FORM AND STRUCTURE OF VARIATION WITHIN LINEAGES OF <u>WYETHIA</u> AND
<u>BALSAMORHIZA</u>

by

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Abstract

This study illustrates a method of comparing morphological aspects of within-species variation to speciation events within larger lineages in an effort to compare the variation which has arisen as a result of ontogeny to that which has been expressed during phylogeny. The source and structure of variation at these different levels of biological organization in the genera _Wyethia_ and _Balsamorhiza_ (Asteraceae, Heliantheae) were studied using different analytical techniques. This approach attempts to illustrate how a deeper understanding of the nature of biological change over time might be gained when these hierarchically related levels of variation are analyzed with appropriate techniques and compared. This study demonstrates a new and potentially valuable application of different methodologies to the examination of evolutionary processes. The relationships within and between _Wyethia_ and _Balsamorhiza_ have presented problems in the past and an attempt was made to clarify the evolutionary patterns among species. The methods of phylogenetic systematics were employed in order to gain a better understanding of these historical relationships. It was found that taxonomic outgroups were valuable mainly in their ability to delimit small clades, which were then used as functional outgroups. The use of functional outgroups permitted a larger number of variables to be used, including a more detailed set of morphological characters and data derived from flavonoid chemistry. More data and the rest of the taxa are required

before relationships among all species can be fully clarified. Small monophyletic groups of species were identified and confirmed from the results of the cladistic analyses. These clades were used to provide a framework within which a the results of the analysis of within-species variation could be viewed. The second part of this study examined morphological variation based on measurements taken from individual plants. Techniques based on principal components analysis were employed to explore this variation for structure and source. Variation in separate data sets describing heads, shoots and leaves was apportioned to taxonomic levels by analysis of variance of PCA scores. Most of the variation was attributable to groups of related species (genera and sections) or to the species themselves. Populations accounted for little of the overall variation. 95% confidence ellipse statistics were calculated for point swarms describing each species. The ellipse results were translated into graphic representations of variation and variable correlation structure from the head, shoot and leaf data for each species. These graphics were then projected onto the branch tips of cladograms so that within-species variation could be compared among species and lineages composed of species. When within-species variation was examined for changes in source and structure it was found that much of it appears to be attributable to the history of a clade. In addition, some unique and unexpected aspect of variation within each species is always apparent and may be related to the speciation event itself. That is, the nature and source of ontogenetic variation

appears to be related to phylogenetic variation. The variation quantified from different hierarchical levels of biological organization appears to demonstrate similar properties of historical conservatism and emergence. These results are examined in the light of current theories which address the nature of biological change over time and are found to be best explained by a new theory of evolution based on nonequilibrium thermodynamics.

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I. INTRODUCTION

This study has attempted to quantify, relate and explain the variation found within and among species and clades of the genera <u>Wyethia</u> and <u>Balsamorhiza</u> (Asteraceae, Heliantheae). For these purposes, different multivariate techniques were used in order to assess the variation present at different levels of biological organization so that all results could be compared. The conceptual basis of such an approach rests on the belief that evolutionary phenomena are manifested through these hierarchically related levels of phylogenetic and ontogenetic differentiation.

The patterns expressed at and above the level of species were summarized and clarified following the methods of phylogenetic systematics (Wiley, 1981). A separate assessment of within-species variation was derived using methods based on principal components analysis. The comparison of results based on these different methods illustrates a new and potentially worthwhile approach to the study of variation at different levels of biological organization. The advantage of this combined use of techniques is that it permits evolutionary processes to be studied in greater depth than any one method used alone could achieve. This approach may permit more direct questions to be asked of the relationships between ontogeny and phylogeny.

One issue addressed in this study regards the monophyly of <u>Wyethia</u> with respect to <u>Balsamorhiza</u>. Justification for the separation of these two taxa has been questioned in the past,

most notably by Weber (1946). In his monograph of Wyethia, Weber included a discussion of Balsamorhiza and commented on its apparent closeness to Wyethia. The species included in these genera are all herbaceous, taprooted perennials restricted to areas west of the Rocky Mts. from southern Canada to northern Mexico. They are also similar in that they possess pistillate, fertile ray florets, a condition that is not common in most other close relatives. Weber's study included chromosome counts from representatives of both genera. He found $n=19$ or $2n=38$ for all species surveyed.

Prior to Weber's study, Sharp (1935) had included Balsamorhiza in his description of several epappose composite genera. Weber modified this taxonomic grouping somewhat, arguing that the lack of a pappus was not, by itself, sufficient to define a genus. He concluded that two of Sharp's species did not belong in Balsamorhiza. Balsamorhiza invenusta and B. bolanderi were subsequently removed from that genus and placed in Weber's section Agnorhiza of Wyethia. Although all other members of Wyethia possess some sort of a pappus, other features of morphology and distribution suggested to him that the inclusion of these species in his section Agnorhiza was a more natural grouping. Weber left Wyethia intact as a genus separate from Balsamorhiza, but he questioned the naturalness of this grouping: "Cytologically and morphologically Wyethia is more closely akin to Balsamorhiza than to any other existing genus, differing only in the leafy-stemmed habit. In fact, if the data now at hand had been available at the time of the original

definition of the genera, it is quite possible that the two would have been regarded as a single genus with two very well-marked subgenera. The presence of connecting links between the pappose and epappose condition in B. sagittata (Sharp,1935) and B. macrophylla would support such an interpretation, and the similar karyotype would be additional confirming evidence."

For the part of this study which examined relationships among species, the methods of phylogenetic systematics were employed to construct and test evolutionary hypotheses. The fourteen species of Wyethia were included in these analyses, along with species of Balsamorhiza. Several taxonomic outgroups were used in initial attempts to polarize the characters and to identify natural groups within the genera. Some of the clades which were confirmed as monophyletic in the initial analyses and which appeared to be relatively plesiomorphic, were used as functional outgroups in later runs (Watrous and Wheeler,1984). This permitted more characters to be included in attempts to achieve better resolution of patterns of speciation.

The use of a different set of data, based on measurements taken fron individuals, and methodology falling under the general heading of exploratory data analysis (Hoaglin, et al., 1983,1985). permitted the assessment of variation at a different level. The data were separated into three groups of variables describing flowering heads, the shoots upon which they develop and the leaves which arise from those same shoots. These sets of data were analyzed separately so that their results could be compared. This part of the study employed principal components

analysis, analysis of variance and the calculation of 95%
confidence ellipse statistics (Jolicoeur, 1968; Jolicoeur and
Mosimann, 1960; Scagel, et al., 1985), based on the results of
the PCAs.

Analysis of variance was used to apportion the variation
present in the sets of morphological data to levels in a
taxonomic hierarchy. That is, I wished to know where, given the
levels of genus, section, species or population, the majority of
the variation occurs. Levels which account for large amounts of
variation in a data set may also be viewed as sources of
differentiation, or as places where organization changes and
organisms diverge. These are the levels where evolutionary
processes are assumed to be most strongly manifested, given the
plant structures represented and the variables defining them.

Using these same sets of data, further analyses based on
95% confidence ellipse statistics were performed to examine
other aspects of within-species variation. The results of these
analyses were made graphic and projected onto the branch tips of
cladograms defining lineages of species. Variation within
species was viewed within the context of variation among species
within and among small, monophyletic groups. I wished to know
what patterns of variation or organization were revealed within
and among species when the results of these different techniques
were compared.

Finally, I wished to compare the explanatory capabilities
of different theories claiming to address the causes of
biological organization and change over time when presented with

these results.

II. MATERIALS AND METHODS

1. PLANTS

The species concept recognized here is defined after Wiley
(1981) as a group of organisms which share membership in a
unique lineage and maintain a group identity. Groups of plants
were excluded from this study if the characteristics defining
them seemed unclear or in dispute. Although hybrids were
commonly encountered in the field, they were easily recognized
and were not included in any of the analyses.

The numbers of individuals representing each species from
which actual measurements were taken are shown in Table I.
Descriptions of collecting sites may be found in Appendix A.
Vouchers for all species have been deposited in the University
of British Columbia Herbarium (UBC). A minimum of five plants
were collected from each site (a "population", as defined here)
and were assumed to be interbreeding. These samples may have
been too small to allow a full assessment to be made of
variation within and among individuals and populations.
Nonetheless, the collections were assumed to provide generally
sufficient material for the analyses performed here. Each
individual was represented by one flowering shoot at anthesis.
Basal leaves were included, when present, but data regarding
them were not included in the analyses based on PCA.

Anthesis was defined as fully opened terminal heads with
anthers and style branches exerted in at least the outermost
whorl of disk florets. This restriction was placed on the

material sampled so that all shoots would be at approximately the same stage of development. In most cases, collections were made such that the heads terminating the central axis of the shoot met these criteria. In a few instances, however, the central heads were just past flowering. This had an effect only on the variable describing numbers of ray florets and is discussed further in the section on measured variables.

All species studied are taprooted perennials with similar root systems, so variables describing roots were excluded here. A collection including whole plants with roots would have been unecessarily cumbersome to store and transport. As well, I had no desire to kill individuals, especially when they were members of a rare or endemic species.

During the sampling, an attempt was made to represent different areas of each species range. For some of the widespread taxa this was not difficult and is reflected in the number of populations representing them. Most of the species of Wyethia and Balsamorhiza were represented by two to seven populations (see Table I and Appendix A). All species of Wyethia were collected, but unfortunately, W. ovata, W. invenusta and W. scabra were only encountered once. These taxa are therefore represented by only five individuals each.

Balsamorhiza was represented by seven species, which certainly did not account for the range of variation in the genus (see Taxonomic Descriptions). It was assumed, however, that the collections were sufficient to assess within-species variation and to gain some further understanding of the

phylogenetic relationships among species of <u>Wyethia</u> and <u>Balsamorhiza</u>. The three species placed in section <u>Artorhiza</u> were included here, but <u>B</u>. <u>deltoidea</u> and <u>B</u>. <u>careyana</u> were represented by only five individuals each. Four species of section <u>Balsamorhiza</u> were examined, all with a sample size greater than five except <u>B</u>. <u>serrata</u>. One of the collections included as <u>Balsamorhiza</u> <u>incana</u> was obtained from a site suppossedly to the south of the range of this taxon,(see Taxonomic Descriptions and Appendix A) but these plants were morphologically indistinguishable from the species.

The four other taxa listed in Table I represent some of the close relatives of <u>Wyethia</u> and <u>Balsamorhiza</u>. These species, with the exception of <u>Helianthus</u> <u>cusickii</u> represent genera which were included as taxonomic outgroups in the phylogenetic analyses. Data from the outgroup species listed in Table I were included in the assessment of within-species variation. This was done in order to compare variation expressed within species of the study group to variation within representative outgroup species. The choice of these particular outgroup taxa was made based solely on their convenience of collection. Species which are sympatric with <u>Wyethia</u> and <u>Balsamorhiza</u> were collected when encountered. These outgroups species, as well as the additional outgroup genera used in the phylogenetic analyses, are all outlined in Taxonomic Descriptions.

2. DATA

All variables used in this study belong to one of two major groups, defined as follows. Measured variables consisted of those things that could be counted or measured on organisms. They include both continuous and discrete variables and were used for the exploratory data analysis section of this study. Categorical variables differed in that character states were chosen and the presence or general condition of an organ or structure was assigned to one of these. Variables of this type were used to construct a partial phylogenetic hypothesis for the taxa of interest.

The measured variables were converted to categorical variables by assigning a state of 0 or 1 to either side of their means in one of the cladistics runs. This analysis was not included in the results of this study, however, because outgroups were represented by only a few species. This was considered an insufficient sample upon which to base character assessment of outgroup genera. As well, I did not have this kind of detailed morphological data for the other taxonomic outgroups employed in the phylogenetic analysis.

A. MEASURED VARIABLES

These data consisted of continuous (lengths and widths, in centimeters) and discrete (numbers of things) variables.

Variables of this kind were used for the assessment of variation based on principal components analysis. Information regarding basal leaves or organs borne on axillary shoots was excluded, since many species lack these structures. All individuals used in this part of the study had at least two leaves attached to the main stem of the flowering shoot, and only these were compared directly (as illustrated in Figure 1). Measurements of phyllaries were taken only from the flower head arising directly from the apex of the main shoot, when more than one inflorescence was present. This restriction was also placed on the variable describing numbers of ray florets, unless those of the central head had fallen and been lost during the collecting. For heads, as for leaves, the attempt was made to avoid any assumptions of homology between inflorescences terminating a central shoot and those arising from axillary buds.

The data gathered from the flowering shoots was divided into three parts for analyses involving apportionment of variation and the descriptions of within-species variation. Descriptions of variables and their acronyms follow.

i. Cauline Leaf Variables

MDLN1 and MDLN2: Lengths of blades of leaves located approximately midway up the axis of the shoot, if more than two leaves were present. These were measured from the apex to the most proximal point of attachment of the blade to the petiole. MDWD1 and MDWD2: The width of the same two cauline leaves at

their widest points. MDPT1 and MDPT2: The lengths of the petioles of the same two cauline leaves.

ii. Shoot Variables

These variables were included as a discrete set of data in the analyses since I wished to examine the variation in numbers of organs which arose from a particular shoot separately from the measurements of the organs themselves. It did not seem reasonable to assume that the number of leaf or axillary shoot meristems initiated on a particular axis was necessarily strongly correlated with the variables describing the mature organs which had arisen from those meristems. #OPP: The total number of oppositely arranged leaves on the shoot. #ALT: The total number of alternately arranged leaves on the shoot. STHT: The height of the main stem axis from its point of attachment at the caudex to the base of the central flower head. #HDS: The total number of flower heads present on a shoot, including both terminal and axillary inflorescences.

iii. Head Variables

With the exception noted below, all measurements were taken from the central head terminating the main axis of the flowering shoot. HDWD: The width of the terminal head, measured across the base of the receptacle. RAY#: The number of ray florets present

on the terminal head. In a couple of instances, these were lost during collecting because the central heads were almost past anthesis. Plants in such condition are noted in the collecting notes in Appendix A. In these cases, ray counts were taken either from axillary heads, if present, or means were taken from the rest of the individuals in the collection. PHLN1, PHLN2, PHNL3: The length from base to apex of three of the outermost phyllaries of the terminal head. PHWD1, PHWD2, PHWD3: The width at their widest point for the same three phyllaries. PH#: The total number of phyllaries for the terminal head.

B. CATEGORICAL VARIABLES

i. Morphological Variables

An initial set of morphological variables was used for the study group and five outgroup genera. These are listed and described in Table II. Because of uncertain affinities and limited data each outgroup was employed independently so that the resulting trees could be compared (Donoghue and Cantino, 1984). Unfortunately, the number of characters that could be used for all members of the study group, as well as for outgroups, was quite small. It was often the case that characters which varied among ingroup species seemed to vary similarly within outgroup genera. Because of this, assessments of polarity were often impossible to make, given the limited

data at hand. These problems are discussed in greater depth in a later section.

Initial analyses employing taxonomic outgroups were sufficient to identify small monophyletic groups of species within Wyethia and Balsamorhiza. In an attempt to improve the resolution of the relationships among species, these clades were employed as functional outgroups (Watrous and Wheeler,1981) in further analyses. This permitted the use of a larger data set consisting of both morphological and chemical variables. Functional outgroups consisted of small collections of taxa which were repeatedly confirmed as monophyletic, regardless of the overall outcome of a given run. The taxa and characters used are shown in Table III and Table IV.

ii. Flavonoid Chemistry

For the purposes of this study, only non-polar flavonoid aglycones (those lacking attached sugars) were examined. These were obtained by washing leaf material in non-polar solvents so that only the contents of the glandular trichomes or the cuticle would be dissolved. The polar flavonoid glycosides which reside in vacuoles are not extracted by this method. These polar compounds were briefly examined for one taxon only (Balsamorhiza sagittata) and were found to consist of glycosides of quercetin and kaempferol. These flavonoids are considered to be rather ubiquitous among angiosperms (Fairbrothers, et al., 1975). Structural differences of surface flavonoids among taxa appeared

to provide more interesting and useful characters. Because of this, the examination of internally sequestered flavonoid glycosides was not considered to be worthwhile and was not pursued further.

Flavonoid aglycones were extracted from air-dried leaves in either dichloromethane or chloroform. The extracts were taken to dryness and chromatographed over Polychlar AT columns using dichloromethane:MeOH (3:1) and gradually increasing amounts of MeOH. Fractions from these columns were further separated on Sephadex LH-20 (MeOH) columns and on polyamide thin-layer chromatograms. Compounds were cleaned over Sephadex LH-20 prior to spectral analysis.

Structural determinations were made based on UV, 1HNMR and MS data, as well as by co-chromatography against standard compounds. Several compounds isolated from some of the species of Wyethia were found to be new natural products. The details of the spectral information leading to the characterization of these new compounds is given elsewhere (McCormick, et al., 1985a; McCormick, et al., 1985b; McCormick, et al., in press). These will not be discussed further here, except as regards their use as characters.

Basic structures representing classes of flavonoids and major substitution patterns are illustrated in Figure 2. A listing of the species of Wyethia and Balsamorhiza for which flavonoids have been characterized is shown in Table V.

Some chemical characters may provide good information with respect to relationships, especially among species of Wyethia.

These include flavonoids with basic structural differences, such as the B-ring attachment of isoflavones. The differences in bonding, protonation and hydroxylation of A-ring carbons 1 and 2, such as those seen in flavonols as opposed to flavanones, may also be important. The ability to provide a flavonoid skeleton with a certain substituent and the specific patterns of methylation or prenylation of compounds may provide useful information as well.

Unfortunately, time and circumstances did not permit the full elucidation of flavonoid aglycones made by all species of Wyethia and Balsamorhiza. However, since representatives from all sections of both genera have been examined, general comparisons were made by co-chromatography for the remaining species. The only characters that could be obtained by this method were the presence of flavanones and prenylated compounds. If any flavanones are present, one will appear as a pink spot on a TLC after appropriate treatment. If prenylated compounds are present, some of these will be flavanones and a series of pink spots will appear. Because of their colors, these compounds are not easily confused with others, but some important chemical characters cannot be evaluated in this way. Isoflavones and methylated flavonols are very different compounds, yet they may both appear as black spots at the non-polar end of a TLC plate. I felt that chemical data of this kind could not be included in the present study, but this information should prove valuable when flavonoids from the remaining taxa are fully identified.

An attempt was also made to gather information on the

flavonoids of outgroups from the literature, but there was not a great amount available. With the single exception of _Flourensia_, outgroup genera appear to produce only methylated flavonols. Some species of _Flourensia_ produce prenylated flavanones (Bohlmann and Jakupovik, 1979) but only a few members of the genus have so far been examined. Available information on outgroup chemistry seemed too sketchy, so these characters were excluded from use in cladistic analysis employing taxonomic outgroups.

3. ANALYSES

A. PHYLOGENETIC SYSTEMATICS

The choice of outgroups for use in cladistic analyses may be a source of difficulty in botanical studies (Funk, 1981; Donoghue and Cantino, 1984). It is often impossible to choose a single, most closely related outgroup. At best, the numerous possibilities can be narrowed down to a few, and this study proved to be no exception. Testing the monophyly of Wyethia with respect to Balsamorhiza and finding polarities for characters required the use of several outgroups and this approach was still not fully successful. I generally chose outgroup taxa from among those which have been considered close to the study group by most workers. Requiring that outgroups be members of the same subtribe as the taxa of interest would have been the simplest approach. Unfortunately, the limits of the subtribes of the Heliantheae is a subject presently in dispute. In the two most recent treatments of the tribe Heliantheae, Wyethia and Balsamorhiza remain together, but in different subtribes. Stuessy (1977) places them in his Helianthinae, while Robinson (1981) thinks they belong in his Ecliptinae. There are a few genera which have been repeatedly placed close to Wyethia and Balsamorhiza by past and present workers. Helianthella, Heliopsis, Encelia, Flourensia and Rudbeckia are considered to

be closely related to the taxa of interest. All were used here for outgroup comparison employing generic outgroups.

I found that I was often very limited in the choice of characters which could be used with taxonomic outgroups. Presence, absence or condition of the pappus, for instance, varies similarly among species of both ingroup and outgroup genera. I suspect that most species possess the information necessary to make some sort of a pappus, but the developmental control of this character seems to vary greatly within outgroups and study groups alike. This problem also exists with other potentially important characters, such as leaf arrangement, number of heads per shoot, presence of basal leaves, leaf venation patterns and others. For Wyethia and Balsamorhiza, these characters tend to be stable enough to be included as part of the generic or sectional definition. However, generic descriptions for some of the outgroups include statements such as, "leaves opposite, at least below", meaning that their arrangement may change to alternate toward the shoot apex. In such a situation it becomes very difficult to decide on a plesiomorphic state without being completely arbitrary. Characters such as these were coded so that change during evolution could be shown to have gone in either direction. This is obvious from Table II, which describes characters used in the initial group of analyses employing taxonomic outgroups.

Two functional outgroups were also used in separate analyses so that additional characters could be included. The first consisted of section Artorhiza of Balsamorhiza and the

second was made up of the species pair <u>Wyethia</u> <u>reticulata</u> and
<u>W</u>. <u>elata</u>. Each of these functional outgroups had been repeatedly
confirmed as monophyletic by earlier analyses. As well, one or
the other clade usually appeared to share the fewest number of
synapomorphies with the other ingroup taxa, according to the
results from the taxonomic outgroup comparisons. The employment
of functional outgroups permitted the use of characters which
could not be used with generic outgroups (Table III and Table
IV).

All phylogenetic analyses were performed using the
systematics package PHYSYS (Farris and Mickevich, 1983). I
wished to examine relationships among species included in these
analyses and to see if the ingroup genera and sections, as they
are presently defined, appeared to be monophyletic. In addition,
the second part of this study required that small lineages of
species be identified and confirmed as monophyletic based on the
results of the cladistic analyses.

