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Rarity and the Phylogeography of the Large-Flowered Piptolobi of Astragalus L. (Fabaceae)

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Jeffrey Wellington White

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Major professor

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RARITY AND THE PHYLOGEOGRAPHY OF THE LARGE-FLOWERED PIPTOLOBI OF *ASTRAGALUS* L. (FABACEAE)

By

Jeffrey Wellington White

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ABSTRACT

RARITY AND THE PHYLOGEOGRAPHY OF THE LARGE-FLOWERED PIPTOLOBI OF *ASTRAGALUS* L. (FABACEAE)

By

Jeffrey Wellington White

Phylogenetic patterns of rarity were explored using a case study group of 51 species of the Large-flowered Piptolobi of *Astragalus* (Fabaceae). The study was divided into three parts: elucidation of a species level phylogeny, quantification of range sizes using areas of occupancy, and assessment of patterns of rarity in the phylogeny.

A morphological cladistic analysis uncovered a highly resolved phylogeny that corresponds well with previous taxonomic work. The Argophyllean clade consisting of 47 species was identified and used in part three.

Areas of occupancy using nine measurement scales (10 to 2560 km) were quantified using a procedure developed to eliminate sampling error associated with standard methods. The program "Minimum Cell Count" searched for minimum areas of occupancy among potential measurement grid placements. Categories of rarity using generally accepted criteria were assigned to each species. Assessment of the fractal properties of each species' distribution revealed that they are generally not fractal. Measurement scale significantly affected rank ordering of species.

Phylogenetic patterns of rarity in the Argophyllean clade of *Astragalus* were assessed using three lines of evidence aimed to address the main hypothesis: Namely, that high rates of diversification in concert with local speciation is associated with rare species clustering in the phylogeny and a preponderance of newly derived rare species. Significant diversification rate variation within the clade was established based a tree asymmetry tests. Two tests were conducted to assess patterns of rarity after range size quantities and rare categories were mapped onto the phylogeny. Rarity is not a

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phylogenetic trait, thus standard comparative methods were not employed; instead, new tests were developed. Phylogenetic clustering of rare was tested by employing a Mantel randomization procedure using matrix values for topological distance among species, and differences in their log area of occupancy. The null hypothesis, that there is no association among matrix values (thus no clustering), was not rejected (p=.089) but results point toward evidence of clustering. A Monte-Carlo procedure that randomized species placement on the phylogeny was employed to test the hypothesis that rare species are more newly derived than expected by chance. The count of 11 rare species found among the 14 terminal pairs of species was not significantly greater than the reference distribution's mean of 9.8 (p=.32).

DEDICATION

in memory of

Richard B. Battelle

Eighth-grade Science Teacher

Mr. Battelle inspired enthusiasm about science and motivated many to aim for high levels of personal achievement. Mr. B. introduced me to botany and inspired my interest and commitment to teaching and to public schools.

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I wish to first thank my guidance committee members for their support and contributions. My advisor, Tao Sang, helped me distill my ideas and offered lots of good advice and constructive criticism. He was flexible and patient from the beginning. Tom Getty asked superb questions and took on a crucial role that supplied continuity during a time of rapid change. Jim Hancock consistently gave upbeat and constructive feedback and helped me understand subtleties within academe. Alan Prather furnished herbarium work space, computational facilities, and advice. My former advisor, Steve Tonsor, played a significant role during the early development of my dissertation work.

Two other professors significantly contributed to my program and work. Peter Murphy graciously offered excellent advice on many occasions, much encouragement, and some exceptional opportunities. His support is greatly appreciated. Don Hall challenged me to think deeply and gave much needed support. I learned a great deal from him about ecology, evolution, and life. Also, thank you Gus de Zoeten.

Mike Sanderson furnished data and shared his insights on the evolution of *Astragalus*. Rupert Barneby offered his gracious help during my visit to New York. Mike Penskar shared his rich understanding of rare plants. Marguerite Halversen provided superb editorial assistance and David Wisner gave expert programming help. The Herbarium staff at NY and RSA assisted during visits and with loans to MSC.

My companion in life, Doreen, gave unending support, love, and tolerance of the many days and nights I spent on this work. Our two children, Nicolas and Anthony, gave seemingly endless smiles and always reminded me of what is most important in life. Thank you Wellington and Colleen White.

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A Brief Overview: Age, Area, and the Evolution of Rare Plants

1.1 INTRODUCTION

Humans are fascinated with rare things. In the case of organisms, an interest in rarity often corresponds with concern about their persistence, particularly when human activities are contributing to their decline. The majority of rare species, however, are probably rare largely for reasons unrelated to human activity. Given the general lack of understanding about natural causes of rarity, it is not surprising that biologists often have difficulty elucidating the factors leading to rare status.

After more than a century of study, general theory regarding the causes and consequences of rarity is just beginning to coalesce. A few general traits are emerging that differentiate rare taxa from common species, including: 1) breeding systems that tend away from outcrossing and sexual reproduction; 2) lower reproductive investment; 3) more limited dispersal; 4) higher levels of homozygosity; and 5) a narrower scope of resource usage (Kunin and Gaston 1997). There are many exceptions to these traits, however. New methods and data are leading to new insights about the nature of

biodiversity dynamics (McKinney and Drake 1998), a large umbrella under which studies of rarity are found.

Rarity, here discussed as a biogeographic attribute, is most commonly measured in terms of range size (area), abundance (number/area), or numbers of populations or localities. Two general processes lead to rare status: demographic decline or incipient local speciation (such as via peripatric speciation or chromosomal rearrangements). Although these two processes are fundamentally different, they are nevertheless difficult to differentiate and may operate simultaneously.

Rarity is not a genealogical trait like morphological traits, chromosome numbers, or DNA sequences. Rather, it is a demographic trait—an aggregate property of the species resulting from its genotype by environment interaction. During speciation events, rare status is not inherited by the derived species; however, traits correlated with biogeographic status may be heritable in some circumstances (Jablonski 1987).

In light of the large number of rare plant species and the increasing number threatened with extinction, understanding the dynamics of their origins and their possible destinies has become more urgent. Indeed, the International Union for the Conservation of Nature's (IUCN) recent publication of the *1997 Red List of Threatened Plants* indicates that more than 33,000 plant species, representing 12.5% of all plant species, are threatened or extinct (Walter and Gillett 1998).

Threatened status is given to species that are more vulnerable to extinction, generally because of declining numbers of individuals or populations through time. As a species approaches extinction, its degree of rarity increases. However, not all rare species are threatened; and although threatened and rare status are highly correlated, they are different attributes. Yet, these two notions are often used interchangeably, especially vulnerability or threat, as a proxy for rarity (Kunin and Gaston 1997). To understand the human role in biodiversity loss and to provide better means for mitigating the effects of human

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activity, we need a better understanding of the similarities and differences of natural and human causes of rarity.

1.2 A BRIEF HISTORY OF RARITY CONCEPTS

Biologists have conjectured about the nature of rarity since before the advent of evolutionary theory. The earliest scientific notions of rarity centered on species' age. Rafinesque (1836) held the view that rare species are young while Lyell (1830-33) believed that rare species are old. While then-current evolutionary theory provided little to settle the debate, it actually led to more complex debate because of the introduction of new concepts about speciation and extinction. Darwin (1872) settled on the view that rare species are heading toward extinction and are therefore old, although he understood the that underlying causes of rarity are complex and include many factors. During the first part of the twentieth century, reiterations of Darwin's notions about rarity and the age of plant species continued to prevail (Fiedler, 1986).

The view that rare plant species are old and going extinct was forcefully challenged by Willis (1916) who, after studying the flora of Ceylon, argued that rare species are newly evolved. Willis set off a vigorous debate about rarity, the age of taxa, and evolution. Significant contributors to this debate included Ridley (1916), Fernald (1918), and others (see Fiedler 1986).

Willis (1922) expanded his theories about rarity in his treatise entitled *Age and Area*, in which he argued that the age of a species corresponds with its area or range size (see also Willis and Yule 1922). The controversy about Willis's concepts of "age and area" diminished several years later following Gleason's (1924 and 1926) pluralistic solution to the debate. Gleason argued that the area or range size of a species (and therefore rare status for some species) is in part a function of its age, and that rare species may be either young or old. Gleason's views on rarity and age have since prevailed.

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By the mid-twentieth century, the debate about rarity in plants broadened to include new contributions from genetics, cytology, speciation, and ecology. Stebbins (1942) was the most significant contributor during this period because of his synthesis of earlier views and his hypotheses concerning rarity that utilized new concepts in genetics, speciation theory and ecology. He also refined theoretical ideas about the geographical distributions of rare plants and, in doing so, described three rarity types based on range size and local abundance. Stebbins laid a groundwork of testable hypotheses, including the hypothesis that rare species are genetically depauperate or that they are poor competitors, which led to decades of research. Stebbins also acknowledged that the ages of species were difficult to determine.

Others who contributed to discussion about rarity in plants during this period include Cain (1940, 1944), Griggs (1940), and Wulff (1943). Simpson (1953) and Wright (1956) made important contributions to general concepts of rarity.

During the early 1960's, Favarger and Contandriopoulos (1961) proposed a new classification for causes of rarity based on cytological attributes, systematic position, and age. Their scheme provided new testable hypotheses about the origins of rarity and was adopted by Stebbins and Major (1965) in their important monograph on endemism and speciation in the California Flora. As was the case with earlier contributors, they acknowledged the limitations associated with determining the age of a species, thus making some aspects of Favarger and Contandriopoulos' hypotheses difficult to test.

In the 1970's, the passage of the Endangered Species Act and the CITIES Convention spurred an increase in protection efforts and studies of rare plants in the United States. Nevertheless, fewer than 370 threatened plant taxa, a small portion of the perceived total, had received federal listing by 1992 (Schemske, *et. al.* 1994; Walter and Gillett 1998). Among listed plants, Schemske, *et. al.* reviewed the research recommendations proposed in 98 recovery plans and found that 96% of the recommendations called for ecological research, 84% for demographic research, and 26% for population genetic research. For

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the last several decades, studies of rarity have continued to focus almost entirely on ecological and population genetics factors. Many of the findings have confirmed earlier hypotheses about rarity while some refute them. For example, Stebbins's hypothesis that rare species are genetically less diverse than common species has often been supported. Exceptions have been found such as some members of the genus *Astragalus* (Karron *et. el.* 1988). Studies of rare plants usually do not isolate simple causes for their status, except when due to the direct effect of human activity.

Other reviews of plant rarity can be found in Kruckeberg and Rabinowitz (1985), Fiedler (1986), and Fiedler and Ahouse (1992). An excellent general discussion of rarity can be found in Gaston (1994).

1.3 SPATIAL ATTRIBUTES OF RARE SPECIES

Central to the notion of rarity is a taxon's spatial distribution. Depending on the scale of measure and the criteria used, taxa that fall below a certain threshold are labeled "rare." Willis (1916), in his study of the flora of Ceylon, divided species into six range size categories: very rare; rare; somewhat rare; somewhat common; common; and very common. His unit of measure was the area derived by drawing a boundary around the location of collection sites. In effect he used range size for categorizing rarity.

Stebbins (1942) noted that spatial patterns of rarity exist at multiple scales, including overall range size, number of populations, and local abundance, leading to different forms of rarity. In a very similar way, Drury (1974 and 1980) described three spatial patterns of rarity: geographically widespread but locally sparse; geographically restricted but locally abundant; and geographically restricted and locally sparse, which are derived for two axis of measure.

Rabinowitz (1981) brought Stebbins's and Drury's spatial categories of rarity together with degree of habitat specificity in her "Seven forms of rarity," now the most

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frequently cited classification system for rarity. Interestingly, the age of species was not included in her classification system despite years of discussion about its importance. Perhaps the frequency with which Rabinowitz's taxonomy of rarity is cited indicates the biologist's preference for attributes that can be studied directly, unlike age.

Local abundance and range size are highly simplified categories that do not capture many of the dimensions of species' distribution, such as number of populations or the number of collecting localities, and are at two ends of a spectrum of spatial scales useful for measuring geographic distributions. Scales of measure employed during studies of species distribution great impact on the interpretation of data (Allen and Hoekstra 1992; Maurer 1999) and thus need to be carefully considered. This is particularly true with rare species because sampling errors are higher compared with more widespread species.

1.4 RARITY, AGE, AND EVOLUTIONARY HISTORY

Stebbins, in 1980, again proposed a major synthesis on causes of rarity. His "synthetic approach" proposed that the study of rarity should take into account ecological factors, the genetic structure of populations, and the evolutionary history of the lineage(s) concerned. To date, nearly all empirical work on rarity has considered only ecological and/or genetic factors (for an exception, see Linder 1995) in spite of the recognized importance of species age toward understanding rare status.

It is curious that few have acknowledged or realized that the whole idea of the age of a species has flaws. Indeed, in the words of G. G. Simpson (1953), ". . . all lineages existing at any one time are of precisely the same age, so how can some be 'young' and some be 'old'? Unless life has arisen in more than one period of Earth history, which is extremely improbable, all must necessarily have undergone the same span of continuous reproduction."

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This leads to important questions about previous authors' ideas about the age of a species. I conjecture that references to "age" have really been references to several different features of lineages, such as time since divergence from a common ancestor, the number of derived versus ancestral traits, and taxonomic distinctness. In the absence of a fossil record, phylogenetic estimation of evolutionary trees provides the best evidence regarding these age-like features. Phylogenetic studies also result in testable hypotheses from which future work can be gauged.

