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UMI

Systematic and Biogeographic Study of a Plant Species Complex:

Aster Section *Eucephalus*

by

Elizabeth Anne Zamluk

BSc., University of British Columbia, 1983

MSc., Dalhousie University, 1992

A Dissertation Submitted in Partial Fulfilment of the

Requirements for the Degree of

DOCTOR OF PHILOSOPHY

in the Department of Biology

We accept this dissertation as conforming

to the required standard

Dr. Geraldine A. Allen, Supervisor (Department of Biology)

Dr. Patrick T. Gregory, Departmental Member (Department of Biology)

Dr. Job Kuijt, Departmental Member (Department of Biology)

Dr. David Duffus, Outside Member (Department of Geography)

Dr. Susan Aiken, External Member (Research Scientist, Vascular Plants, Research Division, Canadian Museum of Nature)

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University of Victoria

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Supervisor: Dr. Geraldine Allen

ABSTRACT

Aster section *Eucephalus* (Nutt.) Munz & Keck is comprised of about 16 taxa in North America (some rare and localized, others abundant and widespread) which appear to form a homogeneous, and probably monophyletic, group. I used a stratified sampling design to select 141 specimens from 1,669 loaned herbarium sheets. I chose morphological characters for analysis on the basis of character descriptions and the taxonomic history of *Aster* section *Eucephalus* species derived from published scientific papers and floras. I calculated similarity indexes based on 33 to 36 characters, using Gower's general similarity coefficient. Thirty-one phenetic groups were found by clustering specimens with UPGMA. The cluster memberships were adjusted by evaluating changes in the eigen values generated during discriminant analysis of "before" and "after" cluster memberships. An axis with increased value indicated that discrimination between the groups had increased relative to the axis, and a decrease showed that the groups were less separated relative to the axis. Those characters that could not be used in discriminant analyses were assessed for gaps or overlaps among groups by applying t-tests and visual inspection of box plots.

Twenty-five phenetic groups remained after the iterative adjustment process. Taxonomic names were assigned to the phenetic groups based on published descriptions. *Aster eastwoodiae* Zaml. *comb. nov.* (*Aster bicolor* was not an available name for this taxon) reinstates a morphologically distinct taxon (*Eucephalus bicolor* Eastwood), previously included in *A. brickellioides* (Greene) Greene, that is endemic to the Klamath region of Oregon and California. *Aster engelmannii* Gray is divided into var. *engelmannii* and var. *monticola* Zaml. *var. nov.* based on size, number of phyllary rows on the involucre, and trichome characteristics. *Aster wasatchensis* (Jones) Blake is separated into var. *wasatchensis* and var. *grandifolius* Zaml. *var. nov.* based on plant size, phyllary colours, and leaf trichome characteristics.

Phenetic groups were used as the bases for cladistic analyses and a hypothesis of

descent was developed from a cladogram derived by coding taxon character means as multi-state characters. Ancestral conditions were inferred from multiple outgroups including *Aster turbinellus* Lindel. *ex.* Hook. *Aster wasatchensis* was hypothesised to be the basal species.

Locality information gathered from herbarium labels was used to produce distribution maps. Biogeographic distribution information combined with cladistic results, and an assumption of a founding taxon from Mexico (Noyes and Rieseberg (1999) hypothesised that New World asters were derived from southern taxa) suggested several biogeographical hypotheses for *Aster* section *Eucephalus*. Four lines of descent were hypothesised to give rise to 1) an ancestral form in the Sierra Nevada; 2) an ancestral form in the Siskiyou Mountains of Oregon, together with *Aster glaucodes* Blake in the Great Basin and the Rocky Mountains; 3) a widespread group including *Aster engelmannii* Gray, *A. vialis* (Bradshaw) Blake, *A. perelegans* Nels. & Macbr., and *A. glaucescens* (Gray) Blake; and 4) *A. wasatchensis* (Jones) Blake in Utah. Taxa could then have developed through the processes of range expansion, isolation and vicariance. *Aster wasatchensis* is probably a palaeoendemic, whereas *A. eastwoodiae*, *A. gormanii* (Piper) Blake, *A. vialis*, *A. glaucescens*, and *A. paucicapitatus* (Robins.) Robins. are probably neoendemics. The current distribution of taxa likely reflects range modifications resulting from climatic changes caused by glaciation, and probably does not indicate the original relative positions of the taxa. Oregon and northern California form one area of species richness and Utah forms another. For these taxa, the coastal ranges exhibit more diversity and a higher rate of endemism. Rarity in *Aster* section *Eucephalus* is probably due to limited habitats and recent origin rather than any particular character trait.

Examiners:

Dr. Geraldine A. Allen, Supervisor (Department of Biology)

Dr. Patrick T. Gregory, Departmental Member (Department of Biology)

Dr. Job Kuiit, Departmental Member (Department of Biology)

Dr. David Duffus, Outside Member (Department of Geography)

Dr. Susan Aiken, External Member (Research Scientist, Vascular Plants, Research Division, Canadian Museum of Nature)

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DEDICATION

This thesis is dedicated to Joan Mary Zamluk (*nee* Harris), my mother, who taught me to appreciate plants, and to Bon van Hardenberg, my husband, and Michael and Peter van Hardenberg, my sons, for being so very patient.

I. INTRODUCTION TO THESIS

The fast disappearance of numerous species from the Earth makes accurate identification of species important, and discovery of evolutionary relationships among taxa essential. The damage to the Earth's biosphere has become so obvious that conventions involving numerous nations have been held to discuss ways to slow down the extinction rate. Canada has joined, to list a few, the Convention on International Trade in Endangered Species of Wild Fauna and Fauna (CITES), the Ramsar Convention (the Convention on Wetlands of International Importance), and the Convention on Biological Diversity. The increased interest in preservation of biodiversity has been accompanied by an escalated demand for inventories of flora and fauna. Assigning a name to an organism requires an easy to use identification key, accompanied by decisive and complete descriptions of the different taxa to which it may belong. Some taxa are easily identified because they have an unusual morphology (*e. g. Thuja plicata* Donn.), have been well studied (*e. g. Rosa*), or are a surviving taxon from a group of almost extinct taxa (*e. g. Ginkgo*). Others can present difficulties because several closely related taxa may share similar morphological characteristics (*e. g. Aster*, *Salix*, *Carex*), and these may not have yet been studied using numerical taxonomic methods. Besides its use in inventories, detailed information about species can be used in further analyses of higher level taxa and in phylogenetic studies.

Biodiversity is a problematic word because of its association with both political action and scientific interests. Political action can involve storming a provincial legislature, spiking trees, or drafting protective federal legislation by a Parliamentary committee. In the scientific community, defining and measuring biodiversity has been mostly handled by ecologists, but systematists have begun to participate as well (Vane-Wright 1996). The initial definition of biodiversity was based on the number of species in random samples of different communities (Fisher *et al.* 1943). Since then, the definition has been expanded to include every level of biological organization, including genetic material (Wilson 1992).

Phylogenetic analysis has recently become important in politics and to international corporations. Biochemical prospecting (the search for pharmaceutically active

compounds) has been influenced by the goal (stated by the Convention of Biological Diversity) of sustainable and equable development of a nation's biological assets (Vane-Wright 1996; Convention on Biodiversity 1999). Costa Rica has limited the activity of biochemical prospectors by declaring ownership of its own biota. Instead, INBio, a company controlled by Costa Rica, provides research companies with biological samples to study. The supplied samples are processed to conceal the identity of the organism, and the container labelled with only a code. If a sample proves interesting, INBio and the research company develop an agreement benefiting both parties, and the identity of the organism is revealed (Janzen 1996). Systematics becomes useful in biochemical prospecting because knowledge of relationships among taxa could shorten the search for new pharmaceutical drugs by directing researchers toward close relatives of a species.

If preservation of genetic diversity is a goal then phylogenetic information can be used to secure some of the genetic diversity of an extinct species by legally protecting, or by collecting and preserving propagative material from closely related species. Recently, plant breeders have begun to preserve genetic material from wild relatives of agricultural crops like potatoes and corn because the original taxa have begun to disappear from Central and South America. Gardeners have started to preserve agricultural and flower genetic diversity by organizing seed swaps and purposely growing heritage gardens. Canada has built a well equipped seed storage facility in Saskatoon, Saskatchewan, in response to the concerns over loss of genetic diversity.

Ironically, in a world with high species extinction rates, circumstances have arisen where systematists, especially those interested in morphology, have been disappearing from government and universities through retirement and death. Morphological studies have gained a reputation for being distinctly old fashioned, and may be less well funded than "modern" approaches using enzymes, chromosomes, and DNA. Molecular and morphological information provide different perspectives on the same question, and each helps move the other toward a more complete understanding of patterns of variation within and among taxa. However, molecular work, whether systematic, medical or pharmaceutical, has no meaning if the researcher cannot correctly identify the research

material.

Systematists are still in pursuit of the elusive goals of general agreement on acceptable techniques, and consistent application of criteria in assigning scientific names to taxa. As an example of disagreement on techniques, cladists are arguing about whether or not quantitative characters can be used in a cladistic analysis; among those who do use quantitative characters, there is a debate on how to code them (Chappill 1989; Felsenstein 1995; Pimentel and Riggins 1987). The nomenclatural debate is not over either, as evidenced by an article which urged botanists to resist the registration of names as part of valid publication (Anderson and Buck 1998), and a week of meetings to discuss nomenclature issues at the 1999 International Botanical Conference in St. Louis. The persistence of confusion and passionate disagreement among systematists is a consequence of the complexity of the task before them. Regardless of these debates, specimens still need to be accurately identified, and the relationships among taxa understood.

The primary goals of this research were to increase the quantity and accuracy of descriptions of a group of species, to develop a hypothesis about the group's evolutionary history, and to combine the phylogenetic hypothesis with the current geographic distribution to generate a hypothesis about its migration history and identify its centre of diversity. This information will be useful in the identification of plants, in working out phylogenetic schemes at the generic and higher taxonomic levels, and give biogeographers well supported distributions to consider.

Modern approaches in Systematics

Classification systems have been described as artificial, natural, numerical, phylogenetic, and phenetic. Artificial systems were designed to make naming and identifying specimens easy. Carolus Linnaeus used an artificial system based primarily on stamen number, fusion, and length as well as style number (Jones and Luchsinger 1979). He formalized the basis for current biological scientific names in the mid-eighteenth century, assigning consistent phrase names to many plants that had been established in botanical gardens of the Netherlands (Stafleu 1971). Although he preferred to use the full

length descriptive names, Linnaeus used 'trivial names', genus and species, in indices and margins to save paper. Use of binomials slowly increased during the next 30 years and has now become standard.

Natural systems developed as taxonomists recognized that certain plant species had "natural affinities" to each other, and must therefore be classified together (Jones and Luchsinger 1979). Concurrent with Linnaeus's artificial system, a natural system using as many characters as possible to classify plants was devised in France by M. Adanson, A. -L. de Jussieu and J. de Lamarck among others, with the intention of finding the structure that God had created (Jones and Luchsinger 1979; Stace 1980). The French taxonomists established the taxonomic orders above genus by creating family and order levels (Jones and Luchsinger 1979). After Charles Darwin published "Origin of Species", systematists started to make classifications that reflected evolutionary relationships.

Systematics has become dominated by numerical taxonomy, of which cladistics and phenetics are sub-disciplines (Sneath 1995). Cladistics developed in an attempt to quantify and add objectivity to the phylogenetic classification process (Stuessy 1990). Willi Hennig, a German entomologist, and W. H. Wagner, an American botanist, separately advocated cladistics.

Hennig (1966) in "Phylogenetic Systematics" presented taxonomic relationships as a hierarchy reflecting the phylogenetic or genealogical relationships between species. He believed that descent could be deduced through logical ordering of observations of facts. Speciation occurred through changes in populations at the fringes of the range of the originating species, and had to involve, eventually, an isolating mechanism resulting in what now is known as vicariant species. He also accepted that hybrid plants could undergo chromosome doubling thereby establishing fertility, and providing a start to a new species (Hennig 1966).

Time and space were vital to Hennig's understanding of evolutionary processes, and were used to deduce relationships between species, assign higher level taxonomic groups, and give direction to character change series (Hennig 1966). He considered reversibility of evolution possible, and listed several acceptable reversals: reappearance of simple

morphological characters, re-establishment of a complex organ in an adult if basic structure was still present in the juvenile stage, reversal of genetic mutations (backward steps), and reduction or disappearance of complex organs (p. 116). Rates of evolution were assumed not to be constant (p. 88). He illustrated the hierarchical relationships among taxa using a tree diagram on which the vertical axis represented time and the horizontal axis approximated relatedness among taxa (Hennig 1966). The tree was rooted in an extinct ancestral species, the internodes were of various lengths, and the nodes bifurcated to represent a speciation event. He called his methods the "Scheme of argumentation" now known as the "Argumentation Method" (Wagner 1980).

Hennig described phylogenetic systematics as an iterative process that would be driven by new information and insights or reciprocal illumination (Hennig 1966). The first step of systematic work was "typological" (or in modern jargon - phenetic analysis) since it was mostly concerned with grouping objects together based on their similarities. The second step was phylogeny (cladistic analysis). The group of taxa being studied was assumed, based on morphological similarities, to be monophyletic *i. e.* all descended from the same ancestor. Hierarchical relationships between species could be found through deduction by looking for special characters that were unique to the group of species that developed from the original or stem species (Hennig 1966). An additional requirement was that these characters be ordered from ancestral to derived. The correctness of a proposed phylogenetic relationship, the result of step two, could be supported by the number and type of facts (*e. g.* ". . . ecological, physiological, geographic, etc." (Hennig 1966, p. 22)) that could be explained by the proposed relationship. Even though there could never be incontrovertible proof that a phylogeny was correct, if new facts could be added without disrupting the proposed hierarchy, and if the new relationships explained previously puzzling phenomena, Hennig argued that it could be tested by how well it met previous criteria, without creating new contradictions, and that reliability increased with the number of characters that supported it. A phylogenetic proposal could be adjusted as new information or insight came to light. According to Hennig, the final goal was to find an underlying set of principles for Biology, explaining the forces that drive evolution,

similar to the fundamental theories of particles and energy which were developed in Chemistry. This final step is most difficult, especially the search for a unifying law, and has been rarely attempted (Hennig 1966).

Wagner, working in Michigan during the 1950s, developed a manual cladistic method which he used for his PhD research on ferns, and then taught to his systematic students (Wagner 1980; Stuessy 1990). Wagner's Groundplan-divergence Method reflected changes during descent based on the assumption that the most common state of a character was ancestral. His method required the establishment of a hypothetical ancestor species with all the ancestral character states (Wagner 1984). Sources of phylogenetic changes were ". . . mutation, combination, selection, isolation and drift" (Wagner 1980, p. 181). Acceptable characters were ". . . any that underwent biological change: morphological, cytological, physiological or chemical. . ." (Wagner 1980, p. 176). His interest was in estimating the amount, direction, and order of change in gene pools of populations but not in placing those populations in actual space or time or in providing a measure of the rate of evolution. Ancestral species were not presumed to be extinct, evolutionary rate of change was irregular, and could be reversible. His method required several steps: assignment of populations to species and varieties (based on phenetics), decisions on direction of character changes, definition of hypothetical ancestral species, numerical estimates of how much each taxon had changed from the ancestral species, and production of a dendrogram based on the numerical estimates of changes (Wagner 1980). Wagner did not consider taxonomic classification a goal, but a possible by-product. He dealt with hybrid plant populations by identifying them based on the assumption that they would have intermediate character states between that of the parental species, and then removing them from the cladistic analysis (Wagner 1984). After analysis was completed, hybrid taxa were reinserted in the appropriate place between parental species. Wagner felt that strong evidence of the validity of the cladogram lay in several areas: it had to agree with phenetic taxonomy, not contradict fossil, distribution, and ecological evidence, and be confirmed by other cladistic methods. He thought that his methods were weak when a group had many extinctions, or had evolved rapidly, or had hybridized extensively. Each

of the processes made assigning ancestral conditions difficult; rapid evolution or hybridization sometimes resulted in character states that were indivisible (Wagner 1980). Wagner agreed with Hennig that new information must be incorporated into the related phylogenetic hypothesis, and it should be revised as necessary (Wagner 1984).

In 1963, Peter Sneath and Robert Sokal published their first book "Principles of Numerical Taxonomy", followed in 1973 by "Numerical Taxonomy", in which they presented their phenetic taxonomic methods as an alternative to phylogenetic because they thought that no scheme could show ". . . information on the degree of resemblance, descent, and rate of evolutionary progress" without becoming too complicated (Sneath and Sokal 1973, p. 10). They wanted to avoid any estimate of evolutionary rate or evolutionary relatedness among taxa. They defined numerical taxonomy as ". . . *the grouping by numerical methods of taxonomic units into taxa on the basis of their character states*" (their italics, Sneath and Sokal 1973, p. 4). A taxonomic unit could be an individual, a population or any level of classifiable groups (*e. g.* species, genus, etc.). Character states were defined as either qualitative or quantitative features that differentiate one organism from another. The interest of Sneath and Sokal was in placing "operational taxonomic units" (OTUs) into unambiguous groups based on unweighted character states, which were usually morphological characters but could include any aspect that could be coded. The principal aim of numerical taxonomy was to increase repeatability and objectivity of any systematic study. Repeatability would be achieved if methods and procedures were accurately described. Objectivity would be more likely if all available characters without previous selection were included, and computers were used to process and evaluate data. Quantitative data would discriminate taxa more easily and clearly because coding data would make characters more explicit.

Interestingly, because of Sneath's and Sokal's (1973) dismissal of phylogenetic analysis methods in their book, Sneath wrote recently that phylogenetic inferences should be made from phenetic data whenever possible, and he indicated that Sokal and he had made a similar statement in their book but had emphasized the differences between phylogenetics and phenetics (Sneath 1995). He pointed out that phenetics was

"information rich" and phylogenetics was "evolutionary history"; therefore they served different purposes, and were useful for achieving different goals (Sneath 1995, p. 285).

An informal survey covering the last 10 years of several systematic journals showed that systematic work has tended to be cladistic, some have used principal components analysis and statistical techniques, and a few used qualitative characteristics and intuition to draw conclusions. Some of the analyses were designed (as a secondary goal to the systematic study of taxa) to evaluate the compatibility of cladograms that had been derived from different types of data. Cladograms developed using chloroplast DNA restriction site data from taxa in *Penstemon* section *Peltanthera* were found to largely agree with results derived from nuclear DNA restriction site data (Wolfe and Elisens 1995). Cladograms based on chloroplast DNA data taken from specimens of *Argyranthemum* (Asteraceae) were found to differ from a cladogram based on morphology but to be similar to one derived from isozymes (Francisco-Ortega *et al.* 1995). Ericaceae was analysed cladistically with morphological, anatomical, and embryological data and found to be paraphyletic (Judd and Kron 1993). Some studies have used numerical taxonomic methods to evaluate morphological similarities among species. One study was of two pine species growing in Mexico and Central America by Matos (1995) in which he found that they could not be separated using multivariate techniques. In another phenetic study, Semple and his colleagues used multivariate techniques to analyse morphology of *Heterotheca* and a section of *Aster* (Semple *et al.* 1988; Semple *et al.* 1991). Allen (1986) used principal components analysis to test morphological limits in two species of *Aster*. Some studies compared cladistic and phenetic results. For example, Jones and Young (1983) considered the relationships within *Aster* at the subgeneric level using several approaches: cladistic, phenetic, and inferences drawn from cytogenetic techniques. They were reluctant to make any changes in the current taxonomic treatments because several equally parsimonious trees were found. Other studies have not been included any numerical analysis. For example, Semple and Brouillet (1980) in a study of *Aster* did not use any numerical analysis to compare taxa below the generic level; they based their arguments on chromosome number and phyllary characteristics. Approaches to systematic

analyses are still diverse and seem to vary depending on the interest and experience of the researcher.

As a bare minimum to avoid researcher bias, every taxonomic treatment needs to be supported by statistical analyses, whether a simple t-test between groups or a complex multivariate study. All information learned about taxa and their relationships is important, and needs to be considered as a whole. Phenetic or multivariate analyses are most helpful at the lower taxonomic levels by identifying hybrids, separating species or varieties, or grouping species into higher taxonomic levels. Cladistic analyses have been used primarily at the genus or higher taxonomic levels, possibly because detailed information necessary for a competent analysis of numerous species is often lacking.

Characters and character analysis

Every systematic study requires characters which describe the organisms being studied. Similarities are useful in placing species together at a higher taxonomic level such as grouping species into sections. Character differences are required, rather than similarities, when comparing species (or any taxa at the same taxonomic rank). Some systematists consider every different characteristic to be a character, *e. g.* red petal colour and white petal colour are two different characters. Others use a more abstract definition which involves assigning different states to a generalized character, *e. g.* red and white petal colour are two states (red, white) of the character of petal colour (Wiley 1980). Sneath, Sokal, Hennig, and Wagner advocated the use of a wide variety of characters from all stages of the life cycle, and the inclusion of every character that varies. Financial and time restraints may, however, impose unavoidable limits to a study and increase the bias.

Before systematic studies can be carried out, analogous characters (those derived from different structures but having the same function) need to be identified in order to avoid finding evolutionary similarities where there are none. Sneath and Sokal assumed that analogous structures would not be used in phenetic analysis very often because detailed examination would quickly reveal underlying dissimilarities (Sneath and Sokal 1973). Wagner argued in the same line; he felt that homologies among plants below class

level were obvious to an expert, and if the species were closely related, this could be tested by conducting hybridization experiments in order to ascertain if the suspected homologous organ or pathway in the hybrid showed intermediate character states (Wagner 1980).

In a phylogenetic study, after homologous characters and their states have been identified, attempts are made to identify the ancestral and derived conditions (Hennig 1966; Wagner 1980). To do this, Hennig used whatever evidence was appropriate for the study taxa, including fossil records; geographical distribution (the character state of the species furthest away (physical distance) from the area assumed to be the place of origin of the group was considered to be most derived); ecological attributes (the species growing in the most different habitat compared to other members of the monophyletic group was assumed to be derived); and ontogeny (the direction of transformation during development could provide information) (Hennig 1966). Several transformed characters occurring together throughout the cladogram were also considered to be derived that the transformed states of those characters were derived (now known as clique analysis) (Hennig 1966). Wagner considered that the most widely distributed state was most likely to be ancestral, and that ancestral attributes tended to occur in the same taxa (Wagner 1980). Ingroup and outgroup comparisons were used to eliminate the possibility of mistaking a character as ancestral when the high frequency had actually resulted from considerable speciation in the group (Wagner 1980 and 1984). Common ingroup characters were assumed to be ancestral unless they were discovered to be different from the outgroup, in which case they were declared to be derived. If direction of change was ambiguous then Wagner recommended that the character be discarded from the study until new information became available. This choice frequently resulted in less than 10 characters being used in a study (Wagner 1980).

Morphological characters are usually the easiest and cheapest data to collect for a systematic study, and have traditionally been the basis for classifications (Stuessy 1990). Data collected from plants may be either vegetative or floral. Vegetative features, such as root, stem, and leaf, are generally more variable than floral, possibly due to the numerous

functions they perform and the modular character of the repeating structures (Stuessy 1990). Floral morphology is less variable, perhaps due to more restricted functions and less time exposed to the climatic selective pressures (Stuessy 1990). Vegetative data has included leaf shape, margin, length, width, venation patterns, epidermis and cuticle features, and some stem features like overall growth patterns and anatomical studies of the pith and the stele. Root characters have been used less frequently but have included growth habits, secondary thickening, and size. Floral morphology included features taken from flowers, fruit, and seed.

Genetic information, which includes study of chromosomes (cytology), enzymes, chloroplast DNA, mitochondrial DNA, and nuclear (including ribosomal) DNA, has become more widely used by some systematists because genetic data were considered closer to the basis of diversity (Stuessy 1990) and DNA was considered a "durable archive" (Williams 1992, p. 11). Various molecules, presumed to change at independent rates, have been used for different taxonomic levels, for example, mitochondrial DNA has been used at the generic level in mammals, whereas ribosomal RNA has been used to discover the origin of mussels (Harvey and Pagel 1991). Plant DNA studies rarely use mitochondrial DNA because it has proven difficult to analyse; instead restriction endonuclease fragmentation and sequencing methods have commonly been applied to nuclear (including ribosomal), and chloroplast DNA. Cytological data (chromosome counts, karyotype (morphology), and behaviour during meiosis) have been helpful in understanding relationships among populations and species. Isozymes, extracted enzymes spotted onto gels and separated by electrophoresis, have been used to assess genetic distances between groups under study. Sometimes, only a few taxa in a monophyletic group are subjected to genetic analysis in order to clarify relationships (Stuessy 1990). Although researchers hope that more resolved phylogenetic trees will be produced by using molecular characters, problems have been identified. For example, substitution events within DNA molecules may not be independent and do not always follow a normal distribution, evolution may occur in bursts rather than at a constant rate, and environmental change may have altered the levels of an allele in a population. Ancestral

states of molecules have been difficult to identify, and to add more confusion, cases of parallel and convergent evolution have been proven (Harvey and Pagel 1991). Despite these problems, phylogenetic hypotheses based on molecular data have often been considered more accurate than those based on morphology.

Biogeographical and ecological information have been used to explain processes, timing, and place of evolutionary events. These areas of study provided raw material that carried the clues to how evolution might have occurred and what mechanisms might have been at work in the past. Some systematists, such as Stuessy, think that these data should be excluded from a phylogenetic study so that they can be used to test the validity of the proposed phylogeny. Biogeographical data have usually been mentioned in any discussion of taxonomy but have not usually been used for classification (Hennig 1966; Sneath and Sokal 1973; Wagner 1980; Stuessy 1990). Sometimes, the distribution has been used to argue for centres of dispersal or to infer trends in character states (Hennig 1966; Cox and Moore 1993). Ecological characters of areas, such as soil type, geology, climatic factors, have sometimes helped to distinguish possible reasons for changes in taxa (Stuessy 1990), for example, specialization by some members of a species which allowed them to grow on a toxic site (Begon *et al.* 1986). Historical information on past climates has also been extremely useful (Stuessy 1990) and has been provided by geographers. Biogeographical data prompted Wegener in 1915 to suggest continental drift. Estimates of continental breakup times have served to establish earliest possible speciation times for some animals, *e. g.* flightless birds (Begon *et al.* 1986). Systematics, ecology, and biogeography generate overlapping sets of information; data collected for one purpose can often be used for another with little adjustment and each complements the other.

Phylogenetic systematics at the moment is the best of the available classification systems. It provides a logical method that, ideally, reflects evolutionary history, contains retrievable information, and groups species of common descent together.

Aster section *Eucephalus* (Nutt.) Munz & Keck

Aster is a member of tribe Astereae of family Asteraceae which is a member of Magnoliopsida. Asteraceae has approximately 1,300 genera encompassing 2,500 species which makes it probably the largest family of Magnoliopsida. The tribe of Astereae was estimated to have over 170 genera and 3,000 species worldwide (Noyes and Rieseberg 1999). Jones and Young (1983) estimated that 200 species of *Aster* occur in North America. Characters that distinguish Astereae from other tribes are connate petals, few stamens (1-5), and an ovary with two carpels (Cronquist 1955). *Aster* section *Eucephalus* (Nutt.) Munz & Keck is among the larger sections of *Aster* (Jones 1980a).

Jones (1980a) revised *Aster* using chromosome number as the "pivotal diagnostic character" (p. 230). Jones and Young (1983) in their phenetic and cladistic analyses of relationships among sections of *Aster*, as defined by Jones (1980a), had to choose only one or two representative species from each because of limitations of their software, and because phylogenetic studies at the subgenus, section, and subsection levels had not been done. Nesom (1994) revised North American *Aster* species using his and other people's published work and his own extensive experience with the genus. In his review of recent *Aster* classifications, he criticised and then dismissed Jones' (1980a &b) revision because it was phenetic. He also did not agree with Jones' and Young's (1983) decision not to segregate the North American Asters after they concluded that two of the most parsimonious cladograms showed "considerable differences in topology" (Jones and Young 1883, p. 83), and that more data were needed to resolve the phylogeny of *Aster*. Nesom considered their choice of *Erigeron* species as a multiple outgroup was poor, and noted that they had concluded that *Aster* species formed a paraphyletic group. He wrote that his revised phylogeny of *Aster* ". . . may not be exactly aligned with What Nature Has Wrought but they are based on detailed observation and broadly based consideration." (Nesom 1994, p. 147). Choosing to use observation and "broadly based consideration" is inconsistent with the goals of numerical taxonomy which strives to eliminate personal bias. Nesom's conclusions may be correct but they are suspect because he used intuition for many of his decisions. A systematic study of one of these sections would provide more

accuracy in the development of overall hypothesis about relationships within *Aster*.

Aster subgenus *Aster* section *Eucephalus* was chosen for this study because it has confusingly similar taxa, has not been subjected to phenetic or cladistic analyses as a group, is of a manageable size (16 species and varieties) for a PhD project, and appears to be a monophyletic group. The monophyletic nature of this section is presumed on the basis of similar morphology and same chromosome numbers. Some species in the section are endemic to small areas and some are extremely widespread which provides an interesting contrast among them. Membership in this section has been modified with the addition of *Aster breweri* (Semple 1988), and division into two sub-sections accompanied by the inclusion of *Aster turbinellus* (Jones 1980). Neither of these studies included a comprehensive numerical taxonomic analysis.

Species considered for this study as part of *Aster* section *Eucephalus* are:

1. *Aster breweri* (Gray) Semple (endemic to California and the western edge of Nevada),
2. *A. breweri* (Gray) Semple var. *multibracteata* (Jeps.) Zamluk *comb. nov.* (endemic to California and western edge of Nevada),
3. *A. brickellioides* (Greene) Greene (endemic to northern California and southern Oregon),
4. *A. brickellioides* (Greene) Greene var. *glabratus* Greene; synonymous with *Aster siskiyouensis* Nels. & Macbr. (endemic to northern California and southern Oregon),
5. *A. engelmannii* Gray (widespread),
6. *A. glaucescens* (Gray) Blake (endemic to southern Washington),
7. *A. glaucodes* Blake (widespread),
8. *A. glaucodes* Blake var. *formosus* (Greene) Kittell (distribution uncertain),
9. *A. glaucodes* Blake var. *pulcher* (Blake) Kearney & Peebles (distribution uncertain),
10. *A. gormanii* (Piper) Blake (endemic in Oregon),
11. *A. ledophyllus* (Gray) Gray var. *ledophyllus* (moderately distributed)

12. *A. ledophyllus* (Gray) Gray var. *covillei* (Greene) Cronq. (endemic to northern California and Oregon),
13. *A. paucicapitatus* Robinson (endemic to the Olympic Mountains and Vancouver Island),
14. *A. perelegans* Nels. & Macbr.(widespread),
15. *A. vialis* (Bradshaw) Blake (endemic to Oregon), and
16. *A. wasatchensis* (Jones) Blake (endemic to Utah)

(Hitchcock and Cronquist 1976; Jones and Young 1983; Munz and Keck 1965; Semple 1988).

Although no one has conducted a numerical analysis of all the species in this section, some previous work has been done. Semple included some species from *Aster* section *Eucephalus* in his chromosomal studies (Semple and Brouillet 1980, Semple, *et al.* 1983, Semple 1985). He also identified *A. breweri* as belonging in section *Eucephalus* (Semple 1988). Semple and Brouillet (1980) and Jones (1980a) included *A. turbinellus* in the section although it has very different chromosome numbers. Eight species in *Aster* section *Eucephalus* have been found to have a somatic chromosome number of $2n = 18$: *Aster breweri*, 3 counts (Semple 1988), 1 count (Anderson *et al.*1974); *A. engelmannii*, 1 count (Semple 1985), 1 count (Semple *et al.* 1983); *A. glaucodes*, 1 count (Jones 1980b), 2 counts (Semple 1985), 1 count (Semple *et al.* 1983); *A. gormanii*, 1 count (Semple 1985); *A. ledophyllus* var. *covillei*, 1 count (Semple 1985); *A. ledophyllus* var. *ledophyllus*, 3 counts (Semple 1985); *A. perelegans*, 1 count (Semple 1985); *A. wasatchensis*, 1 count reported on a herbarium label (Semple, J. and J. Chmielewski, 8890). In contrast, *Aster turbinellus* was reported to be $2n$ ca.= 96, 1 count (Semple *et al.* 1983), 1 count (Semple 1985). Semple has recently retracted the inclusion of *A. turbinellus* in section *Eucephalus* (personal communication). Before phenetic and cladistic analyses were carried out, I collected information on previous descriptions of species in the section in order to determine how previous authors had delineated the taxa, and which characters were considered important diagnostic features.

Taxonomic history of *Aster* section *Eucephalus*

The genus *Eucephalus* Nutt. was first described by Thomas Nuttall in 1841, and the taxonomic rank of the group as a genus or a section has been contentious since its first publication. Nuttall (1841) wrote that the name ". . . alludes to the elegant appearance of the calyx" (p.298). Though the name *Eucephalus* was used by some authors subsequently (Greene 1896-1898; Piper 1906); other authors included the same species in *Aster* (Torrey and Gray 1841; Gray 1884; Greene 1889 and Robinson 1894). Torrey and Gray (1841) discussed *Eucephalus* as a genus, but placed *Eucephalus* species into *Aster*. Greene obviously did not agree, since in later publications he continued to use *Eucephalus* as a genus, while acknowledging the earlier realignment as a synonymy. He considered that the primary differences between *Aster* and *Eucephalus* were in phyllary characters, including their arrangement, shape, size, keel, mid-vein, and pubescence (Greene 1896-1898). Species that he included in *Eucephalus* were *Aster perelegans*, *A. engelmannii*, *A. glaucescens*, *A. ledophyllus*, *A. brickellioides* excluding *A. brickellioides* var. *glabratus*, *A. brickellioides* var. *glabratus*, *A. glaucodes*, *A. paucicapitatus*, and *A. nemoralis*. *Aster nemoralis* was not considered to belong to section *Eucephalus* by any other author.

Jones (1980a) divided section *Eucephalus* (Nutt.) Munz & Keck [California Flora (1959):1194] into two subsections: *Eucephalus* (Nutt.) Bentham & Hooker [*Genera plantarum* (1873) 2:273]; *Turbinelli* (Rydb.) Jones [Brittonia (1980) 32:230-239]. Jones (1980a) placed all taxa that Greene had considered part of *Eucephalus* plus *Aster vialis* and *A. gormanii* (both unknown to Greene) into subsection *Eucephalus* excepting *Aster nemoralis*, *A. glaucodes*, and *A. wasatchensis*. *Aster nemoralis* was placed in *Aster* section *Acuminati* (Alexander in Small) Jones [Brittonia (1980) 32:230-239]. *Aster wasatchensis* was submerged (without explanation) into *A. glaucodes*, then *A. glaucodes* and *A. turbinellus* were placed into subsection *Turbinelli* (Jones 1980a & b). Jones (1980b) placed *A. glaucodes* and *A. turbinellus* together because of similarities involving phyllary characteristics, leaf venation, and inflorescence type. Jones and Young (1983) were not willing to divide the North American Asters into smaller groups because they did not consider the results of their phenetic and cladistic analyses compelling enough to

change the *status quo*.

A more recent revision of North American *Aster* restored many sections, including section *Eucephalus* species, to the genus level (Nesom 1994). He removed *Aster glaucodes* var. *glaucodes*, *A. glaucodes* var. *formosus*, *A. glaucodes* var. *pulcher*, and *A. wasatchensis* from *Eucephalus* and placed them along with *A. horridus* (Wooton & Standl.) Blake (synonym of *Herrickia horrida* Wooton & Standl.) into *Eurybia* (Nutt.) Nesom section *Herrickia* (T. & G.) Nesom [Phytologia (1994): 258]. *Aster wasatchensis* was moved based on similarities with *Aster horrida* of clasping sessile leaves and the presence of green bracts immediately below the involucre; *A. glaucodes* var. *glaucodes* was moved based on similarities with *A. horrida* and *A. wasatchensis* of the leaf base and leaf colour (Nesom 1994). *Aster glaucodes* var. *formosus* was submerged into *Aster glaucodes*. *Aster glaucodes* var. *pulcher* was raised to species level (*Eurybia pulchra* (Blake) Nesom) because it had smaller leaves, acute phyllaries and glandular trichomes than the others (Nesom 1994).

Noyes and Rieseberg (1999) used internal transcribed spacers (ITS) of nuclear ribosomal DNA to develop a phylogeny of members of tribe Astereae. Their study included 26 North American samples (one per species), but did not include any from *Aster* section *Eucephalus*. Their nomenclature for North American *Aster sensu lato* followed Nesom. One of their conclusions was an agreement with Nesom that North American Asters are not closely related to Asian *Aster*. They also pointed out that their study was preliminary because they had used only 55 taxa (less than 2% of all Astereae species).

Aster floral morphology

The flowering heads of *Aster* are highly modified inflorescences, containing several to many small female or bisexual flowers on a common receptacle, all surrounded by an involucre (Harris 1995; Cronquist 1955) (**Figure 1**). Most species in section *Eucephalus* are radiate (with both disk and ray florets) but some are discoid (with only disk florets).

Disk florets, found in the centre of the head, have both male and female organs. The petals are fused completely except for short lobes at the tip (Cronquist 1955). Ray florets

have partially fused petals typically with three longer lobes that form the ray floret limb.

Anthers are connate and release pollen toward the centre of the floret. Pollen is then carried upward by the growth of the style through the centre of the fused anthers (Cronquist 1955).

The ovary has two fused carpels. The style frequently divides into two equal parts after it has grown through the anther tube, and becomes receptive to pollen on certain parts of the surface (Cronquist 1955). Species in section *Eucephalus* always have achenes topped by a feathery pappus which is homologous to the calyx (Harris 1995).

Description of morphological characters of *Aster* section *Eucephalus*

Eucephalus species were described as follows (Greene 1896; Howell 1903; Rydberg 1954): perennials with a caudex, without rosette leaves, and with similarly shaped leaves on the stem; leaves along the stem alternate, sessile, and either lanceolate or oblong; the leaves near the base of the stem are bract-like; inflorescence of heads cymose (*i. e.* with a

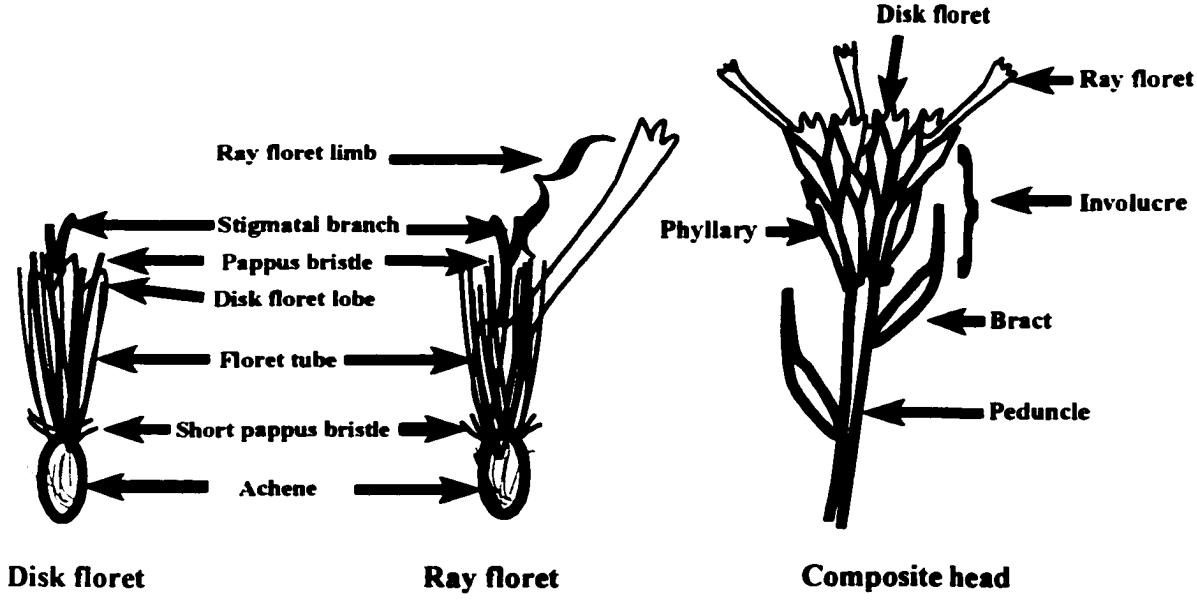


Figure 1: Diagram of an *Aster* head and florets.

head terminating the axis); involucre imbricated, in 3 to 5 rows, with wide phyllaries which are keeled or have a prominent midrib; pappus in two whorls, the inside pappus bristles longer than the floral tube; the longer pappus bristles with expanded tips; ray florets pink, purple, blue or white, few in number and female; disk florets yellow, tubular, and bisexual; stigmatal branches lanceolate and acute; achenes oblong and compressed, hirsute when young and becoming glabrate with age. For eight of the taxa, chromosome counts were reported as $n = 9$ (one to four samples each) (Anderson *et al.* 1974; Jones 1980b, Semple 1985).

Differences in morphological characters among species of *Aster* section *Eucephalus* reported in literature

I compiled descriptions (keeping the original authors' terminology) of *Aster* section *Eucephalus* species and varieties (Table 1). This background information was used to select characters for systematic study, to provide additional detail about each species beyond what was used for this study, and to assign phenetic groups to previously defined taxa.

Table 1: Characteristics reported for *Aster* section *Eucephalus* arranged by species. Information sources are listed at end of table. Names and characters of varieties are enclosed in parentheses.

Species (variety)	Plant height	Growth habit	Underground/ caudex	Leaf sizes and shapes	Sources
Aster breweri plus (var. *multibracteata*)	10-100; (30)	ascending to erect; corymbose or racemosely branched; (strict); few to 20 stems	woody, branched caudex; hard root crown	branch leaves smaller	18; 14; 6; 1
A. brickellioides plus (var. *glabratus*)	60-90; (30-60)	strict, erect, paniculately branched above; (strict); occ. much branched	woody, creeping branched rhizome; woody caudex	smaller above	13; 1; 2
A. engelmannii	20-152; 50-150; 60-90	robust, erect, strict or branched	subrhizomatous or rhizomatous; woody root; woody caudex	largest near mid stem; upper reduced	20; 17; 14; 1; 2
A. glaucescens	30-90, 40-150	slender stems, branched above; erect and corymbose	stout caudex	nearly uniform; numerous	13; 8; 1; 5
A. glaucodes plus (var. *pulcher*)	11-70; 30-50; 13-45	branched	rhizomatous; extensively creeping filiform rootstocks	reduced upward	20; 19; 8
A. gormanii	11-15; 10-30	strict, few branches	short and stout rhizome to slender and branched rhizome	nearly uniform; crowded	1; 5
A. ledophyllus plus (var. *covillei*)	30-80 (30); 30-60, occ. 80	strict, erect; (racemose-corymbose from near middle)	stout, woody caudex	nearly uniform; numerous	15; 13; 1; 5
A. paucicapitatus	25-45; 20-50	no branching, flexuous; erect or ascending	woody root; short caudex, occ. with tap root.	nearly uniform; numerous	16; 1; 5
A. perelegans	30-100; 60-90	branching above	woody caudex, roots fibrous	smaller upward	17; 19; 1; 5
A. vialis	90-120	strict below inflorescence	short, crown-like stock	smaller upward	12; 1; 5
A. wasatchensis	35-65		subrhizomatous		20

Table 1: Continued.

Leaf characters in detail						
Species (variety)	Length cm.	Width cm.	Shape	Tip	Base	Sources
Aster breweri plus (var. *multibracteata*)	2-5; 1-3; 1.25-3.8; 1-5; (3-4)	0.6-2.0; 0.5-2.0; (0.6)	linear-lanceolate; oblong to ovate lanceolate; (linear-lanceolate)	acute; mucronate; (narrowly acuminate)		18; 14; 2; 1; 6
A. brickellioides plus (var. *glabratus*)	3-6; 4-5.5; (3-6); 2-6	1-2;0.5-2.0	oval/elliptic-oblong to linear-oblong; linear-subulate or -lanceolate (ovate-lanceolate to oblong)	acute to obtuse	round	2; 1; 7
A. engelmannii	5-10; 5-3.8; 4-10; 4-11; 2-13.5	1.5-3.5; 0.3-4.6	lanceolate; elliptic to oblong; lance-ovate; broad. lanceolate; or oval to ovate	± acute; or acuminate	rounded or narrowed	15; 14; 2; 1; 20
A. glaucescens	3.5-9.5	0.4-1.5	lanceolate or linear-lanceolate; narrow lance-elliptic	acuminate to acute, mucronate	narrowed	1; 5
A. glaucodes plus (var. *pulcher*)	3-7; 5-7.5;1.4-12.5	0.4-2.5	lanceolate-linear or -oblong; lance-oblong to elliptic or oblong			20
A. gormanii	1.5-3.0; 1.8-3.0	0.3-1; 0.4-1	elliptic; oblong; lance-elliptic	obtuse or acute, apiculate		1
A. ledophyllus plus (var. *covillei*)	3-7; 2-6; 1.5-5.5	0.5-2; 0.4-2	narrow-lanceolate; broad-elliptic; oblong to oblong-lanceolate	acute to obtuse; callous apiculate	round	15; 2; 1; 5
A. paucicapitatus	2-4; 2-3; 1.5-3.4	0.4-1.3; 1.5-3.5	elliptic; lance-elliptic; elliptic-oblong	acute; obtuse & apiculate	rounded or narrowed	15; 1; 5
A. perelegans	2-5; 2.5-6	0.3-1; 0.4-1.1	linear-oblong; lanceolate	acute, rarely obtuse	round	1; 5
A. vialis	2-11; 3.5-6; 7-9	0.5-3.0; 0.8-2.3	elliptic; broadly lanceolate; ovate-lanceolate	acute; apiculate	round	4; 1
A. wasatchensis	1.8-8.5;4-6	0.63-1.3; 0.6-2.4	lanceolate; oblong; oblanceolate			8; 20; 17

Table 1: Continued.

Leaf edges and venation			
Species (variety)	Edge	Venation patterns	Sources
Aster breweri plus (var. *multibracteata*)	entire to ± toothed	3 nerved from base	1
A. brickellioides plus (var. *glabratus*)	entire, occasionally narrowly revolute; (entire)	reticulate veined; 3 nerved from base; indistinctly feather veined	1; 7; 10
A. engelmannii	generally entire; revolute	1 nerved with a pair of weaker, basal or subbasal veins, loosely venose, closely reticulate	1; 5
A. glaucescens	obscurely serrulate, occasionally entire; frequently entire, scabrous-ciliolate	1 nerved and with a pair of weaker veins, somewhat venose; strong conspicuous white midvein and some reticulation of the surface	1; 11
A. glaucodes plus (var. *pulcher*)	entire	when dry reticulate-venulose both sides; 1 nerved, reticulate veined	8; 19
A. gormanii	entire	1 nerved with pair of basal veins	1
A. ledophyllus plus (var. *covillei*)	entire; occasionally few irregular sharp teeth	1 nerved with pair of weak basal veins	1
A. paucicapitatus	entire or nearly	1 nerved with pair of weak lateral veins	1
A. perelegans	entire	1 nerved with pair of weak veins arising from the base; veins inconspicuous; loosely or scarcely reticulate	1; 8; 5
A. vialis	entire or rarely with few sharp teeth	1 nerved with pair of basal veins	1
A. wasatchensis	entire		20

Table 1: Continued.

Species (variety)	Stem, leaf, and involucral bract surfaces				
	On stem	Leaves		On involucre phyllaries	Sources
		upper surface	under surface		
Aster breweri plus (var. *multibracteata*)	glabrate; mod. hirtellous & gland. puberulent; ± gland. to ± tomentulose; (spars. villous-arachnoid; peduncles similar but viscid)	glabrate; woolly pubescent; stipitate gland.; or gland.-hairy (sparingly arachnoid-villous)		glabrate; sparse woolly; stipitate gland.; ± tomentose to gland. hairy; ciliate	2; 1; 6
A. brickellioides plus (var. *glabratus*)	densely stipitate gland.; ± minutely tomentulose; glabrescent (glabrous - occ. gland. below involucre)	sub-coriaceous, glabrous or glabrescent; (glabrous)	± tomentose; (occ. roughish-puberulent)	± tomentose dorsally, occ. glabrescent, (glabrous or occ. minutely gland.)	2; 1
A. engelmannii	subglabrous; ± hairy; long gland.; spars. pilose or near glabrous below and puberulous above	sub-glabrous; slightly gland.; glabrous except on costa where spars. pilose or pilosulous on veins	villous-puberulent; glabrous except pilose on costa	glabrous or pubescent with pilose-ciliate toward apex	2; 15; 1
A. glaucescens	glabrous and somewhat glaucous; scabrous	glabrous and glaucous; scabrous		gland.-puberulous or subglabrous, obscura. lacerate-ciliate	1
A. glaucodes plus (var. *pulcher*)	glabrous, glaucescent; no gland. trich. on peduncles (puberulent to gland. on peduncles)	± coriaceous, margins scarc. scabrous; glaucous; glabrous		glabrous; slightly ciliate	8; 17
A. gormanii	spars. stipitate-glandular	hispidulous-ciliolate, stipitate-glandular	hispidulous-ciliolate, stipitate-glandular	glabrous with pilose-ciliate toward tip	1; 3

Table 1: Continued.

Species (variety)	Stem, leaf, and involucral bract surfaces				Sources
	On stem	Leaves		On involucre phyllaries	
		upper surface	under surface		
Aster ledophyllus plus (var. *covillei*)	± hairy; tomentose or occ. loosely pilose; peduncles glandular and freq. tomentulose (spars. tomentose; pendunc. granular-glandulous); glabrous	± glabrous; slightly hairy; glaucous	cottony; ± tomentose; griseous- or cinereous-tomentose; (spars. tomentose)	finely glandular, obscurely ciliate; (glandular puberulent)	15; 14; 2; 1; 9; 5
A. paucicapitatus	stipitate-glandular and thinly spreading-pilose	stipitate-glandular and thinly spreading-pilose and ciliolate		glandular-puberulent; obscura. glandular and spars. pilosulous, ciliate above	15; 1; 5
A. perelegans	finely incurved-puberulous; minutely scabrous, esp. at margins; occ. glandular	hispidulous-ciliolate, finely roughish-hispidulous; scabrous with close hairs and obscure dots	finely roughish-hispidulous	densely villous-ciliate, puberulous or subglabrous	1; 19; 5
A. vialis	dens. stipitate-glandular & spars. pilose; panicle branches - glandular with spreading hirsute pubescence; glabrous	obs. glandular	spars.-pilose; dull & stipitate-glandular & spars. pilose	stipitate-glandular, occ. obscura. lacerate-ciliolate	4; 1; 5
A. wasatchensis	glandular-puberulent; glabrous	glandular puberulent to glabrous; ± glaucous		glandular	20; 17

Table 1: Continued.

Ray floret characters			
Species (variety)	Colour	Count	Sources
Aster breweri plus (var. *multibracteata*)		0	18
A. brickellioides plus (var. *glabratus*)	pale violet; purple	0; 0-5	2
A. engelmannii	white; purple; rose purple	5-10; 23; 8-13; 8-23	2; 1; 8; 14; 20
A. glaucescens	purple	13; 8	1
A. glaucodes plus (var. *pulcher*)	bright violet; white, violet; pink	14; 10-20	8; 17; 20
A. gormanii	white; dries pink	12	1
A. ledophyllus plus (var. *covillei*)	lavender-purple, pink to lavender, violet to purple; (lavender-purple; deep violet)	2-5; 13; 6-20; 8, 13 or 21; (5-7)	1; 2; 9
A. paucicapitatus	white	12-18; 13, occ. 8 or 12	1; 16; 5
A. perelegans	deep violet; violet or purple; white	6-11; 8, 5; 6 or 7 (to 10)	1; 19; 17
A. vialis		0	4; 20
A. wasatchensis	white or pink	15, 20; 15-25	20; 17

Table 1: Continued.

Disk floret characters					
Species (variety)	Count	Length (cm)	Lobe length (cm)	Style appendages	Sources
Aster breweri plus (var. *multibracteata*)	15; 10-25(35)	0.085-0.11 (0.14)	0.08-0.15;0.01	(filiform, exserted, twining around each other at base)	18
A. brickellioides plus (var. *glabratus*)					
A. engelmannii		1.5-2.5		branches lanceolate; attenuate-subulate	15; 13
A. glaucescens		0.12-0.20			1
A. glaucodes plus (var. *pulcher*)				lanceolate, acute	19
A. gormanii		1.00			
A. ledophyllus plus (var. *covillei*)		0.12-0.20		branches lanceolate	15
A. paucicapitatus		1.0-1.5		branches lanceolate	15
A. perelegans	15-20	0.07-0.12		lanceolate, acute; linear-subulate, hardly acute, equalling the stigmatic portion	19; 13
A. vialis				narrowly oblong-lanceolate	12
A. wasatchensis					

Table 1: Continued.

Achene characters					
Species (variety)	Achene size (cm.)	Achene shape	Number of ribs	Surface	Sources
Aster breweri plus (var. *multibracteata*)	0.3-0.5 by 0.06-0.13	(flat); obovate; compressed obconate	3 - 5	(villous); strigous-pubescent; mod. strigose	6; 8; 18
A. brickellioides plus (var. *glabratus*)		compressed		sparsely pilose to essentially glabrous; (hirsute)	1; 10
A. engelmannii		obovate-oblong with narrowish summit,		appressed pilose; sparsely-pubescent; mostly hairy	1; 8; 10; 5
A. glaucescens				appressed-pilose; hairy throughout	1; 5
A. glaucodes plus (var. *pulcher*)		narrow		pubescent	8
A. gormanii			3	pilose	1
A. ledophyllus plus (var. *covillei*)			5	thinly pilose; glabrous; hirsute at summit	1; 10; 13
A. paucicapitatus		flattened	4	appressed-pilose; sparse; hairy all over	1; 11; 5
A. perelegans		flat	5	short pilose; hirsute turning glabrate at maturity	1; 13
A. vialis	0.3 by 0.1	compressed; oblong; elliptic in x-section, obovate-cuneate to oblanceolate cuneate	2 - 5		1; 4; 12
A. wasatchensis				hairy	20

Table 1: Continued.

	Pappus characters				
Species (variety)	Description	Outer pappus type	Inner pappus type	Colour	Sources
Aster breweri plus (var. *multibracteata*)	thick; double	short fine bristles or none; (short, barbellate); setose; few thin bristles, 0.025-0.1 long	25-40 barbellate bristles, 0.6-0.96 L		1; 6; 14; 18
A. brickellioides plus (var. *glabratus*)		short, setose; barbellate, slightly dilated at apex	bristles somewhat flattened apically	tawny	1; 7
A. engelmannii	graduate; occ. with few short setae	setose	scarcely enlarged apically		1; 5
A. glaucescens	almost double; freq. with few short setae	short setose	dilated apically	brownish	1; 5
A. glaucodes plus (var. *pulcher*)		not thickened	not thickened		19
A. gormanii	somewhat graduate; double	short, setose	enlarged apically	tawny	1; 5
A. ledophyllus plus (var. *covillei*)		few, very short, setose	slightly dilated apically		1; 5
A. paucicapitatus	soft, graduate; copious and fine; unequal bristles but not conspic. double	not dilated	not dilated	brownish white	1; 11; 16
A. perelegans	unequal bristles	short, setose	± dilated apically		1; 19
A. vialis	slightly flattened and enlarged at apex	closely ciliate; few short setae	± dilated apically; closely ciliate	dune	1; 4; 13; 5
A. wasatchensis					

Table 1: Continued.

Head and inflorescence characters							
Species (variety)	Head		Inflorescence branching	Involucre			Sources
	quantity	size (cm.)		shape	size(cm.)	rows	
Aster breweri plus (var. *multibracteata*)	1-3 (7) per branch		cyme; corymbiform, open paniculate or racemiform; naked or leafy-bracteate	broadly campanulate; turbinate cylindrical; subequal	0.7-1.1 H 0.62- 1.0 H	2-3; (4-5); 3-4; (3)	1; 2; 18; 14
A. brickellioides plus (var. *glabratus*)	numerous		elongate-oblong panicle; (leafy corymbiform panicle)	turbinate; (campanulate) imbricate	0.7-0.9; (0.8-0.9)	6; (4-5)	1, 2; 10
A. engelmannii	few to many	2.0-4.5 W	short rounded cyme or panicle with narrow lanceolate or subulate bracts	broadly campanulate; hemispheric; imbricate	0.7-1.0; 0.8-1.2	5-6	1; 15; 14; 5
A. glaucescens	6-14	2.5-3.5 W	leafy branches	broadly campanulate; imbricate	0.6-0.8; 0.7-0.9 H	4-5	1; 5
A. glaucodes plus (var. *pulcher*)	few to numerous		corymbose; contracted corymbs or somewhat racemose	imbricate	0.6-0.9 H X 0.7-0.9 W		20; 19
A. gormanii	single; occ. 2-4	2.0-2.5 W	peduncles 1.5-2.5 cm. L	hemispheric, sub-equal	0.6-0.8	3-4	1; 5
A. ledophyllus plus (var. *covillei*)	few or numerous, occ. single	2.5-4.0 W	corymbosely or thyrsoidly, naked or bracteate; cyme	campanulate; (narrowly campanulate)	0.8-1.0; 0.7-1.1	4-5	1; 2; 13; 5
A. paucicapitatus	solitary or few; less than 4	2.5-4 W; 3-3.5 W	peduncles 1-7 cm. long	hemispheric-campanulate, subequal bracts	0.1-1.0 H	3; 2-3	1; 16; 15; 5
A. perelegans	1 to many	2.0-2.8 W	short rounded cyme or a cymose panicle; corymb	narrow campanulate; imbricated	0.8-1.0; 0.6-0.9	5-7	1; 19; 5
A. vialis	several to numerous	1.0-1.2 H; 1.0-1.5 W	short peduncles, narrow, oblong, leafy panicle; columnar-compound cyme or racemose cyme	turbinate to campanulate; columnar becoming campanulate; imbricated	0.7-0.8; 1.0 H; 0.8-1.0	5-6	1; 12; 5
A. wasatchensis	several to numerous		corymbose		0.80-1.15 L X 0.1-0.2 W; 1.0-1.2 W		20; 17

Table 1: Continued.

Species (variety)	Involucral phyllary characters						
	Phyllary shape			Phyllary tip		Phyllary Base	Sources
	General	Outer	Inner	Outer	Inner		
Aster breweri plus (var. *multibracteata*)	lance-linear to lance-oblong (narrowly ovate to lanceolate)	0.4-0.7 L by 0.07-0.17 W	0.5-1.4 L by 0.06 - 0.28 W	acuminate (acute or acuminate)	acuminate (acute or acuminate)	±pale	1; 2; 18
A. brickellioides plus (var. *glabratus*)	linear or ovate to linear-oblong or oblong	(lanceolate)	(broad lanceolate)	spreading	acute or obtuse, erect	indurate-chartaceous, scarious margin; base ± white	1; 2
A. engelmannii		linear to subulate or lanceolate	lanceolate, lance-ovate to oblong, lance-oblong	attenuate or acuminate	acute, chartaceous; blunter	indurate; chartaceous	1; 2; 5
A. glaucescens	narrow	subulate to lanceolate	ovate to oblong-lanceolate	long, loose	attenuate, short or obsolete, acuminate		20
A. glaucodes plus (var. *pulcher*)	ovate		lanceolate	comm. obtuse, occ. acute	acute		20; 17; 19
A. gormanii	lance-ovate	lanceolate	ovate or oblong-ovate	acute or sub-acuminate	obtuse	indurate-characeous	1; 5
A. ledophyllus plus (var. *covillei*)	narrow	subulate to lanceolate	lance-ovate to oblong	attenuate	acute	short indurate	1; 2; 5
A. paucicapitatus	linear lanceolate	0.8 L		acute	acute	pale, shining-chartaceous	1; 16; 15; 5
A. perelegans	ovate		linear-oblong	acute	acute		1; 17; 5
A. vialis	linear to lanceolate		linear-oblong	acute or acuminate	acute or acuminate	chartaceous	1
A. wasatchensis				acute to attenuate	acute to attenuate	scarious	20

Table 1: Continued.

Species (variety)	Phyllary characters: Edge: General	Edge: Inner	Tip colour	Costa or keel	Sources
Aster breweri plus (var. *multibracteata*)	(occ. purple margined)		green	± keeled, green	1; 2; 18
A. brickellioides plus (var. *glabratus*)	(indurated, scarious margin, ciliate near tip, rarely tinged with purple)	purplish	green to purple	±keeled, green	1; 2
A. engelmannii	narrowly scarious-margined, pilose-ciliate toward apex	purple margined and villous-ciliate	green	± keeled, green; strong mid vein	1; 2; 5
A. glaucescens	lacerate-ciliate; narrowly anthocyanic	narrowly scarious-margin	green; light green	carinate 1 rib	20; 5
A. glaucodes plus (var. *pulcher*)	slightly ciliolate			prominent costa, comm. pink	20; 17; 19
A. gormanii	narrow, lacerate-scarious, pilose-ciliate toward apex, occ. purple tinged		sub-herbaceous; green	prominent costa	1; 5
A. ledophyllus plus (var. *covillei*)	narrow scarious with purple tinge; short, fringed ciliate		outer: herbaceous; others: comm. purple	± keeled, green; strong mid vein or slight keel	1; 2; 5
A. paucicapitatus	narrow, purple			slight keel, green	1; 17; 15; 5
A. perelegans	characeous-indurate, narr. Scarious; villous hyaline ciliate, puberulent		inner: deep purple	strong, green costa	1; 17; 5
A. vialis	slightly purplish tinge		herbaceous	1 nerved, strong costa, ± keeled	1
A. wasatchensis			herbaceous		20

Table 1: Continued. Habitats and distributions.