B. <u>EXPLORATORY DATA ANALYSIS</u>

The analyses included under this heading had two main
purposes. The first was to identify taxonomic levels to which
the variation in the different data sets could be attributed. A
second set of analyses were performed in an attempt to better
understand the relationships between speciation and development

by describing the morphological variation within species and
comparing it to the variation among them. In these analyses, the
data sets used were based on measurements taken from individual
plants, unlike the phylogenetic analyses, which were based on
characters possessed by all members of each species. The
combined use of these methodologies has allowed an assessment to
be made of the variation present at different levels of
biological organization. Time could not be directly related to
developmental change in the present study. Nevertheless, it was
assumed that ontogenetic processes are not completely divorced
from the final product of mature organism. It seemed worthwhile,
therefore, to explore within-species variation in as much detail
as the available data would allow.

The data were divided into three sets of variables
describing shoots, leaves and heads. This was done because I did
not wish to assume that these structures, which arise from
different meristems (induced, leaf and floral, respectively)
would necessarily demonstrate similar patterns of variation. As
well, there are meristematic areas within developing organs,
such as leaves, which may contribute to the final form of the
organ in a relatively independent fashion. Recent work suggests
that variation among different plant structures may be
attributed to different sources, such as the individual plant or
the structure itself (Scagel, et al., 1985; Scagel,1984; Maze,
et al., in press; Robson, et al., in prep.).

This part of the study centered around the use of principal
components analysis (PCA) of a correlation matrix. The

statistical package MIDAS (Fox and Guire, 1976) and the program
ANOVAR (Greig and Osterlin, 1978), provided through the
University of British Columbia Computing Centre, were used for
these analyses. The three different data sets describing heads,
shoots and leaves were analyzed independently so that their
results could be compared. Normality of distribution was checked
using a graphic technique, cumulative frequency distribution of
standardized variables (Zar, 1974). Four of the variables,
PHLN3, PHWD1, PHWD2 and PHWD3 were not normally distributed.
Improvement of these distributions was achieved when a square
root transformation was performed on the first variable and a
log transform on the last three.

The PCA axis scores, for axes with eigenvalues greater than
one, were subjected to analysis of variance in order to
apportion the variation present to different taxonomic levels. I
wished to assess the congruence between actual data polarity, as
expressed in PCA axis scores, and vectors related to different
hierarchical levels. The model used for the analysis was
$Y=A+B(A)+C(AB)+D(ABC)+e$, where Y=PCA axis scores, A=the effect
of genera, B=the effect of sections, C=the effect of species,
D=the effect of populations and e=the residual term. ANOVA was
not used here for the purpose of testing any particular
hypotheses, but instead to apportion variation to these
different hierarchical levels using ratios of sums of squares
for PCA axes with eigenvalues greater than 1.

I also wished to examine in some detail the statistics
describing variation and covariation within the point swarm

representing each species. Eccentricity, theta and area for 95%
confidence ellipses were calculated (Scagel, et al., 1985;
Jolicoeur, 1968; Jolicoeur and Mosimann, 1960) for each point
swarm that described a species. This was done separately for
each data set representing flowering heads, stem leaves and
shoots.

Theta describes the angle between the major vector through
the point swarm for a species and a reference axis relative to
the entire data set (the first PCA axis). Theta offers an
estimate of variable inter-correlations by calculating the
position of each point swarm in variable space relative to all
others. The calculation of eccentricity provides an estimate of
the shape of the point swarm about the vector which summarizes
it. This assesses the strength of variable correlations, with 0
indicating no correlation and 1 indicating strong correlations.
The area of point swarms may be described as the relative size
of each, estimated within the overall variable space. Relatively
large areas imply greater variation among those same variables
for a given point swarm, while small areas indicate little
overall variation.

These statistics allow further descriptions of the data, as
they give some indication of correlation patterns of the
variables describing similar structures among different species.
They also allow some estimate to be made regarding the pattern
of variable relationships for different structures within a
single species. Using these techniques, relative differences in
the interaction of variables describing mature plant structures

were assessed and compared. These estimates of the amount and nature of variation within species were represented graphically as "dry flies", which present a summary of these statistics for each species as a single illustration. This was done so that patterns could be compared visually. The details of their construction are described in the next chapter.

I wished to see what comparisons could be made among descriptions of correlation structure within species when shown graphically at the branch tips of a proposed phylogeny. Only small, monophyletic groups of species were used in these comparisons in an attempt to determine how some of the within-species variation might show pattern or structure within the context of the history of a small lineage. Comparisons involving large areas of cladograms, even when well confirmed, would have been inappropriate because within-species variation was quantified based only on mature structures. As well, theta and eccentricity assign values on a bounded scale and their results, when shown against a large or complex phylogeny, could imply false reversals or parallelisms. For these reasons, only small clades were used to provide the framework of speciation events within which the variation among mature plant structures could be viewed. The descriptions of within-species variation and organization were compared among species and among small lineages composed of species.

III. <u>RESULTS AND DISCUSSION</u>

1. <u>PHYLOGENETIC SYSTEMATICS</u>

A. <u>RESULTS</u>

The results of these analyses are not conclusive with respect to the overall relationships of <u>Wyethia</u> and <u>Balsamorhiza</u>. Figures 3-7 illustrate cladograms resulting from the use of taxonomic outgroups, while Figures 8 and 9 show the different results that were obtained when functional outgroups were employed. Tree lengths and consistency indices are shown with each cladogram. The values for consistency, or ratios of the minimum number of transformations required for expression of the raw data sets to the actual number of changes shown on the trees, are not high for any of these cladograms. The lowest consistency indices were generated with the use of functional outgroups, implying that changes in character states for different variables are not strongly correlated. In general, the use of of each outgroup generated only a single tree. In cases where more than one tree was generated, F-ratios were calculated and only the cladogram giving the lowest value is shown (Brooks, <u>et</u> <u>al</u>., in review).

Based on the use of taxonomic outgroups and morphological data, the results suggest that <u>Wyethia</u> and <u>Balsamorhiza</u> are paraphyletic, implying that some members of <u>Wyethia</u> may have closer relatives among species of <u>Balsamorhiza</u>. Analyses based on the use of <u>Helianthella</u>, <u>Encelia</u>, <u>Heliopsis</u>, <u>Flourensia</u> and

Rudbeckia as taxonomic outgroups are shown in Figures 3-7.

Figures 8 and 9 illustrate cladograms generated with functional outgroups. Section Artorhiza of Balsamorhiza is shown as the outgroup, in Figure 8. In Figure 9 the functional outgroup was derived from the species pair Wyethia reticulata/W. elata. These two small clades were repeatedly confirmed as monophyletic based on results from analyses using taxonomic outgroups. In addition, one or the other functional outgroup was usually represented as having arisen early in the hypothesized lineage and is shown close to the taxonomic outgroup. Analyses using functional outgroups permitted the use of more detailed morphological data. The presence of flavanones and prenyl substituents were also included as characters (Tables III and IV).

The overall results of analyses based on functional outgroups are quite different from those using taxonomic outgroups and the members of the present genera, with few exceptions, now appear to share a more recent common ancestry. In the cladogram which used the Wyethia reticulata/W. elata combination as a functional outgroup, (Figure 9) the members of Balsamorhiza do appear to form a monophyletic group, but part of Wyethia is still paraphyletic with respect to them. In the cladogram using section Artorhiza as the outgroup, (Figure 8) Wyethia and Balsamorhiza do not appear to be paraphyletic, although many of the relationships are still vague. The addition of new data, especially chemical characters, seems to provide stronger evidence of synapomorphies among many species presently

included in Wyethia. The rest of this information is apparently
needed before phylogenetic relationships among all the taxa can
be clarified.

Although a full phylogeny could not be completed, many
species are repeatedly shown to form monophyletic groups within
the present genera. For Wyethia, at least, these groups do not
entirely agree with the present sectional classifications. None
of the sections appear to define monophyletic groups within
Wyethia. I suspect that two of these sections, Wyethia and
Agnorhiza, have been defined almost exclusively by the relative
size of the ranges of the species involved. The possession of a
large range may provide a good character, but it has been
weighted too heavily. Other shared characters must be allowed to
provide evidence of relatedness, as well. Endemism certainly
makes a useful key character, but it does necessarily reveal
much about evolutionary relationships.

I did not have representatives from all species presently
included in Balsamorhiza section Balsamorhiza, and so cannot
present a fuller phylogenetic hypothesis for this genus. I did
not wish to make guesses regarding species definitions and could
not have defended the use of one treatment of section
Balsamorhiza over another. It is not entirely clear why the
definitions of species in this section have remained so vague,
but a great deal of confusion certainly exists. The frequent
hybridization of any taxon in the genus with any other one is
responsible for some of this difficulty and some species may
have arisen in this way, adding to the confusion. In addition,

it seems that many small populations of plants now in section
Balsamorhiza exhibit a great deal of variation with respect to
other populations of the same supposed species. Species
definitions have been attempted several times (Sharp, 1935;
Weber, 1946; Ownbey and Weber, 1943; Cronquist, 1955), but the
criteria by which species are defined seems to vary greatly
among authors. Some phenomenon, perhaps speciation-in-progress,
may be underway here, but it requires examination in far more
depth before possible explanations can be offered. I felt that I
could not rely on the literature and did not wish to be
restricted to the use of herbarium material alone. Careful and
extensive sampling of known numbers of individuals from various
populations or disjuncts are required before this problem can be
dealt with properly.

B. DISCUSSION

In spite of the failure of this study to define the overall
relationships among all species in the genera, several smaller
monophyletic groups were identified based on reasonably strong
evidence. These are further confirmed by the use of section
Artorhiza and the Wyethia reticulata/W. elata species pair as
functional outgroups. Because they are so uncommon, isoflavones
are noted in the following discussion when they have been
identified in a species, even though their presence could not be
used as a character in the present study.

Wyethia mollis is repeatedly shown to share a more recent common ancestry with the endemic species W. invenusta and W. ovata than with other members of section Wyethia. Wyethia mollis is a widespread species, found in Northern California and throughout the Sierra Nevada at mid to high elevations. The two related species, while having only very limited ranges, are near the area covered by W. mollis. Wyethia mollis and W. invenusta both make methylated flavonols, prenylated flavanones and isoflavones. Wyethia ovata makes isoflavones and methylated flavonols. W. bolanderi, another Sierran endemic, makes only methylated flavonols (McCormick et al., 1985b).

Two other endemics, Wyethia reticulata and W. elata, are shown in many of the cladistic analyses to share a relatively close ancestry with the other Sierran species just discussed. These two taxa appear to form a close species pair and share several synapomorphies. These include a genuine lack of any basal leaves arising (independently of flowering shoots) from separate underground caudices. The plants possess only cauline leaves, which are well developed, triangular in shape and alternately arranged. Wyethia reticulata produces isoflavones and methylated flavonols, while Wyethia elata produces only methylated flavonols. Both species are endemic to very small areas along the west slope of the Sierra Nevada, but neither seems to be obviously restricted by geography or habitat differences and both are extremely aggressive within their ranges.

The only other species which completely lacks basal leaves

is _Wyethia_ _scabra_. In many respects, however, this taxon is an
anomaly and appears to possess many autapomorphies. Although
this species makes the isoflavones and prenylated flavanones
characteristic of some other members of _Wyethia_, its leaves are
linear and narrow, with a generally (but not always) alternate
arrangement. In all of the analyses employing generic outgroups
and morphological characters, _W._ _scabra_ is always shown as
having a monophyletic relation to _Balsamorhiza_ _hookeri_. However,
in the cladograms using functional outgroups and a larger number
of variables, _W._ _scabra_ is seen to share a closer ancestral
history with some of the species in section _Wyethia_. Results
based on the use of generic outgroups unite _Wyethia_ _scabra_ and
Balsamorhiza _hookeri_ on what may be the homoplasous characters
of linear leaves and phyllotaxy, which may vary from opposite to
alternate on the same stem. The analyses using functional
outgroups imply that these characters constitute autapomorphies
for both species. _Wyethia_ _scabra_ is native mostly to the deserts
of Utah and its placement with respect to the other members of
Wyethia is still questionable. _Balsamorhiza_ _hookeri_ and the
unidentified species which may be close to it require further
attention as well.

Section _Alarconia_ includes only the two taxa _Wyethia_
helenioides and _W._ _glabra_, both of which produce isoflavones,
flavanones and prenylated compounds. These two are seen to form
a species pair or two members of a trichotomy in all of the
cladistic analyses. There does not, however, appear to be any
strong justification for separating them out as a section. The

results imply that these two species share a relatively close
ancestry with at least some members of section Wyethia, and
perhaps to part of Agnorhiza as well. They have been given
sectional status because of their large, leafy phyllaries, well
developed pappus and huge achenes. These characters certainly
unite the species as a pair, but may not justify sectional
recognition, unless we are to do the same for all good species
pairs.

The placement of all the taxa now included in section
Wyethia remains uncertain. One species in particular, Wyethia
helianthoides, is shown to share a more recent history with some
members of Balsamorhiza than with other species of Wyethia,
based on several of the cladograms. This relation is suggested
repeatedly when taxonomic outgroups were used. Wyethia
helianthoides produces methylated flavonols, as do all members
of Balsamorhiza so far surveyed, but there is no reliable
information yet available on its ability to produce isoflavones.
In the cladistic analyses employing functional outgroups,
W. helianthoides lack of flavanones and prenylated compounds is
seen as either symplesiomorphic or as autapomorphic reversals.
Either way, these cladograms imply W. helianthoides is part of a
monophyletic group including most or all of the present species
of Wyethia.

Some other members of section Wyethia seem to be closely
related to each other, but the details of the relationships
within this group, as well as its ancestry with respect to other
taxa remains ambiguous. Wyethia amplexicaulis, W. angustifolia,

W. longicaulis and W. arizonica, appear in various combinations on most cladograms. Chemically, these four taxa share synapomorphies with some other members of Wyethia in their production of prenylated flavanones (and isoflavones, at least in the case of W. angustifolia).

The two present sections of Balsamorhiza are repeatedly confirmed as outlining monophyletic groups of species, regardless of the outgroup employed. The only exception to this was the anomalous taxon Balsamorhiza hookeri, whose exact relationship to the other species is still uncertain. Section Artorhiza and the other available members of section Balsamorhiza each possess a number of synapomorphies, although their relations to each other are still unclear.

The use of functional outgroups in the systematic section of this study has permitted the use of more detailed morphological and chemical data, and this has proven valuable. Although this additional data lends further support to the apparently monophyletic groups within the two genera, their overall relationships with respect to each other were seen to change dramatically. To me this suggests that most of the taxonomic outgroups share too distant of an ancestry with the study groups. The use of generic outgroups was necessary for the identification of monophyletic collections of species within the study groups, but were of little use in further clarification of relationships, since so few characters could be employed. The main value of taxonomic outgroups, in this study at least, was for the identification of monophyletic functional outgroups,

which could then be used in the further clarification of relationships. Such functional outgroups have the additional advantage of being constructed from data that, at the outset of the study, was equivalent to the data used for the ingroups.

Chemical characters appear to provide strong evidence of synapomorphies for many members of Wyethia. The presence of such relatively rare flavonoids as isoflavones and prenylated flavanones in the remaining taxa should prove to be valuable characters. The full elucidation of flavonoids for all ingroup taxa, as well as better information regarding outgroups is required before good use can be made of this data.

The problems within and between Wyethia and Balsamorhiza have not been fully resolved here. A great deal more information is needed before these relationships can be clarified. The taxa included in section Balsamorhiza must be properly defined, among other things. All of the subspecies presently included in Wyethia scabra are in need of examination as well.

Areas of cladograms which consistently demonstrated monophyletic groups of species, regardless of their relationships to other taxa, were used to form a basis for the second part of this study. I wished to examine the nature of variation among individuals within each species in order to see what patterns might emerge when these descriptions were viewed within the context of small lineages of species. The results of the phylogenetic analyses, while incomplete, provided a sufficiently strong and necessary structural context within which a finer level of variation could be nested.

2. EXPLORATORY DATA ANALYSIS

A. SOURCES OF VARIATION

These analyses were based on the three data sets describing the heads, shoots and leaves of the twenty-five species listed in Table I. Table VI shows the PCA results for these three sets of data. Eigenvalues and the percent variance accounted for by the first two axes are listed along with loadings for variables describing each structure.

I wished to identify the major sources of variation given levels of stratification describing genera, sections, species and populations. Those levels which account for the major amount of variation on a given PCA axis are considered here to be the most strongly differentiated levels. In other words, the polarity expressed by a swarm of data points can be compared with vectors related to different levels in a hierarchy. A strong source of variation can also be viewed as a source of differentiation, or as a place where a change in organization is seen (Maze, et al., 1983; Maze and Parker, 1983; Wheeler and Guries, 1982). Levels which account for larger amounts of variation should also reflect real sources of biological differentiation.

Results of these analyses are shown in Table VII. For variables describing heads, the level of species accounts for the majority of the variation in both principal component axes. This indicates that the vectors related to species agree best with the major axes through the point swarm consisting of head

data. It further implies that, because species account for the
majority of this variation, they are also its primary source. In
other words, one manifestation of speciation among these
organisms appears to be differentiation among variables
describing flowering heads. Sections also account for some of
the variation in the head data, implying that monophyletic
groups account for changes in organization as well.

For leaves and shoots, the majority of the variation
appears at the level of genus and in the residual term which
consists of the variation within populations (between and within
individuals) and measurement error. The amount of variation
accounted for by genera in the shoot and leaf data may be large
due to the relatively great extremes in size, arrangement and
numbers of cauline leaves accounted for by the present generic
groupings. The PCA would indicate this by the relative value of
loadings for these variables. In other words, the genera agree
to some extent with data polarity. In the phylogenetic analyses
employing functional outgroups, a great deal of the polarity in
the data also agreed with the present generic groupings. As
well, the variation attributed to the level of sections in the
head data is likely due to some of the present groupings of
species. This may be especially apparent when species pairs are
given sectional status, such as in <u>Alarconia</u>. The results of the
cladistic analyses have shown that the present sections of
<u>Balsamorhiza</u> appear to be mainly monophyletic. Monophyletic
groups should reasonably account for much of the variation in a
data set, since each lineage would define a point of

differentiation. I do not presently have a completed alternate phylogenetic hypothesis with which to make comparisons. I would expect, though, that monophyletic groupings of organisms should show greater agreement with data polarity than polyphyletic or paraphyletic ones.

Populations account for more of the overall variation among shoots and leaves than do species in PCA 1, but this is reversed for PCA 2. It interesting to note, however, that at no time do populations account for as much variation as does the residual term for any axis through any data set. This implies that populations, at least as they are defined here, do not constitute a particularly important level of biological organization or differentiation (source of variation). It is possible that the sample sizes upon which the populations were based were insufficient to account for differences among populations. Nonetheless, the results presented here imply that populations do not represent a strong source of differentiation for these organisms. Although they may be "significantly" different (this hypothesis was not tested), the differences among populations appear to be trivial when compared to the variation present in the entire data set. This result agrees with several other recent studies (Maze, 1984; Scagel, 1984; Yeh and El-Kassaby, 1980; Robson, et al., in prep.). I would also add that populations may have had the benefit of the doubt in this part of the study, since they are equivalent to species for several taxa due to small sample sizes. Perhaps population differentiation is an organism-specific phenomenon that is not

presently manifested within most of the species described here. This possibility will be addressed when section <u>Balsamorhiza</u> is examined in greater depth, for it may be that differences among disjunct populations are a source of the confusion surrounding some of these taxa.

B. NATURE OF WITHIN-SPECIES VARIATION

Species, and the variation within and among the individuals included within them seemed to be levels worth exploring in greater detail. In my opinion, both individuals and species may be viewed as hierarchically related entities. That is, they constitute real levels of biological organization and are interdependent, but not equivalent. If this is so, then the nature of the relationships between these hierarchies is worth further exploration. It may be possible to better understand evolutionary processes through a search for patterns common to these different levels. I wished to ask what effect speciation (phylogenetic variation) has had upon ontogenetic variation within each species and if any of this can be assessed by observing structures of mature individuals.

Ninety-five percent confidence ellipse statistics (Jolicoeur, 1968; Jolicoeur and Mosimann, 1960) were calculated for each data set describing heads, shoots and leaves for each of the twenty-five species. Included in these analyses were 3 outgroup species, <u>Helianthella</u> <u>californica</u>, <u>H</u>. <u>uniflora</u> and

Rudbeckia occidentalis. Helianthus cusickii, a species from
another closely related genus, was also included.

Because this part of the study was based upon measurements
taken from individuals, it was hoped that variation within
species could be estimated. I did not wish to describe in finer
detail the specific character state changes or a sequence of
such events by which one species differs from another. That was
the purpose for which cladistic analysis was used. The purpose
for which my version of ellipse description analysis was used
(or abused) was to probe the within-species variation for the
details of its structure. This was done in order to see if
within-species variation changed with speciation and, if so, to
determine if any of this could be related to different
hierarchical levels and historical constraints.

The production of these ellipse statistics and the graphics
by which they are represented are far removed by abstraction
from the original raw data. This is necessary in order to made
certain comparisons where pattern and structure cannot be
perceived from a raw data matrix. Techniques similar to those
used here have been employed in recent studies describing
variation among and within individuals and populations (Maze,
et al., 1986b; Scagel, et al., 1985; Robson, et al., in prep.).

Values for theta estimate the placement of a swarm of data
points describing a species in variable space, relative to all
other species represented. In this sense, theta provides an
assessment of the nature of the differences in correlations
among point swarms for each species. It says nothing, however,

about the relative quantity of variation or the degree of inter-relatedness of the variables included in the analysis. Theta gives an abstracted estimate of the nature of organization of structures making up individuals within each species relative to all others.

Estimates of ellipse area give an indication of overall amount of variation for structures within a species relative to those same structures among all species. This permits a quantitative assessment to be made of that variation. For instance, I have asked of the data how much variation exists among cauline leaves in one species compared to variation among all cauline leaves. Within the constraint of the species limits, do leaves vary widely, or are they all rather similar to each other? I wished to ask about the variation different taxa show for homologous structures in order to see if the sources could be identified and the variation explained.

Eccentricity calculations allowed the relative measurement of variable correlations (inter-dependency) to be made for the same structures among the species. Returning to the leaf example, I have asked if a change in length is always accompanied by some equivalent change in width for each leaf, regardless of overall differences between leaves. Both theta and eccentricity, as estimates of correlations, evaluate differences in within-species correlations.