Phylogenetic studies provide new perspectives toward better understanding the origins and destinies of rare plants. In heeding Stebbins call to include evolutionary history in studies of rarity, I undertook a study aimed at assessing phylogenetic patterns of rarity.

1.5 A CASE STUDY OF RARITY FROM A PHYLOGENETIC PERSPECTIVE

The central hypothesis addressed by the case study described here is that high rates of diversification in concert with local speciation result in high proportions of rare species within monophyletic groups of species. The causes of rarity in a group these circumstances would be linked to the causes of diversification and thus would mean that the rare species would have common causes for their rare status. Phylogenetic patterns of rarity may thus result.

The genus *Astragalus* was chosen as a study group because it has a number of useful attributes. More than 400 species have been described in North America, many of which are rare. The taxonomy of the group has been extensively revised, most recently by Barneby (1964), who spent nearly 25 years collecting and studying thousands of living and pressed herbarium specimens. His species concepts are well accepted and have been repeatedly upheld by more recent taxonomic and systematic work. His monograph

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contains data in sufficient detail for both phylogenetic and biogeographic aspects of study. The immense size of the genus precluded a comprehensive study, thus a subgroup was selected. Recent phylogenetic work has unveiled the monophyly of the Large-flowered Piptolobi (Lf-P) group with approximately 51 species and was used for this case study.

This case study is presented in three parts corresponding to the next three chapters of this dissertation. The first part, presented in chapter 2, focuses on the morphological cladistic study that aimed to elucidate phylogenetic relations among the Lf-P of *Astragalus*. Questions addressed during this study include: 1) Is the monophyly of sections in Barneby's Large-flowered Piptolobi sub-phalanx (with a few modifications) supported using morphological data? 2) What are the species level relationships among the members of the group? and 3) What is the utility of morphological characters in resolving interspecific relationships in *Astragalus*.?

In chapter 3, the biogeographic study of the Lf-P group is presented. Questions addressed include: 1) How do range size measures compare when based on different methods of determination and different scales? 2) Are species distribution fractal? 3) Which species meet the rarity criteria used by the IUCN's *1997 Red List of Threatened Plants*? 4) How do values of species richness compare based on differing measurement scales? and 5) Where are the most species rich areas?

Results from the phylogenetic and biogeographic studies were combined and analyzed during the study presented in chapter 4. This third study aimed at assessing phylogenetic patterns of rarity in the Argophyllean clade of *Astragalus*, a monophyletic group identified during the cladistic study. Questions addressed in this third section of the case study include: 1) Is there evidence of diversification rate variation among lineages in the group? 2) Do rare species cluster in the phylogeny? 3) Are newly derived rare species more frequent than expected by chance? Finally, conclusions and a few speculations derived from all the results and the literature are offered.

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A Morphological Cladistic Study of the Large-Flowered Piptolobi of *Astragalus* L. (Fabaceae)

2.1 INTRODUCTION

The genus *Astragalus* includes more than 2500 species and is known as the most species rich genus within the Angiosperms (Sanderson and Wojciechowski 1996; Liston 1994). The North American species number approximately 400 and have been extensively studied by four monographers, most recently by Barneby (1964). Modern phylogenetic studies during the last decade have shed significant light on relationships within the genus as well as the position of *Astragalus* within the tribe Galegeae of the Fabaceae.

The first cladistic study of the genus, based mainly on morphological data, was designed to elucidate relations among sections and resulted in preliminary conclusions about relationships within the genus (Sanderson 1991). Results provided evidence for the monophyly of a number of sections, including *Argophylli*, the largest among the Large-flowered group within Barneby's Piptoloboid phalanx. Sanderson's study had two limitations that should be noted. First, due to computational limitations and the large size of the data set, 113 taxa, the resulting search did not uncover the most parsimonious

trees. Second, outgroup selection was based on taxonomic concepts rather than explicit phylogenetic hypotheses.

Higher level cladistic relationships within *Astragalus* as well as relationships among related genera were later studied using chloroplast DNA restriction site and nuclear ribosomal DNA sequence data. Results from these studies have provided strong support for several higher level clades within North American members. Monophyly of the genus was strongly supported as well as the monophyly of the aneuploids within the paraphyletic euploids (Sanderson and Doyle 1993; Wojciechowski *et al* 1993). Additionally, the monophyly of Barneby's sub-phalanx, the Large-flowered Piptolobi, which includes section *Argophylli* with a few modifications, was also well supported (Sanderson and Doyle 1993).

Phylogenetic relationships below the sectional level have remained elusive due to the lack of phylogenetically informative genetic markers. Indeed, in a review of phylogeny of the tribe Galegeae and *Astragalus*, Sanderson and Liston (1995) emphasize that ". . . in *Astragalus*, morphology appears to be the most useful at the level of section and below." They go on to suggest that the quickest progress toward resolving relationships at lower taxonomic levels will include both molecular and morphological data.

The objectives of the study presented here were twofold: 1) to test the monophyly of sections in Barneby's Large-flowered Piptolobi sub-phalanx (with a few modifications) and to elucidate relationships among species; and 2) to test the utility of morphological characters in resolving interspecific relationships in *Astragalus*.

2.2 METHODS

The present study consists of 51 ingroup taxa and are largely restricted to Barneby's (1964) Large-flowered group of the Piptolobi phalanx (L-fP). Several modifications have been made stemming from previous molecular studies. Three sections, *Desperati*,

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Sarcocarpi, and *Tennesseenses* (representing four, four, and one species, respectively), were excluded because species from these sections have been found by molecular studies to be outside of the otherwise monophyletic L-fP clade (Wojciechowski *et. al.* 1993; Sanderson and Doyle 1993; Sanderson per. com.). The section *Diphysi*, with three species, was included because the widespread and diverse species *A. lentiginosus* of the section has been twice shown to be nested within the L-fP species. Three species within the L-fP have been revised since Barneby's (1964) treatment, resulting in two species additions and one species deletion from the group as follows: *A. tephrodes* var. *eurylobus* has been elevated to the rank of species as *A. eurylobus* (Barneby 1984); *A. castaneiformus* var. *consobrinus* has been elevated to the rank of species as *A. consobrinus* (Welsh 1978); and *A. musimonum* has been reduced to variety status within *A. amphioxys* (Barneby 1989). Species in this study are summarized in table 2.1.

Three outgroup taxa were chosen for this study and are all from within Barneby's Piptolobi phalanx. *Astragalus pomonensis* and *A. trichopodus* are members of the Pacific Piptolobi and *A. douglasii* is a member of the Small-flowered Piptolobi. Results based on cpDNA restriction site data (Sanderson and Doyle 1993) suggest that the above two groups are basal to the Large-flowered Piptolobi.

Data were derived from examination of more than 500 herbarium sheets on loan from NY and RSA as well as published data in Barneby (1964). In a few cases for which data from these two sources were unavailable, Barneby (1989) was consulted. Among the 90 characters screened for use in this study, 37 were excluded due to insufficient variation, significant overlapping variation and/or a high numbers of polymorphic species, or because of difficulty in scoring the character from herbarium specimens.

Species were scored for 53 binary and multistate characters representing 137 binary equivalents (see table 2.2). Thirteen species in the study have infraspecific taxa and for these, data were combined for all varieties within a species resulting in higher average levels of polymorphic characters compared to species without varieties. Among all

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Table 2.1. Species of *Astragalus* included in study. Arrangement by section (all capital letters), followed by subsections when applicable. Taxonomy after Barneby (1964, 1989).

ARGOPHYLLI
- Argophylli
  - *A. argophyllus* Nutt. ex T. & G.
  - *A. zionis* M. E. Jones
  - *A. piutensis* Barneby & Mabb.
  - *A. desereticus* Barneby
  - *A. callithrix* Barneby
  - *A. tephrodes* A. Gray
  - *A. eurylobus* (Barneby) Barneby
  - *A. iodopetalus* (Rydb.) Barneby
  - *A. shortianus* Nutt. ex Torr & Gray
  - *A. cyaneus* A. Gray
  - *A. columbianus* Barneby
  - *A. tidestromii* (Rydb.) Clokey
- Pseudoargophylli
  - *A. waterfallii* Barneby
  - *A. feensis* M. E. Jones
- Neomexicanus
  - *A. neomexicanus* Woot. & Standl.
- Newberryani
  - *A. uncialis* Barneby
  - *A. musiniensis* M. E. Jones
  - *A. loanus* Barneby
  - *A. newberryi* A. Gray
  - *A. eurekensis* M. E. Jones
- Coccinei
  - *A. coccineus* Brand.
- Eriocarpi
  - *A. purshii* Douglas ex Hook.
  - *A. leucolobus* Wats. ex M. E. Jones
  - *A. subvestitus* (Jeps.) Barneby
  - *A. funereus* M. E. Jones
  - *A. utahensis* (Torr.) Torr. & Gray
  - *A. nudisiliquus* A. Nels.
  - *A. inflexus* Dougli. ex Hook.
- Parryani
  - *A. parryi* A. Gray
- Missourienses
  - *A. castaneiformis* S. Wats.
  - *A. consobrinus* (Barneby) Welsh
  - *A. chamaeleuce* A. Gray
  - *A. amphioxys* A. Gray
  - *A. cymboides* M. E. Jones
  - *A. missouriensis* Nutt.
  - *A. accumbens* Sheld.
- Anisus
  - *A. anisus* M. E. Jones

LAYNEANI
- *A. layneae* Green

MOLLISSIMI
- Mollissimi
  - *A. mollissimus* Torr.
- Orthanthi
  - *A. helleri* Fenzl

GIGANTEI
- *A. giganteus* Wats.

MEGACARPI
- *A. megacarpus* (Nutt.) A. Gray
- *A. oophorus* S. Wats.
- *A. beckwithii* Torr. & Gray

LUTOSI
- *A. lutosus* M. E. Jones

PTEROCARPI
- *A. casei* A. Gray ex Brewer & Wats
- *A. pterocarpus* S. Wats
- *A. tetrapterus* A. Gray

DIPHYSI
- *A. lentiginosus* Douglas ex Hook
- *A. iodanthus* S. Wats.
- *A. pseudiodanthus* Barneby

OUTGROUP

DENSIFOLII
- *A. pomonensis* M. E. Jones

TRICHOPODI
- *A. trichopodus* (Nutt.) A. Gray

INFLATI
- *A. douglasii* (Torr. & Gray) A. Gray

Table 2.2. Characters and their states used in the cladistic analysis.

1	Caudex position: 0 = at or above soil surface; 1 = subterranean
2	Duration of plant: 0 = perennial; 1 = short-lived perennial, biennial, or annual
3	Stem growth pattern (ordered): 0 = strongly caulescent; 1 = moderately caulescent; 2 = acaulescent
4	Petiole: 0 = sub-sessile, very short; 1 = well developed
5	Leaflets per leaf (ordered): 0 = greater than 26; 1 = between 5 and 26; 2 = between 3 and 5; 3 = less than 3
6	Leaflet size: 0 = less than 3.9 mm; 1 = greater than 3.9 mm
7	Leaflet folding: 0 = present; 1 = absent
8	Leaflet veination: 0 = midrib visible only; 1 = secondary veins visible; 2 = conspicuously reticulate
9	Leaflet shape: 0 = orbicular-elliptic; 1 = linear
10	Terminal leaflet attachment: 0 = jointed; 1 = confluent
11	Leaflet apex: 0 = rounded; 1 = notched; 2 = acute
12	Stipule connation (ordered): 0 = all free; 1 = connate or amplexical at plant base but free apically; 2 = all connate if only shortly so
13	Stipule texture (ordered): 0 = herbaceous; 1 = papery or membranous; 2 = scarious
14	Leaf pubescence type: 0 = basifixed and appressed; 1 = basifixed and spreading; 2 = medifixed
15	Leaf surface pubescence density: 0 = scanty; 1 = dense
16	Leaf abaxial pubescence density: 0 = scanty; 1 = dense
17	Calyx tube to diameter ratio (ordered): 0 = below 1.3; 1 = between 1.3 and 1.5; 2 = above 1.5
18	Petal color: 0 = white or whitish; 1 = ochroleucous to yellow; 2 = pink to purple; 3 = scarlet
19	Fruit orientation: 0 = erect-ascending; 1 = declined
20	Valve texture (ordered): 0 = membranous to papery, not stiff; 1 = stiffly papery to leathery; 2 = stiffly leathery to woody
21	Valve surface: 0 = smooth or faintly reticulate; 1 = coarsely reticulate
22	Pod drying dark or black: 0 = stramineous to brown; 1 = dark brown to purple, blackish
23	Pod color pattern: 0 = solid; 1 = mottled or speckled
24	Presence of spungy-pithy mesocarp: 0 = absent; 1 = present
25	Fruit septum (ordered): 0 = unilocular; 1 = bilocular but unilocular in the beak; 2 = fully bilocular
26	Fruit persistance: 0 = decidious; 1 = persistant
27	Number of ovules (ordered): 0 = below 14; 1 = between 14 and 18; 2 = above 18
28	Fruit dehiscence: 0 = apical ventral; 1 = apical ventral and through stipe; 2 = ventral and dorsal
29	Stipe: 0 = absent; 1 = present
30	Gynophore (ordered): 0 = absent; 1 = incipient and minute; 2 = present
31	Fruit curvature: 0 = straight, or nearly so; 1 = incurved; 2 = sigmoidal
32	Fruit beak: 0 = absent to cuspidate; 1 = strongly differentiated and upturned; 2 = weakly differentiated and decurved
33	Fruit inflation: 0 = present; 1 = absent
34	Fruit dorsal surface: 0 = smooth; 1 = dorsally grooved; 2 = carinate