Habitats and distributions					
Species (variety)	Habitat description	Political boundaries	Flowering time	Elevation	Sources
Aster breweri plus (var. *multibracteata*)	Open rocky slopes and coniferous forests, (dry rocky slopes); subalpine meadows, open woods; open pine and fir woodlands to tree-line meadows, along streams, in dry washes, and on dry, well drained slopes. Canadian and Hudsonian, (Canadian)	Sierra Nevada from Shasta Co. to Tulare Co and on San Gorgoino Peak, California; adjacent Nevada, (Siskiyou, Trinity and Tehama Counties, California)	July to September, (July-August); (June) July-August (September)	1500-2700	1; 2; 18
A. brickellioides plus (var. *glabratus*)	dry ridges and rocky slopes, (dry forested slopes); dry woods, rocky places. Arid transition zone (arid transition and lower Canadian)	Siskiyou mountains, SW Oregon and adj. California (Siskiyou Mt. area, Josephine and Jackson Co.s, Ore. and adj. Siskiyou Co., Cal.)	July to October; (August to September)	600-2000	1; 2
A. engelmannii	open forests; mountain brush, juniper, Douglas fir, aspen, white fir, lodgepole pine and spruce-fir; meadows; open woods, timbered area. Canadian and Hudsonian; montane	N & SW Alberta to Colorado and NE Nevada and S BC and southward in Cascade Mtns of Wash. Rarely at high elev in Siskiyou Mtns, Calif.; Utah	late June to September	1950-3200; 1800-2000	1; 20; 2; 17; 5
A. glaucescens	open slopes; open woods. Arid transition	region around Mt. Adams, Yakima and Klickitat Co., Wash.; S. to Columbia River	July to October		1; 5
A. glaucodes Blake plus (var. *pulcher*)	calcareous substrates at high elev. and in saline seeps at low or moderate elev., sage brush, pinyon-juniper, mountain brush, ponderosa pine, ryegrass, spruce-fir, Douglas fir, lodgepole pine and hanging garden communities (salt desert shrub, sagebrush, pinyon-juniper, and ponderosa pine)	(Washington and W. Kane Co., Utah), Utah, Idaho and Wyoming, S. to Arizona and Colorado		1220-3050 (825-2136)	20

Table 1: Continued.

Habitats and distributions					
Species (variety)	Habitat description	Political boundaries	Flowering time	Elevation	Sources
Aster gormanii	dry rocky slopes & cliffs. Boreal zone	Mt. Jefferson vicinity, Lane and Jefferson Co., Ore.; Cascade Mountains	July; August		1; 5
A. ledophyllus plus (var. *covillei*)	meadows and open woods; up to timber line. Canadian and Hudsonian	Cascade Mts. of Wash., south to S. Oregon, and adj. N. California as far south as mountains of Trinity and Humboldt Co., Cal. (Crater Lake to Mackenzie Pass)	July to September	1300-1900	1; 2; 5
A. paucicapitatus	ridges and dry slopes; open slopes at moderate to high elev. Boreal.	S. Vancouver Isl., B. C., Olympic Mtns, Wash.	Aug-September		1;5
A. perelegans	dry mountain slopes; open in foothills & at mod. elevations. Arid transition and Canadian; sub-montane, montane	mountains of NE Oregon eastward to SW Montana and Utah; also Nebraska; S Nevada	July-Sept.; July - Aug.		1; 17; 5
A. vialis	Rocky hill sides; open woods, stony hill sides	Willamette Valley, Lane Co. to Douglas Co., Ore.	July to Aug.; July		1; 12; 5
A. wasatchensis	pinyon-juniper, aspen, limber pine and spruce-fir communities. Montane	Garfield, Iron, Millard and Piute Co., Utah	Aug.	1890-3050	20; 17

Sources: 1=Abrams and Ferris 1960; 2=Allen 1993; 3=Blake 1928; 4=Bradshaw 1920; 5=Cronquist 1955; 6=Eastwood 1906; 7=Eastwood 1931; 8=Gray 1884; 9=Greene 1897; 10=Greene 1889; 11=Greene 1896; 12=Henderson 1933; 13=Howell 1903; 14=Jepson 1957; 15=Piper and Beattie 1915; 16=Robinson 1894; 17=Rydberg 1954; 18=Semple *et al.* 1988; 19=Torrey and Gray 1841; 20=Welsh *et al.* 1987.

II. PHENETIC ANALYSIS

INTRODUCTION

In preparation for cladistic analysis and biogeographic studies, taxa must be circumscribed by using sample specimens in a phenetic analysis. Initially, the sample specimens are not assigned to any group. A clustering algorithm is then used to arrange them into groups based on similarities (calculated using morphological characters) between pairs of specimens. Often these clusters can be associated with previously defined taxa; those that cannot be associated may be identified as new taxa. Attributes of each taxon can be precisely and consistently defined by using newly gathered character data. Cladistic and biogeographic analyses use this information.

Character choices

Choice of characters in this study was based on ease of data collection, completeness and condition of specimens, variability of characters among specimens, and theoretical considerations. During phenetic analysis, characters were treated as abstract constructs with various character states. To prevent excessive representation of any type of plant organ, I selected floral and vegetative characters in about equal numbers. If characters were highly correlated, one or more was removed after correlation analysis to prevent related characters from exerting unbalanced influences upon distance calculations and dendrogram construction. I used quantitative, categorical and binary data types to make a thorough description of specimen morphology for use in statistical and cladistic analyses.

Some taxonomists consider reproductive structures more useful in classification because they are less frequently environmentally modified (Jones and Luchsinger 1979). Reproductive structures are probably most informative when systematists are comparing or ordering higher level taxa. Vegetative structures, as opposed to ephemeral floral ones, are more constantly exposed to and subjected to selection by the environment and are probably more useful when recently evolved taxa are being studied. Collecting data from both sources would give balanced information about the distant past and recent influences. Personal bias is impossible to eliminate but by using different techniques to study the data,

a researcher can obtain results reproducible by others.

Assessing ability of dendrogram to represent original data matrix using cophenetic correlations

Distance measures between pairs of specimens may assume a continuous range of values. A dendrogram, by definition, must divide specimens into two groups at each node. The distance of a node from the base may be a compromise that results from averaging conflicting distances between members of one cluster and those of the other. The generated dendrogram will be an approximation of the distances among all members represented. Cophenetic correlations are a measure of the accuracy with which the dendrogram represents the original matrix (Sneath and Sokal 1973). NTSYS programs calculate a matrix of theoretical distances between each pair of specimens based on the dendrogram structure. The structurally based matrix is compared with the original data matrix and a cophenetic correlation coefficient is calculated. The higher the value, the better the fit.

MATERIALS AND METHODS

Specimen and character choices for analysis

This study included species considered by most workers in this group to be members of section *Eucephalus*. *Aster turbinellus* was included because it had been proposed as a new member for the section, although it has since been removed. It could act as a test for the proficiency of analysis methods while simultaneously being evaluated as a possible member. Confidence could be placed in these methods if *A. turbinellus* specimens were grouped together instead of being included in other groups, and *A. turbinellus* specimens could serve as an outgroup during cladistic analysis.

Herbarium specimens were borrowed for this project from CAS, UC, DS, USFS, OSC, RM, JEPS, WILLU, WS, BRY, UTC, UVIC, COLO, UBC, CAN, V, WTU, and WTU(JWT). Label information was collected from herbarium sheets at the University of Victoria and Royal British Columbia Museum. When completed, the data base had

records of 1669 separate collections.

I carried out a pilot study to test data collection techniques and to assess overall variability in section *Eucephalus* by using one herbarium sheet from each included species. These specimens were not randomly chosen, but were the first intact and complete sheets discovered for each species. The assigned species name was omitted on the data sheet to reduce bias in recording and later assessment. More than one hundred characters were measured or assessed. Measurements were made with a flexible tape, small ruler, and calibrated hand lens.

I chose characters carefully, taking into consideration possible environmental influences on phenotypic characters. Under circumstances of poor nutrition or lack of water, a plant may exhibit reduced size, fewer leaves and fewer seeds overall (Richards 1986). Vegetative plasticity can cause problems for a systematist. Nevertheless, phenotypically plastic characters should be considered since they may contribute significantly to species' ability to survive and reproduce in a variety of habitats and, more important, may be of taxonomic significance.

Characters were dropped for several reasons. I initially recorded vesture in considerable detail so that trichome type and distribution contributed more than one third of the total characters. Because of their excessive representation in the data set, the vesture characters were subsequently reduced in number and complexity. Reducing destructive sampling resulted in elimination of disk floret counts, phyllary counts, bract measurements by involucre row and leaf base measurements. Some characters took too much time to collect and were replaced by a simpler method; *e. g.* angle of the leaf tips was assigned to categories rather than measured. Colours of the florets were unreliable in herbarium specimens. Destructive sampling was kept to a minimum although a few disk and ray florets from a terminal head were removed, wetted and measured. Only one measurement was taken for each character per specimen because within plant variation was not of interest during this study. By choosing to measure characters at fixed positions on each specimen, I reduced the impact of within-plant variations. Details of chosen characters are explained in Table 2.

Some species are rare and have been infrequently collected; for example, only seven nonduplicated collections of *Aster vialis* were seen (Table 4). In contrast, *Aster engelmannii* specimens numbered in the hundreds. Because of the different numbers of specimens per species available, I used a stratified sampling scheme to select herbarium sheets for measurement to avoid the possibility with a random sampling design of missing rare species. Varieties were not considered separately from species. The lowest sample size was seven. However, to provide enough specimens to allow multivariate analysis programs to compute correctly, at least 10 specimens of more abundant species were chosen, plus 21 extra sheets. *Aster engelmannii* was not well represented in Canada so four more sheets of this species were randomly selected to include the northerly distribution. After completing the analyses using NTSYS, assigning specimens to clusters, and conducting most of the canonical discriminant analyses, I became aware of the unique morphology of a specimen identified as *Eucephalus bicolor*. I choose three specimens from Alice Eastwood's collections of *E. bicolor* to increase representation of what might be a valid taxon.

Analytical tools

I conducted a search for correlated characters and clusters of specimens in the data set, using commonly available software packages and some specially written dBASE programs to calculate Gower's similarity coefficients for each pair of specimens. SYSTAT (SYSTAT, Inc. 1990) was used for the univariate and discriminant analyses because it allowed the use of command files and was more flexible than other statistical computer packages available to me. NTSYS-pc ver. 1.80 (Applied Biostatistics, Inc. 1994) was used for clustering similarity matrices since it was easily available and is frequently used by other researchers.

Because some characters were not quantitative and therefore could not be standardized using means and standard deviations, I used Gower's general similarity coefficients. Distances between each pair of specimens were calculated using Gower's coefficient (S_G) (Sneath and Sokal 1973). The following equation was used:

$$S_G = \frac{\left(\sum_{i=1}^{n} w_{ijk} s_{ijk}\right)}{\sum_{i=1}^{n} w_{ijk}}$$

where:
S_G = Gower's general similarity coefficient
n = number of characters,
j and *k* = plants being compared,
w = weight,
s = score
i = character being analysed

(Sneath and Sokal 1973, p. 135). Weight (*w*) was used to indicate missing data (1 if data present, otherwise 0). The score (*s*) varied depending on data type and was between 0 and 1 for each character. For binary data and logical characters (T, F), the score was set to 1 if two plants matched and otherwise set to 0. Similarly for categorical data, the score was set to 1 when the two plants had the same value, and otherwise 0. Deriving the score for quantitative characters was more complex, and involved division by the range. For these characters, the score was calculated as:

$$s_{ijk} = 1 - \left(\frac{|X_{ij} - X_{ik}|}{R_i} \right)$$

where:
s_{ijk} = score for character *i* for plants *j* and *k*
j and *k* = plants being compared,
X_{ij} = value of character *i* for plant *j*
X_{ik} = value of character *i* for plant *k*
R_i = range of character *i* for whole data set

(Sneath and Sokal 1973, p. 136).

If two plants had the same character values, the score was 1. If the plants were at extremes of the range of values, the score was 0. All others values were between 0 and 1. The minimum value for Gower's similarity coefficient was 0 and the maximum value was the number of characters being compared, or *n*. I wrote DBASE programs to calculate the similarity matrix.

Table 2: Characters used in morphological analysis: variable name, character, data type and description. Leaf measurements were taken from leaves on the main stem, and floral and involucral characters from the largest mature head.

Variable name	Character	Data type	Description of measurement or coding
A	First leaf shape parameter	quantitative	calculated by quadratic fit to length and width measurements of middle leaf.
A1	Second leaf shape parameter	quantitative	calculated by quadratic fit.
A2	Third leaf shape parameter	quantitative	calculated by quadratic fit.
BRCHCNT	Number of branches	quantitative	count of branches arising from main axis. Did not include secondary branches.
BRCTPDCL	Number of bracts on peduncle	quantitative	count of small bracts immediately below head and above terminal large leaf or branch.
DSKACLNG	Achene length of disk floret (cm.)	quantitative	From base of pappus to base of achene.
DSKACWD	Achene width of disk floret (cm.)	quantitative	From edge to edge across widest part.
DSKLMLNG	Lobe length of disk floret (cm.)	quantitative	From sinus to tip of lobe.
DSKSGLNG	Stigma branch length of disk floret (cm.)	quantitative	From point of branching to tip of stigma.
DSKTBLNG	Tube length of disk floret (cm.)	quantitative	from base to sinus.
DSPPLNG	Pappus length of disk floret (cm.)	quantitative	From base to tip of longest pappus filament.
HDCNT	Number of heads	quantitative	count of every head on specimen.
INVDNS	Density of involucre vesture	categorical ordinal	Estimate by visual inspection of density of all trichomes on involucre. None=0, sparse=1, moderate=1, dense=1.
INVGLND	Involucre vesture glandular	binary	Presence of glandular trichomes on involucre. 1=Yes, 0=No.
INVLNG	Involucre length (cm.)	quantitative	Length of pressed involucre from base to tip of innermost phyllary on terminal head of main axis.
INVPHLCNT	Phyllary count	quantitative	count of number of phyllaries visible on herbarium sheet. About 2/3 of actual total.

Table 2: Continued.

Variable name	Character	Data type	Description of measurement or coding
INVROWS	Number of rows on involucre	quantitative	count of rows of phyllaries.
INVSMPL	Involucre vesture non-glandular	binary	Presence of non-glandular trichomes on involucre. 1=Yes, 0=No.
INVWD	Involucre width (cm.)	quantitative	Width of pressed involucre from edge to edge at centre.
LFBWDNS	Density of middle leaf under surface vesture	categorical ordinal	Estimate by visual inspection of density of all trichomes on middle leaf under surface. None=0, sparse=1, moderate=2, dense=3.
LFBWGLND	Middle leaf under surface vesture glandular	binary	Presence of glandular trichomes on middle leaf under surface. 1=Yes, 0=No.
LFBWSMPL	Middle leaf under surface vesture non-glandular	binary	Presence of non-glandular trichomes on middle leaf under surface. 1=Yes, 0=No.
LFCNT	Number of leaves	quantitative	count of every leaf base or leaf scar visible on the main axis. No count if base of stem was absent.
LFHICLT	Cilia on terminal leaf	binary	1=Yes, 0=No.
LFHIEDG	Margin of terminal leaf	categorical nominal	undulate: 1, few teeth: 2, entire: 3, revolute: 4.
LFHILNG	Length of uppermost leaf (cm.)	quantitative	Same as middle leaf but measured on the first undamaged and accessible terminal leaf that was not a bract.
LFHITP	Tip of uppermost leaf	categorical nominal	Apiculate: 1, acute: 2, acuminate: 3, cuspidate: 4, mucronate: 5, caudate: 6, obtuse: 7.
LFHIWD	Width of uppermost leaf (cm.)	quantitative	edge to edge at widest part.
LFHIWLNG	Length to widest part of uppermost leaf (cm.)	quantitative	from base to widest part of leaf.
LFIN8	Number of leaves in 8 cm.	quantitative	Count of visible leaf bases in 8 cm at middle of main axis.
LFLNG25	Length to ¼ of total length	quantitative	length ¼ distance from base to tip of middle leaf.
LFLNG50	Length to ½ of total length	quantitative	length ½ distance from base to tip of middle leaf.

Table 2: Continued.

Variable name	Character	Data type	Description of measurement or coding
LFLNG75	Length to ¾ of total length	quantitative	length ¾ distance from base to tip of middle leaf.
LFLNGTIP	Length to less than 0.2 cm. of total length	quantitative	length of leaf less 0.2 cm. of middle leaf.
LFMDCLT	Cilia on middle leaf	binary	1=Yes, 0=No.
LFMDEDG	Margin of middle leaf	categorical nominal	undulate: 1, few teeth: 2, entire: 3, revolute: 4.
LFMDLNG	Length of middle leaf (cm.)	quantitative	from base to tip of an easily measured leaf near the middle of the main axis.
LFMDTP	Tip of middle leaf	categorical nominal	Apiculate: 1, acute: 2, acuminate: 3, cuspidate: 4, mucronate: 5, caudate: 6, obtuse: 7.
LFMDWD	Width of middle leaf (cm.)	quantitative	edge to edge at widest part.
LFMDWLNG	Length to widest part of middle leaf (cm.)	quantitative	from base to widest part of leaf.
LFTOOTHED	Presence of any toothed leaf	binary	1=Yes, 0=No.
LFUPDNS	Density of middle leaf upper surface vesture	categorical ordinal	Estimate by visual inspection of density of all trichomes on middle leaf upper surface. None=0, sparse=1, moderate=2, dense=3.
LFUPGLND	Middle leaf upper surface vesture glandular	binary	Presence of glandular trichomes on middle leaf upper surface. 1=Yes, 0=No.
LFUPSMPL	Middle leaf upper surface vesture non-glandular	binary	Presence of non-glandular trichomes on middle leaf upper surface. 1=Yes, 0=No.
LFWD25	Width at ¼ of total length	quantitative	width ¼ distance from base to tip of middle leaf.
LFWD50	Width at ½ of total length	quantitative	width ½ distance from base to tip of middle leaf.
LFWD75	Width at ¾ of total length	quantitative	width ¾ distance from base to tip of middle leaf.

Table 2: Continued.

Variable name	Character	Data type	Description of measurement or coding
LFWDTIP	Width at to less than 0.2 cm. of total length	quantitative	width of leaf less 0.2 cm. of middle leaf.
NODELNG	Internode length (cm.)	quantitative	Length of longest internode at middle of main axis. (Short and long internodes alternate on main stem.)
PHLEDGCI	Middle phyllary edge ciliated	binary	1=Yes or 0=No.
PHLEDGM	Middle phyllary edge membranous	binary	1=Yes or 0=No.
PHLEDGRD	Middle phyllary edge colour	binary	Red: 1=Yes or 0=No.
PHLKLRD	Middle phyllary keel colour- red	binary	Red: 1=Yes or 0=No.
PHLSTWHT	Middle phyllary keel with a white stripe down centre	binary	White: 1=Yes or 0=No.
PHLTP	Middle phyllary tip	categorical nominal	Apiculate: 1, acute: 2, acuminate, cuspidate: 4, mucronate: 5, caudate: 6, obtuse: 7.
PHLTPRD	Middle phyllary tip colour	binary	Red: 1=Yes or 0=No.
PLNTLNG	Plant length (cm.)	quantitative	Length of main axis from where stem attached to rhizome or ground level to top of pappus of terminal floret on main axis. Not recorded if plant was cut above ground level.
RAYCNT	Ray floret count	quantitative	Maximum count of ray florets visible on stem being measured without pulling head apart. Florets were frequently lacking.
RYACLNG	Achene length of ray floret (cm.)	quantitative	From base of pappus to base of achene.
RYACWD	Achene width of ray floret (cm.)	quantitative	From edge to edge across widest part.
RYLMLNG	Limb length of ray floret (cm.)	quantitative	From sinus to tip of limb.

Table 2: Continued.

Variable name	Character	Data type	Description of measurement or coding
RYPPLNG	Pappus length of ray floret (cm.)	quantitative	From base to tip of longest pappus filament.
RYSGLNG	Stigma branch length of ray floret (cm.)	quantitative	From point of branching to tip of stigma.
RYTBLNG	Tube length of ray floret (cm.)	quantitative	from base of tube to base of limb.
STMDNS	Density of stem vesture	categorical ordinal	Estimate by visual inspection of density of all trichomes on middle internode of main axis. None=0, sparse=1, moderate=2, dense=3.
STMGLND	Stem vesture glandular	binary	Presence of glandular trichomes on middle internode of main axis. 1=Yes, 0=No.
STMSMPL	Stem vesture non-glandular	binary	Presence of non-glandular trichomes on middle internode of main axis. 1=Yes, 0=No.

Leaf shape calculations

Shape of a cauline leaf near the middle of the main stem was assessed by measuring the width and length, and widths at ¼, ½, ¾ lengths and 0.2 cm. back from the tip. A quadratic line could be fitted to these measurements because the leaves had simple shapes: lanceolate, linear, ovate or elliptic. SYSTAT module NONLIN (the ESTIMATE command) was used to fit a curve to data for each plant using the following formula:

$$leaf\ width = A + A1 * leaf\ length + A2 * (leaf\ length)^2$$

Parameters A, A1 and A2 were added to the data file and treated as new characters. Each was examined for correlations with other characters.

Analysis of characters

Each character was examined for normality by calculating skewness and kurtosis for the entire data set to identify characters that were skewed, multimodal, or otherwise did not represent a bell-shaped curve.

Correlations among all characters, using data sets of specimens with and without *A. turbinellus*, were run with pairwise deletions: Pearson correlations for quantitative data, Kendall-tau for categorical data, and binary S6 similarity for binary data (Wilkinson 1990). In pairwise deletion, a character with a missing value is removed from calculations along with the opposite character. Using pairwise deletions changes the frequencies between pairs of characters and the differences are reflected in calculations of a sum of squares and cross products. Bonferroni-adjusted probabilities were used for judging significance of the Pearson correlations instead of Bartlett's test because Bartlett's test is affected by nonnormality (Wilkinson 1990). S6 similarity coefficients produce lower correlations and integrate more information than any of the other binary correlation techniques available in SYSTAT. S6 similarity coefficients are calculated using:

$$S_6 = \frac{Number\ of\ pairs\ that\ match}{Number\ of\ pairs\ that\ match\ +\ 2(Number\ of\ pairs\ with\ no\ match)}$$

A data set of ten with five(0,0) and five(1,1) would have an S6 coefficient of 1.00; with 10(1,1) and zero (0,0), it would be 1.00; with five mismatches and five matches, it would be 0.27; three mismatches and seven matches would be 0.66.

Pubescence characters, including density levels and presence or absence of glandular and non-glandular trichomes, were analysed with the TABLE function in SYSTAT to find if any patterns existed among pubescence of stems, leaves and involucres. Because I wanted to retain as many characters as reasonable and this was the first numerical taxonomic study of these species, probability levels were chosen to be low (significance = 0.001 for quantitative data) or, in other words, correlation coefficients had to be greater than 0.400 for one or more variables to be excluded. For categorical data, the correlation coefficients had to be more than 0.500 to be considered significant and S6 binary coefficients more than 0.600.

The data set included characters that were a mix of quantitative, categorical and binary (see Table 2, on page 39) which made impractical simple standardization of the entire data matrix. Problems caused by having different types of data were avoided by

using Gower's general similarity coefficient formula to calculate distances between pairs of specimens.

Six different sets of characters were used for analysis (Table 3). I wanted to know:

1. how cluster membership changed when *Aster turbinellus* was removed from the data set, and whether including ray floret characters caused changes.
2. what clusters were created when only floral characters or only vegetative were

Table 3: Characters used in the six data sets used for phenetic analysis.

Variable name	All	Ray	Tlall	Tlray	Flr	Veg	Variable name	All	Ray	Tlall	Tlray	Flr	Veg
A1	X	X	X	X		X	LF HI LNG	X	X	X	X		X
DSK AC LNG	X	X	X	X	X		LF HI TP	X	X	X	X		X
DSK AC WD	X	X	X	X	X		LF HI WD	X	X	X	X		X
DSK LM LNG	X	X	X		X		LF MD CLT	X	X	X	X		X
DSK SG LNG	X	X	X	X	X		LF MD EDG	X	X	X	X		X
DSK TB LNG	X	X	X	X	X		LF MD LNG	X	X	X	X		X
HD CNT	X	X	X	X	X		LF MD TP	X	X	X	X		X
INV DNS	X	X	X	X	X		LF MD WD	X	X	X	X		X
INV GLND	X	X	X	X	X		LF UP DNS	X	X	X	X		X
INV LNG	X	X	X	X	X		NODE LNG	X	X	X	X		X
INV PHL CNT	X	X	X	X	X		PHL EDG RD	X	X	X	X	X	
INV ROWS	X	X	X	X	X		PHL KL RD	X	X	X	X	X	
INV SMPL	X	X	X	X	X		PHL ST WHT	X	X	X	X	X	
INV WD	X	X	X	X	X		PHL TP	X	X	X	X	X	
LF BW DNS	X	X	X	X		X	RAY CNT	X	X	X	X	X	
LF BW GLND	X	X	X	X		X	RY LM LNG		X		X		
LF BW SMPL	X	X	X	X		X	RY SG LNG		X		X		
LF HI EDG	X	X	X	X			RY TB LNG		X		X		

Notes: All - all specimens without ray floret data. Ray - only specimens with ray florets. Tlall - all specimens but without *Aster turbinellus* specimens. Tlray - only specimens with ray florets but without *A. turbinellus*. Flr - all specimens using only floral characters. Veg - all specimens using only vegetative characters. Variable names were explained in Table 2 on page 39.

used, and how reliable these were.

The data sets were:

1. all 138 specimens (with all ray floret characters removed except ray count since some specimens lacked ray florets);
2. one hundred and eleven specimens (omitting specimens without ray florets but including more ray floret characters);
3. one hundred and twenty-eight specimens (excluding *Aster turbinellus*, and all ray floret characters except ray floret counts);
4. one hundred and one specimens (excluding *Aster turbinellus* and all specimens lacking ray florets but including more ray floret characters);
5. all 138 specimens (using floral characters only, including involucral and disk floret characters, number of heads and ray floret count);
6. all 138 specimens (using vegetative characters only).

NTSYS provided the clustering and phenogram visualization routines. It was used to process similarity matrices of Gower's coefficient produced by DBASE programs. Several clustering techniques were tried: UPGMA (unweighted pair-group arithmetic average clustering), UPGMC (unweighted pair-group centroid clustering), SINGLE (single linkage clustering), FLEXI (flexible clustering), and COMPLETE (complete linkage clustering). Single linkage methods place a candidate into an extant cluster if it is similar to the closest member; complete linkage method compares a candidate with the farthest member (Sneath and Sokal 1973). Flexible linkage methods try to create a compromise between the results from single and complete linkage algorithms by using a parameter to find a midpoint between chained clusters common to single linkage and extreme compact clusters common to complete linkage. Unweighted methods treat every cluster and candidates for the clusters with equal importance. UPGMA algorithms assess a candidate's potential membership in an extant cluster by calculating the mean similarity or dissimilarity of the candidate to every member of the cluster. UPGMC algorithms are similar to those of UPGMA except centroids, instead of means, from each cluster are used in calculations. After each tree was generated, cophenetic correlations were calculated.

The clustering routine that gave the highest cophenetic correlation was used.

Phenograms from the first four data sets were compared and individual specimens were assigned to groups. I initially assigned specimens to groups based on the branching patterns evident in the phenograms rather than by choosing a certain similarity value. Groups were refined by looking for common clusters among phenograms; those individuals that were consistently associated in all four phenograms were assigned to the same group.

Phenograms for the remaining data sets (with only floral or only vegetative characters) were considered separately. Specimens were grouped using the same criteria as for the other phenograms.

Discriminant analysis was used as an exploratory tool to evaluate assignments of specimens to groups. Discriminant analysis uses group centroids for calculations, and eigenvectors point from the origin to those centroids in multivariate space. The eigenvalue for each axis is the sum of the squared values from the projections of the ends of the eigen vectors onto that axis (Kent and Coker 1992). Eigenvalues summarize how close every group is to the axis; groups with eigenvectors with large angles relative to the relevant axis contribute less to the eigenvalue than those with smaller angles. Changes in group membership move the group centroids in multivariate space and alter the eigenvectors. The changes in positions alter the eigenvalue of every axis (Manly 1986). These values are reported as canonical correlations by SYSTAT. Character contributions to the axes are unimportant although correlations between characters and groups can be used to identify any correlation affected by membership changes. SYSTAT computes canonical correlation values (a version of eigenvalues) that measure how well the axes represent the groups in multidimensional space (Wilkinson 1990). Bartlett's residual root test uses chi-square statistics to calculate the significance of the axes by removing them one at a time, starting with the highest dimension (Wilkinson 1990). I rearranged specimens and groups, then evaluated new arrangements by comparing before and after canonical correlation values. If a change in groups caused large decreases in canonical correlation values, it was abandoned; if they increased, it was kept. Characters were

compared between groups by using t-tests or ANOVA, and by inspection of box plots. Decisions were based on the complexity and size of differences, and whether or not they could be attributed to environmental influences.

Discriminant analysis was conducted with SYSTAT (MGLH). Different group sizes were provided to SYSTAT since it defaults to an assumption that groups have equal number of members. Groups with only one member were not included in the analysis. LFHIEDG, LFHITP, LFMDEDG, LFMDTP, and PHLTP were not used in the discriminant analysis because they were nominal (unordered classification) characters. Ray floret characters could not be included because they were lacking in some groups. The characters used were DSKACLNG, DSKACWD, DSKLMLNG, DSKSGLNG, DSKTBLNG, HDCNT, INVDNS, INVGLND, INVLNG, INVPHLCN, INVROWS, INVSMPL, INVWD, LFBWDNS, LFBWGLND, LFBWSMPL, LFHILNG, LFHIWD, LFHIWLNG, LFMDCLT, LFMDLNG, LFMDWD, LFMDWLNG, LFUPDNS, LFUPGLND, LFUPSMPL, NODELNG, PHLEDGRD, PHLKLRD, PHLSTWHT, and RAYCNT.

Mahalanobis distances of specimens from group centroids were calculated using SYSTAT. After specimens were assigned by SYSTAT to a predicted group based on proximity to a centroid, predicted group and actual group assignments were compared. I shifted specimens into predicted groups if the actual groups did not match the predicted. If assigned groups of five or more specimens did not match the predicted groups, analysis was stopped because this provided evidence that the groups were poorly defined.

To illustrate how the discrimination between groups changed before and after the rearrangement of group memberships, graphs for the first two discriminant factors for the original groups and adjusted groups were produced with 90 percent confidence ellipses generated for each group.

Groups close together on phenograms and those sharing the same species identification were compared using univariate techniques such as t-tests or ANOVA for every character. Significance levels were set at 0.01 to keep overlap of character values small. Characters with no variance in one or more groups, therefore not usable for a t-

test, were compared by visual inspection of box plots. Groups were considered distinct if t-tests for several characters showed significant differences or if character box plots did not overlap. For example, if one group had only glandular trichomes on the stem and the other did not, they were considered distinct for that character. On the other hand, if one group had only glandular trichomes on the stem and the other had both non-glandular and glandular trichomes, they were considered not distinct for that character. Complexity of differences was important. A simple set of differences related to lengths or widths might simply imply a poorly grown specimen whereas a complex mixes of differences in colour, vesture and structure lengths could suggest completely distinct groups. If, during the analysis, wide ranges in several characters were noticed, those groups were further scrutinized using graphs to check whether specimens had been grouped incorrectly.

As a further organizing technique, keys were prepared using characters that a field botanist might use. No restrictions based on statistical considerations were placed on the characters used in the identification keys. If two groups were not easily separated, if a group followed several paths in the key, or if a specimen within a group was similar to another group, then group assignments were reconsidered.

An attempt was made to reduce the number of phenetic groups with one or two members. These were compared with groups that were nearby on phenograms, or had been given the same species name on herbarium labels. Using species names as a basis for choosing groups for evaluation may be introducing bias, however experienced taxonomists perceive patterns and connections that may not have been adequately represented by my choice of characters. I wanted to ensure that every reasonable possibility was considered therefore I have used previous identifications as provisional information. Single specimen groups were examined first. Using only the groups under consideration, box plots of each character were placed on the same graph and compared visually. If a character value of the single specimen did not fit within the range of the comparison group, then a disagreement for that character was scored as 1. All disagreements between the specimen and the comparison group were counted. Groups with the lowest number of

disagreements were then evaluated with the single specimen included by comparing canonical correlation values before and after.

Discriminant analyses on the changed groups were conducted using the previously mentioned characters. A specimen was retained in a group if the actual group matched predicted and canonical correlation values did not decrease by large amounts (arbitrarily set at 0.05). Occasionally, larger decreases were accepted if the change could be explained, for example, the specimen was stunted.

Groups with two members were evaluated using a similar technique. If members had been identified as different species, they were added to a test group singly and then together.

After the process of evaluating group membership assignments was completed, discriminant analyses were run on subsets of the groups. The subsets were:

1. only section *Eucephalus* groups (no *Aster turbinellus*),
2. groups collected in Oregon and California,
3. groups occurring in Washington and British Columbia,
4. groups growing in the Canadian and American Rocky Mountain Ranges.

The analyses of subsets were to check that groups were still distinct and to discover if any group member did not match the predicted under the new circumstances.

Descriptive statistics of means, ranges and standard deviations were calculated for each phenetic group. These formed the basis for assigning species names to groups and, if necessary, creating newly named taxa. The statistical information was used in the descriptions of the taxa and preparation of the final identification key.

RESULTS

General description of sample data set

After completing stratified sampling of available herbarium sheets, the number of plants per species, as determined from the herbarium label, varied from seven to 14 (Table 4). Three more plants identified as *Eucephalus tomentellus* or *Eucephalus bicolor* were added near the end of the discriminant analysis.

Tests of assumptions of normality and skew

The data set of 138 specimens and all characters were assessed as a whole to discover how well assumptions of normality were met. Characters examined for univariate normality either met the criteria, were skewed to the right or had a distribution with two or more peaks. The uppermost leaf lengths, plant lengths (excepting one outlier), involucre widths and lengths, and middle leaf widths showed normal or almost normal distributions. Widths of leaves near the top and numbers of heads per plant were skewed to the right. The number of ray florets showed peaks at 8, 12 and 18; one plant (specimen 53, *A. glaucodes*) had 32 ray florets. The pattern of peaks at 0, 8, 12 and 18 numbers of ray florets approximated a Fibonacci series. Lengths of the middle cauline leaves showed three high frequency ranges: 3.0 - 3.5 cm., 5.0 - 5.5 cm., and 7.0 - 8.5 cm. Plant lengths were missing from 30 specimens because they had been collected without basal parts or were missing tops. Ray floret counts on herbarium specimens were not very reliable since florets appeared to fall off easily and were hidden by other plant material. The basic assumption by statistical tests of normally distributed characters was not true for several characters and could not be corrected by transforming data.

Results of correlation analyses

Correlations among characters for 138 specimens have been listed in tables

Table 4: Number of specimens for each species after completing stratified sampling.

Species	Number of Records	Species	Number of Records
Aster breweri	10	*A. ledophyllus*	12
A. brickellioides	12	*A. ledophyllus var. covillei*	1
A. brickellioides var. glabratus syn. *A. siskiyouensis*	1	*A. paucicapitatus*	12
A. engelmannii	14	*A. perelegans*	13
A. glaucescens	10	*A. turbinellus*	10
A. glaucodes	12	*A. vialis*	7
A. gormanii	12	*A. wasatchensis*	12

(quantitative characters in Table 5 and binary characters in Table 6). Density of trichomes on the stem and leaf under surface (with *Aster turbinellus* included: 0.564; without *A. turbinellus*: 0.594) were the only correlated categorical characters. Leaf tips, phyllary tips, and leaf edges were not correlated.

The correlation between number of primary branches and number of heads was not surprising since branches usually ended in a head. Negative correlations between number of leaves and internode length combined with positive correlation between middle leaf size and internode length reflected the tendency toward lower leaf density on taller plants. Longer plants had more leaves, more branches, more phyllaries, and larger leaves but not more heads; number of heads on a plant was not related to size. Number of leaves and number of phyllaries were slightly correlated in the data set with *Aster turbinellus* but the correlation was higher when this species was not included. Number of bracts on the peduncle of the terminal head was correlated with the number of rows on the involucre in the data set with *A. turbinellus*, but not otherwise. *Aster turbinellus* specimens had leafier peduncles and more rows on the involucre than most of the groups. Specimen 119, labelled as *A. turbinellus*, had 47 phyllaries in six rows (more than for other *A. turbinellus* specimens, which averaged 28 phyllaries in five or six rows).

Plant length measurements correlated with lengths to the widest part of middle leaves and with widths of middle and uppermost leaves. Both lengths and widths of the uppermost and middle leaves were more highly correlated in section *Eucephalus* than when *A. turbinellus* was included. High correlation between length of the uppermost leaf and middle leaf in section *Eucephalus* confirmed species descriptions indicating that leaves along the main stem were similar in size.

Leaf size and shape measurements were correlated within a leaf and between middle and uppermost leaves. Shape parameter A was correlated most with the width of the leaf and the width at ¼ length, implying that A was most related to the leaf base width. Parameter A1 was slightly correlated with ¾ lengths and negatively correlated with the two other shape parameters and represented shape best. The last parameter, A2, was

correlated with lengths of leaves. Correlations were not the same for the data set with *A. turbinellus* and the one without.

Sizes of achenes of ray and disk florets were significantly correlated, although no correlation was found with involucre lengths. Pappus lengths for both floret types and disk floret tube length were highly correlated to each other but not very strongly with ray floret tube length. Similarities in size in floret characters probably reflects the same influences during development.

Density estimates of trichomes were compared between different areas of a plant (Table 7). The same density usually occurred throughout the plant but the association was not exact. If trichomes were present on any leaf surface and on the involucre, then the stem always had some trichomes. Plants without trichomes on leaves or involucre might have sparse to no coverage on the stem but never moderate or dense. Trichome density on the involucre could not predict density on a leaf under surface; of the 22 specimens with dense trichomes on the involucre, 20 had high or moderate densities on the leaf under surface; of those lacking trichomes on the involucre, more than 50% had sparse to dense trichomes on the leaf under surface. Density of trichomes on one plant organ was not predictive of densities on the others.

Presence or absence of non-glandular and glandular trichomes on different plant surfaces are summarized in Table 8. Glandular and non-glandular trichomes occurred together more frequently than alone on the stem and leaf under surface. In contrast, involucres had only glandular trichomes more frequently than only non-glandular or a combination. When glandular trichomes were present on the involucre, they were usually present on other surfaces.

Ciliated leaf, ciliated phyllary and membranous phyllary edges were highly correlated. Most edges were ciliated and many arbitrary correlations appeared in the data: glandular trichomes on the involucre and on the stem, non-glandular trichomes on the stem, and a white stripe in the centre of phyllary.

Colours on phyllaries have been used as distinguishing characters by taxonomists who studied this group. Relationships between colours on parts of the phyllary have been

shown in Table 9. Most phyllaries had keels or midribs with a white stripe in the centre, and had red tips and edges. Only 18 specimens had some red on all three (edge, tip and keel), possibly making a distinguishing character combination.

Table 5: Pearson correlation coefficients of characters for 138 specimens (only those with high correlations *i. e.* Bonferroni probabilities were less than 0.001). An asterisk indicates correlation values that differed by >= 0.4 or changed in significance when *Aster turbinellus* was excluded from the data set.

	Number of heads	Number of leaves	Number of leaves in 8 cm.	Length of middle internode
Length of middle internode			-0.825	
Number of branches	0.611			
Plant length		0.688	-0.475	0.495
Length of middle leaf			-0.679	0.696
Length of uppermost leaf			-0.425	0.426: 0.496*
Width of middle leaf			-0.510: -0.558*	0.524: 0.585*
Length to widest point of middle leaf			-0.522	0.571
Number of phyllaries on involucre		0.484: 0.528*		

	Number of bracts on peduncle	Plant length	Length of middle leaf	Length of uppermost leaf
Number of rows on involucre	0.508: 0.262 (NS)*			
Number of phyllaries	0.508: 0.323 (NS)*			
Number of branches		0.472		
Length of middle leaf		0.686		
Length of uppermost leaf		0.573	0.668: 0.729*	
Width of middle leaf		0.642	0.612: 0.665*	0.500
Width of uppermost leaf				0.543
Length to widest part of middle leaf		0.647	0.799	0.583
Length to widest part of uppermost leaf			0.467	0.688

Table 5: Continued.

	A	A1	A2	
Length of middle leaf			0.540: 0.604*	
Width of middle leaf	0.409: 0.432 (NS)*			
Width ¼ distance from leaf base	0.599			
Length ¼ distance from leaf base			0.548: 0.609*	
Length ½ distance from leaf base			0.538: 0.603*	
Width ¾ distance from leaf base		0.480		
Length ¾ distance from leaf base			0.543: 0.610*	
Length less 0.2 cm. from leaf tip			0.540: 0.603*	
A		-0.529: -0.592*		
A2		-0.771		

	Disk achene length	Disk achene width	Disk pappus length	Disk floret tube length
Ray achene length	0.887	0.613: 0.577*		
Ray achene width	0.622	0.688		
Ray pappus length	0.511: 0.423 (NS)*		0.813: 0.779*	0.713: 0.691*
Ray floret tube length				0.495
Ray floret limb length	0.440: 0.430 (NS)*		0.453: 0.437 (NS)*	0.499
Disk tube length			0.757	
Disk achene width	0.583: 0.541*			

	Ray achene length	Ray pappus length	Involucre length	Disk floret stigmatal branch length
Ray achene width	0.613			
Ray pappus length	0.500: 0.397 (NS)*			0.442
Ray floret limb length	0.487	0.467	0.429: 0.528*	
Involucre width	0.417: 0.336 (NS)*	0.408: 0.348 (NS)*		

(NS: not significant.)

Table 6: Binary S6 similarity coefficients of characters from data set of 138 specimens (only those with high correlations *i. e.* coefficients >= 0.600). An asterisk indicates correlation values that differed by >= 0.4 or changed in significance when *Aster turbinellus* was excluded from the data set.

	Red edge on middle phyllary	White central stripe on phyllary	Ciliated edge on middle leaf	Ciliated edge on uppermost leaf	Ciliated edge on phyllary
Glandular trichomes on involucre		0.577 (NS): 0.620	0.605	0.614: 1.000*	
Ciliated edge on middle leaf		0.673			
Ciliated edge on uppermost leaf		0.663	0.986		
Ciliated edge on middle phyllary		0.683	0.781	0.769	
Membranous edge on middle phyllary		0.725	0.804	0.792	0.816
Red phyllary tip	0.840: 0.869*				

	Glandular trichomes on under surface	Glandular trichomes on stem	Glandular trichomes on involucre	Non-glandular trichomes on under surface	Non-glandular trichomes on stem
Glandular trichomes on upper surface	0.758	0.624			
Glandular trichomes on lower leaf surface		0.714			
Non-glandular trichomes on involucre				0.605	
Non-glandular trichomes on upper surface				0.586 (NS): 0.610*	
Non-glandular trichomes on lower leaf surface					0.643
Ciliated edge on middle leaf		0.586 (NS): 0.641	0.605: 0.662*		0.663
Ciliated edge of higher leaf		0.595 (NS): 0.641	0.614: 0.662		0.653
Ciliated edge on phyllary		0.559 (NS): 0.610	0.577 (NS): 0.631*		
Membranous edge on middle phyllary			0.595 (NS): 0.652*		0.633

(NS: not significant)

Table 7: Number of 138 specimens exhibiting various combinations of trichome densities on different surfaces.

	Leaf trichome density (upper surface and under surface) and involucre trichome density			
Stem density	Leaf and involucre lacking	Leaf and involucre sparse	Leaf and involucre moderate	Leaf and involucre dense
Lacking	4			
Sparse	3	9	4	
Moderate		2	10	
Dense		1		1

	Leaf upper surface			
Stem density	Lacking	Sparse	Moderate	Dense
Lacking	12	1	1	
Sparse	14	26	9	1
Moderate	5	24	22	3
Dense	2	8	7	3

	Leaf under surface			
Stem density	Lacking	Sparse	Moderate	Dense
Lacking	12	2		
Sparse	7	25	15	3
Moderate	1	11	33	9
Dense		3	7	10

	Involucre trichome density			
Under surface of leaf	Lacking	Sparse	Moderate	Dense
Lacking	7	8	5	1
Sparse	9	15	7	1
Moderate	2	13	24	10
Dense	2	5	19	10

Note: Blank cells indicate zero values.

Table 8: Number of 138 specimens exhibiting various combinations of glandular and non-glandular trichomes on stem, leaf and involucre.

	Stem	Upper surface	Under surface	Involucre
Non-glandular alone or in combination	107	67	86	53
Glandular alone or in combination	99	75	81	107
Both	82	37	49	42
Non-glandular only	25	30	32	11
Glandular only	17	38	37	65

	Glandular trichomes on leaf surfaces and stem	
Involucre	Absent on leaf and stem	Present on one or more leaf or stem surfaces
Absent	16	15
Present	19	90

Data sets were prepared for use in calculation of Gower's similarity coefficient and for discriminant analysis by removing highly correlated characters and those with missing values. Summaries of retained and removed characters are in Table 10. Some characters had missing values and were removed from the data set: number of branches; plant length; and number of leaves. Number of leaves was also correlated with plant length and number of phyllaries, but not with middle leaf length, and eliminating number of leaves removed one correlation. Some characters were removed because they were remeasurements of

Table 9: Number of 138 specimens exhibiting various combinations of red colouration on tip, edge and keel.

	Edge		Tip		Keel, edge and tip with same colour	Phyllary tip and edge with same colour	White stripe	
Keel colour	Red	Not red	Red	Not red			Present	Absent
Red	18	2	19	1	18	75	9	11
Green	63	55	62	56	50	51	111	7

another character: presence of any toothed leaf, measurements of length and width at ¼, ½, ¾ and near tip positions along a leaf. Number of bracts on the peduncle was not used in the data sets with *Aster turbinellus* because of high correlation with number of rows on the involucre.

Trichome characters were limited to densities on both leaf surfaces and on involucre, plus non-glandular and glandular hairs on leaf underside surface and involucre. Ciliated edge characters for the uppermost leaf and phyllary were removed as was the character for a membranous phyllary edge.

Some correlated characters remained because they were one of a pair of which one had been dropped from the analysis. Thirty-three characters were kept in the first data set (16 floral characters and 15 vegetative characters) (Table 3). Among these, eight were trichome related characters. The data set for plants with ray florets had 36 characters in total and 111 specimens. The number of floral characters exceeded those for vegetative by three. Removing ten *Aster turbinellus* records left 128 in the data set without ray floret detail and 101 specimens in the data set with ray floret detail.

Table 10: Characters retained and removed due to high correlations.

Retained character	Removed character	Other characters correlated with removed character
head count	branch count	plant length
middle leaf length	plant length	head count*; internode length; leaf count; phyllary count*; uppermost leaf length; middle leaf width; middle leaf length to widest part; leaves in 8 cm.
	middle leaf length to widest part	plant length; leaves in 8 cm.; internode length; uppermost leaf length; middle leaf width; uppermost leaf length to widest part*
uppermost leaf length	uppermost leaf length to widest part	length of middle leaf, width of middle leaf *, length to widest part of middle leaf
internode length	leaves in 8 cm.	plant length; middle leaf length; middle leaf width; middle leaf length to widest part; uppermost leaf length
number of phyllaries	leaf count	plant length; phyllary count
uppermost leaf length	uppermost leaf length to widest part	middle leaf length to widest part; width of middle leaf; width of uppermost leaf*
rows on involucre	bracts on peduncle	phyllary count; number of rows on involucre*
A1	A	width of middle leaf; width at ¼ distance from base
	A2	middle leaf lengths; A
disk achene length	ray achene length	ray achene width; ray pappus length*; ray floret limb length; disk achene width; involucre width*
	ray pappus length*	disk pappus length; disk floret tube length; ray achene length*; ray floret limb length, involucre width*; disk floret stigmatal branch length
disk tube length	disk pappus length	ray pappus length; disk floret tube length; ray achene length*; ray floret limb length
disk achene width	ray achene width	ray achene length; disk achene length
red edge on phyllary	red tip on phyllary	none
trichome density on underside of leaf	trichome density on stem	none

Table 10: Continued.

Retained character	Removed character	Other characters correlated with removed character
ciliated edge on middle leaf	membranous edge on phyllary	white stripe in centre of phyllary; glandular trichomes on involucre; non-glandular trichomes on stem; ciliated edge on phyllary; ciliated edge on uppermost leaf
	ciliated edge on phyllary	white stripe in centre of phyllary; glandular trichomes on involucre; glandular trichomes on stem**; non-glandular trichomes on stem; ciliated edge on uppermost leaf; membranous edge on phyllary
	ciliated edge on uppermost leaf	white stripe in centre of phyllary; glandular trichomes on involucre**; non-glandular trichomes on stem
glandular trichomes on lower leaf surface	glandular trichomes on upper leaf surface	glandular trichomes on stem
	glandular trichomes on stem	glandular trichomes on upper leaf surface; non-glandular trichomes on stem; glandular trichomes on involucre; ciliated edge on middle** and uppermost leaves**; ciliated edge on phyllary**
non-glandular trichomes on lower leaf surface	non-glandular trichomes on stem	ciliated edge on middle and uppermost leaves; membranous edge on phyllary
	non-glandular trichomes on upper leaf surface	none

* Significant **without** *A. turbinellus*.** Significant **with** *A. turbinellus*.

Phenetic analysis

I used unweighted pair group method with arithmetic averages (UPGMA), as the clustering algorithm because it returned higher cophenetic regression coefficients than other clustering algorithms (cophenetic regression coefficients measure how well the generated dendrogram matches the original data matrix). The value of 0.68 from UPGMA (which was less than 0.70, considered a poor fit by Rohlf (1994)) was a better fit than other clustering routines: unweighted pair group centroid method (>1 tree, r = 0.08); single link method (>25 trees, r = 0.48); flexible clustering method (1 tree, r = 0.60); and

complete link method (1 tree, r = 0.57). The poor fit from the UPGMA algorithm reflected the similarity among specimens. Double checking the assignments of specimens to groups using discriminate analysis should correct for possible errors in group memberships. Analysis of the other versions of the data set showed similar results; however, those data sets containing ray floret characters were consistently a better fit with the generated dendrogram. The best agreement was for the data set with ray floret characters, including *A. turbinellus* specimens, using the UPGMA routine (r=0.70). UPGMA clustering was used for construction of all phenograms.

For the first four data sets, specimens were assigned to 31 groups (**Figure 2**, **Figure 3**, **Figure 4** and **Figure 5**). I split each phenogram into groups based on the branching patterns in the lower part of the phenogram. The lowest bifurcation on the phenogram for all specimens (**Figure 2**) separates specimen 19 from all the others therefore specimen 19 was placed into a separate group. The remaining specimens were then divided successively into new groups until Gower's general similarity coefficient was about 25. At this level, the topography becomes complex and I separated groups based on the clustering rather than a cut off level; for example, specimens 1, 2, and 10 were put in group1 based on a bifurcation at a coefficient level of 25 whereas groups 2 and 3 were separated at a coefficient level of 27. Groups with the same membership in each phenogram were given the same number. Specimens forming inconsistent associations were each put into a separate group.

Groups created based on the phenogram generated from reproductive characters were given numbers 1 - 22. The phenogram has not been provided because results from the discriminant analysis showed that floral data alone were not successful in separating specimens into stable groups. Discriminant analysis and testing of group assignments found that 11 specimens were not in their predicted group. After those were moved to new groups, a new analysis found three specimens were not in the predicted group. A third analysis, after moving the three specimens to new groups, found 13 more specimens that were not in their predicted groups. Congruence between floral groups and species names was low except for *Aster perelegans* and *A. paucicapitatus*.

Use of only vegetative characters produced less reliable results. Eighteen groups were formed based on the phenogram. Discriminant analysis and testing of group assignments found that 65 specimens were in groups that did not agree with predicted groups. No further analysis was done. Vegetative groups and species names did not match well. Vegetative characters alone could not successfully separate these specimens into stable groups.

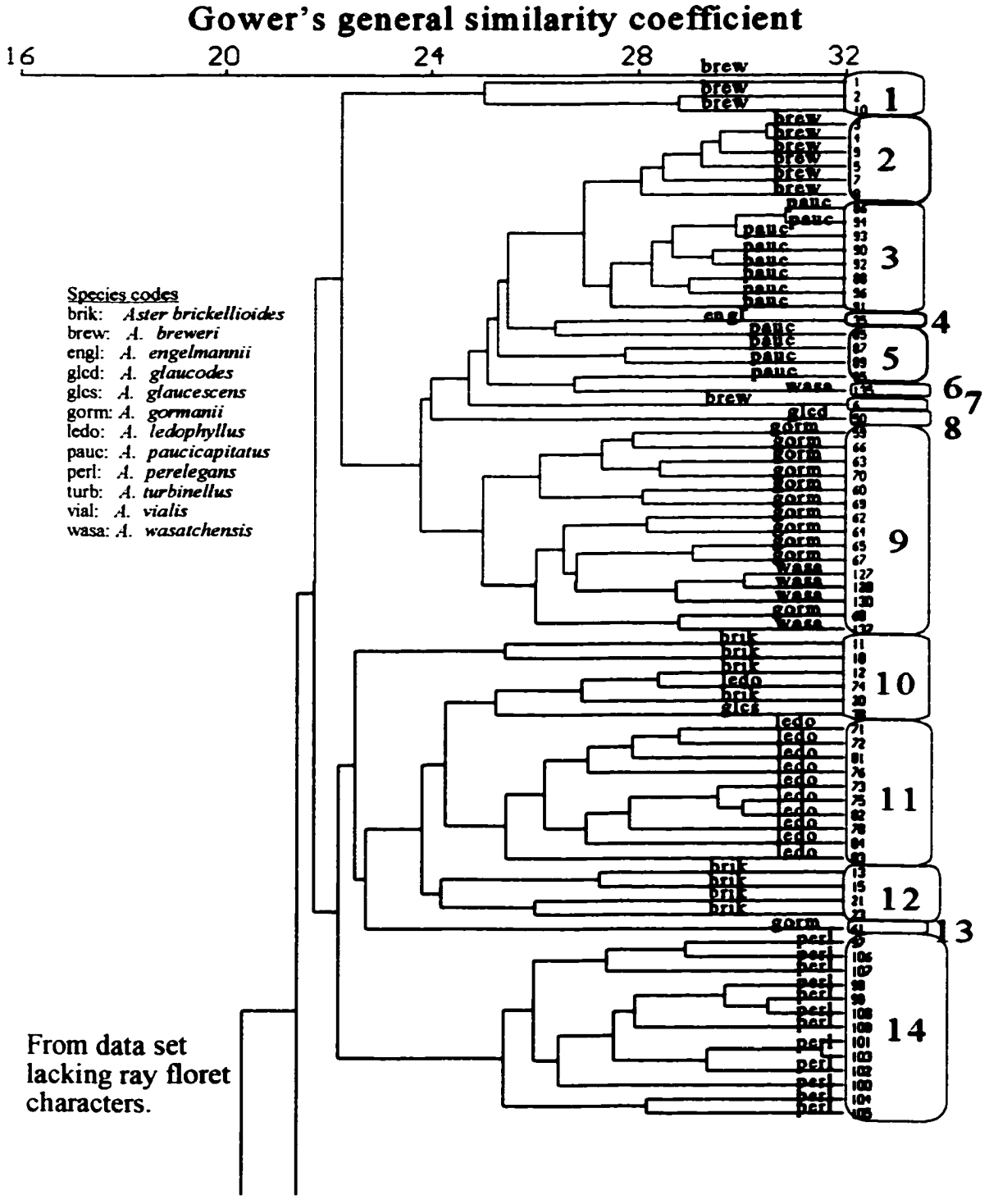


Figure 2: UPGMA cluster analysis of the data set of all specimens, and with ray floret characters omitted. Species names (from herbarium labels) and group assignments are indicated. Large numbers identify groups; small numbers identify specimens.

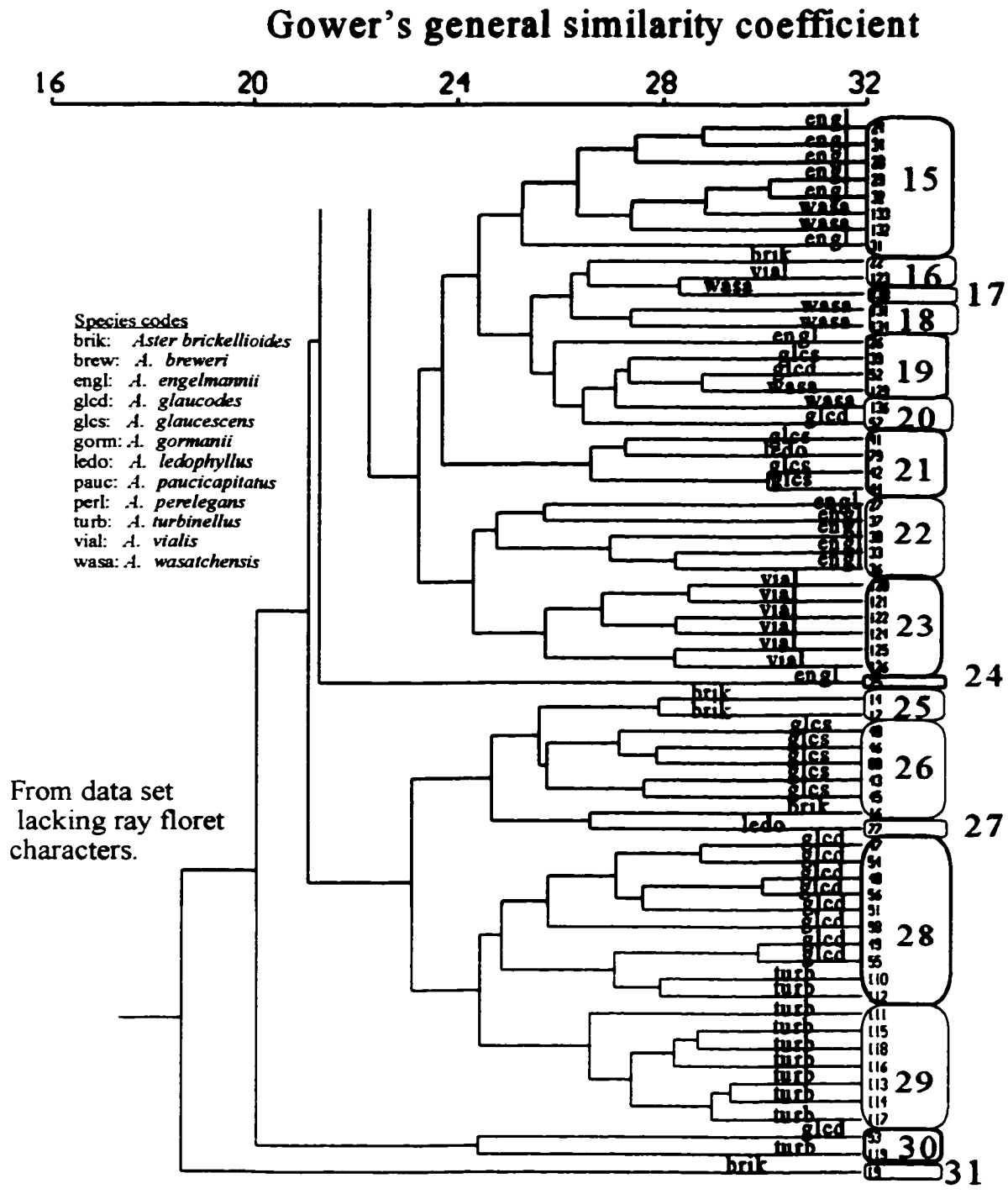


Figure 2: Continued.