Ellipses statistics for each species have been made graphic (Figures 10-12) so that patterns could be more easily noted. The three values which describe some aspect of an ellipse have been

given a common origin and appear as "dry flies". The left half shows values for theta, with a scale running from 80 to -80. The right side of the dry fly consists of two parts. The upper right quadrant gives an estimate of area and its scale runs from 40 to 0, with the horizontal line marking 0. Values closer to zero indicate smaller relative amounts of variation. The lower right quadrant depicts eccentricity, where the horizontal line is given a value of 1, indicating complete correlation among variables. It is given a low value of .6, since variable inter-dependency within these plant structures is rarely any closer to 0 than this. The extremes in scales shown for these dry flies are based on this data set.

Even though some sample sizes were small (only five plants) these statistics are assumed to be reasonably accurate since they were based, ultimately, on a PCA of the entire data set. That PCA is likely stable, and so the statistics derived from it are also stable (Scagel, et al., 1985).

When shown simply as a group of dry flies, it is difficult to pick out any patterns or trends of variation within species which may be due to the ancestry of the species. I wished to compare these dry flies within the context of monophyletic groups derived from phylogenetic analysis. The attempt was made to see where variation appeared to be history-dependent and where it seemed unique within and among small lineages of species.

Among most of the ingroup taxa, theta for shoots never drops below zero on the scale. Almost all of the species in

Wyethia and Balsamorhiza have values for theta somewhere above
zero, where exact values seem to be at least partially dependent
on relatedness. Only Wyethia scabra and Balsamorhiza hookeri,
among ingroup taxa, show theta values for shoots below zero.
This result is seen for the two outgroup species of
Helianthella, as well. It seems likely that the difference in
theta seen for these taxa has to do with the nature of
constraints within which nodes develop on the stems. In these
four species, phyllotaxy may be alternate or opposite, or both
conditions may exist on a single shoot. This situation is never
the case for any of the other ingroup taxa. Cauline leaves of
all other species of Wyethia and section Artorhiza of
Balsamorhiza are always alternate. In all of the other members
of section Balsamorhiza for which I have data, cauline leaves
consist of a single opposite pair. The two ingroup taxa which
show values for theta more similar to those of Helianthella have
been described as anomalous in many other respects. These
results further illustrate the confusing variation found within
these species. Until the phylogenetic relationships are
clarified, the possible historical significance of these
differences in variation structure for shoots of Wyethia scabra
and Balsamorhiza hookeri remain obscure.

Three species of section Artorhiza, a monophyletic group,
are shown in Figure 13 and are compared with the two species of
Helianthella. The shoots of the Balsamorhizas all show low
values for area and values close to one for eccentricity. This
implies that shoot variables are highly inter-correlated and

that differences among shoots do not provide a great source of variation. Other structures, however, appear to be less constrained in their variation. Among flower heads, Balsamorhiza deltoidea demonstrates lower eccentricity than do the other members of this group. This is probably most strongly influenced by phyllaries, which may vary greatly in size among flower heads, providing a unique source of variation for this species compared to the rest of the lineage.

The dry flies representing the two available species of the outgroup Helianthella are quite different from Artorhiza. This is most strongly reflected in theta, area and eccentricity for shoots. The organizanization of shoots in these species differ from Artorhiza in both the nature and quantity of their variation. Area and eccentricity for shoots is greater in Helianthella. As well, shoots of the two outgroup species are quite different from each other, implying that organization of shoots is not highly constrained either within or among species. Within Artorhiza, however, heads and leaves appear to provide greater sources of variation than they do among the outgroup species.

Other lineages of species may also be compared. Figure 14 shows three members of section Balsamorhiza, B. incana, B. macrophylla and B. serrata next to a pair of endemics, Wyethia elata and W. reticulata. The two endemics appear very similar to each other, relative to the Balsamorhiza species, except in eccentricity for leaves. This difference in within-species variable correlations for leaves suggests that

speciation events may be partly manifested as changing sources and intensities of organizational constraint during ontogeny. Some unique pattern of within-species variation appears to exist for each species assessed. As well, the nature, degree and source of this new variation, seen here as the result of many ontogenies, seems to be closely related to lineages composed of species. Historical constraints within monophyletic groups appear to show strong patterns of organization and variation, especially when compared with other clades of somewhat different ancestry.

IV. SUMMARY AND EXPLANATIONS

1. SUMMARY

A. PHYLOGENETIC SYSTEMATICS

In the cladograms employing taxonomic outgroups, Wyethia and Balsamorhiza always appear as paraphyletic taxa, but more exact relationships remain unclear. When functional outgroups are derived from small clades of ingroup species and used for outgroup comparison with a larger set of morphological and chemical variables, the general pattern changes. When the Wyethia elata/W. reticulata outgroup is used, Balsamorhiza appears as a monophyletic group with respect to its present members, but Wyethia is paraphyletic with respect to it. When section Artorhiza is used as the outgroup, the genera do not appear to be paraphyletic. More data and the missing taxa are required before full phylogenetic hypotheses can be constructed for Wyethia and Balsamorhiza. Flavonoid chemistry may provide strong evidence of synapomorphies for many species of Wyethia.

Taxonomic outgroups may give poor results because their relationships to the ingroup taxa are simply too distant. Their real value here was for the identification of functional outgroups, which were used in more detailed analyses. The functional outgroups and other small clades were used to form a framework for the second part of this study, which attempted to relate the pattern of speciation events within and among these

lineages to patterns derived from an analysis of intra-specific variation.

B. EXPLORATORY DATA ANALYSIS

Three different data sets, which consisted of variables describing the shoots, terminal heads and cauline leaves of twenty-five species, including four outgroup species in addition to the ingroup, were examined. The analyses performed here were based on PCA and fall under the general heading of exploratory data analysis. With these techniques I was able to examine morphological data consisting of measured variables taken from individual plants for the sources and structure of among and within-individual variation.

The three data sets were stratified into taxonomic levels defining genera, sections, species, populations and a residual term. The variation present among shoots, heads and leaves was apportioned to each of these. It was found that for heads, the majority of variation could be attributed to species and some to sections. For shoots and leaves, the majority of the variation appeared in the term describing genera. This implies that most of the variation in the data agrees either with lineages of species (genera and sections) or with the species themselves.

Populations were always seen to account for less variation in the data than the residual term. Although the populations may have shown statistically significant differences their importance as a source of variation here is approximately equivalent to measurement error. It is possible that the samples

analyzed here were too small to adequately account for differences among populations. It is also possible that the variation described here is selectively neutral and environmental factors have had little effect. The third possibility is that populations do not constitute an important level of biological organization for these organisms.

Ninety-five percent confidence ellipse statistics were calculated for the point swarms describing each of the twenty-five species. Graphic representations, "dry flies", were derived from these statistics so that patterns describing theta, area and eccentricity for the shoots, heads and leaves of each species could be compared visually. These dry flies were then projected onto the branch tips of cladograms depicting small, monophyletic groups of species. This was done in order to see if any patterns in the source and structure of variation within a species could be attributed to the history of a clade.

New patterns, apparently related to the history of species, emerge when the variation within species is viewed within the context of variation among them. In addition, unpredictable changes in variation and organization are always seen to be present in the abstract description of each species. These unique changes in within and among-individual variation would appear to be part of the manifestation of a speciation event. The emergence of new variation and organization expressed during ontogeny can be related to phylogenetic variation, demonstrating that increases in complexity appear to accompany of both of these evolutionary processes.

2. <u>EXPLANATIONS</u>

This study illustrates a method of comparing aspects of within-species variation to speciation events within small clades. Apportionment of variation to different taxonomic levels has also provided insight into the sources of differentiation for the various plant structures. The use of different multivariate techniques has permitted analyses to be made of variation at different levels of biological organization so that an attempt could be made to relate them. I think this approach will prove to be worthwhile as a method with which the nature of the relationships between ontogeny and phylogeny may be more thoroughly explored. These techniques should permit the development of individuals to be tracked through time for different species, allowing detailed comparisons to be made across phylogenies.

So far, this study has provided an account of how patterns of variation can be analyzed at different hierarchical levels using different methods. The results have been compared in different ways and new patterns have been reported. However, description alone is insufficient. I believe this study has succeeded in examining some of the variation that is the manifestation of evolutionary processes as expressed in these plants. I wish to provide these results with some causal explanation.

Dobzhansky, <u>et al</u>. (1977, pp.506) offer the following definition of at least a part of the evolutionary process. "The

theory of evolution by natural selection advances arguments of
the following general form. Among alternative genetic variants,
some result in features that are useful to their carriers as
adaptations to their environment...useful adaptations become
established in populations.

"To explain a particular adaptation, a valid selectionist
argument has to show (1) that natural selection is involved at
all; and (2) that natural selection favors that particular
adaptation."

As far as can be seen from these results, no adaptations of
any noticeable importance have become established in these
populations with enough force to cause their differentiation.
Genera, which account for the majority of the variation in the
leaf and shoot data, occupy a tremendous diversity of habitats
and, presumably, of selection pressures as well. The level of
species accounts for a great deal of the variation in the head
data. A species such as Balsamorhiza sagittata is sympatric with
B. hookeri, B. macrophylla and Wyethia amplexicaulis, but these
dissimilar species demonstrate a strong source of
differentiation. The identification of relevant selective
forces, given these results, would be exceedingly difficult.
There is no evidence that these organisms have become either
more similar or more different due to environmental factors.
According to the above requirements for a valid selectionist
argument, I find I am unable to demonstrate legitimately that
any evolution by natural selection has taken place here. Perhaps
the sources and organization of the variation described in these

results are the product of evolution by something else.

There are at least two other factors involved in evolution according to Gould and Lewontin (1979) who would perhaps criticize the restrictive definition cited above. "An adaptationist programme has dominated evolutionist thought in England and the U.S. during the past 40 years. It is based on faith in the power of natural selection as an optimizing agent. It proceeds by breaking an organism into unitary 'traits' and proposing an adaptive story for each considered separately. Trade-offs among competing selective demands exert the only brake upon perfection; non-optimality is thereby rendered as a result of adaptation as well. We criticize this approach and attempt to re-assert a competing notion...that organisms must be analysed as integrated wholes... so constrained by phyletic heritage, pathways of development and general architecture that the constraints themselves become more interesting and more important in delimiting pathways of change than the selective force that may mediate change when it occurs."

These insights provide some further understanding of the results presented here. Phylogenetic history does indeed seem to count as a constraint on within species variation. A large amount of the variation quantified here is attributable to genera and sections, implying that shared histories among species have acted as a strong source of differentiation. In addition, if shown dry flies for any two species of Balsamorhiza, section Artorhiza, I could predict that area and eccentricity for shoots will reflect a high degree of constraint

on this source of variation within the third species. I could not make this same prediction for a third species of Helianthella, given the two shown here. That these differences are more likely to be influenced by history than by environment is further evidenced by the fact that Balsamorhiza sagittata is sympatric with Helianthella uniflora, as is B. deltoidea with H. californica (see Appendix A).

The history of a lineage seems to have an impact on the nature and source of both organization and variation within a species. That is, history has partly determined where variation will or will not be extreme among developmentally mature structures and what the nature of this variation will be. This supplies part of the explanation, but it is still incomplete.

There is another aspect to these results which I believe to be neither trivial nor driven by something called "randomness" or "probability". Although these terms often serve to describe the phenomenon, they are not equivalent to its cause. Each dry fly and each branch in a cladogram describes events which are unique and always unpredictable in some way. That is, I can predict that variation within the species of section Artorhiza will be constrained among shoots and will be manifested among heads and leaves, but I will never be able to predict the exact form or source of this new variation. The source and nature of within-species variation is shown to change in a manner which is partly unexpected and unique for each species. These differences in organization demonstrate increases in complexity at the hierarchical level of species. This observation can be related

to the increases in complexity expressed by the structures which make up each flowering shoot. That is, where within-species variation is seen to occur, it is inferred that ontogenetic complexity has increased. The unique variation which arises during speciation in the form of character state changes appears to be accompanied by similarly new and unpredictable variation expressed among and within individuals during ontogeny. I believe the unpredictable changes in the source and nature of variation within and among species and clades demonstrates the manifestation of emergent properties at these different levels of biological organization.

Campbell (1982, pp.101) has discussed the problems arising from the concepts of complexity, increasing complexity and the nature and significance of emergent properties. He approaches the subject by comparing the ideas of Prigogine, a chemist, and Chomsky, a linguist, in the following passages. "The creation of structure depends on how far the system is from equilibrium, and this in turn depends on the rate and amount of exchanges of matter and energy with the surroundings. The distance from equilibrium will be great if there are many exchanges, and very small or nonexistent if there are few. The same laws of physics apply in both cases, but near equilibrium Prigogine says the laws lead to 'doom or destruction', whereas further from equilibrium they may become processes of construction and organization. In this latter case, he adds, probability theory breaks down. Nonequilibrium can therefore be a source of order in open systems, whether these systems are chemical or

biological, revealing a fundamental kinship between life and nonlife. Complexity is maintained in both types.

"The whole question of complexity is one which has proved suprisingly subtle when investigated by modern theorists. Complexity is not just a matter of a system having alot of parts which are related to one another in nonsimple ways. Instead, it turns out to be a special property in its own right and it makes complex systems different in kind from simple ones, enabling them to do things and be things we might not have expected. Chomsky suggests that human language competence, which must be among the most complicated structures in the universe, arises uniquely in evolution at a certain stage of biological complexity. In other words, it appears when, and only when, evolution has lead to an organism as complex as a human being. Chomsky goes on to say, 'This poses a problem for the biologist, since if true, it is an example of true "emergence"- the appearance of a qualitatively different phenomenon at a specific stage of organization.'

"Emergence is not a popular word in modern science. But it is not absolutely taboo, and it is usually associated with complexity."

I do not consider the word or the concept to be at all taboo. On the contrary, I believe the inclusion of the concept of emergence is necessary to an accurate description of biological change over time. The recognition of the emergent properties of a speciation event or an ontogeny supplies the last missing piece required for the understanding of these

results. The appearance of an unpredictable and "qualitatively different phenomenon" with respect to within-species variation is viewed here as the partial manifestation of a speciation event.

It still remains to find a single and complete explanation capable of including and making into a coherent whole all the results of this study. Brooks and Wiley (1986) have provided what I consider to be just such a necessary and comprehensive theoretical explanation. Their Unified Theory of Biology is especially powerful because it is the first theory of evolution ever offered which fits within the formal definition of a deductive Covering Law Model (Hempel, 1966). Brooks and Wiley have based their theory on an expanded view of the Second Law of Thermodynamics as it applies to open systems. They have succeeded in doing this without reducing the processes of biological evolution to the microscopic laws of chemistry and physics. This is obvious from the explanations and predictions stated in the following passages (pp. 154).

"...ontogenesis is a nonequilibrium phenomenon, that organisms are dissipative structures whose temporal sequence of change is caused by an interaction between relatively determinate (regulatory) components and relatively stochastic (structural) components within the genetic and epigenetic architecture each organism possesses... a further amplification of this phenomenon results in the production of new species. Thus, the emergence of new species follows the same process as the emergence of new structures in ontogenesis...

(pp. 350)..."By adopting an explicitly structuralist approach to evolution, we have discovered a number of surprising and, in some cases, counter-intuitive things. We have been able to relate biological evolution to entropy without having to postulate any negentropic properties. This is, we discovered, because the currency of entropic behavior in living systems is information specifying structure and not energy. We have characterized living systems at all functional levels in terms of four cornerstone principles. The principle of irreversibility asserts that biological evolution is one manifestation of the more general phenomenon of cosmological evolution. The principle of individuality amounts to an assertion that origins are essential to understanding evolution, and it also amounts to a rejection of natural kinds in biology. The principle of intrinsic constraints asserts that evolutionary changes are non-random, orderly and constrained by the past history of each species. And the principle of compensatory changes asserts that biological evolution has a conservative tendency which allows the same dynamics to produce both determinism and new variations and options simultaneously. We have shown that information can be produced by entropic phenomenon. This allows many aspects of evolutionary history and evolutionary processes to be tested directly and explicitly...

"The pragmatic aspect of whether or not our theory is considered a new view of biological evolution, or just a reformulation of the consensus depends on two things. First, to what extent is our presentation viewed as providing helpful

explanation for findings which would seem to be anomalous under the current paradigm?...

"Second, we must make some predictions about the kinds of findings research guided by our theory will uncover...

"Biological systems are a combination of deterministic and indeterminate factors; thus, it should be possible to make deterministic predictions about some aspects of evolution. If we are correct, however, the deterministic aspects of evolution are the historical components..."

This theory of history-dependent, nonequilibrium evolution appears necessary and sufficient to explain all of the results presented in this study. First, it explains why lineages should be so important a factor in the sources and nature of the variation quantified here. According to the methods of phylogenetic systematics, the histories of species may be inferred from the unique characters they share with other species. This implies that emergent properties are manifested at the origins of a lineage and are retained in descendants. For example, it would have been impossible to predict that the common ancestor of section <u>Artorhiza</u> should suddenly produce something like arrow-shaped basal leaves. The unique occurence of this character in an ancestral species became an historically preserved synapomorphy which was expressed in later speciation events. It now contributes to the unity of the lineage as a developmental constraint. However, each speciation event in this clade has also been accompanied by some unique and unexpected autapomorphy of its own. That is, emergent properties have

marked the arisal of each species through time and these are expressed through lineages of individuals. Similar patterns of organization and variation are also seen among and within individuals and appear to demonstrate the hierarchical nature of biological organization at a finer level. The use of different analytical methods has permitted the quantification of these phenomena at the levels of individual plants and the structures they produce, species and lineages composed of species. It has been shown that within-species variation demonstrates the same patterns of historical conservatism and emergence as does each speciation event within a clade. Although the details differ, these similar patterns seem to exist from the hierarchical level of lineages, through to the flowering shoots of individual plants. This study has attempted to demonstrate that both history-dependent and unique variation occur at different levels of biological organization and that these are related. These results agree well with the explanations and predictions offered by Brooks and Wiley. I think it is time to take a close and serious look at what new understanding might be gained from their theory of nonequilibrium evolution.

V. EPILOG

Or, can you spell "deductive-nomological"?

Perhaps a final aspect worthy of brief discussion remains with regard to the choice of causal explanations made here. It seems an essential difference has traditionally existed between biological explanations and those used in other disciplines falling under the general heading "natural sciences". This difference has been pointed out rather sharply by at least one physicist philosopher. It has to do with the past failure of evolutionary explanations to fit within the framework of a deductive Covering Law Model (Hempel, 1966). It seems to me that some biologists and philosophers have made fantastic and contorted attempts to provide evolutionary theory with the respectable title of deductive explanation, which it has so far not deserved. (Dobzhansky, et al., 1977; Rosenberg, 1985; Fisher, 1985).

Similar problems may not arise in studies which address the details of biological function because the microscopic laws of chemistry and physics are adequate to explain, for instance, the properties of membranes or the nature of DNA bonding. Functional biology asks "how does it work?" which is a very different question from "how did it come to be?". The fact that a given structure performs a certain function is insufficient to explain why that structure exists (O'Grady, 1984). That is, structures cannot be said to arise in order to perform certain functions.

Leaves, for instance, cannot be said to have evolved in order to conduct photosynthesis, transport solutes and exchange gases. Such an assertion cannot be called a legitimate causal explanation in science. The fact that leaves do exist and perform these functions is a conditional statement. As such, it may be a necessary part of an explanation, but it must remain only a part. The existance of leaves would hardly appear to provide the full explanation of an event describing the existance of leaves.

Hempel (1966, pp. 73) quickly dismisses biological explanations which seek to give living systems such autonomy that they must have their own set of "laws".

"The basic entities and processes posited by a theory, and the laws assumed to govern them, must be specified with appropriate clarity and precision; otherwise, the theory cannot serve its scientific purpose. This important point is illustrated by the neovitalistic conception of biological phenomena. Living systems, as is well known, display a variety of striking features that seem to be distinctly purposive or teleological in character... the remarkable coordination of the many processes in a developing organism which, as though following a common plan, lead to the formation of a mature individual. According to neovitalism, such phenomena do not occur in nonliving systems and cannot be explained by means of the concepts and laws of physics and chemistry alone; rather they are manifestations of underlying teleological agencies...

"This conception may well seem to offer us a deeper

understanding of the remarkable biological phenomena in question...but understanding in this sense is not what is wanted in science, and a conceptual system that conveys insight into the phenomena in this intuitive sense does not for that reason alone qualify as scientific theory. The assumptions made by a theory about underlying processes must be definite enough to permit the derivation of specific implications concerning phenomena that the theory is to explain.

"Testability-in-principle and explanatory import, though crucially important, are nevertheless only minimal necessary conditions that a scientific theory must satisfy..."

I find I must agree with Hempel and it seems that, until recently, evolutionary explanation has been in a sorry state of affairs because of these apparently irreparable flaws. My understanding and respect for science has grown enough in the past few years that I believe Hempel's damning statements cannot be denied. The "New Synthesis" or any other variations on a neo-Darwinian theme simply cannot, by definition, be considered deductive scientific explanation because they do not invoke any natural laws as part of the explanation. Uniquely biological "laws" simply don't count and never have. Probabilities or "chance" events do not count as laws, either. These may serve in a descriptive capacity, but they do not provide cause in the sense that a law does. Natural laws, unlike probabilities, define what appear to be universal regularities. If there are any absolutes in science, they are equivalent to these laws, which are a requisite part of causal explanation. Deductive

science does not really seem to be such an amorphous or mutable thing. Although the meaning of the term "causal explanation" goes far beyond the narrow notions of "hypothesis testing", its structure and limits seem to me to be well defined.

What, then, might constitute a "good" theory of evolution and why should the difference be so important? Hempel (pp. 75) describes some of the necessary properties in the following passage. "In a field of inquiry in which some measure of understanding has already been achieved...a good theory will deepen as well as broaden that understanding. ...such a theory offers a systematically unified account of quite diverse phenomena. It traces all of them back to the same underlying processes and presents the various empirical uniformities they exhibit as manifestations of one common set of basic laws." If "basic laws" cannot be translated into "uniquely biological laws", but are instead defined as "laws of nature", then I cannot see that I have any choice but to at least examine the Unified Theory of Biology presented by Brooks and Wiley (1986). They have succeeded in providing evolutionary phenomena with a single causal explanation based on the expansion of an existing natural law. The charge that this constitutes a reduction of biological entities and processes to the microscopic laws of chemistry and physics is immediatly invalidated by Brooks and Wiley's recognition of emergence. To my mind, reductionism and emergence are mutually exclusive concepts.