Continued on next page

Table 2.2 *Continued*

35	Fruit cross section: 0 = rounded, ob-, or dorsi-ventral compression; 1 = trigonous, triquetrous, or trianglular; 2 = laterally compressed
36	Black caylx hair: 0 = present; 1 = absent or nearly so
37	White calyx hair: 0 = present; 1 = absent or nearly so
38	Pod vestiture: 0 = pubescent; 1 = glabrous or nearly so
39	Flowers per inflorescence (ordered): 0 = below 3; 1 = between 3 and 22; 2 = above 22
40	Flower orientation: 0 = ascending; 1 = declined
41	Keel length (ordered): 0 = less than 22 mm; 1 = between 22 and 29 mm; 2 = above 29 mm
42	Keel incurvature (ordered): 0 = below 40 degrees; 1 = between 40 and 75 degrees; 2 = between 75 and 110 degrees; 3 = above 110 degrees
43	Banner recurvature (ordered): 0 = less than 15 degrees; 1 = between 15 and 32 degrees; 2 = between 32 and 60 degrees; 3 = greater than 60 degrees
44	Anther size (ordered): 0 = between 0.4 and 1.0 mm; 1 = less than 0.4 mm; 2 = greater than 1.0 mm
45	Fruit length to diameter ratio (ordered): 0 = less than 3.3; 1 = between 3.3 and 4.2; 2 = 4.2 and 6.5; 3 = above 6.5
46	Fruit ventral surface: 0 = smooth; 1 = dorsally grooved; 2 = carinate
47	Seed coat purple-speckled: 0 = absent; 1 = present
48	Seed coat texture: 0 = smooth; 1 = pitted and/or wrinkled
49	Seed coat lusture: 0 = dull; 1 = lustrus
50	Bracteoles, well developed: 0 = absent; 1 = present
51	Seed coat dark or black: 0 = absent; 1 = present
52	Wing to banner gradation (ordered): 0 = wing more than 5% longer; 1 = wing between 0% and 5% longer; 2 = wing up 12.5% shorter; 3 = wing more than 12.5% shorter
53	Keel to wing gradation (ordered): 0 = keel longer; 1 = keel up to 22% shorter; 2 = keel more than 22% shorter

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species, a significant correlation exists between the number of varieties and the number of polymorphic characters for a species (Kendall's tau = 0.56, $p < .001$). This correlation remains equally significant after the removal of the outlier *A. lentiginosus* with 36 varieties and 12 polymorphic characters.

Eight quantitative and three meristic characters were included in this study in spite of controversy surrounding their usage in cladistic analyses (Baum 1988; Stevens 1991; Thiele 1993). Data for these characters were taken largely from Barneby (1964) rather than directly from herbarium sheets because Barneby's data represents a far greater sampling of individuals than could possibly be achieved in this current study. Barneby presents continuous measures as ranges rather than as means and standard deviations. In order to make use of the gap-coding procedure of Archie (1985), the standard deviation of measures for a species was conservatively estimated by dividing the range by two. Polymorphic coding was used in the few cases when a species exhibited broad variation that overlapped otherwise discrete patterns of variation among other species.

Quantitative and meristic characters were ordered following the suggestion of Thiele (1993). Six qualitative characters, scored based on data from Barneby (1964), were also ordered because variation among species for these characters was derived from the qualitative assessment of underlying continuous variation along a single axis. Among 2862 cells in the data matrix, 20 (<0.7%) had missing data. Among the 135 cells with polymorphic coding, 71 had fewer character states than were possible, potentially providing phylogenetic information (see table 2.3).

A search for most parsimonious trees was undertaken using PAUP* 4 (Swofford 1998) on a Macintosh G-3 computer. A heuristic search strategy was employed using 100 random addition sequence replicates with TBR swapping with the following options in effect: steepest decent, multrees, zero length branches collapsed, and maxtrees set to 20,000.

Table 2.3.
Polymorph
D = 2&3. E

Taxon
argophyllus
zionis
piutensis
deseretianus
callithrix
tephrodes
eurylobus
iodopetalus
shortianus
cyaneus
columbianus
tidestromii
waterfallii
fecnis
mecmexicanu
umbellis
musiniensis
lcanus
newberryi
eurekensis
coccineus
purshii
leucolobus
subvestitus
fumereus
utahensis
nudisiliquus
inflexus
parryi
castaneiform
consobrinus
chamaeleuce
amphioxys
cymboides
missouriensi
accumbens
anisus
layneae
mollissimus
helleri
giganteus
megacarpus
ochrorus
beckwithii
lutosus
casei
pterocarpus
tetrapterus
lentiginosus
iodanthus
pseudiodanth
pomonensis
trichopodus
douglasii

Table 2.3. Taxon by character data matrix. Characters as in Table 2.2. Polymorphic taxa are coded as follows: A = 0&1, B = 0&2, C = 1&2, D = 2&3, E = 0&1&2. Unknown = ?. The last three taxa are outgroups.

Taxon	1111111111222222222233333333334444444444555512345678901234567890123456789012345678901234567890123
argophyllus	00C11100002010112202A0000020001110000010022102 0A01021
zionis	20111100002120112202101000200011100010100221020A01021
piutensis	00C11100002010112201100000200211100000100121010AA1121
desereticus	00111110002011112001100000100211100100100221013??1?22
callithrix	01111000000011112202000000200011110100100121020011021
tephrodes	00C1110000B12A1A220C11000020001110000A100221020AA0121
eurylobus	00C1111000002 11A220211001020001110010 0C00221020AA0121
iodopetalus	00111100002021102202110000200011100101100221020010022
shortianus	00211100000010112202110000200011100100100221020111021
cyaneus	002111100000101122021000002000111200001002210200010 21
columbianus	000111000020A0002002110000200011100011100221A20111012
tidestromii	01C1111000001111200210000020001112001010022112111 10C1
waterfallii	0011110100B0101022010010C021000010100010022122111 1021
feenis	01111100000021102201 1000C020001011110010012122011 0021
neomexicanus	000101000020111122A11000102000101000001102210200011 31
uncialis	00212110002012112201000000200011120100001121020A11021
musiniensis	00212010002012112201000100200011100000000121010110021
loanus	00211110000012112001000000200111000000010022101???0?21
newberryi	0021111000B022112201100000200211100000 10A121000A11121
eurekensis	00211100002012112102100000200011100000100C21020010021
coccineus	0021110000B011112301000000200011100000 1020120B0A00120
purshii	00211100002021112E01A100A02002111A0000 1002210E1A00121
leucolobus	00111100002021112202100010200111111A100100221020111021
subvestitus	0011110000B011112001100010000011100100100221000100021
funereus	00111100000011112201100000000011100100101121000001020
utahensis	00011100000011112201100000200211100100100221110011121
nudisiliquus	0001110000B011112202000000200011100100100221000101121
inflexus	0000110000B011112202100000200211110100100221010A00121
parryi	0000110A000011A020021000002000111100001001211100010D1
castaneiformis	0021110000B012112001000000 2000A010000010022102 0A11121
consobrinus	0021110000B012112001000000 2000A010000010022102 0A11122
chamaeleuce	00C1111000001211 2C011111002000001 0000A100221020111021
amphioxys	0111110000B01211220211A0002200A11200001002211201110 21
cymboides	0021111000B012112A0101010020000012200010022102011 0021
missouriensis	00C1111000BAC211220211000121000A12E000100221020111021
accumbens	00111100000012112101110001210000121000 10033002???0?01
anisus	00111100000012112201100120220000100100100121010001121
layneae	10011100000011112001101 0C020011111A010200221321111021
mollisimus	01C1A100000011112E0C1000102000AAA10000CA0211011101121
helleri	00110100000011112301100020200??0110100101001 0????0?D1
giganteus	0001A0100020011121020000112000101001012102210 10000121
megacarpus	00111111000010002B0000100020020000000010022100010 1121
oophorus	0001111000E010002C1000100020020000010111023100010 1021
beckwithii	0000111100E010000C0200101020021A1A0101100231020001122
lutosus	10011100000211102B0000000021020000000A00221010000021
casei	10001100A1E1001122111110002101101200 1A100221C20A01031
pterocarpus	1000300011210011221111100002101A1120001100221020A11031
tetrapterus	1000110010210000 2E1111100021011112000A100221120111031
lentiginosus	0A01111A00E010002E010010102000AA0A000AC002210A1AA0121
iodanthus	0000110100000000 2B1110101021001 11AA000100121200AA1121
pseudiodanthus	1000110000001110121A1110101000111100001002211001000 21
pomonensis	0000011100000000 0A0000000020000000000021022101010 0021
trichopodus	0000A10A000010001A1000000121200 0A020002102210A0A011D1
douglasii	00011100000000AA0A0000100020010A00000AC002310A0A0?021

2.3 RESU

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2.3 RESULTS

The search uncovered 12 most parsimonious trees of 489 steps, including autapomorphies with a consistency index (excluding uninformative characters) of 0.47 and a retention index of 0.51. Although these values seem low, it should be pointed out that these two measures are highly correlated with each other and are significantly negatively correlated with the number of study taxa. The consistency index is in line with other morphological cladistic studies of plants (Sanderson and Donoghue 1996). The strict consensus tree (figure 2.1) is well resolved and contains only three unresolved nodes with three branches each. A randomly chosen tree among the 12 most parsimonious trees is shown in figure 2.2.

Contrary to assumptions made about relationships among the ingroup and outgroup taxa, four *a priori* chosen ingroup taxa, the three species of section *Megacarpi*, and *A. lentiginosus* of section *Diphysi*, are nested among the outgroup taxa. Among the three taxa chosen as outgroups, *A. pomonensis* and *A. trichopodus*, both members of the Pacific Piptolobi, form a clade, whereas *A. douglasii* is several nodes from the branch leading to the other two outgroups. For purposes of rooting, the branch leading to *A. pomonensis* and *A. trichopodus* was used because it leads to two of the three chosen outgroups (see figure 2.1).

Section *Diphysi* is polyphyletic with the widespread species *A. lentiginosus* placed among the outgroup taxa and the remaining taxa, *A. iodanthus* and *A. pseudiodanthus*, as highly derived taxa within the tree. Sections *Mollissimi*, *Pterocarpi*, and *Megacarpi* are monophyletic (although *Megacarpi* is nested among outgroup taxa). Section *Argophylli* is paraphyletic with four sections, *Layneani, Gigantei*, *Pterocarpi,* and *Mollissimi*, and the two species of *Diphysi* nested within. This monphyletic assemblage, plus the monotypic section *Lutosi,* are members of a lineage designated here as the Argophyllean Clade.

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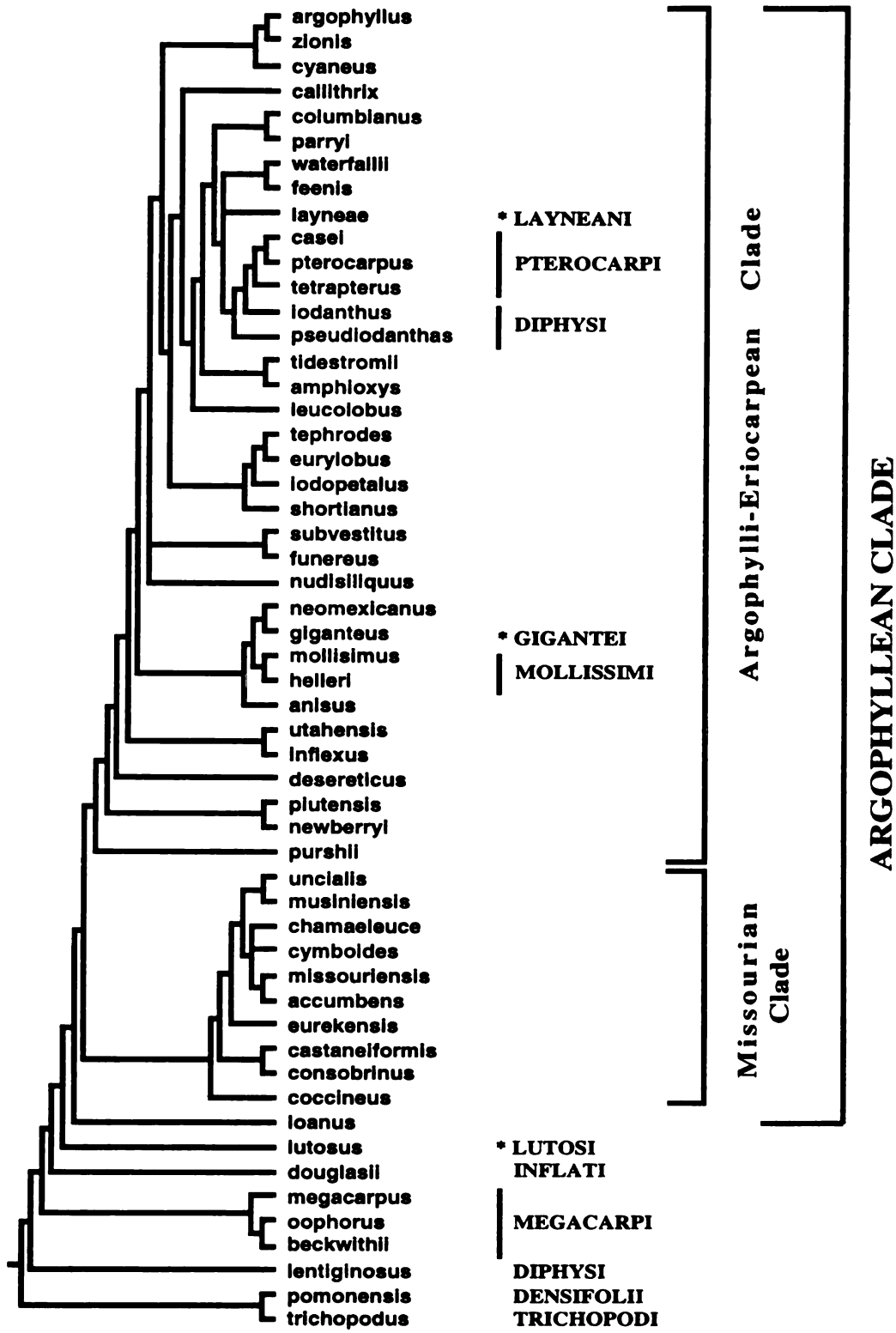


Figure 2.1 Strict consensus of 12 most parsimonious trees recovered. Sections names are in all capital letters. Monotypic sections are denoted by (*).

