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Hunt Institute was dedicated in 1961 as the Rachel McMasters Miller Hunt Botanical Library, an international center for bibliographical research and service in the interests of botany and horticulture, as well as a center for the study of all aspects of the history of the plant sciences. By 1971 the Library's activities had so diversified that the name was changed to Hunt Institute for Botanical Documentation. Growth in collections and research projects led to the establishment of four programmatic departments: Archives, Art, Bibliography and the Library.

A TAXIMETRIC ANALYSIS OF ERYSIMUM

Margaret H. Goodhue

Dec. 17, 1970

Goodhue -

Grade - 1<sup>st</sup> 1/2 - A

Talk - C

Final Paper - B

Final Grade - B

The genus, Erysimum, is a group of plants widespread throughout Europe, the United States, and southern Canada. It is a member of the family, Cruciferae, of which twenty genera are listed for the state of Colorado (Rossbach, 1958). Several other keys have been constructed for the Colorado species of this genus, notably those of Harrington (1964), Rydberg (1906), and Weber (1967). An examination of these keys reveals much inconsistency and disagreement as to the names and descriptions of the species.

Dr. William Weber, of the University of Colorado Herbarium, suggested that a study of Erysimum be confined to an examination of certain local specimens which exhibit petal coloration not described by Rossbach. These plants, occupying areas along the eastern slope of the Rocky Mountains at altitudes between, approximately, 7000 and 8500 feet, Weber believes to be hybrids. I have found that Rossbach does, in fact, list the species, E. capitatum, as possessing petals in just such shades of yellow, brick-red, and orange-brown or, in the Southwest, a purplish maroon. It is not clear from Rossbach's description whether these colors appear in one inflorescence - as I found them - or whether they occur on separate plants, though the former must certainly be the case.

Harrington lists six Colorado species of Erysimum : E. nivale, E. wheeleri, and E. repandum being distinct, and E. amoenum being a synonym for E. wheeleri. E. capitatum is not listed, as it is by Rossbach, whose key to the thirty-three United States species includes about seven found in Colorado. The nomenclature here approximates that of Harrington, with the above-mentioned exception. In addition, E. argillosum is added and E. wheeleri excluded. Weber's key lists just four species of Erysimum, E. cheiranthoides and E. inconspicuum being absent possibly because the area in Colorado which the book refers to is a limited one, and only Front Range species are described. It is curious that all authors include E. repandum in their keys, noting that this species is common on the plains and in waste places and roadsides, yet I did not see a representative of this group among the University of Colorado Herbarium collection. What is more, with the exception of one collecting site in the vicinity of Palmer Lake, north of Colorado Springs, all of the plants which I collected were taken from roadbeds or otherwise disturbed areas nearby.

Further questions arose as I continued to make collections. For example, certain specimens in the Herbarium called E. capitatum, taken from Lookout Mountain and La

Veta Pass, were purple-petaled forms (I am assuming - perhaps incorrectly - that this was the original color), yet upon visiting these locations I discovered only the multicolored inflorescence described by Rossbach. Relative to this is the fact that other Herbarium specimens of this same name, from Cuchara Valley and the area north of Eldora, also show the same petal coloring. Weber, however, considers this group one of two types of E. asperum, the other possessing clear yellow flowers. He states that it is these two types which represent extremes in variation and which are undergoing hybridization. According to Weber, neither their nomenclature nor their breeding behavior has been resolved.

Harrington considers E. nivale and E. wheeleri to be separate species, with E. amoenum a synonym for the latter. Weber feels that the caespitose E. amoenum is a lavender petaled form of E. nivale. In still another source, the Denver Museum of Natural History Pictorial number 13, a long-stemmed, pink-petaled form is given the name E. amoenum, and described as having been found at both Red Mountain Pass near Ouray, where I collected several such plants, as well as on Mt. Evans, where I also saw a single specimen.

It is not surprising that Green (1896) wrote, "Amer-

ican species are not reducible to defined groups...", when referring to this genus, and he was critical of Linnaeus for having classified Erysimum on technicalities of the seed pod which resulted in four species that actually represent four genera. One of these is Cheiranthus, which Greene says forms, together with Erysimum, one natural genus. Davis and Heywood (1963) state an opinion similar to Greene's when they write, "In Erysimum and Isatis (Cruciferae) there seem to be no natural taxa (with <sup>the</sup> possible exception of a series for small groups of closely allied species) between the genus and the species!"

I am certainly not well acquainted with the genus, nor have I made an intensive effort to identify specimens which I intuitively feel to be representative of groups taken from the twenty or so major collecting areas within the state. My original plan concerning research on this group was ecologically oriented, with as much cytological evidence as could be successfully gained to supplement the study. It is therefore impossible for me to suggest reasons for the puzzling nature of Erysimum, other than the more obvious ones: insufficient collecting so that the more extreme variants are not represented, and inadequate field notes which do not include accurate

descriptions of color, particularly, leaving the sometimes changed hues of the dried herbarium specimens the only source of this information. Added to this is the probability that in some areas, particularly those already mentioned, crosses between individuals have produced offspring which flower at different times during the growing season, hence a single trip to such a site would reveal the presence of only a fraction of the individuals which would appear during the season. Inasmuch as biennial, as well as perennial and annual species occur in this genus, a form may not appear during a single growing season, and observations the following year - or in two years - are required.

Dr. G. Appan suggested the use of Taximetrics as an aid in handling data from what appeared to be great variation among my specimens. In view of the difficulty in identifying the species, it seemed worthwhile to employ the programs of CHARANAL and Graph-Cluster-Analysis in an attempt to find natural clusters and other related information which could supplement existing classifications. The questions concerning the hybrid groups might, I thought, find some answers by virtue of their relative positions in the clustering procedure.

Collecting was begun in late June of 1970, when

flowering first appeared in those plants growing at altitudes of 4700' to 7500'. The first collections were made at Owl Canyon, north of Fort Collins, Lookout Mountain, near Golden, Cuchara Valley, near Walsenburg, and El Dorado, south of the Boulder area. At each of these locations floral buds were selected at varying stages of development and fixed in a solution of three parts absolute ethyl alcohol to one part glacial acetic acid. Field notes included date of collection, altitude, exposure, amount of sun the plants would receive during the day, habitat description, and a list of other plant species present. A soil sample was also taken at each collection site. I felt it always desirable to obtain several photographs of *Erysimum* as well, since a pictorial record of the habitat is secured, and because petal colors change upon drying. Twelve to fifteen plants were then picked at random and placed in a press as permanent specimens.

Later collections were made at intermediate altitudes: Red Rock Lake on the Brainerd Lake road, the Rio Grand Camp Ground east of Pagosa Springs, La Veta Pass, Gothic, and a site eight miles east of Gunnison. In August, specimens were gathered at altitudes of 10,000' and above: at Cumberland Pass, Niwot Ridge, and Mount Evans. Sampling was made from several other locations as well.

During the late weeks of August and early September, return trips were made to each one of the collecting sites to get plants in the fruiting stage. In most cases, plants had been marked by one of several methods to ensure retrieval at the later date.

Representative specimens from most of the sites were examined in order to construct a list of characters, or descriptors, of phenotypic variation against which all plants in the study could be compared. In this way, the input for CHARANAL was designed. In order to avoid the selection of those characters which clearly were due to environmental factors, no descriptors such as stem length, or the quality of a growth habit, such as caespitose, were included. From my field notes I chose altitude, amount or quantity of sunlight, direction of exposure, and the location of the collecting area itself as extrinsic characters, since information of a purely environmental nature can be used for the CHARANAL input. Phenotypic characters selected for this preliminary "character analysis" are as follows:

Qualitative and Quantitative Characters

- (1) Petal color: yellow (1), pink (2), purple (3), orange (4), shades of orange and deep red throughout raceme (5), pale purple (6).