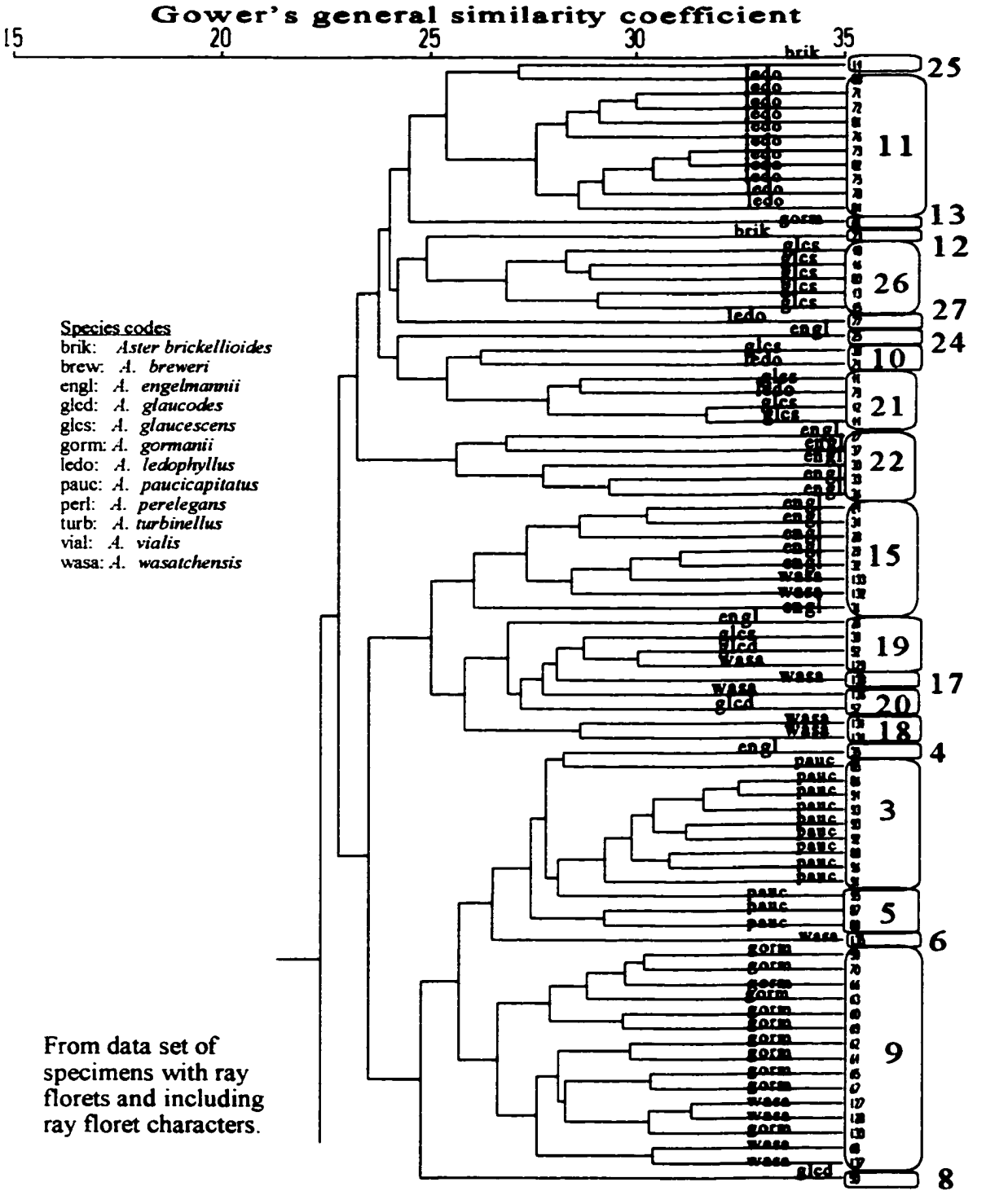
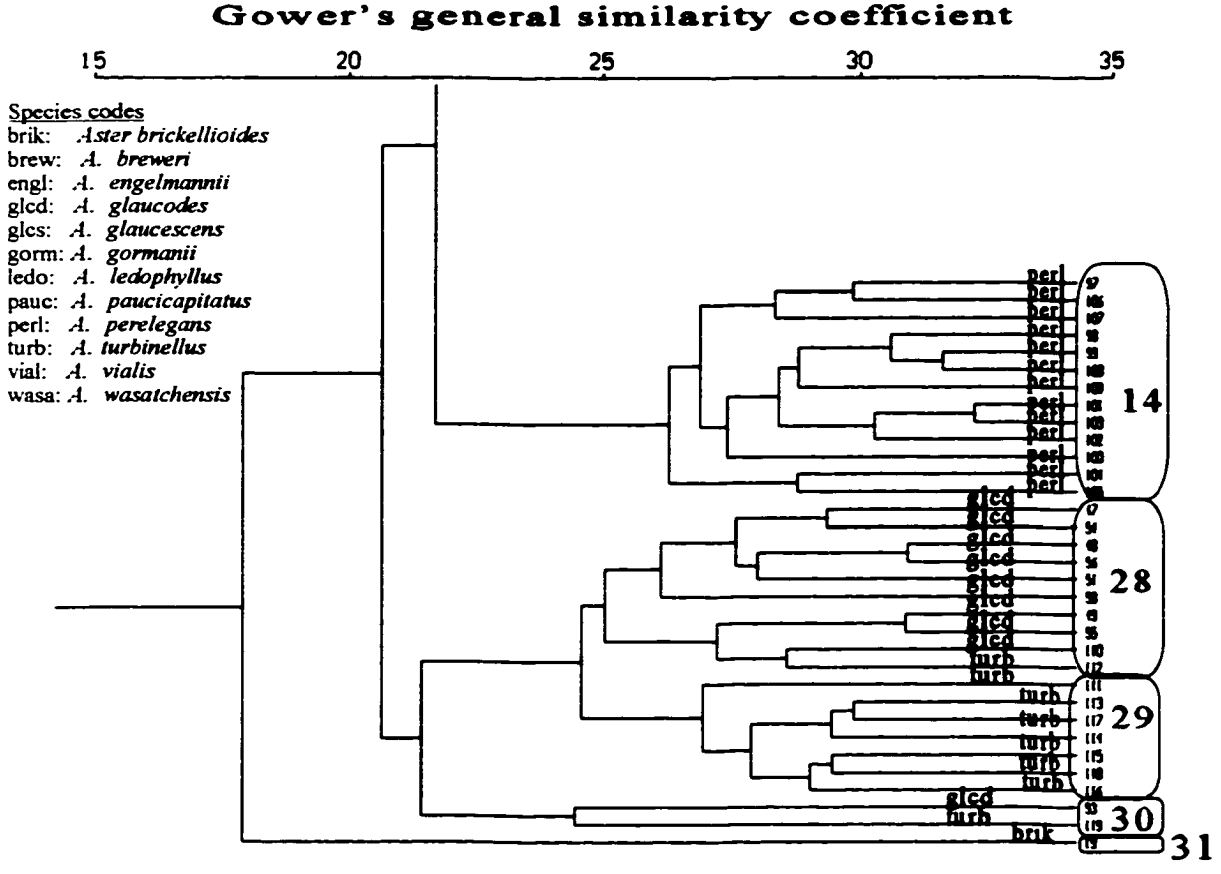


Figure 3: UPGMA cluster analysis of the data set constituted only of specimens with ray florets, and with ray floret characters included. Species names (from herbarium labels) and group assignments are indicated. Large numbers identify groups; small numbers identify specimens.



From data set of specimens with ray florets and including ray floret characters.

Figure 3: Continued.

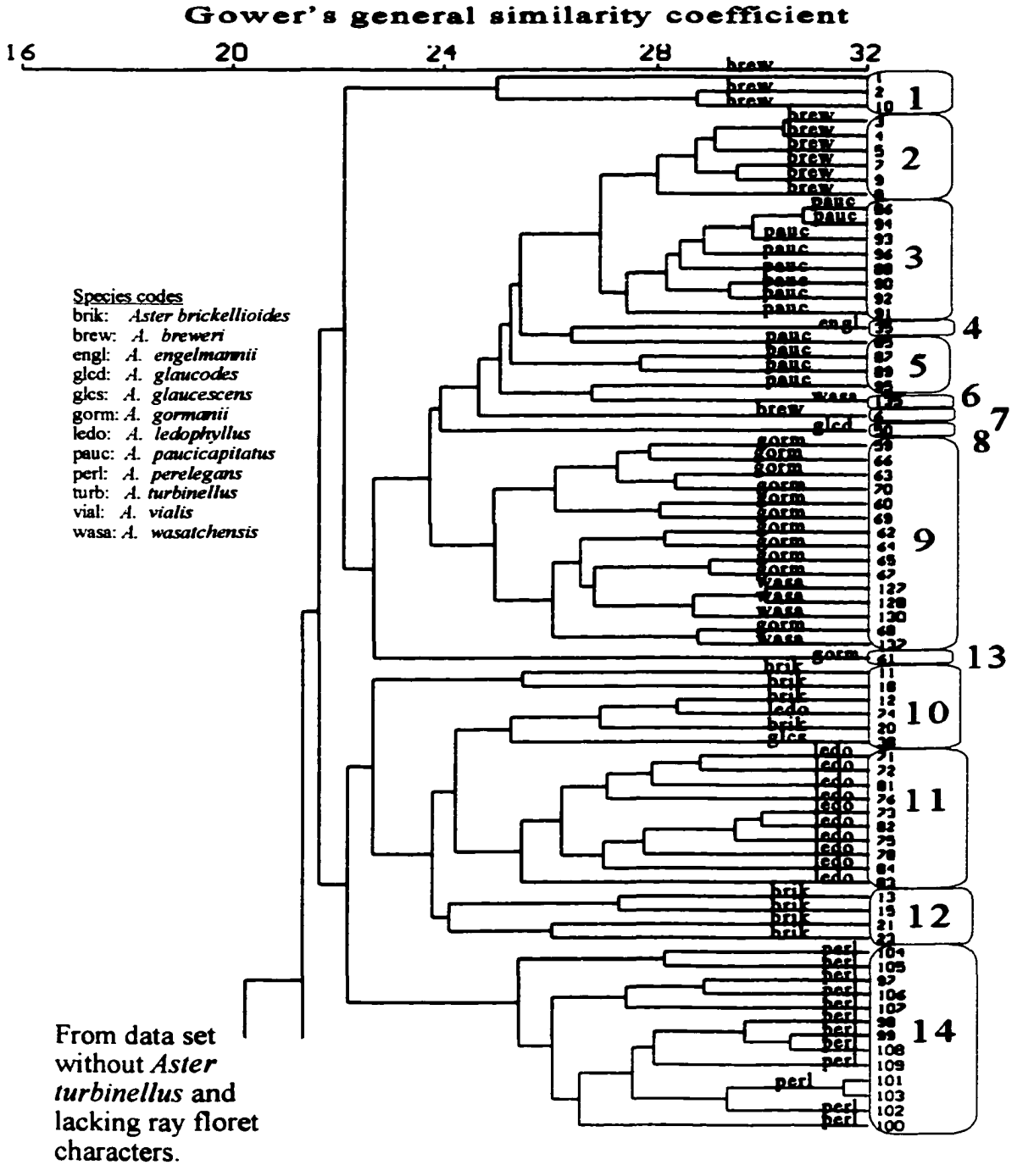
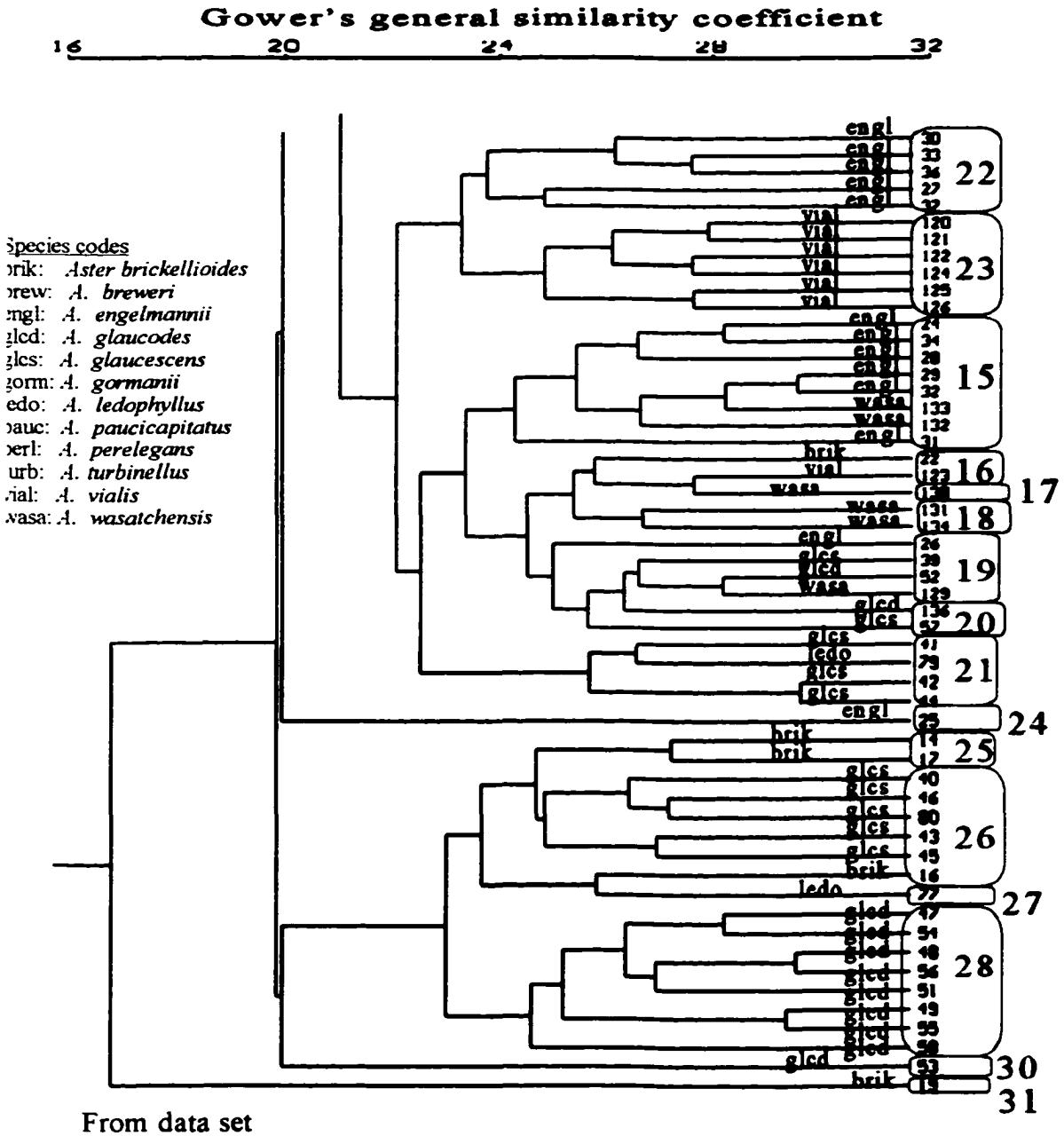


Figure 4: UPGMA cluster analysis of the data set excluding *Aster turbinellus* specimens, and with ray floret characters omitted. Species names (from herbarium labels) and group assignments are indicated. Large numbers identify groups; small numbers identify specimens.



From data set without *Aster turbinellus* and lacking ray floret characters.

Figure 4: Continued.

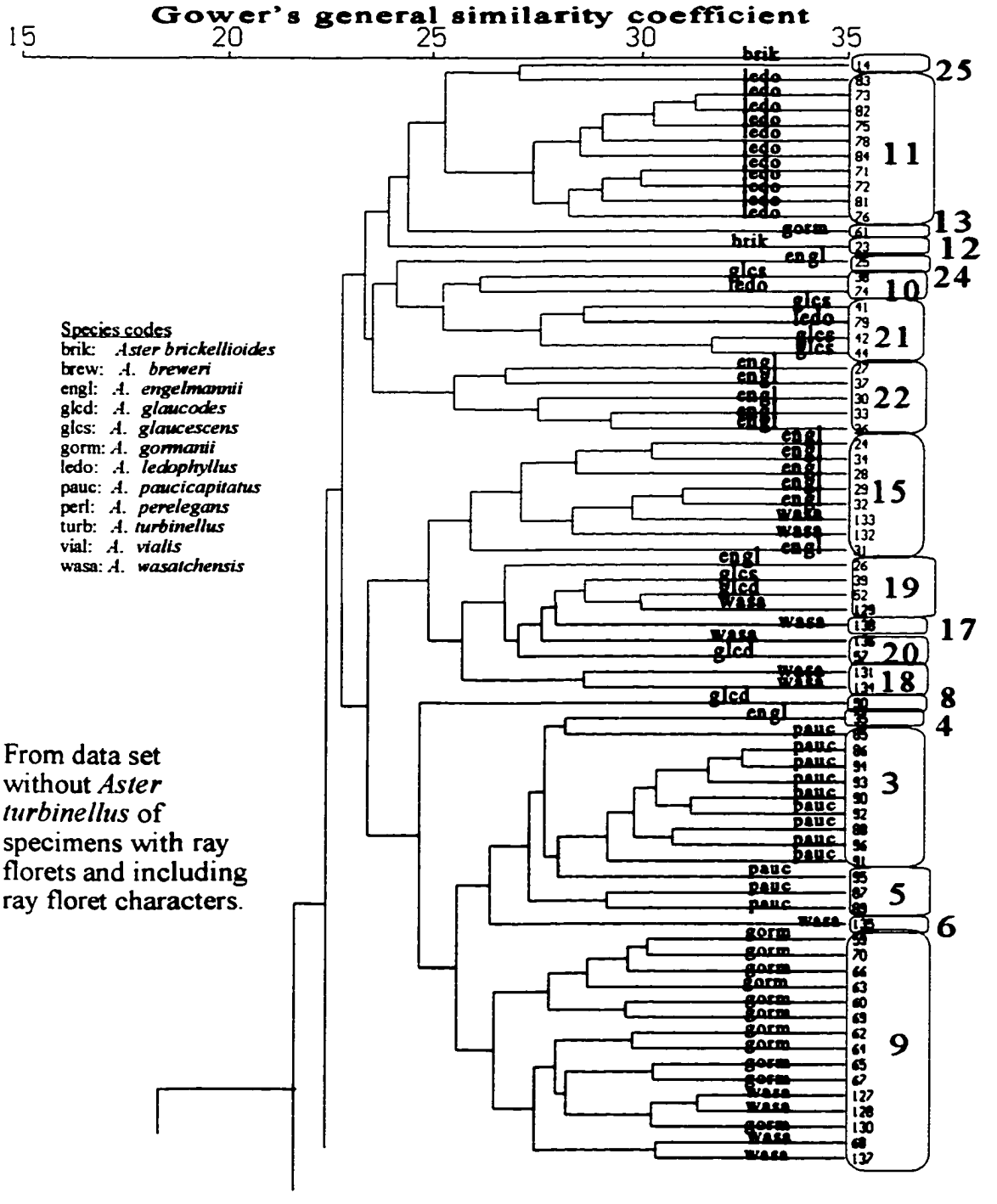


Figure 5: UPGMA cluster analysis of the data set excluding *Aster turbinellus* specimens and those without ray florets, and with ray floret characters included. Species names (from herbarium labels) and group assignments are indicated. Large numbers identify groups; small numbers identify specimens.

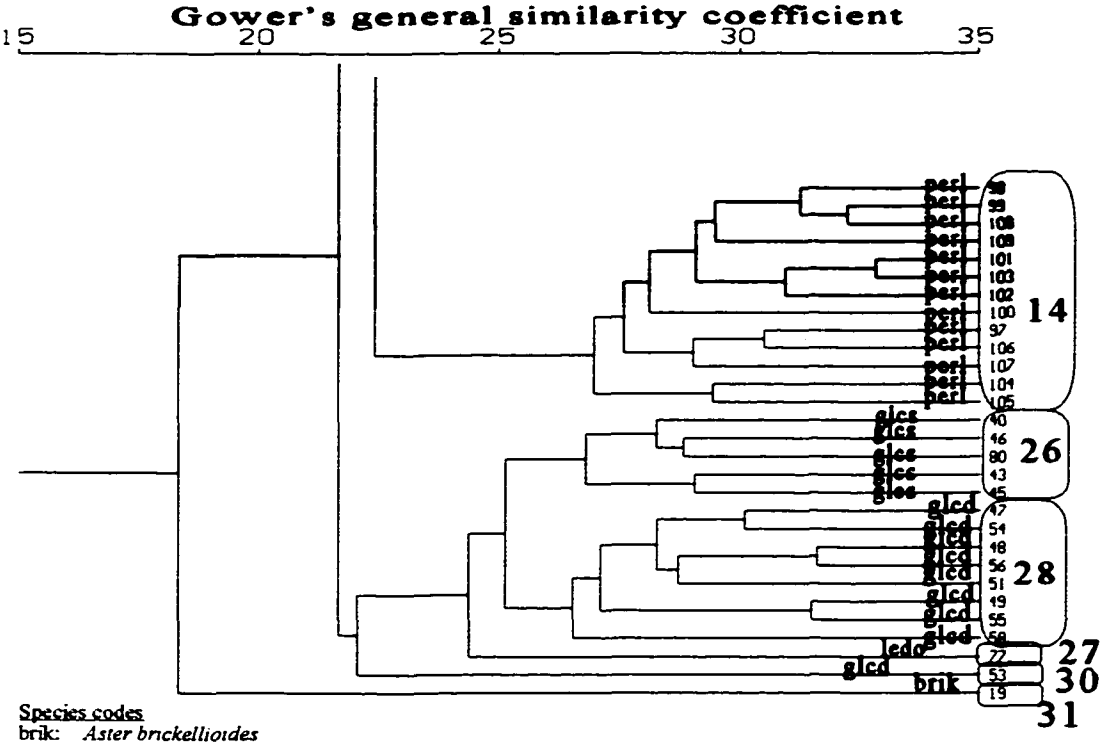


Figure 5: Continued.

Comparison between phenetic groups and herbarium sheet determinations

Species names, based on herbarium sheet determinations, and the group assignments did not correspond exactly for individual specimens (**Figure 2**). *Aster perelegans* was the only species exclusively in one group. Five taxa were in two or three groups: *A. breweri*, *A. gormanii*, *A. paucicapitatus*, *A. turbinellus*, and *A. vialis*. Six taxa were in four or more groups: *A. brickellioides*, *A. engelmannii*, *A. glaucodes*, *A. glaucescens*, *A. ledophyllus*, and *A. wasatchensis*.

Comparison among phenograms

Effects of including or excluding *Aster turbinellus*

Phenograms for the data set of all specimens, excluding ray floret characters, were very similar with or without the inclusion of *Aster turbinellus* (**Figure 2** and **Figure 4**). Group 29 (comprised only of *A. turbinellus*) was missing, and the other two groups that contained *A. turbinellus* and *A. glaucodes* specimens remained in the same position on both phenograms. Groups 25, 26, and 27 (mostly *A. brickellioides* and *A. glaucescens*) were placed in the same large cluster as the *A. glaucodes* specimens in both phenograms. The removal of *A. turbinellus* specimens had no effect on the structure, which implies that *A. glaucodes* and *A. turbinellus* specimens had similar Gower's general similarity coefficients. *Aster wasatchensis* was not associated with *A. glaucodes* or *A. turbinellus* in either phenogram.

Phenograms from the data sets using ray characters with and without *Aster turbinellus* were similar but had one change (**Figure 3** and **Figure 5**). On the phenogram with *A. turbinellus*, group 28 (*A. glaucodes* specimens) was associated with it in a separate cluster from all other groups. When *A. turbinellus* was not included, group 26 (mostly *A. glaucescens* specimens) and group 27 (*A. ledophyllus*, specimen 77), which had been associated with groups 11 to 13 (mainly *A. ledophyllus*) and 25 (*A. brickellioides*), were moved to join groups 28 and 30 (*A. glaucodes* specimens).

Effects of including or excluding ray floret characters

The addition of ray floret characters and removal of specimens lacking ray florets produced a phenogram that matched the raw data better than that produced for the first data set; *i. e.* it had a higher cophenetic regression coefficient of 0.70 (**Figure 2** and **Figure 3**). Groups 1, 2, 4, 7, 16 and 23 consisting exclusively of specimens without ray florets were omitted from this analysis. Group 31 *(A. brickellioides*, specimen 19) remained distinctly different from other specimens. The other groups could be clustered into larger associations based on the topography of the phenograms. The phenograms could each be divided into four major associations; in the first phenogram (**Figure 2**), they were given numbers and in the second (**Figure 3**), letters (Table 11). For simplicity, three small groups (24, 30, and 31) were not assigned numbers or letters. The phenogram that did not include ray floret characters had associations composed of five to nine groups each; the phenogram that did include ray floret characters had associations composed of one to nine groups each. The largest association A was comprised of association 1, parts of association 3 (groups 15, 17, 18, 19, and 20), and parts of association 4 (groups 25, and 26). The remaining groups of association 3 were placed into association B which also had all but one group of association 2. Group 14, *Aster perelegans*, was isolated from the others. The remaining two groups of association 4 were placed with group 30 into association D. When ray floret characters were added, Group 25, represented by a single specimen of *A. brickellioides* with ray florets, shifted from an alignment with association 4 to one with association B. Groups with many members remained in stable alignment with each other even if they were shifted between large clusters. Most of the differences between phenograms came from the movement of smaller groups.

Table 11: Taxa included in associations among phenetic groups based on (i) all specimens; with ray floret characters omitted (indicated by number) and (ii) specimens with ray florets; with ray floret characters included (indicated by letters).

All specimens - no ray floret characters.	Specimens with ray florets - with ray floret characters.	Phenetic group numbers	Taxa included in groups	Specimens identified as a taxon compared to total
1	not included	1, 2	*Aster breweri*	10 of 10
1	A	3, 5	*A. paucicapitatus*	12 of 12
1	A	4	*A. engelmannii*	1 of 14
1	A	6	*A. wasatchensis*	1 of 12
1	A	9	*A. wasatchensis*	4 of 12
1	A	9	*A. gormanii*	11 of 12
1	A	8	*A. glaucodes*	1 of 12
2	B	10	*A. brickellioides*	4 of 12
2	B	10	*A. ledophyllus*	1 of 13
2	B	10	*A. glaucescens*	1 of 10
2	B	11	*A. ledophyllus*	11 of 13
2	B	12	*A. brickellioides*	4 of 12
2	B	13	*A. gormanii*	1 of 12
2	C	14	*A. perelegans*	13 of 13
3	A	15	*A. engelmannii*	6 of 14
3	A	15	*A. wasatchensis*	2 of 12
3	not included	16	*A. brickellioides*	1 of 12
3	not included	16	*A. vialis*	1 of 7
3	B	17	*A. wasatchensis*	1 of 12
3	B	18	*A. wasatchensis*	7 of 12
3	B	19	*A. wasatchensis*	1 of 12
3	B	19	*A. engelmannii*	1 of 14
3	B	19	*A. glaucodes*	1 of 12
3	B	19	*A. glaucescens*	1 of 10
3	B	20	*A. wasatchensis*	1 of 12
3	B	20	*A. glaucodes*	1 of 12
3	A	21	*A. glaucescens*	3 of 10
3	A	21	*A. ledophyllus*	1 of 13
3	B	22	*A. engelmannii*	4 of 14
3	not included	23	*A. vialis*	7 of 7
4	not included	25	*A. brickellioides*	2 of 12
4	A	26	*A. brickellioides*	1 of 12
4	A	26	*A. glaucescens*	5 of 10
4	A	27	*A. ledophyllus*	1 of 13
4	D	28	*A. glaucodes*	8 of 12
4	D	28	*A. turbinellus*	2 of 10
4	D	29	*A. turbinellus*	7 of 10

Discriminant analysis of phenetic groups

When groups with one member were removed from the data set, 129 cases organized into 22 groups remained. Discriminant analysis showed that specimen 39, *Aster glaucescens* was closer to the group 20 centroid therefore I moved it into group 20. Further testing on the new groups found matches between assigned group numbers and those predicted. Three axes from the discriminant analysis of the "before"groups (specimens clustered based on phenograms' topographies) have been graphed (**Figure 6**).

Univariate F tests among the "before" groups found that all characters were significantly different ($p < 0.0001$). Multivariate tests using Wilks' lambda, Pillai trace and Hotelling-Lawley trace and theta were all significant ($p < 0.001$). The complexity of the data set was reflected in the thirteen discriminant axes with significant canonical correlation values.

Characters correlated with the axes have been summarized (Table 12). The first five discriminant axes were most affected by number of ray florets, trichome characteristics, and phyllary colours. Lengths of leaves, head counts, and internode lengths did not become important until the sixth to thirteenth axes.

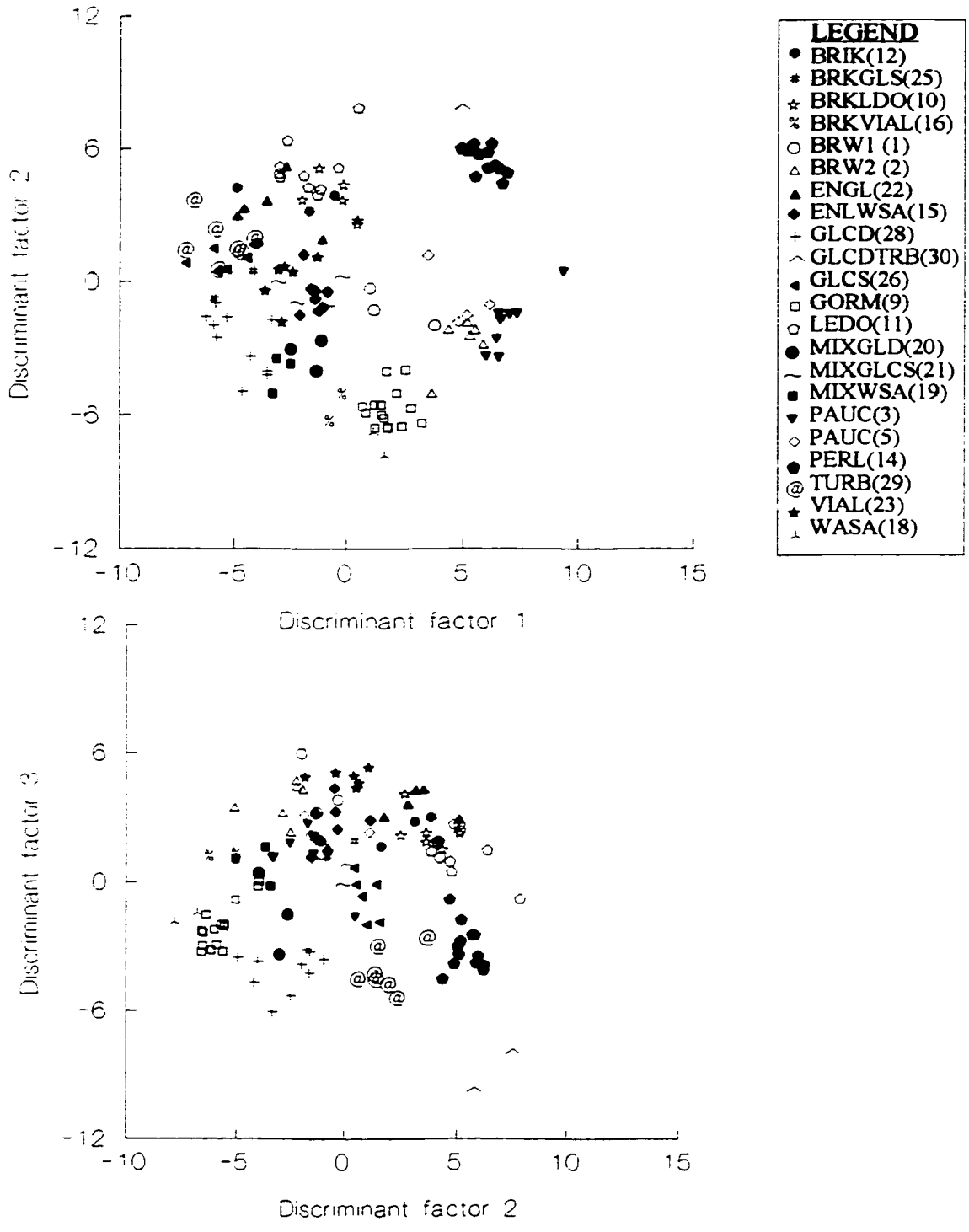


Figure 6: First three discriminant factor axes for the 22 "before" phenetic groups. Top graph with factors 1 and 2 on the axes. Bottom graph with factors 2 and 3 on the axes.

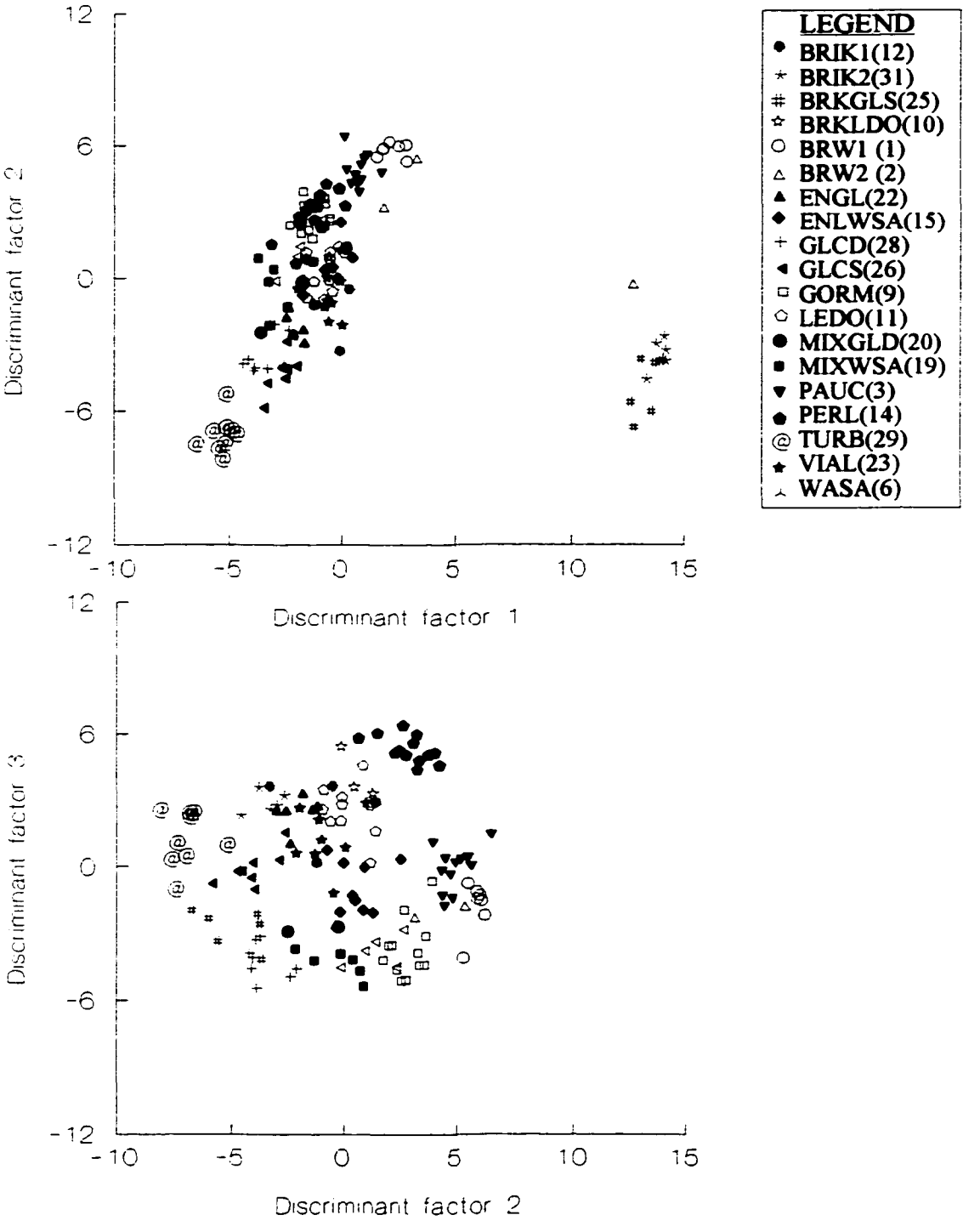


Figure 7: First three discriminant factor axes for the 19 "after" phenetic groups. Top graph with factors 1 and 2 on the axes. Bottom graph with factors 2 and 3 on the axes.

Examination of cluster assignments

The poor fit of the phenogram to the data matrix, as suggested by the cophenetic index, implied that some specimens had not been optimally placed. Reexamination of the cluster memberships was necessary to assess the ability of the algorithm to place such morphologically similar specimens into groups. Since this was the first time that I had used NTSYS and Gower's similarity coefficient, I wanted to check the results of combining these methods. Evaluations were done by looking for anomalies (*i. e.* groups with overlapping character ranges), inspecting box plots of character distributions, and using t-tests to evaluate the distinctiveness of two groups that came into question. If group memberships were changed, I used discriminant analysis to assess perturbations for all the groups by comparing "before" and "after" correlations between group locations in multivariate space and discriminant axes. While evaluating group memberships, I started by considering groups that were difficult to separate in a dichotomous key or had characters with unusually large ranges, followed by those that shared the same species identification on the herbarium label. I tried to place small groups into larger groups (first, one-member groups, then two-member groups). Assessing every combination of every group was impractical; by choosing for consideration groups that had the same species identifications I increased the probability of finding clusters that were mistakenly separated or joined. As mentioned, I added three *Eucephalus bicolor* specimens to the data set in order to include group 31 (originally determined to be *E. bicolor* before being transferred into *Aster brickellioides*) in a discriminant analysis.

Membership assessments of groups with overlapping or extreme character ranges

A simple dichotomous key (not shown) for 31 phenogram-based groups required 92 steps to resolve. Group 9 was unusual because the range in leaf length was large compared with the other groups, as were groups 28 and 29 because they seemed to have overlaps. Although well separated on the phenogram which included ray floret data, Groups 10 and 11 were difficult to distinguish in the key.

To illustrate my methods and decision processes, I describe in detail how group 9 (of interest because of large range in leaf sizes) was assessed. The t-tests of all quantitative characters comparing the two species in group 9, labelled on the herbarium sheets as *Aster gormanii* and *A. wasatchensis*, showed that seven quantitative characters were significantly different at significance level of 0.01: number of leaves in 8 cm., internode length, length and width of middle leaf, disk floret pappus length, ray achene width, and leaf shape parameter A1 (an illustrated example of leaf size differences: **Figure 8**). Among the characters that were binary or categorical, eight characters were of different fixed values. Based on these differences between the two taxa, group 9 was split into two groups, one containing *A. gormanii* and the other containing *A. wasatchensis*. Specimen 135, group 6, *A. wasatchensis*, then could be examined to find if it more closely resembled the *A. gormanii* or *A. wasatchensis* group. Specimen 135 resembled each group in many respects but also showed nine differences, mostly involving size. It more closely resembled *A. wasatchensis* than *A. gormanii*. Differences from *A. wasatchensis* were number of leaves in 8 cm., length of the internode, plant length, middle leaf length and width, uppermost leaf length, disk floret achene width, ray floret achene length and presence of a non-membranous phyllary edge. The *A. wasatchensis* subset of group 9 was merged into group 6 and the remaining specimens were left as Group 9. Discriminant analysis on the preceding changes showed no differences between the assigned group number and the predicted. Canonical correlation values for the first thirteen axes and groups increased. The changes were kept. Using these methods of analyses and decision making, groups 10, 11, 28, and 29 were evaluated in a similar fashion.

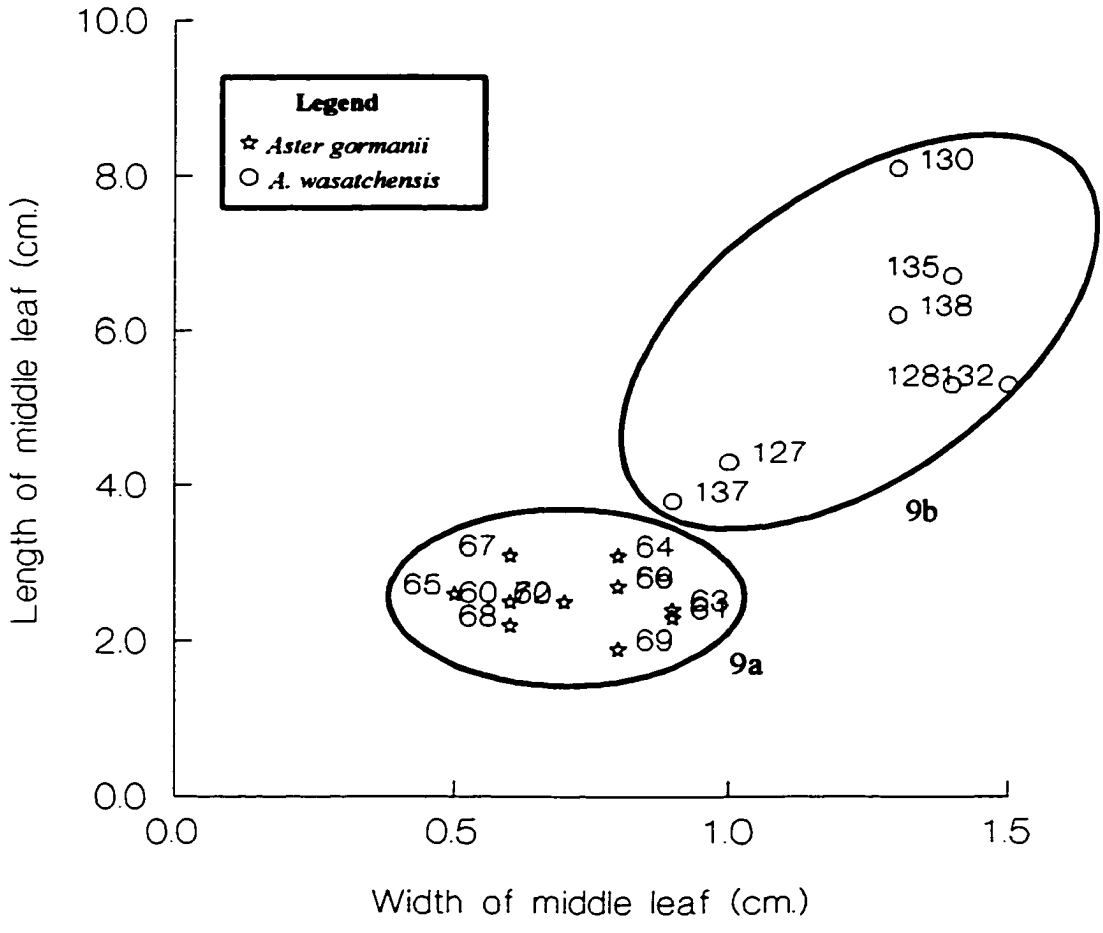


Figure 8: Middle leaf length vs width for group 9 with data points labelled with specimen number. Groups created during the assessment process have been enclosed.

To summarize changes in membership after the first round of analyses were completed:

1. group 9 was separated into two groups; one group (all *Aster wasatchensis* specimens) was merged with group 6, and the remaining specimens (all *A. gormanii*) were left as group 9.
2. Group 11 was left unchanged.
3. Specimen 38 (*A. glaucescens*), from group 10, had middle leaves that were almost twice as long as the others so it was treated as a new group, 33.

4. Group 21 was separated into two groups based on leaf size, number of phyllaries, and disk and ray floret length differences: specimens 41 and 79 (*A. glaucescens* and *A. ledophyllus*) remained as group 21, and specimens 42 and 44 (both *A. glaucescens*) were assigned to a new group 32.
5. Group 28 was compared with group 29 (suspect because of overlapping characters); specimens 110 and 112 (both *A. wasatchensis*) were moved into group 29, thereby leaving only *A. glaucodes* specimens in group 28. T-tests comparing group 28 and 29 found significant differences in 12 characters, including ray floret characters, trichome densities and widths of uppermost leaves.

Cluster assignment tests based on specimen identifications

Groups 1 and 2, both identified as *Aster breweri*, were compared using t-tests and discriminant analysis. They differed in length of the uppermost leaf and length to the widest part of the middle leaf. Joining the groups decreased the canonical correlation values so they were retained as separate groups.

Specimen 6 or group 7, *A. breweri*, was compared with groups 1 and 2. Specimen 6 was most similar to group 2. Discriminant analysis found that assigned groups matched those predicted and that the first thirteen canonical correlation values were still significant. Differences after including specimen 6 in group 2, between groups 1 and 2 were plant length (group 1: 41.4±24.0 cm.; group 2: 69.8 ±9.1 cm.), length to widest part of middle leaf (group 1: 0.8±0.4 cm.; group 2: 1.8± 0.5) and uppermost leaf length (group 1:2.1 ±0.3; group 2:3.3±0.2). Groups 1 and 2 were merged again to evaluate if group discrimination could be improved but were kept separate when discrimination did not improve.

Groups 3 and 5, both *Aster paucicapitatus*, were separated on the phenogram (**Figure 2**) by specimen 35, *A. engelmannii*, and were compared to discover if they could be placed together. T-tests found that disk floret tube lengths, involucre lengths, ray and disk floret

pappus lengths were significantly different. All these characters reflected smaller heads, therefore group 5 was merged into group 3.

Group 9, with all but one *Aster gormanii*, was tested with discriminant analysis to discover if group 13, specimen 61, the isolated *A. gormanii*, could be placed with the other similarly identified specimens. Predicted groups matched actual groups. Fourteen canonical correlation values, instead of thirteen, were found significant. One correlation increased while six decreased and the others were unchanged. Specimen 61 was left in group 9.

Specimen 138, group 17, *Aster wasatchensis*, was compared with groups 15, 18, 19 and 20 to discover if it closely resembled any of them. Group 17 matched group 19 best, and the two groups were joined. A discriminant analysis was run, correlation of the groups to axes increased for one axis and decreased for eight. Specimen 138 was kept in group 19 because of the increase.

To summarize the additional changes from the original phenetic group memberships, 29 groups remained (seven with one member and six with two):

1. groups 3 and 4 were merged,
2. specimen 6 (group 7) *Aster breweri*, was included with group 2,
3. group 13 was merged into group 9 by that bringing all *A. gormanii* specimens together, and
4. specimen 138 (group 17) was placed into group 19.

Placement of singleton groups

Attempts were made to place small groups into larger groups. Comparison groups were chosen based on proximity on phenograms and species identifications on the herbarium sheets. The following did not closely resemble any larger group and were retained as separate groups:

1. group 4 (specimen 35, *Aster engelmannii*);
2. group 8 (specimen 50, *A. glaucodes*);
3. group 27 (specimen 77, *A. ledophyllus*);

4. group 31 (specimen 19, *A. brickellioides*).

The following were reassigned to other groups:

1. group 24 (specimen 25, *A. engelmannii*) into group 22;
2. group 33 (specimen 38, *A. glaucescens*), previously separated from group 10, into group 26.

After considering all the single specimen groups, 27 groups were left; four were single specimens. Six groups contained only two specimens.

Placement of two-member groups

Some groups were eliminated.

1. Group 21 was eliminated when specimen 79 (*A. ledophyllus*) was placed into group 11, and specimen 41 (*A. glaucescens*) into group 25.
2. Group 16 with specimen 22, *Aster brickellioides*, and specimen 123, *A. vialis*, was separated and specimens examined individually. Specimen 123 was placed into group 23. Specimen 22, the remaining member of group 16, was included in group 26, thereby removing group 16.
3. Group 18 was removed when specimens 131 and 134 (both *Aster wasatchensis*) and specimen 136, (*A. wasatchensis*) were merged into group 19.

One group could not be placed into a larger group.

1. Group 32 (both *A. glaucescens*) remained because the separated members could not be placed into a larger group, nor could the intact group be merged into another.

One group was split into two.

1. Two new single member groups were created when specimen 119 (*Aster turbinellus*), one member of group 30, was made into a new group, 34. The remaining member (specimen 53, *A. glaucodes*) could not be placed into a larger group.

With these changes, another attempt was made to place the small groups remaining. Rather than making changes one by one, the most likely associations were used based on which group was most similar to the small group under consideration.

1. Group 4 (specimen 35) was put into group 15,
2. group 27 (specimen 17) was placed into group 25, and
3. group 32 (specimens 42 and 44) was added to group 26.
4. When a discriminant analysis was run on the new combinations, specimen 16 in group 26 was found to belong in group 25. Specimen 16 was switched and analysis run again.
5. Specimen 26 was found to belong to group 25 instead of group 19 and it was moved. Discriminant analysis was done again. Actual group assignments matched predicted, and eight canonical correlation values increased while four decreased: increases ranged from 0.001 to 0.029, and decreases were from 0.001 to 0.004.

Effect of adding *Eucephalus bicolor* specimens

Adding three more specimens of *Eucephalus bicolor* enabled the inclusion of group 31 in the discriminant analysis. Specimen 18 (*A. brickellioides*) was found to belong in group 31. It was shifted and the discriminant analysis was rerun. The actual groups matched the predicted groups, and the correlation values for all axes increased.

Analysis of new phenetic groups

Twenty-three phenetic groups remained with four groups containing one specimen. Group 14 was largest with 13 members. Groups with 9-12 members were groups 3, 9, 11, 15 and 29. When species names were compared with the new groups, five species were found in their own unique groups: *Eucephalus bicolor*, *A. gormanii*, *A. paucicapitatus*, *A. perelegans* and *A. vialis*. *Aster turbinellus* was in one group excepting one specimen. *Aster breweri* occurred in two groups instead of three. *Aster glaucescens*,

A. wasatchensis, *A. ledophyllus*, and *A. engelmannii* specimens were each in three groups, *A. brickellioides* specimens were in four groups, and *A. glaucodes* were in five groups.

Groups with two or more members were given names created from species names of members; if more than one group had the same name then a numeric suffix was added. Single specimens not assigned to a large group were named with a short species code with a suffix of the specimen key number.

For the adjusted groups, all univariate tests and multivariate tests of characters were significant. Discriminant analysis found nine characters were significantly correlated (>0.70) with groups (Table 12); several had changed: middle leaf with a ciliated edge, middle leaf length, some vesture characters and red edge on phyllary. These correlation values measure how the characteristics of specimens in each group compare with those in other groups, and change as group memberships change. As an example, when a group with a wide range of leaf lengths was adjusted by removing those specimens with different lengths to another group of specimens with similar leaf lengths, then the correlation value between leaf length and groups would increase. This increase in correlation between character and groups may not cause a similar increase in canonical correlation values derived from discriminant analysis.

Discriminant axes are placed to maximize the differences among groups and do not directly reflect variation in individual characters. However, characters are indirectly associated with axes through relationship between groups and axes. Looking at the characters that show the highest correlation with the axes suggest which ones would best discriminate between groups (Table 12). The main changes between the "before" and "after" groups were the surprising correlation of middle leaf edge with cilia as the only significant character with the first axis, and the shift of leaf lengths and widths to axes two and four from their original positions. Before adjustments, middle leaf length had not been correlated with any significant axis, and width was correlated with the sixth axis. Pubescence and colour of phyllary characters remained correlated with the first five axes.

The graph of discriminant axes one and two of the adjusted groups shows how most groups were alignment at an angle slightly more than 45° to the axes and obscured each

other (top graph: **Figure 7**). This resulted from most groups having middle leaf edges with cilia. Clearer separation of the groups can be seen on the graph of discriminant axes two and three (bottom graph: **Figure 7**).

Making no change except removing group 29 (TURB) from the data set, another discriminant analysis was run. All characters, thirteen axes, and all multivariate tests were significant. Correlations between characters and the discriminant axes changed when *Aster turbinellus* was removed, excepting the first axis which was still mainly correlated with the character of middle leaf edge with cilia (Table 12). Axes 1 to 11 were correlated with at least two characters, often a combination of size, phyllary colour or pubescence. A graph of discriminant axes one and two showed most of the groups overlaid similarly to previous analysis (**Figure 7**) excepting groups 31 and 25 which were clearly separated

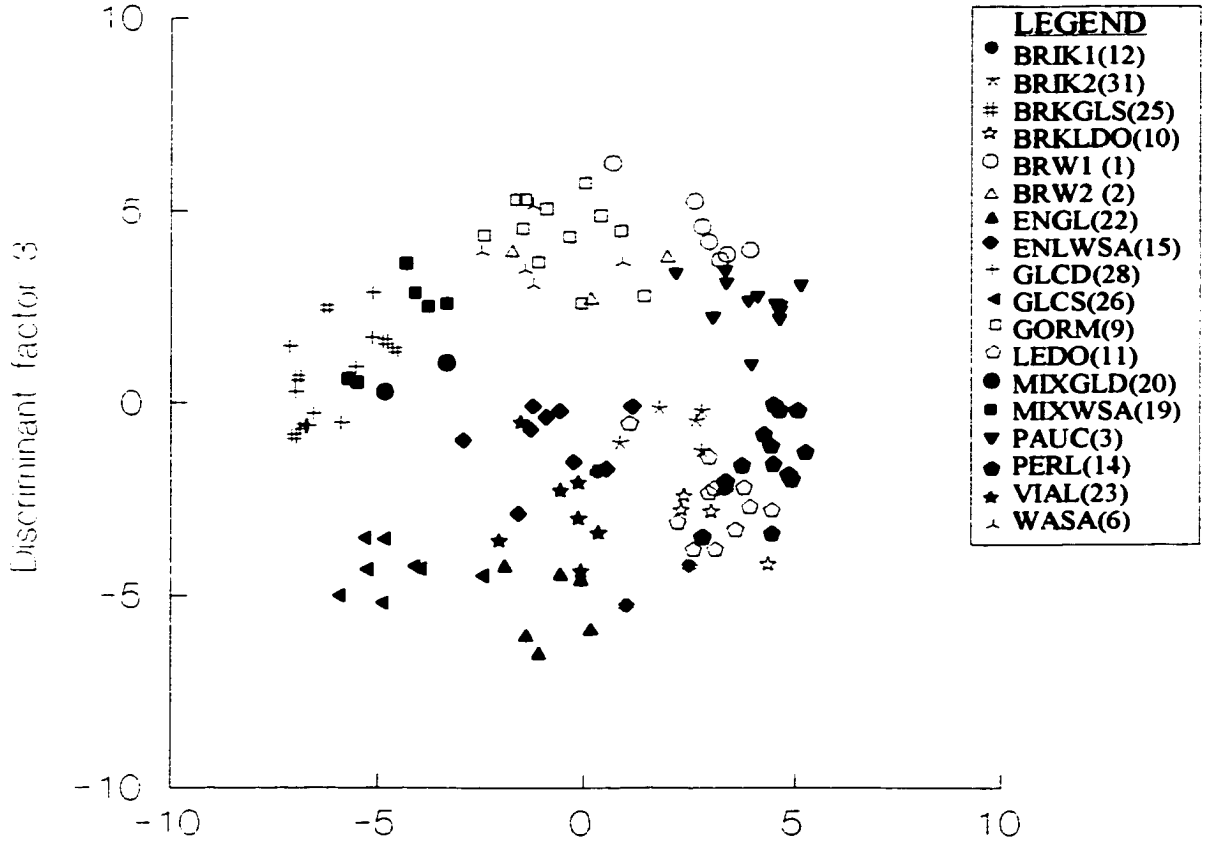


Figure 9: Discriminant factor axes 2 and 3 for section *Eucephalus* adjusted phenetic groups (group 29 (TURB) removed).

from each other as well as the other groups. A graph of discriminant axes 2 and 3 has

Table 12: Characters found to have high correlations with either the "before" or "after" phenetic groups or highly correlated with the first ten discriminant axes of the "after" phenetic groups.

Character	Groups based on phenogram			Adjusted groups			
	Correlation value	Rank	Correlated discriminant axes	Correlation value	Rank	Correlated discriminant axes	
	with *Aster turbinellus*			with *Aster turbinellus*			*Eucephalus* only
Middle leaf edge with cilia	0.43	21	15	0.94	1	1, 2	1
White stripe on phyllary	0.88	1	1, 2, 3, 4	0.81	2	3, 4	4
Middle leaf length	0.66	10	16	0.8	3	2, 5, 9	2, 3
Trichome density on leaf under surface	0.77	5	7	0.79	4	5	2, 5
Rows on involucre	0.75	7	17	0.79	4	2, 3	3
Ray floret count	0.76	6	3, 4, 5, 6	0.76	5	5, 8	5, 6, 7
Non-glandular trichomes on involucre	0.80	4	1, 5	0.76	5	7	2
Glandular trichomes on leaf under surface	0.83	2	1, 4, 8	0.72	6	2, 7	7
Non-glandular trichomes on leaf under surface	0.81	3	2, 5	0.70	7	3	2
Middle leaf width	0.70	8	6	0.69	8	4	4
Internode length	0.62	11	6	0.69	8	9	8
Glandular trichomes on leaf upper surface	0.67	9	11	0.67	9	16	7
Red edge on phyllary	0.80	4	2, 5	0.67	9	6	3
Trichome density on leaf upper surface	0.67	9	12	0.66	10	2	8
Red keel on phyllary	0.60	12	20	0.60	13	4	4
Trichome density on involucre	0.55	14	21	0.60	14	10	10
Disk floret achene length	0.60	12	3	0.59	14	6	6
Glandular trichomes on involucre	0.50	18	19	0.54	16	10	10
Non-glandular trichomes on leaf upper surface	0.53	16	14	0.54	16	11	9
Disk floret achene width	0.56	13	9, 20	0.53	17	9	none
Disk floret stigmatal branch length	0.47	21	9	0.35	25	15	9

been presented instead (**Figure 9**).

I also investigated discrimination among groups from particular geographic regions. Subsets based on geographic distributions were created, invariable and insignificant characters in each subset were removed and discriminant analyses were done for each.

One subset included groups 1, 2, 9, 10, 11, 12, 23, 25, 26 and 31, which occur in Oregon or California. Width of the involucre, disk floret achene width, phyllary keel colour and white stripe on the centre of the phyllary were removed from the character set because they were insignificant (with probabilities > 0.01). All the characters, multivariate tests, and seven axes were significant. The characters that best discriminated the groups were middle leaf edge with cilia, middle leaf length, trichome density on leaf underside, trichome density on the leaf underside, number of rows on the involucre, non-glandular

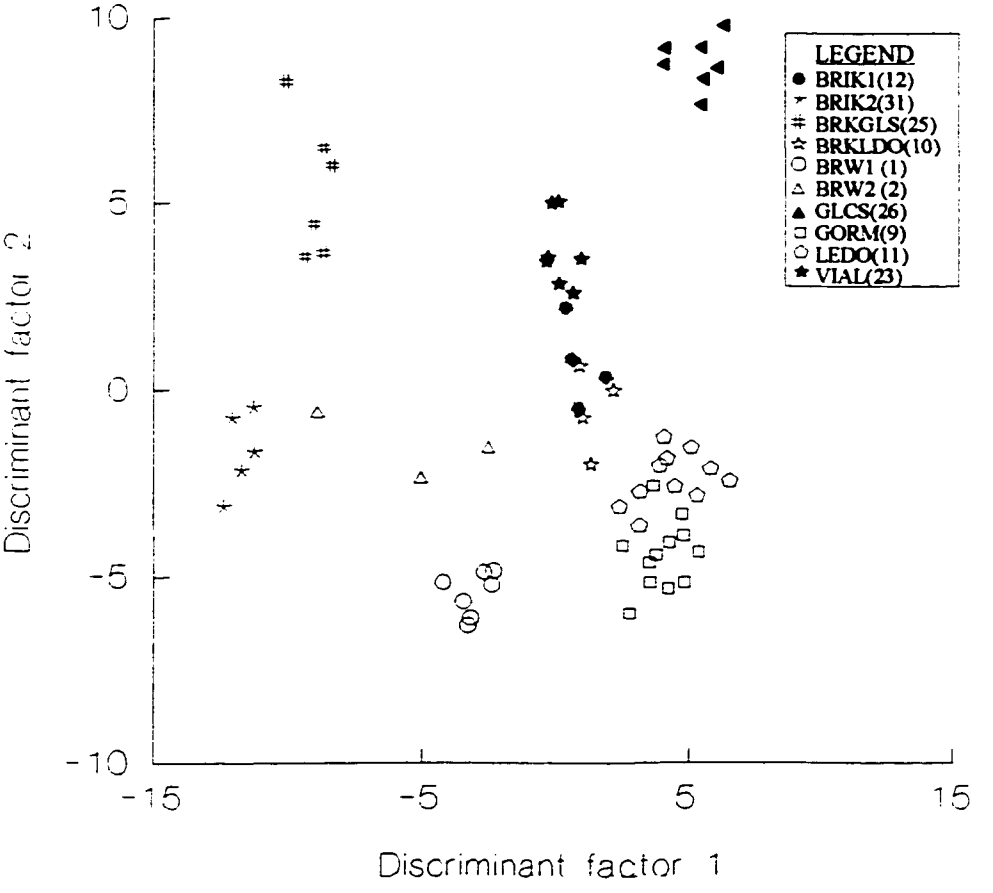


Figure 10 : Discriminant factor axes 1 and 2 for California and Oregon adjusted phenetic groups.

trichomes on leaf undersurface, glandular trichomes on the leaf upper surface, non-glandular trichomes on involucre, and middle leaf length. On the graph of axes one and two, each specimen was represented by a group symbol (**Figure 10**).

