2B. Leaves sessile. Eglandular leaf hairs type F and K. Glandular hairs, when present, type Q. Interfascicular cambium. Vessel distribution patterns 1 and 2. Vessels narrow. Xylem rays medium or wide. Duplex achenial hairs. Pappus hairs fluked. Anther auricles absent.

Subgroup 2C. Leaves commonly petiolate. Eglandular leaf hairs type B and K. Vessel distribution pattern 7. Vessels medium or wide. Xylem rays wide. Duplex achenial hairs. Ovarian crystals elongate or intermediate hexagonal.

Subgroup 2D. Leaves sessile. Vessel distribution patterns



2, 3 or 5. Vessels narrow. Xylem rays narrow. Pith collapsed. Duplex achenial hairs absent. Ovarian crystals isodiametric.

Subgroup 2E. Leaves petiolate often with palmate veins.

Vessel distribution pattern 7. Vessels wide. Duplex achenial hairs absent. Anther auricles sterile.

Subgroup 3. Leaves petiolate. Eglandular leaf hairs types 1 and/or 2. Interfascicular cambium. Vessel distribution patterns 4 and 5. Nodes quinquelacunar and trilacunar. Pith intact and lignified. Duplex achenial hairs rare. Achenial crystals frequent, druses. Anther fibrous layer polarised. Filament collar cylindrical. Anther auricles sterile. Ray florets 4+ nerved with staminodes. Pappus hairs clubbed.

#### GROUP V

Leaves petiolate. Eglandular leaf hairs type C. Glandular leaf hairs type P. Phloem lignified. Pith lignified. Resin canals absent. Duplex achenial hairs thick-walled. Achenial crystals, druses. Filament collar cylindrical. Anther auricles sterile. Pappus hairs clubbed.

#### GROUP VI

Leaves petiolate. Interfascicular cambium. Vessel distribution pattern 5. Vessels wide. Xylem rays narrow. Resin canals usually absent. Phloem lignified. Cortical sclereids. Duplex achenial hairs thick-walled. Achenial crystals, crystal mixture. Anther auricles fertile. Fibrous layer transitional. Pollen grains lophate.



APPENDIX III

COMPUTER TYPE-OUT

Columns 1 and 2 fusing species and/or group(s)

Column 3 denotes the fusion products

Column 4 is a measure of information gain on group  
formation (employed as an expression of  
dissimilarity in Diagrams 1 - 5).