- (2) Presence of different intensity of color on top few petals: deeper yellow (1), orange and deep red (2), deeper red-brown (3), deeper purple (4), no difference in color (5).
- (3) Angle made by silique with stem: divaricate (1), ascending (2), right angle pedicel - silique descending (3), right angle pedicel - silique ascending (4).
- (4) Length of silique: .3 cm (1), 2-4 cm. (2), 4-6 cm. (3), 6-8 cm. (4), > 8cm. (5).
- (5) Silique shape: flat (1), spherical (2), 4-sided (3), 4-sided and prominently keeled (4), 4-sided and slightly keeled (5), oval (6).
- (6) Pedicel length:  $\frac{4}{5}$  as long as silique (1),  $\frac{4}{3}$  to  $\frac{4}{2}$  as long as silique (2),  $\frac{4}{10}$  as long as silique (3), 1.2 times as long as silique (4), 3 times as long as silique.
- (7) Pedicel hairs: numerous (1), moderately numerous (2), sparse (3).
- (8) Basal leaf margin: slightly waved (1), strongly waved (2), entire (3).
- (9) Lower leaf shape: broadly and bluntly oblanceolate (1), narrowly elongate (2), oblanceolate with acute tip (3).
- (10) Foliar hairs: moderately numerous (1), very numerous (2),

- combination (3).
- (11) Seed color: yellow brown (1), red brown (2).
  - (12) Seed size: 1.5 mm. (1), 1.0 mm. (2), less than 1.0 mm. (3).
  - (13) Seed morphology: 3-sided and winged on one side (1), distal appendage (2), winged on one long side (3).
  - (14) Number of seeds in silique: 2 (1), 8 (2), 18-35 (3).
  - (15) Form: single (1), branched (2), numerous branches (3).
  - (16) Petal length: 3-13 mm. (1), 13-23 mm. (2).
  - (17) Petal width: 1-3mm. (1), 3-5 mm. (2), 5-13 mm. (3).
  - (18) Petal hairs: present and 2-forked (1), present and 3-forked (2), some 3-, some 2-forked (3).

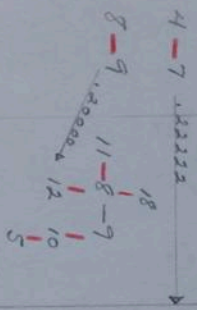
Had the input for CHARANAL combined characters for both the fruiting and flowering specimens, there would have been too much missing information and the results could not have been accepted as reliable. Therefore, two separate runs were made: one for floral, vegetative, and ecological characters, the other for fruit, vegetative, and ecological characters. The results of the input led to an elimination of the following descriptors in preparation for the Graph-Clustering-Analysis input: pedicel hairs, seed color, seed size, and petal length. The amount of information which the first three of these characters shared with all others was low, and petal length

was found to vary in proportion to petal width. For the Graph input, some minor modifications of certain character states seemed advisable and, of course, all extrinsic, ecological characters were necessarily dropped.

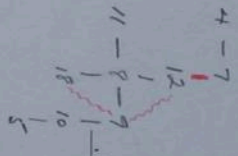
An attempt was made to combine fruit, flower, and vegetative characters for a single Graph analysis, but as this did not yield a satisfactory clustering of the specimens, two separate analyses were made: one for plants in flower, and another for the fruiting specimens. The results of the printout are on the following pages.

It is apparent that a good clustering of the objects again failed to occur at significant C-values, so that nothing can be concluded from these results. A solution to this dilemma most probably lies with a reassessment of characters and character states and the addition of new, "good" characters. I admit to having examined my specimens individually, concentrating more on minute morphological patterns, while I should have <sup>looked at</sup> many of them at one time for larger pattern similarities and differences. Properties of my plants which I had overlooked are: compact vs. elongate vs. indifferent inflorescence, length of inflorescence, distance between pedicels, and ratio of inflorescence length to stem length. It was Dr. Rogers' trained eye that saw these patterns, and it was all of him who added a most intriguing dimension to biology for us.

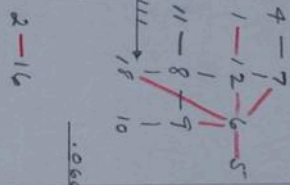
L 1      L 2  
 $\Sigma = 1000$        $\Sigma = .850000$



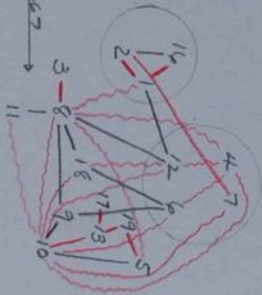
L 3  
 $\Sigma = .77778$



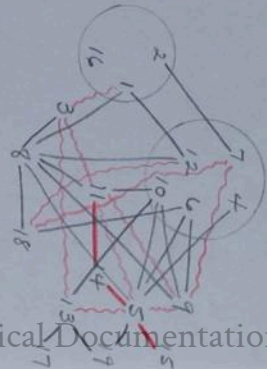
L 4  
 $\Sigma = .66667$



L 5  
 $\Sigma = .60000$



L 6  
 $\Sigma = .55556$

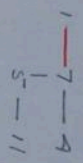


GRAPH - CLUSTERS - ANALYSIS  
 FRUITS, FLOWERS, VEGETATIVE  
 CHARACTERS COMBINED

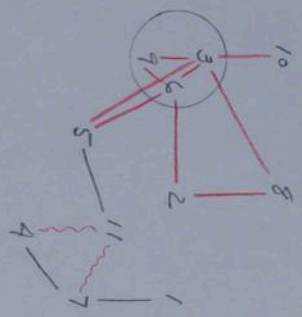
L 1  
Q = .77778



L 2  
Q = .66667

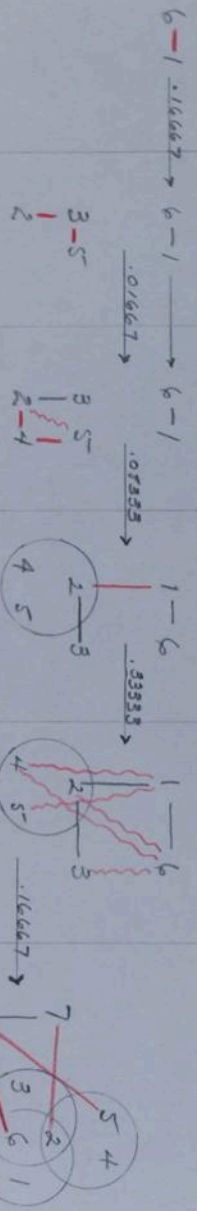


L 3  
Q = .55556



GRAPH - CAUSTIC - ANALYSIS  
FLOWERS & VEGETATIVE CHARACTERS

L1	L2	L3	L4	L5	L6
$C = .66667$	$C = .60000$	$C = .58333$	$C = .50000$	$C = .33333$	$C = .16667$



GRAPH-CLUSTER-ANALYSIS  
FRUITS & VEGETATIVE CHARACTERS

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## TAXONOMIC CHARACTERS: A BRIEF OPINIONATED DISCUSSION

Basic to an understanding of taxonomic characters is the point that the character is a tool, not a captor, of the taxonomist. It then follows that the character can be defined and delimited by the taxonomist. It further follows that different workers may have widely different concepts concerning taxonomic characters.