The subset for Washington state, British Columbia and Alberta included groups 3, 11, 14, 15, 19, 22, and 26. Middle leaf edge with cilia, glandular trichomes on involucre, and disk floret tube length were removed from the character set. After the discriminant analysis was completed, all characters, all multivariate tests and all six axes were significant. Characters that separated the groups were density of trichomes on the leaf undersurface, middle leaf length, phyllary colours, glandular trichomes on leaf undersurface, trichome density on the leaf undersurface, non-glandular trichomes on the involucre, white stripe on the centre of the phyllary, middle leaf length and width, number

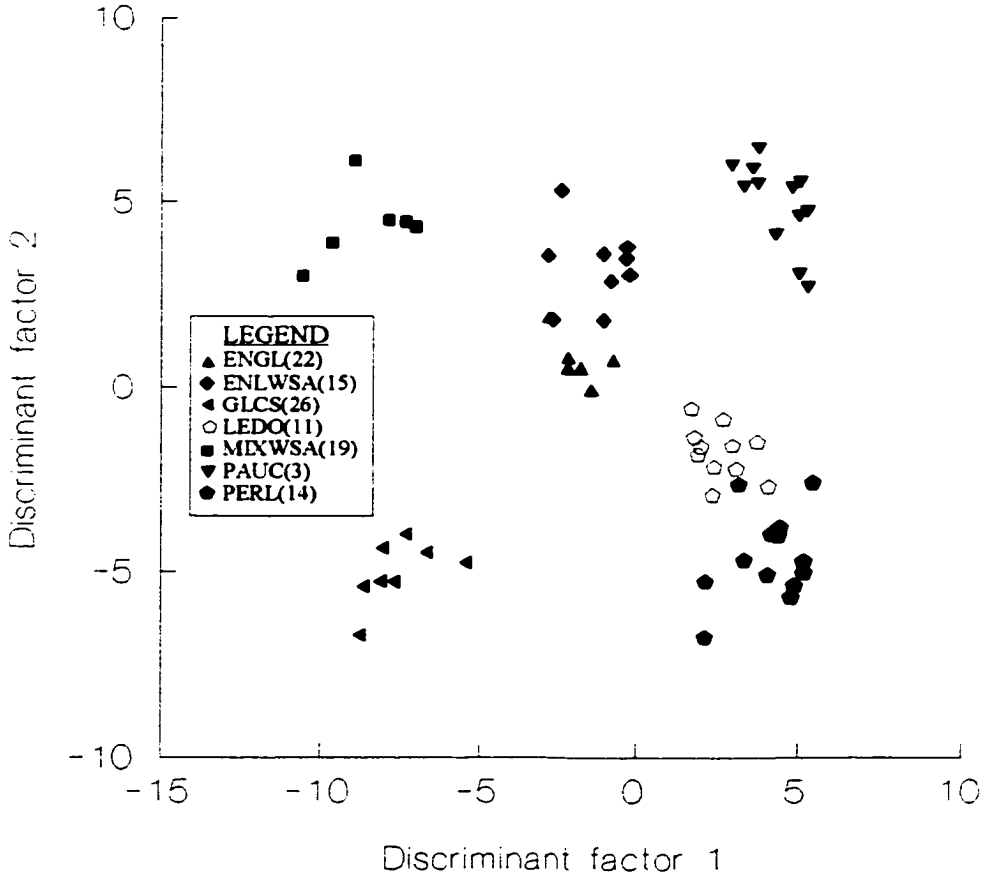


Figure 11: Discriminant factor axes 1 and 2 for northern adjusted phenetic groups.

of rows on the involucre, internode length, glandular trichomes on the leaf undersurface, and uppermost leaf length. The first two axes were used to graph discriminant values (**Figure 11**).

The last subset was for an analysis of groups (6, 14, 15, 19, 22, and 28) with specimens found growing in the Rocky Mountain Ranges. Number of heads, disk floret tube length, disk floret lobe length and white stripe on the phyllary were not included in the character set. The discriminant analysis found all characters, all multivariate tests, and five axises significant. Characters that separated the groups were middle leaf width, glandular trichomes on the leaf undersurface, internode length, number of ray florets, involucre width, and colour on the edge of the phyllary. The first two factors were used to illustrate the relationships among the groups (**Figure 12**).

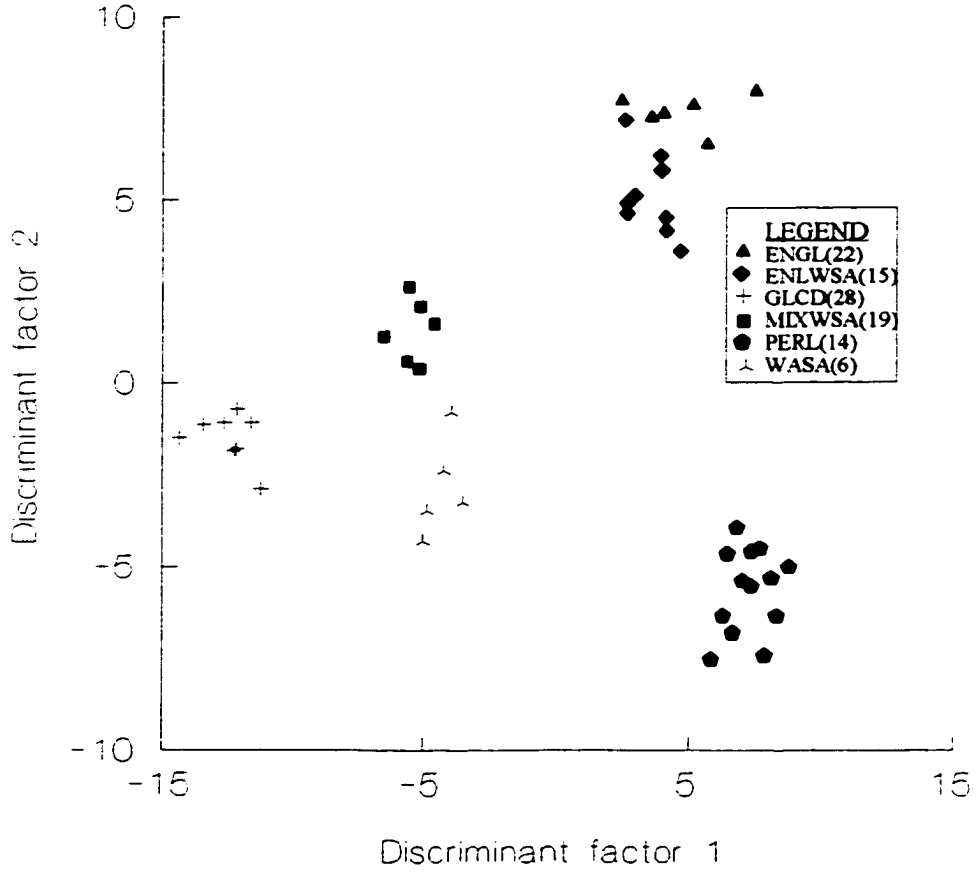


Figure 12: Discriminant factor axes 1 and 2 for Rocky Mountain Ranges adjusted phenetic groups.

Statistics for phenetic groups

Ranges, means and standard deviations of all characters for all the adjusted phenetic groups are in Table 13. Groups are arranged in alphabetic order of names.

Table 13: Ranges, means and standard deviations of all characters by phenetic group. The number of specimens in each group is in the second column. Character abbreviations are in Table 2 (page 39).

Group name and number	N	PLNT LNG		HD CNT		BRCH CNT		LF CNT	
		Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD
BRIK1 (12)	4	38.8-64.2	51.6 ±14.1	3-38	14.8 ±16.3	3-26	11.8 ±10.7	27-43	34.0 ±7.8
BRIK2 (31)	5	48.3-66.0	57.2 ±8.0	5-72	27.2 ±26.4	4-20	11.4 ±7.6	29-34	31.5 ±3.5
BRK22 (16)	1	52.2		6		5		33	
BRKGLS (25)	6	30.5-53.5	39.2 ±8.7	1-20	8.8 ±6.2	2-11	7.4 ±3.5	16-31	24.6 ±5.5
BRKLDO (10)	4	25.5-58.0	39.1 ±13.6	4-9	6.3 ±2.6	3-15	9.3 ±4.9	13-28	20.5 ±7.1
BRW1 (1)	7	27.4-69.1	41.4 ±24.0	1-37	14.0 ±12.3	10-24	14.7 ±8.1	17-27	21.7 ±5.0
BRW2 (2)	3	63.4-76.2	69.8 ±9.1	4-15	10.7 ±5.9	21-24	22.5 ±2.1	26-30	28.0 ±2.8
ENGL (22)	6	91.0-107.3	101.4 ±9.0	5-41	13.3 ±14.0	5-7	6.0 ±1.0	32-42	37.3 ±5.0
ENLWSA (15)	9	47.1-102.2	72.2 ±21.1	1-16	8.8 ±5.1	4-10	6.9 ±2.5	25-49	37.1 ±8.0
GLCD (28)	8	33.8-41.5	37.1 ±3.2	10-31	18.5 ±8.2	5-12	7.8 ±3.1	14-20	16.5 ±2.6
GLCS (26)	8	86.3-159.5	102.7 ±31.8	4-59	18.1 ±17.6	5-20	12.0 ±6.4	38-75	53.2 ±13.7
GLD50 (8)	1	44.5		112		15		16	
GLD53 (30)	1	39.8		17		14		20	
GORM (9)	12	13.8-31.5	22.4 ±5.1	1-5	1.7 ±1.2	0-11	4.4 ±4.2	18-36	24.6 ±5.3
LEDO (11)	11	21.0-84.5	43.4 ±17.9	1-17	8.9 ±5.3	0-18	8.9 ±6.0	15-57	31.4 ±11.0
MIXGLD (20)	2	41.2-64.5	52.9 ±16.5	8-23	15.5 ±10.6	6-11	8.5 ±3.5	22-37	29.5 ±10.6
MIXWSA (19)	6	30.7-78.0	58.7 ±17.4	4-40	17.5 ±13.2	3-16	7.7 ±4.5	16-31	22.3 ±4.9
PAUC (3)	12	20.5-53.6	29.2 ±10.0	1-4	2.2 ±1.3	0-8	2.7 ±2.8	18-32	24.3 ±5.1
PERL (14)	13	30.5-77.4	45.2 ±12.8	3-17	8.6 ±4.2	3-30	11.1 ±7.6	22-74	37.6 ±13.0
TURB (29)	9	62.5-67.2	65.2 ±2.4	7-80	38.1 ±26.9	11-20	16.3 ±4.7	27-28	27.7 ±0.6
TURB119 (34)	1			33					
VIAL (23)	7	77.0-117.5	98.3 ±19.6	5-134	64.1 ±50.8	0-29	19.8 ±13.5	30-45	36.0 ±7.9
WASA (6)	5	24.3-42.5	31.5 ±9.3	2-12	5.0 ±4.0	1-11	5.4 ±3.8	16-26	21.0 ±4.3

Table 13: Continued.

Group name and number	BRCT PDCL		NODE LNG		LF IN 8		LF MD LNG		LF HI LNG	
	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD
BRIK1 (12)	1-3	2.0 ±0.8	0.7-1.9	1.2 ±0.5	6-10	7.5 ±1.7	2.5-5.8	4.0 ±1.5	0.8-2.5	1.9 ±0.8
BRIK2 (31)	1-4	2.2 ±1.1	0.9-1.2	1.1 ±0.1	7-10	8.4 ±1.1	2.3-4.4	3.4 ±0.9	1.2-2.3	1.8 ±0.5
BRK22 (16)	3		1.5		6		7.4		4.8	
BRKGLS (25)	1-3	2.0 ±0.6	0.5-1.5	1.0 ±0.3	7-10	8.2 ±1.3	3.0-5.9	4.3 ±1.1	1.0-2.6	1.9 ±0.5
BRKLDO (10)	1-9	4.8 ±3.3	0.7-1.6	1.1 ±0.4	6-10	8.0 ±1.8	2.7-4.8	3.7 ±1.0	1.6-3.1	2.2 ±0.7
BRW1 (1)	2-5	2.9 ±1.1	0.7-2.1	1.4 ±0.6	4-10	6.7 ±2.1	2.6-4.3	3.2 ±0.6	1.6-2.6	2.1 ±0.3
BRW2 (2)	2-3	2.7 ±0.6	0.9-2.5	1.7 ±0.8	6-7	6.3 ±0.6	3.2-5.0	4.1 ±0.9	3.1-3.5	3.3 ±0.2
ENGL (22)	1-5	2.5 ±1.4	2.0-2.6	2.2 ±0.2	3-6	4.5 ±1.0	7.0-9.6	8.1 ±1.0	3.1-4.4	3.7 ±0.5
ENLWSA (15)	1-4	1.9 ±0.9	0.7-2.5	1.7 ±0.5	4-11	6.0 ±2.1	5.3-8.2	6.6 ±1.1	1.7-5.0	3.9 ±1.0
GLCD (28)	1-3	1.8 ±0.9	1.1-2.7	1.8 ±0.5	3-6	4.8 ±1.0	5.3-10.9	7.7 ±1.8	1.2-5.5	3.4 ±1.2
GLCS (26)	2-6	4.1 ±1.2	1.0-2.0	1.4 ±0.3	6-11	7.7 ±1.6	6.2-9.2	7.9 ±1.1	2.6-5.4	4.2 ±0.9
GLD50 (8)	1		1.3		6		4.7		2.7	
GLD53 (30)	2		3.4		3		6.1		2.5	
GORM (9)	0-2	1.0 ±0.6	0.3-1.0	0.6 ±0.2	10-18	13.6 ±2.1	1.9-3.1	2.5 ±0.3	1.2-2.9	1.9 ±0.6
LEDO (11)	1-4	2.2 ±1.0	0.5-1.8	1.1 ±0.4	7-15	9.3 ±2.4	3.0-5.3	4.2 ±0.8	1.5-3.2	2.1 ±0.5
MIXGLD (20)	2-7	4.5 ±3.5	1.2-1.4	1.3 ±0.1	6-7	6.5 ±0.7	5.9-7.0	6.5 ±0.8	2.8-3.1	3.0 ±0.2
MIXWSA (19)	1-3	1.7 ±1.0	1.9-3.0	2.4 ±0.4	3-4	3.3 ±0.5	6.2-9.2	7.9 ±1.3	2.1-4.1	3.2 ±0.9
PAUC (3)	0-3	1.5 ±1.1	0.6-1.3	0.9 ±0.2	7-13	9.1 ±1.8	2.5-3.9	3.2 ±0.5	1.1-3.0	2.2 ±0.6
PERL (14)	1-6	2.8 ±1.3	0.5-1.4	0.9 ±0.3	6-14	10.3 ±1.8	3.0-5.8	4.2 ±0.9	0.9-2.5	1.6 ±0.4
TURB (29)	4-22	9.0 ±5.8	1.8-2.6	2.2 ±0.3	3-6	3.8 ±1.0	6.2-9.6	7.5 ±1.2	1.1-3.4	2.2 ±0.7
TURB119 (34)	15		1.1		6		1.7		1.0	
VIAL (23)	1-4	2.9 ±1.1	1.2-2.1	1.6 ±0.3	5-9	6.3 ±1.5	5.7-8.6	7.2 ±1.1	2.4-5.2	3.6 ±1.0
WASA (6)	0-2	1.2 ±0.8	0.9-1.8	1.3 ±0.4	4-9	6.6 ±2.1	3.8-8.1	5.6 ±1.8	1.3-2.2	1.9 ±0.4

Table 13: Continued.

Group name and number	LF MD WD		LF HI WD		LF TOOTH		LF MD WLNG		LF HI WLNG	
	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD
BRIK1 (12)	0.7-1.7	1.1 ±0.4	0.2-0.4	0.3 ±0.1	0		0.4-2.0	1.1 ±0.7	0.2-1.0	0.5 ±0.4
BRIK2 (31)	0.7-1.4	1.0 ±0.3	0.2-0.7	0.4 ±0.2	0-1	0.2 ±0.4	1.0-2.1	1.6 ±0.5	0.3-1.2	0.7 ±0.3
BRK22 (16)	1.7		0.9		0		1.5		0.4	
BRKGLS (25)	0.7-1.5	1.2 ±0.3	0.2-0.8	0.5 ±0.2	0		0.2-2.7	1.3 ±0.9	0.1-1.0	0.6 ±0.4
BRKLDO (10)	0.5-1.5	1.0 ±0.4	0.2-0.6	0.4 ±0.2	0		0.9-2.6	1.4 ±0.8	0.1-1.5	0.5 ±0.7
BRW1 (1)	0.6-1.5	1.1 ±0.3	0.4-1.1	0.7 ±0.3	0		0.4-1.6	0.8 ±0.4	0.3-0.8	0.5 ±0.2
BRW2 (2)	0.6-1.4	1.1 ±0.4	0.6-0.8	0.7 ±0.1	0-1	0.3 ±0.6	1.3-2.3	1.8 ±0.5	0.5-1.2	0.8 ±0.4
ENGL (22)	1.6-3.6	2.5 ±0.8	0.5-1.1	0.8 ±0.2	0-1	0.3 ±0.5	2.5-4.0	3.3 ±0.5	1.1-2.2	1.5 ±0.5
ENLWSA (15)	1.5-2.3	1.9 ±0.3	0.5-1.8	0.9 ±0.4	0-1	0.2 ±0.4	1.6-3.5	2.5 ±0.6	0.3-2.5	1.3 ±0.7
GLCD (28)	0.7-1.6	1.2 ±0.3	0.5-1.2	0.8 ±0.3	0-1	0.1 ±0.4	0.5-3.5	2.3 ±1.1	0.3-1.1	0.7 ±0.3
GLCS (26)	0.6-1.6	1.1 ±0.3	0.2-0.6	0.3 ±0.1	0-1	0.1 ±0.4	2.3-4.4	3.2 ±0.8	0.5-2.9	1.4 ±0.9
GLD50 (8)	1.2		0.7		0		0.9		0.5	
GLD53 (30)	0.6		0.3		0		0.8		0.5	
GORM (9)	0.5-0.9	0.7 ±0.1	0.3-1.7	0.6 ±0.4	0		0.6-1.1	0.9 ±0.2	0.4-1.0	0.7 ±0.2
LEDO (11)	0.6-1.8	1.1 ±0.4	0.2-0.7	0.4 ±0.1	0-1	0.2 ±0.4	0.7-2.6	1.7 ±0.7	0.3-0.8	0.5 ±0.2
MIXGLD (20)	0.7-0.8	0.8 ±0.1	0.4-0.6	0.5 ±0.1	0		0.5-1.5	1.0 ±0.7	0.2-1.0	0.6 ±0.6
MIXWSA (19)	1.3-2.4	1.9 ±0.4	0.6-1.0	0.8 ±0.2	0		2.0-4.3	3.2 ±1.1	0.4-1.5	0.8 ±0.4
PAUC (3)	0.5-1.2	0.8 ±0.2	0.2-1.0	0.6 ±0.2	0-1	0.1 ±0.3	0.5-1.6	1.0 ±0.3	0.3-1.0	0.6 ±0.2
PERL (14)	0.3-1.0	0.7 ±0.2	0.2-0.6	0.3 ±0.1	0		0.6-1.9	1.2 ±0.4	0.3-0.7	0.5 ±0.2
TURB (29)	0.3-2.0	1.1 ±0.5	0.1-0.8	0.4 ±0.2	0		0.8-4.7	2.7 ±1.3	0.3-1.0	0.6 ±0.2
TURB119 (34)	1.4		0.4		0		1.0		0.2	
VIAL (23)	1.6-2.9	2.3 ±0.5	0.5-1.2	0.8 ±0.2	0-1	0.3 ±0.5	2.0-4.5	3.1 ±0.9	0.6-2.4	1.3 ±0.6
WASA (6)	0.9-1.4	1.2 ±0.2	0.3-0.7	0.6 ±0.2	0		0.5-2.5	1.4 ±0.7	0.2-0.7	0.5 ±0.2

Table 13: Continued.

Group name and number	LF MD TP		LF HI TP		LF MD EDG		LF HI EDG		LF MD CLT		LF HI CLT	
	Range	Mean± SD	Range	Mean± SD	Range	Mean± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD
BRIK1 (12)	1-5	3.0 ±2.3	1-5	3.5 ±1.9	3		3		1		1	
BRIK2 (31)	1-5	2.4 ±1.5	1-5	2.2 ±1.1	3-4	3.8 ±0.4	3-4	3.8 ±0.4	0		0	
BRK22 (16)	5		5		3		3		1		1	
BRKGLS (25)	3-5	4.5 ±0.8	3-5	4.0 ±1.3	3-4	3.2 ±0.4	3		0		0	
BRKLDO (10)	3-5	3.5 ±1.0	3-5	2.8 ±1.5	3		3		1		1	
BRW1 (1)	4-5	4.9 ±0.4	4-5	4.6 ±0.8	3		3		1		1	
BRW2 (2)	4-5	4.3 ±0.6	4-5	3.0 ±1.7	2-3	2.7 ±0.6	3		0-1	0.7 ±0.6	0-1	0.7 ±0.6
ENGL (22)	4-6	5.2 ±0.8	4-6	4.3 ±1.6	2-3	2.5 ±0.5	3		1		1	
ENLWSA (15)	3-5	4.6 ±0.9	3-5	4.2 ±1.0	2-4	2.9 ±0.6	3-4	3.1 ±0.3	1		1	
GLCD (28)	2-5	4.4 ±1.1	2-5	5.1 ±1.0	3		3		1		1	
GLCS (26)	2-5	4.0 ±1.1	2-5	2.9 ±1.0	2-3	2.8 ±0.5	3		1		1	
GLD50 (8)	4		4		3		3		1		1	
GLD53 (30)	5		5		3		3		1		1	
GORM (9)	2-7	4.3 ±1.5	2-7	3.7 ±1.3	3		3		1		1	
LEDO (11)	3-6	4.8 ±0.8	3-6	3.3 ±1.3	2-3	2.9 ±0.3	3		1		1	
MIXGLD (20)	5		5	3.5 ±2.1	3		3		1		1	
MIXWSA (19)	3-5	4.7 ±0.8	3-5	4.5 ±1.4	3		3		1		1	
PAUC (3)	2-7	4.6 ±1.4	2-7	3.2 ±1.3	3		3		1		1	
PERL (14)	2-5	3.3 ±1.4	2-5	2.7 ±1.3	3		3		1		1	
TURB (29)	2-5	2.7 ±1.3	2-5	3.7 ±1.6	3		3		1		0-1	0.9 ±0.3
TURB119 (34)	5		5		3		3		1		1	
VIAL (23)	3-5	4.4 ±1.0	3-5	4.1 ±1.5	2-3	2.9 ±0.4	3		1		1	
WASA (6)	2-5	4.4 ±1.3	2-5	4.4 ±0.9	3		3		1		1	

Table 13: Continued.

Group name and number	STM GLND		STM SMPL		STM DNS		LF UP GLND		LF UP SMPL		LF UP DNS	
	Range	Mean± SD	Range	Mean± SD	Range	Mean± SD	Range	Mean± SD	Range	Mean± SD	Range	Mean± SD
BRIK1 (12)	0-1	0.3 ±0.5	1		1-2	1.3 ±0.5	0		0-1	0.5 ±0.6	0-1	0.5 ±0.6
BRIK2 (31)	0		1		2-3	2.6 ±0.5	0		0		0	
BRK22 (16)	1		0		2		0		0		0	
BRKGLS (25)	0-1	0.3 ±0.5	0		0-1	0.3 ±0.5	0-1	0.2 ±0.4	0-1	0.2 ±0.4	0-1	0.3 ±0.5
BRKLDO (10)	0-1	0.8 ±0.5	1		2-3	2.3 ±0.5	0-1	0.8 ±0.5	0-1	0.8 ±0.5	1-3	2.0 ±0.8
BRW1 (1)	1		0-1	0.9 ±0.4	1-2	1.6 ±0.5	0-1	0.7 ±0.5	0-1	0.9 ±0.4	1-2	1.7 ±0.5
BRW2 (2)	1		0-1	0.7 ±0.6	1		0-1	0.3 ±0.6	1		1	
ENGL (22)	0-1	0.8 ±0.4	1		1-2	1.2 ±0.4	0-1	0.3 ±0.5	0-1	0.7 ±0.5	0-1	0.8 ±0.4
ENLWSA (15)	1		0-1	0.9 ±0.3	1-2	1.6 ±0.5	0-1	0.7 ±0.5	0-1	0.7 ±0.5	1-2	1.1 ±0.3
GLCD (28)	0-1	0.1 ±0.4	0-1	0.3 ±0.5	0-1	0.4 ±0.5	0		0		0	
GLCS (26)	0-1	0.3 ±0.5	0-1	0.4 ±0.5	0-1	0.5 ±0.5	0-1	0.1 ±0.4	0-1	0.1 ±0.4	0-2	0.5 ±0.9
GLD50 (8)	1		0		2		1		0		2	
GLD53 (30)	0		1		1		0		0		0	
GORM (9)	1		1		1-3	1.7 ±0.8	1		0-1	0.5 ±0.5	1-3	2.2 ±0.7
LEDO (11)	0-1	0.5 ±0.5	1		1-3	2.3 ±0.6	0		1		1-2	1.2 ±0.4
MIXGLD (20)	1		0		1		1		0		1	
MIXWSA (19)	0-1	0.8 ±0.4	0-1	0.3 ±0.5	0-3	2.0 ±1.3	1		0		1-2	1.3 ±0.5
PAUC (3)	1		1		1-3	1.8 ±0.6	1		0-1	0.6 ±0.5	1-3	1.7 ±0.6
PERL (14)	1		1		2-3	2.2 ±0.4	0-1	0.8 ±0.4	1		1-3	1.7 ±0.6
TURB (29)	0-1	0.2 ±0.4	1		1-2	1.4 ±0.5	0-1	0.1 ±0.3	0		0-1	0.1 ±0.3
TURB119 (34)	0		1		3		0		1		2	
VIAL (23)	1		1		1-2	1.7 ±0.5	1		0-1	0.3 ±0.5	1	
WASA (6)	1		0-1	0.4 ±0.5	1-3	2.4 ±0.9	1		0-1	0.2 ±0.4	1-2	1.6 ±0.5

Table 13: Continued.

Group name and number	LF BW GLND		LF BW SMPL		LF BW DNS		INV GLND		INV SMPL		INV DNS	
	Range	Mean± SD	Range	Mean± SD	Range	Mean± SD	Range	Mean± SD	Range	Mean± SD	Range	Mean± SD
BRIK1 (12)	0-1	0.3 ±0.5	1		2		1		0-1	0.3 ±0.5	1-2	1.8 ±0.5
BRIK2 (31)	0		1		3		0		1		2-3	2.8 ±0.4
BRK22 (16)	1		0		1		1		0		2	
BRKGLS (25)	0-1	0.3 ±0.5	0		0-1	0.3 ±0.5	0-1	0.8 ±0.4	0		0-3	1.7 ±1.2
BRKLDO (10)	0-1	0.5 ±0.6	1		2-3	2.5 ±0.6	0-1	0.8 ±0.5	0-1	0.8 ±0.5	2-3	2.3 ±0.5
BRW1 (1)	1		0-1	0.9 ±0.4	2		0-1	0.9 ±0.4	1		2	
BRW2 (2)	0-1	0.3 ±0.6	1		1		1		1		1	
ENGL (22)	0-1	0.3 ±0.5	0-1	0.8 ±0.4	1		0-1	0.8 ±0.4	0-1	0.5 ±0.5	0-2	1.0 ±0.6
ENLWSA (15)	1		0-1	0.3 ±0.5	1-2	1.9 ±0.3	1		0-1	0.1 ±0.3	1-3	2.2 ±1.0
GLCD (28)	0		0		0		0-1	0.3 ±0.5	0-1	0.1 ±0.4	0-1	0.4 ±0.5
GLCS (26)	0-1	0.3 ±0.5	0-1	0.1 ±0.4	0-1	0.4 ±0.5	1		0-1	0.1 ±0.4	1-2	1.4 ±0.5
GLD50 (8)	1		1		2		1		1		1	
GLD53 (30)	0		1		1		0		1		1	
GORM (9)	1		0-1	0.1 ±0.3	1-3	2.0 ±0.6	0-1	0.5 ±0.5	0		0-3	0.9 ±1.1
LEDO (11)	0		1		3		1		0-1	0.1 ±0.3	2-3	2.5 ±0.5
MIXGLD (20)	1		0		1		1		0		1-2	1.5 ±0.7
MIXWSA (19)	1		0		1		1		0		1-3	2.2 ±1.0
PAUC (3)	1		1		1-3	1.9 ±0.5	1		1		1-3	2.3 ±0.6
PERL (14)	1		1		1-3	2.0 ±0.6	0-1	0.7 ±0.5	1		1-3	2.6 ±0.7
TURB (29)	0-1	0.1 ±0.3	0-1	0.6 ±0.5	0-3	0.9 ±0.9	0-1	0.1 ±0.3	0		0-1	0.2 ±0.4
TURB119 (34)	0		1		3		0		1		3	
VIAL (23)	0-1	0.9 ±0.4	1		1-2	1.4 ±0.5	1		0-1	0.3 ±0.5	1-2	1.9 ±0.4
WASA (6)	1		0-1	0.4 ±0.5	1-2	1.8 ±0.4	1		0		2-3	2.8 ±0.4

Table 13: Continued.

Group name and number	INV LNG		INV WD		INV ROWS		INV PHL CNT		PHL TP	
	Range	Mean±SD	Range	Mean±SD	Range	Mean± SD	Range	Mean± SD	Range	Mean± SD
BRIK1 (12)	0.8-1.0	0.9 ±0.1	0.8-1.1	0.9 ±0.1	3-5	4.0 ±1.2	11-26	19.0 ±6.8	1-3	1.8 ±1.0
BRIK2 (31)	0.7-1.0	0.8 ±0.1	0.7-0.9	0.8 ±0.1	4-5	4.4 ±0.5	19-30	24.0 ±4.0	2-3	2.2 ±0.4
BRK22 (16)	1.0		1.1		3		16		3	
BRKGLS (25)	0.7-1.1	1.0 ±0.1	0.9-1.2	1.1 ±0.1	3-4	3.5 ±0.5	14-20	17.8 ±2.6	2-4	3.3 ±0.8
BRKLDO (10)	1.0-1.2	1.1 ±0.1	0.8-1.3	1.1 ±0.2	4-5	4.5 ±0.6	19-28	22.5 ±4.4	2-3	2.8 ±0.5
BRW1 (1)	0.7-0.9	0.8 ±0.1	0.5-1.2	0.9 ±0.2	2		9-14	12.0 ±1.8	3-4	3.7 ±0.5
BRW2 (2)	0.8-0.9	0.9 ±0.1	1.0-1.2	1.1 ±0.1	2		13-16	14.0 ±1.7	3-4	3.7 ±0.6
ENGL (22)	0.9-1.1	1.0 ±0.1	1.1-1.7	1.4 ±0.3	4-5	4.3 ±0.5	20-34	25.0 ±5.1	2-5	3.5 ±1.4
ENLWSA (15)	0.8-1.2	1.1 ±0.1	1.1-1.6	1.3 ±0.2	3-4	3.3 ±0.5	12-36	18.1 ±7.4	2-5	2.9 ±1.4
GLCD (28)	0.7-0.8	0.7 ±0.0	0.7-1.0	0.8 ±0.1	3-4	3.5 ±0.5	11-19	13.9 ±2.9	3-7	6.0 ±1.5
GLCS (26)	0.7-1.1	0.9 ±0.1	0.8-1.5	1.1 ±0.2	3-4	3.8 ±0.5	16-37	25.1 ±7.4	2-4	3.4 ±0.9
GLD50 (8)	1.0		0.8		3		10		7	
GLD53 (30)	0.9		1.1		4		24		5	
GORM (9)	0.7-1.2	0.8 ±0.1	0.8-1.4	1.1 ±0.2	2-3	2.3 ±0.5	11-19	15.2 ±2.7	2-4	2.6 ±0.8
LEDO (11)	0.7-1.2	0.9 ±0.2	0.8-1.6	1.1 ±0.2	3-5	3.9 ±0.5	13-28	19.3 ±4.5	2-4	3.2 ±0.6
MIXGLD (20)	0.7-0.8	0.8 ±0.1	0.6-1.1	0.9 ±0.4	3-4	3.5 ±0.7	15-20	17.5 ±3.5	2-5	3.5 ±2.1
MIXWSA (19)	0.7-1.0	0.9 ±0.1	0.6-1.2	0.9 ±0.2	2-3	2.7 ±0.5	10-16	11.8 ±2.3	2-7	5.2 ±2.2
PAUC (3)	0.6-1.2	0.9 ±0.1	1.1-1.7	1.4 ±0.2	2-3	2.2 ±0.4	11-19	15.3 ±2.5	2-3	2.1 ±0.3
PERL (14)	0.7-0.9	0.8 ±0.1	0.6-1.1	0.9 ±0.2	3-5	4.2 ±0.7	14-28	20.5 ±4.0	2-3	2.3 ±0.5
TURB (29)	0.9-1.2	1.1 ±0.1	0.6-1.2	0.9 ±0.2	5-6	5.6 ±0.5	20-36	27.9 ±4.8	7	
TURB119 (34)	1.0		0.7		6		47		5	
VIAL (23)	0.8-1.2	1.0 ±0.1	0.7-1.9	1.1 ±0.4	3-4	3.7 ±0.5	17-20	19.0 ±1.2	2	
WASA (6)	0.8-1.0	0.9 ±0.1	0.8-1.6	1.1 ±0.3	2-3	2.4 ±0.5	10-18	12.8 ±3.1	2	

Table 13: Continued.

Group name and number	DSK AC LNG		DSK AC WD		DS PP LNG	
	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD
BRIK1 (12)	0.15-0.39	0.24 ±0.11	0.05-0.10	0.09 ±0.03	0.59-0.80	0.68 ±0.10
BRIK2 (31)	0.21-0.35	0.25 ±0.06	0.04-0.10	0.07 ±0.02	0.55-0.64	0.60 ±0.04
BRK22 (16)	0.30		0.07		0.70	
BRKGLS (25)	0.27-0.49	0.38 ±0.09	0.05-0.12	0.08 ±0.03	0.66-0.78	0.72 ±0.05
BRKLDO (10)	0.20-0.43	0.32 ±0.10	0.06-0.12	0.09 ±0.03	0.70-0.80	0.75 ±0.04
BRW1 (1)	0.30-0.50	0.42 ±0.07	0.08-0.11	0.10 ±0.01	0.60-0.90	0.76 ±0.13
BRW2 (2)	0.40-0.50	0.45 ±0.05	0.05-0.10	0.07 ±0.03	0.70-1.00	0.83 ±0.15
ENGL (22)	0.45-0.50	0.47 ±0.02	0.06-0.18	0.12 ±0.04	0.60-0.90	0.74 ±0.10
ENLWSA (15)	0.36-0.51	0.43 ±0.05	0.04-0.10	0.07 ±0.02	0.70-0.92	0.81 ±0.08
GLCD (28)	0.14-0.26	0.21 ±0.03	0.03-0.06	0.05 ±0.01	0.59-0.81	0.72 ±0.07
GLCS (26)	0.29-0.52	0.43 ±0.08	0.07-0.15	0.09 ±0.03	0.60-0.76	0.66 ±0.05
GLD50 (8)	0.36		0.05		0.67	
GLD53 (30)	0.24		0.07		0.76	
GORM (9)	0.20-0.45	0.32 ±0.06	0.05-0.13	0.08 ±0.02	0.55-0.75	0.63 ±0.06
LEDO (11)	0.22-0.50	0.34 ±0.09	0.04-0.11	0.07 ±0.02	0.60-0.85	0.72 ±0.07
MIXGLD (20)	0.23-0.35	0.29 ±0.08	0.06-0.07	0.07 ±0.01	0.55-0.62	0.59 ±0.05
MIXWSA (19)	0.20-0.30	0.25 ±0.04	0.03-0.09	0.05 ±0.02	0.59-0.79	0.66 ±0.08
PAUC (3)	0.27-0.54	0.41 ±0.08	0.07-0.17	0.12 ±0.03	0.72-0.90	0.79 ±0.06
PERL (14)	0.21-0.41	0.33 ±0.06	0.05-0.10	0.08 ±0.02	0.47-0.80	0.68 ±0.09
TURB (29)	0.13-0.27	0.21 ±0.05	0.03-0.07	0.05 ±0.01	0.48-0.66	0.56 ±0.06
TURB119 (34)	0.16		0.03		0.52	
VIAL (23)	0.22-0.50	0.37 ±0.14	0.07-0.10	0.09 ±0.01	0.63-1.00	0.82 ±0.12
WASA (6)	0.17-0.26	0.21 ±0.04	0.04-0.05	0.05 ±0.01	0.68-0.88	0.74 ±0.08

Table 13: Continued.

Group name and number	DSK TB LNG		DSK LM LNG		DSK SG LNG	
	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD
BRIK1 (12)	0.50-0.70	0.59 ±0.09	0.10-0.20	0.13 ±0.05	0.12-0.24	0.17 ±0.06
BRIK2 (31)	0.40-0.57	0.48 ±0.06	0.05-0.32	0.16 ±0.11	0.09-0.20	0.15 ±0.05
BRK22 (16)	0.60		0.15		0.15	
BRKGLS (25)	0.54-0.66	0.60 ±0.04	0.10-0.16	0.13 ±0.02	0.10-0.29	0.21 ±0.06
BRKLDO (10)	0.50-0.65	0.58 ±0.06	0.10-0.12	0.11 ±0.01	0.12-0.21	0.18 ±0.04
BRW1 (1)	0.60-0.80	0.68 ±0.09	0.10-0.30	0.19 ±0.08	0.20-0.35	0.27 ±0.06
BRW2 (2)	0.60-0.90	0.73 ±0.15	0.15-0.30	0.22 ±0.08	0.10-0.30	0.23 ±0.12
ENGL (22)	0.55-0.72	0.62 ±0.06	0.07-0.20	0.13 ±0.05	0.19-0.26	0.22 ±0.03
ENLWSA (15)	0.52-0.98	0.69 ±0.13	0.09-0.16	0.13 ±0.02	0.21-0.30	0.25 ±0.03
GLCD (28)	0.47-0.65	0.56 ±0.06	0.10-0.15	0.12 ±0.02	0.16-0.21	0.18 ±0.02
GLCS (26)	0.51-0.62	0.56 ±0.04	0.07-0.15	0.11 ±0.03	0.10-0.21	0.18 ±0.04
GLD50 (8)	0.63		0.09		0.20	
GLD53 (30)	0.60		0.05		0.14	
GORM (9)	0.40-0.60	0.50 ±0.06	0.09-0.19	0.13 ±0.03	0.12-0.20	0.17 ±0.02
LEDO (11)	0.52-0.65	0.60 ±0.04	0.08-0.16	0.12 ±0.02	0.12-0.30	0.21 ±0.05
MIXGLD (20)	0.46-0.56	0.51 ±0.07	0.11-0.16	0.14 ±0.04	0.18-0.23	0.21 ±0.04
MIXWSA (19)	0.48-0.72	0.56 ±0.08	0.07-0.12	0.11 ±0.02	0.12-0.26	0.18 ±0.06
PAUC (3)	0.51-0.82	0.63 ±0.09	0.12-0.18	0.15 ±0.02	0.12-0.25	0.19 ±0.03
PERL (14)	0.32-0.75	0.56 ±0.11	0.06-0.15	0.10 ±0.02	0.11-0.25	0.20 ±0.04
TURB (29)	0.45-0.60	0.50 ±0.05	0.07-0.12	0.10 ±0.02	0.11-0.22	0.16 ±0.04
TURB119 (34)	0.42		0.05		0.12	
VIAL (23)	0.51-0.80	0.63 ±0.10	0.10-0.20	0.16 ±0.04	0.09-0.25	0.18 ±0.05
WASA (6)	0.50-0.62	0.57 ±0.05	0.09-0.13	0.10 ±0.02	0.15-0.21	0.18 ±0.03

Table 13: Continued.

Group name and number	RAY CNT		RY AC LNG		RY AC WD		RY PP LNG	
	Range	Mean± SD	Range	Mean±SD	Range	Mean± SD	Range	Mean±SD
BRIK1 (12)	0-4	1.0 ±2.0	0.16		0.06		0.61	
BRIK2 (31)	0-6	3.8 ±2.3	0.23-0.30	0.26 ±0.03	0.04-0.07	0.05 ±0.01	0.50-0.57	0.54 ±0.04
BRK22 (16)	0							
BRKGLS (25)	0-8	4.8 ±3.8	0.23-0.40	0.34 ±0.07	0.06-0.10	0.08 ±0.02	0.65-0.86	0.73 ±0.10
BRKLDO (10)	0-7	1.8 ±3.5	0.47		0.07		0.72	
BRW1 (1)	0							
BRW2 (2)	0							
ENGL (22)	4-12	8.5 ±2.6	0.35-0.50	0.45 ±0.05	0.10-0.15	0.12 ±0.02	0.70-0.83	0.75 ±0.06
ENLWSA (15)	7-20	14.2 ±4.2	0.31-0.52	0.40 ±0.06	0.04-0.15	0.08 ±0.04	0.62-0.88	0.74 ±0.09
GLCD (28)	8-19	13.8 ±3.6	0.12-0.28	0.20 ±0.06	0.03-0.07	0.04 ±0.01	0.55-0.75	0.66 ±0.06
GLCS (26)	5-12	8.8 ±2.4	0.24-0.52	0.38 ±0.09	0.05-0.13	0.09 ±0.03	0.58-0.73	0.63 ±0.05
GLD50 (8)	14		0.35		0.04		0.65	
GLD53 (30)	32		0.20		0.07		0.72	
GORM (9)	3-14	9.4 ±3.5	0.26-0.43	0.31 ±0.05	0.03-0.11	0.08 ±0.03	0.52-0.71	0.61 ±0.05
LEDO (11)	6-20	11.5 ±4.1	0.23-0.50	0.34 ±0.09	0.04-0.13	0.07 ±0.03	0.64-0.86	0.71 ±0.08
MIXGLD (20)	12-15	13.5 ±2.1	0.27-0.35	0.31 ±0.06	0.06-0.09	0.08 ±0.02	0.50-0.63	0.57 ±0.09
MIXWSA (19)	8-14	11.0 ±2.5	0.16-0.31	0.26 ±0.05	0.06-0.07	0.06 ±0.00	0.50-0.72	0.59 ±0.07
PAUC (3)	7-13	10.7 ±2.0	0.25-0.47	0.36 ±0.06	0.06-0.16	0.11 ±0.03	0.65-0.90	0.73 ±0.07
PERL (14)	5-8	6.8 ±1.0	0.22-0.41	0.33 ±0.06	0.06-0.11	0.08 ±0.01	0.50-0.75	0.64 ±0.08
TURB (29)	10-18	13.6 ±2.5	0.11-0.28	0.19 ±0.05	0.04-0.10	0.06 ±0.02	0.47-0.60	0.52 ±0.04
TURB119 (34)	16		0.16		0.08		0.56	
VIAL (23)	0							
WASA (6)	10-18	13.6 ±3.0	0.16-0.26	0.20 ±0.04	0.03-0.07	0.05 ±0.02	0.61-0.73	0.66 ±0.05

Table 13: Continued.

Group name and number	RY TB LNG		RY LM LNG		RY SG LNG	
	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD
BRIK1 (12)	0.15		0.62		0.12	
BRIK2 (31)	0.18-1.00	0.44 ±0.38	0.90-1.20	1.05 ±0.13	0.10-0.15	0.12 ±0.02
BRK22 (16)						
BRKGLS (25)	0.37-0.41	0.40 ±0.02	1.10-1.70	1.45 ±0.26	0.10-0.25	0.16 ±0.07
BRKLDO (10)	0.42		1.15		0.16	
BRW1 (1)						
BRW2 (2)						
ENGL (22)	0.32-0.60	0.48 ±0.13	1.20-1.50	1.35 ±0.12	0.12-0.30	0.17 ±0.06
ENLWSA (15)	0.35-0.82	0.48 ±0.14	1.05-2.20	1.64 ±0.30	0.12-0.30	0.20 ±0.06
GLCD (28)	0.35-0.50	0.41 ±0.06	0.70-1.35	0.96 ±0.25	0.15-0.20	0.18 ±0.02
GLCS (26)	0.25-0.40	0.31 ±0.06	0.76-1.42	1.22 ±0.21	0.12-0.36	0.19 ±0.08
GLD50 (8)	0.36		0.90		0.12	
GLD53 (30)	0.27		1.00		0.12	
GORM (9)	0.25-0.42	0.35 ±0.04	0.70-1.62	0.93 ±0.24	0.10-0.21	0.15 ±0.03
LEDO (11)	0.23-0.50	0.39 ±0.08	1.10-1.90	1.39 ±0.25	0.10-0.29	0.18 ±0.06
MIXGLD (20)	0.30-0.35	0.33 ±0.04	0.70-1.30	1.00 ±0.42	0.17-0.23	0.20 ±0.04
MIXWSA (19)	0.30-0.42	0.34 ±0.04	1.00-1.90	1.31 ±0.32	0.12-0.23	0.19 ±0.04
PAUC (3)	0.35-0.41	0.38 ±0.03	1.05-1.62	1.25 ±0.17	0.12-0.22	0.17 ±0.04
PERL (14)	0.22-0.48	0.34 ±0.07	0.60-1.51	1.04 ±0.22	0.12-0.26	0.19 ±0.04
TURB (29)	0.24-0.42	0.31 ±0.06	0.70-1.30	1.07 ±0.20	0.11-0.16	0.13 ±0.02
TURB119 (34)	0.35		0.75		0.10	
VIAL (23)						
WASA (6)	0.26-0.42	0.35 ±0.07	0.71-1.20	1.01 ±0.18	0.13-0.22	0.17 ±0.04

Table 13: Continued.

Group name and number	PHL EDG RD		PHL TP RD		PHL KL RD		PHL ST WHT	
	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD
BRIK1 (12)	1		1		0		1	
BRIK2 (31)	1		1		0-1	0.2 ±0.4	1	
BRK22 (16)	0		0		0		1	
BRKGLS (25)	0-1	0.8 ±0.4	1		0-1	0.2 ±0.4	1	
BRKLDO (10)	1		0-1	0.8 ±0.5	0		1	
BRW1 (1)	0-1	0.1 ±0.4	0-1	0.4 ±0.5	0		1	
BRW2 (2)	0		0-1	0.3 ±0.6	0		1	
ENGL (22)	1		0-1	0.8 ±0.4	0		1	
ENLWSA (15)	1		1		0		1	
GLCD (28)	0-1	0.5 ±0.5	0-1	0.5 ±0.5	0-1	0.5 ±0.5	1	
GLCS (26)	1		1		0-1	0.1 ±0.4	1	
GLD50 (8)	0		0		0		1	
GLD53 (30)	0		0		0		0	
GORM (9)	0-1	0.1 ±0.3	0-1	0.2 ±0.4	0		0-1	0.9 ±0.3
LEDO (11)	1		1		0-1	0.1 ±0.3	0-1	0.9 ±0.3
MIXGLD (20)	1		1		1		1	
MIXWSA (19)	0-1	0.5 ±0.5	0-1	0.5 ±0.5	0		1	
PAUC (3)	0-1	0.1 ±0.3	0-1	0.1 ±0.3	0		0-1	0.9 ±0.3
PERL (14)	1		1		0-1	0.8 ±0.4	0	
TURB (29)	0-1	0.3 ±0.5	0		0		1	
TURB119 (34)	0		0		0		0	
VIAL (23)	0-1	0.6 ±0.5	0-1	0.6 ±0.5	0		1	
WASA (6)	0		0		0		1	

Correspondence between phenetic groups and recognized taxa

I compared the descriptions collected from the literature (Table 1) with the means and ranges calculated for the phenetic groups (Table 1), and attempted to assign a recognized taxonomic name to each group. The type specimen of *Aster vialis* and an isotype of *Aster wasatchensis* were among the herbarium specimens that I examined for this study. I found placement of some specimens into any described taxon of section

Eucephalus impossible, and have concluded that some were misidentified, or on reexamination found some to be incomplete or poorly grown (as indicated by small size (compared to other specimens similarly identified) or insect infestation). First I will discuss groups that fit well with a description, then the puzzling groups, and finally the single specimens.

Phenetic groups that could be easily placed were TURB, TRB119, BRKGLS, BRKLDO, BRW1, BRW2, GLCD, GLCS, GORM, LEDO, PAUC, PERL, and VIAL (Table 14). Differences from the literature reports were noted in the table.

Assigning BRIK1 and BRIK2 to a previously described taxonomic group was a challenge because the nomenclature of *Aster brickellioides* has a complex history. Greene assigned the taxon to *Seriocarpus tomentellus* (Greene 1889a), then later transferred it to *Aster brickellioides* (Greene, 1889b) because of similarities with *Aster ledophyllus*. Seven years later, he transferred several taxa, including *A. brickellioides*, into *Eucephalus* (Greene 1896). In that move, he renamed *A. brickellioides* var. *brickellioides* as *Eucephalus tomentellus*, and *A. brickellioides* var. *glabratus* as *Eucephalus glabratus* (Greene 1896). Eastwood (1931) described *Eucephalus bicolor* after concluding that it differed from *E. tomentellus* because of denser trichome coverage on the leaf underside, and more numerous ray florets. Abrams and Ferris (1960) placed *Eucephalus bicolor* in synonymy with *A. brickellioides*, and adjusted the taxon description to state that leaf under surfaces could be lacking trichomes, or be sparsely, moderately or densely covered in trichomes. Their description amended the number of ray floret to allow for the presence of ray florets, which led to later confusion because character ranges became too large to be useful in accurately identifying taxa.

I placed the phenetic groups BRIK1 and BRIK2 by using the original descriptions of *Eucephalus tomentellus* (Greene 1889a) and *E. bicolor* (Eastwood 1931). BRIK1 was most similar to *E. tomentellus* because of similarities in the number of ray florets, and the sparse to moderate trichome coverage on the stem, leaf undersurface and involucre. BRIK2 was most similar to the description of *E. bicolor* especially because of the dense trichome coverage on the leaf undersurface. *Eucephalus bicolor* had not been transferred

to *Aster*. Although I did not receive loans of the types for these two taxa, I examined several specimens determined by Eastwood as *E. bicolor*, and used these to confirm the name assignments of BRIK2 specimens. I also examined several specimens determined by others as *E. tomentellus* (in some cases before Eastwood had described *E. bicolor*) and found that some were better determined as *E. bicolor*.

Assigning BRIK1 specimens to *Aster brickellioides* (synonym for *E. tomentellus*) did not require a nomenclature change, but BRIK2 required a new name. A simple transfer of *Eucephalus bicolor* to *Aster* was not possible because two other taxa have been already been named *A. bicolor* (details in the Taxonomy chapter, page 159). In honour of Alice Eastwood, I propose the new combination *Aster eastwoodiae* Zamluk *comb. nov.*

Aster engelmannii Gray has been divided into two varieties represented by ENGL and ENLWSA, *A. engelmannii* Gray var. *engelmannii* and *A. engelmannii* Gray var. *monticola* Zaml. *var. nov.* respectively (Table 14). The lectotype of *Aster engelmannii* (Watson 515, Nevada, designated by Cronquist (1955)) was not available to me. Characters that separate these varieties are leaf lengths, internode lengths, plant heights, leaf pubescence and number of rows of phyllaries on the involucre. I propose to assign ENGL to var. *engelmannii* because the specimens in this group were on average taller than ENLWSA, and the group was exclusively comprised of specimens previously identified as *A. engelmannii*.

Recognizing the morphological differences between WASA and MIXWSA as varieties of *Aster wasatchensis* seems appropriate (Table 14). WASA specimens were recognized as var. *wasatchensis*, and MIXWSA as a new variety, *Aster wasatchensis* var. *grandifolius* Zaml. *var. nov.* Comparison between characteristics of the isotype of *A. wasatchensis* and those of WASA and MIXWSA showed that it fit best into WASA, showing that designating WASA as var. *wasatchensis* was correct.

Groups not easily fitting into a taxon described in the literature were single specimens BRK22, GLD50, GLD53, and group MIXGLD. The single specimens seem to be misidentifications, and belong in other sections of *Aster*. MIXGLD appears to be composed of (1) a stunted specimen of *Aster glaucescens* (it matches the description of

that taxon in most characters except size), and (2) a short bushy example of *A. glaucodes* (it appears to have been grazed).

Table 14: Disposition of phenetic groups into recognized taxa. Phenetic groups were compared to previously published descriptions (Table 1, page 20).

Phenetic group	Taxon name	Comments
TURB and TRB119	*Aster turbinellus*	TRB119 may be only the top of a plant and based on head characteristics was correctly identified. All other specimens previously identified as *A. turbinellus* were assigned to TURB, and assumed to be correct.
BRIK1	*Aster brickellioides* Greene	Refer to text for extensive comments.
BRIK2	*Aster eastwoodiae* Zamluk *comb. nov.*	See text for comments.
GLCD	*Aster glaucodes* Blake	Specimens agreed with published descriptions of *A. glaucodes* except specimens completely lacked trichomes on leaves.
GORM	*Aster gormanii* (Piper) Blake	Stem pubescence can be dense sometimes, not just sparse as reported, otherwise similar to published descriptions.
PAUC	*Aster paucicapitatus* (Robins.) Robins.	Differences from reports in literature are presence of branches, uppermost leaves are half the length of middle leaves, stem pubescence is variable and can be dense, measured ray floret limb lengths and involucre heights are larger, and phyllaries are green with a white stripe not purple.
PERL	*Aster perelegans* Nels. & Macbr.	Differences from previous reports are that the involucres are frequently covered with glandular trichomes and the involucre has three to five rows of phyllaries not five to seven. Otherwise, statistics corresponded well to published descriptions.
VIAL	*Aster vialis* (Brads) Blake	Measured specimens are from 77 cm. to 117 cm. tall instead of the reported 90 to 120 cm. Leaf widths are wider than reported 3.0 cm. The pubescence on the stem was observed not to be dense. The number of involucre rows observed was three or four not five or six. Type was available for study and was assigned to this group.
BRW1 and BRW2	BRW1: *Aster breweri* (Gray) Semple var. *multibracteata* (Jepson) Zamluk *com. nov.* BRW2: *Aster breweri* (Gray) Semple var. *breweri*	*A. breweri* specimens examined for this study, had two, rarely three, involucre rows rather than two to five rows reported in the literature. Measurements of specimens previously not included in the phenetic study that had been determined as var. *multibracteata* by Jepson were consistent with BRW1 statistics which provides evidence that the correct BRW group was assigned to var. *multibracteata*.

Table 14: continued.

Phenetic group	Taxon name	Comments
GLCS	*Aster glaucescens* (Gray) Blake	Descriptions reported no trichomes on stem or leaf surfaces but GLCS contains specimens with trichomes. The type specimen was not available, but specimens, not included in the phenetic analysis, from the same area and identified as *A. glaucescens* by Suksdorf were found to be consistent with GLCS characteristics.
BRKGLS	*Aster siskiyouensis* Nels. & Macbr.	BRKGLS resembles descriptions of *Aster brickellioides* var. *glabratus*. At the start of my research, I was not aware that this taxon had been renamed *Aster siskiyouensis* Nels. & Macbr. (1913). Phenetic analysis showed that it was sufficiently different from *A. brickellioides* to be a separate species.
BRKLDO	*Aster ledophyllus* (Gray) Gray var. *covillei* (Greene) Cronq.	BRKLDO specimens occasionally have dense coverage of trichomes on the leaf upper surface. The lack of ray florets in some of specimens in BRKLDO have probably led taxonomists to place these specimens in *A. brickellioides* rather than in *A. ledophyllus*.
LEDO	*Aster ledophyllus* (Gray) Gray var. *ledophyllus*	Characteristics of LEDO match the published descriptions well.
ENGL and ENLWSA	ENGL: *Aster engelmannii* Gray var. *engelmannii* ENLWSA: *A. engelmannii* Gray var. *monticola* Zaml *var. nov.*	ENGL and ENLWSA match descriptions of *Aster engelmannii* found in the literature probably because the ranges given for characters like plant length and leaf sizes are large. See discussion in text.
WASA and MIXWSA	WASA: *Aster wasatchensis* (Jones) Blake var. *wasatchensis* MIXWSA: *Aster wasatchensis* (Jones) Blake var. *grandifolius* Zaml. *var. nov.*	WASA and MIXWSA fit into the descriptions from the literature of *Aster wasatchensis*. WASA specimens are shorter than the range of heights reported and MIXWSA a little taller. See discussion in text.

DISCUSSION AND CONCLUSIONS

Stratified sampling, although initially designed to ensure the inclusion of rare taxa, produced a data set that represented the geographic distribution of the Asters being studied. The different types of data, lack of normality and skew to most of the characters were successfully accommodated by using Bonferroni-adjusted probabilities, dropping correlated characters and using Gower's general similarity coefficients.

Jones and Young (1983) treated *Aster glaucodes* as a segregate from *Aster* section *Eucephalus*, and used it in a phenetic analysis which also included representative species from all sections of *Aster*. On their resulting phenogram, *Aster glaucodes* was placed below section *Eucephalus*, in the same position as on the phenograms from this study. The agreement between these two studies, despite the use of different characteristics, provides evidence that the methods used in this study are reasonable. The subsequent reorganisation of some cluster memberships corrected the poor fit of the phenogram to Gower's coefficients by examining anomalous groups, and by attempting to place small groups into larger groups.

Correlation analysis

Characters may be correlated because they reflect the same developmental processes, because they respond similarly to environmental influences, or because a character state may occur in many taxa and by chance show a high correlation with another common character. Most of these associations reflect the consequence of descent from a common ancestor, developmental processes, or response to environmental traits.

The lack of correlation between number of heads and plant length, although length is highly correlated with number of branches, leaf lengths and phyllaries number, implies that number of heads is not simply a function of plant vigour. Each taxon has a slightly different phylogenetic history, and even though plant vigour and number of heads may be correlated within a taxon, differences among groups may cause the correlation to be low over the entire data set.

The similarity between sizes of achenes of ray and disk florets was expected based on reports of linked development of the different parts of the *Aster* head (Harris 1995), but the lack of correlation with involucre lengths was not. This suggests that development of the involucre may be regulated differently from that of floret development.

Correlations between the two trichome types and among the various trichome densities on the various surfaces were low; the highest was between stem and upper surface of the leaf in both type and densities; the lowest was between vesture characters of the involucre and other surfaces. Trichome characteristics of one organ were unreliable in predicting those of other organs. The vesture on the involucre was often different from that of the stem and leaf surfaces. Density levels were varied among the surfaces, and would be better described in overlapping terms, *i. e.* none to sparse or moderate to dense, than by using single categories.

Analysis techniques and group realignments

Different phenograms contained large groups with identical memberships, suggesting that clustering based on Gower's coefficient and UPGMA routine worked satisfactorily. Placement of specimens with the same species names in the same general area of phenograms was evidence that the analyses were reasonable. The low cophenetic index may have resulted from the high number of possible positions for the smaller groups on the phenogram. Lack of correspondence between herbarium identifications and specimen groups may be due to misidentifications, plus the presence of varieties and undescribed taxa. Eleven groups contained one or two members; the large number of small groups resulted from attempts to establish groups with the same members in the four phenograms. The use of other techniques to test the assignments placed many smaller groups with larger groups, and improved the discrimination between groups. "Before" and "after" changes in correlations of groups with the axes was a more subtle evaluation of group membership modifications than the cruder technique of comparing specimen distances from centroids. Use of this method resulted in more compact groups with members more closely associated with the group centroid. The correlation of characters with groups was

also useful, because the nature of shifts could be pinpointed. Using univariate tests and box plots allowed every character, including categorical characters (*i. e.* leaf tips) and characters that were lacking on some specimens (*i. e.* ray florets), to be included in the comparisons among groups. Simple counting of differences was useful in reducing the number of discriminant analyses required.

Reasons for the shifts in membership lie in the limitations imposed to build a phenogram and in the way similarities and distances are calculated. UPGMA phenograms are built on compromises between the calculated similarities of member pairs. Similarities between members could have the same value although very different characters contributed to it; for example, presence of glandular trichomes and absence of non-glandular trichomes would have the same effect as absence of glandular trichomes and presence of non-glandular trichomes. Gower's general similarity coefficient gives categorical data different levels of influence than quantitative because quantitative characters would rarely equal one or zero. The effect of categorical data would vary with the prevalence of agreement within a data set; one with many mismatches would lower the influence of the categorical characters. Results from any analysis always need to be checked using other methods such as discriminant analysis and univariate statistical tests. Following the preparation of an identification key, the success of the clustering can be evaluated by annotating herbarium specimens and by examining living material. If the new material proves to be easy to identify using the key then the clustering methods can be assumed to be successful. Otherwise, the character data set can be modified by adding new characters, more specimens and redoing the analysis. For example, adding more specimens of *Eucephalus bicolor*, caused a change in group membership of a previously defined group, and recognition of the new group increased the discrimination among all the groups.

The discriminant analyses with subsets of groups were interesting because the discriminant axes became associated with different characters; the results were reassuring because all the actual members matched the predicted. The characters correlated with the

discriminant axes were frequently the same as those used in the literature descriptions to distinguish among groups.