Brooks and Wiley have constructed a theory of biological change which has permitted a full explanation of the results

presented here without the need to tell a single "just-so" story, and it has done so strictly within the formal boundaries of deductive scientific explanation. As well, I believe it has permitted the aquisition of a better understanding of how evolutionary processes might be manifested by the organisms I have studied. In addition, suggestions have been made regarding new ideas for future research, an exceedingly valuable commodity in science. If no deeper understanding can be achieved, or no new knowledge obtained, given past theories, then it is time to thank the old for what light it could shed and look to the new. This is, I believe, something that is long overdue in biology. We have not had a revolution since 1859. It is time.

VI. <u>TAXONOMIC DESCRIPTIONS</u>

I. <u>WYETHIA</u>

The 14 presently recognized species of <u>Wyethia</u> are, in general, easily distinguished. They are described below in an abbreviated version of Weber's (1946) monograph. I had no wish to rewrite this excellent paper and my disagreements with Weber mostly concern the groupings of species into sections. Direct quotations are used where a description or grouping seemed questionable. These have been discussed elsewhere.

<u>Wyethia</u> Nutt., Jour. Acad. Phila. 7:39. 1834

<u>Alarconia</u> DC., Prodr. 5:537. 1836

<u>Melarhiza</u> Kellogg, Proc. Calif. Acad. Sci. 1(ed.2):37. 1873

Herbaceous, taprooted perennials, the aerial shoots mostly leafy and glabrous to variously pubescent. Well developed basal leaves present in most taxa. Cauline leaves alternate and ranging from linear to deltoid, entire to dentate. Heads solitary to several, usually radiate. Phyllaries 2 to 4-seriate, herbaceous to coriaceous, linear to ovate. The outermost series in some taxa are foliaceous and very large. Receptacle convex, paleae firm, conduplicate and persisting after the fall of the achenes (cypselae). Disk florets yellow, perfect, tubular-campanulate, 5-lobed. Anther appendages ovate, the bases sagittate. Style branches slender, attenuate, hirsutulous

(pollen-receptive) for their entire length. Ray florets
pistillate and fertile, mostly yellow (white in <u>W.</u>
<u>helianthoides</u>), oblong-lanceolate. Disk achenes quadrangulate to
rhomboidal in cross-section, glabrous to variously pubescent.
Ray achenes similar, but more compressed dorsally and trigonal.
Pappus usually an uneven crown of persistant, laciniate scales,
prolonged into awns at the angles of the achenes in some taxa,
entirely lacking in a few.

The ranges of all species are restricted to areas of North
America west of the Rocky Mts. Type species: <u>W.</u> <u>helianthoides</u>
Nutt.

A. AGNORHIZA

<u>Agnorhiza</u> (Jeps.)Weber. "Basal leaves absent or greatly
reduced; leaves falsly triple-nerved by the accentuation of two
of the lowermost nerves or by anastomoses of the lateral
nerves... Five of the six species included in this section are
very restricted in their distributional area, one of these,
<u>W.</u> <u>reticulata</u> being known definitly from a very small area near
Rescue, El Dorado Co., Cal. They are apparently species of long
standing, conservative, and depleted of biotypes. <u>W.</u> <u>scabra</u>,
included in this section by reason of the triple-nerved leaves
and lack of basal leaves, does not possess the broad leaves
characteristic of the other species."

1. <u>Wyethia</u> <u>ovata</u> Torrey and Gray.

Stems 1-3 dm. high, much exceeded by the cauline leaves. Plants silky-villous, becoming glabrate. "Basal leaves reduced to scales or club-shaped rudiments." Cauline leaves broadly ovate with subcordate bases, blades 7-20 cm. long, mostly mucronate at the apices, entire, coriaceous and coarsly reticulate, "...two of the lowermost lateral nerves usually conspicuous, giving the leaves a triple-nerved appearance." Petioles well developed. Heads several, almost sessile and clustered in the axils of the uppermost leaves. Outer phyllaries few, foliaceous and broadly linear. Florets glabrous, the rays yellow and few in number. Achenes ca. 10 mm. long, glabrous. Pappus shallow and coroniform with short awns at the angles.

In the past, plants have been collected on hillsides and mountain slopes from Tulare, Los Angeles, Riverside, Orange and San Diego Cos., Cal. It seems likely that the species range may have shrunken considerably in the last century. I have only seen it twice in the field even after a reasonably thorough search.

2. Wyethia bolanderi (A.Gray) Weber.

Stems slender, purplish, 1.5-3 dm. high. Plants glandular to glabrous. "Basal leaves reduced to scale-like bracts." Cauline leaves ovate with truncate to cordate bases, blades entire, 4-12 cm. long, coriaceous and coarsly reticulate with mucronate apices, "...pinnately veined or tending to have a triple-nerved appearance..." Petioles well-developed. Heads solitary and terminal. Outer phyllaries few, foliaceous, ovate. Florets glabrous, rays yellow. Achenes ca. 7 mm. long, glabrous,

epappose.

As it flowers in the early spring, I did not have the opportunity to collect these plants myself and it was only sampled once for this study. It is recorded to range through the Sierra Nevada foothills from Butte to Mariposa Co., Cal.

3. Wyethia reticulata Greene

Plants ca. 6 dm. high, glandular and somewhat hispid, becoming scabrous. "Enlarged basal leaves absent." The cauline leaves several, the largest 12-15 cm. long, ovate to deltoid and entire to serrulate, with truncate to cordate bases. Petioles well-developed. "Two of the lowermost lateral nerves usually more conspicuous than the rest, giving the leaf a triple-nerved appearance." Heads 1-4. Outer phyllaries unequal, lance-linear. Florets sparsely glandular, yellow. Achenes ca. 6 mm. long, glabrous, with a minute, awnless, coroniform pappus.

Plants are found only in the vicinity of Rescue/Cameron Park, El Dorado Co., Cal. and are considered endangered. Although this species has a very restricted range in the chaparral-covered low foothills of the Sierra Nevada, it seems to be abundant and aggressive in that area.

4. Wyethia elata H.M.Hall

Plants 5-10 dm. high, glandular and with a dense pubescence. "Enlarged basal leaves absent." Cauline leaves several, the largest ca. 15-20 cm. long, lance-ovate to deltoid,

entire to dentate, the bases truncate to cordate. Petioles well-developed. "The principal veins prominent beneath, two of the lower lateral ones usually conspicuous, giving the leaf a triple-nerved appearance." Heads 1-4. Outer phyllaries unequal, lanceolate. Disk florets glabrous, the rays glandular, yellow. Achenes 8-12 mm. long, mostly glabrous. Pappus coroniform wiith short awns at the achene angles.

Found in open pine woods of the Sierra Nevada foothills in Mariposa, Madera, Fresno and Tulare Cos., Cal. The range of this species may have shrunken during the last century, but where it is present, plants are abundant.

5. <u>Wyethia</u> <u>invenusta</u> (Greene) Weber

Plants 3-6 dm. high, pilose and glandular. "Enlarged basal leaves absent." Largest cauline leaves 15-20 cm. long, lance-ovate, entire, with mostly truncate bases. Petioles well-developed. "...the principal veins prominant beneath, two of the lowermost lateral ones often conspicuous, giving the leaves a triple-nerved appearance." Heads mostly soliitary,"...discoid, or with a few short ray flowers." Outer phyllaries unequal, foliaceous, lanceolate. Florets glabrous, yellow. Achenes 7-8 mm. long, glabrous,"...the apex developing knob-like projections on the angles. Pappus absent."

This species is said to be distributed through open woodlands of the s. Sierra Nevada, in Fresno, Tulare and Kern Cos., Cal. The species proved extremely difficult to locate, partly because much of the range was inaccessable due to fires

and the effects of landslides in the area during the time the
field work was done. My single collection consisted of plants
which do not completely fit Weber's description of the species,
but are even less similar to any others. This potential
inconsistancy will hopefully be cleared up in a future study,
but it seemed to present no serious problem here.

6. Wyethia scabra Hook.

Stems several, 1.5-4 dm. high, slender and whitish. Plants
hispid to harshly scabrous throughout. "Enlarged basal leaves
absent." Cauline leaves numerous, the largest 3-15 cm. long,
stiff, linear, entire and mainly sessile, narrowed at the bases,
the apices mucronate. "...the nerves very pale, the lateral ones
confluent toward the margin, giving the leaves a triple-nerved
appearance." Heads solitary, terminal. Outer phyllaries
numerous, linear, attenuate. Disk florets glabrous, the rays
pubescent, yellow. Achenes 6-8 mm. long, glabrous. Pappus short
and coroniform, awns lacking.

Plants have been collected in deserts from central and sw.
Wyo. to ne. and central Utah. Weber recognized two additional
varieties to the species. His description of these follow:

"Wyethia scabra is a polytypic species with three
morphologically recognizable, geographically discontinuous
races. Their morphological discontinuity is manifested by
differences in the shape and indument of the phyllaries. The
most striking departure from the historical type of the species
is found in the race (var. attenuata) inhabiting Kane Co., Utah

and adjacent Coconino Co., Ariz. In this race the phyllaries are extremely long, narrow and very loosely imbricate, with the stout hairs tending to be restricted to the margins. In the second race (var. canescens), occupying the adjacent corners of Ariz., N.M., Colo., and Utah, separated from the first by the canyons of the Colorado and Green rivers, a dense over-all pubescence of short, stiff hairs completely covers the phyllaries, which are very closely imbricate, the outer having conspicuously recurved tips. When this variety does not winter-kill, the upper portion of the stem sometimes branches, an unusual condition in the genus.

"The species in the original sense is found in Wyo. and Utah. The pubescence of the phyllaries is somewhat intermediate, but only a few specimens from s. cent. Utah, where this race approaches the distributional area of var. canescens, might be said to exhibit primary intergradation."

Only one collection of plants, fitting the description and distribution of var. attenuata, were included in this study. A several-day search for other representatives of the species was unsuccessful. It is possible that var. scabra and var. canescens were past flowering by the time my collecting had extended into their ranges. It was hoped that this lack of specimens would not have too detrimental an effect on this study's ability to respond to the main issues addressed here.

B. ALARCONIA

<u>Alarconia</u> DC., Prodr. 5:537.1836, as genus;

Nutt. in Trans. Am. Phil. Soc. II.7:353.1840, as section.

"Heads very large, solitary, the outer series of phyllaries greatly exceeding the disk. Basal and cauline leaves elliptic-ovate, very large. Achenes 10-15 mm. long, the largest in the genus. Pappus calyx-like, conspicuous, often prolonged into stout awns on the angles. Median vascular bundles of corolla-lobes well developed."

7. <u>Wyethia glabra</u> A.Gray

Plants 1.5-4 dm. high, glandular and glabrous to sparsly pilose. "Basal leaves very large, 3.5-4 dm. long...pinnately veined...", oblong to elliptic. Margins entire and often undulate, bases narrowed to short petioles. Cauline leaves similar, ca. 1.5 dm. long. Heads usually solitary and terminal, very large. Outer phyllaries very large, ovate, foliaceous. Florets slightly glandular, yellow. Achenes 10-12 mm. long, puberulent above. Pappus an uneven crown with short, broad awns.

I did not have the opportunity to collect this myself because of its early flowering time. Although only one collection was made for this study, plants have been found through the Coast ranges from Mendicino to San Luis Obispo Cos., Cal.

8. <u>Wyethia helenioides</u> (DC.) Nutt.

Plants 3-6 dm. high, densly tomentose, becoming glabrate

with age. "Basal leaves very large, about 3 dm. long...pinnately veined...", oblong to elliptic, mainly entire, bases abruptly narrowed to short petioles. Cauline leaves similar but smaller, 1-2 dm. long. Heads mostly solitary, terminal, very large. Outer phyllaries very large, unequal, lance-ovate, foliaceous. Disk florets with pubescent lobes; the rays glabrous, yellow. Achenes 12-15 mm. long, pubescent above. Pappus coroniform, uneven, with short, broad awns.

The range of this species overlaps that of the other member of the section in the Coast ranges from Mendocino to San Luis Obispo Cos., Cal. In addition, W. helenioides occurs in the w. foothills of the Sierra Nevada, from El Dorado to Mariposa Cos., Cal. It also blooms in the early spring and I have not collected it myself.

C. WYETHIA (EUWYETHIA).

"True Wyethia" A.Gray in Brewer, Watson and Gray, Bot. Calif. 1:349.1876, as section.

"Basal leaves present, much larger than the cauline leaves, lanceolate in general outline. Phyllaries graduate, subequal, erect and appressed, not or only slightly exceeding the disk. Median vascular bundles of corolla lobes usually lacking. Achenes 6-10 mm. long.

"From a geological standpoint Euwyethia is probably the most recent section of the genus. The species, for the most part, occupy extensive areas; they have a broad range of

habitats and are apparently aggressive."

9. <u>Wyethia</u> <u>mollis</u> A. Gray

Plants densly tomentose, becoming glabrate in age. "Basal leaves 2-4 dm. long...pinnately veined...", lanceolate to oblong, entire, bases narrowed to well developed petioles. Cauline leaves similar but smaller. Heads 1-3. Outer phyllaries few, herbaceous, lance-ovate. Disk florets with pubescent lobes, rays glabrous, yellow. Achenes 8-10 mm. long, pubescent above. Pappus coroniform with long awns.

The species range extends from the s. Cascades of Lake Co., Ore., through the Sierra Nevada to Fresno Co., Cal. and adjacent Nev.

10. <u>Wyethia</u> <u>helianthoides</u> Nutt.

Plants 3-5 dm. high, pilose. "Basal leaves large, but narrower than those of <u>W</u>. <u>amplexicaulis</u> ...abruptly or gradually narrowed to the petiole, the lateral nerves ascending...", 1-3 dm. long, lance-elliptic, usually entire. Cauline leaves smaller,"...sessile to amply petiolate...", entire. Heads solitary, terminal. Phyllaries numerous, thin, herbaceous, lance-linear, with spreading hairs. Disk florets glabrous, rays slightly pilose, white. Achenes 8-10 mm. long, pubescent. Pappus a shallow, laciniate crown, often with short, thin awns.

The species ranges from the Blue and Ochoco mts. of Ore., through s. Ida., ne. Nev., sw. Mont. and w. Wyo. in mountain

meadows and clearings.

11. Wyethia angustifolia (DC.) Nutt.

"Plant 1.5-6 dm. high, from almost scapose to tall and leafy, softly appressed-pubescent to hirsute and scabrous. Leaves very variable, the basal large, the cauline reduced upward,...long-petiolate to sessile, tapered at both ends or sometimes the bases of the upper ones almost cordate, entire or sometimes irregularly serrate- or undulate-margined...", 15-35 cm. long, lance-linear to lance-ovate. Heads mostly 1 (to 3). Phyllaries numerous and lanceolate, with ciliate margins. Disk florets with pubescent or glabrate lobes. Rays yellow with pubescent or glabrate tubes. Achenes ca. 8 mm. long, slightly pubescent. Pappus a shallow crown with thin awns.

The species ranges from sw. Wash. and Ore., w. of the Cascade-Sierra axis to Tulare and San Luis Obispo Cos., Cal., from sea level to ca.2,000 m..

These plants appear to express a great deal of within-species variation, as Weber noted. "Wyethia angustifolia displays a great range of variation between local populations, one extreme being an almost scapose, low-growing form, somewhat localized in the San Francisco Bay area, the other a tall, leafy form most well marked in collections from Ore.. However, the species does not appear to exhibit sufficient morphological or geographic discontinuity to warrant nomenclatural recognition of the various forms for which taxonomic status has been proposed."

12. Wyethia longicaulis A.Gray

Plants 3-6 dm. high with a sparse, fine pubescence. "Basal leaves oblong-lanceolate, 15-40 cm. long,...glossy, acute, entire or denticulate, sessile or tapering to a usually short petiole; lateral veins ascending." Cauline leaves similar but smaller, sessile. Heads 1-4. Outer phyllaries foliaceous, lanceolate. Disk and ray florets glabrous. Achenes ca. 7 mm. long with a short, lobed coroniform pappus.

Plants are said to be found on open slopes of the n. Coast ranges in e. Humboldt, adjacent Trinity and ne. Mendocino Cos., Cal. I was able to locate it only once in the Mendocino Nat. For.

13. Wyethia amplexicaulis (Nutt.) Nutt.

Plants glabrous and resin-varnished. "Basal leaves very large, oblong-lanceolate, 20-40 cm. long...entire, sometimes denticulate or...shallowly dentate, pinnately veined...gradually narrowed to the short petiole..." Cauline leaves similar but smaller and sessile, usually with clasping bases, entire or denticulate. "Heads large, several (occasionally solitary), the terminal head largest." Outer phyllaries subequal, foliaceous, lance-ovate. Florets yellow, glabrous. Achenes 8-10 mm. long, glabrous. Pappus coroniform, sometimes with thin awns.

Plants are common in open grasslands and woods at mid-altitudes in sw. Mont and through Ida., se. Wash., and e. Ore., w. to the Columbia Gorge, s. to se. Wyo, adjacent Colo, n. Utah

and ne. Nev.

Weber noted, "_Wyethia_ _amplexicaulis_ is the most widely distributed species in the genus, overlapping the distributional areas of _W_. _helianthoides_, _W_. _arizonica_ and _W_. _scabra_."

Wyethia _arizonica_ A.Gray

"Similar to _W_. _amplexicaulis_, But densly hirsute-pubescent, becoming scabrous, or sometimes glabrate, the leaves narrower and smaller, with slender petioles, only the uppermost cauline leaves sessile or somewhat clasping. Disk flowers pubescent on the lobes. Ray flowers yellow, dorsally hirsute." Plants are found on dry hills and mountain slopes, w. Colo. and adjacent Utah, Ariz. and N.M.

II. <u>BALSAMORHIZA</u>

The organisms included in <u>Balsamorhiza</u> Nutt. have proven difficult to group. Species and subspecies have been re-organized several times (Sharp, 1935; Weber, 1946; Ownbey and Weber, 1943; Cronquist, 1955). This reflects the confusion which seems to surround attempts to delimit species in this genus. The clarification of <u>Balsamorhiza</u> will hopefully be the subject of a future study. For the present, the species are used in a somewhat general sense, as described. Particular difficulties and the assumptions made with respect to them are noted throughout the following taxonomic descriptions, following Cronquist's (1955) treatment.

Heads solitary, or several in some, radiate, the rays pistillate and fertile, mostly yellow. Phyllaries mostly herbaceous, the outer sometimes foliaceous. Paleae firm, persistant. Disk florets numerous, mostly yellow, anther bases sagittate,style branches slender, the submarginal stigmatic lines hispidulous throughout, or toward apices only. Pappus usually lacking, disk achenes compressed-quadrangular. "...scapiform perennials with rosettes of large basal leaves, often with one or more much reduced, generally bractlike cauline leaves."

"About 12 species...all taprooted perennials. In the section <u>Artorhiza</u> the taproot is very large and deep-seated, and is surrmounted by a multicipital caudex bearing...several rosettes of leaves. In the section <u>Eubalsamorhiza</u> the taproot is

smaller and more carrotlike...the leaves of all the species are similar on juvenile plants, being elliptic and entire. By progressive stages the adult-type leaves are eventually produced."

Cronquist describes part of the difficulty in the assignment of particular identities to some members of Balsamorhiza in the following.

"The taxonomic difficulties of the genus arise largely from the weakness or absence of genetic barriers, so that any two species will hybridize where they grow together. In most cases these hybrids do not swamp the parents, occuring instead only in the immediate area of contact, with local introgression seldom detectable for more than a few hundred yards. Several of these hybrids have been mistaken in the herbarium for distinct species, and have been named as such. B. terebinthacea (Hook.) Nutt. was evidently based on a hybrid between B. deltoidea and B. hookeri ..." He goes on to list other named hybrids. Although several collections of hybrids were made during the field work, data from them were not used for any of the analyses and they are not mentioned further here.

A couple of species, such as B. rosea were omitted because attempts to locate them were unsuccessful. The only taxa described here are those that were included in the study.

A. ARTORHIZA

Plants with a large, woody root and a multicipital caudex.

Basal leaves deltoid to sagittate, entire to crenate. Cauline leaves much smaller than the basal, alternate, lance-linear, entire. Rays yellow.

1. Balsamorhiza sagittata (Pursh) Nutt.

Basal leaves cordate to triangular-hastate, up to 30 cm. long. Petioles well developed. Plants with a fine, woolly pubescence. Stems 2-8 dm. high. Cauline leaves few, small, alternate and linear. Heads usually solitary, terminal. Outer phyllaries few, lanate-tomentose. Achenes glabrous, epappose.

Common on open hillsides and flats up to high elevations, s. B.C. to s. Cal., w. of the Cascade-Sierra axis, e. to Mont., S.D. and Colo. This is the most widespread species in the genus. It is easily recognizable and often forms a major component of sagebrush and ponderosa pine vegetation.

2. Balsamorhiza careyana A.Gray

"...stem 2-10 decimeters tall, scapiform but usually with several strongly reduced narrow leaves..." Basal leaves up to 30 cm. long, with cordate to triangular-hastate bases, usually rather stiff and veiny, slightly hirsute, sometimes glandular, on long petioles. Heads usually several, rather small. Phyllaries slightly woolly, not much enlarged. Rays tend to persist on the achenes and become whitish as they dry. Achenes pubescent.

Grows in open, dry places e. of the Cascades from s. B.C.

to c. Ore. I have only one collection of reasonable certain
identity.

3. Balsamorhiza deltoidea Nutt.

"...stem 2-10 dm. tall, scapiform, but usually with
several, strongly reduced narrow leaves; central head large...
lateral heads when present obviously smaller..." Basal leaves up
to 30 cm. long with triangular-hastate to cordate bases, usually
crenate margined, slightly hirsute and glandular. Outer
phyllaries rather large and foliaceous, slightly woolly. Rays
"...soon deciduous, not becoming papery; achenes glabrous."
Plants range from s. Van. I., w. of the Cascades, to s. Cal.
Only one collection could be included here.