For the purposes of this class, a taxonomic character was defined as "a single basis for comparison, defined over the study". Let us dissect this definition. The fundamental point of this definition is its intrinsically stated parameter, i. e., it is "defined over the study". Although an apparent arbitrariness of taxonomic characters is discernible simply in the fact that they may be given different definitions by different taxonomists, this definition goes so far as to state that even characters in its own sense of the word may differ simply by virtue of having jurisdiction over a different group of organisms and/or functions. It does the taxonomist well to think upon this apparent arbitrary nature of his prime tools, as they are the tools with which he tries to interpret the objective reality of the evolutionary relationships among organisms. Such a definition of the field over which a character is defined should, perhaps, be clarified to read: "defined over the organism(s)<sup>studied and for the function(s)</sup> desired"; such a definition may lead into a discussion of classificatory characters (a "classification" being understood in this paper to mean an evolutionarily accurate one) vs. key characters. The questions

good  
point

They need not be mutually  
exclusive!

raised in the two preceding sentences will be considered later in this paper.

Returning to the definition of a taxonomic character adopted for the purpose of this class, the first part of it (i. e., "a single basis for comparison") tempts further consideration. It is in this portion of the definition that the intrinsic purpose of the character is delimited, to the full extent which this definition considers such delimitation. The purpose of a taxonomic character is to serve as a basis for comparison. Exactly how such a comparison is to be made and what is to be gained from it are among the most important questions of technique and philosophy within taxonomy. That this definition of a character states that it is a basis for comparison, rather than an answer in itself is, in a way, a statement of the distinction between the character and the resultant comparison, with the link between the two being the judgment of the taxonomist. Stated another way, the taxonomist makes the comparison, using the characters; the characters themselves do not make the comparison.

One final point to be considered in the above-stated definition of a taxonomic character is the consideration of a character as a single basis for comparison. The word "single" in the definition is not in actuality necessary, inasmuch as it does not preclude naturally interdependent characters, characters comprised of several other characters, or characters which are given relatively different weights when used for comparison(s) (again a consideration not entering into the definition of a taxonomic character presently under discussion). A character may certainly not be considered

The point  
may be  
valid -  
but I  
need  
some  
more  
explanation  
to understand  
it!

single in that it reflects natural forces which act on all facets of all living organisms. The word "single", in this case, merely repeats that already said by using the article "a".

Now let us return, in reverse order, to two points mentioned earlier in this paper. The distinction between classificatory and key characters was noted, under the more general topic of the functions of characters. While classificatory characters need not necessarily differ from key characters, the different employment of each carries with it such a possibility. A classification, in the biological sense, is meant to reflect the evolutionary history of a given group. A key, on the other hand, is generally accepted as a tool for identifying organisms. In dichotomous keys, the idea is to accomplish, by means of "yes-no" questions, the quickest possible identification of a given specimen or group of specimens. Such a utilitarian function need not (and, if it is to maintain its maximum efficiency, often can not) account for such intricacies as evolution has produced in the natural world. Classifications, on the other hand, have the purpose and the responsibility of portraying such intricacies as are necessary for an accurate appraisal of the evolutionary relationships among organisms. Tabular keys (designed to identify while at the same time serving to store information concerning the organisms under study) notwithstanding, the functions of classificatory and key characters can be seen to be as different as the functions of classifications and keys themselves. Key characters need only provide maximum efficiency of separation of taxa by successive "yes-no" decisions, whereas classificatory characters must serve as the indicators of true evolutionary relationships.

*I think it important to point out the word "may".*

Thus we are led to consider the other of the two above-mentioned points, that of the apparent arbitrary nature of taxonomic characters. The taxonomist should not look upon his characters as being arbitrary. They have a specific function, and thus should not be chosen arbitrarily. The desired function of a given character should be the factor which determines its treatment and utilization by the taxonomist. Evolutionarily accurate classifications are objective realities which the taxonomist attempts to approach as nearly as possible in his work. If taxonomic characters are to be among his tools in such work, his skill in choosing and employing them must surely weigh heavily in his ultimate attainment of his goals.

Good Paper A  
Final Made A

A Taximetric Study of Species Variation of *Physocarpus*

Claire Lynn Robbins  
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Abstract

This is a preliminary study of the species variation in the genus *Physocarpus*. It is based on herbarium material for *P. Alternans*, *P. Intermedius*, *P. Monogynus*, and *P. Opulifolius*. The taximetric program CHARANAL was used in the development and structuring of ten characters. The graph-clustering-analysis method was used in the generation of a classification, and an explanation of its operation is given. This analysis indicates that the specimens examined can be grouped into two species, *P. Alternans* being the only distinct, well-defined species. Indication is given that varietal variation is operating in the other species grouping.

## A Taximetric Study of Species Variation of *Physocarpus*

Claire Lynn Robbins  
University of Colorado

### Introduction

Certain species of the genus *Physocarpus* common to Colorado have provided a taxonomic problem of some confusion. *Physocarpus* is in the family Rosaceae, order and suborder Rosaceae, and tribe Spireaoideae. It is a shrub ground cover common to the foothills and ravines of the central Rocky Mountain Range. Previous studies of the species of *Physocarpus* indicate confusion as to the number and composition of valid species. Specifically, it has been questioned whether *P. Monogynus* and *P. Intermedius* are distinct.

Species included in this study are *P. Alternans*, *P. Intermedius*, *P. Monogynus*, and *P. Opulifolius*. The taximetric methods CHARANAL and the graph-clustering-analysis technique have been used in this study to develop a classification. An explanation of the operation and use of the graph-clustering-analysis technique is included for the purpose of showing how the classification was determined.

### Population Samples

For this preliminary study of the species variation of *Physocarpus* all specimens examined were chosen from the collections of the Herbarium of the University of Colorado. It is obvious therefore, that a final classification must be contingent upon further research and field collections. A total of thirtyone specimens were examined. These specimens were divided between the four species in this manner; *P. Alternans* and *P. Opulifolius* were represented by four specimens each. Nine specimens of *P. Intermedius* were included, and fourteen specimens of *P. Monogynus* completed the collection.

It was decided to limit this analysis of *Physocarpus* to studies of phenotypic variation since the exclusive use of herbarium material did not provide sufficient data for analysis of ecological, reproductive, or chromosomal material.

#### Character Selection

The first step in this analysis was that of discovering, structuring and evaluating characters. The taximetric method CHARANAL was used as an aid for structure and evaluation. CHARANAL is a computer-aided technique developed by the Taximetrics Laboratory of the University of Colorado, which is based on an information theory model. (Rogers and Appan, 1969) This method measures how information is distributed between the states of each character, and between pairs of characters by examining the total information of each character or state and the information shared between states and characters<sup>1</sup>.

A total of 35 characters were examined. Thirteen were analyzed with the use of CHARANAL, and the following 10 characters were retained after evaluation and restructuring.