Preparing identification keys was useful in finding conflicts between groups. Several versions of the key had to be prepared and member assignments to groups were reevaluated based on questions raised during the process.

Was *Aster turbinellus* part of *Aster* section *Eucephalus*?

Aster turbinellus specimens were well separated from other groups on the graphs of the discriminant axes, and were easy to separate in the dichotomous key. They lacked the similar leaf shapes and sizes that are diagnostic of section *Eucephalus*. On the phenograms, *A. turbinellus* and *A. glaucodes* were placed together indicating that they were similarly different from other specimens in the analysis, although not necessarily truly similar to each other. However, closer examination of the characters (Table 13) showed that *A. turbinellus* was much taller, had larger numbers of heads, branches and leaves per plant, had almost four times as many bracts on the peduncle, had narrower leaves, and had more rows and phyllaries on the involucre than *A. glaucodes*. The placement of *A. glaucodes* and *A. turbinellus* together in *Aster* section *Eucephalus* subsection *Turbinelli* (Jones 1980b) has not been supported by this analysis. Although not all the taxa in section *Eucephalus* have been assessed for chromosome count, all known counts are $n = 9$; in contrast, *Aster turbinellus* was reported to be $n = 48$. For these reasons, I conclude that *Aster turbinellus* does not belong in *Aster* section *Eucephalus*, and that subsection *Turbinelli* should be removed.

How well did only vegetative and only floral characteristics work in defining groups?

Both reproductive and vegetative characteristics were necessary to generate phenograms that could be used to place specimens into well-separated groups. Using only one or the other group of characters resulted in many members that did not match the group predicted by discriminant analysis. Possibly, if more characters had been included in each category, the clustering program would have generated more stable groups. The

need to use both types of characters may reflect the phylogenetic closeness and phenetic similarity of the taxa; for more divergent taxa, reproductive characters may have been all that was required.

Which data set generated the clusters most similar to the final groups?

None of the phenograms had structures that could be used to exactly reproduce the final groups. However the data set with ray floret characters was most similar. The presence or absence of *A. turbinellus* made no difference. I reconsidered the phenogram to discover if a line at a specific coefficient value could be drawn on the phenogram to reproduce memberships in the clusters after adjustment. Coefficient values between 25 and 27 were closest.

Recommendations on previously suggested modifications in *Aster* section *Eucephalus*

Jones (1980b) submerged *Aster wasatchensis* into *A. glaucodes* without explanation, and then placed them with *A. turbinellus* into subsection *Turbinelli*. On all phenograms, *Aster wasatchensis* specimens were distinct from the large group of *A. glaucodes* specimens. *Aster wasatchensis* specimens were different from *A. glaucodes* specimens in size, vesture characteristics, and phyllary colours, but similar in many reproductive characters. I concluded that *A. wasatchensis* should be considered a separate species from *A. glaucodes*. Similarly, even though *Aster turbinellus* and *A. glaucodes* were placed together on the phenograms, comparison of their characteristics showed many differences. Her creation of subsection *Turbinelli* was unnecessary since *A. turbinellus* does not belong in *Aster* section *Eucephalus*, and *A. wasatchensis* is a distinct species from *A. glaucodes*.

III. CLADISTICS

INTRODUCTION

Willi Hennig used the analogy of a torn map to explain his ideas about discovering evolutionary relationships (Hennig 1966). The map stands for the complete, well defined actual path that species followed as they evolved. Time causes the tearing of the map. The groups or clades are represented by pieces, and characters are roads, lakes and coastlines printed on them. A researcher, when trying to reassemble the map, needs to have all the bits that came from the correct section of map, and none that belong in a different section. After characters or landmarks have been identified on most pieces, the researcher tries to fit them together again. Outgroups could be considered the boundaries of the map. Problems come from missing pieces (from extinctions or lack of information), extra pieces (from other evolutionary paths) and distortions from pieces changing shapes (different evolutionary rates or profound environmental effects). After assembling the map (that is completing cladistic analyses), the researcher can then argue that based on these features or those features, this arrangement of map pieces fit together better or no worse than other arrangements. Proposed arrangements would be accepted until new information was found and the phylogenetic hypothesis supported or changed.

Cladistic techniques begin with simplifying character data, usually, into binary states. Data are organized into a matrix with rows representing taxa, and columns representing characters. Taxa are arranged on a hierarchical, bifurcating dendrogram so that the numbers of changes in character states from base to tip are minimized.

The purposes of this part of the study were to

1. estimate the order of descent for member species of section *Eucephalus* using cladistic techniques, and
2. to develop methods for using complex data in such an analysis.

Phylogenetic reconstruction with a recently evolved genus, such as *Aster*, is difficult because ancestral conditions are not clear. Wagner parsimony, which does not restrict the hypothesis of the direction of change, was used for all these analyses. Ancestral conditions were deduced from the most parsimonious trees produced by analyses with

several outgroups specified. Multiple outgroups are useful when the sister group is not known because using a single outgroup could prejudice the cladistic analysis if an inappropriate outgroup was chosen. Multiple outgroups improve estimates of ancestral states because more information about characters' states outside the ingroup is available.

Coding characters into binary states can introduce researcher bias. Even presence and absence data, already scored as binary, may need to be interpreted because every specimen in a group may not have the particular characteristic being scored. In section *Eucephalus*, 12 taxa had 80% or more specimens with glandular trichomes on the stem, one taxon had 50% specimens with them, and four taxa had 30% or fewer specimens with them. A difference in frequency may suggest an evolutionary shift, genetic variability, or the influence of an unknown environmental factor. The ability of some members of a taxon to express a particular phenotype provides evolutionary information. What is important in cladistics - the unfailing expression of a phenotype or the occasional expression of a phenotype? A researcher makes a choice by choosing a threshold, and a choice must be made whether the character is qualitative, categorical or quantitative.

Several cladists question the use of categorical and quantitative characters in cladistic analysis (Chappill 1989, Pimentel and Riggins 1987) and an introductory cladistic method primer does not even discuss quantitative data (Wiley *et al.* 1991). Continuous data are perceived as very difficult to manage. The main problems revolve around how continuous data can be changed, without bias, into discrete categories. Using gap coding methods, derived from Theile's paper (1993) on treatment of morphometric data, Chandler and Crisp (1996) assigned values to continuous characters before using PAUP to do the cladistic analysis. Since PAUP permits up to 32 states per character, they could use standardised means as a measure of evolutionary distances. Gap analysis was not appropriate for most of the quantitative characters used in this study because ancestral states were unknown, thereby invalidating step one of Thiele's method that requires means to be sorted into size order in order to create an ". . . ordered set of states" (Thiele 1993, p. 283).

A cladistic analysis, such as this one, being conducted on recently evolved taxa, cannot be meaningfully completed without using quantitative characters because too few qualitative characters distinguish taxa. Eliminating quantitative data from cladistic analyses removes data that are reproducible, subject to statistical analysis and clearly defined. My approach to character choice and coding was pragmatic. I needed to use a mix of qualitative and quantitative characters, and coding that was simple, clearly reproducible, and easily performed. I used unordered character states thereby avoiding assumptions about the direction of evolution. I used two different approaches (described below) in coding ranges and means of characters for each taxon:

1. simple binary coding for all characters with thresholds chosen with reference to the overall average of each character;
2. simple binary coding for qualitative characters, and multiple state coding for continuous and categorical characters with unmanipulated thresholds calculated with arithmetic averages of taxon means and standard errors.

MATERIALS AND METHODS

PHYLIP (Phylogeny Inference Package) version 3.57c by Felsenstein (1995) was used for the cladistic analysis because it was available free over the Internet, and ran on a personal computer (IBM clone). MIX (Mixed method parsimony program) 3.5c, one of the component programs of PHYLIP, was used to generate the most parsimonious trees, *i. e.* those with the lowest total numbers of steps for all characters. MIX accepts binary characters, and allows specification of weight and ancestral state for each. Wagner parsimony, which freely permits changes between "0" and "1", was always chosen. MIX was run with multiple searches that started with a randomly chosen group each time (Jumble option). Ancestral states were specified after an analysis with multiple outgroups was completed. MIX writes up to 100 of the shortest trees to a file. Where necessary, CONSENSE (Consensus tree program) 3.5c was used to produce a maximum likelihood consensus tree.

Cladograms were recreated with MOVE (Interactive mixed method parsimony program) 3.5c and different branches were moved around to experiment with various versions of the tree. MOVE made it possible to generate a parsimonious tree with more compatible characters than produced by MIX, and to find different, usually longer, trees with more compatible characters. MOVE can be used for character by character analysis of a tree.

The structure of cladograms can be critically examined with multiple sets of rearranged data generated from SEQBOOT 3.5c, which resamples data by using bootstrap, jackknife or permutation techniques. Each of the multiple data sets randomly generated by one of the resampling methods should be different from each other. The generated data sets can then be used in MIX, and the resulting trees compared to those produced from the unaltered data set. The bootstrap routine in PHYLIP randomly samples characters in the original data set so that representations of some character states are eliminated and others simultaneously increased. This simulates introduction of newly collected data (Felsenstein 1995). The jackknifing routine in PHYLIP theoretically produces similar result to bootstrapping but differs because the number of characters in the original data set is reduced by randomly eliminating half the characters (Felsenstein 1995). Reorganizing the data set by permuting the characters for all groups at once is equivalent to removing all taxonomic structure, and makes it possible to compare the number of steps produced from this unorganized data set with those generated by other methods. If the estimated tree from MIX has fewer steps than the disorganized one, then meaningful structure is probably present (Felsenstein 1995). Experimentation with the various numbers of permuted data sets showed that 25 permutations were necessary to estimate lengths of unstructured cladograms.

No specific number of times to repeat the random reordering of taxa was recommended in MIX documentation so some experimentation was done. A test data set was submitted with jumbles of 150, 1,000 and 2,000 times; jumbling 2,000 times gave more trees than for 150 or 1,000 times. Trees had the same number of steps.

Choice of characters and thresholds

Not every character used in the phenetic analyses was appropriate for a cladistic analysis. Characters were omitted as having no useful cladistic information if no significant differences were found among taxon means. If a character distribution was multi-modal, then the character was retained in the study based on the assumption that the peaks reflected real differences among taxa. Homoplasious characters with extremely high step counts, more than six, were often dropped from the data set on the assumption that they carried little evolutionary information because they were under environmental influences, or were highly polymorphic within the monophyletic group.

Ranges and means of taxa are possible sources for coding characters for cladistic analyses. Range statistics reduce the distinctions among taxa since the potential for overlap is increased. Maximum and minimum measurements of characters within a taxon may be largely influenced by growing conditions; the lowest measurement may result from poor nutrition or an inhospitable habitat, and the highest from growth in an excellent habitat. Although influenced by the lowest and highest character values within a group, the mean of each taxon estimates the "usual" value of a character because the influence of extreme measurements is diminished. I considered both ranges and means as coding sources.

A character with two states can be fully specified with one column in a data matrix; multiple states can be specified for a character by using several columns and fractionally weighting them (Wiley *et al.* 1991). When using binary coding to represent multiple states, an additional column is added to the data matrix for each state and each taxon is assigned a zero or one as appropriate. All the columns relating to the multiple state character are assigned weights so that the total of their weights equals the weight of a simple binary coded character. Non-additive character coding was used in this study because a complex relationship between character states was not known; additive coding reflects transformation series that ". . . consist of subsets of related characters" (Wiley *et al.* 1991, p. 38). Categorical characters can be prepared by using the non-additive binary coding method or by choosing a rare category and scoring it as "1" while scoring all

others as "0". Continuous measures and ordered categorical characters can also be prepared with non-additive binary coding methods or by simplifying them into binary codes by comparing either taxon ranges or means to a selected threshold.

Two cladistic analyses were completed using simple binary coding in which one column was used for each character. One analysis was conducted using taxon ranges of quantitative characters and the other used taxon means. The choice of the threshold at which a character was assigned a "0" or a "1" was based on discontinuities or the mean for the whole data set. For example, in a bimodal distribution, the threshold would be chosen in the "valley" between the two "peaks." All analyses were iterative. I changed the threshold during the initial phases of a cladistic study if a small shift eliminated several steps. Results are reported based on final threshold values.

Coding techniques for ranges and means for the first two analyses differed slightly from each other because range coding required two tests whereas means coding needed one. For the analysis using range values, each character of a group was assigned "1" if character values of all taxon members were greater than or equal to the chosen threshold; "0" if all character values were lower; "?" if values were missing; and "b" if range values fell on both sides of the threshold. Data prepared for analyses using taxon means did not have the "b" option but could be "0", "1" or "?."

The third analysis was of taxon means. For each quantitative and ordered categorical character, means from each taxon within section *Eucephalus* were arithmetically averaged and the standard error calculated. The standard error is the standard deviation of taxon means (Steel and Torrie 1980). Assuming taxa character means were normally distributed, and taxon means found in the tails of the distribution were of evolutionary interest, thresholds were chosen to separate means that fell into the "tails." Three matrix columns were created for each quantitative and ordered categorical character, and assigned a weight of one. The first column was for those taxa with means more than one standard error lower than the grand mean (arithmetic average of taxon means), the second was for those with means within one standard error of the grand mean, and the third was for those taxa with means more than one standard error greater than the grand mean.

Unordered categorical data, such as leaf tip type, were assigned a column for each category, and each column given a weight of one. Qualitative characters were coded with one column, thresholds were set to 1%, and each character given a weight of three.

Cladistic analysis with taxa derived from phenetic analysis.

Taxa usually considered members of section *Eucephalus* were used as the monophyletic ingroup. *Aster turbinellus*, BRK22, GLD50 and GLD53 were used as outgroups.

Results from three analyses are reported:

1. *Eucephalus* taxon ranges coded in simple binary format,
2. *Eucephalus* taxon means coded in simple binary format with ancestral conditions deduced from multiple outgroups,
3. *Eucephalus* taxon means coded with the non-additive binary coding method with ancestral conditions deduced from multiple outgroup.

SEQBOOT was used to produce twenty-five permuted data sets from each data set. The permuted data sets were each jumbled 20 times by MIX to provide a test for actual structure in the cladograms.

The consistency index for a tree was calculated by dividing the number of characters used in the analysis by the number of steps. When the index was calculated for the third analysis, adjustments were made for the different weights per character.

After the cladistic analyses were completed, a choice was made between the different variations discovered and a hypothesis of descent was proposed. Evaluation was based on the number of most parsimonious trees produced, the total number of steps on the most parsimonious trees, the presence of structure in the generated cladogram, the consistency index for trees and the percentage of homoplasious characters. Characters were mapped onto the preferred cladogram to show how well or poorly they support the structure.

RESULTS

Section *Eucephalus* taxon ranges prepared with simple binary coding without outgroups or ancestral states

Seventeen phenetic groups with 35 characters were used in this cladistic analysis (Table 15). The starting group was jumbled 2,000 times. One hundred trees (each with 312 steps) were generated by MIX, then used as input to the CONSENSE program (**Figure 13**). Nineteen, or 54%, of the characters needed nine or more steps. The consistency index was 0.11 which is considered a low value (Wiley *et al.* 1991). Permutations of the data set 25 times when jumbled 20 times by the MIX program found trees that varied from 314 to 317 steps with differences that ranged from two to five more steps than the original data. The small difference in total steps between the cladograms suggests cladograms generated from taxon ranges have little meaningful structure. Because of the high percentage of homoplasious characters and the low consistency index, both indications that a well-supported cladogram was not produced, no further analyses were conducted.

Table 15: Character thresholds used in analysis of section *Eucephalus* taxon ranges with simple binary coding.

Character	Threshold	Character	Threshold	Character
Quantitative or categorical characters				**Binary characters**
Bracts on peduncle - count	5	Leaf shape - A1 parameter	1.1	Involucre vesture non-glandular
Disk floret pappus length	0.64 cm.	Leaves: number in 8 cm.	10	Involucre vesture glandular
Disk floret lobe length	0.14 cm.	Middle leaf width	1.6 cm.	Leaf under surface vesture non-glandular
Edge of middle leaf	revolute	Middle leaf length	5.0 cm.	Leaf under surface vesture glandular
Head count	7	Phyllary tip	blunt	Leaf upper surface vesture glandular
Uppermost leaf length	4.5 cm.	Plant length	75 cm.	Leaf upper surface vesture non-glandular
Uppermost leaf width	0.6 cm.	Ray floret count	8	Middle phyllary edge red
Internode length	2.2 cm.	Ray floret stigma branch length	0.18 cm.	Phyllary keel red
Involucre width	0.9 cm.	Ray floret limb length	1.2 cm.	Phyllary tip red
Involucre vesture density	2	Rows on involucre - count	4	Phyllary with white stripe
Leaf under surface vesture density	2	Stem vesture density	2	Stem vesture non-glandular
Leaf upper surface vesture density	2			Stem vesture glandular

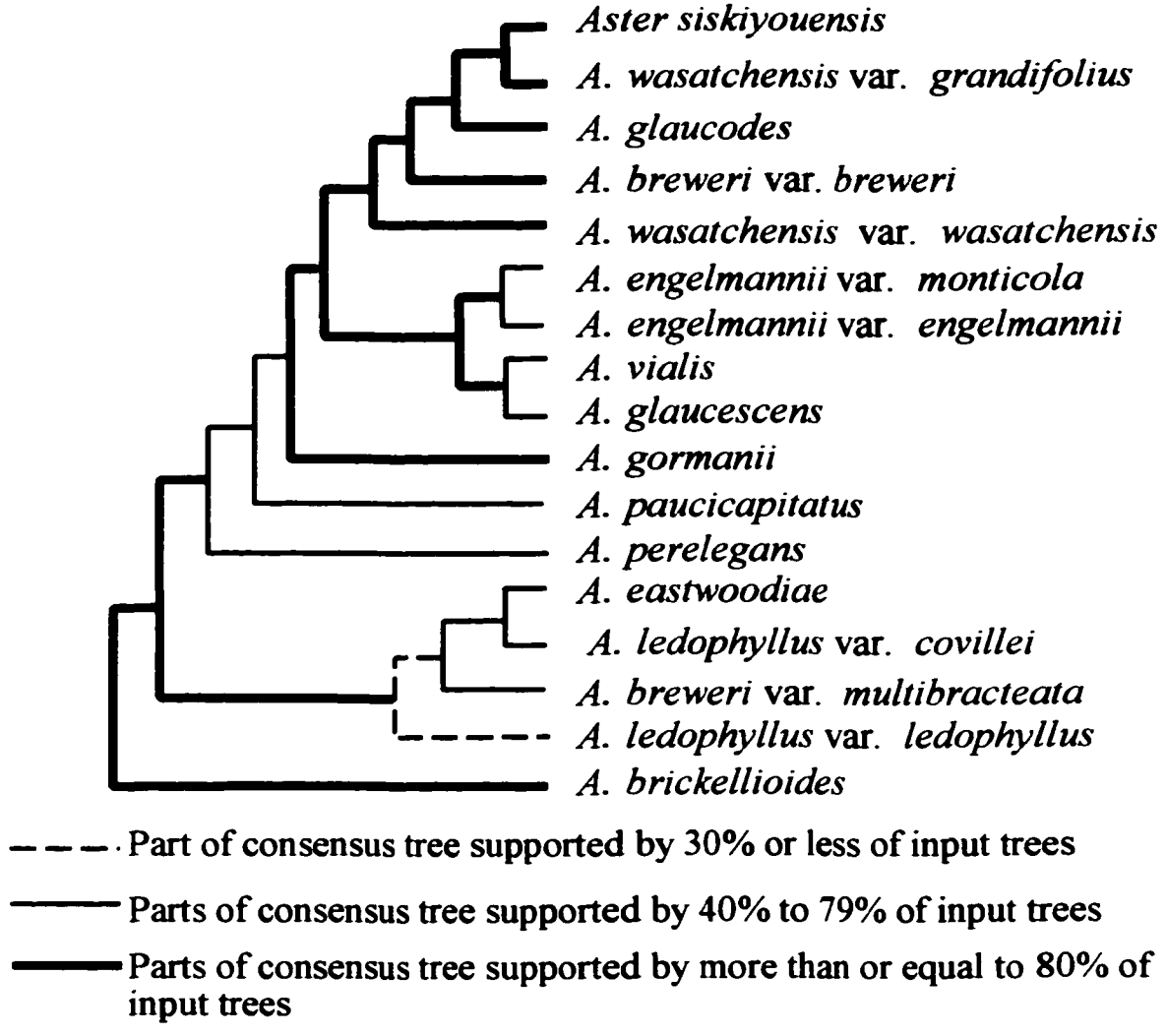


Figure 13: Unrooted maximum likelihood consensus tree for 100 input trees of 312 steps produced from taxon ranges. Qualitative, quantitative and categorical characters were coded as binary. No outgroup or ancestral conditions specified.

Section *Eucephalus* taxon means prepared with simple binary coding, and with ancestral states specified

Seventeen phenetic groups with 47 characters were used (Table 16). Most thresholds were different from the analysis of taxon ranges, and ancestral states were specified for all characters (Table 16). The data set was jumbled 2,000 times and three trees with 130 steps were found (**Figure 14**). They were not summarized with CONSENSE. Trees had a consistency index of 0.36; with the autapomorphies removed (characters that defined a terminal taxa and had only one step), the CI was 0.33. Trees had three, or 6%, characters requiring more than four steps, seven characters were autapomorphies, and 20 characters, including the autapomorphies, had consistency indexes of 0.50 or higher. Twenty-five permutations of the data set, jumbled 20 times by the MIX program, produced trees that varied from 149 to 161 steps with differences that ranged from 17 to 31 more steps than the original data. Trees from the original data set were 12% to 19% shorter. Cladograms had structure, were supported by 28% of the characters, and tree 2 had one less homoplasious character than the other two.

Two areas of difference among the trees were in the position of node 1, and the arrangement of *Aster vialis* and *A. wasatchensis* var. *monticola* above node 1 (**Figure 14**). In tree 1, above node 1, *A. vialis* and *A. wasatchensis* var. *monticola* formed a sister group to *A. engelmannii* and *A. breweri*. In tree 2, this was changed because *A. vialis* was placed below *A. engelmannii* and *A. breweri*, while *A. engelmannii* var. *monticola* was placed as an ancestor to *A. vialis*. In tree 3, node 1 was moved closer to the root than on trees 1 and 2.

Reconstruction of the preceding trees using MOVE found them to be 130 steps long with seven compatible characters. Compatible characters for the three trees were the autapomorphies (glandular trichomes on the stem and the involucre, and white stripe in the centre of phyllary) plus number of heads, density on the middle leaf upper surface, phyllary tip, and phyllary tip red. While using MOVE, I could not find a shorter tree or increase the number of compatible characters.

Table 16: Character thresholds and deduced ancestral states used in cladistic analysis of section *Eucephalus* taxon means with simple binary coding.

Character	Thres.	Ances.	Character	Thres.	Ances.	Character	Thres.	Ances.
Bracts on peduncle - count	2.7	0	Involucre width	1.0 cm.	0	Phyllary tip	blunt	1
Disk floret achene length	0.33 cm.	0	Leaf under surface vesture non-glandular	0.2	0	Phyllary tip red	0.2	1
Disk floret achene width	0.07 cm.	0	Leaf under surface vesture glandular	0.2	1	Phyllary with white stripe	0.2	1
Disk floret lobe length	0.12 cm.	0	Leaf under surface vesture density	1.5	0	Plant length	60 cm.	0
Disk floret pappus length	0.67 cm.	1	Leaf upper surface vesture density	1.5	0	Ray floret achene length	0.33 cm.	0
Disk floret stigma branch length	0.18 cm.	0	Leaf upper surface vesture non-glandular	0.2	0	Ray floret achene width	0.07 cm.	0
Disk floret tube length	0.59 cm.	0	Leaf upper surface vesture glandular	0.2	0	Ray floret count	8	1
Heads - count	6	1	Leaves - number in 8 cm.	8	0	Ray floret limb length	1.3 cm.	0
Uppermost leaf length	3.0 cm.	1	Middle leaf edge	revolute	0	Ray floret pappus length	0.67 cm.	0
Uppermost leaf width	0.6 cm.	1	Middle leaf length	4.6 cm.	1	Ray floret stigma branch length	0.17 cm.	1
Internode length	1.5 cm.	1	Middle leaf tip	blunt	0	Ray floret tube length	0.42 cm.	0
Involucre length	1.0 cm.	0	Middle leaf width	1.0 cm.	1	Stem vesture density	1.5	1
Involucre vesture density	1.5	1	Middle leaf edge with cilia	0.5	1	Stem vesture glandular	0.2	1
Involucre vesture glandular	0.2	1	Phyllary count	19	0	Stem vesture non-glandular	0.2	1
Involucre vesture non-glandular	0.2	0	Phyllary edge red	0.2	1	Toothed leaf	0.2	0
Involucre rows - count	3.5	0	Phyllary keel red	0.2	0			

Note: Ances. = deduced ancestral state from previous analysis of same data set using multiple outgroups. Thres. = character threshold limit used to assign binary values for each taxon. 0: ancestral state ≤ threshold. 1: ancestral state > threshold.

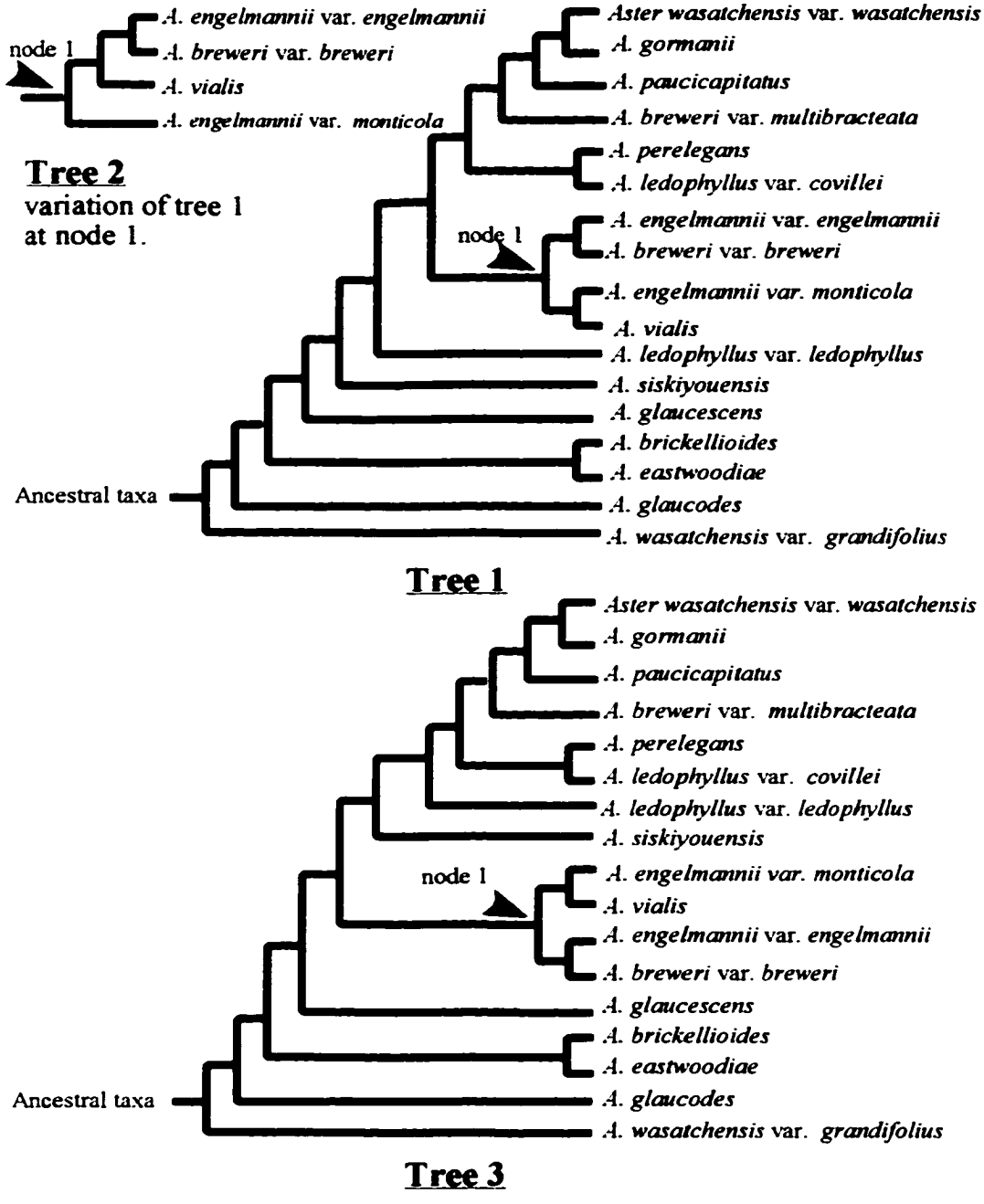


Figure 14: Three rooted trees, 130 steps long, generated from section *Eucephalus* taxon means. Qualitative, quantitative and categorical characters were coded as binary. Ancestral conditions were specified.

Section *Eucephalus* taxon means coded as simple binary or multi-state characters with ancestral states specified

Seventeen phenetic groups were analysed using 22 quantitative or categorical and 12 binary characters. Character coding details and deduced ancestral states are in Table 17. The data set was jumbled 2,000 times and 1 tree with 105 steps was found (**Figure 15**). The tree's consistency index was 0.53; with the autapomorphies removed, it was 0.51. Four characters (12%) required more than four steps, five characters were autapomorphies, and 27 characters (including the autapomorphies) had consistency indexes of 0.50 or higher. The cladogram was 9% to 12% shorter than the unstructured trees produced when twenty-five permutations of the data set were jumbled 20 times by the MIX program. The cladogram had more structure and a higher consistency index than resulted from the previous analyses.

Reconstruction of the tree using MOVE found fourteen compatible characters of which five were autapomorphies: involucre without glandular trichomes, ray floret with short limb, stem without glandular trichomes, stem without non-glandular trichomes, and no white stripe on phyllary. Other compatible characters were number of heads, internode lengths, uppermost leaf length, middle leaf widths, leaf tip types, middle leaves with cilia, leaf upper surface with no or sparse coverage of trichomes, and number of involucre rows. While using MOVE, I could not find a shorter tree or increase the number of compatible characters.

Table 17: Character thresholds and deduced ancestral states used in cladistic analysis of section *Eucephalus* taxon means with non-additive or simple binary coding.

Character	Thres.		Ances.	Character	Thres.		Ances.
Characters coded with the non-additive binary method							
Bracts on peduncle - count	Low	1.4	~2.4	Middle leaf - length to widest part (cm.)	Low	1.0	~1.9
	High	3.3			High	2.8	
Disk floret achene width (cm.)	Low	0.06	≤0.06	Middle leaf tip	mucronate		mucronate
	High	0.1			caudate		
Disk floret lobe length (cm.)	Low	0.1	~0.14		blunt		
	High	0.17		Middle leaf width (cm.)	Low	0.8	~1.3
Disk floret pappus length (cm.)	Low	0.66	~0.72		High	1.8	
	High	0.79		Ray floret count	Low	1.9	≥ 12.2
Disk floret stigma branch length (cm.)	Low	0.17	~0.20		High	12.2	
	High	0.23		Ray floret limb length (cm.)	Low	0.9	~1.2
Disk floret tube length (cm.)	Low	0.53	~0.60		High	1.4	
	High	0.66		Stem vesture density	Low	0.9	~1.6
Heads - count	Low	1.7	~14.6		High	2.3	
	High	28.9					
Uppermost leaf length (cm.)	Low	1.8	~2.6	**Characters coded with the simple binary method**			
	High	3.5		Uppermost leaf edge	revolute		not revolute
Uppermost leaf width (cm.)	Low	0.4	~0.6	Uppermost leaf - length to widest part (cm.)	1.1		≤1.1
	High	0.8					
Internode length (cm.)	Low	0.9	~1.4	Involucre vesture glandular	0.1		with glandular trichomes
	High	1.9					
Involucre length (cm.)	Low	0.8	~0.9	Leaf under surface glandular	0.1		with glandular trichomes
	High	1.0					
Involucre rows - count	Low	2.5	~3.3	Leaf upper surface glandular	0.1		with glandular trichomes
	High	4.2					
Leaf under surface vesture density	Low	0.7	~1.6	Middle leaf edge with cilia	0.1		with cilia
	High	2.5					
Leaf upper surface vesture density	Low	0.4	~1.1	Phyllary tip	blunt		not blunt
	High	1.8		Phyllary edge colour	0.1		no red
Leaves - number in 8 cm.	Low	5.0	~7.5	Phyllary tip colour	0.1		no red
	High	9.9		Phyllary with white stripe	0.1		with white stripe
Middle leaf length (cm.)	Low	3.2	~5.2	Stem vesture glandular	0.1		with glandular trichomes
	High	7.2		Stem vesture non-glandular	0.1		with non-glandular trichomes

Note: Ances. = deduced ancestral state from previous analysis of same data set using multiple outgroups. Thres. = character threshold limits used to assign binary values for each taxon. ~: ancestral state approximates the listed arithmetic mean value.

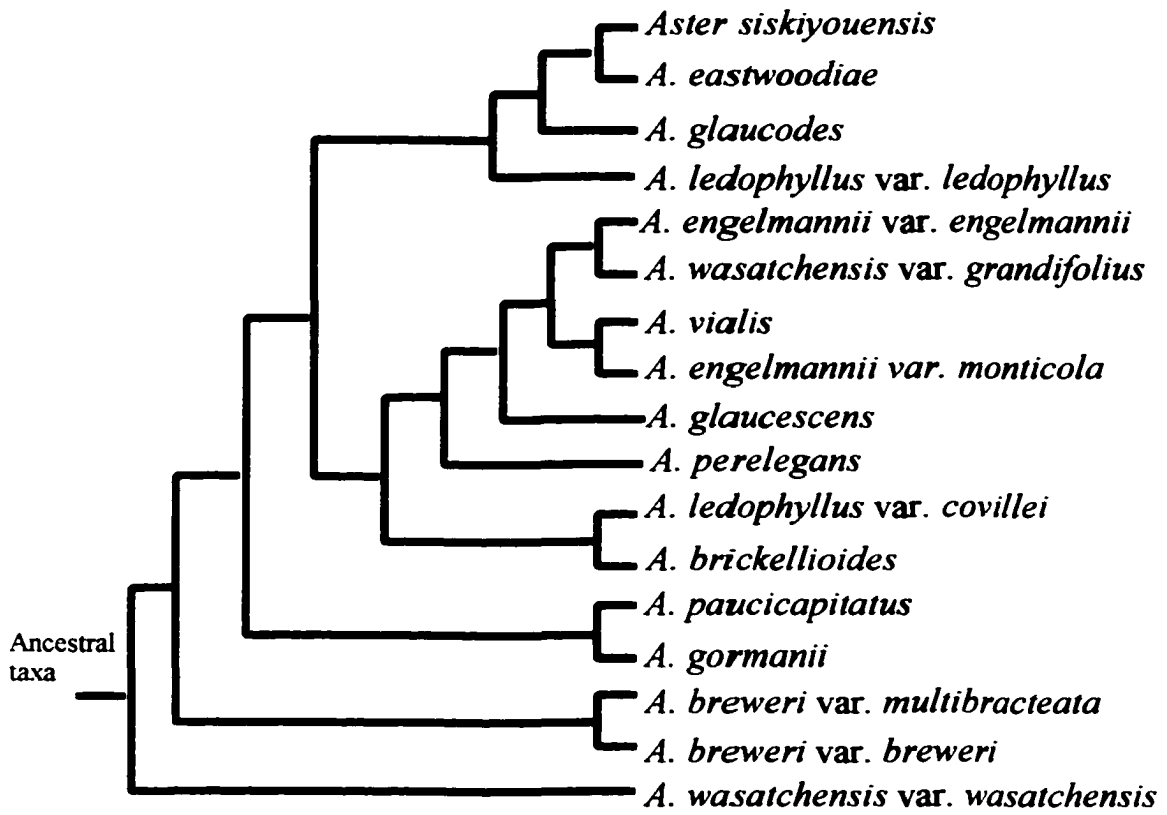


Figure 15: Most parsimonious tree, 105 steps long, generated from section *Eucephalus* taxon means. Qualitative characters were coded as binary. Quantitative and categorical characters were coded as multi-state. Ancestral conditions were specified.

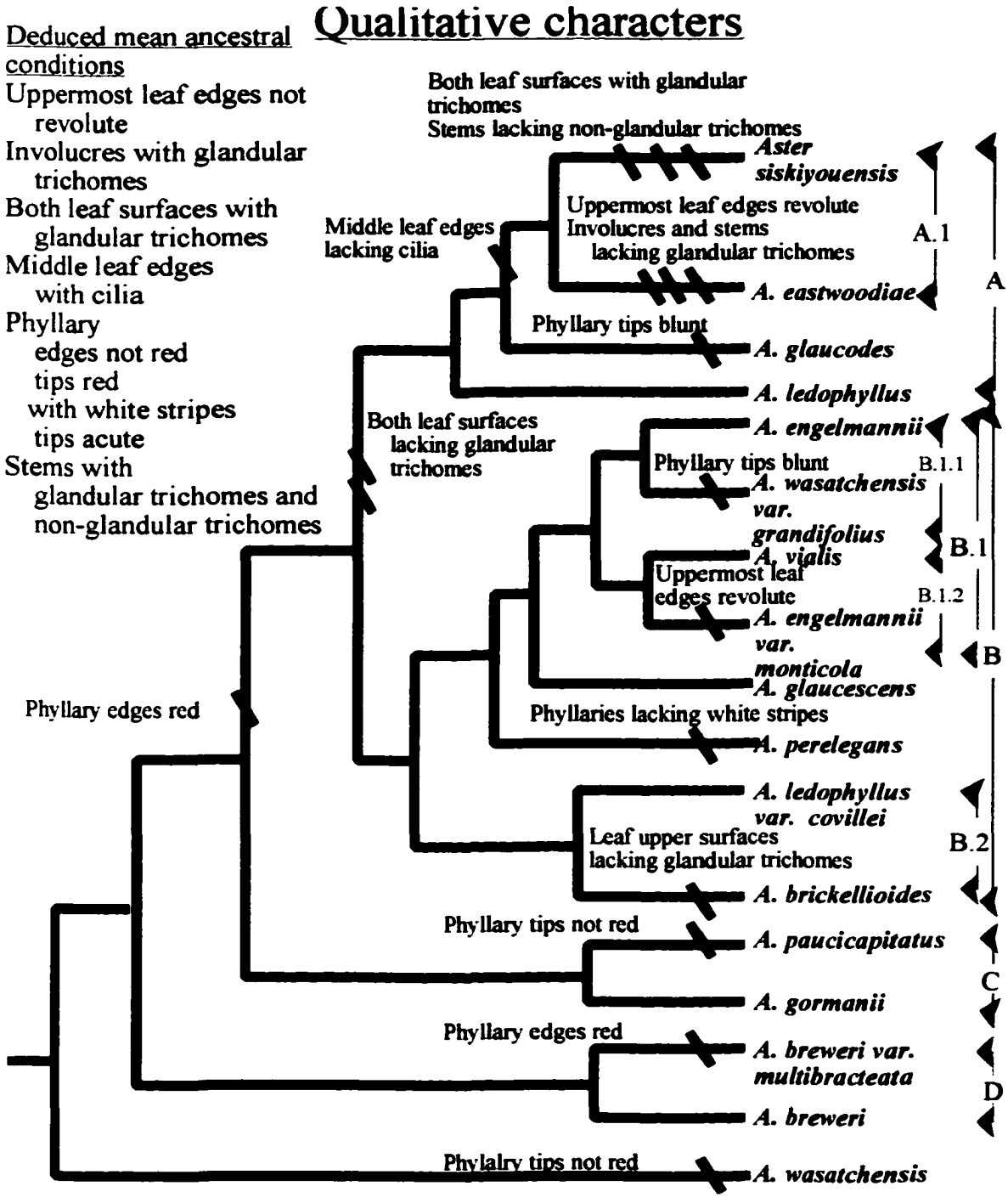
Character distributions on preferred cladogram

The cladistic analysis of taxon quantitative and categorical character means coded as multi-state produced one rooted tree that had the highest consistency index, and a larger number of compatible characters than the other analyses. Characters were separated into three subsets before being mapped onto the cladogram: qualitative (**Figure 16**), vegetative (**Figure 17**), and reproductive (**Figure 18**). Clades were identified to facilitate discussion.

Characters are considered to support the structure if only one step occurs and it does not define a terminal taxon. Large portions of the cladogram structure were not supported by any qualitative character (**Figure 16**). Four characters were autapomorphies that do not provide any information useful in establishing structure: stems lacking non-glandular trichomes, involucres and stems lacking glandular trichomes, and phyllaries without a white stripe. Clades A and B were distinguished from Clades C and D only by the colour on phyllaries' edges, and that character state was reversed in Clade D. Lack of cilia on the middle leaves' edges, the only supporting qualitative character, separated Clade A.1 from the rest. The combination of no glandular trichomes on either leaf surface separates Clade A from other taxa, but within Clade A, *Aster siskiyouensis* has glandular trichomes and in Clade B, *A. brickellioides* has none. The quantitative and categorical characters were needed to develop a well-supported hypothesis.

Some multi-state quantitative characters were found by MOVE to be compatible (*i. e.* one step long) with cladogram structure. Since MOVE does not distinguish between single and multiple state characters, it may mistakenly find a character compatible. For example, internode length, a compatible character according to MOVE, was actually two steps long. One step occurred on the branch where Clade C was partially distinguished from the others by short internodes, and the second step occurred on the branch where Clade B.1.1 was partially distinguished by long internodes (**Figure 17**). MOVE detected the support provided by each partial character. Vegetative quantitative and categorical characters supported most of the cladogram but no vegetative character could distinguish Clade D from the other clades (**Figure 17**); it was separated based on ray floret counts

and disk floret characters (**Figure 18**). Reproductive character distributions did not completely support the cladogram either; the division of Clade A and B was explained only by trichome characters. Every type of character was necessary to develop the hypothesis of descent.



Rooted cladogram from analysis of taxon means: qualitative characters coded as binary, quantitative and ordered categorical characters coded as multi-state.

Figure 16: Qualitative character distributions mapped onto cladogram of taxon means coded using multi-state characters.

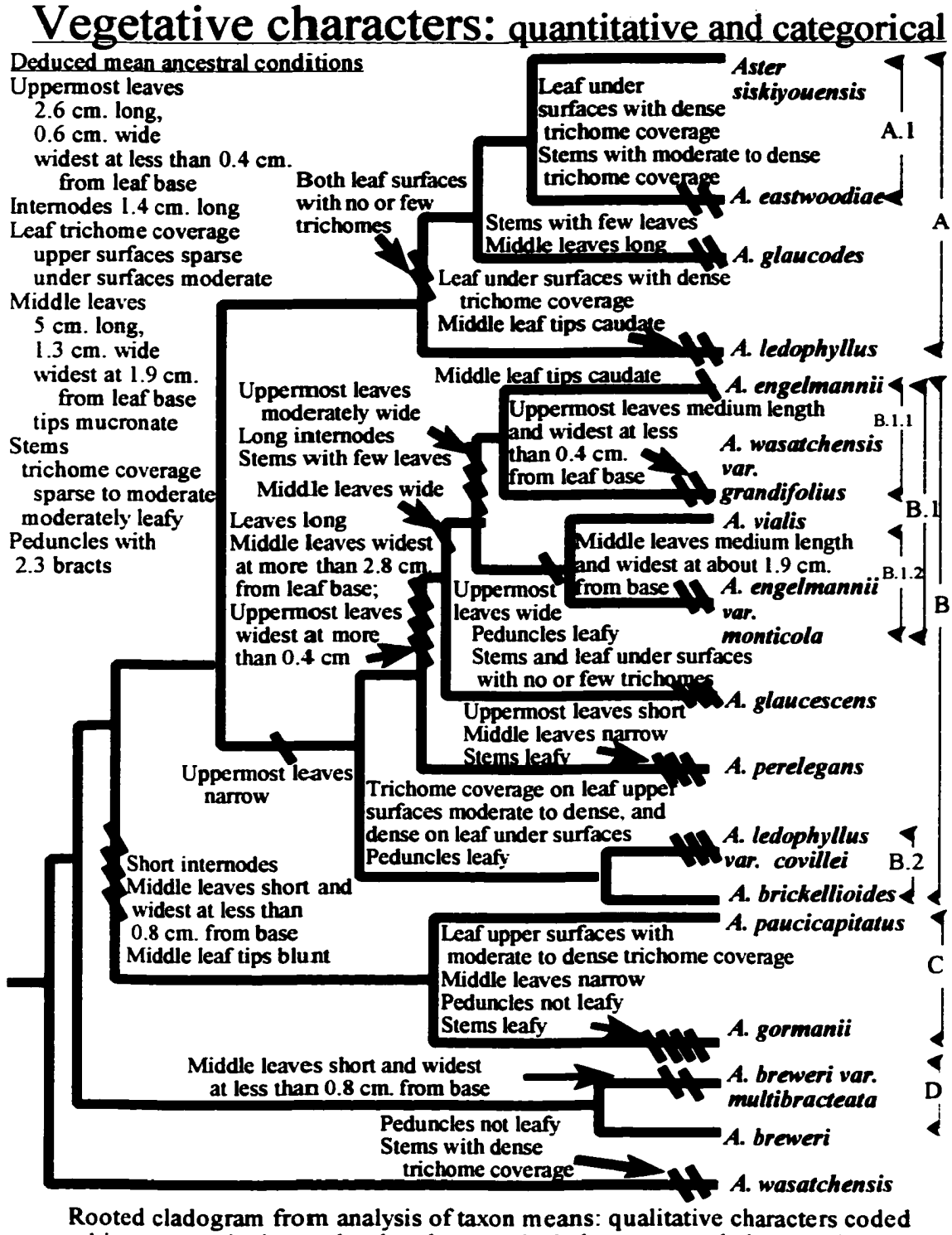


Figure 17: Vegetative quantitative and categorical characters mapped onto cladogram of taxon means coded using multi-state characters.

Reproductive characters: quantitative and categorical

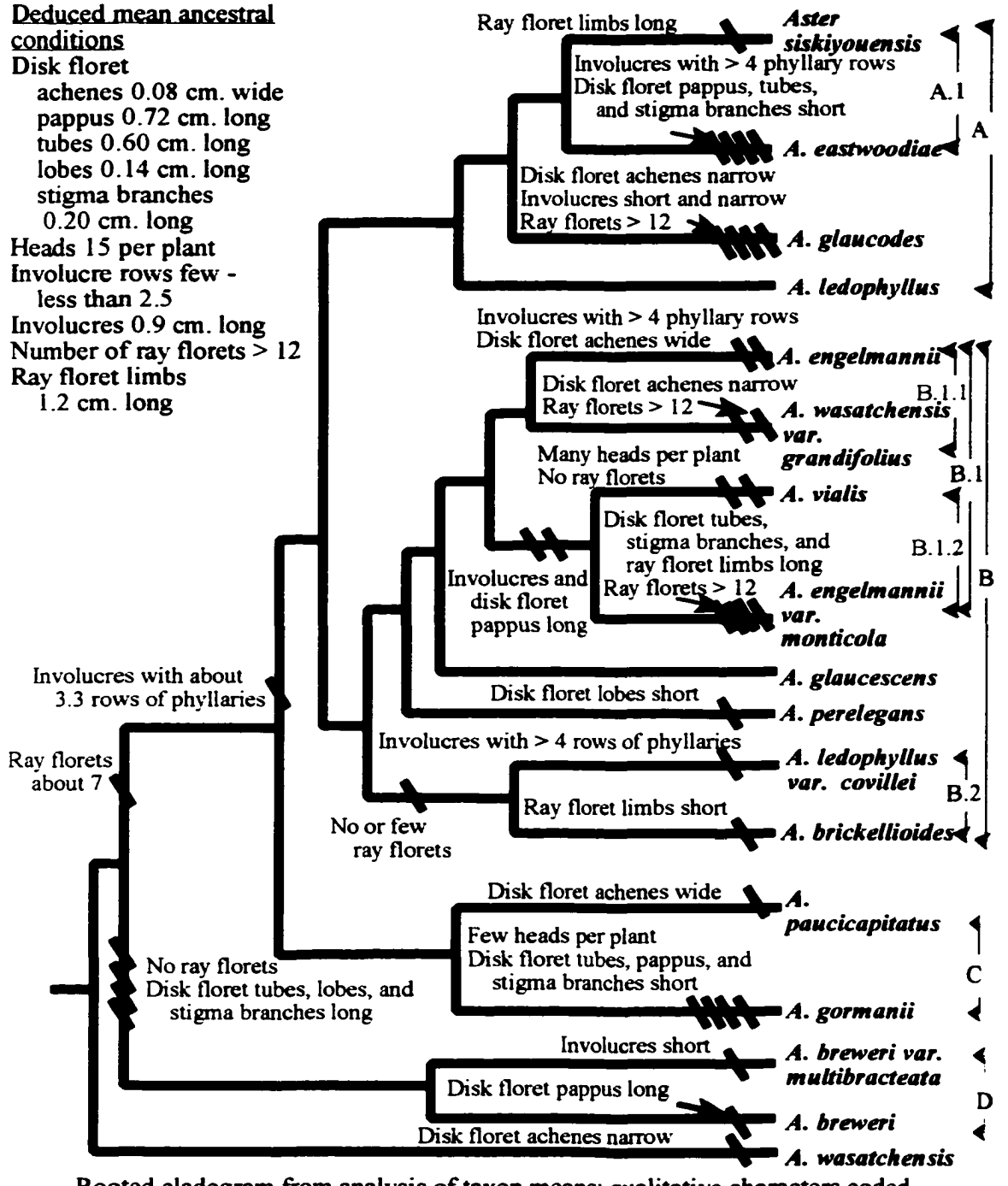


Figure 18: Reproductive quantitative and categorical characters mapped onto cladogram of taxon means coded using multi-state characters.

Ancestral species description deduced from cladogram

A description of the ancestral species was assembled from the deduced ancestral states derived from the two cladistic analyses of taxon means (Table 17). The ancestral species is conjectured to be as follows: stem short with many flower heads, each with more than twelve ray florets; leaves near the middle of the main axis frequent (averaging about 1/cm.), approximately 5 cm. long by 1 cm. wide with a non-revolute, untoothed, ciliated edge, mucronate tip; internodes about 1.4 cm. long; upper most leaves approximately 3 cm. long by 0.5 cm. wide, about 1.5 times shorter than the leaves in the middle of the stem; glandular trichomes on all surfaces; stem moderately covered with both glandular and non-glandular trichomes; middle leaves sparsely covered with trichomes on the upper surfaces, and moderately covered with them on the under surface; pedicles with two bracts; involucres about 0.9 cm. long, with approximately three rows of many acute tipped phyllaries; phyllaries without red on tips and edges, with white central stripe; disk achenes narrow; disk florets moderately long; ray floret limbs around 1.2 cm. long; disk floret stigmatal branches approximately 0.20 cm. long.

Most of the cladistically deduced ancestral states for the characters were close to arithmetic averages of taxa from section *Eucephalus* except for narrow disk floret achenes, short lengths to the widest part of the uppermost leaves, and numerous ray florets on a head. These differences from the average indicate that the ancestral states have not defaulted to the most common condition but have been polarized by the outgroups.

DISCUSSION

Techniques

Choice of range or mean statistics for coding characters

When range statistics were used for coding characters, extreme values were emphasized. As mentioned, range statistics increase the probability that groups overlap, which results in a decrease in separation. Separating the groups was a problem because

the taxa have recently evolved and many have not had enough time to become clearly distinct.

Use of means decreased the problem of overlap in analyses. Means can be affected by the amount of skew in the taxon, and possibly could reflect a value that does not occur within the group. Sample size would influence the estimate of the mean since larger samples would estimate the actual population more accurately. Estimates of variability within taxa were not used but might have provided information about the degree of outbreeding within a taxon with for example, low variability would be expected in an asexually reproducing group. Variability might be included in a cladistic analysis by coding it as a new character.

Choice of characters and thresholds

A complex mix of characters was needed to develop a hypothesis of descent. During data collection, potentially useful new characters were observed. Thickness of the leaf blade might have helped to define trees, because some specimens have almost translucent leaves while others are very opaque. Inflorescence bracts were consistently much shorter and narrower in some taxa than in others. Trichome characters from the pedicel would have improved discrimination among some groups. Stem thickness might also have been a good character since some taxa were noticeably thin stemmed while others were invariably thick. Many of the characters used in this study are environmentally influenced, but can still be used successfully in distinguishing taxa.

For the second analysis, setting thresholds was subjective though objectivity was attempted. The technique of setting the threshold, followed by adjustments, resulted in trees with fewer steps. Threshold levels chosen to reflect differences among groups could cause problems if, by coincidence, a taxon mean happened to be close to the threshold value, in which case means not significantly different if tested statistically could nevertheless be given different values. Some apparent homoplasy resulted from this type of artifact.

Multi-state character coding of the quantitative and categorical characters gave better results than simple binary coding. Thresholds were objective since they were based on calculations, but choosing to use one unit of standard error to calculate limits was subjective. The ancestral states were more precisely estimated with the multi-state character coding simply because divisions were more fine than used in simple binary coding. The ancestral estimates between the two methods usually agreed, and when they did not, the estimated state was close in value to a threshold.

Effect of using ranges or means on tree structure

The difference between step counts from permuted data sets and those from the cladistic analysis was helpful in culling analysis results; results from the taxon range data set were eliminated for this reason. Analyses using taxon means did produce structured trees that were shorter than those from permuted data sets. Finding structure in a cladogram is not, by itself, a reason to accept a hypothesis of descent, but lack of structure is good reason to abandon or modify the analysis.

Use of MOVE to find trees with more compatible characters

Using MIX with many jumbles generated the shortest trees, but frequently some adjustments to the structure resulted in trees with more compatible characters. It was necessary to use MOVE, or a similar program, to find those with higher comparability but with more steps because the MIX program can only produce the most parsimonious trees. MOVE was most efficient when taxa were arranged into a structure based on a consensus tree and then further arranged to evaluate structures found on other cladograms. MOVE was helpful during the initial phases of a cladistic analysis because it was possible to compare character distributions between different hypothesis of descent, and to try different taxa at the root, but it became less useful as the data set was fine tuned by eliminating characters with high levels of homoplasy.

Cladistic study

Cladograms from the two analyses using coded taxon means showed only one repeated association, that between *Aster engelmannii* var. ***monticola*** and *A. vialis* (**Figures 14** and **15**). *Aster paucicapitatus* and *A. gormanii* were near each other in both cladograms (also evident on the consensus tree derived from coding ranges(**Figure 13**)), as were *A. eastwoodiae* and *A. glaucodes*. The largest inconsistency was in the position of *A. wasatchensis* at the root on the cladogram from the third analysis, and its position as a recently derived taxon in the second analysis. The result from the third analysis is more likely to be correct because more precisely defined characters were used to develop it. Selective pressure may cause a character to change from the ancestral condition in either direction; an organ may become more numerous or larger, or it may become less numerous or smaller. Changes in either direction may contribute to speciation, and using the multi-state coding methods of this study captures some of these changes.

On all the cladograms derived from coding taxon averages (**Figures 14** and **15**), varieties of *Aster wasatchensis*, *A. ledophyllus*, and *A. engelmannii* were not paired as varieties. The varieties of *A. wasatchensis* were extremely separated which suggests to me that *A. wasatchensis* var. *grandifolius* may be a hybrid between *A. wasatchensis* and *A. glaucodes* or *A. engelmannii* (possibilities suggested by its positions on the cladograms). The separation of the two *A. ledophyllus* varieties is not as extreme, and could be explained by hypothesising that *A. ledophyllus*, *A. siskiyouensis*, *A. brickellioides*, and *A. eastwoodiae* form a species complex that resembles their ancestral taxon. The *A. engelmannii* varieties are the least separated of the variety pairs on the cladograms, perhaps reflecting their similarity to *A. vialis* which has caused instability in the cladogram derived from averages coded as single states. Possibly, both cladograms are incorrect, and adding new characters to the cladistic analysis would result in pairing of all the varieties.

Ancestral species characteristics

The probable ancestral species characteristics have been described earlier. The compact size, for an Aster, and plentiful floral display with small achenes suggests windy

and unprotected conditions with high competition for pollinators.

Derived trends in characters

The members of Clade A have the most complex combinations of vesture characteristics. Derived characteristics seem to be the complete loss of trichomes from leaves and stems, loss of glandular trichomes on the involucre and on the stem, and loss of cilia on the leaf edge.

Derived reproductive characteristics seem to be the reduction in number or complete lack of ray florets on heads, large reductions or increases in the number of heads per plant, and increasing number of phyllary rows on the involucre. The only trend to show no reversals was the increasing number of rows.

No single trend is apparent in the sizes of leaves, internode lengths, and heights of plants. Taxa seem to be changing in both directions, some becoming shorter, and others taller. Several reversals have occurred.

How these ancestral conditions and the trends within section *Eucephalus* compare to those in other sections is difficult to answer because similar studies have not been done. Certainly, the loss of ray florets is well worth studying with different approaches. The existence of heads with and without ray florets on the same plant implies that developmental pathways may be the key to the presence of ray florets.

CONCLUSIONS

The cladogram developed from taxon means using multi-state coding for quantitative and categorical characters provides the best hypothesis of descent. This puts *Aster wasatchensis* at the root as the taxon most similar to the ancestral species. A cladistic analysis by Jones and Young (1983) shows *Aster glaucodes* as an ancestor to representative taxa from *Aster* section *Eucephalus*. Their study used characters that differed from those used in this study. Dissimilarities between these studies suggests that using only a few taxa, as they did, to represent a section could be misleading. Results from this cladistic study did not support Jones' and Young's suggestion that *A. glaucodes*

belongs in a sub-section of section *Eucephalus*. The separation by Nesom (1994) of *A. wasatchensis* and *A. glaucodes* from *Eucephalus* into *Eurybia* is not supported either, and they would be best treated as members of genus *Eucephalus*.

Now that a hypothesis about descent, within *Aster* section *Eucephalus*, has been presented, taxa can be compared with more accuracy because similarities among them attributable to descent can be removed during a statistical analysis. Chromosome, enzyme, molecular, and hybridization studies can be conducted to evaluate the hypothesis, especially among *Aster ledophyllus*, *A. siskiyouensis*, *A. brickellioides*, *A. eastwoodiae*, and *A. glaucodes*. A close relationship between *A. engelmannii* and *A. wasatchensis* var. *grandifolius* was suggested by the hypothesis of descent and would merit detailed evaluation; *Aster wasatchensis* var. *grandifolius* may be a hybrid between *A. engelmannii* and *A. wasatchensis*. Transplantation studies would help identify morphological differences referable to environmental influences. Of particular interest to me would be transplantation experiments with the two varieties of *A. engelmannii* to find out if the difference in size and pubescence are the consequence of environment or genetics.

Returning to the analogy of Hennig's torn map, all the pieces of the map were present and those that did not belong, were removed during the phenetic analysis. Perhaps the map is not completely torn yet and some of the pieces still are connected making clear separations among taxa awkward. Adjustments to the hypothesis as more information becomes available through more research will no doubt improve on what has been proposed, but a reasonable order of descent has been developed in this study.

IV. TAXONOMY

This chapter contains a diagnosis of *Aster* section *Eucephalus*, an identification key, and descriptions of each member taxon. Type information and synonymies have been incorporated into taxon descriptions. Excluded taxa have been listed. Formal diagnoses of the new taxa, with comments, are provided separately. Descriptions were developed from statistics derived in Chapter 2, from habitat descriptions and floret colours recorded on herbarium labels, from reported chromosome counts found in papers or on herbarium labels, and from observations made while annotating specimens.

Description of *Aster* section *Eucephalus*

Section *Eucephalus* (formalized by Jones (1980a) [type species *Aster perelegans* Nels. & Macbr.]) is distinguished from other sections of *Aster* by the presence of a double pappus with dilated bristles, involucre bracts with a prominent keel or obvious mid-vein, and reduced bracts on the lower stem (Gray 1884, Greene 1896, Tidestrom 1925). Other important but not unique characters are a perennial habit, sessile cauline leaves, stems leafy to the top, flattened achenes, absence of rosette leaves, presence of a non-woody caudex, the usually imbricated involucre, and heads with less than 21 ray florets. The description of the section has been changed (Table 18).

In the field, *Aster* section *Eucephalus* species can be identified by checking for each of the following characteristics:

1. absence of rosette leaves,
2. presence of small bracts or leaf scars on the lower portion (approximately the lower quarter) of the stem (**Figure 20** shows the small and reddish bracts near the base on several stems),
3. cauline leaves without a petiole,
4. cauline leaves with similar simple shapes in the upper portion of the stem (**Figure 21**), and
5. non-herbaceous phyllaries on the involucre (**Figure 19** illustrates the light coloured and frequently imbricated involucre).

Table 18: *Aster* section *Eucephalus* description.