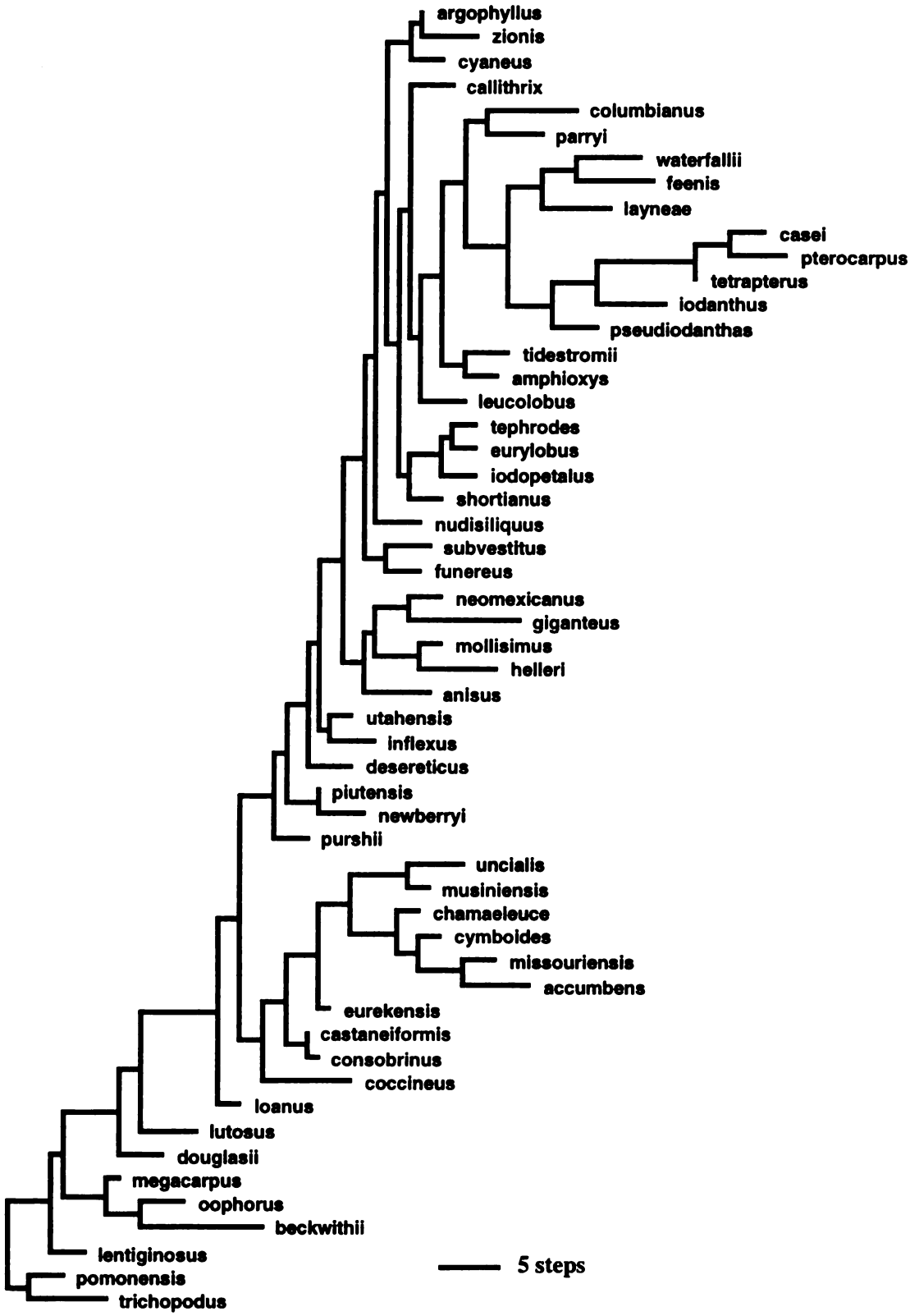


Figure 2.2 A randomly chosen tree among the 12 most parsimonious trees. Branch lengths are proportional to inferred evolutionary changes.

The Argophyllean species are found principally in two sub-clades that correspond well with Barneby's subsections in section *Argophylli*. The Missourian Clade includes 10 of the 13 species of subsections *Missourienses*, *Newberryani*, and monotypic section *Coccinei*. The Argophylli-Eriocarpean Clade, with 35 species, includes five sections (discussed above), the species of subsections *Eriocarpi* and *Argophylli* (both of which are paraphyletic), the monophyletic subsection *Pseudoargophylli*, plus the three remaining monotypic subsections, *Parryani*, *Neomexicani*, and *Anisi*. *Astragalus amphioxys* and *A. newberryi* are dispersed within the later clade while *A. loanus* is basal to both.

Assessment of support for phylogenetic findings presented here met with computational limitations. Both bootstrap and decay analyses were attempted but were truncated due to tree buffer overflow. This is not surprising given the large number of taxa, the low character to taxon ratio, and the high level of homoplasy in the data set.

2.4 DISCUSSION

Results correspond well with Barneby's (1964) taxonomy, which can be regarded as a coarse phylogenetic hypothesis, at least for higher levels. Nearly all sections and subsections were found to be monophyletic or nearly so if a few modification are made. The most notable exceptions are section *Argophylli*, and subsections *Argophylli* and *Eriocarpi*, which are paraphyletic with numerous small sections and subsections nested within. These findings are not surprising in light of Barneby's tendency to put the more divergent species in their own sections or subsections.

Perhaps the most significant finding of this study is the placement of section *Megacarpi* (three species) and *A. lentiginosus* between *A. douglasii* and the two outgroup taxa used for rooting, *A. pomonensis* and *A. trichopodus*. The placement of *Megacarpi* and *A. lentiginosus* is contrary to the results of Sanderson and Doyle (1993), and in the case of *A. lentiginosus*, is contrary to the results of Wojciechowski *et. al.* (1993).

Astragalus oophorus, a member of section *Megacarpi*, and *A. lentiginosus* were placed in highly derived positions nested well within the L-fP clade, according to results reported by Sanderson and Doyle (1993).

Explanations for these contradictory results include several possibilities. The placement of *A. lentiginosus*, a species in section *Diphysi*, near the base of the tree may be due to the high number of polymorphic characters--12 for the species. Eight of the twelve characters are polymorphic for all character states, rendering them equivalent to missing data. The two other species of section *Diphysi*, *A. iodanthus* and *A. pseudiodanthus*, were placed in a highly derived position within the Argophyllean clade. To the extent that *Diphysi* is a good group and that the number of polymorphic characters for *A. lentiginosus* resulted in basal placement of the species, these findings are consistent with those of the above molecular studies. Interestingly, Barneby placed *A. lentiginosus* in the Small-flowered Piptolobi sub-phalanx where the designated outgroup species *A. douglasii* is found.

Another explanation for these findings results from the choice of outgroup taxa, one species from the Small-flowered Piptolobi, and two species from the Pacific Piptolobi. The relationship among these two sub-phalanxes with respect to the Large-flowered Piptolobi may be more complex than either Barneby's taxonomy or previous molecular studies would suggest. More importantly, results presented here suggest that the Large-flowered Piptolobi (as modified for this study) is not monophyletic, in spite of findings from molecular studies. In his discussion of the Piptolobi phalanx, Barneby suggests that the various species can be advantageously grouped into series and presumably phylogenetic affinity, but he acknowledges the difficulty of placement of the Pacific Piptolobi because they have attributes of both the Large- and Small-flowered Piptolobi.

Perhaps more telling than the placement of the above lineages is that fact that assessment of support values (bootstrap and decay indices) failed to conclude due to the number of trees generated in the analysis. Although it is common for large numbers of

trees to be produced when character/taxa ratios are low, it is also possible that levels of homoplasy are sufficiently high such that assessment of the robustness of the phylogenetic reconstruction is inhibited. Indeed, given the evidence that *Astragalus* is part of a larger clade (together with the genus *Oxytropis* and other members of the tribe Galegeae) that has undergone an increase in diversification rates relative to sister groups, it is entirely possible that diversification has proceeded more rapidly than the evolution of characters assessed in this study. This explanation is consistent with the findings that no molecular markers have yet been found adequate for resolving among species relationships within the genus (Sanderson, per. com.)

Future studies aimed at assessing monophyly of the sub-phalanxes and their relationships to one another will be needed before more definitive conclusions can be drawn about this group. Nevertheless, findings here and elsewhere lend considerable support to the conclusion that a large majority of Large-flowered Piptolobi species form a monophyletic clade, notwithstanding the few modifications mentioned above. The relationship of the L-fP clade to other Piptolobi awaits future studies.

Results from this study provide evidence for the utility of morphological characters for elucidating relationships among species in *Astragalus*. A few qualifications are offered, however. First, the effect of a low character to taxa ratio, which leads to short branch lengths, needs to be addressed to overcome the problem of assessing support. Addressing this issue by analyzing a smaller study group is likely to help but undoubtedly will result in some characters becoming uninformative. Second, as was concluded by Sanderson (1991), high levels of homoplasy among morphological characters in *Astragalus* are likely to frustrate efforts to resolve relationships among larger groups. Perhaps the greatest future utility of morphological features will derive from the discovery and assessment of new features hitherto not used in phylogenetic studies such as this.

An additional consideration regarding the use of morphology stems from the common finding that phylogenetic hypotheses based on morphology frequently do not correspond

to those based on molecular data. The assessment of new morphological characters combined with more refined choices of ingroup and outgroup taxa are likely to lead to more robust hypotheses of relationships. The same can be said for the discovery of molecular markers with sufficient variation for inferring among species relationships. Progress developing both these lines of evidence and a combined analysis may yield stronger hypotheses.

In summary, phylogenetic results correspond well with Barneby's (1964) taxonomic concepts after a few modifications. Some results are contrary to previous molecular findings. Morphological data have proven very useful in resolving among species relationships. However, results should be considered preliminary because of the difficulty in assessing support as well as issues concerning the relationship between the ingroup and the outgroup taxa. More definitive conclusions about relationships within and among the Large-flowered Piptolobi await better taxon sampling and additional data.

3

Rarity and the Biogeography of the Large-Flowered Piptolobi of *Astragalus* L.

3.1 INTRODUCTION

For centuries, biologists have catalogued and studied the spatial distribution of organisms. As new concepts regarding distribution patterns have emerged and the processes leading to these patterns have been elucidated, new spatial measures have also been developed. At least a dozen biogeographic measures have been used to characterize range size during the last two decades (Gaston 1994).

The choice of geographic measures and measurement scales depends on both the aims of the study and practical limitations. An unfortunate consequence of the wide variety of measures and scales that have been used is that comparisons among studies are often difficult. This condition is improving, however, due to recent trends in collecting and storing biogeographic data.

Distributional point data are now emerging as one of the most useful forms for quantifying spatial distributions for a number of important reasons. Point data can represent a variety of attributes about an organism, depending on the goals of the

investigator. For example, points can be used to represent individuals or collections of individuals for studies focused at local scales. Points can also be used to represent populations or collection localities for larger scale studies. Furthermore, other parameters can be linked to the points, such as dates, measurement scales, and error estimates.

Equally important is the convertibility of point data into other biogeographic quantities, including abundance and range size measures such as area of occupancy and area of extent. Recent advances in Geographical Information Systems (GIS) software technology have significantly reduced the difficulty of converting point data into these biogeographic parameters.

Another important trend in studies of geographic distributions is the increasing use of grids for summarizing the range size of organisms and for calculating species richness. Range size in the form of area of occupancy is generally based on the presence or absence of organisms within grid cells and is simply the number of cells occupied multiplied by the cell area. For convenience, many use grids that correspond to latitude and longitude lines. This methods works well for small and local areas, but at larger scales, grids need to be based on equal area cells to control for diminishing cell sizes as the poles are approached.

The use of area of occupancy measures to summarize point data has two important benefits: 1) the area can be summarized at any scale of interest as long as the cell size is not smaller than the scale in which the data was collected or substantially larger that the overall geographic extent; and 2) the use of multiple scales can be examined to determine the fractal properties of an organism's distribution.

In spite of these benefits, summarizing point data in the form of area of occupancy has a drawback that is commonly overlooked. The measure, when based on arbitrarily placed grids, can result in high levels of sampling error among organisms found at few localities and with small range sizes. This problem is particularly worrisome in studies purporting to compare rare and widespread species. For example, if an organism is

found at four localities that are less distant from each other than the distance across a grid cell, the calculated area of occupancy can vary by a factor of four, depending on where the grids are placed. This problem can be eliminated by testing different placements of grids to find the minimum area of occupancy measures.