- (1) Leaf width: (1) 0.0 - 1.0 cm., (2) 1.1 - 2.0 cm., (3) 2.1 - 2.9 cm., (4) 3.0 - 4.0 cm.
- (2) Leaf length: (1) 0.0 - 1.0 cm. (2) 1.1 - 2.7 cm.  
(3) 2.8 - 3.5 cm. (4) 3.6 - 4.0 cm.
- (3) Petiole length: (1) 0.0 - 0.4 cm. (2) 0.5 - 0.9 cm.  
(3) 1.0 - 2.0 cm.
- (4) Number of spurs: This character was judged on the basis of the number of spurs present on 10.0 cm. of branch measuring from the node.
  - (1) 7 - 10 spurs (2) 5 - 6 spurs
  - (3) 2 - 4 spurs (4) 0 - 1 spur
- (5) Number of flowers in corymb: (1) less than 10 flowers,  
(2) more than 10 flowers

1 For a detailed examination of CHARANAL, refer to Legendre (1970).

- (6) Appearance of veins: (1) same as blade, (2) distinct from blade
- (7) Pubescence of veins: (1) complete, (2) partial, (3) absent
- (8) Pubescence of top surface of leaf: (1) complete, (2) partial, (3) absent
- (9) Pubescence of lower surface of leaf: (1) complete, (2) partial, (3) absent
- (10) Pubescence of petiole: (1) complete, (2) partial, (3) absent

Because of the nature of this taxonomic problem, specifically an extremely high degree of similarity between all species, it proved difficult to discover characters that would effectively separate the specimens into distinct groups. This fact supports the conclusions drawn in this analysis.

#### Development of a Classification

Having developed and refined those characters useful in making a classification, it was necessary to apply these to the objects being studied to discover the relationships between the objects. One method of doing this is the use of a measure of similarity. In this study the taximetric similarity-graph-clustering technique was used. (Rogers and Appan, 1969) This method was developed by Wirth, Estabrook and Rogers (1966). It is based on a graph theory model and is intended to replicate the procedures used by a classical taxonomist in making a classification. The model is based on three assumptions about the nature of a classification. A classification for a collection of objects is a hierarchical, two dimensional partitioning of objects into mutually exclusive groups. Similar objects should be grouped together, and partitions should exist between groups. (Legendre, P., 1970)

Using these assumptions a similarity measure is defined. This function varies between zero and one. Zero indicates complete dissimilarity and one indicates complete similarity.

The general structure of the similarity measure may be described in this manner. The similarity between two objects, A and B, is equal to the sum of all similarities of all character values for objects A and B, divided by the total number of characters. This basic structure has been refined for special cases and the taxonomist has been given freedom to determine partial similarities between character states. (Legendre, P., 1970) This similarity measure is computed for each pair of objects in the study.

Clusters are then formed using this similarity function. For the purpose of this technique, a cluster is defined as follows: A collection of objects is isolated for some fixed value of similarity, if each object in the collection is less similar to every object outside the collection than that fixed similarity. An acceptable cluster is a collection of objects which is isolated for some fixed value of similarity but which contains no smaller cluster isolated for the same fixed value.<sup>2</sup> This members of a cluster show discontinuity with non-members, and clusters cannot be further subdivided without the subclusters being less isolated than the whole. Two objects are linked at a given level of similarity if the value of the computed similarity function is greater than or equal to the level of similarity considered. All pairs of objects at least as similar as some fixed value are linked. The aggregates of linked objects constitute clusters. This process forms a partition of the objects into equivalence classes, or clusters. Clusters formed at a low level of similarity will be composed entirely of clusters of a partition formed for a higher similarity value.

The clustering process is hierarchical when considered along an axis of decreasing similarity. At first, each object forms a separate, disjoint cluster. The similarity value is then lowered until a point where two objects join to form a cluster. This process is continued until all objects are linked in one cluster. With each cluster there is associated a similarity value, C, which is the largest fixed similarity value for which the cluster remains inter-linked.

2. France, G.T., D.J. Rogers, and F. White, 1969, p.1224

Two other measures are also built into this technique. The moat is a numerical value of isolation of a C-level cluster. The moat gives an indication of the distance between a cluster and the next object to join it. The moat value is found by subtracting from the value of the C-level of the cluster, the C value of its most similar non-member. The internal continuity of a cluster also provides useful information. For any cluster the maximum number of connections can be determined. The ratio between the number of existing connections and the total number of possible connections provides a measure of the internal continuity. As this ratio approaches one, the degree of internal connectedness approaches the maximum.

Two visual methods of reading the output are provided for analysis of the results. Each emphasizes different aspects of the classification generated by the method. The use of subgraphs makes it possible to see exactly how the cluster memberships change as the similarity value decreases. Subgraphs are constructed for each similarity level in a manner such that every pair of objects having a similarity value at least as great as the given C value is connected by a line. Three types of lines are used to distinguish the different types of connections. The red lines represent the similarities which connect previously unconnected groups. The pencil lines represent internal structure which existed at the previous C-level, and the blue lines represent those additional connections which have formed at the present C-level within existing clusters. Circles drawn around cluster members represent subclusters of maximal internal connection.

The skyline plot presents a summary of the clustering analysis by showing the clusters that are formed, their value of similarity, the hierarchical relationship and the measure of isolation associated with each cluster. The object numbers are placed along the horizontal axis and the similarity scale is plotted along the vertical axis. Horizontal lines indicate cluster membership. The moat is represented by the distance from one horizontal line to the one directly beneath it.

## Results

The results of the computer analysis are presented here by use of the subgraphs and the skyline plot. Ten levels of clustering are represented.

### Discussion of Results

The analysis of this study indicates that the specimens examined can only be separated into two species groups. *P. Alternans* is shown to be distinct and well-defined. No species variation is shown between the other three groups of specimens. The species definition of *P. Alternans* is indicated by a moat of 0.42. These specimens join the main cluster in the tenth level of similarity,  $C = 0.58$ .

The results also indicate a variety definition by the joining of two specimens of *P. Monogynus* at a C-level of 0.74 in the ninth similarity level. Evaluation of this indication must be reserved until after further research, since these specimens derive their independence through high similarity with *P. Alternans*. It is possible that this varietal difference is solely a function of character choice. It is also possible that this is an indication of hybridization between *P. Alternans* and the other species.

The clustering in levels 1 through 8 indicates conspecific variation. Specimens are added to a main cluster at regular intervals of 0.02 or 0.04 degrees of similarity. The decision to include specimens of *P. Monogynus*, *P. Intermedius* and *P. Opulifolius* in one species is justified by both the regular intervals of C-levels and the high degree of internal connectedness shown at the C values 0.80 and 0.74.

The results of this study in part support the results of the previous work of other researchers. The main difference lies in the fact that this study finds no species differentiation between *P. Monogynus* and *P. Opulifolius*. It is possible that this can be explained by the fact that these specimens were added to the study





L8 C=.80

$\frac{68}{120}$

H1(42,43) 40 10  
 16 32 12(13,14,15,17)  
 18 11 23 20  
 21 22 24  
 26(31) 27  
 28(29,33)

.06  
 →

L9 C=.74

$\frac{120}{153}$

H1(42,43) 40 10  
 16 32 12(13,14,15,17)  
 18 11 20 23  
 21 22  
 24(31) 27 28  
 25-30 24

.16  
 →

L10 C=.58

$\frac{8}{171}$

H1(42,43) 40 10  
 16 32 12(13,14,15,17)  
 18 11 20 23  
 21 22  
 24(31) 27 28  
 25 30 24

1  
 (2,3,4)

25 → 25-30  $\frac{1}{1}$  .06 →

1  
 2  
 3  
 4

after the completion of CHARANAL and thus the characters selected may not reflect existing differences. That no species differentiation was found between specimens of *P. Monogymus* and *P. Intermedius* supports past research. It is possible that with further research and field collection that a varietal classification could be made for these two groups. This is indicated in the present study by a relatively good initial separation of these two groups at high C values, such as 0.86.

The taximetric methods used in this analysis have facilitated the process of the research. CHARANAL proved to be very useful in the difficult task of character selection. Selection of good characters is the key to the analysis of these species of *Physocarpus*. The fact that character selection proved to be a difficult problem supports the conclusions that only two species groups can be defined.