Cronquist also recognizes a taxon he calls B. careyana var.
intermedia, whose description sounds identical to that for
B. deltoidea, except that its ray florets persist and become
papery in age. He gives no justification for the apparently
overwhelming importance of this single character. The situation
seems confusing and in need of further study.

B. BALSAMORHIZA (EUBALSAMORHIZA) 12

most of the taxa in this section possess a small, carrot-
like taproot. All have well developed basal leaves with margins
ranging from serrate to pinnatifid to bipinnately compound.
Cauline leaves are usually limited to a single, opposite pair.
Heads solitary, terminal.

The confusion surrounding the taxonomic groupings of

entities reaches its zenith in this section. Although the section itself seems mostly natural, the species and subspecies have been shifted around several times and are greatly in need of further study.

4. <u>Balsamorhiza hookeri</u> Nutt.

Taproots small and crowns simple. Stems "...0.6-4 dm. tall, with one or more inconspicuous, linear, entire or toothed-pinnatifid bract near the base." Basal leaves 1-4 dm. long, pinnate to bipinnately compound, the divisions narrow. Heads solitary, terminal. Phyllaries linear to ovate, pubescent at least on margins. Achenes glabrous, epappose.

"Dry, rocky outcrops in the foothills and lowlands; distribution apparently discontinuous; dry plains of c. Wash., w. as far as Bingen; apparently totally absent from Ore.; w.c. Ida., e. to sw. Wyo. and nw. Colo., s. to Cal. and s. Utah...

"This species shows a most confusing pattern of intraspecific variability, only partly correlated with geography..." Cronquist recognizes at least 5 subspecies of <u>B. hookeri</u>. Plants resembling <u>B. hookeri</u> ssp. <u>lagocephala</u> (Sharp)Cronq. were used in this study.

5. <u>Balsamorhiza incana</u> Nutt.

Crowns simple, stems 1.5-7 dm. tall. Basal leaves 1-4.5 dm. long, pinnately divided, "...the divisions 1.5-6 cm. long, entire or with a few coarse teeth or segments, broader than in

B. hookeri and B. hirsuta, sometimes as much as 4 cm. wide; a pair of reduced, but still fairly well developed and pinnatifid cauline leaves commonly borne just above the base of the...stem..." Plants covered with a long, silky white tomentum. Heads solitary, terminal. Phyllaries woolly, "...with ovate or lanceolate base, sometimes merely pointed, sometimes with long, reflexed, subcaudate apex..." Achenes glabrous, epappose.

"Meadows and other moderately moist to moderately dry open places, in generally more mesic habitats than B. hookeri; moderate elevations in the mts. of ne. Ore. and se. Wash., e. through n. Ida. to n. and w.c. Wyo. and se. Mont." One collection (#8411, see Appendix A.) was made outside this range, but fits the species description in other respects and so was included here.

7. Balsamorhiza serrata Nels.& Macbr.

Stems 1-4 dm. tall,"...often with a pair of much reduced leaves near the base..." Plants with a simple crown. Basal "...leaves green, scabrous and strongly reticulate-veiny, petiolate, the blade 4-20 cm. long...varying from deltoid-ovate and merely sharply serrate, to evidently pinnatifid, often even on the same plant, but nearly all plants with some merely toothed leaves..." Heads solitary, terminal. Phyllaries glabrate to strongly pubescent, lance-linear. Achenes glabrous, epappose.

Plants occur infrequently on dry, rocky hillsides and outcrops in Ore. and s. Wash., e. of the Cascades.

7. Balsamorhiza macrophylla Nutt.

Plants are larger than other species in this section and resemble members of Artorhiza in the possession of large taproots and multi-branched crowns. Plants glandular with a long, sparse pubescence. Stems 3-10 dm. high with a single, well developed pair of cauline leaves, pinnatifid to pinnately compound. Basal leaves 3-6 dm. long, pinnately compound, the divisions entire to coarsly few-toothed. Heads solitary, terminal, large. Phyllaries rather long and foliaceous, lanceolate. Achenes glabrous, epappose.

Plants occur in open areas at rather high elevations from n. Utah, n. to se. Ida., through w. Wyo. and n. to Mont.

III. TAXONOMIC OUTGROUPS

Several other taxa were also used for outgroup comparison and these are described in the following section. All of these are considered closely enough related to Wyethia and Balsamorhiza to at least be included in the tribe Heliantheae. That is, they are mostly perennials or annuals with herbaceous phyllaries, tailless anther bases, and stigmatic lines which are marginal and run the length of the style branches. Paleae or pappus, when present, are composed of scales or awns.

Within the Heliantheae there has been some dispute over the limits of some of the subtribes and the inclusion of some genera in them (Stuessy, 1976; Robinson, 1981). The attempt was made to utilize outgroup genera whose closeness to the study taxa is generally agreed upon. These include Helianthella, Encelia, Heliopsis, Flourensia and Rudbeckia. Collections were also made for use in the analysis of within-species variation. Species were chosen for this based mostly on their sympatry with Wyethia and Balsamorhiza. In other words, if I came across them while in the field, I collected them. The genera represented include Helianthella, Helianthus and Rudbeckia .

A. HELIANTHELLA Torrey & Gray

The following descriptions are condensed from Weber's (1952) monograph of the genus. He recognized 8 species of herbaceous, taprooted perennials. "The leaves may be either cauline or basal. Basal rosettes of leaves are usually formed by buds which do not produce a flowering stem during the current season. Flowering stems rarely possess large basal leaves, although the lower pairs of cauline leaves are sometimes quite large. The leaves of the basal rosette are similar in shape, texture and indument to those of the stem.

"The lowermost cauline leaves are always opposite, while the uppermost leaves may be alternate or opposite. In some species, leaves are occasionally produced three at a node. The leaf margins are always entire. The leaf blades are simple and range in shape from linear to ovate-lanceolate. Venation is pinnate, but most leaves appear to be triple-nerved because of the accentuation of two of the lowermost lateral nerves.

"All species are more or less hirsute or strigose...the pubescence of the foliage and stem becomes more sparse as the organs elongate...individuals are scabrous or glabrate at maturity. In most species, the inflorescence is a single, terminal head. A few small axillary heads are sometimes present but these often abort... the phyllaries range in outline from ovate to obtuse...to lanceolate or lance-linear...In a few species the outermost phyllaries are greatly enlarged and leaf-like. Paleae...oblanceolate, acute, conduplicate and deciduous with the mature fruits or falling...after anthesis. Ray florets neuter, yellow. Disk florets perfect, yellow, purple or

brownish. Disk corollas lack median vascular traces. Anthers with ovate appendages and sagittate bases. Style branches slender, terete or flattened, minutely pubescent from base to apex. Achenes laterally compressed, often slightly wing-margined, cuneate-obovate to obcordate, pubescent to glabrous. Pappus of slender, persistant awns and a short lacreate crown, or lacking. N=15."

Of the 8 species recognized by Weber (1952), only 2 were actually collected for use in the study of within-species variation. These are described below. For the phylogenetic analysis employing Helianthella as a taxonomic outgroup, characters were taken from the generic description above. The species described below were used in the PCA-based analyses.

1. Helianthella uniflora (Nutt.) Torrey & Gray

Stems 4-12 dm. high, often somewhat hirsute, becoming scabrous, simple or few-branched. Leaves mostly lance-elliptic. "...enlarged basal leaves absent, the cauline leaves in 3-6 opposite pairs, the middle pairs largest, 3-nerved from below the middle... short-petioled or sessile, the blades 12-25 cm. long, the upper sessile. Heads solitary and terminal,...a few supressed lateral heads often present..." Phyllaries subequal, lanceolate-attenuate,"...the outermost frequently elongated and leaf-like..." Florets yellow. Achenes"...6-7 mm. long, narrowly obovate, ciliate above, appressed-pubescent on the lateral faces; pappus of two slender awns...intermediate squamellae short or obsolete."

Plants are found through the Rocky Mts., intermountain plateaus and ranges of the Great Basin from s. Ida., se. Ore. and sw. Mont., s. to n. Nev., s. Utah and nw. Colo.,"...in a wide variety of habitats..."

Individuals used in this study fit the description of var. douglasii (T.& G.) Weber.

2. Helianthella californica A.Gray

Plants 1.5-6 dm. high, hirsutulous, becoming scaberulous. "...leaves oblong-lanceolate, 5-26 cm. long, tapering to elongate petioles, the lowermost cauline leaves opposite; heads usually solitary on long peduncles;...phyllaries lanceolate, densly pubescent to ciliate or glabrate..." Achenes compressed, 6-10 mm., glabrous, epappose.

The representative used here was var. nevadensis (Greene) Jepson, which apparently differs from the species in its achenes, "...which always bear two short, persistant awns and usually several low intermediate squamellae."

The variety ranges from s. Ore., to Kern Co., Cal., through the Sierra Nevada, e. to Washoe Co., Nev and w. of the Central Valley to Lake Co., Cal. It is replaced by the species on the w. side of the Valley.

B. HELIANTHUS L.

Mostly perennial, sometimes annual herbs, including ca. 60 species (Hitchcock, et al., 1955). The cauline leaves simple, at least the lowermost ones opposite. Ray florets yellow, neutral. Disk florets perfect and fertile, the anthers with entire or slightly sagittate bases, the style branches flattened, hispidulous, as are their appendages. Phyllaries subequal, mostly herbaceous. Paleae persistant. Achenes thick, but somewhat compressed, usually glabrous. Pappus mostly of two deciduous awns. Only one species was included in assessment of within-species variation. It is described below.

1. Helianthus cusickii A.Gray

Perennial plants 2-12 dm. tall, the stems arising from the crown of a thickened taproot, often freely branching, hirsute to scabrous. Leaves lanceolate to somewhat linear, entire, 3-12 cm. long, apparently triple-nerved, subsessile and opposite, at least below. Phyllaries lance-linear, usually with spreading hairs.

Plants in dry plains and foothills of e. Ore., sw. Ida. and ne. Cal., n. between the Columbia R. and the Cascades to Ellensburg, Wash.

C. RUDBECKIA L.

Plants mostly perennial, some annual. Cauline leaves

alternate, entire to pinnatifid. Heads radiate or discoid, the rays neutral, the disk florets perfect and fertile. Anthers with sagittate or obtuse bases, style branches flattened and with hirsute appendages. Phyllaries subequal or unequal, mostly herbaceous. Receptacle conic or columnar. Achenes quadrangular or somewhat flattened, glabrous. Pappus a short, toothed crown, or lacking.

This North American genus contains about 24 species and was used here for outgroup comparison. Morphological characters were taken from Hitchcock, et al. (1955). The following species was also used in the exploratory data analysis part of this study.

1. Rudbeckia occidentalis Nutt.

Plants perennial, 5-20 dm. tall, glabrate or with short pubescence. Cauline leaves alternate, up to 25 cm. long, broadly ovate to elliptic with subcordate bases, entire to serrate, petioles short. Heads discoid. Pappus a short crown.

Plants in woodlands from sw. Mont. and nw. Wyo. to Wash, Utah and Cal.

D. HELIOPSIS Pers.

Herbaceous perennials, rarely annuals with opposite, petiolate cauline leaves. The ray florets yellow, pistillate and fertile, their corollas persisting on the achenes and becoming

papery. Disk florets perfect and fertile, the anthers mostly with entire bases, the style branches flattened and with short, hirsute appendages. Phyllaries subequal, at least the apex herbaceous. Receptacle conic. Achenes usually quadrangular. Pappus a short, few-toothed crown, or lacking.

This genus contains about 6 species native to the New World. It was used here for outgroup comparison only, based on descriptions in Hitchcock, et al. (1955).

E. ENCELIA Adans.

Low, branching shrubs with alternate, mostly entire leaves. Heads solitary or in panicles, radiate or discoid. Ray florets neutral. Disk florets fertile. Phyllaries 2 to 3-seriate. Receptacle convex. Paleae scaricus and deciduous with the achenes. Achenes flat, obovate, pubescent. Pappus of two slender awns, or none.

The genus includes about 14 species native from the sw. U.S., s. to Peru, Chile and the Galapagos Ids..

Morphological information was taken from Munz and Keck (1968) for use in outgroup comparison.

F. FLOURENSIA DC.

Resinous shrubs with alternate, lanceolate to oval, reticulately-veined leaves. Heads solitary or in panicles, radiate or discoid. Ray florets neutral. Disk florets perfect and fertile. Phyllaries 2 to 4-seriate, subequal, lanceolate to ovate, herbaceous. Paleae scarious and deciduous with the achenes. Anthers with ovate appendages and cordate-sagittate bases. Style branches with short, hispidulous appendages. Achenes thickened or somewhat compressed, silky-villous at least on margins. Pappus mostly of two persistant awns, rarely deciduous or lacking.

Blake (1921) recognized 23 species, 14 of which are native to w. S. America and 9 to Mexico. Only one of the species, F. cernua enters the sw. U.S. The genus was used for taxonomic outgroup comparison.

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APPENDIX A - PLANT COLLECTIONS

1. Wyethia

Wyethia amplexicaulis (Nutt.) Nutt.
   Hwy. 10 between Cle Elum and Teanaway, by Camp Illahee
   turnoff. Kittitas Co., Wash. Weedy roadside with grasses,
   Pinus ponderosa, Symphoricarpos, Lomatium, Balsamorhiza
   sagittata.
   8401, Nicholls and Robson, June 6, 1984.

Wyethia amplexicaulis (Nutt.) Nutt.
   I-84, 12 mi. SE of Pendleton, below viewpoint for S-bound
   lanes. Umatilla Co., Ore. Mesic hillside with grasses,
   Lupinus sulphureus, Rosa, Castilleja, Balsamorhiza
   sagittata.
   8405, Nicholls and Robson, June 6, 1984.

Wyethia amplexicaulis (Nutt.) Nutt.
   Hwy 89, ca. 2 mi. W of Garden City, Rich Co., Utah. Clay
   depression in damp meadow with grasses, Melilotus,
   Geranium, Artemisia.
   8433, Robson, July 20, 1984.

Wyethia amplexicaulis (Nutt.) Nutt.
   Road to Tony Grove Lake, 25 mi. E of Logan, Cache Nat.
   For., Cache Co., Utah. Meadow on dolomite soil with nearby
   Picea engelmannii, Abies lasiocarpa.
   8434c, Barkworth and Robson, July 21, 1984.

Wyethia amplexicaulis (Nutt.) Nutt.
   Hwy. 75, ca. 10 mi. N of Sun Valley/Ketchum, Sawtooth Nat.
   For., Blaine Co., Ida. On moist, sandy soil with Artemisia,
   Eriogonum and nearby Populus tremuloides, Pinus contorta.
   8436, Robson, July 23, 1984.

Wyethia amplexicaulis (Nutt.) Nutt.
U.S.F.S. Rd. 40, ca. 35 mi. S of Pomeroy, Umatilla Nat.
For., Garfield Co., Wash. In open areas between stands of
Pinus ponderosa with grasses, Helianthella uniflora.
8508, Robson, June 18, 1985.

Wyethia amplexicaulis (Nutt.) Nutt.
Ca. 3 mi. along trail to Jardine Juniper, 12 mi. E of
Logan, Cache Nat. For., Cache Co., Utah. Open montane
meadow on dolomite soil with grasses, Artemisia,
Balsamorhiza macrophylla, Helianthella uniflora.
8511a, Barkworth and Robson, June 23, 1985.

Wyethia amplexicaulis (Nutt.) Nutt.
Hwy. 47, within a 1 mi. radius of Lower Mesa Falls, Targhee
Nat. For., Fremont Co., Ida. Clearings among Populus
tremuloides, Pinus contorta with grasses, Wyethia
helianthoides and hybrids.
8513, Robson, June 24, 1985.

Wyethia angustifolia (DC.) Nutt.
Along Sonoma Mt. Rd. N of Penngrove, Marin Co., Cal.
Roadside with dry grasses, Quercus.
8414, Nicholls and Robson, June 13, 1984.

Wyethia angustifolia (DC.) Nutt.
Corner of Eel River and Van Arsdale Rds., between Lake
Pillsbury and Potter Valley, Mendocino Co., Cal. Gravelly
bank by running ditch with grasses, Toxicodendron, Pinus
ponderosa, Ceanothus, Arctostaphylos, Lotus, Melilotus,
Trifolium.
8416, Robson, June 21, 1984.

Wyethia angustifolia (DC.) Nutt.
Hwy. 36, ca. 13 mi. E of Bridgeville, Humboldt Co., Cal.
Moist rocky slope with grasses, Plantago.
8417, Robson, June 21, 1984.

Wyethia angustifolia (DC.) Nutt.
    Hwy. 4, 0.7 mi. W of Arnold, Calaveras Co., Cal. In weedy
roadside ditch, plants with insect damage.
8421, Robson, June 24, 1984.

Wyethia angustifolia (DC.) Nutt.
    On Hwy. 49, 16.4 mi. N of Jackson, Amador Co., Cal.
B1-5, Maze, May, 1985.

Wyethia angustifolia (DC.) Nutt.
    Sutter Creek, Amador Co., Cal.
C1-5, Maze, May, 1985.

Wyethia angustifolia (DC.) Nutt.
    Pacific Angwin College, Napa Co., Cal.
D1-5, Maze, May, 1985.

Wyethia angustifolia (DC.) Nutt.
    Jasper Ridge Biological Preserve, Santa Clara Co., Cal. For
chemistry only.
1772, Bohm, May, 1984.

Wyethia angustifolia (DC.) Nutt.
    Napa-Bothe State Park, Napa Co., Cal. It is illegal to take
plants from a state park and it is not necessary. Such an
act is indicative of a lazy and arrogant character. This
collector did it twice. For chemistry only.
1774, 1775, Bohm, May, 1984.

Wyethia arizonica A.Gray
    Hwy. A89, 12.4 mi. S of Flagstaff, Coconino Co., Ariz. In
gravelly, damp depression by road with grasses, Pinus
ponderosa, Quercus, Melilotus.
8430, Robson, July 16, 1984.

Wyethia arizonica A.Gray
    Ca. 16 mi. along road to Warner Lake from jct. with Hwy.
    191 S of Moab, Manti-La Sal Nat. For., Grand Co., Utah. In
    damp, rocky clay with grasses, Quercus, Artemisia, Lupinus,
    Sedum.
    8432, Robson, July 18, 1984.

Wyethia bolanderi (A.Gray) Weber
    Ca. 2 mi. W of Dobbins, Yuba Co., Cal. Most rays lost.
    1786, Bohm, May 1, 1984.

Wyethia elata H.M.Hall
    Hwy. 49, 4 mi. N of Ahwahnee, Mariposa Co., Cal. Dry
    roadside clay with grasses, Pinus ponderosa, Quercus
    kelloggii, Arctostaphylos, Lupinus, Clarkia, Madia.
    8422, Robson, June 25, 1984.

Wyethia elata H.M.Hall
    Rd. 222, 1.5 mi. S of North Fork, Madera Co., Cal. Gravelly
    roadside clay with grasses, Toxicodendron, Ceanothus, near
    Pinus sabiniana, Quercus douglasii, Arctostaphylos.
    8426, Robson, July 10, 1984.

Wyethia glabra A.Gray
    Solano Co., Cal.
    3223, Warnock and McCormick, March 16, 1984.

Wyethia helenioides (DC.) Nutt.
    Ca. 21 mi. S of Hollister on Panoche Rd., San Benito Co.,
    Cal. Along roadside in oak woodland.
    A1-5, Maze, May, 1985.

Wyethia helenioides (DC.) Nutt.
    Mi. 74, Hyw. 101, Mendocino Co., Cal.
    1786, Bohm, April 26, 1984.

Wyethia helianthoides Nutt.
    1.1 mi. along rd. to Red Rock Lakes Bird Sanctuary from
    jct. Hwy. 20, Fremont Co., Ida. Open meadow with grasses,
    this population almost out of bloom.
    8514, Robson, June 25, 1985.

Wyethia helianthoides Nutt.
    Near shores of Alturas Lake, off Hwy. 75 between Galena
    Summit and Obsidian, Sawtooth Nat. For., Blaine Co., Ida.
    Open areas among Pinus contorta, with grasses,
    W. amplexicaulis and hybrids Artemisia, Arnica, Potentilla.
    8515, Robson, June 26, 1985.

Wyethia helianthoides Nutt.
    Along rd. to Bull Trout Lake, ca. 35 mi. NE of Lowman, Hwy.
    21 Boise Nat. For., Boise Co., Ida. In damp, rocky
    clearings among Pinus contorta with few grasses,
    Ranunculus, Senecio.
    8516, Robson, June 26, 1985.

Wyethia invenusta (Greene) Weber
    Hwy. 155 (=Evans Rd.) at jct. of Alta Sierra Rd., Sequoia
    Nat. For., Kern Co., Cal. Very small pop. in sandy soil
    with grasses, Pinus ponderosa, Calocedrus decurrens,
    Quercus kelloggii, Asclepias.
    8427, Robson, July 11, 1984.

Wyethia longicaulis A.Gray
    U.S.F.S. Rd. 1N02, 8 mi. S of Lake Pillsbury, Mendocino
    Nat. For., Lake Co., Cal. Dry, gravelly soil with grasses,
    near Pinus ponderosa, Pseudotsuga menziesii, Arbutus
    menziesii, Arctostaphylos.
    8415, Robson, June 20, 1984.

Wyethia mollis A.Gray
    Hwy. 395, 2 mi. S of Ore. border, Goose Lake Valley, Modoc
    Co., Cal. Roadside, grassy rangeland.
    8410, Nicholls and Robson, June 7, 1984.

Wyethia mollis A.Gray
    Hwy. 89, ca. 5 mi. NW of Greenville, near W shore of Lake
Almanor, Plumas co., Cal. In rocky, thin clay with grasses,
Pinus ponderosa, Calocedrus decurrens, Arctostaphylos,
Lupinus, Helianthella californica, Balsamorhiza deltoidea.
8418b, Robson, June 22, 1984.

Wyethia mollis A.Gray
    USFS Rd. 07 (=Henness Pass Rd.), ca. 6 mi. E of jct. Hwy
89, 9 mi. S of Sierraville, Tahoe Nat. For., Sierra Co.,
Cal. In damp, rocky, granitic soil with grasses, Pinus
ponderosa, Abies concolor, Ribes.
8419, Robson, June 23, 1984.