In this chapter, I explore how grid size and placement affects the area of occupancy measures based on distributional-dot data for 51 species of the Large-flowered Piptoloboid (Lf-P) group of *Astragalus* (discussed in Chapter 2). Results are used to quantify the fractal geometry of the species distributions as well as for classifying their range-size rarity. Seven specific questions are addresses for the study group: 1) How do area of occupancy measures based on the arbitrary placement of grids compare with grids placed to minimize the number of grid cells occupied? 2) How does this latter measure compare with area of extent measures? 3) Which of the species meet the rarity criteria used by the International Union for the Conservation of Nature's (IUCN) *1997 Red List of Threatened Plants*? 4) How do area of occupancy measures compare when different measurement scales are used? 5) Are the species' distributions fractal and how do they compare? 6) How do values of species richness compare based on different measurement scales? and 7) Where are the most species rich areas located?

3.2 STUDY SYSTEM AND METHODS

3.2.1 The Large-flowered Piptolobi of *Astragalus*

Barneby's (1964) revision of the North American members of *Astragalus* provides the data for this study. Barneby presents distributional point maps of nearly every species covered in the revision based on more than 25 years of study that included thousands of specimens from the field and from herbarium collections.

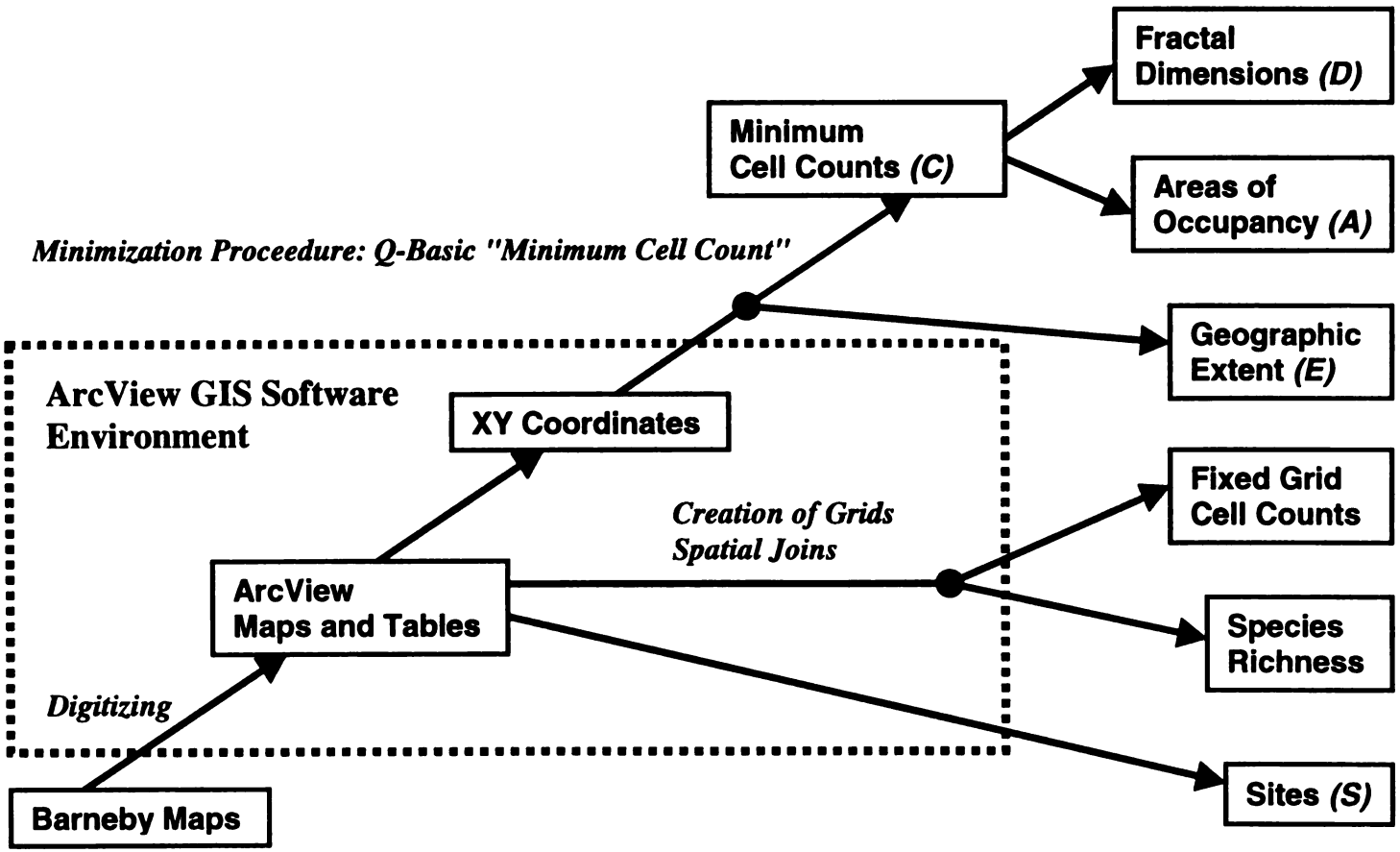
3.2.2 Data handling in the ArcView GIS environment

Geographic data were digitized and a large proportion of data manipulations were done within the ArcView 3.x GIS software environment (Environmental Systems Research Institute 1998), as shown in figure 3.1. Approximately 3000 points representing localities derived from Barneby's distributional point maps were utilized. Point data, hereafter called sites and denoted by ***S***, were entered as latitude-longitude positions. ArcView maps were manipulated using an equal-area cylindric map projection as shown in figure 3.2 . The "equal-area cylindric" projection was chosen because meridians are perpendicular to latitude circles throughout the map area.

A series of nine fixed position grids were created using an Avenue script (the programming language used within the ArcView environment) created specifically for this procedure by the programming staff at Environmental Systems Research Institute (ESRI). This script, "GridPoly," appears in Appendix B. Beginning with 10 km x 10 km square cells (100 km^2), a sequence of grids was created, with each cell larger in area than the preceding one by a factor of four. A total of nine grids were created with the largest cell size equaling 6,553,600 km^2. Linear dimensions of these cells are referred to as the scale of measure and are symbolized by ***J***. Scales began at 10 km and continued to 2,560 km.

The location of the initial 10 km grid was chosen randomly. From this initial position, additional grids were created such that cells at smaller scales nested perfectly within the cells at higher scales. Table 3.1 provides details about the scales, areas of measure, and number of cells created for this study. Figure 3.3 shows the overall distribution of the group together with the 320 km grid (cell area = 102,400 km^2), whereas figure 3.4 shows the 40 and 80 km scale grids overlaying Utah. Point data, corresponding to sites ***S***, were linked to the individual cells in the grids using the ArcView "spatial join" feature. This feature creates database linkages among attributes that overlap grid cells. The number of cells occupied for each of 51 species at 9 spatial

Figure 3.1
Flow chart showing relations and sequence of data transformation



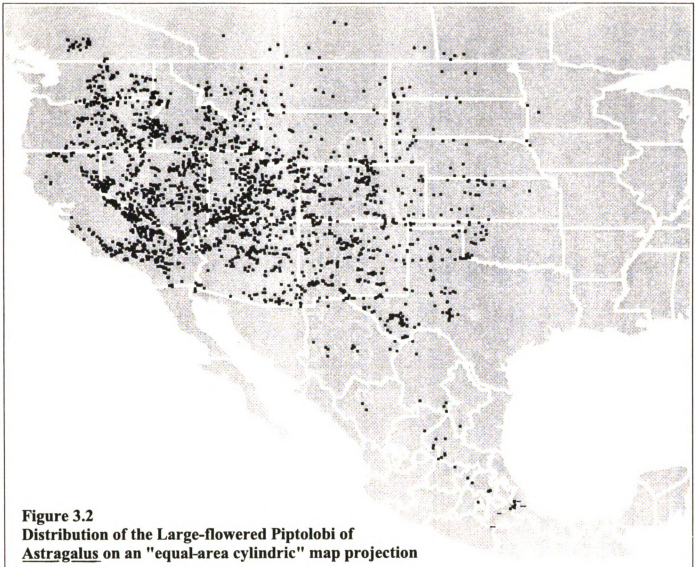


Figure 3.2
Distribution of the Large-flowered Piptolobi of
Astragalus on an "equal-area cylindric" map projection

Table 3.1 Scales, measurement areas, and number of grid cells used in this study.

Scale (J) in km	**Measurement area (J^2) in km^2**	**Number of grid cells**
10	100	102,400
20	400	25,600
40	1,600	6,400
80	6,400	1,600
160	25,600	400
320	102,400	100
640	409,600	25
1,280	1,638,400	6+
2,560	6,553,600	1+

Figure 3.3 320 km grid overlaying western North America

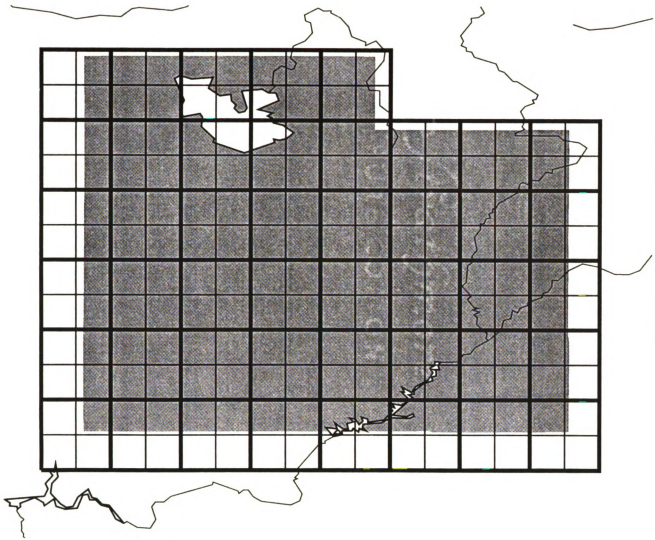


Figure 3.4
Grids overlaying Utah

scales was tabulated. Species richness values for each cell were also tabulated. Equal-area normalized coordinates for each site were exported for use in determining minimum cell counts and geographic extents.

3.2.3 Minimum cell counts, area of occupancy, geographic extent, and fractal dimensions

Minimum cell counts C were determined by the following procedure. Grids were numerically moved in a 2 km step search procedure in both the X and the Y directions until all possible unique positions were assessed. The smallest cell counts were retained. At the 10 km scale, 25 different positions were assessed. Each larger scale was also searched using 2 km steps resulting in four times the number of positions assessed compared to the previous scale. This procedure was carried out with "Minimum Cell Count," written in Q-Basic specifically to accomplish this search (see Appendix C). Minimum cell counts are referred to simply as cell counts and are denoted by C_j for scale of measure J.

A species area of occupancy at each scale J, denoted by A_j, was calculated by multiplying the cell counts by J^2 (referred to as the measurement area). Each species had up to nine measures for area of occupancy depending on the geographic extent of the species.

The geographic extent of each species, denoted by E, was calculated by multiplying the coordinate range in both the X and the Y directions. Range values were rounded up to the nearest 10 km because the smallest cells were created with a measurement scale of 10 km. Measurement scale bias is thus kept constant among area measures.

A summary of measures is as follows:

- S = Sites: number of localities recorded by Barneby (1964).
- J = Scale: linear dimension of grid cell
  [10, 20, 40, 80, 160, 320, 640, 1280, & 2560 km]
  Little j used as a scale identifier.
- J^2 = Measurement area at scale J.
- C_j = Cell count or cells occupied at scale J
- A_j = Area of occupancy at scale J. $A = CJ^2$.
- E = Geographic extent.

A comparison of fixed grid versus minimized area of occupancy measures was carried out using cell counts directly for scales J = 10 and 160 kms. Correlations, both Spearman and Pearson, were run to assess relations among sites S, cell counts C_{10}, and geographic extent E. In order to assess at which scales the largest changes occurred in the rank order of species by area of occupancy A, each scale was compared with the next larger scale using a sequential ranking procedure. Ordinary ranks, which give ties the same average rank, introduce a large amount of variation at higher scales not pertinent to these comparisons. Sequential ranks provide a unique rank for each species and, in the case of ties, do not change the ranks used at the previous scale. The sequential rank procedure was accomplished by first sorting species by A_{10} and then assigning ranks. Next, species were sorted first on A_{20} and second on A_{10}, followed by ranking. This series of steps continued until ranks were assigned at all scales. A count of rank changes and the magnitude of changes were calculated for each pair of scales compared.

Area of occupancy A was used to calculate the fractal dimensions D of each species using the following equation (Peigten *et. al.* 1992):

$$D = \frac{\partial \log A}{\partial \log J^2} \qquad (3.1)$$

where J^2 is the measurement area. This equation can be reorganized into:

$$D_{j_1 j_2} = \frac{Log\ A_{j_1} - Log\ A_{j_2}}{Log\ J_1^2 - Log\ J_2^2} \qquad (3.2)$$

where J_1^2 and J_2^2 are the scales of measurement.

Another frequently used fractal dimension is the box-counting dimension D_B, used specifically for count data. The dimension D is numerically related to D_B in the following way (Peigten *et. al.* 1992) and is presented here for comparisons with other studies:

$$D_B = 2 - 2D \qquad (3.3)$$

Fractal dimensions were calculated for each pair of sequential scales using equation 3.2 and resulted in eight comparisons for each species. Log J^2 was plotted versus log A_{10} to express the fractal dimension as the slopes of the lines connecting the individual points for a species.

The degree to which a species distribution is fractal was assessed by calculating the standard deviation among a sequential triplet of dimensions (four sequential scales).

Standard deviations of zero are considered perfectly fractal, whereas standard deviations between zero and 0.05 are considered nearly fractal.