The clustering analysis method was relied upon as the major tool for the development of a classification. Its merit is borne out in the results. The most useful aspects of this method in making a classification were the measure of isolation, the moat, and the measure of internal continuity, and their visual representations in the subgraphs and the skyline.

#### Summary

This preliminary study of species variation in the genus *Physocarpus* was limited to an analysis of phenotypic variation. Two taximetric methods were used. CHARANAL aided in the selection of ten characters. The graph-similarity-clustering technique was used in the development of the classification. An explanation of the use and operation of this method is included. The results indicate that *P. Alternans* is a well defined species, and that the classifications of *P. Intermedius*, *P. Monogymus* and *P. Opulifolius* show no species variation. Contributing factors in this classification are considered.

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5

This is an excellent  
paper -  
You have demonstrated  
independent judgement  
and also employed  
our programs very  
intelligently - A+

A Taximetric Study of Two Species of  
Castilleja (Scrophulariaceae).

Erik Olgeirson

Taximetrics, Fall 1970

Summary:

Two species of the North American genus, Castilleja (Scrophulariaceae) -- C. miniata Lindl. and C. rhexifolia -- were chosen as the subjects of a computer-aided classification. The techniques employed are those developed in conjunction with the Taximetrics Laboratory, University of Colorado, Boulder, Colorado.

The taximetrics program consists of two fundamental parts: (1) The selection and scrutiny of characters derived from the objects(organisms)in the study; and (2) Grouping (clustering)of these same objects into a hierarchial classification by means of a similarity index obtained from the characters ultimately chosen in part(1).

The Character Analysis -- CHARANAL -- technique(1), was found to be especially valuable to this study because of the taxonomic complexity of Castilleja; this manifests itself in extreme phenotypic variability. The results of this analysis are described graphically in Figure 1.

The results of the Clustering Analysis are represented by Figure 2. These results are significant in supporting the original allegation concerning the lack of disjunction between C. miniata and C. rhexifolia, but the conclusions from this procedure must be minimally drawn with great care, due to the size and distribution limitations imposed by the objects used.

## 1, Introduction

The use of computerized analyses in making taxonomic delimitations have numerous existing and potential applications. The methods of this study are those developed in conjunction with the Taximetrics Laboratory, University of Colorado, Boulder, Colorado. Herein two fundamental steps are taken: (1) The selection and scrutiny of characters observable from the objects(organisms)in the study; and (2) Grouping(clustering)of these same objects into a hierarchical classification by means of a similarity index obtained from the characters ultimately chosen in part(1).

It is implicit within the framework of this program that the computing machine operates as a 'data arranger', having no abilities of its own in making qualitative decisions and adjustments; and must be given no disposition toward making strict quantifications of the data which it receives. The sole function of the computer is to serve as a collator of the information generated by the intuitive experience of the worker and his conscientious attitude. In this way these methods make no attempt to transgress or rearrange taxonomy as a human invention and function, but rather to attempt ramification of the human technique.

Taximetrics procedures have been given special distinction as a taxonomic methodology aiding in the description of problem groups(Wirth, Estabrook, & Rogers, 1966; Prance, Rogers, & White, 1969; Rogers & Appan, 1969). Taximetrics becomes most applicable to problems involving groups which

are complex for reasons of group size, phenotypic variation, distribution (geographically and ecologically), high indices of hybridization, or previously confused taxonomy.

## 2. The Problem

Castilleja is a North American genus of the Scrophulariaceae. It occurs primarily throughout the mountainous and plains states westward from the Mississippi, from Canada into Mexico.

The difficulties of this genus are well-appreciated and are best described by Heckard (1962, 1964, 1968). Included in the information gathered for the genus are graphic representations of the definition of its obscurity: marked variability in chromosome number within almost all species; experimentally produced interspecific and intergeneric hybrids (often fertile through  $F_2$ ); root parasitism; and phenotypic variability. The last point, in particular, serves to make taxonomic interpretations by conventional techniques abstruse to the point of frustration.

The two species used in this study -- Castilleja miniata Lindl. and C. rhexifolia Rydb. -- occur throughout the state of Colorado where elevations exceed 8000 feet. The elevational distribution extends to 14,000 feet, and the plants are most common at the higher end of the scale. They are sympatric, and may seemingly not be defined on the grounds of observable habitat preference and subsequent mutual exclusion. Moreover, their phenotypic characteristics do not provide any immediately obvious pattern of reliable separation. Although chromosome studies have not been made

for the specimens in this particular study, indications from other detailed experimentation(Heckard, 1968)show no evidence inclining one to hope for conclusions of a taxonomic nature being derived from cytological data.

Phenotypic and cytological confusion are impetus for more intensified study of both these facets -- with more precise information gathered ecologically -- in order to improve our understanding of the variability inherent in Castilleja. It is nearly tacit that this sort of understanding is the only approach one can make initially with the ultimate purpose of making a reliable classification.

In this way this study is entirely preliminary. Its approach is directed squarely at obtaining some insights into the variation which the two species chosen embody. Because of the disagreement of conventionally used characters with collected specimens, it was deemed most advantageous to seek new characters and to attempt to discover not only the potential relatedness of these, but also the possible inter-relatedness of selected conventional descriptors.

The number of specimens(objects)used for this study is admittedly small, and does not adequately describe the geographical/ecological range of the taxa -- even for Colorado alone. However, the results presented here are believed to support the original allegation that the two taxa are not describable as specific entities on the basis of phenotypic characteristics.

The Taximetric method has been rewarding to this problem because it so uniquely approaches the area of characters. Both the results from the application of

CHARANAL and Graph Analysis will be discussed below.

### 3. Character Analysis -- CHARANAL

A character is best described as a single basis for the comparison of objects(organisms)within a particular study. Its discovery is an intuitive process often described as the ability of the observer to recognize patterns. In the case of living organisms, the patterns which are observed are assigned a genetic function. Although we do not totally understand the transduction of the genetic information into expression of form and function, we may still be fairly assured that the repetition of patterns is indicative of a genetic pattern. The selection of characters also integrally involves the finer description of these characters into character states. Just as the characters describe the organisms, the states of the character describe the characters. For a more detailed discussion of characters see Rogers & Estabrook, 1967.

The CHARANAL method is a computerized technique related to non-parametric statistics, but in a loose sense, as it utilizes Information Theory rather than Probability Theory. Basically, the character data developed for a set of organisms(the study)by a Taxonomist is measured by the computer in terms of how the information in each character is distributed between the states of the character; and how information is distributed between each pair of characters. In this way one will discover those characters and character states which give the most information about the objects in the study. Even more important, the total effect of the

technique is to reveal how the organisms in the study relate to each other. For a complete discussion of the CHARANAL program see Legendre, 1970a.

CHARANAL is of particular interest to the study of Castilleja because of the phenotypic variability within the genus. This diversity not only is evident between species, but is especially strong intraspecifically; creating a good deal of confusion for the worker attempting to identify species. Castilleja minlata and C. rhexifolia are two species whose recognition is especially nebulous due to this variability. If these are truly separate and distinct taxa, any information contributing to the understanding of character inter-relatedness will be of prime value in establishing a method by which they may be delimited. If it should at some time be discovered that they are synonymous, this same sort of information will contribute further in describing this synonymy, and the overlapping description of any other species of Castilleja.

Figure 1. is a graphic representation of the inter-relatedness of the characters used in this study (a listing of these characters and their states is given in Table 1.). This figure is a visual aid showing that characters relate differentially to each other, and that these relationships may be further defined in terms of which states of characters have inter-relatedness.