Wyethia mollis A.Gray
    Hwy. 431 at jct. of Gale St., near N Lake Tahoe, Washoe
Co., Nev. In dry rocky, granitic soil with grasses, Pinus
ponderosa, Calocedrus decurrens, Arctostaphylos, Lonicera,
Purshia, Balsamorhiza sagittata.
8425b, Robson, June 28, 1984.

Wyethia ovata Torrey and Gray
    Hwy. 74, ca. 5 mi. S of Mtn. Center, near Lake Hemet, San
Bernardino Nat. For., Riverside Co., Cal. Very sandy
granitic soil with grasses, Pinus ponderosa, Artemisia,
Arctostaphylos, Ceanothus.
8429, Robson, July 15, 1984.

Wyethia reticulata Greene
    Jct. of La Canada and Cameron Park Dr., Cameron Park, El
Dorado Co., Cal. In Rescue stony, sandy loam with grasses,
Ceanothus, Salvia.
8423, Ayres and Robson, June 27, 1984.

Wyethia reticulata Greene
    Deer Valley Rd., .2 mi. W of Green Valley, Rescue, El
Dorado Co., Cal. In Argonaut clay loam with grasses,
Toxicodendron, Adenostema fasciculata, Quercus.
8424, Ayres and Robson, June 27, 1984.

Wyethia scabra var. attenuata Weber
    10 mi. N of Kanab on Hwy.89, Kane Co., Utah. On red sand
    dunes with Artemisia, Purshia, Yucca, Eriogonum, Juniperus,
    Quercus, grasses.
    8431, Robson, July 17, 1984.

2. Balsamorhiza

Balsamorhiza careyana A. Gray
    Jct. of Hwy. 395 and Hwy. 74 at Nye, Umatilla Co., Ore. In
    rocky, exposed lava with various grasses.
    8407, Nicholls and Robson, June 7, 1984.

Balsamorhiza deltoidea Nutt.
    On Hwy. 89 near W shore of Lake Almanor, ca. 5 mi. NW of
    Greenville, Plumas Co., Cal. Clearing in rocky, thin,
    drying clay with Pinus ponderosa, Calocedrus decurrens,
    Arctostaphylos, Rosa, Ceanothus, Lupinus, Helianthella
    californica, Wyethia mollis.
    8418c, Robson, June 22, 1984.

Balsamorhiza hookeri var. lagocephala (Sharp) Cronq.
    14 mi. W of Vantage, Grant Co., Wash.
    8504, McIntosh and Hawkes, May 17, 1985.

Balsamorhiza hookeri var. lagocephala (Sharp) Cronq.
    Colockum Pass, S of Malaga, Kittitas Co., Wash. In dry,
    rocky, basaltic soil with Artemisia tridentata, Agropyron
    spicatum, Lithophragma parviflora, Eriogonum.
    8501, Maze, Scagel and Robson, May 1, 1985.

Balsamorhiza incana Nutt.
    Old Cabbage Hill Rd., 1 mi. N of jct. I-84, 14 mi. SE of
    Pendleton, Umatilla Co., Ore. Drying, rocky hillside with
    grasses.
    8406, Nicholls and Robson, June 7, 1984.

<u>Balsamorhiza incana</u> Nutt.
>Ukiah city limit, Umatilla Co., Ore. Along roadside at
>margin of moist pasture with various grasses.
><u>8409</u>, Nicholls and Robson, June 7, 1984.

<u>Balsamorhiza incana</u> Nutt.
>Along Hwy. 395, Goose Lake Valley, N of Alturas, ca. 41 mi.
>S of Ore. border, Modoc Co., Cal. Grassy roadside.
><u>8411</u>, Nicholls and Robson, June 7, 1984.

<u>Balsamorhiza incana</u> Nutt.
>On Hwy. 126, 14.7 mi. S of Asotin, Asotin Co., Wash. On
>roadside with grasses, <u>Medicago sativa</u>.
><u>8509</u>, Robson, June 19,1985.

<u>Balsamorhiza macrophylla</u> Nutt.
>Along road to Tony Grove Lake, Cache Nat. For., ca. 25 mi.
>E of Logan, Cache Co., Utah. 2 collections made, separated
>by ca. 1000 ft. elev. In grassy clearings of dolomite soil
>among <u>Picea engelmannii</u>, <u>Abies lasiocarpa</u>.
><u>8434a</u>,<u>b</u>, Barkworth and Robson, July 21, 1984.

<u>Balsamorhiza macrophylla</u> Nutt.
>Trail to Jardine Juniper, ca. 12 mi. E of Logan, Cache Co.,
>Utah. In open montane meadow of dolomite soil with
><u>Artemisia</u>, <u>Wyethia amplexicaulis</u>, <u>Helianthella uniflora</u>.
><u>8511b</u>, Barkworth and Robson, June 23, 1985.

<u>Balsamorhiza sagittata</u> (Pursh) Nutt.
>Entrance to Blue Lake Camp, Modoc Nat. For., Modoc Co.,
>Cal. On rocky hillside with <u>Artemisia</u>, <u>Pinus ponderosa</u>,
><u>Wyethia mollis</u>, grasses.
><u>8412</u>, Nicholls and Robson, June 7, 1984.

<u>Balsamorhiza sagittata</u> (Pursh) Nutt.
>Hwy. 431 at jct. of Gale St., near N Lake Tahoe, Washoe
>Co., Nev. In dry, rocky, granitic soil with grasses, <u>Pinus
>ponderosa</u>, <u>Calocedrus decurrens</u>, <u>Arctostaphylos</u>, <u>Lonicera</u>,
><u>Purshia</u>, <u>Wyethia mollis</u>.
><u>8425a</u>, Robson, June 28, 1984.

Balsamorhiza sagittata (Pursh) Nutt.
 0.7 mi. S of Galena Summit on Hwy. 75, Sawtooth Nat. For.,
 Blaine Co., Ida. On damp, rocky hillside with Artemisia,
 Gilia, Potentilla, grasses.
 8437, Robson, July 24, 1984.

Balsamorhiza sagittata (Pursh) Nutt.
 23 mi. S of N border of Umatilla Nat. For., on U.S.F.S. Rd.
 40, between Pomeroy and Troy, Garfield Co., Wash. On rocky
 clearings with Lupinus, Helianthella uniflora, grasses.
 8507a, Robson, June 18, 1985.

Balsamorhiza serrata Nels. & Macbr.
 On Hwy. 395 S of Nye, Umatilla Co., Ore. Mesic, rocky
 roadside with Lupinus, Phlox, Astragalus.
 8408, Nicholls and Robson, June 7, 1984.

   3. Outgroups

Helianthella californica var. nevadensis (Greene) Jepson
 Hwy. 89 ca. 5 mi. NW of Greenville, near W shore of Lake
 Almanor, Plumas Co., Cal. In rocky, thin clay with grasses,
 Pinus ponderosa, Calocedrus decurrens, Arctostaphylos,
 Lupinus, Balsamorhiza deltoidea, Wyethia mollis.
 8418a, Robson, June 22, 1984.

Helianthella californica var. nevadensis (Greene) Jepson
 3 mi. E of Alleghany on Co. Rd. S309, 7.8 mi. E of jct.
 with Co. Rd. S180, Sierra Co., Cal. In sandy, dry, granitic
 soil with grasses, Pinus ponderosa, Abies concolor,
 Arctostaphylos, Mimulus.
 8420, Robson, June 23, 1984.

Helianthella uniflora var. douglasii (T. & G.) Weber
 23 mi. S of N border of Umatilla Nat. For., on U.S.F.S. Rd.
 40 between Pomeroy and Troy, Garfield Co., Wash. In rocky
 clearings with grasses, Lupinus, Balsamorhiza sagittata.
 8507b, Robson, June 18, 1985.

<u>Helianthella</u> <u>uniflora</u> var. <u>douglasii</u> (T. & G.) Weber
    Trail to Jardine Juniper, ca. 12 mi. E of Logan, Cache Nat.
    For., Cache Co., Utah. In open montane meadows of dolomite
    soil with <u>Artemisia</u>, <u>Wyethia</u> <u>amplexicaulis</u>, <u>Balsamorhiza</u>
    <u>macrophylla</u>.
    <u>8511c</u>, Barkworth and Robson, June 23, 1985.

<u>Helianthus</u> <u>cusickii</u> A. Gray
    Mi. 13 on Hwy. 240 through Hanford Nuke Reserve, Benton
    Co., Wash. Weedy roadside with grasses, <u>Salsola</u>, <u>Brassica</u>.
    <u>8404</u>, Nicholls and Robson, June 7, 1984.

<u>Rudbeckia</u> <u>occidentalis</u> Nutt.
    At E. J. Harney Viewpoint on Hwy. 204, ca. 2 mi. W of
    Tollgate, Umatilla Co., Ore. In rocky, disturbed area with
    grasses, <u>Potentilla</u>, <u>Penstemon</u>.
    <u>8517</u>, Robson, June 27, 1985.

Table I. List of species and numbers of individuals from which measurements were taken.

SPECIES	CASES
Wyethia amplexicaulis	38
Wyethia angustifolia	35
Wyethia arizonica	10
Wyethia helianthoides	21
Wyethia longicaulis	5
Wyethia mollis	20
Wyethia elata	10
Wyethia reticulata	10
Wyethia bolanderi	15
Wyethia invenusta	5
Wyethia ovata	5
Wyethia scabra	5
Wyethia helenioides	10
Wyethia glabra	10
Balsamorhiza macrophylla	19
Balsamorhiza serrata	5
Balsamorhiza incana	20
Balsamorhiza hookeri	11
Balsamorhiza deltoidea	5
Balsamorhiza careyana	5
Balsamorhiza sagittata	19
Helianthella californica	10
Helianthella uniflora	23
Rudbeckia occidentalis	7
Helianthus cusickii	6

Table II. Characters used with taxonomic outgroups and ingroup species.

Character	W. amplexicaulis	W. angustifolia	W. arizonica	W. helianthoides	W. longicaulis	W. mollis	W. elata	W. reticulata	W. bolanderi	W. invenusta	W. ovata	W. scabra	W. helenioides	W. glabra	B. sagittata	B. deltoidea	B. careyana	B. incana	B. hookeri	B. macrophylla	B. serrata	Helianthella	Flourensia	Rudbeckia	Heliopsis	Encelia
# heads/shoot 0 - 1 - 2 1 - many	2	1	2	0	1	1	1	1	0	1	2	0	1	1	1	1	2	0	0	0	0	1	2	1	1	1
leaf margin 0 - 1 - 2 entire-divided	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	2	2	2	1	0	0	1	1	0
cauline leaves 0 - 1 - 2 alt. - opp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	2	2	1	1	0	0	2	0
basal leaves 0 - 1 abs. pres.	2	2	2	2	2	2	0	0	1	2	2	0	2	2	2	2	2	2	2	2	2	1	0	0	0	0
leaf shape 0 - 1 - 2 lin. - ovate	1	1	1	1	1	2	2	2	2	2	2	0	1	1	0	0	0	1	0	1	1	1	1	2	2	2
petioles 0 - 1 - 2 long - abs.	2	1	0	0	1	0	0	0	0	0	0	2	0	0	1	0	0	2	0	0	1	1	1	1	1	1
caul. venation 0 - 1 3-nerv. - retic.	1	1	1	1	1	1	0	0	1	1	1	0	1	1	0	0	0	1	1	1	1	0	1	0	1	1
ray flrts. 0 - 1 neut. - pist.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	0
achenes 0 - 1 quad. - flat.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1

Table III. Characters used with Balsamorhiza section Artorhiza
as functional outgroup.

Characters (states):

- basal lvs. (0 – 1 : pres. – abs.)
- pappus (0 – 1 : abs. – pres.)
- cauline arr. (0 – 1 – 2 : alt. – opp.)
- caul. venation (0 – 1 : 3-nrv. – retic.)
- # heads/shoot (0 – 1 – 2 : 1 – few – sev.)
- lf. marg. (0 – 1 : ent. – div.)
- caul. shape (0 – 1 – 2 – 3 : lin. – lan. – ov. – delt.)
- caul. lvs. (0 – 1 : sm/few – lg/many)
- phyllaries (0 – 1 : many – few)
- achene pubesc. (0 – 1 – 2 : glab. – pubesc.)
- petioles (0 – 1 : none – long)
- flavanones (0 – 1 : abs. – pres.)
- prenyls (0 – 1 : abs. – pres.)

Taxon	basal lvs.	pappus	cauline arr.	caul. venation	# heads/shoot	lf. marg.	caul. shape	caul. lvs.	phyllaries	achene pubesc.	petioles	flavanones	prenyls
Artorhiza	0	0	0	0	1	0	0	0	0	0	0	0	0
W. amplexicaulis	0	1	0	1	2	0	1	1	1	0	0	1	1
W. angustifolia	0	1	0	1	1	0	2	1	1	0	1	1	1
W. arizonica	0	1	0	1	2	0	3	1	1	0	1	0	0
W. helianthoides	0	1	0	1	0	0	2	1	1	0	1	1	0
W. longicaulis	0	1	0	1	1	0	2	1	1	1	1	1	1
W. mollis	1	1	0	1	1	0	2	1	1	0	1	0	1
W. elata	0	0	0	0	1	0	2	1	1	1	1	0	0
W. reticulata	0	0	0	0	1	0	0	1	1	1	1	0	1
W. bolanderi	0	1	0	1	0	0	2	1	1	1	1	1	1
W. invenusta	1	1	1	1	1	0	2	1	1	1	1	0	0
W. ovata	0	1	0	1	2	1	2	1	1	0	1	1	0
W. scabra	0	1	0	1	0	0	1	1	1	0	1	1	0
W. helenioides	0	0	2	1	0	0	0	1	1	0	0	0	1
W. glabra	0	0	1	1	0	0	1	1	1	0	1	1	1
B. incana	0	0	2	1	0	0	1	1	1	0	1	1	0
B. hookeri	0	0	2	1	0	1	0	1	0	0	1	0	0
B. macrophylla	0	0	0	1	0	1	0	0	1	0	1	0	0
B. serrata	0	0	0	1	1	1	1	1	1	0	1	0	0

Table IV. Characters used with the species pair <u>Wyethia</u> <u>reticulata</u>/<u>W.elata</u> as functional outgroup.

Character	W. reticulata/elata	W. amplexicaulis	W. angustifolia	W. arizonica	W. helianthoides	W. longicaulis	W. mollis	W. bolanderi	W. invenusta	W. ovata	W. scabra	W. helenioides	W. glabra	B. incana	B. hookeri	B. macrophylla	B. serrata	B. sagittata	B. deltoidea	B. careyana
basal lvs. 0 - 1 abs. - pres.	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
pappus 0 - 1 pres. - abs.	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	1	1	1	1
cauline arr. 0 - 1 - 2 alt. - opp.	0	0	0	0	0	0	0	0	0	0	1	0	0	2	1	2	2	0	0	0
caul. venation 0 - 1 3-nrv. - retic.	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	0
# heads/shoot 0 - 1 - 2 1 - few - sev.	1	2	1	2	0	1	1	0	1	2	0	0	0	0	0	0	0	1	1	2
lf. marg. 0 - 1 ent. - div.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0
caul.shape 0 - 1 - 2 - 3 delt.-ov.-lan.-lin.	0	2	2	2	2	2	1	1	1	1	3	2	2	2	3	2	2	3	3	3
caul. lvs. 0 - 1 lg/many - few/sm.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
phyllaries 0 - 1 many - few	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	1	1	1
achene pubesc. 0 - 1 - 2 glab. - pubesc.	0	1	1	0	2	0	2	0	0	0	0	1	1	0	0	0	0	0	0	2
petioles 0 - 1 long - none	0	1	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	1
flavanones 0 - 1 abs. - pres.	0	1	1	1	0	1	1	0	1	0	1	1	1	0	0	0	0	0	0	0
prenyls 0 - 1 abs. - pres.	0	1	1	0	0	1	1	0	1	0	1	1	1	0	0	0	0	0	0	0

Table V. List of flavonoids from species so far surveyed.

Wyethia angustifolia - isoflavones, flavanones, prenylated
flavanones, prenylated isoflavones, prenylated
dihydroflavonol, dihydrooxepin ring

Wyethia scabra - isoflavones, flavanones, prenylated
flavanones, methylated flavonols

Wyethia reticulata - isoflavones, methylated flavonols

Wyethia elata - dihydroflavonols, methylated flavones,
methylated flavonols

Wyethia bolanderi - methylated flavonols

Wyethia ovata - isoflavones, methylated flavonols

Wyethia invenusta - isoflavones, flavanones, prenylated
flavanones, methylated flavonols

Wyethia glabra - isoflavones, flavanones, prenylated
flavanones, chalcone

Wyethia helenioides - isoflavones, flavanones, prenylated
flavanones, methylated flavonols

Balsamorhiza sagittata - methylated flavonols

Balsamorhiza deltoidea - methylated flavonols

Balsamorhiza careyana - methylated flavonols

Balsamorhiza macrophylla - methylated flavonols

Table VI. Results of PCA for three sets of morphological variables.

Axis	1	2
	HEAD DATA	
Eigenvalue	5.451	1.905
HDWD	-.30188	.34683
RAY	.01780	.60984
PHLN1	-.38009	.15667
PHLN2	-.37914	.14409
PHLN3	-.37859	.15806
RECPHLN3	.38795	.14598
RECPHWD2	.38836	.15479
RECPHWD3	.38830	.14129
PH#	.15776	.61014
	SHOOT DATA	
Eigenvalue	1.5974	1.0689
OPP	-.23763	.84803
ALT	.58857	-.25366
STHT	.54393	.39200
	LEAF DATA	
Eigenvalue	3.2833	1.6229
MDLN1	.42969	.34533
MDLN2	.45898	.25998
MDWD1	.47538	.09426
MDWD2	.48051	.04774
MDPT1	.31098	-.58706
MDPT2	.22608	-.67628

Table VII. Sources of variation by strata.

A=GENUS   B=SECTION

C=SPECIES   D=POPULATION

E=RESIDUAL

HEAD VARIABLES

PCA 1 = 60.57%   PCA 2 = 21.17%

A = 7.739   A = 1.892

B = 13.685   B = 2.354

C = 25.142   C = 6.761

D = 5.710   D = 4.712

E = 8.295   E = 5.514

SHOOT VARIABLES

PCA 1 = 39.94%   PCA 2 = 26.72%

A = 16.094   A = 8.466

B = 3.966   B = 1.284

C = 4.355   C = 5.729

D = 5.853   D = 2.813

E = 9.672   E = 8.428

LEAF VARIABLES

PCA 1 = 54.72%   PCA 2 = 27.05%

A = 22.050   A = 8.571

B = 5.433   B = 1.300

C = 5.967   C = 5.799

D = 8.018   D = 2.848

E = 13.251   E = 8.531

Figure 1. Measurements used in exploratory data analysis.

Shoots - 4 variables

Heads - 9 variables

Cauline Leaves - 6 variables

5 genera

6 sections

25 species

57 populations

329 individuals
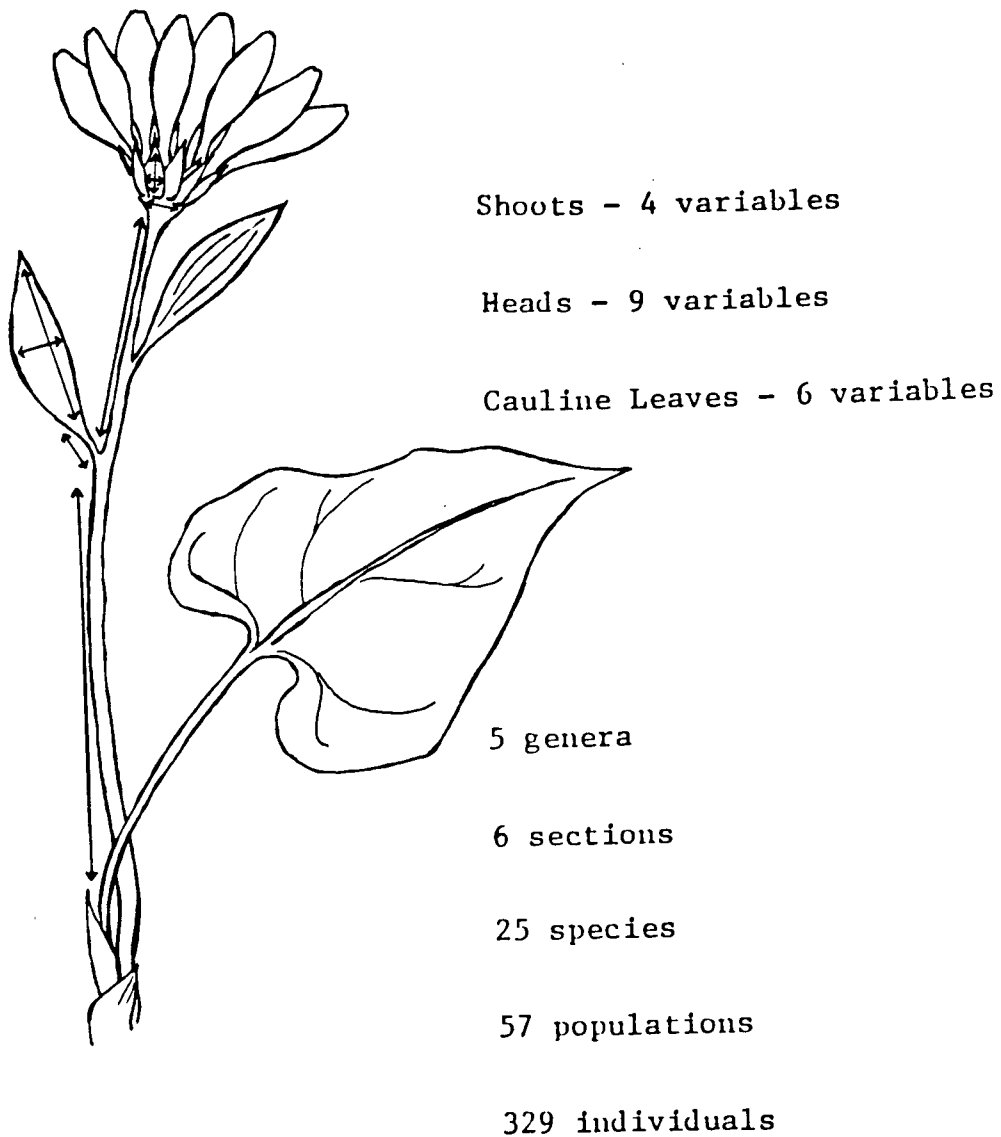
Figure 2. Classes of flavonoids and major substitution patterns.
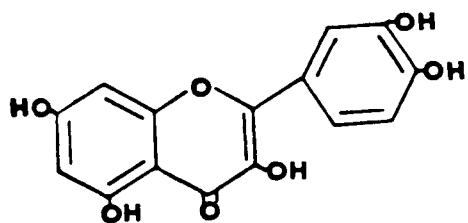
flavonol
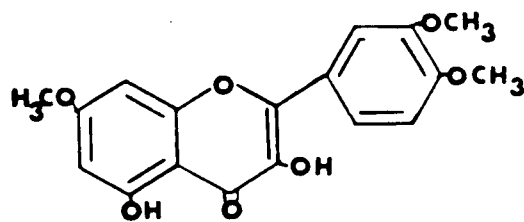
methylated
flavonol
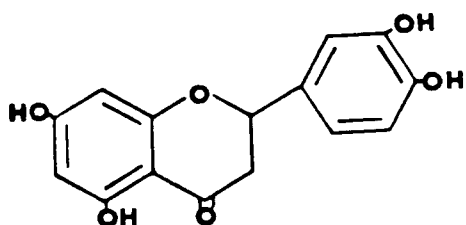
flavanone
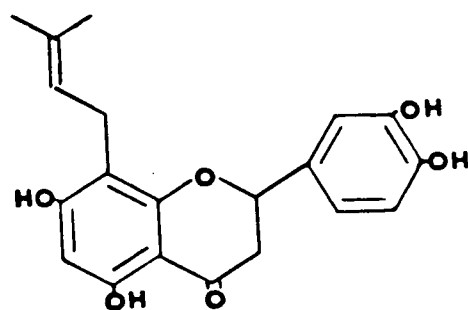
prenylated
flavanone
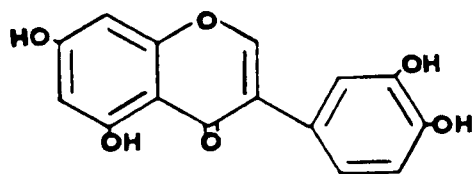
isoflavone

Figure 3. Cladogram using Helianthella as taxonomic outgroup.