3.2.4 Species richness

Species richness values, that is, the number of species represented in a grid cell, were tabulated for each fixed grid cell at each scale. Means, variances, and coefficients of dispersion (CD) were calculated among all cells (when occupied) within a given scale. Kolmogorov-Smirnov tests for goodness of fit with respect to a Poisson distribution were carried out.

3.2.5 Categories of rarity used in this study

Rare categories were defined in terms of two measures: area of occupancy A_{10} and geographic extent E. Using both the IUCN Red List guidelines as well as guidelines adopted by the Joint Nature Conservation Committee, the criteria are defined as follows:

- Very Rare, ***R1*** $A < 100$ km^2 $E < 100$ km^2
- Rare, ***R2*** 100 km^2 $< A <$ 500 km^2 100 km^2 $< E <$ 5000 km^2
- Somewhat Rare, ***R3*** 500 km^2 $< A <$ 2000 km^2 5000 km^2 $< E <$ 20000 km^2
- ***Common*** 2000 km^2 $< A$ 20000 km^2 $< E$

3.3 RESULTS

3.3.1 Fixed grid versus minimum cell counts

Nearly all species in the study showed significantly higher cell counts based on fixed grids compared to minimized cell counts. Figure 3.5 shows levels of inflation at scales 10 and 160 km for all species in the study. Average inflation error at the smallest scale of 10 km is 14%, whereas at the intermediate scale of 160 km is 49%. Overall, inflation rates are largest for species with the smallest distributions and inflation rates rise as the measurement scale increases.

The cell count measures for the species *Astragalus helleri* found in Vera Cruz, Mexico, provide a good illustration of the error introduced by using arbitrarily placed fixed grids. Figure 3.6 shows the locations of the three sites and the position of the fixed grids for scales J = 160 and 320 km. As chance would have it in this case, the three sites for the species fall in three different 160 km cells, even though they are at most 36 km apart. The intersection of grid lines happens to fall within the triangle created by the three points. A comparison of fixed grid and minimized cell counts show sizable inflation through the 160 km scale (see table 3.2).

3.3.2 Geographic measures and resulting rare categories

Species values for number of sites S, minimum cell counts C, and geographic extents E, are given in table 3.3. Cell counts for areas larger than a species' geographic extent are by definition equal to 1 and are indicated with shading in table 3.3. The four rarest species (*A. desereticus, A. columbianus, A. eurylobus, A. accumbens*) have geographic

Figure 3.5
Fixed grid cell count inflation
compared to minimum cell counts

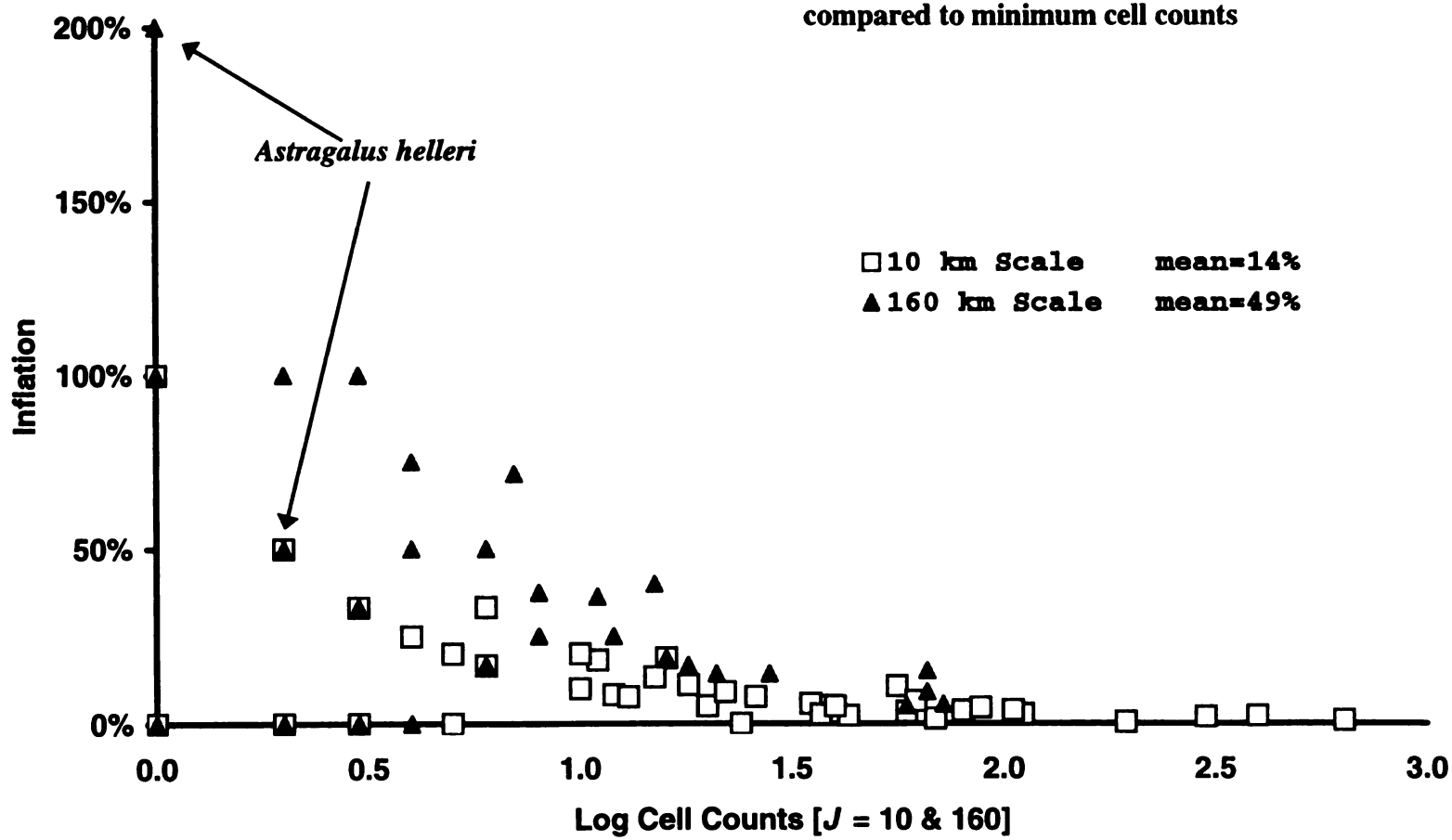


Figure 3.6
The three sites of Astragalus helleri in Mexico

Table 3.2 Comparison of fixed grid and minimized cell counts for *Astragalus helleri*.

Cell Counts	Scale of measure *(J)*								
	10	**20**	**40**	**80**	**160**	**320**	**640**	**1280**	**2560**
Fixed grid	3	3	3	3	3	1	1	1	1
Minimized	2	2	1	1	1	1	1	1	1
Inflation	50%	50%	200%	200%	200%	--	--	--	--

Table 3.3 Sites *S*, minimum cell counts *C*, and geographic extent *E* for each species. Sorted by C_{10} values. Area of occupancy *A* (km^2) is equal to CJ^2. Shaded cells are scales that are larger than the species' area of extent.

Species Code	*Sites (S)*	Cells counts *(C)* at scale *(J)*, in kilometers									Geographic Extent *(E)* $(km)^2$
		10	20	40	80	160	320	640	1280	2560	
dese	*1*	1	1	1	1	1	1	1	1	1	100
colu	*1*	1	1	1	1	1	1	1	1	1	100
eury	*2*	1	1	1	1	1	1	1	1	1	100
accu	*2*	1	1	1	1	1	1	1	1	1	100
unci	*2*	2	1	1	1	1	1	1	1	1	400
fune	*3*	2	1	1	1	1	1	1	1	1	200
loan	*3*	2	2	1	1	1	1	1	1	1	400
hell	*3*	2	2	1	1	1	1	1	1	1	400
call	*3*	2	2	2	2	1	1	1	1	1	4,800
subv	*3*	3	2	2	2	1	1	1	1	1	2,700
pter	*4*	3	2	2	2	2	1	1	1	1	5,400
neom	*5*	4	3	3	1	1	1	1	1	1	3,500
luto	*5*	5	4	2	2	1	1	1	1	1	4,200
cons	*5*	5	5	4	2	1	1	1	1	1	9,900
anis	*6*	5	4	2	1	1	1	1	1	1	700
pseu	*6*	5	4	3	3	2	1	1	1	1	22,000
feen	*7*	5	5	4	3	1	1	1	1	1	9,900
cyan	*7*	6	3	3	2	1	1	1	1	1	6,000
leuc	*8*	6	4	3	2	1	1	1	1	1	12,800
iodo	*11*	10	8	7	6	2	1	1	1	1	47,500
giga	*12*	10	8	7	6	3	3	1	1	1	294,000
musi	*12*	10	9	7	5	3	1	1	1	1	46,800
cymb	*13*	10	7	5	3	2	1	1	1	1	13,300
wate	*14*	11	9	8	6	4	2	1	1	1	203,500
zion	*16*	12	9	7	5	3	2	1	1	1	40,000
nudi	*14*	13	8	5	4	2	1	1	1	1	29,700
cast	*15*	13	10	8	4	2	1	1	1	1	55,100
eure	*17*	15	14	10	5	2	1	1	1	1	34,500
tide	*20*	16	10	6	4	2	1	1	1	1	50,400
tetr	*21*	18	15	13	10	6	3	2	1	1	374,400
piut	*22*	20	16	12	7	4	2	1	1	1	77,700
case	*25*	22	16	12	8	4	2	1	1	1	107,300
mega	*25*	24	20	16	12	7	4	2	1	1	588,000

Continued

Table 3.3 *continued*

cocc	***30***	26	22	14	10	6	2	1	1	1	225,000
parr	***39***	35	30	19	10	4	2	1	1	1	79,200
cham	***43***	37	28	23	12	6	3	1	1	1	144,400
shor	***41***	39	32	22	13	8	4	2	1	1	434,000
layn	***46***	40	31	23	13	6	3	1	1	1	148,500
infl	***60***	43	33	23	14	8	4	2	1	1	199,500
teph	***64***	56	45	35	22	11	5	2	1	1	496,800
utah	***64***	59	50	39	21	8	4	2	1	1	318,200
ioda	***68***	62	51	41	26	12	4	2	1	1	374,400
ooph	***72***	69	59	48	31	16	7	3	2	1	634500
argo	***87***	80	71	57	38	21	9	4	2	1	1,092,000
beck	***97***	88	76	57	35	18	8	4	1	1	1,379,400
amph	***114***	105	92	69	38	15	7	3	1	1	792,000
newb	***119***	111	98	82	59	28	11	5	2	1	1,626,200
miss	***201***	194	179	151	117	66	25	9	4	1	3,569,600
moll	***320***	300	262	210	142	66	23	9	3	1	4,275,000
purs	***426***	397	337	241	132	59	21	8	3	1	3,376,800
lent	***739***	637	505	345	188	72	24	7	3	1	3,013,200

extents equal to 100 km^2, the smallest measurement area and smallest scale used in this study.

Spearman and Pearson correlations among sites S, cell counts C_{10}, and geographic extent E, are shown in table 3.4. Among the three pairwise comparisons, a nearly perfect correlation was found between sites S and minimum cell counts C_{10}. Figure 3.7 shows histograms of sites and cell counts. Figure 3.8 shows histograms of areas of occupancy A_{10} and geographic extent E. Figure 3.9 is a bivariate plot of the latter. Kolomogorov-Smirnov tests for normality returned the following probabilities: log S = 0.978; log C_{10} = log and A_{10} = 0.944; log E = nil. Assuming 95% confidence levels, normality for the log number of sites S is not rejected while log cell counts C_{10} and log areas of occupancy A_{10} are just marginally rejected. Normality for log extent E is rejected.

Species in this study were categorized for rarity by area of occupancy A_{10} and geographic extent E. A summary of results appear in table 3.5, with dual-categorical tabulation presented in table 3.6, which has been formatted to correspond with figure 3.9. Rare categories for individual species appear in Appendix A. The locations of the 17 species categorized as "rare" or "very rare" for at least one type of measure are mapped in figure 3.10. The four "very rare" species, R1-R1 categories, are coded black on the map. These species are very rare by both measures. Nine species fall in the "rare" category, R2-R2 for both measures, and are coded light gray. Four additional species are in the R2 category for area of occupancy but are either "somewhat rare," R3, or "common" in terms of geographic extent. These species are thus considered "rare" by only one category and are also color-coded light gray.

Table 3.4 Spearman (Pearson) correlations among the three principal geographic measures.