16+	15=	370	0.0000	324+	322=	422	0.0300	230+	65=	474	0.0556
34+	33=	371	0.0000	55+	50=	423	0.0303	277+	99=	475	0.0556
37+	36=	372	0.0000	287+	286=	424	0.0303	295+	420=	476	0.0556
71+	70=	373	0.0000	290+	288=	425	0.0303	352+	328=	477	0.0564
78+	74=	374	0.0000	54+	53=	426	0.0313	318+	134=	478	0.0571
79+	76=	375	0.0000	218+	204=	427	0.0313	87+	426=	479	0.0573
127+	126=	376	0.0000	384+	336=	428	0.0324	423+	56=	480	0.0455
162+	160=	377	0.0000	398+	305=	429	0.0333	156+	397=	481	0.0579
274+	273=	378	0.0000	115+	104=	430	0.0360	279+	278=	482	0.0583
303+	302=	379	0.0000	224+	222=	431	0.0369	299+	67=	483	0.0588
349+	332=	380	0.0000	399+	395=	432	0.0374	124+	123=	484	0.0588
359+	339=	381	0.0000	43+	42=	433	0.0381	125+	484=	485	0.0588
350+	343=	382	0.0000	21+	18=	434	0.0392	400+	477=	486	0.0603
347+	345=	383	0.0000	29+	20=	435	0.0392	418+	455=	487	0.0613
358+	357=	384	0.0000	381+	417=	436	0.0404	259+	257=	488	0.0614
364+	362=	385	0.0000	52+	48=	437	0.0404	311+	308=	489	0.0614
320+	314=	386	0.0049	113+	85=	438	0.0404	460+	212=	490	0.0618
335+	380=	387	0.0049	249+	245=	439	0.0407	435+	472=	491	0.0630
353+	340=	388	0.0076	393+	270=	440	0.0414	227+	86=	492	0.0631
361+	312=	389	0.0081	264+	263=	441	0.0415	321+	403=	493	0.0632
183+	178=	390	0.0085	137+	414=	442	0.0417	235+	234=	494	0.0643
382+	387=	391	0.0088	35+	26=	443	0.0429	60+	59=	495	0.0645
202+	201=	392	0.0090	428+	436=	444	0.0431	91+	483=	496	0.0645
300+	272=	393	0.0090	404+	401=	445	0.0438	410+	471=	497	0.0646
366+	365=	394	0.0090	24+	22=	446	0.0438	443+	434=	498	0.0646
77+	374=	395	0.0098	101+	100=	447	0.0439	459+	453=	499	0.0654
122+	121=	396	0.0104	370+	14=	448	0.0441	467+	492=	500	0.0655
155+	153=	397	0.0116	394+	217=	449	0.0444	439+	239=	501	0.0656
306+	379=	398	0.0122	419+	372=	450	0.0455	151+	150=	502	0.0659
375+	75=	399	0.0147	41+	450=	451	0.0455	497+	499=	503	0.0666
338+	331=	400	0.0149	10+	9=	452	0.0463	47+	45=	504	0.0667
177+	175=	401	0.0152	429+	211=	453	0.0465	109+	430=	505	0.0667
360+	391=	402	0.0157	250+	244=	454	0.0465	129+	128=	506	0.0667
116+	114=	403	0.0175	433+	31=	455	0.0483	317+	233=	507	0.0686
179+	176=	404	0.0189	192+	191=	456	0.0488	490+	214=	508	0.0693
89+	88=	405	0.0196	252+	251=	457	0.0488	228+	474=	509	0.0694
383+	346=	406	0.0244	416+	351=	458	0.0496	363+	197=	510	0.0694
309+	307=	407	0.0250	458+	409=	459	0.0477	422+	327=	511	0.0698
174+	173=	408	0.0256	216+	215=	460	0.0500	142+	141=	512	0.0699
356+	329=	409	0.0270	297+	285=	461	0.0500	448+	13=	513	0.0714
341+	334=	410	0.0270	190+	171=	462	0.0513	161+	465=	514	0.0721
323+	386=	411	0.0271	187+	186=	463	0.0513	407+	304=	515	0.0732
388+	348=	412	0.0275	243+	241=	464	0.0524	209+	84=	516	0.0735
64+	62=	413	0.0278	291+	377=	465	0.0526	271+	440=	517	0.0737
136+	135=	414	0.0278	389+	315=	466	0.0537	466+	503=	518	0.0738
283+	282=	415	0.0278	427+	63=	467	0.0541	446+	27=	519	0.0750
330+	313=	416	0.0278	82+	66=	468	0.0541	188+	463=	520	0.0769
412+	402=	417	0.0286	319+	411=	469	0.0541	390+	408=	521	0.0778
44+	32=	418	0.0294	406+	344=	470	0.0549	208+	199=	522	0.0787
40+	39=	419	0.0294	470+	444=	471	0.0548	449+	337=	523	0.0787
296+	294=	420	0.0294	28+	19=	472	0.0556	480+	479=	524	0.0787
342+	333=	421	0.0294	413+	61=	473	0.0556	139+	138=	525	0.0789