Figure 1a. treats all characters in the study as 2-state characters. The relationships plotted here are designed so that one may make a reciprocal if...then statement concerning any two characters and/or any two different character states.

For example, from the figure, If character 1...Then character 4; and If character 1/1...Then character 4/1(If lower stem puberulent...Then cauline leaves puberulent); and visa-versa. Similarly character 4/1 has a reciprocity of description with character 5/1. Characters 5 and 7 have no relationship.

In Figure 1b., where all characters are regarded as having the appropriate number of states assigned to them, the relationships are slightly altered in some cases. Here the If...Then statement -- If 1/1...Then 4/1(If 4/1...Then 1/1)becomes more complicated, because this relationship no longer stands. It must become: If 1/1...Then 4/1; If 4/1...Then 1/1, or sometimes 1/3. Other such examples may also be derived from the figure.

The inter-relationships in Figure 1. were derived from examination of the Conditional Probability matrices given in the CHARANAL printout. The comparative information values given numerically in these matrices may be used to indicate the comparative degree to which character states relate to other character states(see the examples above).

The inter-relationships are most useful in delimiting a potential scheme of character relationships, which, if reproducible for like sets of data, may well indicate an underlying mechanism of genetic control. Such an indication would be invaluable in discovering isolated gene pools. If well-structured this model could potentially be used to resolve certain ambiguities presented by complex gene manipulations(supergenes, polygeny, pleiotropy, etc.)and the immense variability of factors concerning habitat.

Figure 1. Character Inter-Relatedness

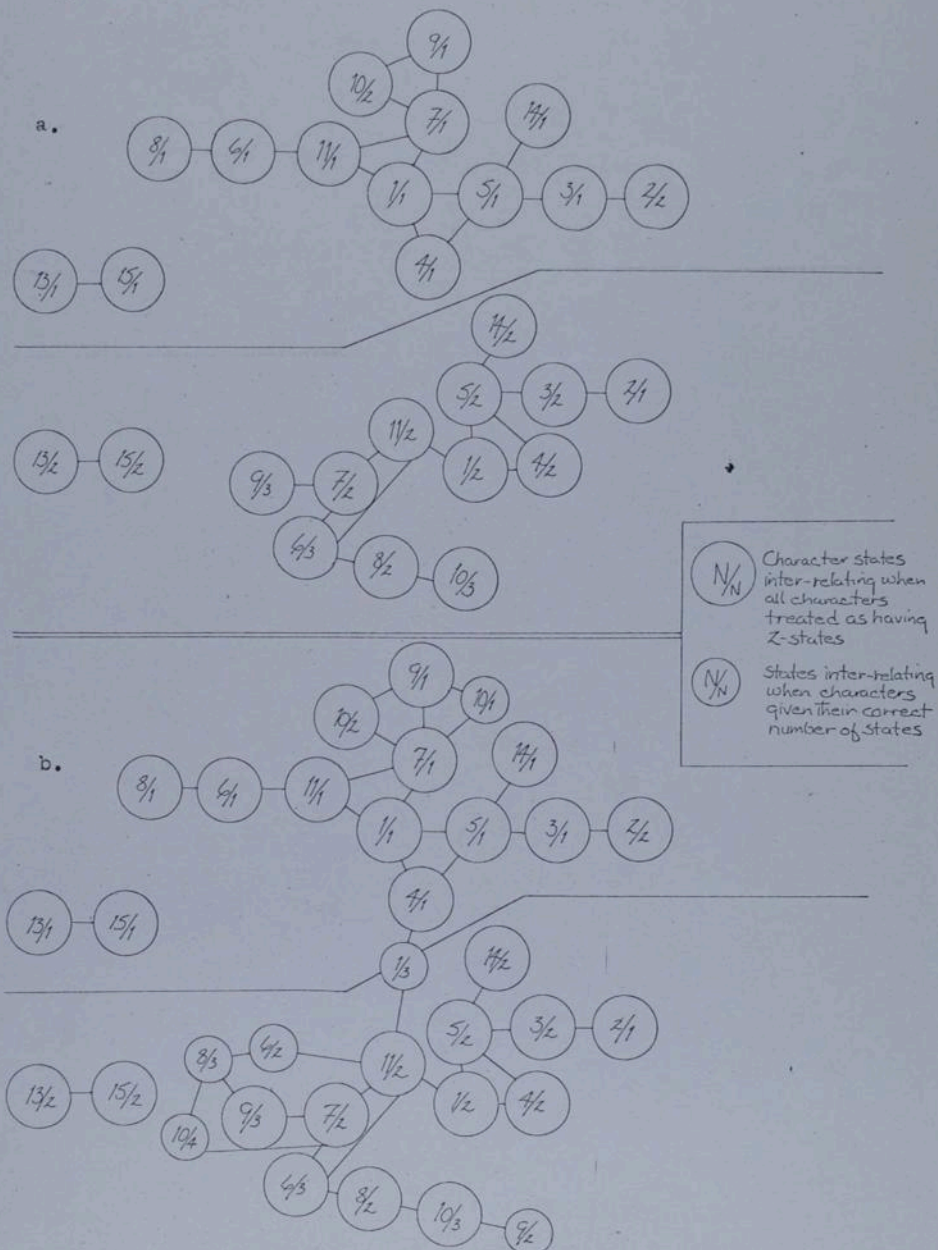


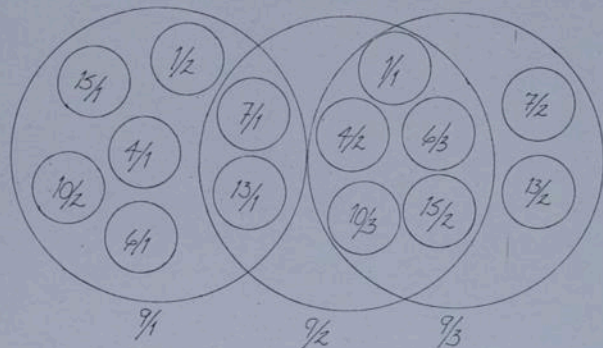
Table 1. Characters &amp; Character States

1. Pubescence of the Lower Stem	/1 puberulent /2 villous /3 sparsely villous
2. Pubescence of the Upper Stem	/1 villous /2 sparsely villous
3. Pubescence of the Rachis of the Inflorescence	/1 villous /2 lanate
4. Pubescence of the Cauline Leaves	/1 puberulent /2 sparsely villous
5. Pubescence of the Leaf-Base	/1 glabrous /2 pubescent
6. Pubescence of the Bracts of the Inflorescence	/1 villous over the entire surface /2 puberulent over the entire surface /3 villous on margins & veins, puberulent between
7. Lobation of the Upper Leaves	/1 cleft into several divisions /2 entire
8. Lobation of the Bracts of the Inflorescence	/1 deeply cleft, below middle /2 not deeply cleft, above middle /3 entire to minutely lobed
9. Shape of the lobes of the Upper Leaves	/1 central lobe lanceolate /2 central lobe ovate /3 lobes absent
10. Shape of the lobes of the Bracts of the Inflorescence	/1 central lobe lanceolate /2 central lobe ovate-lanceolate /3 central lobe broadly ovate /4 lobes absent
11. Color of the Bracts of the Inflorescence	/1 rose /2 crimson
12. Shape of the Lower Leaves	/1 linear-lanceolate /2 ovate-lanceolate

Table 1. Continued

13. Length of the Inflorescence	/1 short and broad at maturity /2 elongate and narrow at maturity
14. Length of the Galea	/1 7-9mm. long; shorter than the tube /2 10-15mm. long; equal to or longer than the tube
15. Habitat	/1 open, meadow-like situation /2 closed, forest-like situation

Figure 2. Results of SUMRAT



(for description of Characters and Character States see Table 1.)