Tree Length – 310
Consistency Index – 59%
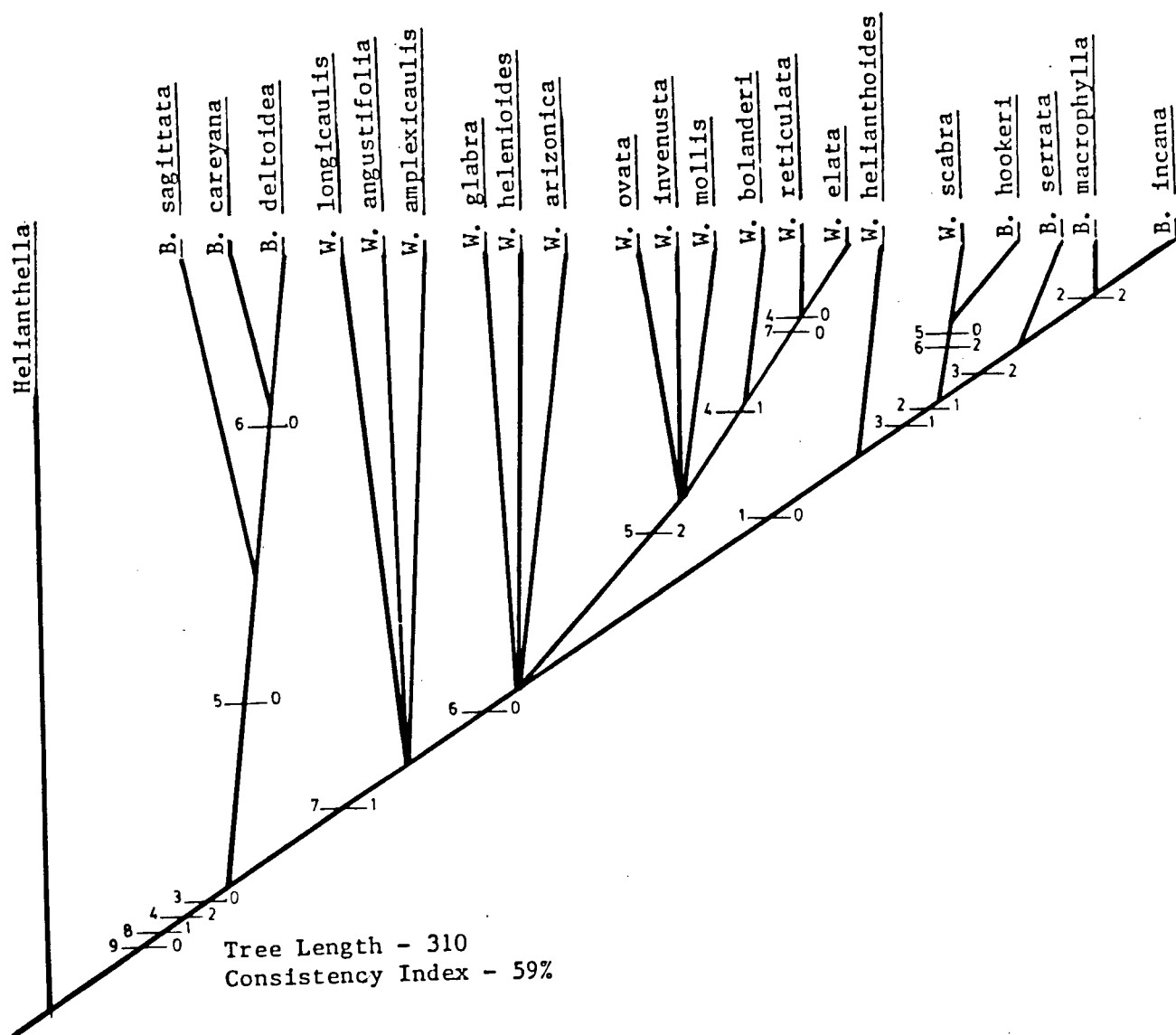
Figure 4. Cladogram using <u>Encelia</u> as taxonomic outgroup.

Tree Length — 310
Consistency Index — 59%
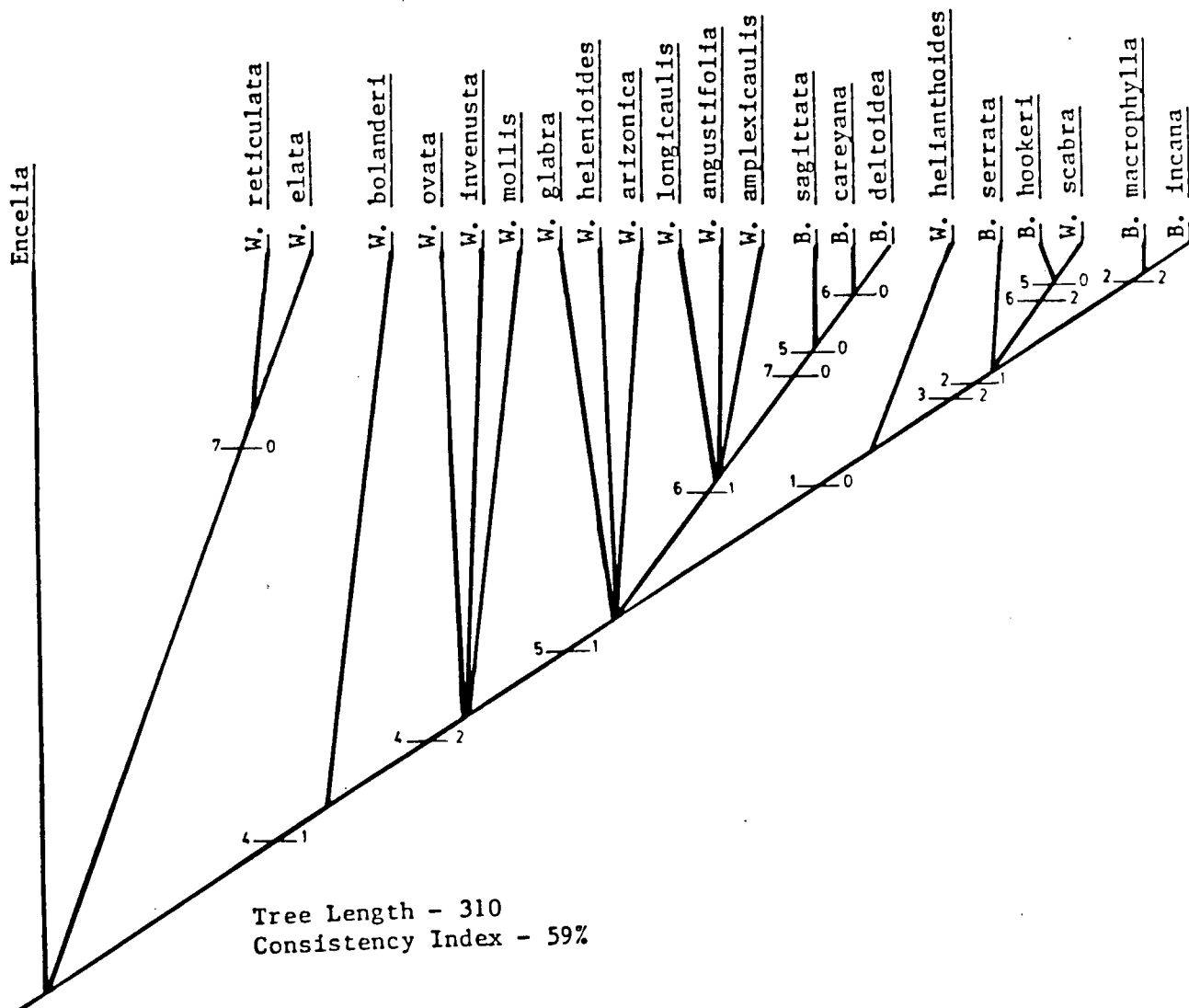
Figure 5. Cladogram using Heliopsis as taxonomic outgroup.

Tree Length - 310
Consistency Index - 34%
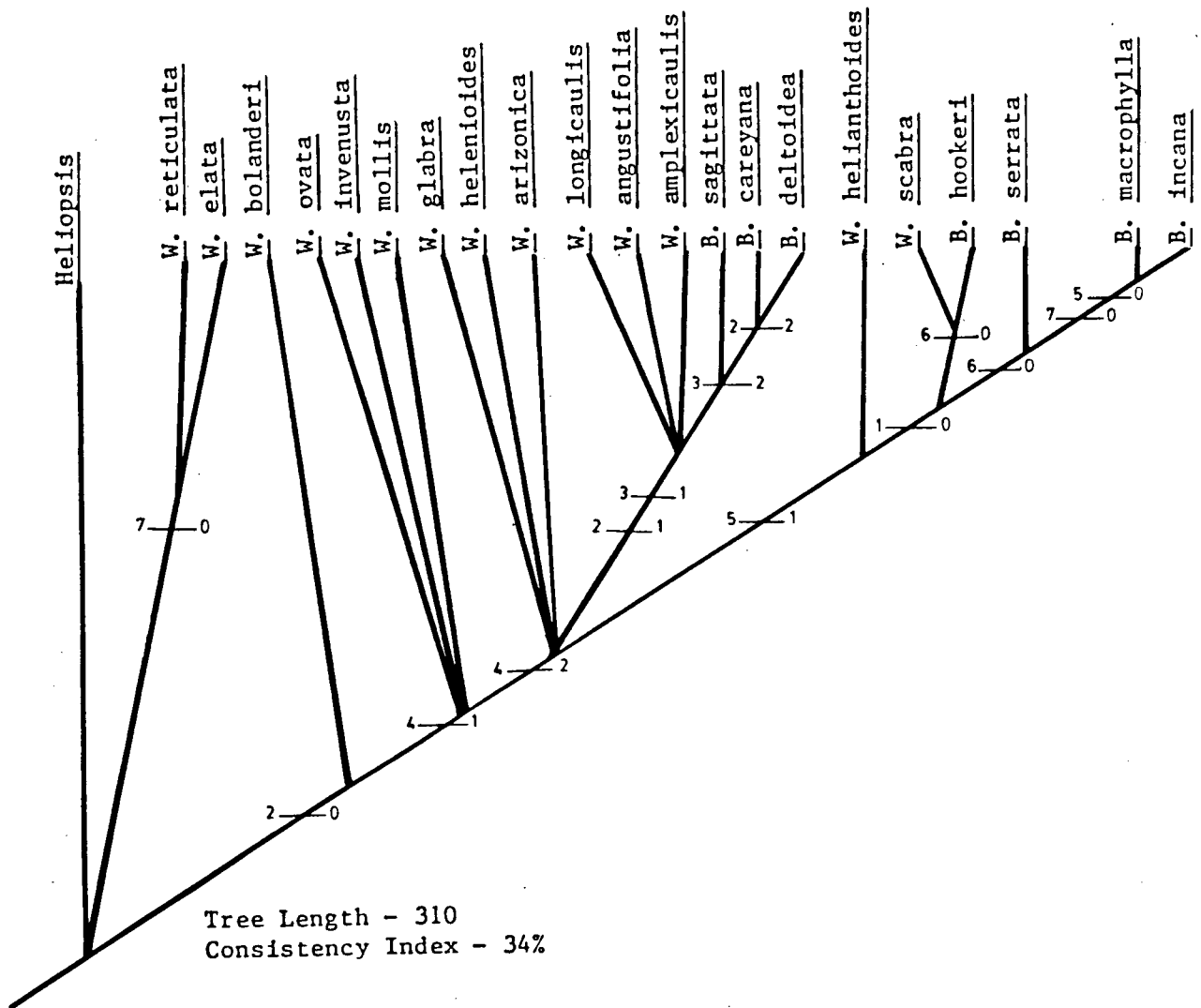
Figure 6. Cladogram using <u>Flourensia</u> as taxonomic outgroup.

Tree Length - 310
Consistency Index - 62%
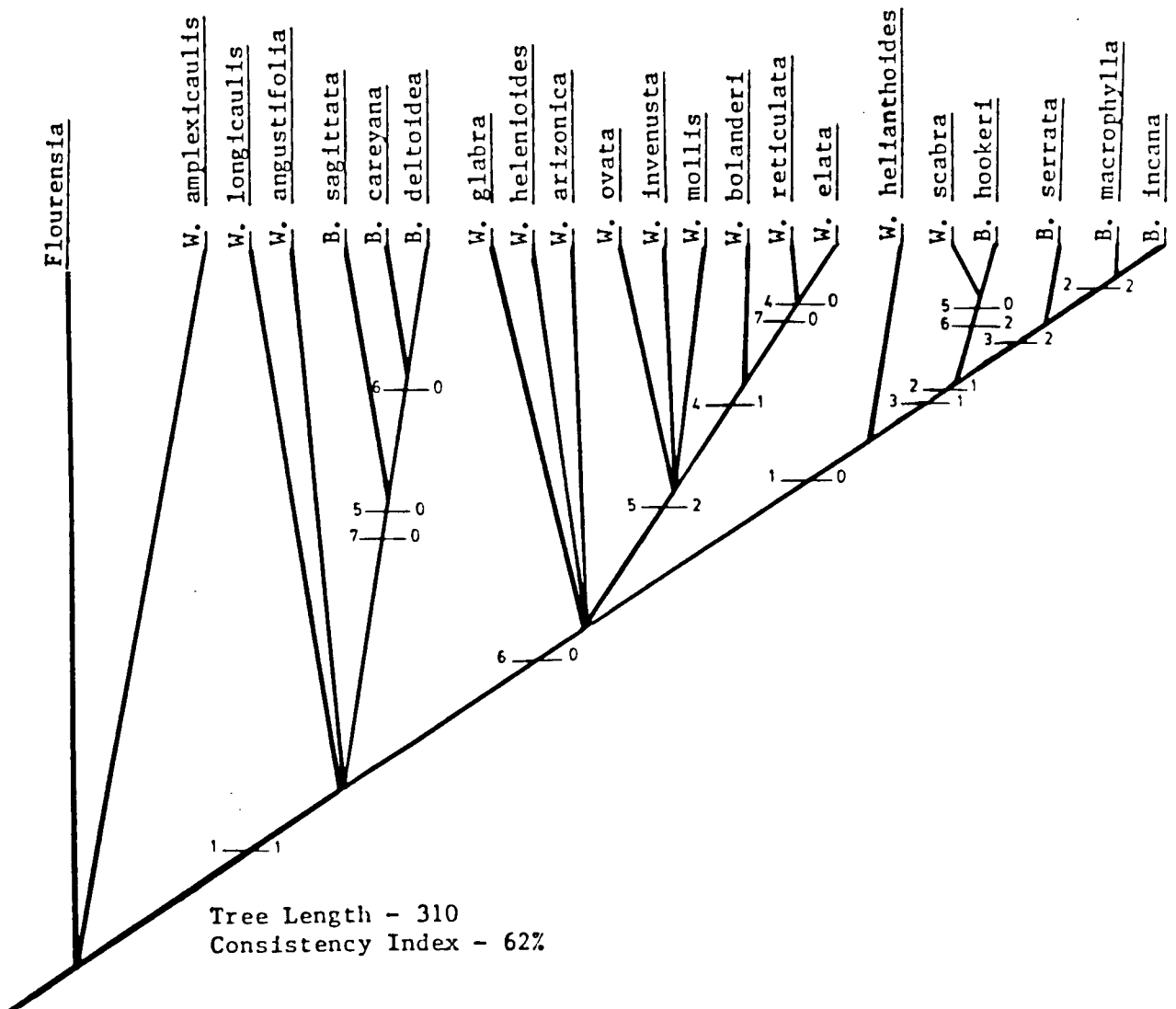
Figure 7. Cladogram using Rudbeckia as taxonomic outgroup.

Tree Length — 290
Consistency Index — 58%
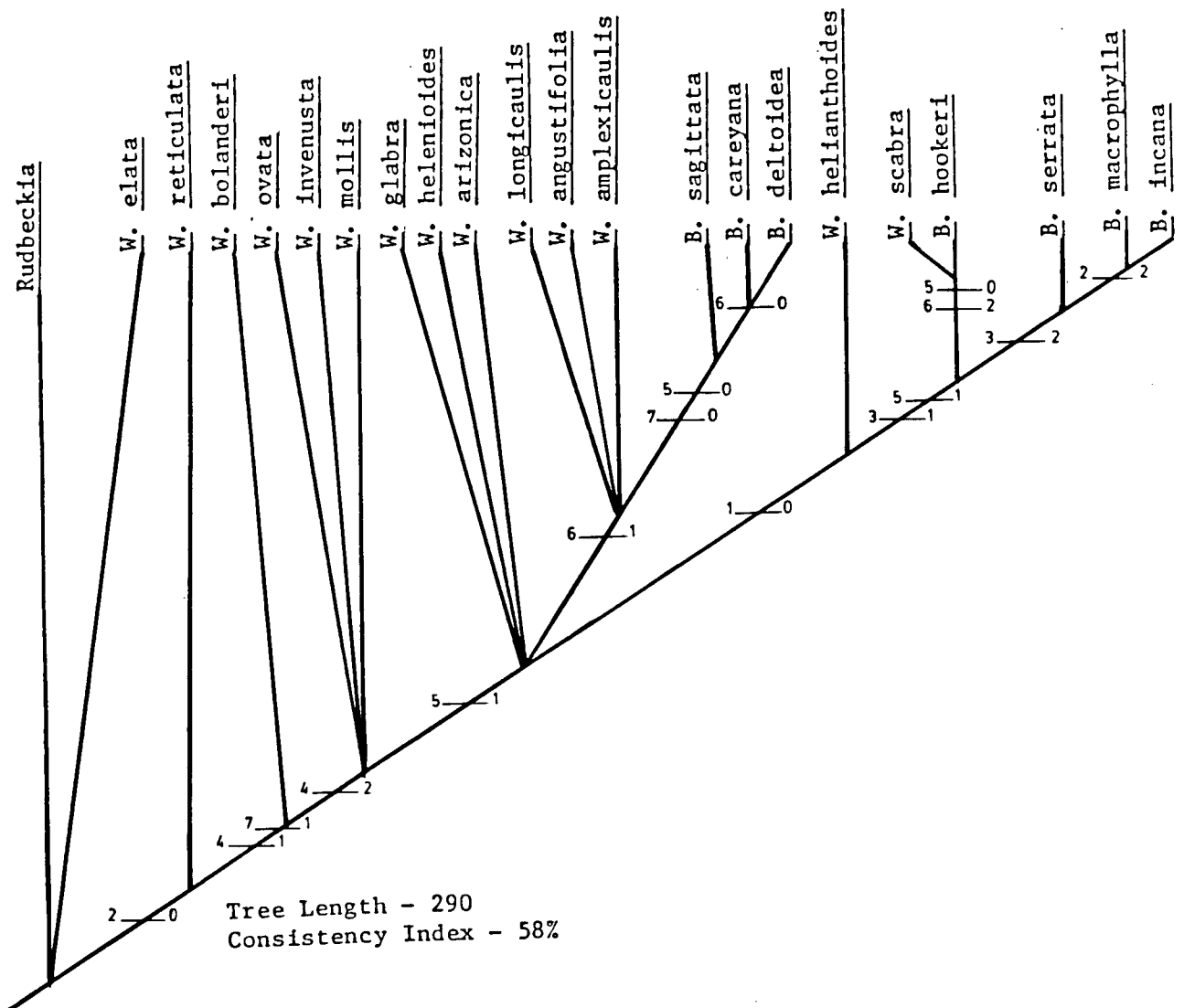
Figure 8. Cladogram using <u>Balsamorhiza</u> section <u>Artorhiza</u> as functional outgroup.