	Log sites S	Log minimum cell count C_{10}
Log minimum cell count C_{10}	.997 (.996)	
Log geogrphic extent E	.956 (.934)	.958 (.941)

Figure 3.7
Number of sites and minimum cell counts C_{10}

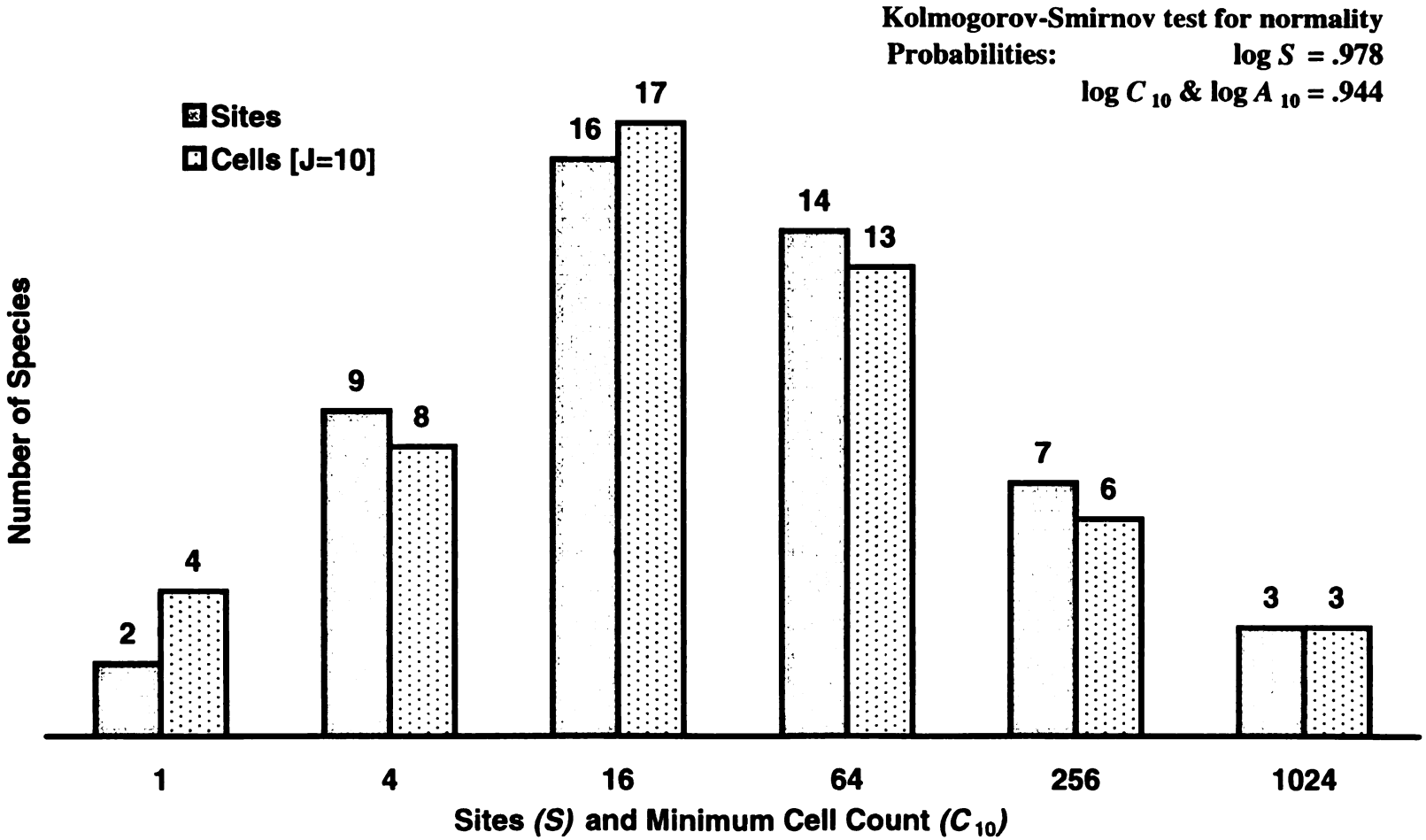


Figure 3.8
Area of occupancy A_{10} and Geographic extent E

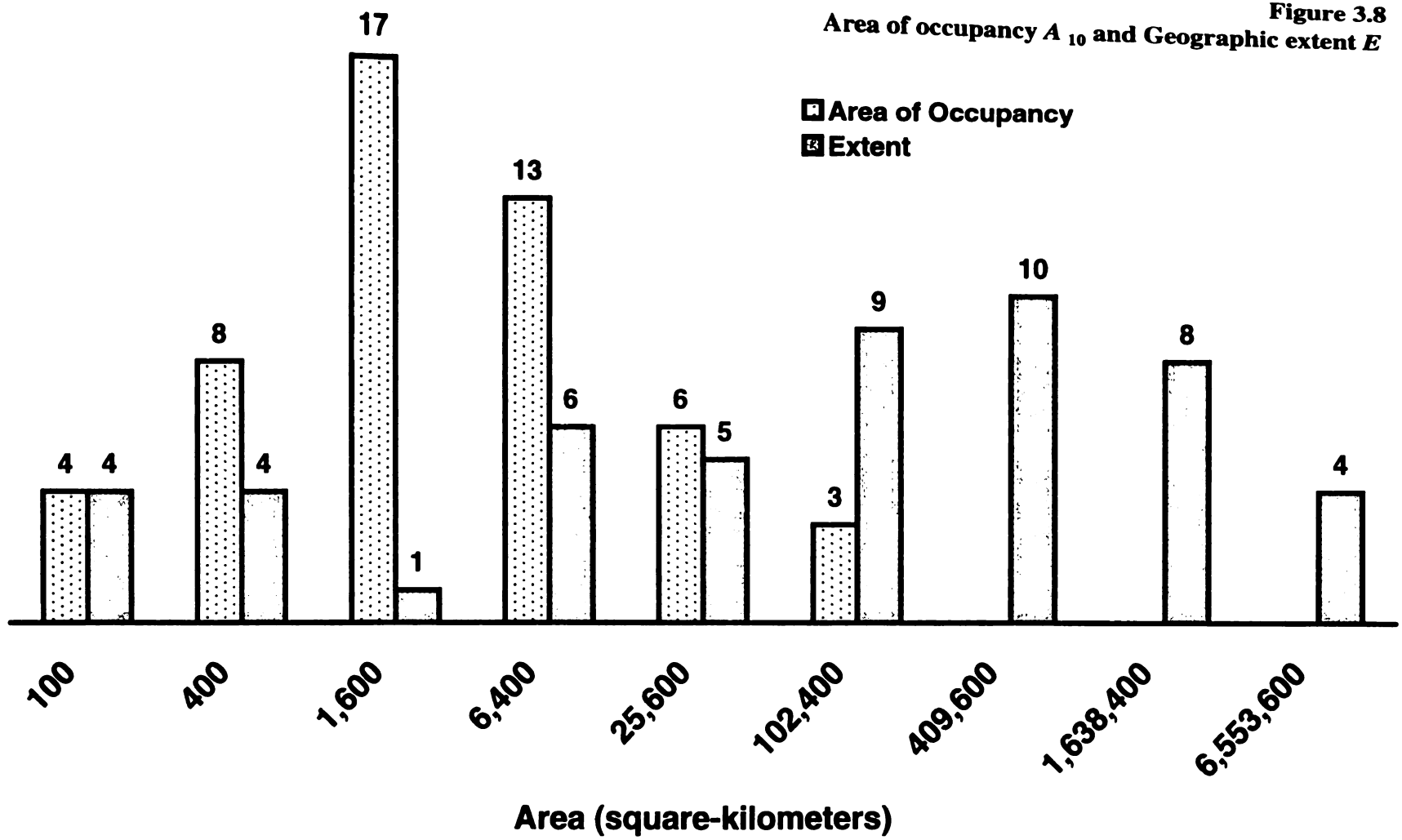


Figure 3.9
Log area of occupancy A_{10} versus Log geographic extent E

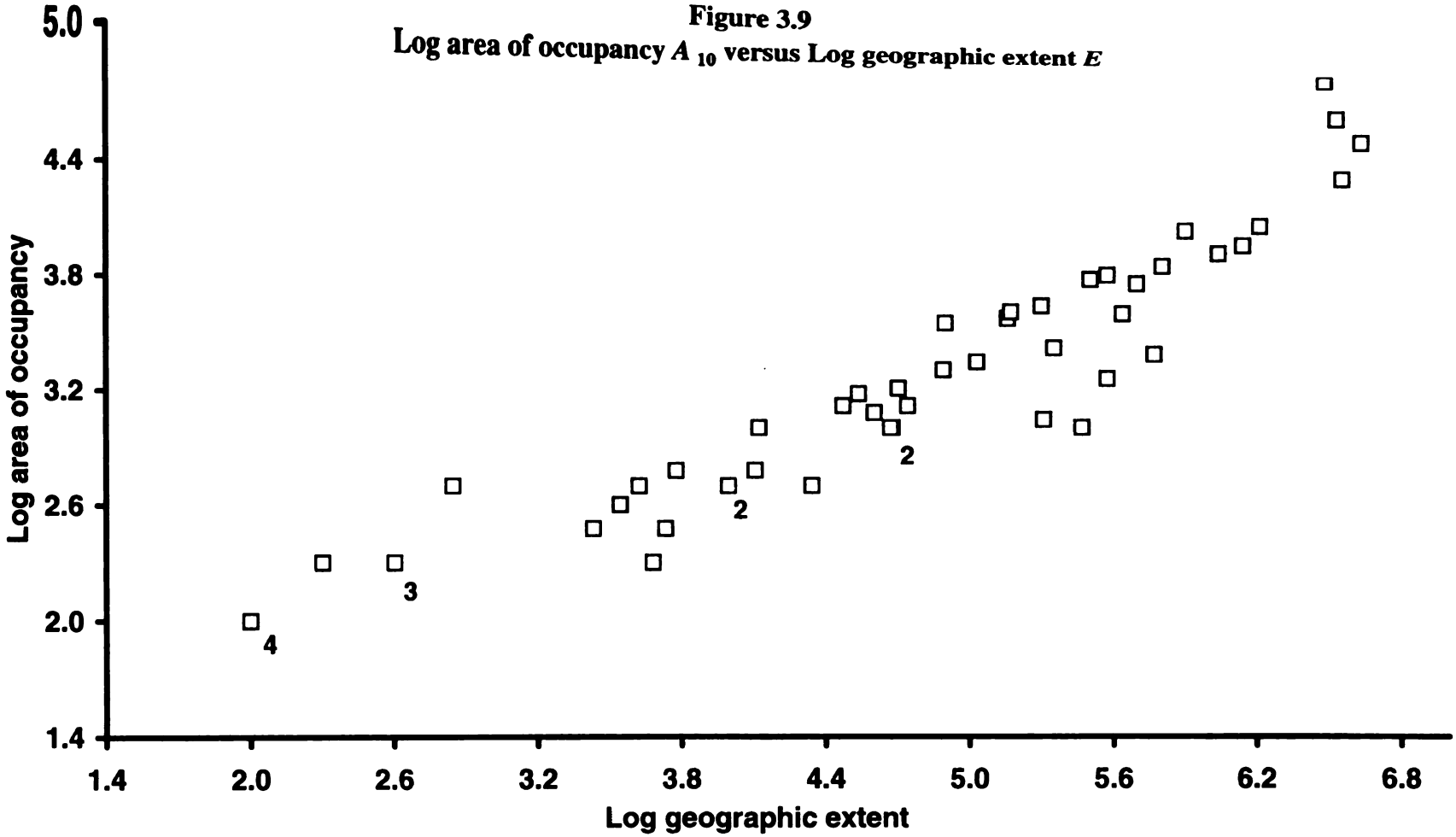


Table 3.5 Categories of rarity applied in this study.

	Area of Occupancy (A_{10})		Geographic Extent (*E*)	
Category	**Criteria**	**In Study**	**Criteria**	**In Study**
R1	≤100 km^2	4 (8%)	≤100 km^2	4 (8%)
R2	100-500 km^2	13 (25%)	100-5000 km^2	9 (18%)
R3	500-2000 km^2	14 (27%)	5000-20000 km^2	6 (12%)
Common	>2000 km^2	20 (39%)	>20000 km^2	32 (63%)

Table 3.6 Species categorized by area of occupancy *A* and geographic extent *E* rarity.

Area of Occupancy (A_{10})					
	Common				20
	R3			3	11
	R2		9	3	1
	R1	4			
		R1	***R2***	***R3***	***Common***
		Geographic Extent (*E*)			

■ ***A. columbianus*** (Washington State)

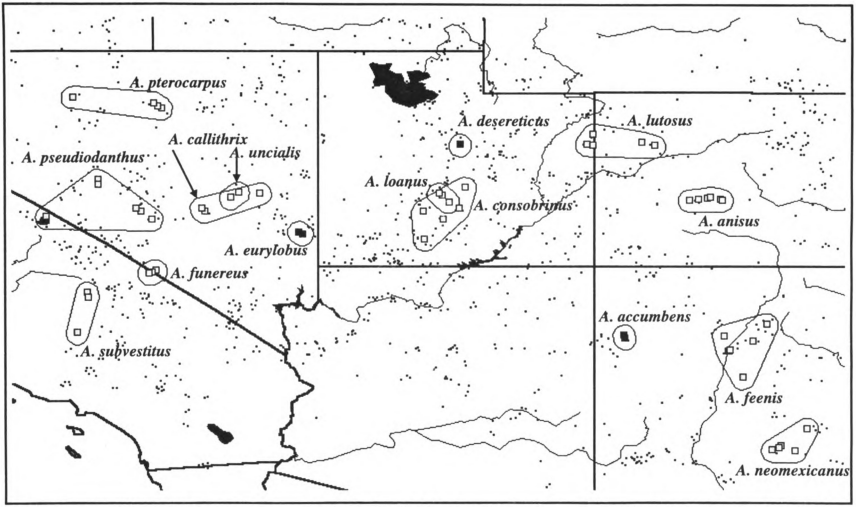


Figure 3.10 Location of rare and vary rare species of the Lf-P *Astragalus*

□□□ ***A. helleri*** (Vera Cruz, Mexico)

3.3.3 Among scale comparisons

Pairwise Spearman and Pearson correlations among scales, based on areas of occupancy ***A***, are shown in table 3.7. The highest correlations were found at the smallest scales of measure. Further, correlations were always highest for scales nearest in size. Figure 3.11 is a chart of the values in table 3.7.

The sequential ranks of species at each scale are given in table 3.8. Shaded cells in the table indicate rank changes for a species. The number of species with changes in rank varied from as low as 2 at the largest scales to a high of 26 (or 51%) between scales [***J*** = 40 and 80 km]. The magnitude of rank changes, taking into account the size of each rank change, varied similarly. Figure 3.12 provides a summary of these changes.