	Description
Habit	perennial with short rhizomatous root or caudex; stems of different maturity may occur on same plant.
Basic chromosome count	9
Cauline leaves	sessile and with similar shapes. Edges entire, frequently fringed with cilia and may have two or three teeth. Edges in some species revolute. Uppermost leaves usually half the length of leaves found at middle of main stem. Leaves numerous. Shapes lanceolate, elliptic, ovate to linear.
Trichomes	non-glandular trichomes usually villous but may be scabrous depending on species. Glandular trichomes may be stalked, obvious or obscure, but never branched.
Lowest leaves	bracts; often dry or deciduous by flowering.
Inflorescence	simple, corymbose or raceme; often with 1 to 3 bracts, rarely up to 9.
Disk florets	numerous, perfect, tubular, usually yellow but can be infused with red or purple pigment.
Ray florets	lacking or varies in number between 3 to 20; a single peripheral row; violet, lilac, purple, pink, blue or white.
Involucre	imbricated in 2 - 5 series.
Involucre bracts	keeled or with obvious midrib, broad, concave shape, edges usually membranous and tattered. Outer bracts frequently shorter than inner bracts. Edges, tips and keels may be red. Bracts often have a white stripe in centre. Trichomes often found on top third of phyllary but may be throughout.
Pappus	white, cream, or tawny unequal bristles, and extending above corolla; in two whorls but outside whorl may be difficult to observe. Longer bristles have expanded tips.
Achene	oblong, flat, ridged, hirsute while young, frequently glabrate when old.
Stigmatal branches	lanceolate with acute tip or ovate with obtuse tip; may be tinted with purple.

Figure 19: *Aster eastwoodiae*. French Hill, California.

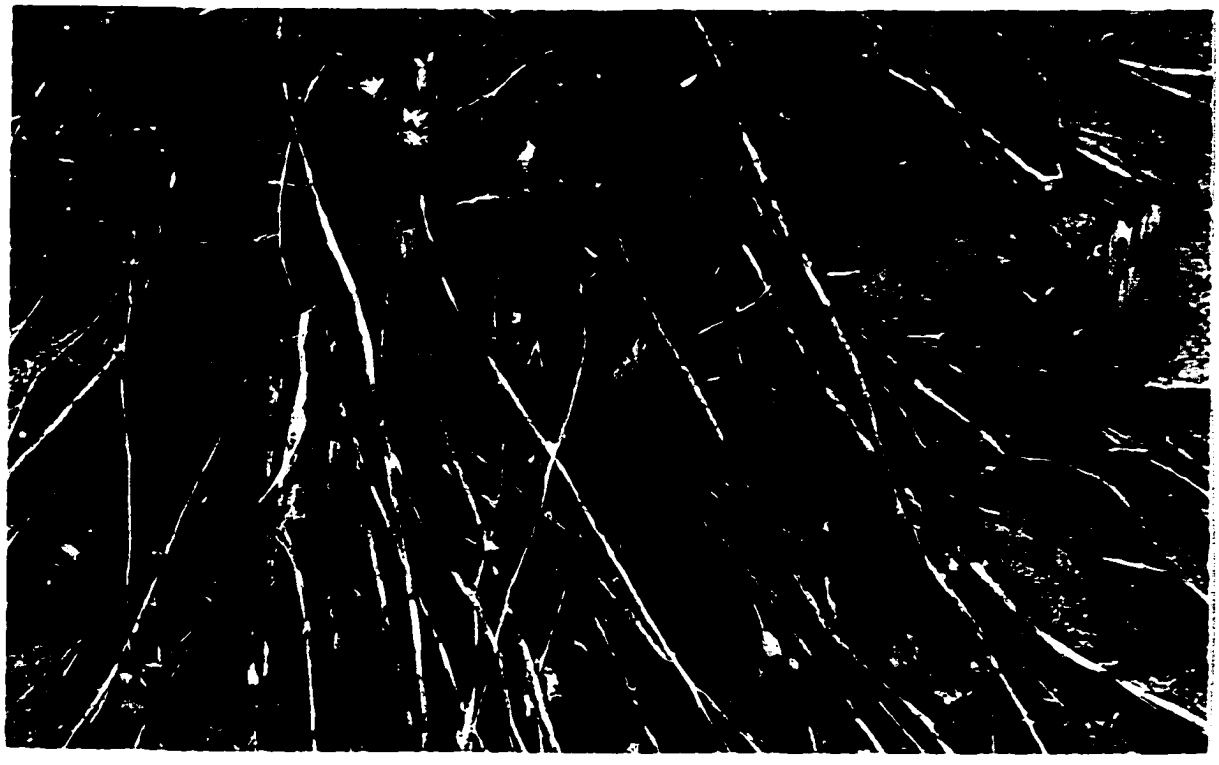


Figure 20: *Aster ledophyllus* in early stage of development. Mt. Hood, Oregon.

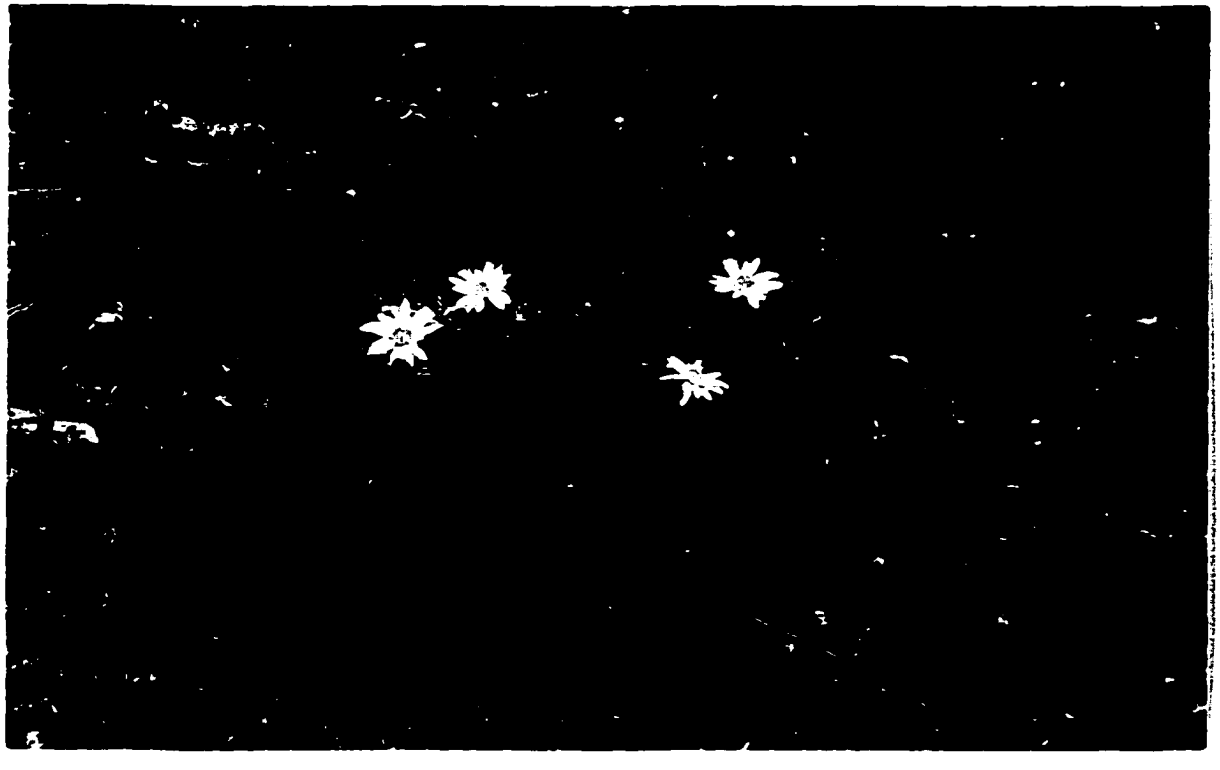


Figure 21: *Aster paucicapitatus*. Olympic National Park, Washington.

Formal diagnosis of new taxa

These new varieties are not considered to be validly published in this thesis. Formal nomenclatural changes will be made elsewhere, in accordance with ICBN rules for valid publication.

Aster engelmannii Gray, Am. J. Sci. Ser. II. (1862) 33:238; Syn. Fl. N. Am. (1884) 1,2:199.

var. *engelmannii*

Leaves elliptic, strongly imbricated involucre with 4 or 5 rows of phyllaries, average height 100 cm. (91 - 107 cm.), trichomes may be lacking from leaf upper surface, stem sparsely covered with leaves (3 - 6 leaves in 8 cm.). [Synonymies: *Aster elegans* T. & G. var. *engelmannii* Eaton, in Bot., in US Geol. Expl. 40th Par. (1871) 5:144, "*engelmanni*". *Eucephalus engelmannii* (Gray) Greene, Pittonia (1896) 3:54. Lectotype at YU (not seen): Watson, 515. From East Humboldt and Clover Mts., Nevada. Typification is debatable because Piper (1906) cited a different type as Lyall, *s. n.* from the Cascade Mountains, latitude 49° N.]

var. *monticola* Zamluk *var. nov.*

Planta 47 - 102 cm.; foliis superficialis trichomata; caulis foliatius (4-11 per 8 cm.); involucro infirmus imbricatus 3-4 serialis.

Leaves lanceolate, weakly imbricated involucre with 3 or 4 rows of phyllaries, average height 72 cm. (47 - 102 cm.), trichomes always present on leaf upper surface, stem densely covered with leaves (4 - 11 leaves in 8 cm.). [Holotype at RM (344970) (have seen): Lowry, P. P., 2857. East of Teton Pass, Teton Co., Wyoming. August 11, 1979.]

Comments

Differences between the above taxa are not extreme. Variation in plant height and leaf density could be affected by poor nutrition, and the absence of trichomes may not be taxonomically significant because I have observed specimens with trichomes on one plant

organ and not on another. The differences in the number of rows and in the amount of imbrication of the phyllaries on the involucre seem to be consistent within the specimens and seem to be taxonomically important. Intermediates were observed. Differences between the two taxa are not large enough to merit placing them at the species level but recognizing them at the variety level will allow researchers to discern the morphological differences between them.

Aster wasatchensis (Jones) Blake, Contrib. U. S. Nat. Herb. (1925) 25:526.

var. *wasatchensis*

Internode at middle of stem less than 1.9 cm. long, average height 32 cm. (24 - 42 cm.), average middle leaf length 5.6 cm. (3.8 - 8.1 cm.), average middle leaf width 1.2 cm. (0.5 - 2.5 cm.), average number of heads 5 (2 - 12). [Synonymies: *Aster glaucus* var. *wasatchensis* Jones, Proc. Calif. Acad. (1895) 2,5:694. *Eucephalus wasatchensis* (Jones) Rydb., Fl. Rocky Mnts. (1917): 878. *Eurybia wasatchensis* (Jones) Nesom, Phytologia (1994) 77(3): 262. Holotype at BRY (have seen isotype from RM); isosyntype at US (236650): M. E. Jones, 5861. Tate Mine, near Marysvale, Piute Co., Utah. August 22, 1894.]

var. *grandifolius* Zamluk *var. nov.*

Planta 31 - 78 cm.; caulis internodia > 1.8 cm.; foliis longus 6.2 - 9.2 cm., latus 1.5 - 2.3 cm.; capitula 4 - 40.

Internode at middle of stem greater than 1.8 cm. long, average height 59 cm. (31 - 78 cm.), average middle leaf length 7.9 cm. (6.2 - 9.2 cm.), average middle leaf width 1.9 cm. (1.5 - 2.3 cm.), average number of heads 18 (4 - 40). [Holotype at RM (152451), isotype at UTC (21233) (have seen): Maguire & Richards, 15731. Cedar Canyon, Iron Co., Utah. August 5, 1934.]

Comments

The differences between these two varieties of *A. wasatchensis* are largely size differences, and further studies might prove them to be due to growing conditions. Another possibility, based on the association of var. *grandifolius* and *A. engelmannii* on the cladogram, could be that var. *grandifolius* is a hybrid between var. *wasatchensis* and *A. engelmannii*. I recognized the groups because the phenetic analysis showed that they were distinct from each other.

Key to taxa in *Aster* section *Eucephalus*

1a. No ray florets 2

1b. Ray florets present 8

2a. Phyllaries on involucre in 2 or 3 rows; phyllaries approximately equal in length; middle leaf length less than 5.5 cm. 3

2b. Phyllaries on involucre with more than 2 rows; or shorter phyllaries shorter than inner; or middle leaf length greater than 5.5 cm. 4

3a. Uppermost leaves greater than 3.0 cm. long; and plants generally longer than 60 cm.

Aster breweri* var. *breweri

3b. Uppermost leaves less than 2.8 cm. long; and plants generally shorter than 70 cm.

Aster breweri* var. *multibracteata

4a. Leaf edge revolute; stem and leaf under surface usually densely (rarely moderately) covered in non-glandular trichomes; middle leaves 2.3-4.4 cm. long by 0.7-1.4 cm. wide ***Aster eastwoodiae***

4b. Leaf edge not revolute; or trichomes lacking from stem or leaf under surface; or middle leaves longer or wider 5

5a. Stem and leaf under surface usually with no trichomes (infrequently with only glandular trichomes); upper leaf surface usually with no trichomes (rarely sparsely covered with only glandular trichomes or with non-glandular trichomes); involucre with usually moderately to densely covered in only glandular trichomes (rarely lacking trichomes) ***Aster siskiyouensis***

5b. Stem or leaf under surface with non-glandular trichomes; or upper leaf surface moderately to densely covered with trichomes; involucre with non-glandular trichomes 6

6a Plants taller than 75 cm.; uppermost leaf 2.4 - 5.2 cm. long by 0.5 - 1.2 cm. wide; middle leaf 5.7 - 8.6 cm. long by 1.6 - 2.0 cm. wide; pedicel with moderate to dense coverage of glandular trichomes mixed with sparse to moderate coverage of non-glandular trichomes ***Aster vialis***

6b Plants shorter than 75 cm.; or leaves different in size; pedicel either lacking trichomes or lacking non-glandular trichomes on pedicel 7

7a Disk floret achene 0.20 - 0.43 cm. long; leaf upper surface with sparse to dense coverage of trichomes; average number of heads 6 (4-9); plant 25 - 58 cm. tall ***Aster ledophyllus* var. *covillei***

7b Disk floret achene length 0.15 - 0.39 cm. long; leaf upper surface usually lacking trichomes (rarely sparsely covered with only non-glandular trichomes); average number of heads 15 (3-38); plant 38 - 64 cm. tall ***Aster brickellioides***

8a Both stem and leaf under surfaces usually densely (rarely moderately) covered with trichomes on stem and leaf under surface; leaves with revolute edges; leaf edge lacking cilia ***Aster eastwoodiae***

8b Either stem or leaf under surfaces lacking trichomes, or sparsely to moderately covered with trichomes; or leaf edges not revolute; or leaves with cilia 9

9a Middle leaf greater than 5.8 cm. long and uppermost leaf less than 2.5 cm. long; plant generally greater than 85 cm. tall 10

9b Plants smaller in leaf length or height 12

10a Middle leaf 0.6 - 1.6 cm. wide and uppermost leaf 0.2 - 0.6 cm. wide; 6 - 11 leaves/8 cm.; internode 1.0 - 2.0 cm. long; stem and leaf under surface either usually missing trichomes (rarely very sparse coverage)

Aster glaucescens

10b Leaves wider; different number of leaves/8 cm.; or internodes shorter or longer; or stem or leaf under surface sparsely to moderately covered with trichomes 11

11a Involucre strongly imbricated with 4 or 5 rows; leaves elliptic; average number of heads 13 (5-41); average height 100 cm. (91-107 cm.); ray florets 4 - 13; 3 - 6 leaves/8 cm.; main stem usually straw coloured and usually greater than 0.4 cm. in diameter; middle leaf 6.2 to 9.6 cm long by 1.6 to 3.6 cm. wide

Aster engelmannii* var. *engelmannii

11b Involucre weakly imbricated with 3 or 4 rows; leaves lanceolate; average number of heads 9 (1 - 16); average height 72 cm (34-102 cm.); ray florets 7 - 20; 4 - 11 leaves/ 8 cm.; main stem usually dark and usually less than 0.4 cm. in diameter; middle leaf 5.3 to 8.2 cm. long by 1.5 to 2.3 cm. wide

Aster engelmannii* var. *monticola

12a Middle leaf 2.5 - 3.9 cm. long by 0.5 - 1.2 cm. wide; involucre weakly imbricated with 2 - 3 rows; involucre with mix of non-glandular and glandular hairs; both leaf surfaces with glandular trichomes; phyllary green with or without thin red edge and tip, and with white central stripe; heads 1 - 4
Aster paucicapitatus

12b Middle leaf longer than 4.0 cm. or wider than 1.2 cm.; or involucre with more than 3 rows; or involucre lacking trichomes or not a mix; or one or both leaf surfaces lacking glandular trichomes; or phyllary with red edge, tip and keel; or lacking white stripe 13

13a Leaves with glandular trichomes on both surfaces; involucre moderately or densely covered with only glandular trichomes; middle leaf 3.8 - 8.1 cm. by 0.9 - 1.4 cm.; internode length 0.9 - 1.8 cm.; phyllary without red on edge, tip or keel ***Aster wasatchensis* var. *wasatchensis***

13b One or both leaf surfaces lacking glandular trichomes; or involucre with non-glandular trichomes; or involucre lacking or sparsely covered in trichomes; or middle leaf shorter than 3.8 cm. or wider than 1.4 cm.; or internode length greater than 1.8 cm.; or phyllary with red on tip, edge, or keel 14

14a Trichomes lacking on both leaf surfaces; plant shorter than 60 cm. 15

14b One or both leaf surfaces with trichomes or plant taller than 60 cm. 16

15a Middle leaf 5.3 - 10.9 cm. long by 0.7 - 1.6 cm. wide; leaf edge lacking cilia; light blue-green leaves with wrinkled appearance when dry; disk floret achene 0.14 - 0.26 cm. long by 0.03 - 0.06 cm. wide
Aster glaucodes

15b Middle leaf 3.0 - 5.9 cm. long by 0.7 - 1.5 cm. wide; leaf edge usually with cilia; light green leaves with smooth appearance when dry; disk floret achene 0.27 - 0.49 cm. long by 0.05 - 0.12 cm. wide ***Aster siskiyouensis***

16a Middle leaf length < 3.2 cm.; involucre with 2 - 3 rows; stem with mix of non-glandular and glandular trichomes; leaf upper surface always with glandular trichomes and occasionally mixed with non-glandular trichomes; involucre either lacking trichomes or with only glandular trichomes ***Aster gormanii***

16b Longer leaves; or involucre with more than 3 rows; stem lacking trichomes or not a mix; leaf upper surface lacking glandular trichomes; involucre with non-glandular trichomes 17

17a Middle leaf 5.3 - 8.2 cm. long by 1.5 - 2.3 cm. wide; uppermost leaf 0.5 - 1.8 cm. wide; leaf under surface always with small glandular trichomes and occasionally non-glandular trichomes; leaf edges with cilia; pedicel not densely covered in glandular trichomes ***Aster engelmannii* var. *monticola***

17b Middle leaf longer than 8.2 cm. or shorter than 5.3 cm. or narrower than 1.5 cm.; or uppermost leaf narrower than 1.5 cm.; or leaf under surface lacking glandular trichomes; or leaf edge without cilia; or pedicel densely covered in glandular trichomes 18

18a None or only glandular trichomes on leaf under surface 23

18b Non-glandular trichomes on leaf under surface 19

19a Dark green or dark purple central stripe on green phyllary with very distinct purple tip and edge; involucre clearly imbricated; involucre sparsely to densely covered with non-glandular and usually glandular trichomes ***Aster perelegans***

19b Phyllary with central white stripe or lacking purple edge and tip; or involucre not clearly imbricated; or involucre lacking non-glandular trichomes 20

20a Dense trichome coverage on leaf under surface 21

20b Sparse to moderate trichome coverage on leaf under surface 22

21a Ray florets 0 to 7; bracts 1 to 9 on peduncle; leaf upper surface usually with mix of glandular and non-glandular trichomes; leaf under surface moderately to densely covered with non-glandular trichomes; involucre usually with mix of non-glandular and glandular trichomes (rarely with only glandular trichomes); pedicel moderately covered with mix of glandular and non-glandular trichomes

Aster ledophyllus* var. *covillei

21b Ray florets 0 to 20; bracts 1 to 4 on peduncle; leaf upper surface with non-glandular trichomes; leaf under surface densely covered with only non-glandular trichomes; involucre always with glandular trichomes (rarely mixed with non-glandular); pedicles moderately to densely covered in glandular trichomes

Aster ledophyllus* var. *ledophyllus

22a Leaf upper surface sparsely to densely covered with a mix of non-glandular and glandular trichomes; involucre moderately to densely covered with usually both non-glandular and glandular trichomes

Aster ledophyllus* var. *covillei

22b Leaf upper surface never with glandular trichomes; involucre sparsely to moderately covered with glandular (rarely with non-glandular trichomes)

Aster brickellioides

23a Internode length 1.9 - 3.0 cm.; 3 - 4 leaves/8 cm.; middle leaf 6.2 - 9.2 cm. long by 1.3 - 2.4 cm. wide ***Aster wasatchensis* var. *grandifolius***

23b Internode length 0.5 - 1.5 cm.; 7 - 10 leaves/8 cm.; middle leaf 3.0 - 5.9 cm. long by 0.7 - 1.5 cm. wide ***Aster siskiyouensis***

Species and variety descriptions

Aster breweri (Gray) Semple var. breweri, Syst. Bot. (1988) 13(4): 545.

Brewer's Golden Aster. (Phenetic group BRW2, page 108).

SYNONYMIES

BASIONYM: *Chrysopsis breweri* Gray, Proc. Amer. Acad. Arts (1865-1866) 6:542. [Holotype at GH (not seen): Brewer, 2692. Alpine Co., California. "Near Sonora Pass and Ebbett's Pass, in the Sierra Nevada, common at the elevation of 4,000-8,000 ft."] OTHER SYNONYMS: *Heterotheca breweri* (Gray) Shinners, Field and Lab. (1951) 29:71. *Eucephalus breweri* (Gray) Nesom, Phytologia (1994) 77:254.

POSSIBLE SYNONYMIES (Semple *et al.* 1988)

Chrysopsis gracilis Eastw., Bot. Gaz. (1906) 41:291. [Holotype at POM (not seen): E. B. Copeland, *s. n.* August 17, 1903. Mount Eddy, California, elevation 2225 m.] It was excluded from *Chrysopsis* by Semple *et al.* (1988) and placed in synonymy with *Aster brickellioides*. Eastwood's description indicates that the involucre has five rows of glandular phyllaries. The five rows of phyllaries on the involucre suggests that placing *Chrysopsis gracilis* as a synonym *A. breweri* var. *breweri* might be an error since all *Aster breweri* specimens, seen by me so far, have only two or three rows, not 5.

Chrysopsis wrightii Gray, Syn. Fl. N. Amer. (1884) 1, 2:445. [Holotype at GH (not seen): Wright, *s. n.* San Bernardino Mts, California.] Similarly to *C. gracilis* above, Semple *et al.* (1988) excluded it from *Chrysopsis*, and placed it as a synonym of *Aster breweri*.

Habit: *Height*: 63 - 76 cm.. *Branching*: 21 - 24 leafy branches on main stem. *Internode length in middle of main stem*: 0.9 - 2.5 cm. *Leaf density at middle of main stem*: 6 - 7 leaves in 8 cm.

Chromosome number: $n = 9$ (Anderson *et al.* 1974 and Semple 1988). **Flowering time**: Early July - late September.

Leaves: *Shape*: lanceolate. *Middle leaf*: 3.2 - 5.0 cm. long by 0.6 - 1.4 cm. wide. *Uppermost leaf*: 3.1 - 3.5 cm. long by 0.6 - 0.8 cm. wide. *Middle leaf tip*: cuspidate or acute or mucronate. *Uppermost leaf tip*: acute or mucronate. *Leaf edge*: entire and ciliated (may have one or two teeth on leaf edge). *Leaf upper surface*: dried specimens frequently with an overall pattern of light patches resembling dots.

Vesture: *Both leaf surfaces*: sparsely covered with only non-glandular trichomes (rarely with mix of non-glandular and glandular trichomes). *Stem*: sparsely covered with mix of glandular and non-glandular trichomes (rarely sparsely covered with only glandular). *Involucre*: sparsely covered with non-glandular and glandular trichomes. *Peduncle*: moderately covered in glandular and non-glandular trichomes just below head.

Number of heads: 4 - 15. **Peduncle**: 2 or 3 bracts.

Involucre: *Imbrication*: 2 or 3 rows. *Phyllary length*: 0.8 - 0.9 cm. *Width of pressed involucre*: 0.9 - 1.2 cm.

Phyllaries: *Phyllary tip*: acuminate or cuspidate. *Colour*: white central stripe, rarely tipped with red, no red on edges or keels.

Disk florets: *Achene*: 0.40 - 0.50 cm. long by 0.05 - 0.10 cm. wide. *Achene description*: lanceolate moderately covered in stiff trichomes. *Pappus length*: 0.7 - 1.0 cm. *Pappus description*: double pappus with outer circle about 0.15 cm. long. *Floret tube length*: 0.6 - 0.9 cm. *Floret lobe length*: 0.10 - 0.30 cm. *Floret colour*: yellow.

Ray florets: *Number of ray florets*: 0.

Distribution and ecology: California and rarely in Douglas and Washoe counties, Nevada (**Figure 22**). Specimens were collected from several soils: dry and rocky; granitic; sandy; and well drained granite slopes. They occurred in lodgepole pine and red fir woods, and in forest openings. *Elevation*: 550-3,450 m.

Notes: Figure 5437 (p. 265) found in the "Illustrated Flora of the Pacific States" (Abrams and Ferris 1960) appears to be incorrectly labelled as *Chrysopsis breweri*; it more closely resembles *Aster brickellioides* in the imbrication of the involucre.

Aster breweri (Gray) Semple var. *multibracteata* (Jepson) Zamluk *comb. nov.* (Phenetic group BRW1, page 108).

SYNONYMY

BASIONYM: *Chrysopsis breweri* Gray var. *multibracteata* Jepson, Man. Fl. Pl. Calif. (1925):1037. [Holotype at JEPS (not seen): J. W. Congdon, *s. n.* Sisson (Mt. Shasta City), Siskiyou Co., California.]

Habit: *Height*: 27 - 70 cm. *Branching*: 10 - 24 leafy branches on main stem. *Internode length in middle of main stem*: 0.7 - 2.1 cm. *Leaf density at middle of main stem*: 4 - 10 leaves in 8 cm.

Chromosome number: unknown. **Flowering time:** Middle of July to late August.

Leaves: *Shape*: linear or lanceolate. *Middle leaf*: 2.6 - 4.3 cm. long by 0.6 - 1.5 cm. wide. *Uppermost leaf*: 1.6 - 2.6 cm. long by 0.4 - 1.1 cm. wide. *Middle leaf tip*: cuspidate or mucronate. *Uppermost leaf tip*: cuspidate, acuminate or mucronate. *Leaf edge*: entire and ciliated.

Vesture: *Leaf upper surface*: moderately (occasionally sparsely) covered with mix of non-glandular and glandular trichomes (rarely with only glandular or only non-glandular). *Leaf under surface*: moderately covered with mix of non-glandular and glandular trichomes (rarely only glandular). *Stem*: sparsely to moderately covered with a mix of glandular and non-glandular trichomes (rarely with only glandular). *Involucre*: moderately covered with mix of glandular and non-glandular trichomes (rarely with only non-glandular).

Number of heads: 1 - 37. **Peduncle**: 2 to 5 bracts.

Involucre: *Imbrication*: slightly imbricated with 2 or 3 rows of phyllaries approximately equal in length. *Phyllary length*: 0.7 - 0.9 cm. *Width of pressed involucre*: 0.5 - 1.2 cm.

Phyllaries: *Phyllary tip*: acuminate or cuspidate. *Colour*: white central stripe, occasionally tipped with red, rarely red on edges and never red on keels.

Disk florets: *Achene*: 0.30 - 0.50 cm. long by 0.08 - 0.11 cm. wide. *Pappus length*: 0.6 - 0.9 cm. *Pappus description*: bristly with expanded tips; double pappus not evident. *Floret tube length*: 0.6 - 0.8 cm. *Floret lobe length*: 0.10 - 0.30 cm. *Floret colour*: yellow.

Ray florets: *Number of ray florets*: 0.

Distribution and ecology: California and Nevada (**Figure 23**). Collectors reported finding specimens growing on granite or sandy soils in open forests of mountain hemlock, pine and red fir. *Elevation*: 1,300 - 3,900 m.

Aster brickellioides (Greene) Greene, Pittonia (1889) 2:16-17.

Brickellbush Aster or Rayless Leafy Aster. (Phenetic group BRIK1, page 105).

SYNONYMIES

BASIONYM: *Sericocarpus tomentellus* Greene, Pittonia (1889) 1:283. [Holotype at NDG (056413) (not seen): T. Howell near Waldo, Josephine Co., Oregon, July 1888.] OTHER SYNONYMIES: *Eucephalus tomentellus* (Greene) Greene, Pittonia (1896) 3:55. *Aster tomentellus* (Greene) Frye & Rigg, NW Fl. (1912): 385. *Eucephalus brickellioides* (Greene) Nesom, Phytologia (1994) 77:254.

Not *Aster tomentellus* Hook. & Arn., Bot. Beech. Voy. (1833):146 which was assigned to *Corethrogyne filaginifolia*.

Greene assigned *Aster brickellioides* to three different taxa over seven years. First he considered it to be *Seriocarpus tomentellus* (1889), then changed his mind and placed it as *Aster brickellioides* (1889), and finally as *Eucephalus tomentellus* (1896). When Frye & Rigg (1912) transferred *E. tomentellus* to *Aster*, they mistakenly (because the name was already in use) assigned it to *Aster tomentellus*. Nesom (1994), recognizing the segregates of *Aster*, renamed it *Eucephalus brickellioides*.

Habit: *Height*: 40 - 64 cm. *Branching*: 3 - 26 branches on main stem. *Internode length in middle of main stem*: 0.7 - 1.9 cm. *Leaf density at middle of main stem*: 6 - 10 leaves in 8 cm.

Chromosome number: unknown. **Flowering time:** Late July to middle August.

Leaves: *Shape*: lanceolate or oblanceolate. *Middle leaf*: 2.5 - 5.8 cm. long by 0.7 - 1.7 cm. wide. *Uppermost leaf*: 0.8 - 2.5 cm. long by 0.2 - 0.4 cm. wide. *Middle leaf tip*: mucronate or apiculate. *Uppermost leaf tip*: mucronate but could be apiculate or acuminate. *Leaf edge*: entire and ciliated.

Vesture: *Leaf upper surface*: no trichomes or sparsely covered with only non-glandular trichomes. *Leaf under surface*: moderately covered with only non-glandular trichomes (rarely mix of non-glandular and glandular). *Stem*: sparsely (rarely moderately) covered with only non-glandular trichomes (rarely a mix of non-glandular and glandular trichomes). *Involucre*: moderately (rarely sparsely) covered with only glandular trichomes (rarely with mix of glandular and non-glandular).

Number of heads: 3 - 38 heads. **Peduncle**: 1 - 3 bracts.

Involucre: *Imbrication*: clearly imbricated in 3 to 5 rows. *Phyllary length*: 0.8 - 1.0 cm. *Width of pressed involucre*: 0.8 - 1.1 cm.

Phyllaries: *Phyllary tip*: apiculate but can be acute or acuminate. *Colour*: white central stripe, with red on tips and edges, but never red on keels.

Disk florets: *Achene*: 0.15 - 0.39 cm. long by 0.05 - 0.10 cm. wide. *Pappus length*: 0.6 - 0.8 cm. *Floret tube length*: 0.5 - 0.7 cm. *Floret lobe length*: 0.10 - 0.20 cm.

Ray florets: *Number of ray florets*: 0 - 9. *Colour*: violet. *Achene*: 0.16 - 0.32 cm. long by 0.06 - 0.07 cm. *Pappus length*: 0.6 cm. *Floret tube length*: 0.4 - 0.6 cm. *Floret limb length*: 0.6 - 1.6 cm.

Distribution and ecology: Jackson, Josephine and Klamath counties, Oregon, and in California (**Figure 24**). Collectors reported finding specimens in wooded areas, in forest openings, and rocky cliffs with northern, eastern and south eastern exposures. Soils were dry shallow rocky clay and plants were found in rock crevices. *Elevation*: 1,300-2,400 m.

Aster eastwoodiae **Zamluk** *comb. nov.*

(Phenetic group **BRIK2**, page 105).

SYNONYMY

BASIONYM: *Eucephalus bicolor* Eastw., Proc. Calif. Acad. (1931) IV. 20:157. [Holotype at CAS (2940) (not seen): Eastwood, 2214. French Hill, California, above Adams Station, September 14, 1912.]

Direct transfer of the specific epithet of *bicolor* to *Aster* was not possible because the name was already in use: *Aster bicolor* Dietr. ex. D. C. Prod. (1821) (later assigned to *Aster longifolius*); *Aster bicolor* Nees. (1832) (later assigned to *Solidago bicolor*).

Habit: *Height*: 48 - 66 cm. *Branching*: 4 - 20 branches on main stem. *Internode length in middle of main stem*: 0.9 - 1.2 cm. *Leaf density at middle of main stem*: 7 - 10 leaves in 8 cm.

Chromosome number: unknown. **Flowering time:** Early August to early October.

Leaves: *Shape*: oblanceolate. *Middle leaf*: 2.3 - 4.4 cm. long by 0.7 - 1.4 cm. wide. *Uppermost leaf*: 1.2 - 2.3 cm. long by 0.2 - 0.7 cm. wide. *Middle leaf tip*: acute or mucronate. *Uppermost leaf tip*: acute or cuspidate. *Leaf edge*: revolute and not ciliated; occasionally with one or two teeth near leaf tip.

Vesture: *Leaf upper surface*: no trichomes. *Leaf under surface*: densely (rarely moderately) covered with only non-glandular trichomes. *Stem*: densely (occasionally moderately) covered with only non-glandular trichomes. *Involucre*: densely (rarely moderately) covered with only non-glandular trichomes; older heads have fewer trichomes. *Peduncles*: densely covered with matted tomentulose trichomes.

Number of heads: 5 - 72 heads. **Peduncle**: 1 - 4 bracts.

Involucre: *Imbrication*: 4 - 5 rows. *Phyllary length*: 0.7 - 1.0 cm. *Width of pressed involucre*: 0.7 - 0.9 cm.

Phyllaries: *Phyllary tip*: acute or acuminate. *Colour*: white central stripe, red on tips and edges; red occasionally on keels.

Disk florets: *Achene*: 0.21 - 0.25 cm. long by 0.04 - 0.08 cm. wide. *Achene description*: golden brown. *Pappus*: 0.55 - 0.64 cm. long. *Pappus description*: double with short hairs about 0.04 cm. long; flaring tips. *Floret tube length*: 0.40 - 0.57 cm. *Floret lobe length*: 0.10 - 0.32 cm. *Floret colour*: yellow but sometimes red. *Style branch colour*: yellow.
Ray florets: *Number of ray florets*: 0 - 6 ray florets; may be variable within a population. *Colour*: violet or lilac. *Achene*: 0.23 - 0.30 cm. long by 0.04 - 0.07 cm. wide. *Pappus*: 0.52 - 0.57 cm. long. *Floret tube length*: 0.18 - 1.00 cm. *Floret limb length*: 0.90 - 1.20 cm.

Distribution and ecology: Curry and Josephine counties in Oregon, and Gasquet mountains, Del Norte, California (**Figure 25**). Specimens were collected in shallow rocky, clay loam soil, and in drier areas around a swamp. They occurred in chaparral. *Elevation*: 95-1,000 m.

Aster engelmannii Gray var. *engelmannii*, Am. J. Sci. Ser. II. (1862) 33:238. Engelmann's Aster. (Phenetic group ENGL, page 109).

SYNONYMIES

BASIONYM: *Aster engelmannii*, Am. J. Sci. Ser. II. (1862) 33:238 (in footnote without characters); Syn. Fl. N. Am. (1884) 1,2:199. [Lectotype at YU (not seen): Watson 515, from East Humboldt and Clover Mts., Nevada.] OTHER SYNONYMIES: *Aster elegans* T. & G. var. *engelmannii* Eaton, in Bot., in US Geol. Expl. 40th Par. (1871) 5:144, "*engelmanni*". *Eucephalus engelmannii* (Gray) Greene, Pittonia (1896) 3:54.

Typification is debatable because Piper (1906) cited a different type as Lyall *s. n.* from the Cascade Mountains, latitude 49° N.

Habit: *Height*: 91 - 107 cm. *Branching*: 5 - 16 branches on main stem. *Internode length in middle of main stem*: 2.0 - 2.6 cm. *Leaf density at middle of main stem*: 3 - 6 leaves in 8 cm.

Chromosome number: $n = 9$ (Semple *et al.* 1983 and Semple 1985). **Flowering time:** Early July to late August.

Leaves: *Shape*: elliptic. *Middle leaf*: 7.0 - 9.6 cm. long by 1.6 - 3.6 cm. wide. *Uppermost leaf*: 3.1 - 4.4 cm. long by 0.5 - 1.1 cm. wide. *Middle leaf tip*: mucronate, caudate or cuspidate. *Uppermost leaf tip*: acuminate, mucronate, cuspidate, caudate or acute. *Leaf edge*: entire and ciliated, occasionally with few teeth.

Vesture: *Leaf upper surface*: sparsely covered (rarely without trichomes) with only non-glandular trichomes (rarely with mix of mix of glandular and non-glandular, or rarely only glandular). *Leaf under surface*: sparsely covered only non-glandular trichomes (rarely with only glandular, or rarely with mix of glandular trichomes and non-glandular). *Stem*: sparsely (rarely moderately) covered with mix of small glandular and non-glandular trichomes (rarely with only non-glandular). *Involucre*: moderately (rarely lacking trichomes or sparsely) covered with mix of glandular and non-glandular trichomes (occasionally with only glandular).

Number of heads: 5 - 41. **Peduncle**: 1 - 5 bracts.

Involucre: *Imbrication*: 4 or 5 rows. *Phyllary length*: 0.9 - 1.1 cm. *Width of pressed involucre*: 1.1 - 1.7 cm.

Phyllaries: *Phyllary tip*: acuminate, acute, cuspidate or mucronate. *Colour*: white central stripe, with red on tips (rarely without), on edges but no red keels.

Disk florets: *Achene*: 0.45 - 0.50 cm. long by 0.06 - 0.18 cm. wide. *Achene description*: obovate with long, slim trichomes. *Pappus length*: 0.6 - 0.9 cm. *Pappus description*: hairs with small bristles and flaring at tip. *Floret tube length*: 0.55 - 0.72 cm. *Floret lobe length*: 0.07 - 0.20 cm. *Floret colour*: yellow.

Ray florets: *Number of ray florets*: 4 - 12. *Floret colour*: violet, purple, or white. *Achene*: 0.35 - 0.50 cm. long by 0.10 - 0.15 cm. wide. *Pappus length*: 0.70 - 0.83 cm. *Floret tube length*: 0.32 - 0.60 cm. *Floret limb length*: 1.2 - 1.5 cm.

Distribution and ecology: Alberta and British Columbia in Canada. Colorado, Idaho, Montana, Nevada, Utah, Washington, and Wyoming (**Figure 26**). Plants were found by collectors growing on wooded hillsides, in meadows, in seep meadows, and on sagebrush

grasslands. They were in shady places or in small openings. Soils were calcareous gravelly loam, and loam. They were collected from gentle, moderate and steep slopes. *Elevation*: 300-3,700 m.

Aster engelmannii Gray var. *monticola* Zamluk *var. nov.*

(Phenetic group ENLWSA, page 109).

[Holotype at RM (344970) (have seen): Lowry, P. P. 2857. East of Teton Pass, Teton Co., Wyoming. August 11, 1979.]

Habit: *Height*: 47 - 102 cm. *Branching*: 4 - 10 branches on main stem. *Internode length in middle of main stem*: 0.7 - 2.5 cm. *Leaf density at middle of main stem*: 4 - 11 leaves in 8 cm.

Chromosome number: unknown. **Flowering time:** early July to late August.

Leaves: *Shape*: lanceolate. *Middle leaf*: 5.3 - 8.2 cm. long by 1.5 - 2.3 cm. wide. *Uppermost leaf*: 1.7 - 5.0 cm. long by 0.5 - 1.8 cm. wide. *Middle leaf tip*: mucronate but could be acuminate. *Uppermost leaf tip*: mucronate but could also be acute or cuspidate. *Leaf edge*: entire or revolute with cilia (occasionally with few teeth).

Vesture: *Leaf upper surface*: sparsely (rarely moderately) covered with mix of glandular and non-glandular trichomes, or with only non-glandular trichomes (rarely with only glandular. *Leaf under surface*: moderately (rarely sparsely) covered with mix of glandular and non-glandular trichomes (occasionally with only glandular). *Stem*: sparsely or moderately covered with mix of glandular and non-glandular trichomes (rarely only glandular). *Involucre*: densely (occasionally sparsely or rarely moderately) covered with only glandular trichomes (rarely with mix of glandular and non-glandular).

Number of heads: 1 - 16. **Peduncle**: 1 - 4 bracts.

Involucre: *Imbrication*: 3 or 4 rows. *Phyllary length*: 0.8 - 1.2 cm. *Width of pressed involucre*: 1.1 - 1.6 cm.

Phyllaries: *Phyllary tip*: acute and could also be mucronate or cuspidate. *Colour*: with white central stripe, with red on tips, edges, but never on keels.

Disk florets: *Achene*: 0.36 - 0.51 cm. long by 0.04 - 0.10 cm. wide. *Pappus length*: 0.70 - 0.92 cm. *Floret tube length*: 0.52 - 0.99 cm. *Floret lobe length*: 0.09 - 0.16 cm. **Ray florets**: *Number of ray florets*: 7 - 20. *Colour*: white, pink, or magenta. *Achene*: 0.31 - 0.52 cm. long by 0.04 - 0.15 cm. wide. *Pappus length*: 0.62 - 0.88 cm. *Floret tube length*: 0.35 - 0.82 cm. *Floret limb length*: 1.1 - 2.2 cm.

Distribution and ecology: Alberta and British Columbia, Canada. Colorado, Idaho, Montana, Utah, and Washington, Wyoming (**Figure 27**). Plants were collected in subalpine meadows, from a damp river bottom, in lodge pole pine forests, and in openings in coniferous forests. They were reported on moist gravelly loam, clay loam, sandy soil, and on talus. *Elevation*: 970-3,400 m.

Aster glaucescens (Gray) Blake, Rhodora (1928) 30:278. Klickitat Aster.

(Phenetic group GLCS, page 109).

SYNONYMIES

BASIONYM: *Aster engelmannii* Gray var. *glaucescens* Gray, "*engelmanni*", Syn. Fl. N. Amer. II (1884): 200. [Holotype at US (75863): Suksdorf, 11. Washington territory, Washington.] OTHER SYNONYMIES: *Eucephalus glaucescens* (Gray) Greene, Pittonia (1896) 3:56. [Lectotype at GH: Suksdorf, 31. Mt. Paddo (Adams), Washington.] *Eucephalus glaucophyllus* Piper, Contr. U. S. Nat. Herb. (1906) 11:570. [Holotype: Suksdorf, 118. Mt. Paddo (Adams), Washington.] *Aster glaucophyllus* (Piper) Frye & Rigg, NW Fl. (1912): 385. *Eucephalus serrulatus* Greene: Pittonia (1896) 3:55. [Isotype at WS (121291) (not seen): Suksdorf, 1563. Mt. Paddo, Washington.] *Aster serrulatus* (Greene) Frye & Rigg: NW Fl. (1912): 385.

Not: *Aster glaucescens* Wenderoth ex. Nees. (1832) which has been assigned to *Aster laevis*. Blake (1928) wrote that ". . . *Aster glaucescens* Wenderoth . . . occurs as a synonym only (of *Aster cyaneus* Hoffm. ∝ *glaucus* (Hoffm.)

Nees, Gen. & Sp. Asterac. 132. 1832) so does not invalidate further use of the name." (p. 228).

Habit: *Height*: 86 - 160 cm. *Branching*: 5 - 23 branches on main stem. *Internode length in middle of main stem*: 1.0 - 2.0 cm. *Leaf density at middle of main stem*: 6 - 11 leaves in 8 cm.

Chromosome number: unknown. **Flowering time:** late July to early October.

Leaves: *Shape*: linear. *Middle leaf*: 6.2 - 9.2 cm. long by 0.6 - 1.6 cm. wide. *Uppermost leaf*: 2.6 - 5.4 cm. long by 0.2 - 0.6 cm. wide. *Middle leaf tip*: mucronate or cuspidate, otherwise could be acute or acuminate. *Uppermost leaf tip*: mucronate or cuspidate but may also be acute or acuminate. *Leaf edge*: entire and with cilia; occasionally with few teeth.

Vesture: *Leaf upper surface*: with no trichomes (rarely moderately covered with only glandular or rarely only non-glandular trichomes). *Leaf under surface*: lacking trichomes (occasionally sparsely covered with only glandular or rarely only non-glandular trichomes). *Stem*: with no trichomes or sparsely covered with only non-glandular trichomes (rarely with only glandular or rarely with mix of glandular and non-glandular). *Involucre*: sparsely (occasionally moderately) covered with only glandular trichomes (rarely with mix of non-glandular and glandular).

Number of heads: 4 - 59. **Peduncle**: 2 - 6 bracts.

Involucre: *Imbrication*: 3 or 4 rows. *Phyllary length*: 0.7 - 1.1 cm. *Width of pressed involucre*: 0.8 - 1.5 cm.

Phyllaries: *Phyllary tip*: cuspidate, acute or acuminate. *Colour*: white central stripe, with red on tips and edges, and rarely red on keels.

Disk florets: *Achene*: 0.29 - 0.52 cm. long by 0.07 - 0.15 cm. wide. *Pappus length*: 0.60 - 0.76 cm. *Floret tube length*: 0.51 - 0.62 cm. *Floret lobe length*: 0.07 - 0.15 cm.

Ray florets: *Number of ray florets*: 5 - 12. *Colour*: purple or blue. *Achene*: 0.24 - 0.52 cm. long by 0.05 - 0.13 cm. wide. *Pappus length*: 0.58 - 0.73 cm. *Floret tube length*: 0.25 - 0.40 cm. *Floret limb length*: 0.8 - 1.4 cm.

Distribution and ecology: Yakima, Klickitat and Skamania counties in Washington (**Figure 28**). Found in pine forest growing on moist, loamy soil, and growing in volcanic sand, and rocky soil in semi-open brush. *Elevation*: 800 - 1,500 m.

Aster glaucodes Blake var. *glaucodes*, Proc. Biol. Soc. Wash.(1922) 35:174. Blue Leaf Aster. (Phenetic group GLCD, page 108).

SYNONYMIES

BASIONYM: *Eucephalus glaucus* Nutt., Trans. Am. Phil. Soc. (1840) 2,7:299. [Holotype at BM (not seen): Nuttall *s. n.* Towards the sources of the Platte, and in the Rocky Mts.] OTHER SYNONYMIES: *Aster glaucus* T & G. (*nom. illeg.*), Syn. Fl. N. Am. (1841) 2:159, 503. *Eurybia glauca* (Nutt.) Nesom, Phytologia (1994): 77(3): 260.

Not: *Aster glaucus* Nees. Syn. Aster. (1818): 23.

Habit: *Height*: 34 - 42 cm. *Branching*: 3 - 12 branches on main stem. *Internode length in middle of main stem*: 1.1 - 2.7 cm. *Leaf density at middle of main stem*: 3 - 6 leaves in 8 cm.

Chromosome number: $n = 9$ (Semple *et al.* 1983; Semple 1985). **Flowering times**: late June to middle September.

Leaves: *Shape*: linear or oblong; when dry blade has bullate texture apparently caused by shrinkage of the leaf veins. *Colour*: blue-green. *Middle leaf*: 5.3 - 10.9 cm. long by 0.7 - 1.6 cm. wide. *Uppermost leaf*: 1.2 - 5.5 cm. long by 0.5 - 1.2 cm. wide. *Middle leaf tip*: mucronate or cuspidate, otherwise acute. *Uppermost leaf tip*: mucronate or caudate but can be acuminate. *Leaf edge*: entire and ciliated; can have a few teeth.

Vesture: *Both leaf surfaces*: no trichomes. *Stem*: lacking trichomes (rarely sparsely covered with only non-glandular (rarely with only non-glandular)). *Involucre*: lacking trichomes (rarely sparsely covered with only glandular (rarely with non-glandular). *Peduncle*: no trichomes.

Number of heads: 10 - 31. **Peduncle**: 1 - 3 bracts.

Involucre: *Imbrication*: 3 or 4 rows. *Phyllary length*: 0.7 - 0.8 cm. *Width of pressed involucre*: 0.7 - 1.0 cm.

Phyllaries: *Phyllary tip*: obtuse but can be acuminate or mucronate. *Colour* : white central stripe, equally probable that phyllaries are without red on tips, edges or keels, or they will have red on tips, edges or keels (rarely lacking red on tips alone or red on keels alone).

Disk florets: *Colour*: purple, or yellow browning to red-brown. *Achene*: 0.14 - 0.26 cm. long by 0.03 - 0.06 cm. wide. *Achene description*: sparsely covered with trichomes. *Pappus length*: 0.59 - 0.81 cm. *Pappus description*: double pappus not evident. *Floret tube length*: 0.47 - 0.65 cm. *Floret lobe length*: 0.10 - 0.15 cm. *Style branch colour*: purple.

Ray florets: *Number of ray florets*: 8 - 19. *Colour*: lavender, bright blue, or white. *Achene*: 0.12 - 0.28 cm. long by 0.03 - 0.07 cm. wide. *Pappus length*: 0.55 - 0.75. *Floret tube length*: 0.35 - 0.50 cm. *Floret limb length*: 0.7 - 1.4 cm.

Distribution and ecology: Arizona, Colorado, Idaho, New Mexico, Utah, and Wyoming. Specimens were collected from forests and meadows, rabbit brush grasslands, aspen groves, and pinyon and juniper woods. It was reported growing on talus, stream banks, in moist soil pockets, and on rocky soil. Distribution map: (**Figure 29**). *Elevation*: 650-3,500 m.

Notes: Three varieties for *Aster glaucodes* have been recognized in the literature: var. *glaucodes*, var. *pulcher* (Blake) Kearney & Peebles and var. *formosus* (Greene) Kittell. In "The Manual of the Plants of Colorado", var. *formosus* was distinguished from var. *glaucodes* by its obtuse phyllaries and hairy pedicels (Harrington 1954). The "Great Basin Naturalist Memoirs" divides var. *pulcher* from var. *glaucodes* based on the glandular trichomes on the involucre and peduncles of var. *pulcher* (Welsh *et al.* 1981). The descriptions of var. *pulcher* and var. *formosus* show remarkable similarity but because no collections of var. *formosus* were included in this study, this variety and its overlap with var. *pulcher* could not be evaluated.

Aster glaucodes Blake var. *pulcher* (Blake) Kearney & Peebles, Proc. Biol. Soc. Wash.(1922) 35:174. (No corresponding phenetic group).

SYNONYMIES

BASIONYM: *Aster glaucodes* Blake ssp. *pulcher* Blake, Proc. Biol. Soc. Wash.(1922) 35:174. [Holotype at US (326729) (not seen): Jones, M. E., 6037. Elk Ranch, Utah, September 12, 1894.] OTHER SYNONYMY: *Eurybia pulchra* (Blake) Nesom, Phytologia (1994) 77(3): 261.

Flowering times: middle September to middle of October.

Vesture: *Peduncle*: below head densely covered in glandular trichomes.

Distribution and ecology: Arizona and Utah. Collectors reported it growing in sandy soil in woodlands and on a dry hillside. Distribution map: **(Figure 29)**. *Elevation*: 1,500-2,500 m.

Notes: see notes of *Aster glaucodes* var. *glaucodes*.

Aster glaucodes Blake var. *formosus* (Greene) Kittell, Fl. Ariz. and N. Mex. (1941): 404. (No corresponding phenetic group).

SYNONYMIES

BASIONYM: *Eucephalus formosus* Greene, Pittonia (1900) 4:156. [Holotype at US (369184): Baker, 659. Pagosa Peak. Colorado. August 23, 1899.] OTHER SYNONYMIES: *Aster glaucus* T. & G. (*nom. illeg.*) var. *formosus* A. Nels., New Man. Rocky Mountains (1909):513. *Eurybia glauca* (Nutt.) Nesom, Phytologia (1994): 77(3): 260.

Phyllaries: *Phyllary tip*: "all obtuse" (Harrington 1954, page 574).

Distribution and ecology: ". . . from southern Colorado" (Harrington 1954, page 574).

Notes: see notes of *Aster glaucodes* var. *glaucodes*.

***Aster gormanii* (Piper) Blake,** Rhodora (1928) 30:278. Gorman's Aster.

(Phenetic group GORM, page 108).

SYNONYM

BASIONYM: *Eucephalus gormanii* Piper, Proc. Biol. Soc. Wash. (1916) 29: 101, "*gormani*". [Holotype at WS (50205) (not seen): Gorman, 2851. Hanging Valley, Mount Jefferson, Cascade Mountains.]

Habit: *Height*: 14 - 32 cm. *Branching*: none - 12 branches on main stem. *Internode length in middle of main stem*: 0.3 - 1.0 cm. *Leaf density at middle of main stem*: 10 - 18 leaves in 8 cm.

Chromosome number: $n = 9$ (Semple 1985). **Flowering time:** middle of July to middle of August.

Leaves: *Shape*: linear and slightly elliptic, while others oblanceolate. *Middle leaf*: 1.9 - 3.1 cm. long by 0.5 - 0.9 cm. wide. *Uppermost leaf*: 1.2 - 2.9 cm. long by 0.3 - 1.7 cm. wide. *Middle leaf tip*: mucronate but can be acute or acuminate or obtuse. *Uppermost leaf tip*: mucronate but can be acute or acuminate or cuspidate. *Leaf edge*: entire and ciliated.

Vesture: *Leaf upper surface*: densely or moderately (rarely sparsely) covered with only glandular trichomes or mix of glandular and non-glandular trichomes. *Leaf under surface*: moderately (occasionally densely or sparsely) covered with either only glandular trichomes (rarely with mix of non-glandular and glandular). *Stem*: sparsely (occasionally moderately or densely) covered with mix of glandular trichomes and non-glandular trichomes. *Involucre*: lacking trichomes or moderately (occasionally sparsely or rarely densely) covered with only glandular trichomes.

Number of heads: 1 - 5. **Peduncle**: 0 - 2 bracts.

Involucre: *Imbrication*: 2 or 3 rows. *Phyllary length*: 0.7 - 1.2 cm. *Width of pressed involucre*: 0.8 - 1.4 cm.

Phyllaries: *Phyllary tip*: acute, acuminate or cuspidate. *Colour*: white central stripe (rarely without), no red on tips, edges or keels (rarely with red on tips or edges).

Disk florets: *Achene*: 0.20 - 0.45 cm. long by 0.05 - 0.13 cm. wide. *Pappus length*: 0.55 - 0.75 cm. *Floret tube length*: 0.40 - 0.60 cm. *Floret lobe length*: 0.09 - 0.19 cm.
Ray florets: *Number of ray florets*: 3 - 14. *Colour*: buds - purple; open - white. *Achene*: 0.26 - 0.43 cm. long by 0.03 - 0.11 cm. wide. *Pappus length*: 0.52 - 0.71 cm. *Floret tube length*: 0.25 - 0.42 cm. *Floret limb length*: 0.7 - 1.6 cm.
Distribution and ecology: Clackamas, Jefferson, Linn, and Marion counties in Oregon (**Figure 30**). Reported from fully exposed, dry, and rocky sites. *Elevation*: 1,200 - 1,900 m.

Aster ledophyllus (Gray) Gray var. *covillei* (Greene) Cronq,

Vasc. Pl. Pac. NW (1955) 5:89. (Phenetic group BRKLDO, page 109).
SYNONYMIES

BASIONYM: *Eucephalus covillei* Greene, Pittonia (1897) 3:162. [Holotype (not seen): Coville, *s. n.* Near Crater Lake in 1896.] OTHER SYNONYMIES: *Aster covillei* (Greene) Peck, Man. High. Pl. Ore. (1941):725. *Eucephalus ledophyllus* (Gray) Greene var. *covillei* (Greene) Nesom, Phytologia (1994) 77(3):255.

Habit: *Height*: 25 - 58 cm. *Branching*: 3 - 15 branches on main stem. *Internode length in middle of main stem*: 0.7 - 1.6 cm. long. *Leaf density at middle of main stem*: 6 - 10 leaves in 8 cm.
Chromosome number: $n = 9$ (Semple 1985). **Flowering time:** late July to late August.
Leaves: *Shape*: lanceolate or oblanceolate. *Middle leaf*: 2.3 - 4.8 cm. long by 0.5 - 1.5 cm. wide. *Uppermost leaf*: 1.5 - 3.1 cm. long by 0.2 - 0.6 cm. wide. *Middle leaf tip*: acuminate but can be mucronate. *Uppermost leaf tip*: acute but can be mucronate. *Leaf edge*: entire and ciliated.
Vesture: *Leaf upper surface*: moderately (rarely dense or sparsely) covered with mix of non-glandular and glandular trichomes (occasionally with only non-glandular or rarely with only glandular). *Leaf under surface*: moderately or densely covered with mix of

glandular and non-glandular trichomes (occasionally only non-glandular). *Stem*: moderately (rarely densely) covered with mix of glandular and non-glandular trichomes (rarely only non-glandular trichomes). *Involucre*: moderately (rarely densely) covered with mix of non-glandular and glandular trichomes (rarely with only glandular or rarely only non-glandular). *Peduncle*: with glandular trichomes.

Number of heads: 4 - 9. **Peduncle**: 1 - 9 bracts.

Involucre: *Imbrication*: 4 or 5 rows. *Phyllary length*: 1.0 - 1.2 cm. *Width of pressed involucre*: 0.8 - 1.3 cm.

Phyllaries: *Phyllary tip*: acute or acuminate. *Colour*: white stripe in centre, with red on tips and edges, and never red on keels (rarely with red on edges alone).

Disk florets: *Achene*: 0.20 - 0.43 cm. long by 0.05 - 0.12 cm. wide. *Pappus length*: 0.70 - 0.80 cm. *Floret tube length*: 0.50 - 0.65 cm. *Floret lobe length*: 0.10 - 0.12 cm. *Floret colour*: yellow but can have red pigment. *Style branches*: purple.

Ray florets: *Number of ray florets*: 0 - 12. *Colour*: violet, purple, or blue. *Achene*: 0.22 - 0.47 cm. long by 0.05 - 0.07 cm. wide. *Pappus length*: 0.50 - 0.72 cm. *Floret tube length*: 0.30 - 0.70 cm. *Floret limb length*: 0.9 - 1.2 cm.

Distribution and ecology: Northern California, Oregon and Washington (**Figure 31**). Plants were collected from subalpine forests, dry meadows and pumice slopes. Soils were dry loam, gravelly or rocky. They were found on moist hillsides and in damp meadows. Exposure was partial shade and in full sun. *Elevation*: 1,200-2,600 m.

***Aster ledophyllus* (Gray) Gray var. *ledophyllus*,** Proc. Amer. Acad. (1880) 16: 98 (without characters). Cascade Aster. (Phenetic group LEDO, page 109).

SYNONYMIES

BASIONYM: *Aster engelmannii* Gray var. *ledophyllus* Gray, Proc. Amer. Acad. (1872) 8:388, "*ledophylla*". [Holotype at GH: Hall, 242. They were collected high up in the Cascade Mountains, Oregon.] OTHER SYNONYMY: *Eucephalus ledophyllus* (Gray) Greene, Pittonia (1896) 3:55.

Habit: *Height*: 21 - 85 cm. *Branching*: 0 -18 . *Internode length in middle of main stem*: 0.5 - 1.8 cm.. *Leaf density at middle of main stem*: 7 - 15 leaves in 8 cm..

Chromosome number: $n = 9$ (Semple 1985). **Flowering time:** middle July to early September.

Leaves: *Shape*: linear but can be ovate . *Middle leaf*: 3.0 - 5.3 cm. long by 0.6 - 1.8 cm. wide. *Uppermost leaf*: 1.5 - 3.2 cm. long by 0.2 - 0.9 cm. wide. *Middle leaf tip:* mucronate but can be acuminate, cuspidate or caudate. *Uppermost leaf tip*: acute but can be acuminate, mucronate or cuspidate. *Leaf edge*: entire and ciliated; leaves may be toothed.

Vesture: *Leaf upper surface*: sparsely (occasionally moderately) covered with non-glandular trichomes. *Leaf under surface*: densely covered with non-glandular trichomes. *Stem*: moderately (occasionally densely or rarely sparsely) covered with mix of small glandular and long non-glandular trichomes (occasionally with only non-glandular). *Involucre*: moderately or densely covered with either only glandular trichomes (rarely with mix of glandular and non-glandular).

Number of heads: 2 - 17. **Peduncle**: 1 - 4 bracts.

Involucre: *Imbrication*: 3, 4 or 5 rows. *Phyllary length*: 0.7 - 1.2 cm. *Width of pressed involucre*: 0.8 - 1.6 cm.