Tree Length — 390
Consistency Index — 60%
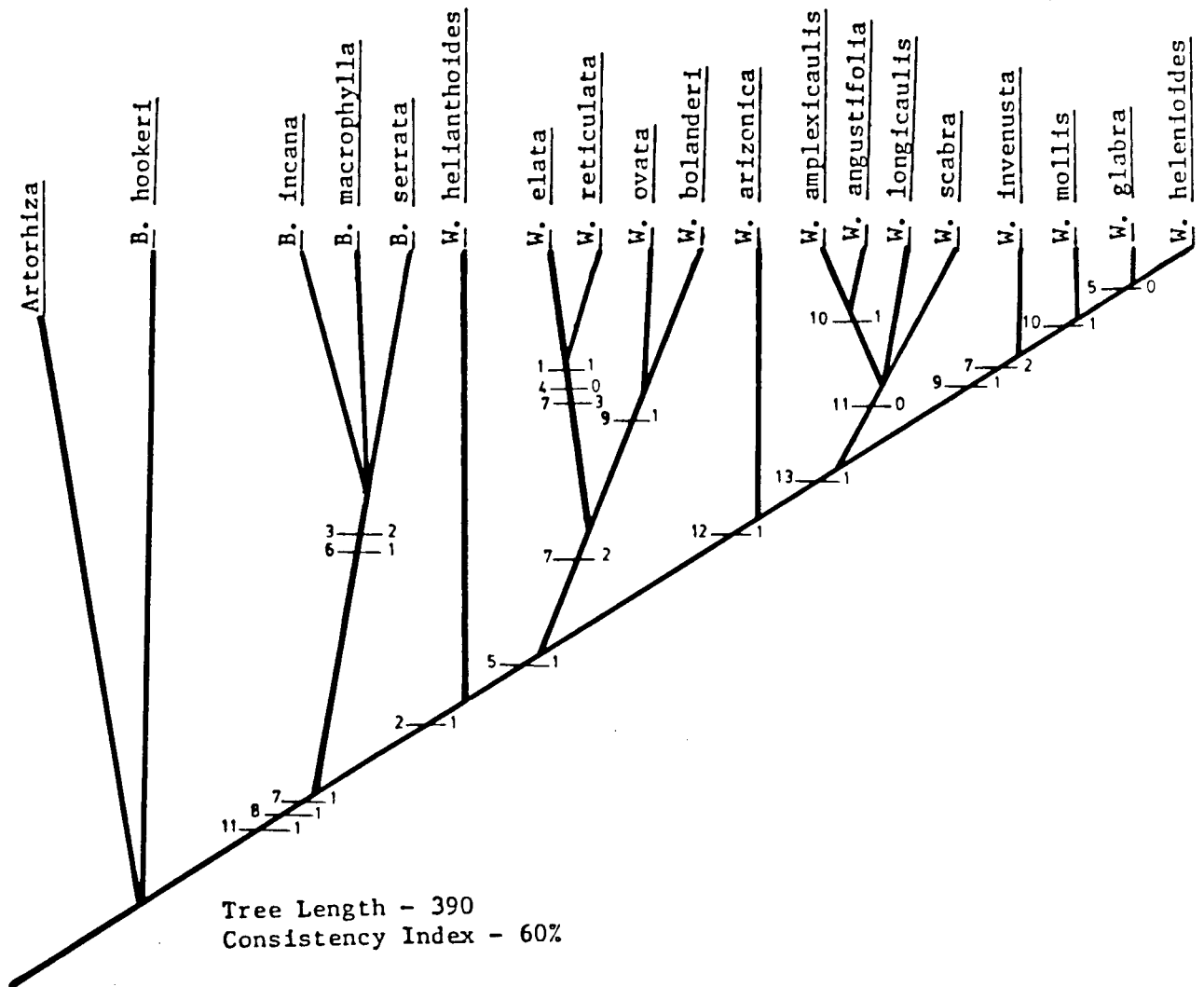
Figure 9. Cladogram using species pair <u>Wyethia reticulata</u>/<u>W.</u> <u>elata</u> as functional outgroup.

Tree Length — 450
Consistency Index — 51%
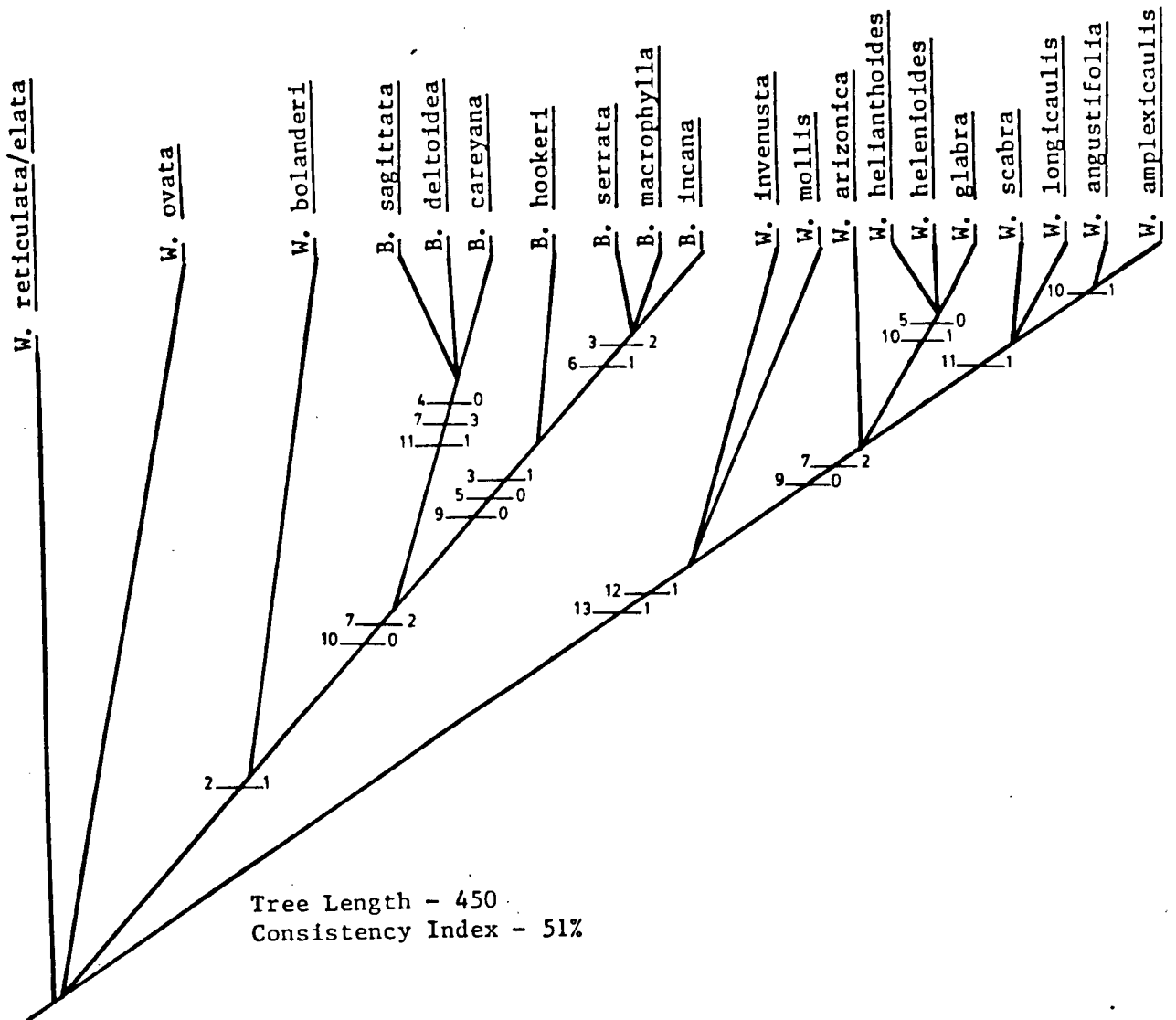
Figure 10. Dry flies of species.
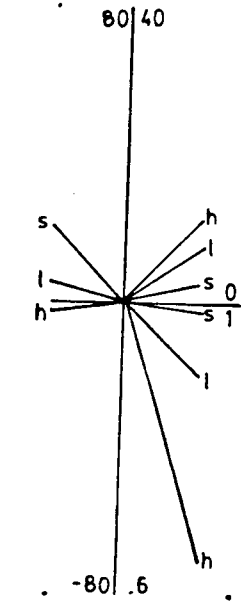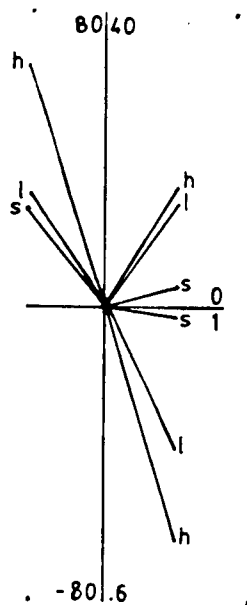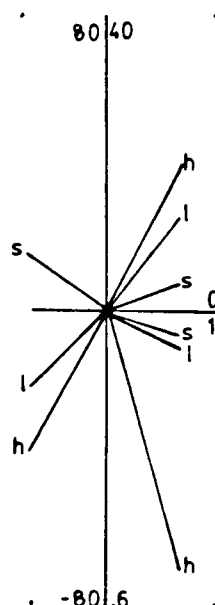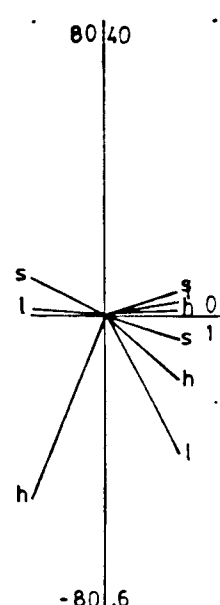
W. amplexicaulis   W. angustifolia   W. arizonica   W. longicaulis
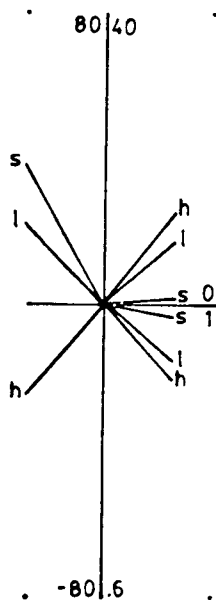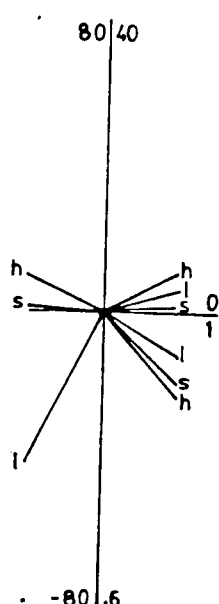
W. mollis   W. helianthoides   W. helenioides   W. glabra

122
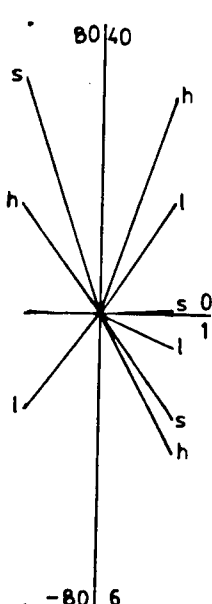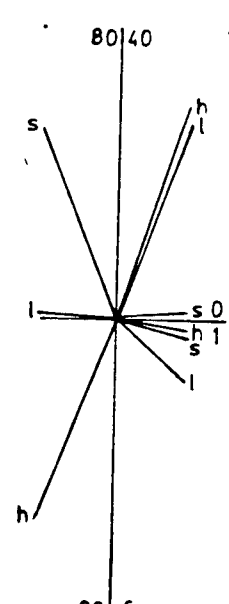
Figure 11. Dry flies of species.
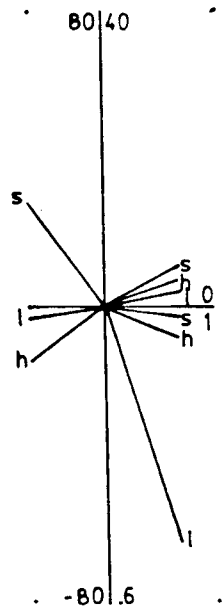
W. reticulata
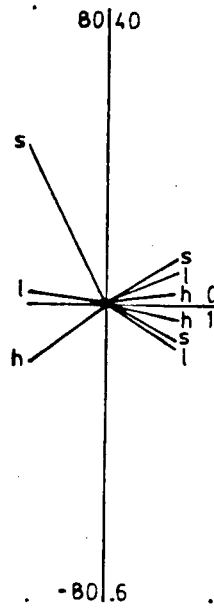
W. elata
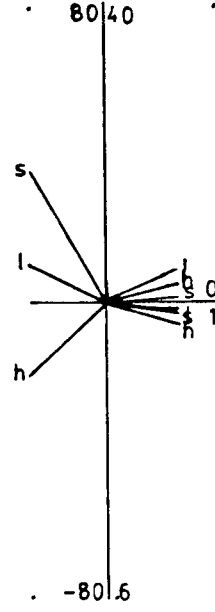
W. invenusta
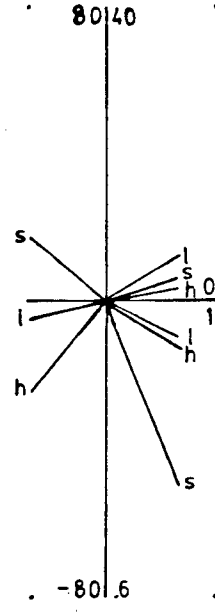
W. ovata
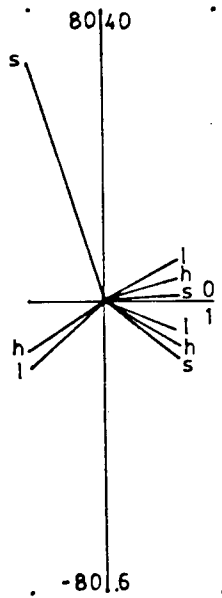
W. bolanderi
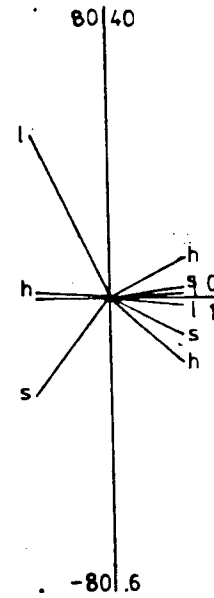
W. scabra
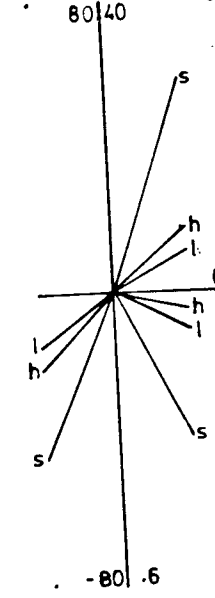
Helianthella
californica
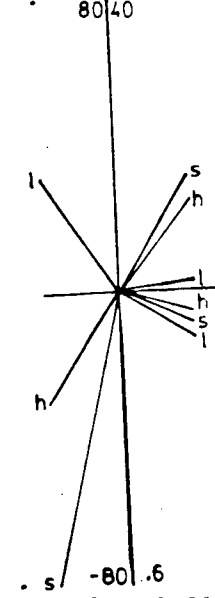
Helianthella
uniflora

Figure 12. Dry flies of species.
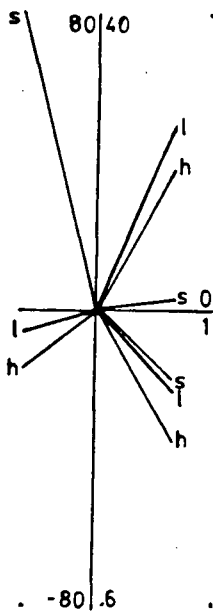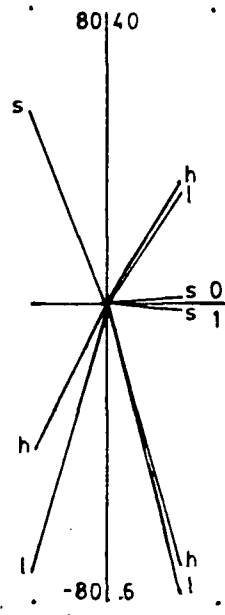
B. macrophylla   B. incana   B. serrata   B. hookeri
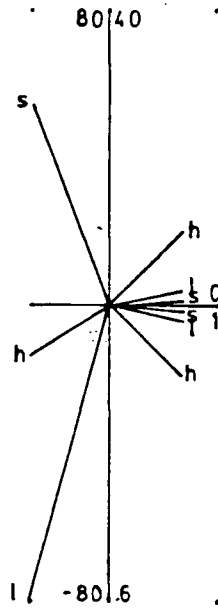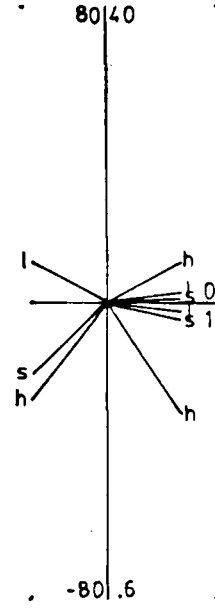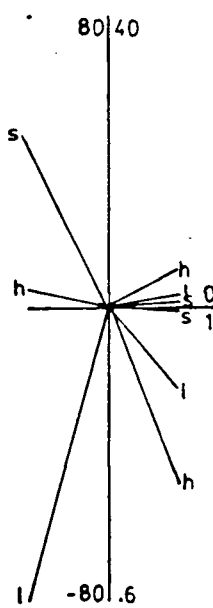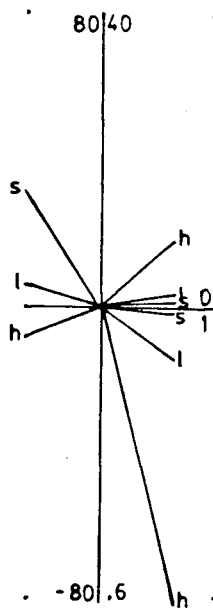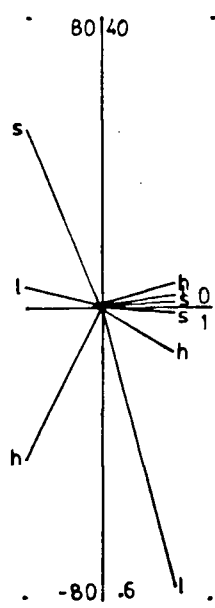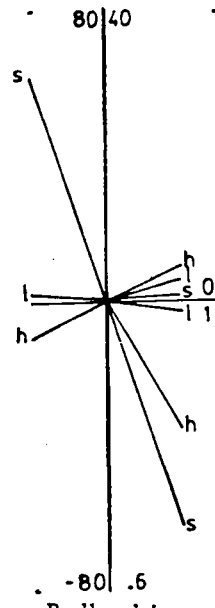
B. sagittata   B. deltoidea   B. careyana   Rudbeckia occidentalis   Helianthus cusickii
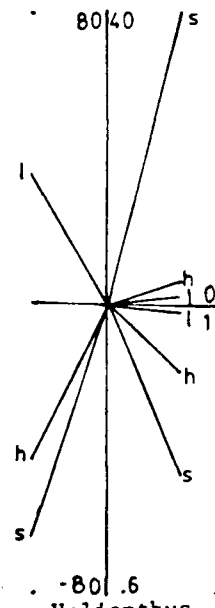
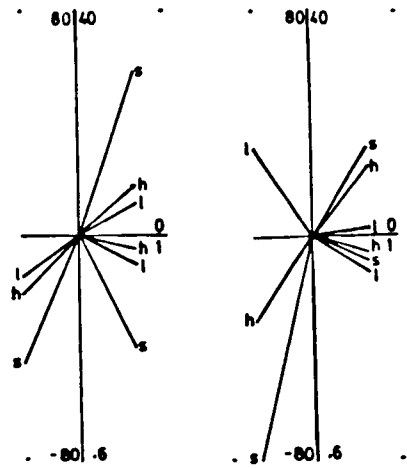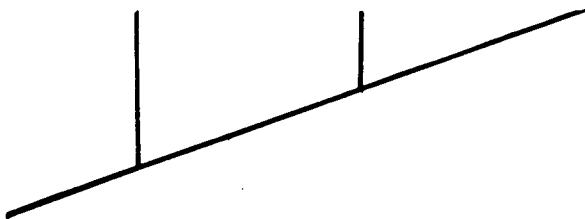Figure 13. Cladograms with dry flies for <u>Balsamorhiza</u> section <u>Artorhiza</u> and two species of <u>Helianthella</u>.
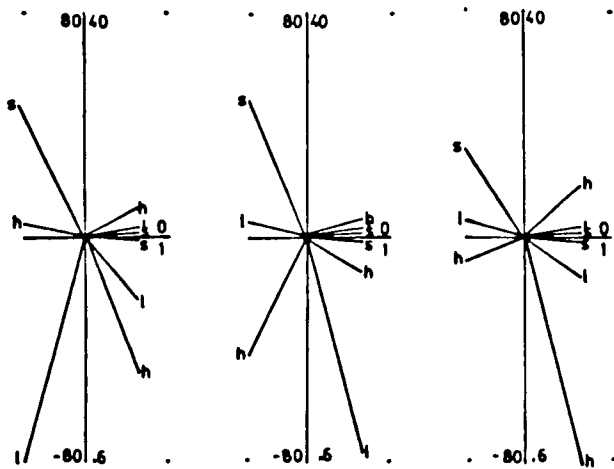
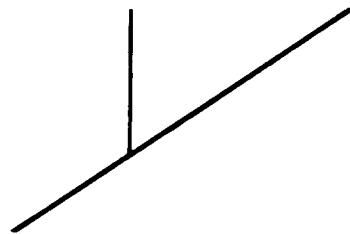| <u>**B.** <u>sagittata</u></u> | <u>**B.** <u>careyana</u></u> | <u>**B.** <u>deltoidea</u></u> | <u>Helianthella</u> <u>californica</u> | <u>Helianthella</u> <u>uniflora</u> |

Figure 14. Cladograms with dry flies for three species of Balsamorhiza section Balsamorhiza and the Wyethia reticulata/W. elata species pair.

B. serrata   B. incana   B. macrophylla   W. elata   W. reticulata