152+	502+	526	0.0803	8+	2+	579	0.1054	544+	610+	632	0.1392
30+	519+	527	0.0803	425+	57+	580	0.1061	553+	584+	633	0.1394
376+	485+	528	0.0809	355+	506+	581	0.1061	583+	624+	634	0.1396
468+	96+	529	0.0811	421+	326+	582	0.1061	588+	633+	635	0.1407
106+	105+	530	0.0821	5+	4+	583	0.1083	447+	102+	636	0.1414
461+	325+	531	0.0825	181+	169+	584	0.1085	522+	577+	637	0.1422
223+	431+	532	0.0832	517+	514+	585	0.1088	157+	481+	638	0.1425
475+	98+	533	0.0833	568+	572+	586	0.1093	523+	617+	639	0.1436
229+	189+	534	0.0833	120+	92+	587	0.1095	242+	614+	640	0.1443
213+	210+	535	0.0833	182+	172+	588	0.1098	573+	196+	641	0.1444
486+	518+	536	0.0833	371+	549+	589	0.1106	258+	556+	642	0.1451
11+	452+	537	0.0843	515+	586+	590	0.1119	570+	478+	643	0.1452
513+	12+	538	0.0844	432+	58+	591	0.1129	207+	576+	644	0.1481
180+	462+	539	0.0854	269+	268+	592	0.1140	601+	632+	645	0.1492
193+	164+	540	0.0855	524+	564+	593	0.1151	619+	587+	646	0.1502
72+	373+	541	0.0857	49+	593+	594	0.1123	606+	646+	647	0.1454
145+	144+	542	0.0857	529+	552+	595	0.1157	602+	205+	648	0.1528
542+	512+	543	0.0798	456+	166+	596	0.1162	578+	1+	649	0.1549
298+	476+	544	0.0858	378+	554+	597	0.1171	643+	581+	650	0.1557
438+	81+	545	0.0861	516+	496+	598	0.1184	248+	640+	651	0.1557
493+	103+	546	0.0869	560+	240+	599	0.1192	639+	608+	652	0.1560
495+	437+	547	0.0871	487+	589+	600	0.1195	541+	94+	653	0.1569
527+	498+	548	0.0875	97+	598+	601	0.1209	540+	520+	654	0.1573
491+	548+	549	0.0836	221+	206+	602	0.1212	550+	117+	655	0.1583
226+	225+	550	0.0877	301+	289+	603	0.1212	615+	528+	656	0.1584
385+	469+	551	0.0878	534+	165+	604	0.1216	170+	83+	657	0.1585
509+	473+	552	0.0883	159+	158+	605	0.1220	625+	93+	658	0.1597
445+	521+	553	0.0890	107+	530+	606	0.1250	658+	620+	659	0.1605
415+	267+	554	0.0897	539+	596+	607	0.1263	246+	651+	660	0.1612
489+	284+	555	0.0906	555+	590+	608	0.1267	442+	17+	661	0.1619
260+	488+	556	0.0906	494+	200+	609	0.1268	220+	69+	662	0.1622
112+	110+	557	0.0909	292+	580+	610	0.1275	648+	662+	663	0.1535
354+	310+	558	0.0909	23+	600+	611	0.1277	154+	638+	664	0.1623
265+	256+	559	0.0911	148+	147+	612	0.1282	266+	219+	665	0.1634
454+	464+	560	0.0914	545+	131+	613	0.1290	665+	628+	666	0.1524
111+	505+	561	0.0924	457+	599+	614	0.1297	451+	38+	667	0.1636
482+	276+	562	0.0925	561+	557+	615	0.1298	634+	649+	668	0.1645
508+	500+	563	0.0939	510+	275+	616	0.1312	622+	666+	669	0.1657
51+	547+	564	0.0962	575+	574+	617	0.1314	571+	293+	670	0.1658
90+	405+	565	0.0966	143+	567+	618	0.1316	653+	73+	671	0.1667
441+	261+	566	0.0969	546+	231+	619	0.1320	254+	253+	672	0.1667
140+	525+	567	0.0972	595+	591+	620	0.1321	629+	652+	673	0.1671
531+	316+	568	0.0977	533+	280+	621	0.1325	607+	664+	674	0.1692
133+	108+	569	0.0980	621+	562+	622	0.1274	569+	132+	675	0.1694
119+	118+	570	0.0980	565+	95+	623	0.1335	669+	645+	676	0.1721
507+	532+	571	0.0992	7+	579+	624	0.1344	656+	647+	677	0.1740
511+	536+	572	0.0997	594+	623+	625	0.1356	637+	203+	678	0.1756
46+	504+	573	0.1000	25+	611+	626	0.1366	609+	663+	679	0.1780
563+	68+	574	0.1034	597+	585+	627	0.1375	673+	677+	680	0.1783
232+	535+	575	0.1049	603+	627+	628	0.1359	592+	676+	681	0.1788
198+	195+	576	0.1049	558+	551+	629	0.1378	680+	681+	682	0.1790
392+	194+	577	0.1052	566+	559+	630	0.1385	670+	682+	683	0.1780
6+	3+	578	0.1053	167+	163+	631	0.1390	657+	604+	684	0.1791



654+ 684= 685 0.1789	618+ 691= 703 0.2022	720+ 716= 721 0.2380
655+ 80= 686 0.1800	659+ 703= 704 0.1972	631+ 149= 722 0.2429
616+ 675= 687 0.1833	641+ 696= 705 0.2029	692+ 543= 723 0.2472
247+ 237= 688 0.1833	613+ 701= 706 0.2045	538+ 537= 724 0.2484
660+ 688= 689 0.1743	582+ 706= 707 0.2058	711+ 719= 725 0.2506
255+ 501= 690 0.1847	702+ 689= 708 0.2134	725+ 723= 726 0.2508
667+ 626= 691 0.1857	679+ 707= 709 0.2162	642+ 697= 727 0.2519
612+ 146= 692 0.1868	695+ 699= 710 0.2167	726+ 721= 728 0.2556
262+ 630= 693 0.1872	369+ 694= 711 0.2178	728+ 668= 729 0.2663
238+ 184= 694 0.1877	705+ 709= 712 0.2187	722+ 729= 730 0.2757
367+ 185= 695 0.1892	636+ 168= 713 0.2195	661+ 724= 731 0.2842
678+ 644= 696 0.1913	713+ 710= 714 0.1999	715+ 730= 732 0.2999
693+ 526= 697 0.1917	396+ 130= 715 0.2250	281+ 732= 733 0.3059
635+ 685= 698 0.1919	650+ 712= 716 0.2251	368+ 731= 734 0.3080
698+ 674= 699 0.1951	605+ 236= 717 0.2302	734+ 733= 735 0.3003
687+ 683= 700 0.1956	708+ 717= 718 0.2252	424+ 735= 736 0.3296
686+ 700= 701 0.2000	714+ 718= 719 0.2228	727+ 736= 737 0.4165
672+ 690= 702 0.2011	704+ 671= 720 0.2319	