One last function of the CHARANAL program taken advantage of this study is an operation designed to indicate which Character(s) indicate the most about all the other characters being used. This is called the SUMRAT value. This is obtained from the sum of the ratios representing the amount of information that any given character has in common with all other characters, divided by the information of the character with which the given character is compared in the ratio. The results of SUMRAT are given in Figure 2. For this particular study it was discovered that character 9 best described all the other characters in the study. After discovering this relationship, those objects grouping into each of the three states of character 9 were further investigated. This scrutiny revealed that certain character states of seven characters used in the study defined the objects. This definition totally separates those objects falling into 9/1 and 9/3, but overlaps in the case of 9/2. Character 9/2 is composed of objects most like those in 9/3, but somewhat like those in 9/1, yet the objects in 9/2 are distinct for the character state of 9 which they possess.

This system may be used, in some cases, to construct a classification. I believe that it relates equally valuable information, complimentary to the system of Character Inter-relatedness described above. In 9/1, characters 1/2, 4/1, 6/1, 7/1, 10/2, 13/1, and 15/1 all have some relationship to each other -- which may have genetic implications -- but overall show a greater cohesion to the expression of the character trait 9/1. As in the above discussion, usefull

If... Then statements may be made, and elaborated upon.

#### 4. Cluster Analysis: Subgraphs

The major process involved with clustering is the development of the Subgraphs. These are represented as Figure 3. The conventions used in the subgraphing are explained at the bottom of the last page included in the figure.

The evaluation of this model has been made according to the rough parameters described by Rogers & Appan(1969).

The major clusters fall into two definitions: homogenous and heterogenous. For definition of these and other terms see Table 2(page 12). The majority of subclusters are of the heterogenous variety. The single homogenous unit(objects 17,18, and 19)may prove to be of some interpretive value and will be discussed below.

In this study, due to the lack of correlation between habitat and/or geographical distribution found for the members of the various subclusters, the possible interpretations which might be given the data is considerably narrowed(for a detailed discussion of subcluster interpretation,see Rogers & Appan, 1969).

In the terminal cluster, three subclusters may be identified -- according to size, 1.= 25, 26, 9, 8, 7, 4, 5, 2, 12, 13, 16, 11, and 21; 2.= 27, 24, 28, 14, 6, 10, 23, 22, 1, and 15; 3.= 17, 18, 19, and 3. The larger of these two, because of lack of connectedness, may be indicative of two subspecies. There is, however, no ecological and/or geographical information to substantiate this, so that the possibility stands until further investigation is

Table 2. Definition of Terms

Moat. The moat is a value of cluster isolation, indicating the amount of decreasing 'C-value' (similarity) which must be obtained before the cluster under consideration will suffer any changes. Such changes may include the addition of new objects and/or new internal connections.

'C-value'. The 'C-value' is a measure of similarity obtained for any two given objects, a and b, by dividing the number of characters for which the same state has been attributed to objects a and b, by the total number of characters in the study (Legendre, 1970b.).

Internal Connection. An internal connection is one that occurs between two objects that previously were included in the membership of the cluster involved.

External Connection. An external connection is one generated by the addition of a new object to a cluster, or in some cases, the original formation of a cluster.

Homogenous Cluster. Homogenous clusters are those in which the majority of members join at high 'C-values', and in which the internal connectedness is tight.

Heterogenous Cluster. Heterogeneity of a cluster is indicated by cluster members joining at various 'C-values' (not less than .80000), and by a general dearth of internal connectedness.

made. Examination of the characters possessed by the objects contained in the three memberships does show that each cluster can be defined on the basis of certain characters. Cluster 1. is best described by characters 10/3 and 9/3, and in comparisons of all characters possessed by the membership is equally alike to clusters 2 and 3. Cluster 2. is defined by characters 10/2 and 9/1, and is most similar, overall, to cluster 3. Cluster 3, is outlined by characters 10/1 and 9/3, and is more like cluster 2.

The interpretation arrived at (Rogers & Appan, 1969) is that the objects in this study are representative of a reticulate pattern of phenotypic characteristics, which may only be partially defined on the basis of one character (possibly two) with any distinctness. This one character is character 10, which describes the shape of the lobes of the bracts of the inflorescence. The difficulty in using this character is its extreme variability. It is therefore possible that this variability has not been well-represented in this study, or that the small number of specimens has created a fortuitous grouping by this character which may not withstand the testing of a larger number of objects. For a visual idea of the variability of bract size and lobation, see Appendix I.

Even the articulators (objects bringing together distinct clusters) do not give any good insights into the nature of the clustering. It is supposed that, by definition, these articulators are in some way unique. However, they may

only be so singular in terms of character ratios that establish the similarities. This is said because these objects have no uniqueness which could be used to develop good biological criteria for classification.

The single homogenous cluster (cluster 3, above) also leads one to an as-yet unresolvable quandry. This sub-cluster should be considered as having some significance because of its early tight connectedness and high 'moat' value. However, the only demonstrable difference between these objects and all others in the study is the state of character 10, which they exclusively possess. The difficulties in using this character for separation have been discussed above.

Inherent in the term reticulate is the idea of being interwoven. This perhaps is a most fitting term of description for Castilleja, and, in terms of this genus, can be qualified as indicating an overall pattern of phenotypic flux. It is probable -- with reference to this study -- that the populations which these objects represent are highly dynamic and diverging (possibly due to ecological opportunism of the sort which favors subspeciation), or it may be that the expression of the variation shown is simply not well enough understood.

## 5. Conclusions

From the results of Character Analysis and Clustering Analysis described above, it is concluded that the complex taxonomic problem of Castilleja will only commence on