Phyllaries: *Phyllary tip*: acuminate but can be acute or cuspidate. *Colour*: white central stripe (rarely without), with red on tips and edges, but rarely with red on keels.

Disk florets: *Achene*: 0.22 - 0.50 cm. long by 0.04 - 0.11 cm. wide. *Achene shape*: linear. *Pappus length*: 0.60 - 0.85 cm. *Pappus description*: double with outside bristles about 0.09 cm. long; pappus covered with small bristles and dilated at tip. *Floret tube length*: 0.52 - 0.65 cm.. *Floret lobe length*: 0.08 - 0.16 cm. *Floret colour*: purple. *Colour of style branches*: red.

Ray florets: *Number of ray florets*: 6 - 20. *Colour*: blue-purple. *Achene*: 0.23 - 0.50 cm. long by 0.04 - 0.13 cm. wide. *Pappus length*: 0.65 - 0.86 cm. *Floret tube length*: 0.23 - 0.50 cm. *Floret limb length*: 1.1 - 1.9 cm.

Distribution and ecology: Oregon, Washington, and rarely in California (**Figure 32**). Specimens were collected from fully exposed sites in dry rocky open woodlands, on subalpine banks, in alpine meadows, pumice slopes, and open grass lands. Soils were well drained gravelly loam, moist sand, and shallow clay loam. *Elevation*: 450 - 2,250 m.

Aster paucicapitatus (Robins.) Robins, Proc. Amer. Acad. (1894) 29: 329-330. Olympic Aster. (Phenetic group PAUC, page 108).

SYNONYMIES

BASIONYM: *Aster engelmannii* var. (?) *paucicapitatus* Robins., Proc. Amer. Acad. (1891) 26: 176. [Syntypes at GH: Piper, 926 and 934 collected August and September 30, 1890 in the Olympic Mountains, Washington. Piper, 926 designated as lectotype by A. G. Jones (1984).] OTHER SYNONYMY: *Eucephalus paucicapitatus* (Robins.) Greene, Pittonia (1896) 3:56.

Habit: *Height*: 20 - 54 cm. *Branching*: none - 8 branches on main stem. *Internode length in middle of main stem*: 0.6 - 1.3 cm. *Leaf density at middle of main stem*: 7 - 13 leaves in 8 cm.

Chromosome number: unknown. **Flowering time:** late July to late August.

Leaves: *Shape*: oblong. *Middle leaf*: 2.5 - 3.9 cm. long by 0.5 - 1.2 cm. wide. *Uppermost leaf*: 1.1 - 3.0 cm. long by 0.2 - 1.0 cm. wide. *Middle leaf tip*: mucronate but can be acute or cuspidate, cuspidate or obtuse. *Uppermost leaf tip*: acute but can be acuminate, cuspidate, or mucronate. *Leaf edge*: entire and ciliated; sometimes with few teeth.

Vesture: *Leaf upper surface*: moderately (occasionally sparsely or rarely densely) covered with mix of non-glandular and glandular trichomes (occasionally with only glandular). *Leaf under surface*: moderately (rarely densely or rarely sparsely) covered mix of glandular and non-glandular trichomes. *Stem*: moderately (occasionally sparsely or rarely densely) covered with mix of glandular and non-glandular trichomes. *Involucre*: moderately (occasionally densely or rarely moderately) covered with mix of non-glandular

and glandular trichomes. *Peduncle*: moderately to densely covered in a mix of non-glandular and glandular trichomes.

Number of heads: 1 - 4. **Peduncle**: 0 - 3 bracts.

Involucre: *Imbrication*: 2 or 3 rows. *Phyllary length*: 0.6 - 1.2 cm. *Width of pressed involucre*: 1.1 - 1.7 cm.

Phyllaries: *Phyllary tip*: acute. *Colour*: white central stripe (rarely without), without red on tips, edges or keels (rarely with red on tip and edge).

Disk florets: *Achene*: 0.27 - 0.54 cm. long by 0.07 - 0.17 cm. wide. *Pappus length*: 0.72 - 0.90 cm. *Floret tube length*: 0.51 - 0.82 cm. *Floret lobe length*: 0.12 - 0.18 cm. *Floret colour*: yellow.

Ray florets: *Number of ray florets*: 7 - 13. *Colour*: white. *Achene*: 0.25 - 0.47 cm. long by 0.06 - 0.16 cm. wide. *Pappus length*: 0.65 - 0.90 cm. *Floret tube length*: 0.35 - 0.41 cm. *Floret limb length*: 1.1 - 1.6 cm.

Distribution and ecology: Vancouver Island, British Columbia, and Olympic Peninsula, Washington (**Figure 33**). Plants were collected on open alpine slopes, on scree, in alpine meadows, and talus. They grew in non-limestone soil on Marble Mountain, Vancouver Island. *Elevation*: 850 - 3,300 m.

***Aster perelegans* Nels. & Macbr.**, Bot. Gaz. (1913)56:477. Elegant Aster. (Phenetic group PERL, page 108).

SYNONYMIES

BASIONYM: *Eucephalus elegans* Nutt., Trans. Amer. Phil. Soc. (1841)7:298. [Holotype is at BM (not seen): Nuttall, *s. n.* Oregon plains and the Blue Mountains of the west. Possible isotype at GH.] OTHER SYNONYMIES: *Aster elegans* (Nutt.) T. & G., Fl. N. Amer. (1841) 2:159. *Eucephalus perelegans* (Nels. & Macbr.) Weber, Phytologia (1982) 51(6):374. *Eucephalus frigidus* Gandoger, Bull. Soc. Bot. France (1918) 4:40, "*Encephalus*". [Holotype(not seen): Rydberg and Bessey, 5113. Henry's Lake, Idaho.] *Eucephalus scaber* Gandoger, Bull. Soc. Bot. France (1918) 4:40, "*Encephalus*". [Holotype (not seen): Leiberg, 5. Bitter Root Forest Res., Montana.]

Not *Aster elegans* Hook, J. D., Thompson, T. ex. C. B. Clarke: Comp. Ind.(1855): 44.

Not *Aster elegans* Hort. Par. ex. Gray: Syn. Fl. N. Am. (1884)1,2:184.

Not *Aster elegans* Nees.: Syn. Aster (1831): 20.

Not *Aster elegans* Willd.: Sp. Pl. (1803)3:2042.

Eucephalus frigidus Gand. and *E. scaber* Gand. were placed in synonymy with *A. perelegans* by Cronquist (1955).

Habit: *Height*: 33 - 77 cm. *Branching*: 3 - 30 branches on main stem. *Internode length in middle of main stem*: 0.5 - 1.4 cm. *Leaf density at middle of main stem*: 6 - 14 leaves in 8 cm.

Chromosome number: unknown. **Flowering time:** early July to late August.

Leaves: *Shape*: linear with a slightly wider base. *Colour*: blue green. *Middle leaf*: 3.0 - 5.8 cm. long by 0.3 - 1.0 cm. wide. *Uppermost leaf*: 0.9 - 2.5 cm. long by 0.2 - 0.6 cm.

wide. *Middle leaf tip*: either mucronate or acute but could be acuminate. *Uppermost leaf tip*: acute (rarely mucronate). *Leaf edge*: entire and ciliated.

Vesture: *Leaf upper surface*: moderately or sparsely (rarely densely) covered with mix of glandular and scabrous non-glandular trichomes (occasionally with only non-glandular scabrous). *Leaf under surface*: moderately (rarely sparsely or rarely densely) covered with mix of glandular and non-glandular scabrous trichomes. *Stem*: moderately (occasionally densely) covered with mix of glandular and non-glandular trichomes. *Involucre*: densely (occasionally moderately or sparsely) covered with mix of glandular and non-glandular trichomes (occasionally only non-glandular).

Number of heads: 3 - 17. **Peduncle**: 1 - 6 bracts.

Involucre: *Imbrication*: clearly imbricated with 3, 4 or 5 rows. *Phyllary length*: 0.7 - 0.9 cm. *Width of pressed involucre*: 0.6 - 1.1 cm.

Phyllaries: *Phyllary tip*: acute (occasionally acuminate). *Colour*: dark green or purple central stripe; greenish with purple tips and edges.

Disk florets: *Achene*: 0.21 - 0.41 cm. long by 0.05 - 0.10 cm. wide. *Pappus length*: 0.48 - 0.80 cm. *Floret tube length*: 0.3 - 0.8 cm. *Floret lobe length*: 0.06 - 0.15 cm. *Floret colour*: purple, or dirty yellow with purple tips. *Style branch colour*: purple.

Ray florets: *Number of ray florets*: 5 - 8. *Colour*: purple, or blue. *Achene*: 0.22 - 0.41 cm. long by 0.06 - 0.11 cm. wide. *Pappus length*: 0.50 - 0.72 cm. *Floret tube length*: 0.22 - 0.48 cm. *Floret limb length*: 0.6 - 1.5 cm.

Distribution and ecology: Colorado, Idaho, Montana, Nevada, Oregon, Utah, and Wyoming (**Figure 34**). Plants were collected from open ridges, sage brush communities, aspen stands, grassy granite slopes, and grassy meadows. Soils were described as shallow loam, dry and rocky, clay loam, and sandy loam. *Elevation*: 1,160 - 3,200 m.

***Aster siskiyouensis* Nels. & Macbr.,** Bot. Gaz. (1913) 56:477. Siskiyou Rayless Aster. (Phenetic group BRKGLS, page 109).

SYNONYMIES

BASIONYM: *Aster brickellioides* Greene var. *glabratus* Greene: Pittonia (1889) 2:17. [Holotype at US (60809) (not seen): Toward the summits of the Siskiyou Mountains, Oregon, September 2, 1889.] OTHER SYNONYMIES: *Eucephalus glabratus* (Greene) Greene, Pittonia (1896) 3:56. *Aster glabratus* (Greene) Blake ex. M. E. Peck, Man. High. Pl. Ore. (1941):726.

POSSIBLE SYNONYMY

Eucephalus glandulosus Eastw., Proc. Calif. Acad. (1931) series 4, 20: 157-158. [Holotype at CAS (171599) (not seen): Eastwood, 2152. Near Waldo, Josephine Co., September 11, 1912.]

Not *Aster glabratus* Kuntz., Rev. Gen.(1891):318.

Not *Aster glabratus* Krause, Strum, Fl. Deutschland, (1905) ed. 2 8:57.

Not *Aster glabratus* B. Fedtsch., Rastit. Turkest. (1915):731.

Habit: *Height*: 30 - 54 cm.. *Branching*: 2 - 11 branches on main stem. *Internode length in middle of main stem*: 0.5 - 1.5 cm. *Leaf density at middle of main stem*: 7 - 10 leaves in 8 cm.

Chromosome number: unknown. **Flowering time:** Early July to middle August.

Leaves: *Shape*: lanceolate. *Middle leaf*: 3.0 - 5.9 cm. long by 0.7 - 1.5 cm. wide. *Uppermost leaf*: 1.0 - 2.6 cm. long by 0.2 - 0.8 cm. wide. *Middle leaf tip*: mucronate, or cuspidate. *Uppermost leaf tip*: mucronate, cuspidate, or acute. *Leaf edge*: entire (occasionally revolute) and not ciliated.

Vesture: *Leaf upper surface*: without trichomes (occasionally sparsely covered with only non-glandular trichomes or only glandular trichomes). *Leaf under surface*: without trichomes (occasionally sparsely covered with glandular trichomes). *Stem*: without trichomes (occasionally sparsely covered with glandular trichomes). *Involucre*: sparsely

or moderately (rarely with no trichomes or rarely densely) covered with glandular trichomes.

Number of heads: 1 - 20. **Peduncle**: 1 to 3 bracts.

Involucre: *Imbrication*: 3 or 4 rows. *Phyllary length*: 0.7 - 1.1 cm. *Width of pressed involucre*: 0.9 - 1.2 cm.

Phyllaries: *Phyllary tip*: acute, acuminate or cuspidate. *Colour*: white central stripe, with red on tips and edges (rarely on tips alone) and rarely red on keels.

Disk florets: *Achene*: 0.27 - 0.49 cm. long by 0.05 - 0.12 cm. wide. *Pappus length*: 0.66 - 0.78 cm. *Floret tube length*: 0.54 - 0.66 cm. *Floret lobe length*: 0.10 - 0.16 cm.

Ray florets: *Number of ray florets*: 0 - 8. *Colour*: blue or blue violet. *Achene*: 0.23 - 0.40 cm. long by 0.06 - 0.10 cm. wide. *Pappus length*: 0.65 - 0.86 cm. *Floret tube length*: 0.37 - 0.41 cm. *Floret limb length*: 1.1 - 1.7 cm.

Distribution and ecology: Jackson, Josephine, Klamath and Curry counties, Oregon. Humboldt, Trinity, Siskiyou, Del Norte counties, California (**Figure 35**). Collectors reported finding specimens growing among rocks; on drier ground in a swampy area; in dry stony situations; on sandy slopes; in quartz dionite; on serpentine. They were collected in chaparral and in the shade of fir trees. *Elevation*: 750 - 2,300 m.

Aster vialis (Bradshaw) Blake, Rhodora (1928) 30:228. Wayside Aster.

(Phenetic group VIAL, page 108).

SYNONYMIES

BASIONYM: *Eucephalus vialis* Bradshaw, Torreya (1921) 20:122. [Isotype at US (984315) (not seen): Bradshaw, 1944. Rocky hillsides, Willamette Valley, Ore.] OTHER SYNONYMY: *Seriocarpus sipei* Henderson: Madroño (1933) 2:105. [Holotype at ORE (120451) (have seen isotype): Henderson, L. F., 15708. Ten miles from Eugene, Oregon.]

Habit: *Height*: 77 - 118 cm. *Branching*: 9 - 29 branches on main stem. *Internode length in middle of main stem*: 1.2 - 2.1 cm. *Leaf density at middle of main stem*: 5 - 9 leaves in 8 cm.

Chromosome number: unknown. **Flowering time:** July.

Leaves: *Shape*: lanceolate - elliptic. *Middle leaf*: 5.7 - 8.6 cm. long by 1.6 - 2.9 cm. wide. *Uppermost leaf*: 2.4 - 5.2 cm. long by 0.5 - 1.2 cm. wide. *Middle leaf tip*: mucronate (rarely acuminate). *Uppermost leaf tip*: mucronate (occasionally acute, caudate or acuminate). *Leaf edge*: entire and ciliated; occasionally with a few teeth.

Vesture: *Leaf upper surface*: sparsely covered with either only glandular trichomes (rarely with mix of glandular and non-glandular). *Leaf under surface*: sparsely or moderately covered with mix of non-glandular and glandular trichomes (rarely only non-glandular). *Stem*: sparsely or moderately covered with mix of non-glandular and glandular trichomes. *Involucre*: moderately (rarely sparsely) covered with only glandular trichomes (rarely mix of glandular and non-glandular).

Number of heads: 5 - 134. **Peduncle**: 1 - 4 bracts.

Involucre: *Imbrication*: 2, 3 or 4 rows. *Phyllary length*: 0.7 - 0.8 cm. *Width of pressed involucre*: 0.7 - 1.9 cm.

Phyllaries: *Phyllary tip*: acute. *Colour*: white central stripe, occasionally with red on tips and edges but never red on keels.

Disk florets: *Achene*: 0.22 - 0.50 cm. long by 0.07 - 0.10 cm. wide. *Pappus length*: 0.63 - 1.00 cm. *Floret tube length*: 0.51 - 0.80 cm. *Floret lobe length*: 0.10 - 0.20 cm.

Ray florets: *Number of ray florets*: 0.

Distribution and ecology: Lane and Douglas counties, Oregon, and Siskiyou and Humboldt counties, California (**Figure 36**). I assigned two herbarium specimens from California to *A. vialis* (one in Humboldt county, collected in 1919 by J. P. Tracy, 5304 (at UC (205151)) and the other in Siskiyou county, collected in 1964 by R. Waring, 567 (at OSC (119648)). Plants were collected from open dry woods, either in shade or sun. *Elevation*: 200 - 1,800 m.

Aster wasatchensis (Jones) Blake var. *grandifolius* Zamluk *var. nov.* Big leafed Markagunt Aster. (Phenetic group MIXWSA, page 109).

[Holotype at RM (152451), isotype at UTC (21233) (have seen): Maguire & Richards, 15731. Cedar Canyon, Iron Co., Utah. August 5, 1934.]

Habit: *Height*: 30 - 78 cm. *Branching*: 3- 16 branches on main stem. *Internode length in middle of main stem*: 1.9 - 3.0 cm. *Leaf density at middle of main stem*: 3 - 4 leaves in 8 cm.

Chromosome number: $n = 9$.

Chromosome count from herbarium label (Semple, J. and J. Chmielewski, 8890); collected in San Pete county, Utah. **Flowering time:** middle July to late August.

Leaves: *Middle leaf*: 6.2 - 9.2 cm. long by 1.3 - 2.4 cm. wide. *Uppermost leaf*: 2.1 - 4.1 cm. long by 0.6 - 1.0 cm. wide. *Middle leaf tip*: mucronate (occasionally acuminate). *Uppermost leaf tip*: mucronate (occasionally caudate, acute or cuspidate). *Leaf edge*: entire and ciliated.

Vesture: *Leaf upper surface*: sparsely (occasionally moderately) covered with only glandular trichomes. *Leaf under surface*: sparsely covered with glandular trichomes. *Stem*: densely (rarely sparsely or densely) covered with mix of glandular and non-glandular trichomes (occasionally only glandular trichomes). Rarely without trichomes. *Involucre*: densely (rarely sparely or moderately) covered with glandular trichomes. *Peduncle*: densely covered with tipped glandular trichomes.

Number of heads: 4 - 40. **Peduncle**: 1 - 3 bracts.

Involucre: *Imbrication*: 2 or 3 rows. *Phyllary length*: 0.7 - 1.0 cm. *Width of pressed involucre*: 0.6 - 1.2 cm.

Phyllaries: *Phyllary tip*: obtuse (rarely acute, mucronate or acuminate). *Colour*: white central stripe; with red on tips and edges together or without red on tips and edges together, but never red on keels.

Disk florets: *Achene*: 0.20 - 0.30 cm. long by 0.03 - 0.09 cm. wide. *Pappus length*: 0.59 - 0.79 cm. *Floret tube length*: 0.48 - 0.72 cm. *Floret lobe length*: 0.07 - 0.12 cm.
Ray florets: *Number of ray florets*: 8 - 14. *Colour*: white or pink. *Achene*: 0.16 - 0.31 cm. long by 0.06 - 0.07 cm. wide. *Pappus length*: 0.50 - .72 cm. *Floret tube length*: 0.30 - 0.42 cm. *Floret limb length*: 1.0 - 1.9 cm.
Distribution and ecology: Utah and Wyoming (**Figure 37**). Plants were collected in pine, aspen-fir, and spruce woods. They were on rocky steep slopes and by stream sides. *Elevation*: 2,250 - 2,850 m.

Aster wasatchensis (Jones) Blake var. *wasatchensis*, Contrib. U. S. Nat. Herb. (1925) 25:526. Markagunt Aster. (Phenetic group WASA, page 109).

SYNONYMIES

BASIONYM: *Aster glaucus* var. *wasatchensis* Jones, (1895) Proc. Calif. Acad. 2,5:694. [Holotype at BRY and RM (have seen); isosyntype at US (236650): M. E. Jones 5861. Tate Mine, near Marysvale, Piute Co., Utah. August 22, 1894.]
OTHER SYNONYMIES: *Eucephalus wasatchensis* (Jones) Rydb., Fl. Rocky Mnts. (1917): 878. *Eurybia wasatchensis* (Jones) Nesom, Phytologia (1994) 77(3): 262.

Habit: *Height*: 24 - 43 cm. *Branching*: 1 - 11 branches on main stem. *Internode length in middle of main stem*: 0.9 - 1.8 cm. *Leaf density at middle of main stem*: 4 - 9 leaves in 8 cm.
Chromosome number: unknown. **Flowering time:** early July to late August.
Leaves: *Shape*: linear to slightly lanceolate. *Colour*: blue-green. *Middle leaf*: 3.8 - 8.1 cm. long by 0.9 - 1.4 cm. wide. *Uppermost leaf*: 1.3 - 2.2 cm. long by 0.3 - 0.7 cm. wide. *Middle leaf tip*: mucronate (occasionally acute). *Uppermost leaf tip*: mucronate (occasionally acuminate or cuspidate). *Leaf edge*: entire and ciliated.
Vesture: *Leaf upper surface*: moderately or sparsely covered with only glandular trichomes (rarely mix of glandular and non-glandular). *Leaf under surface*: moderately (rarely sparsely) covered with only glandular trichomes (occasionally a mix of glandular

and non-glandular). *Stem*: densely (rarely moderately or rarely sparsely) covered with only glandular trichomes (occasionally with mix of glandular and non-glandular). *Involucre*: densely (rarely moderately) covered with only glandular trichomes. *Peduncle*: moderately to densely covered with glandular trichomes.

Number of heads: 2 - 12. **Peduncle**: 0 - 2 bracts.

Involucre: *Imbrication*: 2 or 3 rows. *Phyllary length*: 0.8 - 1.0 cm. *Width of pressed involucre*: 0.8 - 1.6 cm.

Phyllaries: *Phyllary tip*: acute. *Colour*: white central stripe; no red.

Disk florets: *Achene*: 0.17 - 0.26 cm. long by 0.04 - 0.05 cm. wide. *Pappus length*: 0.74 - 0.88 cm. *Floret tube length*: 0.50 - 0.62 cm. *Floret lobe length*: 0.09 - 0.13 cm.

Ray florets: *Number of ray florets*: 10 - 18. *Colour*: white or pink. *Achene*: 0.16 - 0.26 cm. long by 0.03 - 0.07 cm. wide. *Pappus length*: 0.61 - .073 cm. *Floret tube length*: 0.26 - 0.24 cm. *Floret limb length*: 0.7 - 1.2 cm.

Distribution and ecology: Coconino, Arizona, and Utah (**Figure 38**). Plants were collected from aspen, and juniper communities. Soils were sandy loam, gravelly, clay, and degraded limestone. *Elevation*: 2,000 - 3,200 m.

DISTRIBUTION MAPS

North America

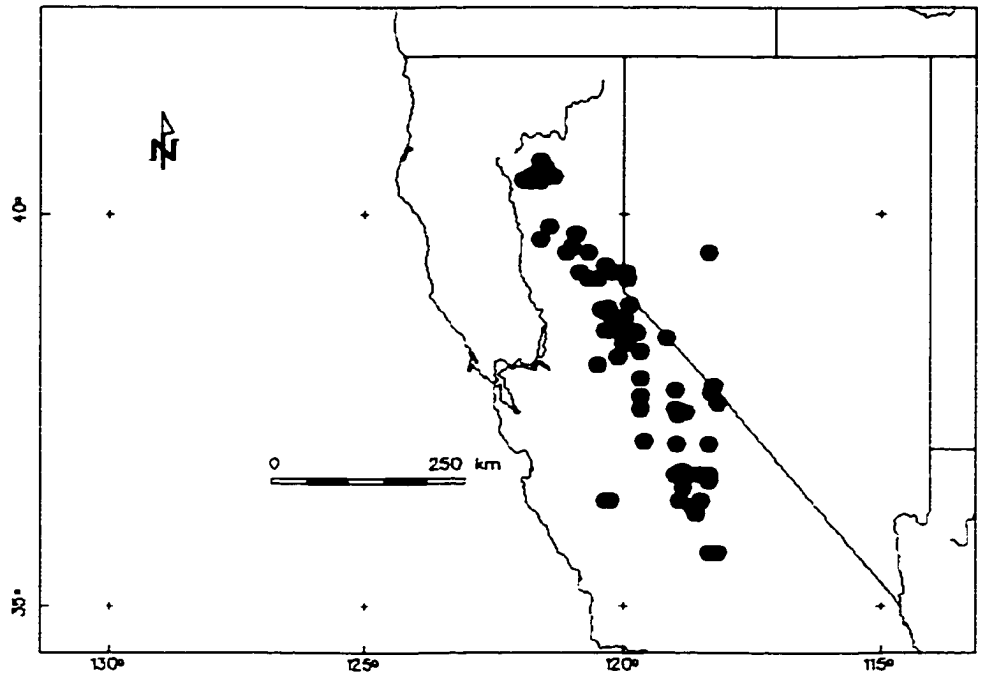


Figure 22: Distribution of *Aster breweri* (Gray) Semple var. *breweri*.

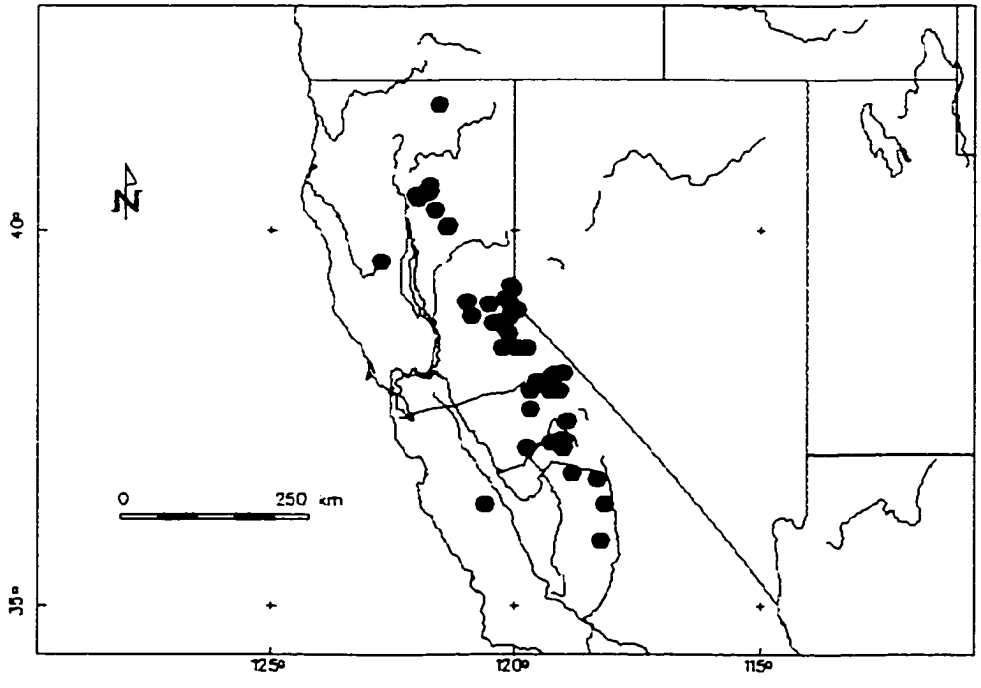


Figure 23: Distribution of *Aster breweri* (Gray) Semple var. *multibracteata* (Jepson) Zamluk *comb. nov.*

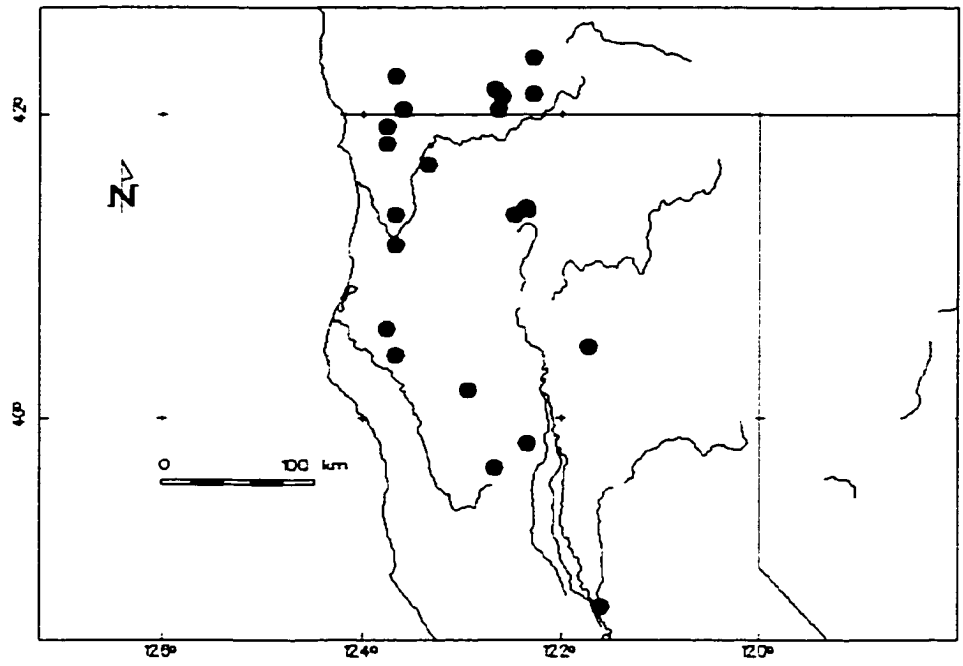


Figure 24: Distribution of *Aster brickellioides* (Greene) Greene.

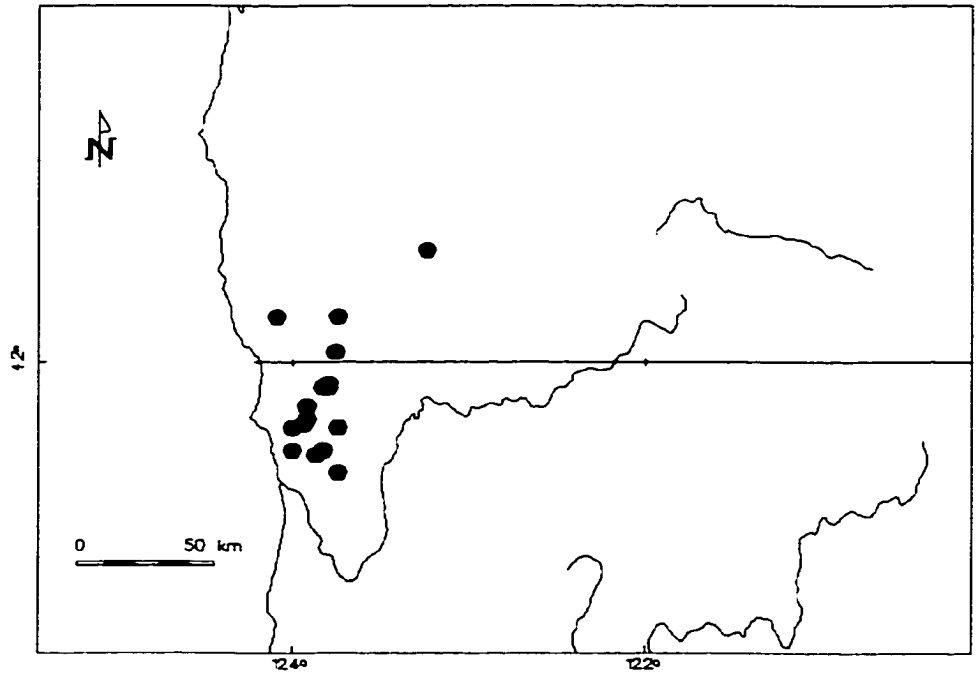


Figure 25: Distribution of *Aster eastwoodiae* Zamluk *comb. nov.*

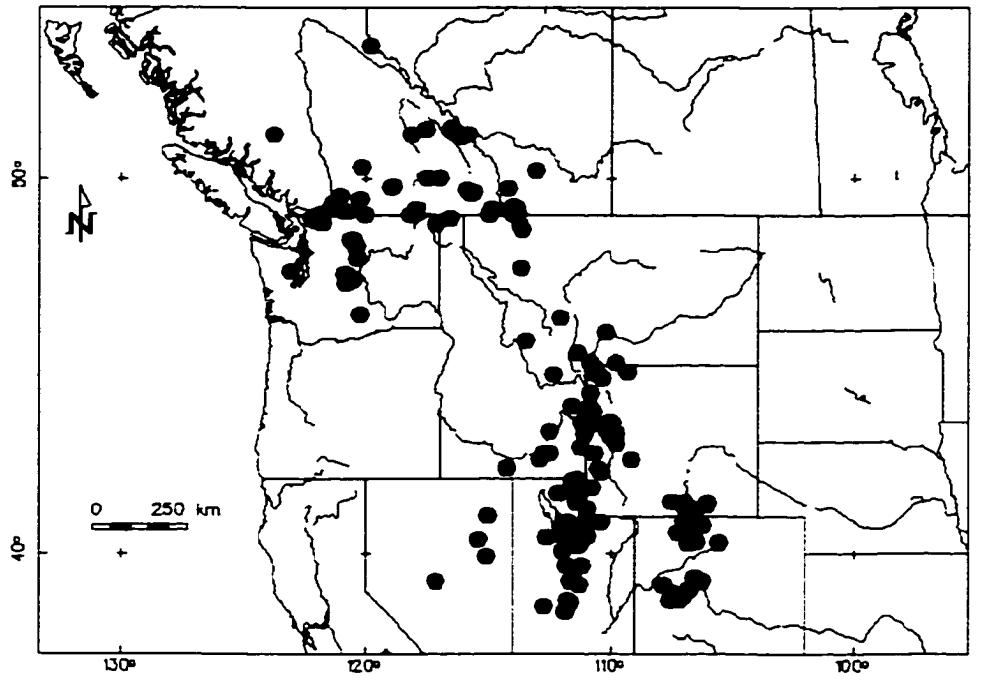


Figure 26: Distribution of *Aster engelmannii* Gray var. *engelmannii*.

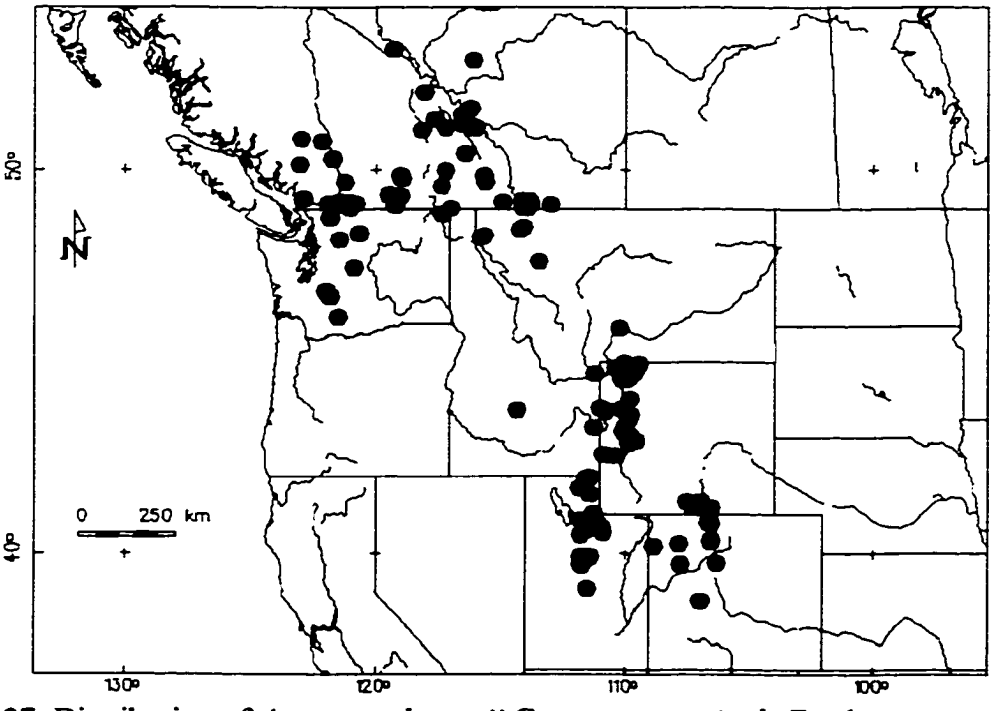


Figure 27: Distribution of *Aster engelmannii* Gray var. *monticola* Zaml. *var. nov.*

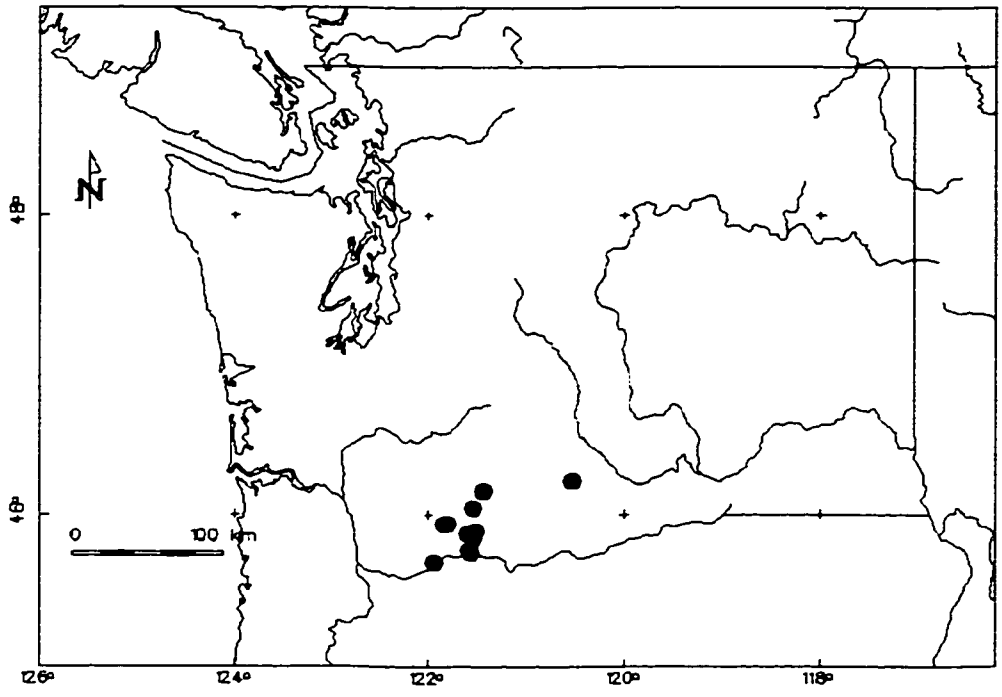


Figure 28: Distribution of *Aster glaucescens* (Gray) Blake.

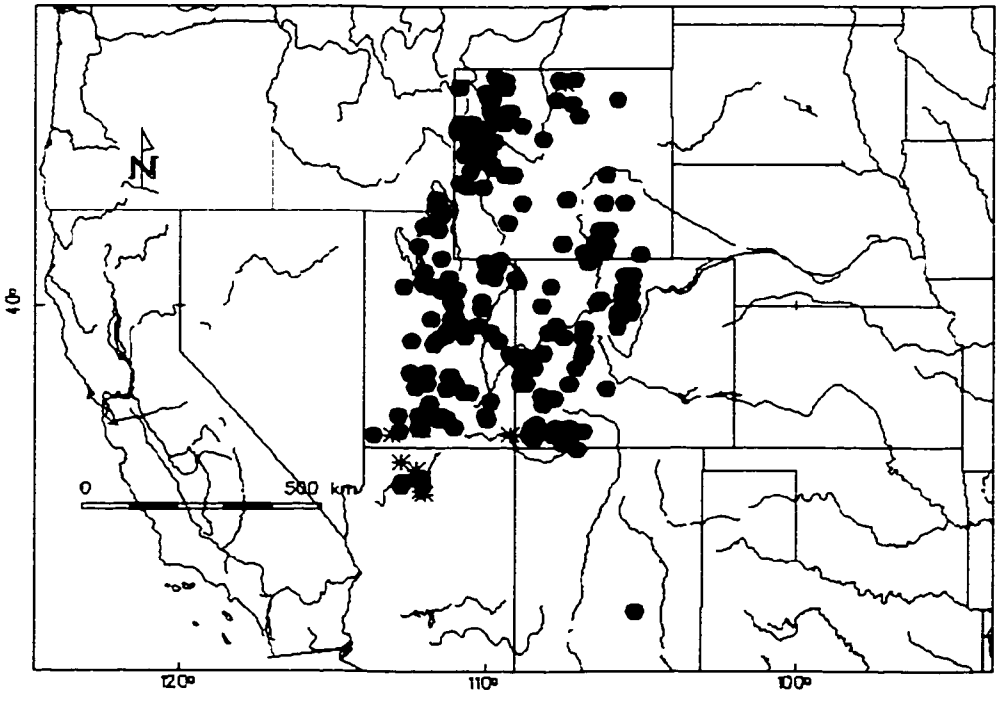


Figure 29: Distribution of *Aster glaucodes* Blake var. *glaucodes* (dots) and *Aster glaucodes* Blake var. *pulcher* (Blake) Kearney & Peebles (asterisks).

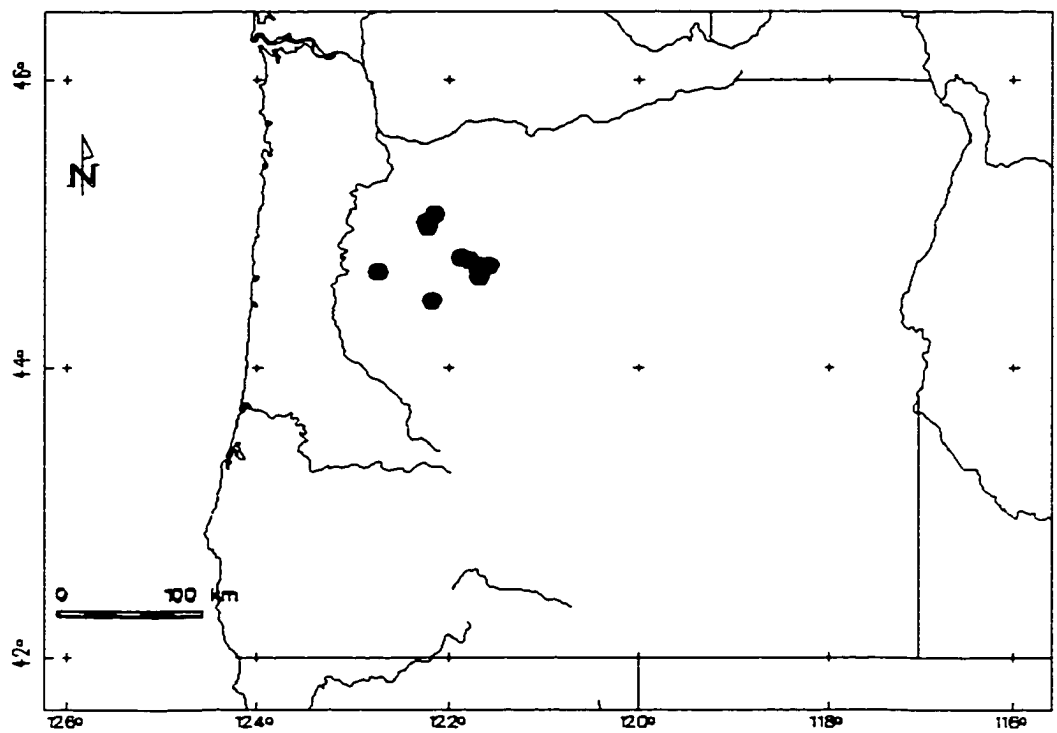


Figure 30: Distribution of *Aster gormanii* (Piper) Blake.

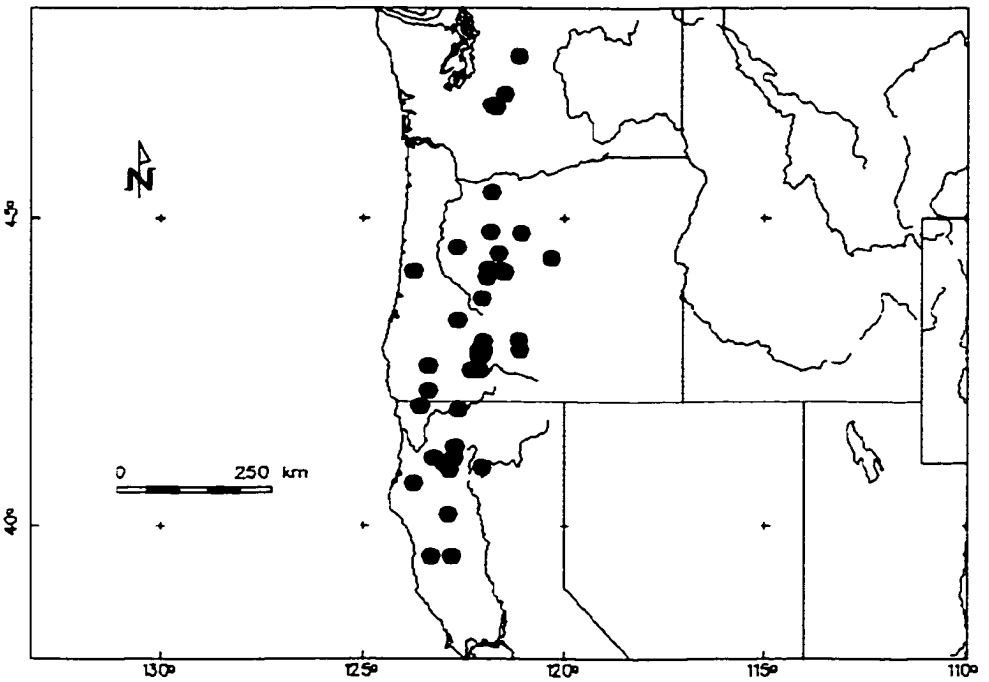


Figure 31: Distribution of *Aster ledophyllus* (Gray) Gray var. *covillei* (Greene) Cronq.

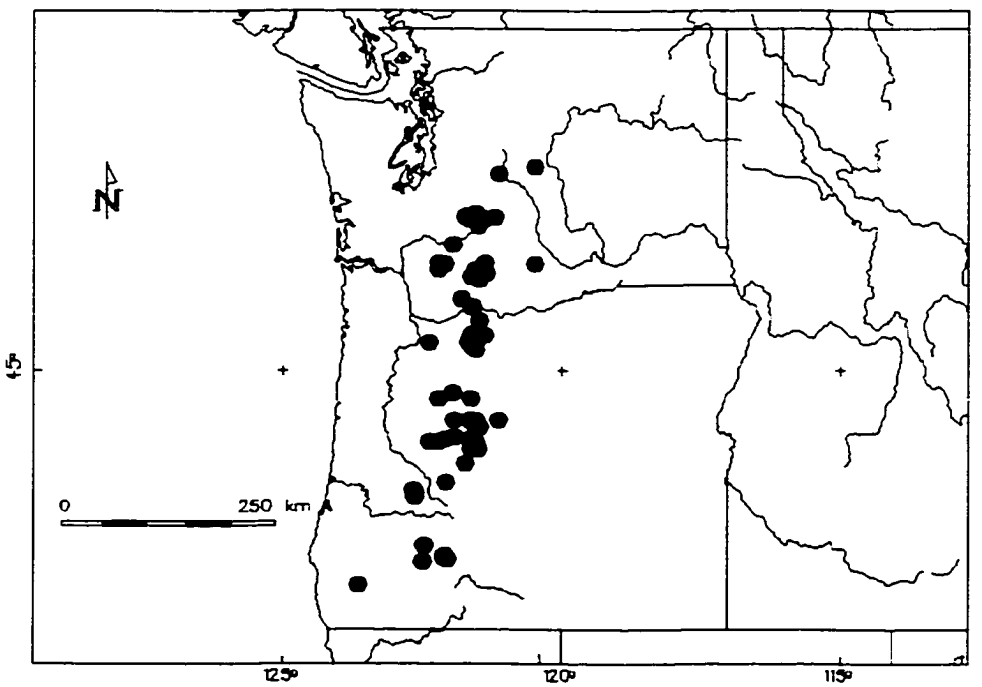


Figure 32: Distribution of *Aster ledophyllus* (Gray) Gray var. *ledophyllus*.

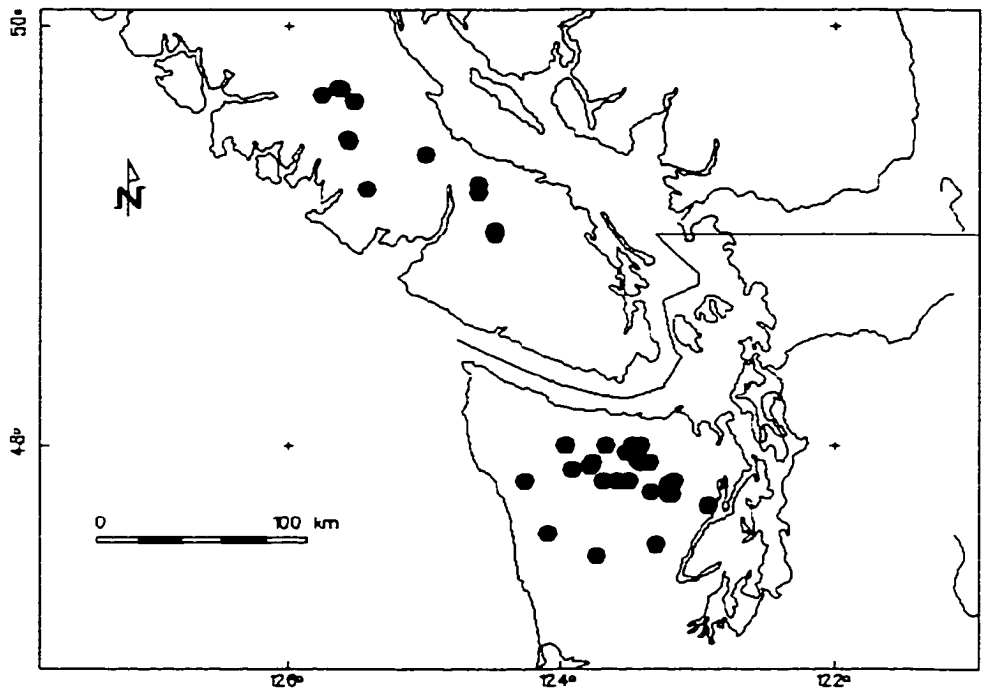


Figure 33: Distribution of *Aster paucicapitatus* (Robins.) Robins.

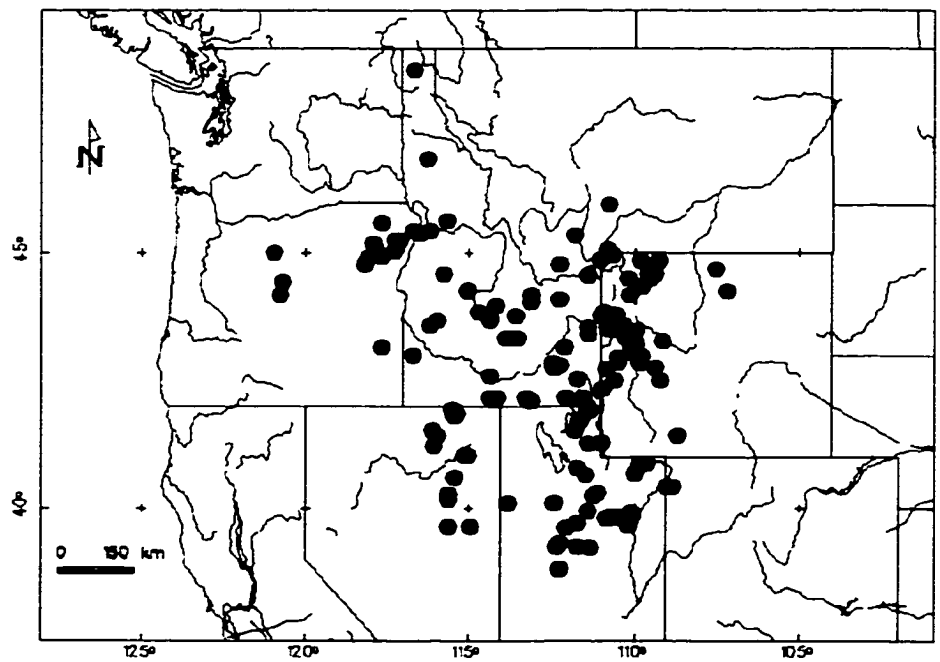


Figure 34: Distribution of *Aster perelegans* Nels. & Macbr.

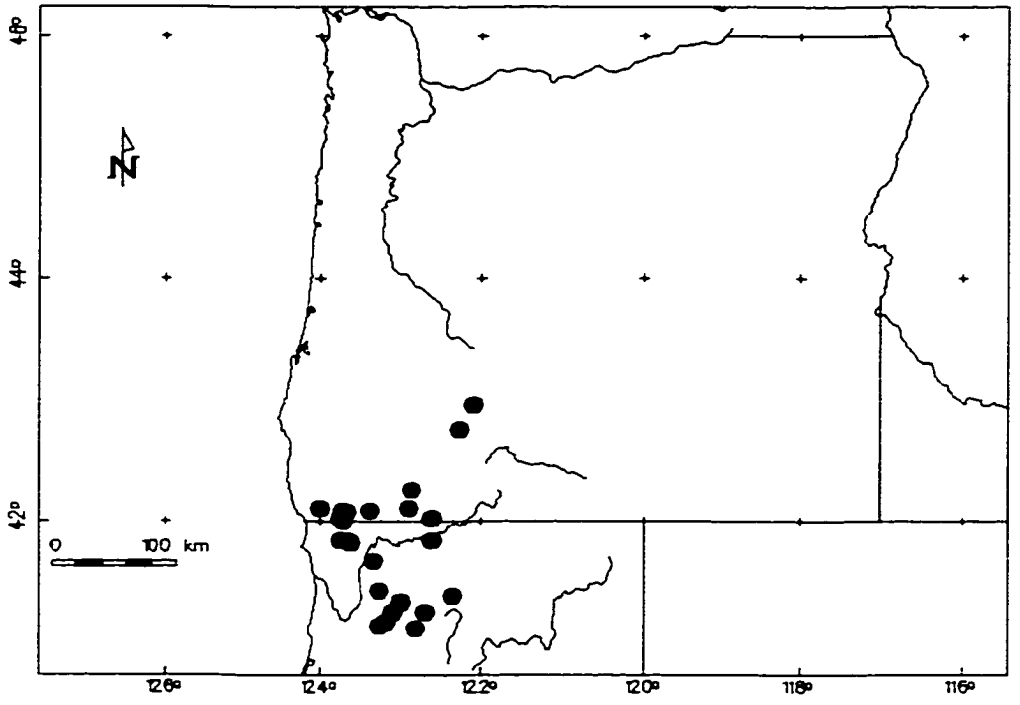


Figure 35: Distribution of *Aster siskiyouensis* Nels. & Macbr.

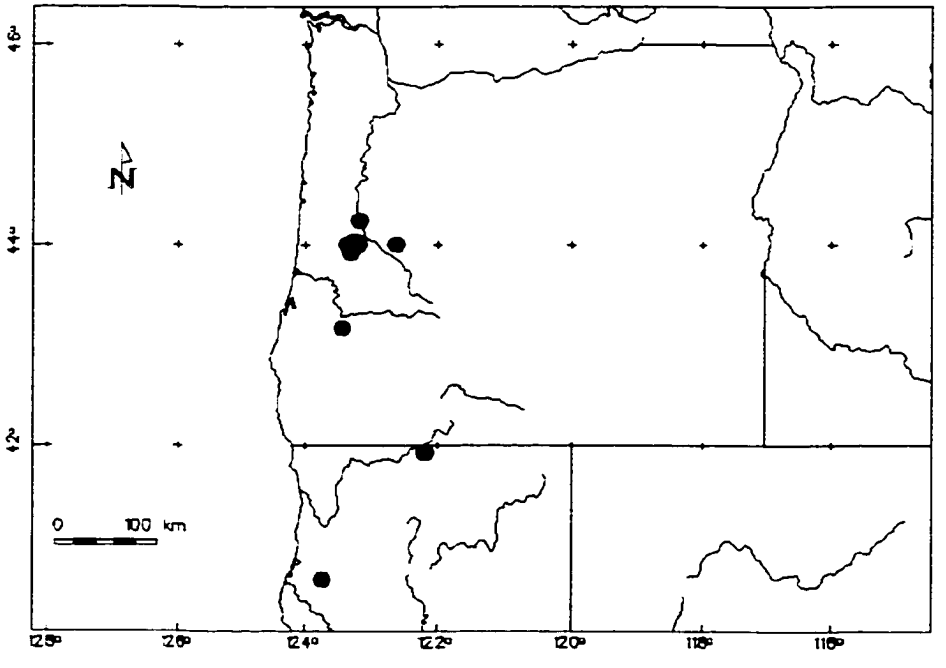


Figure 36: Distribution of *Aster vialis* (Bradshaw) Blake.

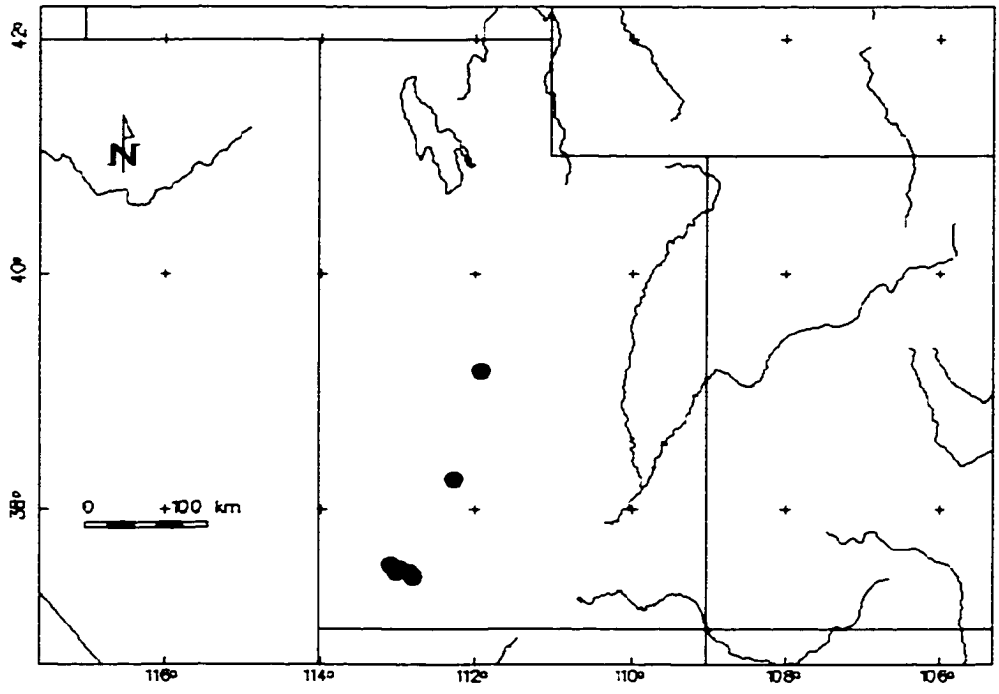


Figure 37: Distribution of *Aster wasatchensis* (Jones) Blake var. *grandifolius* Zamluk *var. nov.*

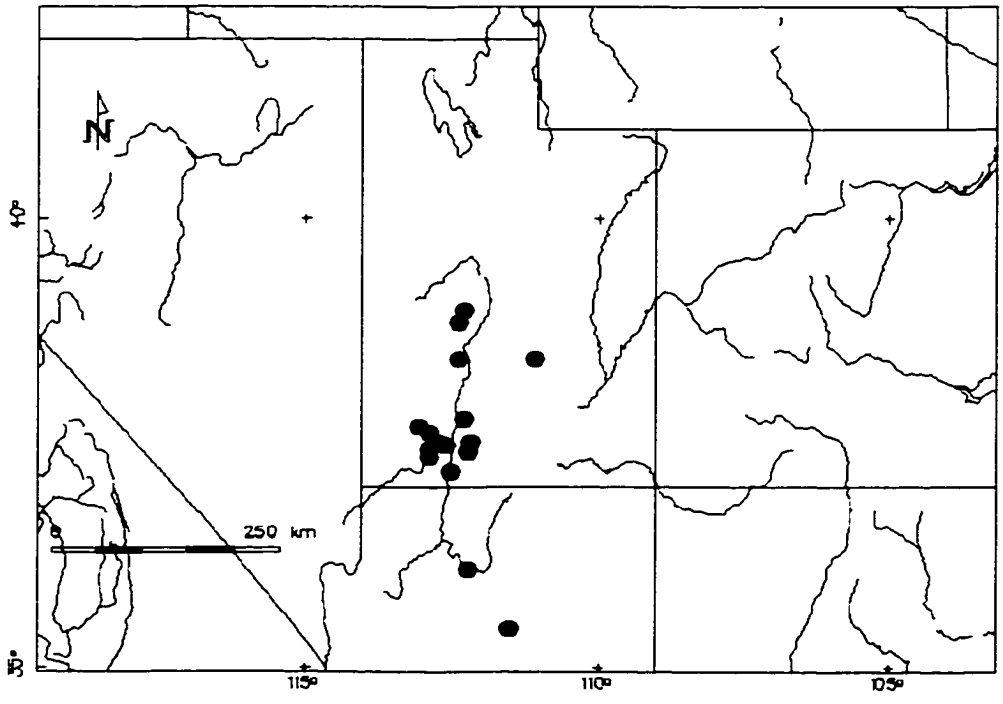


Figure 38: Distribution of *Aster wasatchensis* (Jones) Blake var. *wasatchensis*.