resolution when a better understanding of character rela-

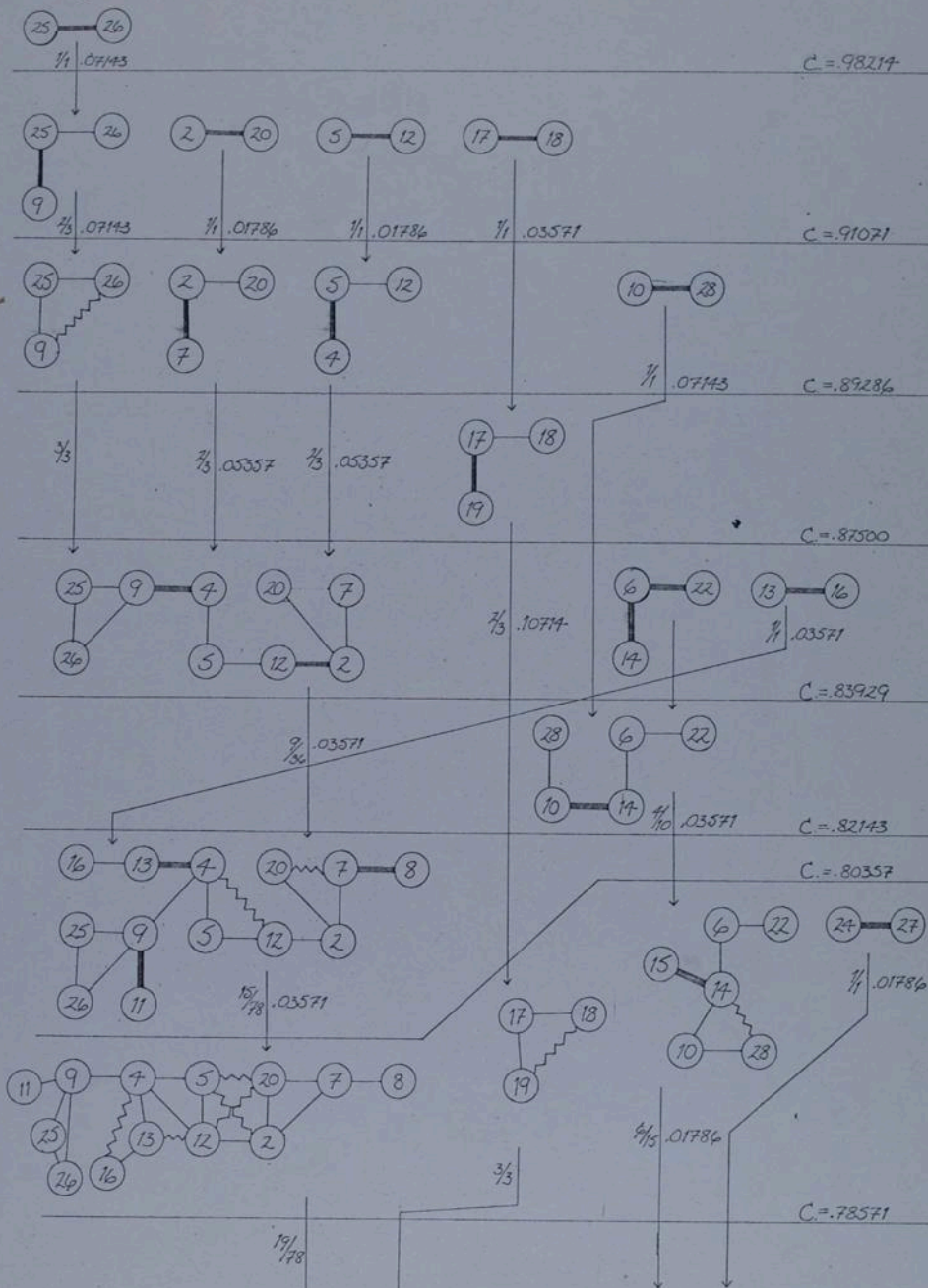
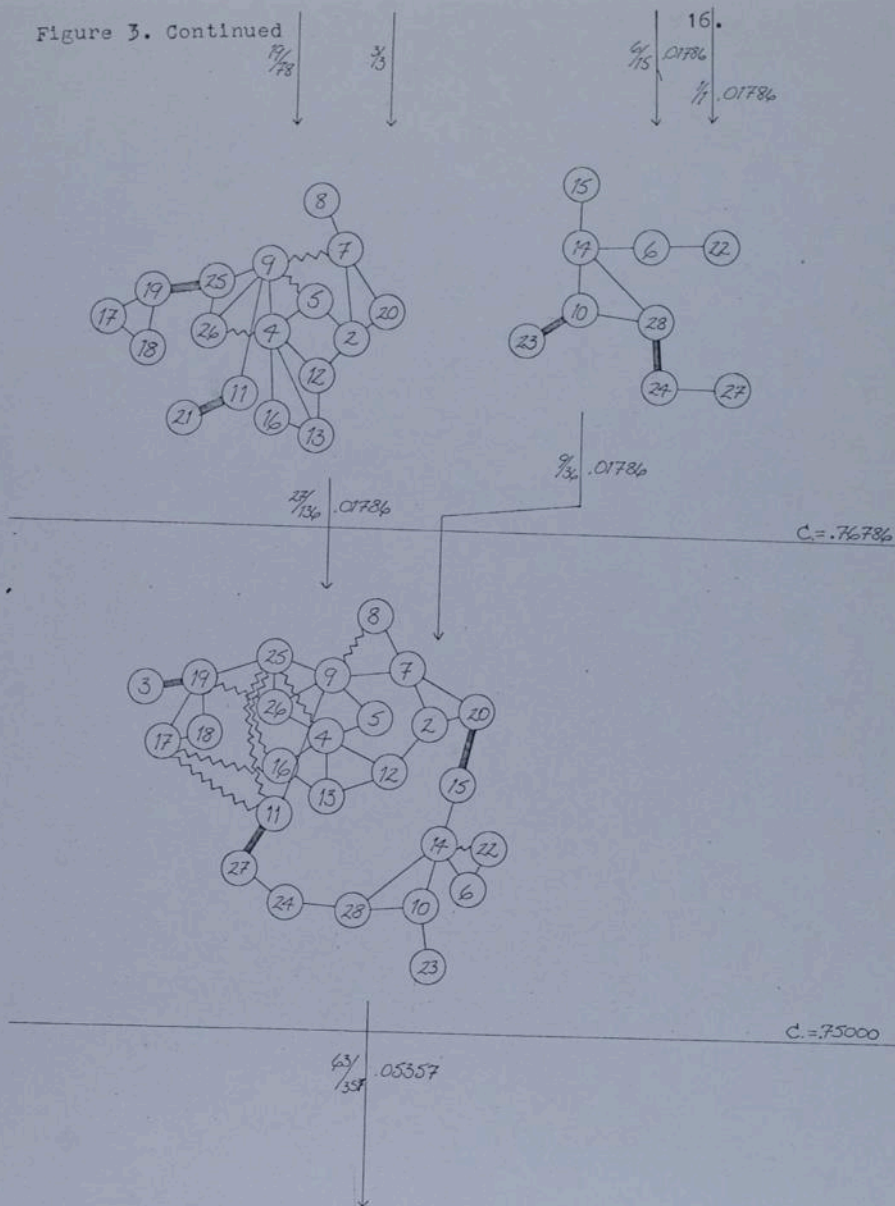
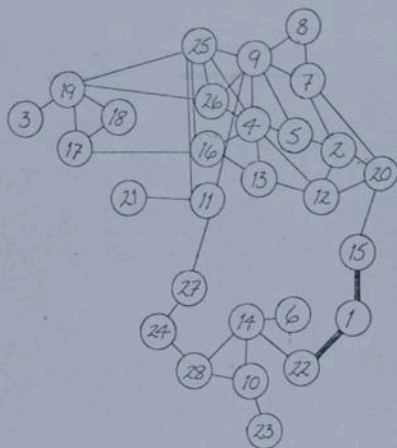


Figure 3. Continued



$\frac{64}{101}$  .05357  
↓



$C = .69643$

$\frac{82}{1578}$

Conventions





-  Primary (external) connection
-  Internal Connection
-  Previous Internal or External connection
-  An object in the study

Table 3. Listing of Objects by Their Conventional  
Taxon Assignment.

---

---

Castilleja *minista* Lindl.

Objects: 1  
3  
11  
16  
17  
18  
19  
20  
21  
22  
23  
24  
27  
28

Castilleja *rhexifolia* Rydb.

Objects: 2  
4  
5  
6  
7  
8  
9  
10  
12  
13  
14  
15  
25  
26

tionships is gained. The Taximetrics methodologies lend themselves very well in this respect.

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Appendix I.

Illustrations of the diversity in bract size and lobation for the objects in the study; including the species Castilleja miniata and C. rhexifolia.



302 ERO



271 ERO



317 ERO



267 ERO



121 ERO



566 E20



53A20



53B20



H8 E20



H8 E20



H8 E20



H8 E20



86CW



42



86EM



565Ero



565Ero



121 ERO



218 ERO



513 ERO



543 ERO



42.EM



42.EM



42.EM



328.ER0