Taxa excluded from *Aster* section *Eucephalus*

Aster nemoralis Ait. Hort. Kew. (1789) 3: 198. Greene (1896-1898) suggested that *A. nemoralis* had affinities with *Eucephalus* based on leafy stems, reduced leaves on the lower stem, corymbose inflorescence and lack of radical leaves therefore he reassigned it to *Eucephalus nemoralis* (Ait.) Greene. The name *E. nemoralis* seems to have never been used since.

Aster turbinellus Lindl. Comp. Bot. Mag. (1835) 1: 98. Semple and Brouillet decided to include this taxon in section *Eucephalus* despite a base chromosome count of 8 (rather than 9) because of the phyllary characteristics. Jones (1980) completely removed it and *Aster glaucodes* from section *Eucephalus* by placing both into a new section *Turbinelli*. I do not consider *A. turbinellus* part of section *Eucephalus* and find subdividing the section unnecessary.

Eucephalus macounii Greene [Isotype at CAS (328): Macoun 447, near Victoria, B. C.] was later determined to be *Aster radulinus* Gray (Cronquist 1955).

Eucephalus ericoides Nutt. was placed in synonymy with *Aster ericoides* L. when *Eucephalus* was moved into *Aster*.

Eucephalus albus Nutt. was placed into *Aster ptarmicoides* (Nees.) T & G. Fl. N. A. (1841) 2:160.

V. BIOGEOGRAPHY

INTRODUCTION

The history of the geographic distribution of members of the tribe Astereae, especially those from North America, has recently been investigated through the cladistic analysis of chloroplast DNA (Xiang and Semple 1996) and ITS sequences (Noyes and Rieseberg 1999). Nesom (1994) and Jones (1980a) included minor discussions of biogeography and phylogeny in their revisions of the tribe. Noyes and Rieseberg (1999) have throughly reviewed the phylogenetic and biogeographic research published on members of Astereae. Interest has focussed on the origins of North American Astereae whether as migrants from Eurasia, Africa or South America, or evolving in place. Sequence data from many taxa are still not available, however some work has been done. Xiang and Semple (1996) found (from chloroplast restriction site data) that North American *Aster* taxa were closely related to Eurasian taxa, and originated in North America. Noyes and Rieseberg (1999) based their conclusions on results from less than 2% of the species in Astereae. They noted that the lower nodes of their cladograms were poorly resolved. Nonetheless, in contrast to Xiang and Semple (1996), they concluded (based on their cladistic analysis of ITS sequence data) that North American Astereae are more closely related to each other than to Eurasian and Southern hemisphere taxa. Their results suggested that the ancestral taxa may have been shrubs or trees, and originated from the Southern hemisphere. More information is obviously needed before these issues will be resolved. The North American segregates of *Aster* are inferred to have evolved in North America (Xiang and Semple 1996).

The current distribution of species of *Aster* section *Eucephalus* has presumably changed over time as a result of environmental and speciation events. The Pleistocene Epoch, and the current interglacial have been the most important factors in the current distribution because of associated climate changes south of the 49th parallel and movement of continental ice across British Columbia and Alberta (Pielou 1979). The current interglacial period was estimated to begin about 10,000 years ago (Pielou 1979). Most of Canada is still undergoing the process of recolonization.

By applying the phylogenetic hypothesis developed in the Cladistics chapter, a hypothesis of range expansion and contraction can be inferred. Areas of high species richness or with rare taxa are of particular interest because they can be protected by law and their biodiversity preserved.

MATERIALS AND METHODS

Over sixteen hundred specimens were examined and assigned taxon names using the key and taxon descriptions presented in the Taxonomy chapter. The relationship between the cladogram and the extant distributions of the taxa were illustrated by combining the distributions of the taxa with the preferred cladogram. The taxon distributions were smoothed by me into simple shapes which may enclose areas that currently do not actually contain any specimens, and cannot be substituted for the actual distributions presented in the Taxonomy chapter.

RESULTS

When I used simplified shapes to outline the extant distribution of a taxon, I did not expect to gain any insight into the possible migration patterns of the taxa but the shape did seem to be instructive because several of the endemic taxa could be enclosed in a circle (*Aster gormanii*, *A. eastwoodiae* and *A. glaucescens*) whereas all other taxon distributions were best simplified into ovals or rectangles (**Figure 39 - Figure 43**).

Map 1 (**Figure 39**) shows the hypothesised relationship among *Aster wasatchensis*, the two *A. breweri* varieties, and the sister group of *A. gormanii* and *A. paucicapitatus*. This relationship is consistent with a simple migration from Utah westward into California, then northward. Alternately, *A. wasatchensis* and *A. breweri* could be descendants of a more widespread taxon covering an area from the Californian coast to the southern Rockies, *A. wasatchensis* differentiating in the eastern portions of the ancestor's range and *A. breweri* to the west. *Aster gormanii* and *A. paucicapitatus* would then be established by populations migrating northward. Establishing the time of speciation is difficult, but the morphologically indistinguishable populations of *A. paucicapitatus* on the

Olympic Mountains and on Vancouver Island must have resulted from recolonization since both areas are presumed to have been covered by glaciers. *Aster paucicapitatus* could have evolved in a southern part of North America, perhaps from populations of *A. gormanii*, before or during the last glacial period, or may have differentiated in the north before populations migrated south as the climate cooled.

Map 2 (**Figure 40**) might reflect either a shift southward of already differentiated *Aster paucicapitatus* and *A. gormanii*, or speciation of some *A. breweri* populations. Eventually, both varieties of *A. ledophyllus*, and *A. brickellioides* could arise from these populations. An alternative possibly is descent from a common ancestor from which two lines developed: one leading to *A. ledophyllus* and *A. brickellioides*; the other to *A. glaucodes*.

Map 3 (**Figure 41**) could be seen in three ways:

1. *A. ledophyllus* var. *ledophyllus* could be the source for *A. glaucodes* through a south-east migration followed by a new north-west migration leading to *A. eastwoodiae* and *A. siskiyouensis*;
2. *A. ledophyllus var. ledophyllus* could be the original source for *A. glaucodes* through a south-east migration as well as *A. eastwoodiae* and *A. siskiyouensis* by a migration southward.
3. *Aster glaucodes* and *A. ledophyllus* might be vicariant species derived from a widely distributed taxon that had undergone range contraction due to climate changes, and had left behind widely separated populations. Populations left in Arizona or Utah would have established *A. glaucodes*. The other populations might have evolved into *A. ledophyllus*, which then split into two lines of descent, one producing *A. siskiyouensis* and *A. eastwoodiae* while the other gave rise to *A. ledophyllus* var. *covillei* and *A. brickellioides*.

My preference is for option 3 because it does not rely on migrations, and encompasses the influence of climate change.

Map 4 (**Figure 42**) suggests, because of the proximity of the extant taxa, that speciation events leading to *A. glaucescens* and *A. perelegans* may have occurred among

populations of a widespread species derived from, or ancestral to *A. ledophyllus* var. *covillei* and *A. brickellioides*. *Aster glaucescens* could evolved in place from populations of *A. perelegans*.

Map 5 (**Figure 43**) cannot be easily explained as a pattern of migration, since the phylogenetic hypothesis requires *A. glaucescens* to be the ancestral source for both varieties of *A. engelmannii*, *A. wasatchensis* var. *grandifolius*, and *A. vialis*. In order for this to happen, populations of *A. glaucescens*, or the ancestral taxon, would have had to migrate south and east, undergone speciation into *A. engelmannii* and *A. wasatchensis* var. *grandifolius* which then would have spread in all directions. *Aster glaucescens* may have good dispersal capabilities but its current distribution does not provide supporting evidence. A less complicated proposal would be that an ancestral taxon eventually produced *Aster perelegans*, *A. engelmannii*, *A. vialis* and *A. wasatchensis* var. *grandifolius*. *Aster wasatchensis* var. *grandifolius* may be a hybrid between *A. engelmannii* and *A. wasatchensis*, and, if so, could be eliminated from the hypothesis. *Aster vialis* might be result from isolated populations of *A. engelmannii* var. *monticola*. The possibility that the two varieties of *A. engelmannii* were caused by glaciation which later rejoined is an interesting idea that may merit further investigation.

If the ancestor of *Aster* section *Eucephalus* is presumed to have arrived from Mexico (Noyes and Rieseberg 1999), the hypothesis of an original widespread taxon that undergoes vicariance in different parts of its range becomes more reasonable since it simplifies the migration patterns (**Figure 44**). The restriction of *Aster* section *Eucephalus* to the western part of the North American continent can be then explained by an origin in Mexico, combined with unfavourable climatic conditions or competition in the prairie regions that have prevented an eastward spread. Repetitive range expansion and contraction with associated speciation explains much of the current distributions in the non-glaciated regions, and complete eradication followed by recolonization explains the distributions north of the 49th parallel.

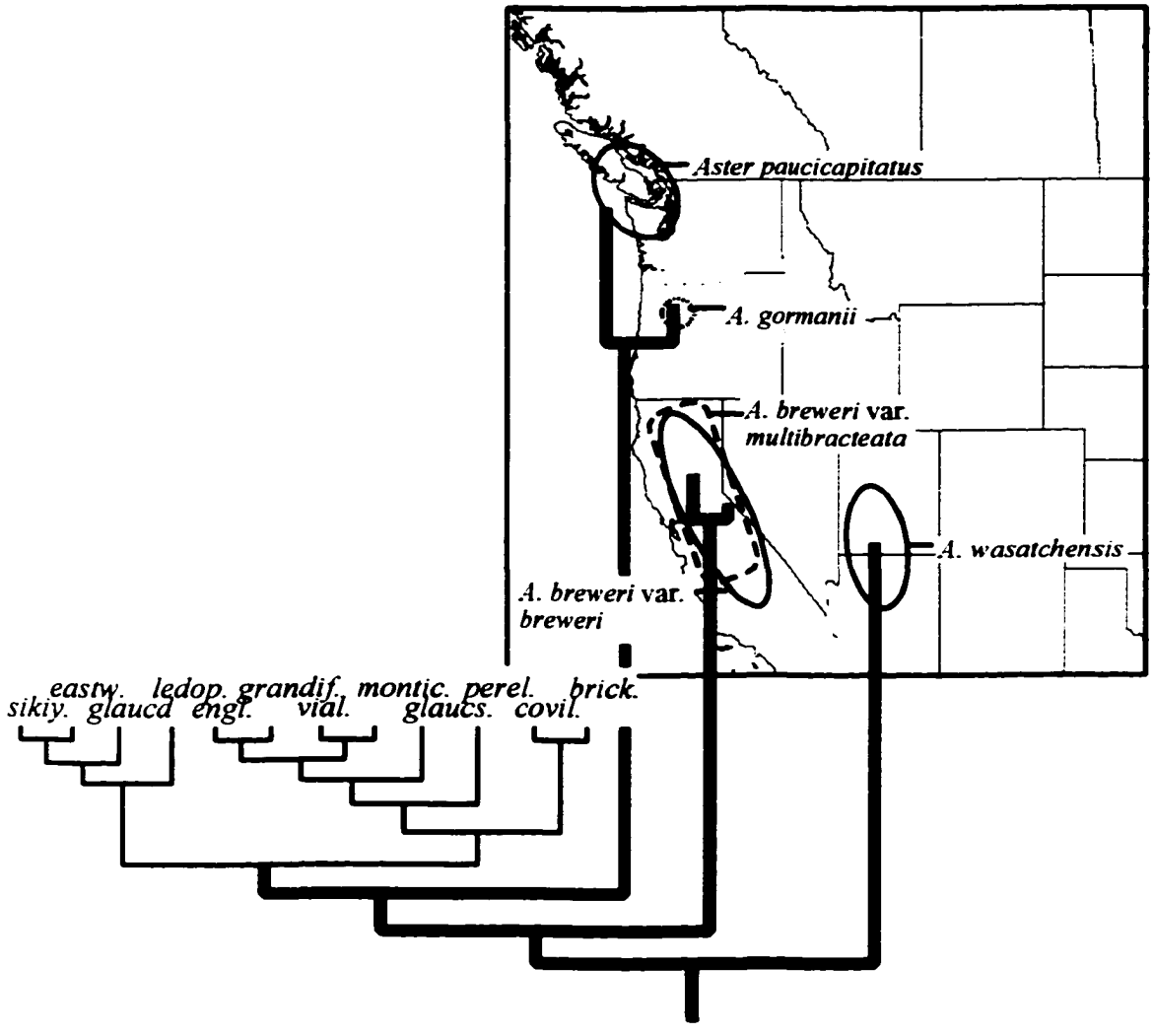


Figure 39: Map illustrating the hypothesised relationships among taxa near the cladogram base.

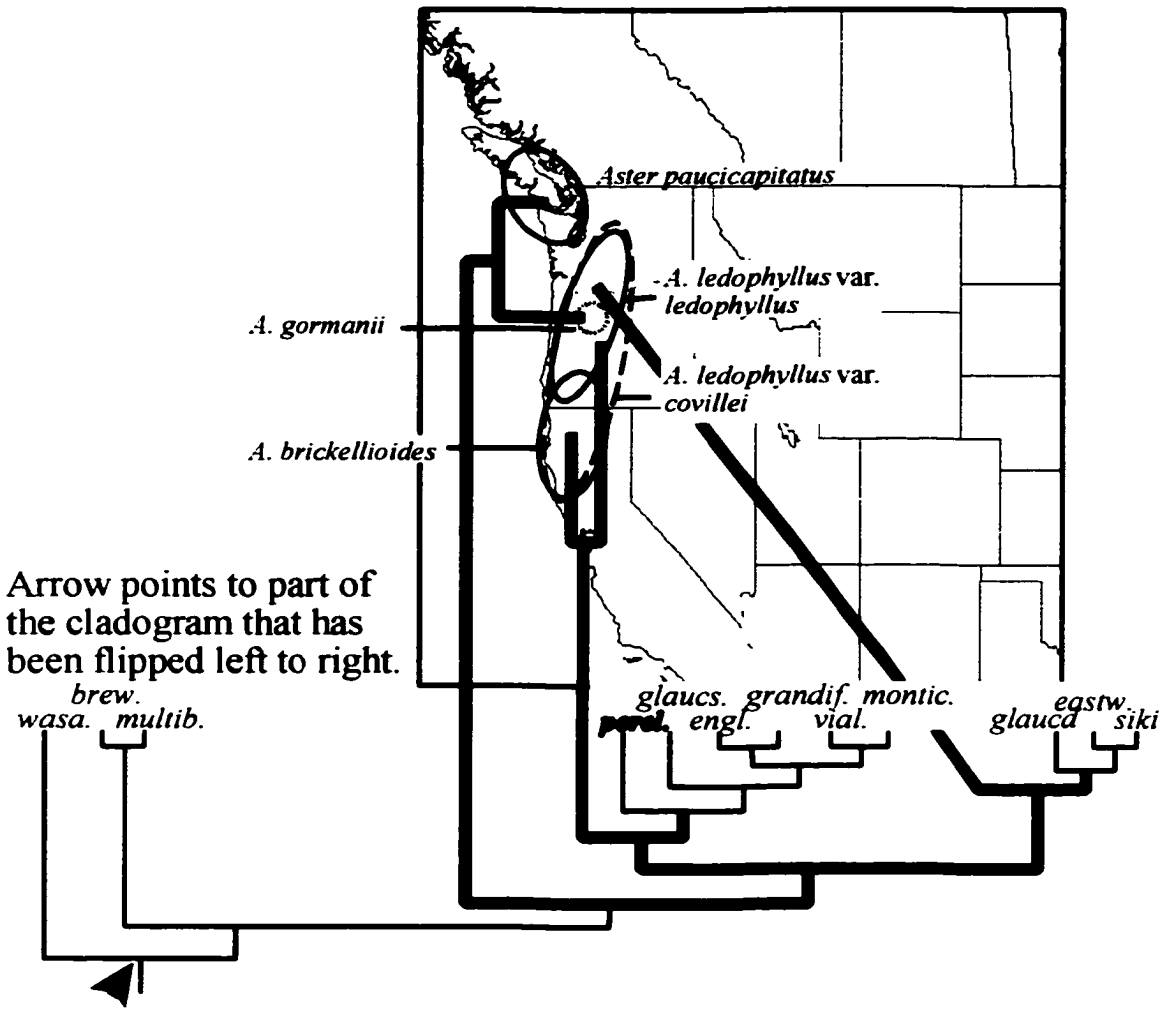


Figure 40: Map illustrating the hypothesised relationships among taxa found in the Coastal mountains.

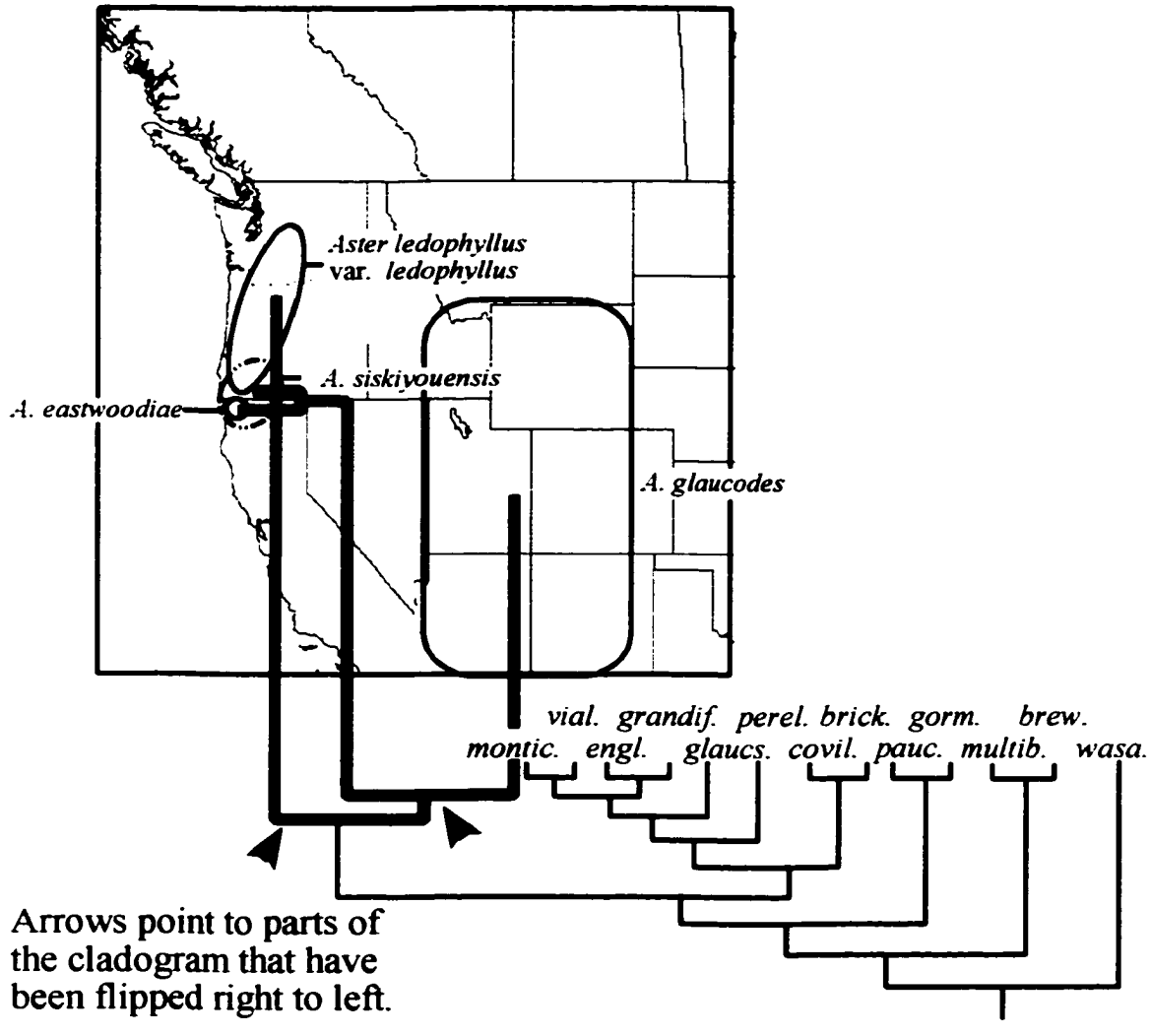


Figure 41: Map illustrating the hypothesised relationships among some taxa of the Coastal mountains and *Aster glaucodes*.

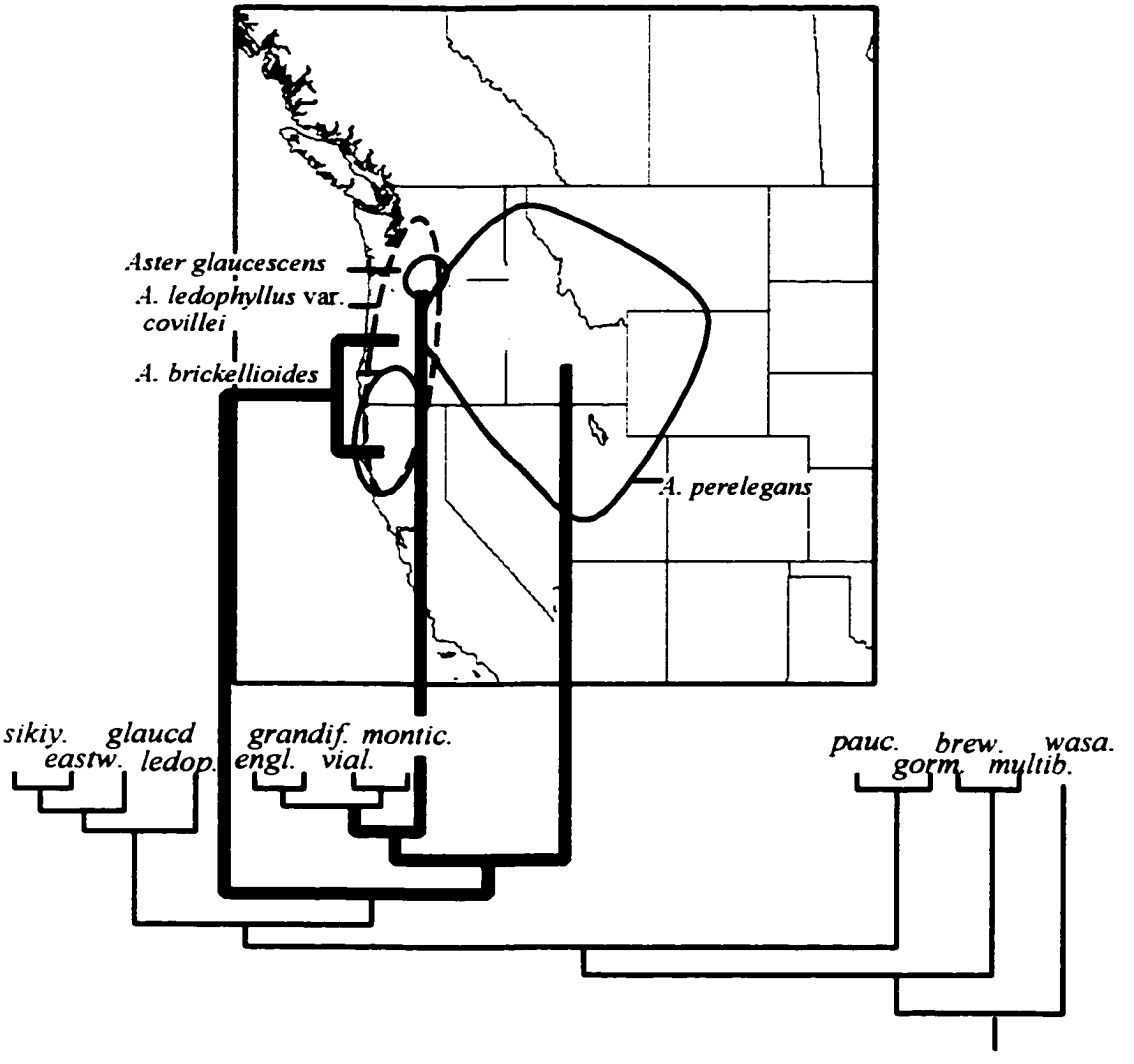


Figure 42: Map illustrating the hypothesised relationships among some taxa of the Coastal mountains and *Aster perelegans*.

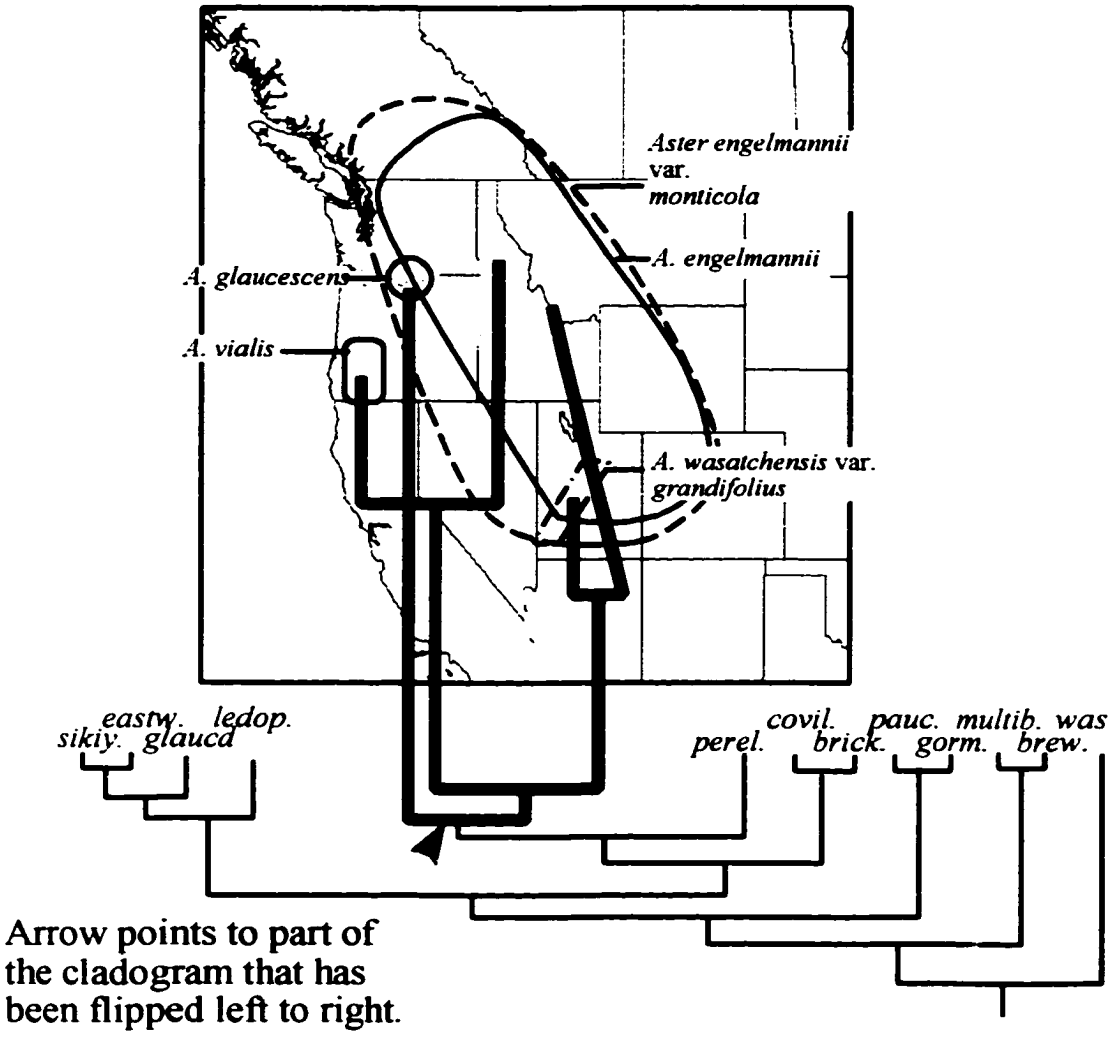


Figure 43: Map illustrating the hypothesised relationships among *Aster engelmannii*, *A. vialis* and *A. wasatchensis* var. *grandifolius*.

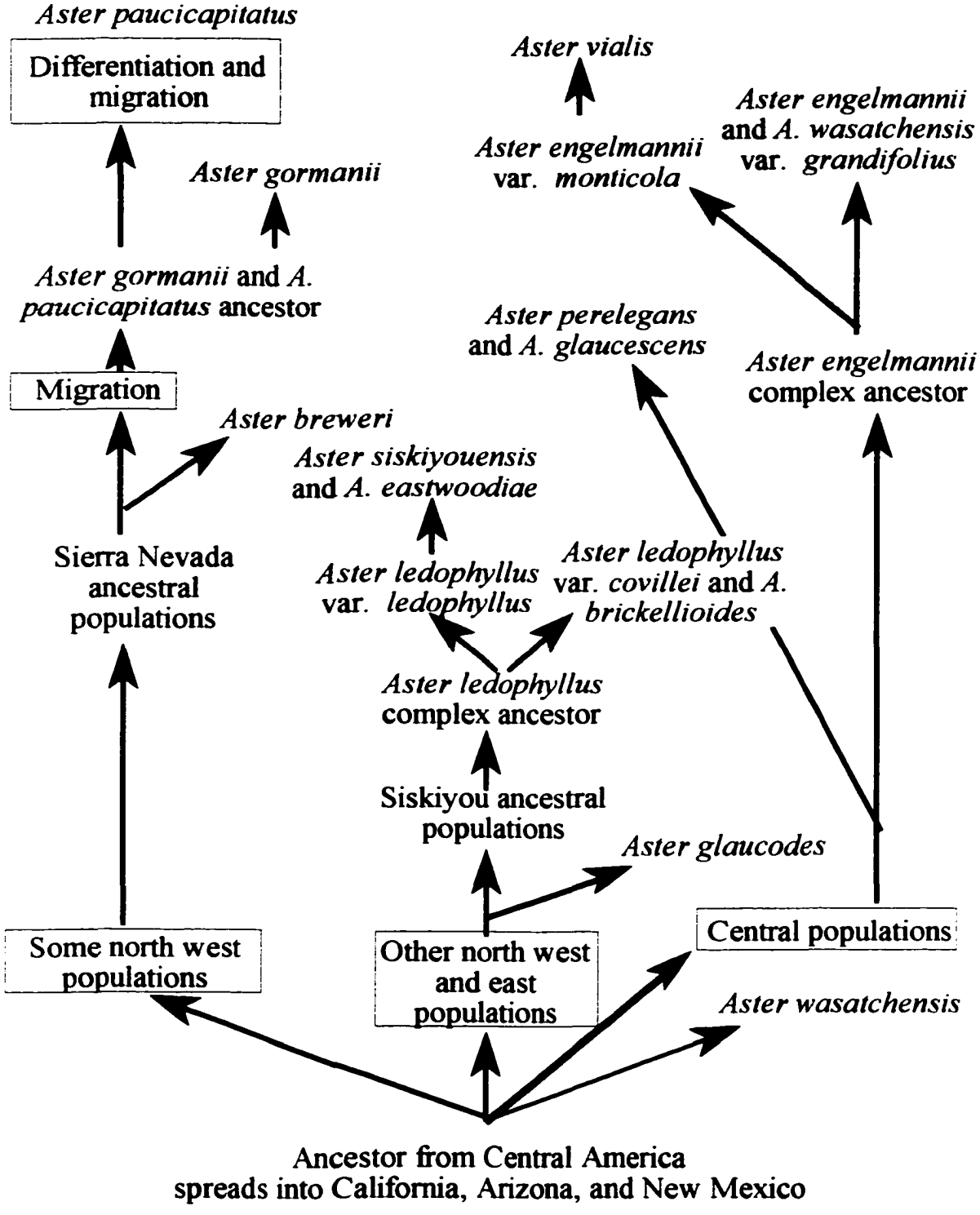


Figure 44: Summary of biogeographic hypothesis derived from the phylogenetic hypothesis and extant distributions of *Aster* section *Eucephalus*.

DISCUSSION AND CONCLUSIONS

According to vicariance biogeography theory, climatic or other barriers lead to the breakup of an ancestral species into isolated groups which are then likely to adapt differently to different kinds of new conditions. This could result in some groups of the ancestral species persisting in their original form while other groups diverged to give rise to new species. Those groups unable to adapt to changed conditions would go extinct, possibly creating gaps between related taxa. Distribution of species would alter with conditions as progeny migrated, expanding the range, or as populations disappeared, causing a decrease.

A clue to whether a taxon is expanding or contracting its range might be found in the simplified shapes applied to the current distributions of taxa. *Aster siskiyouensis*, *A. eastwoodiae*, *A. gormanii*, and *A. glaucescens* distributions could be enclosed in a circle which may be an indication that the current populations are still expanding into nearby suitable habitats, but it could reflect the distribution of favourable habitats. Support for the idea comes from *Aster siskiyouensis* and *A. eastwoodiae*, which, according to the phylogenetic hypothesis of the Cladistics chapter, are two of the most recently derived taxa. On the other hand, *A. gormanii* (a much older taxon than *A. siskiyouensis* and *A. eastwoodiae*) refutes the idea unless a common ancestral species to *A. gormanii* and *A. paucicapitatus* is presumed. Both sister taxa then could be considered recently evolved, and *A. gormanii* range could be expected to increase. *Aster glaucescens* could also have the potential to expand its range, whether as a recovery from a drastic range contraction, or because it was derived from a population of a widespread species.

Ellipses and rectangles might reflect migrations north and south, and could indicate taxa successful in adapting to climatic changes caused by glaciation. *Aster perelegans* distribution was simplified into a lopsided rectangle which might point to either range contraction, or migration through a narrow favourable region into an area with many suitable habitats. It is the only taxon with a range that extends directly eastward from Oregon to the American Rocky Mountains.

Influence of geographical distributions on phylogenetic hypothesis

Cladistic analysis is a useful tool but has clear limitations, related to the necessity of simplifying data and the mechanics of creating trees. Cladograms cannot represent a widespread species that may undergo several vicariance events at different times because of the assumption that a species may give rise to only two descendant species. Presuming a widespread ancestral species simplifies the hypothesis of descent, especially when the geographic distributions are considered. If the least complicated theory is preferred then modifications to the phylogenetic hypothesis are acceptable.

Assuming a widespread ancestral taxon that leads to four different lineages simplifies the phylogenetic hypothesis. The four postulated lineages are:

1. *Aster wasatchensis*, probably the oldest taxon, a palaeoendemic;
2. the "Sierra Nevada ancestral populations" leading to *A. breweri*, *A. gormanii* and *A. paucicapitatus*. Perhaps, with the cooling and drying caused by glaciation, the southern populations of *A. breweri* were restricted to warmer conditions, and the northern populations were able to adapt, eventually giving rise to *A. gormanii* and *A. paucicapitatus*;
3. a lineage leading to the "Siskiyou ancestral populations" and to *Aster glaucodes*. *Aster glaucodes* is a widespread taxon found in the hot and dry south western states, and has developed some morphological diversity (taxonomists have recognized three varieties) suggesting that it evolved early in the history of the group. The "Siskiyou ancestral populations" hypothesized to have lead to an ancestral taxon may still be extant as the two varieties of *A. ledophyllus*. *Aster ledophyllus* var. *covillei* and *A. brickellioides* were found to be sister groups, and share many morphological characteristics. *Aster ledophyllus* var. *ledophyllus* was hypothesized to be an ancestor to *A. siskiyouensis* and *A. eastwoodiae*. *Aster eastwoodiae* might be a very recent descendant of *A. siskiyouensis* since its range is encompassed by that of *A. siskiyouensis*;
4. a lineage derived from populations of the founding taxon that migrated north from the central part of the original range giving rise to two groups of

descendants. One group led to *Aster perelegans* and *A. glaucescens*. The simplest assumption would be that *Aster glaucescens* evolved from populations of *A. perelegans*. The second group produced an ancestral taxon that evolved into *A. engelmannii* and its associated sister groups. *Aster wasatchensis* var. *grandifolius*, one of the sister groups, is problematic because its placement as such implies an intimate association with *Aster engelmannii* but its geographic location puts it close to *Aster wasatchensis*; both associations could be explained if it is a hybrid between the two taxa. *Aster vialis* is geographically isolated from other sister groups; it could be a remnant from a previous range expansion and contraction of *A. engelmannii*.

None of my proposed adjustments contradict the original phylogenetic hypothesis, only the assumption that one species could give rise to only two others needed to change to allow for more. Possibly, more biogeographic research may show that this group evolved from North American taxa, or has migrated from Asia, or has not been strongly influenced by climatic change. The phylogenetic hypothesis might change as new information becomes available. This hypothesis is meant to provide a basis for discussion and to offer direction to further investigation.

Current distributions of section *Eucephalus* taxa

The current ranges of section *Eucephalus* taxa probably do not reflect accurately (especially the northern taxa) the geographic positions during which speciation events occurred. Glaciation and later retreat of glaciers probably forced species ranges to move south and then north again.

In the western part of section *Eucephalus* species ranges, taxa are limited to smaller geographic areas than those found further east in the Rocky Mountains and the Purcell range. In other words, all species but one in the eastern part of the overall range are widespread and numerous. The species richness of section *Eucephalus* is higher in the Coastal mountains than in the Rocky mountains. This phenomenon of higher species richness and increased endemism may, in some part, be attributed to the latitudinal trend;

i. e. endemism and species richness increase as the latitude decreases (Myers and Giller 1988). The trend cannot be strictly applied to section *Eucephalus* since species richness decreases in the most southern parts of the overall range, which implies that these species thrive in cool habitats, an idea supported by their success in subalpine and alpine areas. The ability of these taxa to become established and persist in cool habitats supports the proposal that their ranges may been modified during climate change, and detracts from the suggestion that they are derived from a taxon migrating from a presumably warm southern origin.

The movement of species that propagate with wind-borne seed is not restricted to the directions of the prevailing winds and any direction of dispersal is possible at different times during the year. The plants, once established, can probably survive adverse conditions and develop rapidly every summer because all taxa in this section of *Aster* have underground rhizomes. Lack of pollinators may not be a large problem to the persistence of individuals since they may vegetatively reproduce through the extension of rhizomes. If pollination does not occur, dissemination to new sites may be eliminated because seeds may not develop.

The distribution of section *Eucephalus* outlines the Coastal mountain ranges, the Rockies and the Purcell mountains. Differences between the ranges might explain the east-west divergence in species richness; many of the Coastal mountains have a volcanic origin (creating an complex of discontinuous habitats) and the Rockies, the Purcells, and Vancouver Island mountain ranges originated from uplift.

Centres of diversity for section *Eucephalus* were simple to identify because they were places of most confusion on the overall map. The Siskiyou mountains is currently the area with the highest number of species. More study of species in this area may lead to a better phylogenetic hypothesis since some of these taxa may be ancestral to other members of the section.

I could not separate Vancouver Island *Aster paucicapitatus* specimens from those on the Olympics using morphological data. They are probably a homogenous population and from the same origin. Areas where *A. paucicapitatus* currently grows were heavily

glaciated therefore the extant populations probably are from recent colonizations. Some arguments have been made for glacial refugia on Vancouver Island where some plants may have survived. If the plants on the Island mountains are descendants of survivors from refugia, then the limited genetic pool should have resulted in some evidence of morphological differences from those found on the Olympic mountains. If seeds or pollen were found in lake or sea bottom cores then some hypothesis on the changing distributions could be developed. I would like to know if *A. paucicapitatus* grew on southern Vancouver Island several thousand years ago. If it was found to occur, then the current distribution gap could be attributed to lose of habitat or competition, but if it was not found, then persistence in a refugia on Vancouver Island, or nearby, becomes a stronger possible explanation.

Aster vialis is of special interest because it is a rare endemic under legislative protection in the USA. On the cladogram, it was closely associated with *A. engelmannii* var. *monticola*. *Aster vialis* could be simply a rayless variety of *A. engelmannii*.

VI. OVERALL CONCLUSIONS

The analytical techniques developed and tested during this study have yielded groups which have been successfully used in annotating herbarium specimens, cladistic and biogeographic analyses. These techniques are most helpful when applied to morphologically similar taxa that require several characteristics to separate them. Gower's general similarity coefficient was helpful in establishing clusters, and providing a starting hypothesis. It could be further modified to make better use of binary and categorical characters. Examining the group memberships by inspecting box plots and t-tests of characters lead to the discovery of questionable groups. Using eigen values from discriminant analyses provided means to gauge the effect of changes in group memberships. This study would have been improved if larger sample sizes had been used and varieties, rather than only species, had been included in the stratified design. In hindsight, specimens collected in the Oregon/California border region should have been more intensely sampled. I did not realize, when I began this study, that section *Eucephalus* taxa were so richly represented in this area.

Cladistic analysis using taxon averages coded as multi-state characters produced one most parsimonious cladogram that was used to develop a phylogenetic hypothesis. *Aster* section *Eucephalus* was found to be a monophyletic group that includes *Aster breweri* (Gray) Semple, *A. breweri* (Gray) Semple var. *multibracteata* (Jeps.) Zamluk *comb. nov.*, *A. brickellioides* (Greene) Greene, *A. engelmannii* Gray var. *engelmannii*, *A. engelmannii* Gray var. *monticola* Zaml. *var. nov.*, *A. eastwoodiae* Zaml. *comb. nov.*, *A. glaucescens* (Gray) Blake, *A. glaucodes* Blake, *A. glaucodes* Blake var. *formosus* (Greene) Kittell, *A. glaucodes* Blake var. *pulcher* (Blake) Kearney & Peebles, *A. gormanii* (Piper) Blake, *A. ledophyllus* (Gray) Gray var. *ledophyllus*, *A. ledophyllus* (Gray) Gray var. *covillei* (Greene) Cronq., *A. paucicapitatus* (Robins.) Robins., *A. perelegans* Nels. & Macbr., *A. siskiyouensis* Nels. & Macbr., *A. vialis* (Bradshaw) Blake, *A. wasatchensis* (Jones) Blake var. *grandifolius* Zaml. *var. nov.* and *A. wasatchensis* (Jones) Blake var. *wasatchensis*. *Aster glaucodes* was found to be a member of section *Eucephalus*; no evidence justified

placing it into a subsection. *Aster wasatchensis*, according to this study, was the oldest taxon in the group, and was sufficiently morphologically different from *A. glaucodes* is be considered a separate species. Nesom's decision (1994) to elevate *Aster glaucodes* var. *pulcher* to species level, then place it, *A. glaucodes* var. *glaucodes* and *A. wasatchensis* into *Eurybia* rather than *Eucephalus* was not supported by this study.

Several changes in taxonomic designations are suggested. *Aster eastwoodiae* Zaml. was a new combination that recognized *Eucephalus bicolor* Eastw. in order to delineate a morphologically distinct taxon previously included with *A. brickellioides*. *Aster breweri* var. *multibracteata* was found to be a valid taxonomic group, and need not be combined with var. *breweri*. *Aster engelmannii* was divided into two varieties based on size, involucre size and trichome characteristics: *Aster engelmannii* var. *engelmannii* and *Aster engelmannii* var. *monticola*. *Aster wasatchensis* was separated into two varieties based on size differences and leaf trichome characteristics: *Aster wasatchensis* var. *wasatchensis* and *Aster wasatchensis* var. *grandifolius*. The more clearly defined taxa will lead to correct identifications and better estimates of distributions. Molecular and genetic work will be more precise because identifications will be accurate. Comparative analysis among taxa can be done with more precision than previously possible.

The phylogenetic hypothesis developed with cladistic analysis was slightly modified by considering the possible existence of widespread ancestral taxa from Mexico that underwent vicariance in several parts of its range to eventually produce several lineages. Allowing this small modification simplified the proposed migration patterns and associations among several disjunct taxa.

Based on the biogeographical analysis and the phenetic analysis of this group, there seems to be no particular reason related to the morphology of rare taxa which explains their rarity. Rarity in this section seems to be a result of geography and evolutionary history, one taxon might be a palaeoendemic (*Aster wasatchensis*) and others appear to be neoendemics (*Aster eastwoodiae*, *A. glaucescens*, *A. gormanii*, *A. paucicapitatus*, and *A. vialis*). Even without human interference, these endemic taxa would be at risk of extinction because of naturally limited availability of habitats.

Specific steps to preserve this group are probably unnecessary, excepting *Aster vialis*. Because many of these taxa can be found in mountainous regions, they have already been protected by chance through the creation of managed areas, provincial, state and national parks in Canada and the United States. *Aster vialis* is under direct threat of extinction because of its location in the highly populated area around Eugene, Oregon. Hopefully, the identification of new sites in California will lead to discoveries of more populations of *A. vialis*.

In Canada, *Aster engelmannii* is well protected in Provincial and National Parks, and appears to be in a range expansion phase. On Vancouver Island, some *Aster paucicapitatus* populations are under no threat from human activity because they are in very inaccessible locations, and others are protected by Strathcona Park. *Aster paucicapitatus* does not seem to be in danger of extinction. If the warming climatic changes continue, I would expect northward range expansions into Canada of *Aster ledophyllus* and *A. perelegans*, as well as shifts of all the taxon ranges northward. Hopefully, the changes in ranges can be monitored over the next century, and facts, rather than speculation, will provide the basis for the biogeographical hypothesis.

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APPENDIX

List of herbarium specimens used in analyses

Specimen number	Phenetic group	Assigned taxon	Collector	Site
7	1	*Aster breweri* var. *multibracteata*	Smith, G. L. & Neilson, A. H. 2654	Pyramid Peak, El Dorado, California
6	1	*A. breweri* var. *multibracteata*	Winkelman, H. G. 229	Mercur Peak, Tuolumne, California
9	1	*A. breweri* var. *multibracteata*	McGregor, E. A. 56	Half Moon Lake, El Dorado, California
3	1	*A. breweri* var. *multibracteata*	Quibell, C. H. 4867	Bear Creek, Fresno, California
5	1	*A. breweri* var. *multibracteata*	Beane, L. 373	Huntington Lake, Fresno, California
4	1	*A. breweri* var. *multibracteata*	Howell, J. 16790	Shedon Creek, Madera, California
8	1	*A. breweri* var. *multibracteata*	Smith, L. S. 2155	Robertson Flat, Placer, California
1	2	*A. breweri*	Bacigalupi, R., Constance, L. & Nasir, E. 4358	Webber Lake, Sierra, California
10	2	*A. breweri*	Thomas, H. A. & Thomas, J. H. 4606	Mono Creek, Fresno, California
2	2	*A. breweri*	Smith, C. N. 717	Sunday Peak, Kern, California
85	3	*A. paucicapitatus*	Kruckeberg, A. R. 2775	Hurricane Ridge, Clallam, Washington
94	3	*A. paucicapitatus*	Kruckeberg, A. R. 6113	Sunnybrook Meadows, Jefferson, Washington
88	3	*A. paucicapitatus*	Leach, L. 2034	Skyline Trail, Clallam, Washington
89	3	*A. paucicapitatus*	Elmer, A. D. E. 2601	Olympic Mts., Clallam, Washington
91	3	*A. paucicapitatus*	Davies, B. W. & Davies, D. 1880	Golden Hinde Mtn., BC
86	3	*A. paucicapitatus*	Rollins, R. C. & Chambers, T. S. 2676	Constance Pass, Jefferson, Washington
93	3	*A. paucicapitatus*	Helmrich, H. E. 387	Marmot Pass, Jefferson, Washington
96	3	*A. paucicapitatus*	St. John, H. 5766	Sol Duc-Bogacheil Divide, Clallam, Washington
90	3	*A. paucicapitatus*	Thompson, J. W. 5570	Mt. Angeles, Clallam, Washington
87	3	*A. paucicapitatus*	Thompson, J. W. 9949	Marmot Pass, Jefferson, Washington
95	3	*A. paucicapitatus*	Thompson, J. W. 9966	Mt. Colonel Bob, Grays Harbour, Washington
92	3	*A. paucicapitatus*	Warrington, P. D.	Mt. Arrowsmith, BC
137	6	*A. wasatchensis*	Goodrich, S. 17402	Fillmore, Millard, Utah
127	6	*A. wasatchensis*	Jean, C. CEBR 70	Markagunt Plateau, Iron, Utah
130	6	*A. wasatchensis*	Welsh, S. L., Taylor, K. & Thorne, K. 14313	Paunsagunt Plateau, Garfield, Utah
128	6	*A. wasatchensis*	Lommasson, T. 22	Crazy Hollow Pasture, Millard, Utah

Specimen number	Phenetic group	Assigned taxon	Collector	Site
135	6	*A. wasatchensis*	Thorne, K., Kass, R. & Tuhy, J. 6424	Church Mesa, Washington, Utah
50	8	*A. wasatchensis*	Rossbach, G. B. 5463	Rainbow Point, Kane, Utah
67	9	*A. gormanii*	Nissila, P. & Cooney, C.	Baty Butte, Nat. For. Rd. 54, Clackamas, Oregon
69	9	*A. gormanii*	Peck, M. E. 18836	Harney Lake, Jefferson, Oregon
60	9	*A. gormanii*	Peck, M. E. 18838	Harney Lake, Jefferson, Oregon
62	9	*A. gormanii*		no site,
59	9	*A. gormanii*	Leach, L. 4413	Mt. Jefferson, Marion, Oregon
61	9	*A. gormanii*	Peck, M. E. 18846	Jefferson Park, Linn, Oregon
64	9	*A. gormanii*	Whitehead, G. 1907	Scorpion Mtn, Marion, Oregon
66	9	*A. gormanii*	Woodbridge, M.	Wash Creek Butte ,N.F. Rd 54, Clackamas, Oregon
70	9	*A. gormanii*	Peck, M. E. 18847	Mt. Jefferson Wilderness Area, Linn, Oregon
63	9	*A. gormanii*	Thompson, D. D. 286	Breitenbush Lake, Jefferson, Oregon
65	9	*A. gormanii*	Woodbridge, M.	Wash Creek Butte ,N.F. Rd 54, Clackamas, Oregon
68	9	*A. gormanii*	Bluhm, W. L.	Marten Buttes, Marion, Oregon
12	10	*A. brickellioides*	Baker, M. S. 10679	Black Butte, Glenn, California
74	10	*A. ledophyllus* var. *covillei*	Stansell, V.	Sanger Lake, Del Norte, California
11	10	*A. brickellioides*	Peck, M. E. 4626	Ashland-Klamath Falls Road, Jackson, Oregon
20	10	*A. ledophyllus* var. *covillei*	Howell, J. T. 19245	Glenn County, Glenn, California
78	11	*A. ledophyllus*	Sheldon, E. P.	Mt. Rainier, Pierce, Washington
82	11	*A. ledophyllus*	Thompson, J. W. 1654	Crater Lake, Klamath, Oregon
76	11	*A. ledophyllus*	Franklin, J. F. & Dyrness, C. T. 117	Frissel Pt., Linn, Oregon
72	11	*A. ledophyllus*	Gilkey, H. M. 14	Mt. Adams, Yakima, Washington
79	11	*A. ledophyllus*	Coville, F. V. & Applegate, E. I. 1197	Mt. Jefferson, Linn, Oregon
75	11	*A. ledophyllus*	Leach, L. 4664	Cispus Pass, Lewis, Washington
73	11	*A. ledophyllus*	Abrams, L. R. 12095	Crater Lake, Klamath, Oregon
71	11	*A. ledophyllus*	Andrews, R. 391	Horse Creek Trail, Lane, Oregon
83	11	*A. ledophyllus* var. *covillei*	Coville, F. V. & Applegate, E. I. 355	Crater Lake, Klamath, Oregon
84	11	*A. ledophyllus*	Henderson, L. F.	McKenzie Pass, Linn, Oregon
81	11	*A. ledophyllus*	Grant, J. M.	Bewett Pass, Chelan, Washington
21	12	*A. brickellioides*	Keck, D. D. 6442	Black Butte, Glenn, California
23	12	*A. brickellioides*	Applegate, E. I. 4481	Horse Creek, Klamath, Oregon

Specimen number	Phenetic group	Assigned taxon	Collector	Site
15	12	*A. brickellioides*	Heller, A. A. 12242	Mount Eddy, Siskiyou, California
13	12	*A. brickellioides*	Tracy, J. P. 17043	South Fork Mountain, Humboldt, California
105	14	*A. perelegans*	Maguire, B. & Holmgren, A. H. 27057	Slickrock Creek, Wallowa, Oregon
98	14	*A. perelegans*	Fertig, W. 11580	White Rock Mtn., Sublette, Wyoming
103	14	*A. perelegans*	Harrison, O. C. 91	Grey's River area, Lincoln, Wyoming
100	14	*A. perelegans*	Hartman, R. L. 28398	Burnt Ridge, Teton, Wyoming
97	14	*A. perelegans*	Atwood, N. D. 13222	Jarbridge Mountain, Elko, Nevada
101	14	*A. perelegans*	Nelson, A. & Macbride, J. F. 1271	Ketchum, Blaine, Idaho
99	14	*A. perelegans*	Peck, M. E. 4411	Rock Creek Canyon, Baker, Oregon
108	14	*A. perelegans*	Hurd, R. M. 369	Dry Fork, Sheridan, Wyoming
106	14	*A. perelegans*	Atwood, D. 16484	Pinedale Range Station, Sublette, Wyoming
107	14	*A. perelegans*	Welsh, S. L. 3432	Tavaputs Plateau, Duchesne, Utah
109	14	*A. perelegans*	Cronquist, A. 1835	Henry's Lake, Fremont, Idaho
102	14	*A. perelegans*	Nelson, B. E. & Fonken, G. 7097	Tensleep Canyon, Upper, Washakie, Wyoming
104	14	*A. perelegans*	Nelson, A. & Nelson, E. 6547	Jackson's Lake, Teton, Wyoming
35	15	*A. engelmannii* var. *monticola*	Meyer, F. G. & Meyer, L. E. 2398	Piney Lake, Middle, Sublette, Wyoming
31	15	*A. engelmannii* var. *monticola*	Nelson, B. E. & Nelson, S. 17558	Service Creek, Routt, Colorado
132	15	*A. wasatchensis* var. *grandifolius*	Eastwood, A. & Howell, J. T. 7300	Cedar Breaks, Iron, Utah
24	15	*A. engelmannii* var. *monticola*	Macoun, J. M. 26361	Chilliwack River, BC
32	15	*A. engelmannii*	Ogilvie, R. T.	Crowsnest area, Alberta
29	15	*A. engelmannii* var. *monticola*	Beamish, K. I., Luitjens, J., Carey, K. & Campbell, S. 750281	Slocan, BC
133	15	*A. wasatchensis*	Higgins, L. 11245	Brian Head, Iron, Utah
28	15	*A. engelmannii* var. *monticola*	Roller, K. J.	Manning Park, BC
34	15	*A. engelmannii* var. *monticola*	Williams, R. L. 160	Green Mt., Carbon, Wyoming
22	16	*A. siskiyouensis*	Applegate, E. I. 11457	Sand Ridge, Josephine, Oregon
52	19	*A. glaucodes*	Semple, J. & Chmielewski, J. 8890	Wasatch Plateau, Sanpete, Utah

Specimen number	Phenetic group	Assigned taxon	Collector	Site
129	19	*A. wasatchensis* var. *grandifolius*	Jones, M. E. 6037	Elk Ranch, Piute, Utah
131	19	*A. wasatchensis* var. *grandifolius*	Hitchcock, C. L., Rethke, R. V. & van Raadshooven, R. 4620	Cedar City, Iron, Utah
134	19	*A. wasatchensis* var. *grandifolius*	Welsh, S. L. & Christensen, E. M. 2642	Cedar Creek, Iron, Utah
138	19	*A. wasatchensis* var. *grandifolius*	Goodrich, S. 15135	John Williams Canyon, Millard, Utah
136	19	*A. wasatchensis* var. *grandifolius*	Taye, A. 3553	Cascade Creek, Piute, Utah
39	20	*A. glaucescens*	Ryan, B. 486	Red Mountain, Skamania, Washington
57	20	*A. glaucodes*	Neese, E. 2500	Crescent Creek, Garfield, Utah
33	22	*A. engelmannii*	Maguire, B. 3832	Mt. Timpanogos, Utah, Utah
37	22	*A. engelmannii*	Passey, H. B. 59	Hodge's Pasture, Cache, Utah
27	22	*A. engelmannii*	Brandegee, T. S. 129	Yakima Co., Yakima, Washington
25	22	*A. engelmannii*	Taye, A. 692	Willow Canyon, South, Tooele, Utah
30	22	*A. engelmannii*	Turner, G. T. 209	Black Mesa Exp. Range, Pstur 3, Gunnison, Colorado
36	22	*A. engelmannii*	Malte, M. O. & Watson, W. R. 2462	Castle mountain, Alberta
125	23	*A. vialis*	Bradshaw, R. V. 823	Eugene, Lane, Oregon
121	23	*A. vialis*	Constance, L. 951	Eugene, Lane, Oregon
122	23	*A. vialis*	Peck, M. E. 20280	Ten Mile, Douglas, Oregon
120	23	*A. vialis*	Mason, G.	Mt. Pisgah, Lane, Oregon
126	23	*A. vialis*	Henderson, L. F. 15896	Spencer Butte, Lane, Oregon
124	23	*A. vialis*	Henderson, L. F. 15708	Spencer Butte, Lane, Oregon
123	23	*A. vialis*	Brown, R. 230	Spencer Butte, Lane, Oregon
16	25	*A. siskiyouensis*	Semple, J. & Heard, S. 8492	Etna Mountain, Siskiyou, California
17	25	*A. siskiyouensis*	Whittaker, R. H.	Lake Mountain, Josephine, Oregon
14	25	*A. siskiyouensis*	Ground, C. A. 644	Preston Peak, Siskiyou, California
77	25	*A. siskiyouensis*	Kildale, D. K. 9103	Preston Peak, Siskiyou, California
26	25	*A. siskiyouensis*	Emmel, J. F. 93	Caribou Lake, Siskiyou, California
41	25	*A. siskiyouensis*	Gorman, M. W. 5922	Crater Lake, Klamath, Oregon
46	26	*A. glaucescens*	Suksdorf, W. N. 11040	Kressenberg, Klickitat, Washington
38	26	*A. glaucescens*	Howell, T. J.	Cimcoe Mountain, Klickitat, Washington
40	26	*A. siskiyouensis*	Howell, T.	Coast Mountain, Josephine, Oregon
43	26	*A. glaucescens*	Suksdorf, W. N. 9471	Falcon Valley, Klickitat, Washington
45	26	*A. glaucescens*	Suksdorf, W. N. 5842	Falcon Valley, Klickitat, Washington

Specimen number	Phenetic group	Assigned taxon	Collector	Site
42	26	*A. glaucescens*	Jolley, R.	Baldy Peak, Klickitat, Washington
44	26	*A. glaucescens*	Suksdorf, W. N. 10635	Underwood, Skamania, Washington
80	26	*A. ledophyllus*	Henderson, L. F.	McKenzie Pass, Linn, Oregon
54	28	*A. glaucodes*	Maguire, B., Piranian, G. & Richards Jr., B. L. 12628	Grey's River Valley, Lincoln, Wyoming
56	28	*A. glaucodes*	Maguire, B. & Snell, R. 16026	Tony Grove Lake, Cache, Utah
58	28	*A. glaucodes*	Lewis, M. E. & Lewis, E. T. 3796	Ephraim Canyon, Sanpete, Utah
55	28	*A. glaucodes*	Lewis, M. E. 4997	Birch Creek, Sanpete, Utah
47	28	*A. glaucodes*	Haas, W. H. 46	Mesa Verde National Park, Montezuma, Colorado
49	28	*A. glaucodes*	Thorne, K. 9584	Weber River, Middle Fork, Weber, Utah
51	28	*A. glaucodes*	Porter, J. M. 4166	Deep Creek, Wayne, Utah
48	28	*A. glaucodes*	Jones, M. E. (Mrs.)	American Ink Canyon, Utah
113	29	*A. turbinellus*	Hasse, H. E.	Pulasli Co., Pulaski, Arkansas
117	29	*A. turbinellus*	Hall, E.	Athens, Menard, Illinois
111	29	*A. turbinellus*	Waterfall, U. T. 15202	Heavener, Le Flore, Oklahoma
116	29	*A. turbinellus*	Davis, J.	Hannibal, Marion, Missouri
112	29	*A. turbinellus*	Glatfelter, N. M.	St. Louis, St. Louis, Missouri
114	29	*A. turbinellus*	Freeman, C. C. 2823	Shoal Creek, Cherokee, Kansas
110	29	*A. turbinellus*	McDonald, F. E.	East Alton, Madison, Illinois
118	29	*A. turbinellus*	Brooks, R. E. & Kuhn, C. 20555	Huzzah Creek, Crawford, Missouri
115	29	*A. turbinellus*	Davis, J.	Hannibal, Marion, Missouri
53	30	*Aster*	Umbach, L. M. 561	Midvale, Salt Lake, Utah
18	31	*A. eastwoodiae*	Howell, T.	Coast Mountain, Josephine, Oregon
139	31	*A. eastwoodiae*	Eastwood, A. 12285	Adams, Del Norte, California
19	31	*A. eastwoodiae*	Eastwood, A. 12164	Gasquet Mts, Del Norte, California
140	31	*A. eastwoodiae*	Eastwood, A. 12133	Gasquet Mts, Del Norte, California
141	31	*A. eastwoodiae*	Eastwood, A. 2187	Boundary Hill, Del Norte, California
119	34	*A. turbinellus*	Hitchcock, A. S. 719	Cherokee County, Cherokee, Kansas