3.3.4 Fractal geometry of species distributions

Table 3.9 gives each species' fractal dimensions ***D*** for the eight pairs of scales compared. Note that a significant portion of the cells in the table are shaded, indicating ***D*** when it is equal to 1. As previously mentioned, this occurs when the scales of measure exceed the geographic extent of a species. Visual inspection of this table reveals that species' distribution are generally not fractal across scales. Indeed, no species is perfectly fractal across the full range of scales examined in this study. Scale-area curves on a log-log plot are shown in figure 3.13. The slope between each pair of points is equal to ***D***. The bold diagonal line graphically represents the position where geographic extent equals measurement scale, and ***D***, therefore, equals 1.

The four rarest species (*A. desereticus, A. columbianus, A. eurylobus, A. accumbens*) do not have fractal dimensions because they are too rare. Four additional species, *A. uncialis, A. funereus, A. loanus,* and *A. helleri,* have sufficiently small range sizes such that they do not have a sequence of three dimensions for comparison. Among

Table 3.7 Spearman (Pearson) correlations among scales for areas of occupancy A.

Scale (J)	**10**	**20**	**40**	**80**	**160**	**320**	**640**
20	.993 (.994)						
40	.987 (.989)	.991 (.993)					
80	.974 (.974)	.977 (.980)	.986 (.989)				
160	.952 (.945)	.954 (.953)	.960 (.964)	.975 (.981)			
320	.898 (.897)	.900 (.907)	.911 (.922)	.925 (.944)	.944 (.972)		
640	.795 (.810)	.798 (.823)	.799 (.839)	.813 (.869)	.835 (.907)	.879 (.944)	
1280	.584 (.654)	.584 (.664)	.586 (.679)	.591 (.714)	.607 (.756)	.637 (.798)	.719 (.867)

Figure 3.11
Pairwise spearman correlations among scales

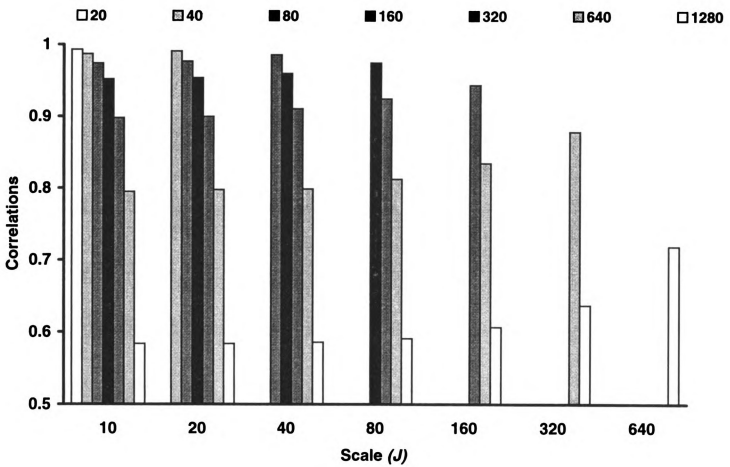


Table 3.8 Sequential rank of species at each scale based on area of occupancy ***A***. Ranks were not determined for the largest scale [***J***=2560] because all species have the same area. Shaded cells indicate rank changes. See text for further details.

Species Code	Sequential rank for each scale (*J*), sorted at *J*=10							
	10	**20**	**40**	**80**	**160**	**320**	**640**	**1280**
dese	1	1	1	1	1	1	1	1
colu	2	2	2	2	2	2	2	2
eury	3	3	3	3	3	3	3	3
accu	4	4	4	4	4	4	4	4
unci	5	5	5	5	5	5	5	5
fune	6	6	6	6	6	6	6	6
loan	7	7	7	7	7	7	7	7
hell	8	8	8	8	8	8	8	8
call	9	9	9	11	11	11	11	11
subv	10	10	10	12	12	12	12	12
pter	11	11	11	13	18	18	18	18
neom	12	12	14	10	10	10	10	10
luto	13	14	12	14	13	13	13	13
cons	14	18	18	17	16	16	16	16
anis	15	15	13	9	9	9	9	9
pseu	16	16	16	18	19	19	19	19
feen	17	19	19	19	17	17	17	17
cyan	18	13	15	15	14	14	14	14
leuc	19	17	17	16	15	15	15	15
iodo	20	21	23	27	25	25	25	25
giga	21	22	24	28	28	33	33	33
musi	22	24	25	24	26	26	26	26
cymb	23	20	20	20	20	20	20	20
wate	24	25	27	29	29	28	28	28
zion	25	26	26	25	27	27	27	27
nudi	26	23	21	21	21	21	21	21
cast	27	27	28	23	23	23	23	23
eure	28	29	29	26	24	24	24	24
tide	29	28	22	22	22	22	22	22
tetr	30	30	32	32	33	34	36	36
piut	31	31	30	30	30	29	29	29
case	32	32	31	31	31	30	30	30
mega	33	33	34	35	37	37	37	37

Continued

Table 3.8 *continued*

cocc	34	34	33	33	34	32	32	32
parr	35	36	35	34	32	31	31	31
cham	36	35	37	36	35	35	34	34
shor	37	38	36	37	38	38	38	38
layn	38	37	38	38	36	36	35	35
infl	39	39	39	39	39	39	39	39
teph	40	40	40	41	41	42	42	42
utah	41	41	41	40	40	40	40	40
ioda	42	42	42	42	42	41	41	41
ooph	43	43	43	43	44	44	44	45
argo	44	44	44	45	46	46	46	46
beck	45	45	45	44	45	45	45	44
amph	46	46	46	46	43	43	43	43
newb	47	47	47	47	47	47	47	47
miss	48	48	48	48	49	51	51	51
moll	49	49	49	50	50	49	49	49
purs	50	50	50	49	48	48	48	48
lent	51	51	51	51	51	50	50	50

Count of changes	**18**	**20**	**26**	**23**	**11**	**3**	**2**
Magnitude of changes	**32**	**35**	**50**	**38**	**18**	**4**	**2**

Figure 3.12
Sequential rank changes across scale

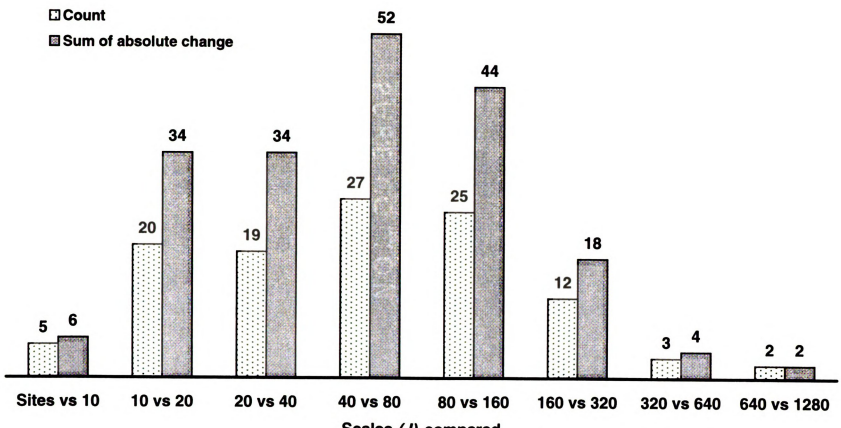


Table 3.9 Fractal Dimensions ***D*** for each species between reference scales. Shaded cells indicate ***D*** values which are 1 by definition. List sorted as in table 3.3. Doubly underlined values represent scales for which the species' distribution is perfectly fractal; singly underlined represents nearly fractal distributions.

Species Code	Fractal Dimensions *D* between reference scales *J*							
	10-20	20-40	40-80	80-160	160-320	320-640	640-1280	1280-2560
dese	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
colu	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
eury	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
accu	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
unci	0.50	1.00	1.00	1.00	1.00	1.00	1.00	1.00
fune	0.50	1.00	1.00	1.00	1.00	1.00	1.00	1.00
loan	1.00	0.50	1.00	1.00	1.00	1.00	1.00	1.00
hell	1.00	0.50	1.00	1.00	1.00	1.00	1.00	1.00
call	1.00	1.00	1.00	0.50	1.00	1.00	1.00	1.00
subv	0.71	1.00	1.00	0.50	1.00	1.00	1.00	1.00
pter	0.71	1.00	1.00	1.00	0.50	1.00	1.00	1.00
neom	0.79	1.00	0.21	1.00	1.00	1.00	1.00	1.00
luto	0.84	0.50	1.00	0.50	1.00	1.00	1.00	1.00
cons	1.00	0.84	0.50	0.50	1.00	1.00	1.00	1.00
anis	0.84	0.50	0.50	1.00	1.00	1.00	1.00	1.00
pseu	0.84	0.79	1.00	0.71	0.50	1.00	1.00	1.00
feen	1.00	0.84	0.79	0.21	1.00	1.00	1.00	1.00
cyan	0.50	1.00	0.71	0.50	1.00	1.00	1.00	1.00
leuc	0.71	0.79	0.71	0.50	1.00	1.00	1.00	1.00
iodo	0.84	0.90	0.89	0.21	0.50	1.00	1.00	1.00
giga	0.84	0.90	0.89	0.50	1.00	0.21	1.00	1.00
musi	0.92	0.82	0.76	0.63	0.21	1.00	1.00	1.00
cymb	0.74	0.76	0.63	0.71	0.50	1.00	1.00	1.00
wate	0.86	0.92	0.79	0.71	0.50	0.50	1.00	1.00
zion	0.79	0.82	0.76	0.63	0.71	0.50	1.00	1.00
nudi	0.65	0.66	0.84	0.50	0.50	1.00	1.00	1.00
cast	0.81	0.84	0.50	0.50	0.50	1.00	1.00	1.00
eure	0.95	0.76	0.50	0.34	0.50	1.00	1.00	1.00
tide	0.66	0.63	0.71	0.50	0.50	1.00	1.00	1.00
tetr	0.87	0.90	0.81	0.63	0.50	0.71	0.50	1.00
piut	0.84	0.79	0.61	0.60	0.50	0.50	1.00	1.00
case	0.77	0.79	0.71	0.50	0.50	0.50	1.00	1.00
mega	0.87	0.84	0.79	0.61	0.60	0.50	0.50	1.00

Continued

Table 3.9 *continued*

cocc	0.88	0.67	0.76	0.63	0.21	0.50	1.00	1.00
parr	0.89	0.67	0.54	0.34	0.50	0.50	1.00	1.00
cham	0.80	0.86	0.53	0.50	0.50	0.21	1.00	1.00
shor	0.86	0.73	0.62	0.65	0.50	0.50	0.50	1.00
layn	0.82	0.78	0.59	0.44	0.50	0.21	1.00	1.00
infl	0.81	0.74	0.64	0.60	0.50	0.50	0.50	1.00
teph	0.84	0.82	0.67	0.50	0.43	0.34	0.50	1.00
utah	0.88	0.82	0.55	0.30	0.50	0.50	0.50	1.00
ioda	0.86	0.84	0.67	0.44	0.21	0.50	0.50	1.00
ooph	0.89	0.85	0.68	0.52	0.40	0.39	0.71	0.50
argo	0.91	0.84	0.71	0.57	0.39	0.42	0.50	0.50
beck	0.89	0.79	0.65	0.52	0.42	0.50	0.00	1.00
amph	0.90	0.79	0.57	0.33	0.45	0.39	0.21	1.00
newb	0.91	0.87	0.76	0.46	0.33	0.43	0.34	0.50
miss	0.94	0.88	0.82	0.59	0.30	0.26	0.42	0.00
moll	0.90	0.84	0.72	0.45	0.24	0.32	0.21	0.21
purs	0.88	0.76	0.57	0.42	0.25	0.30	0.29	0.21
lent	0.83	0.73	0.56	0.31	0.21	0.11	0.39	0.21

the remaining 43 species, 7 are perfectly fractal across four scales of measure (three measures of D), and 14 additional species have nearly fractal dimensions across four or more scales. By this criterion, nearly 50% of species show a high level of fractalness across at least four scales of measure. On the other hand, among 166 sequences of four scales (three measures of D), only 29 (17%) of them are fractal by this criterion. These sequences are indicated by underlining in table 3.9. Perfectly fractal sequences are doubly underlined, whereas nearly fractal sequences are singly underlined.

As a group, D was highest at the smallest scales and declined with the larger scales. Within scale variance increased with increasing scale owing to the smaller number of species with range sizes at large scales (see figure 3.14).

3.3.5 Species richness

Species richness among individual cells varied substantially with scale. At the smallest scale (J = 10 km), species richness averages just greater than one species per cell (when occupied) with a maximum of three species per cell. The largest scale analyzed (J = 640 km) had an average of more than seven species per cell and a maximum of 23 species per cell. Table 3.10 shows species richness counts among the six scales analyzed.

Kolmogorov-Smirnov tests for a goodness of fit with a Poisson distribution returned very low probabilities (data not shown). Coefficients of dispersion, CD (variance/mean, expressed as a decimal), are shown in table 3.10. CDs were less than 1.0 for scales J = 10, 20, and 40 km, indicating that at these scales, species distributions are repulsed (i.e., contrary to clumped). Species richness counts are clumped at scales J = 80, 160, 320, and 640 km. A plot of mean and variance values among scales (not shown) indicates values cross between scales 40 and 80 km. This suggests that, with respect to species richness, cell counts may have a Poisson distribution at a scale near 60 km.

Figure 3.14
Fractal dimensions across scales

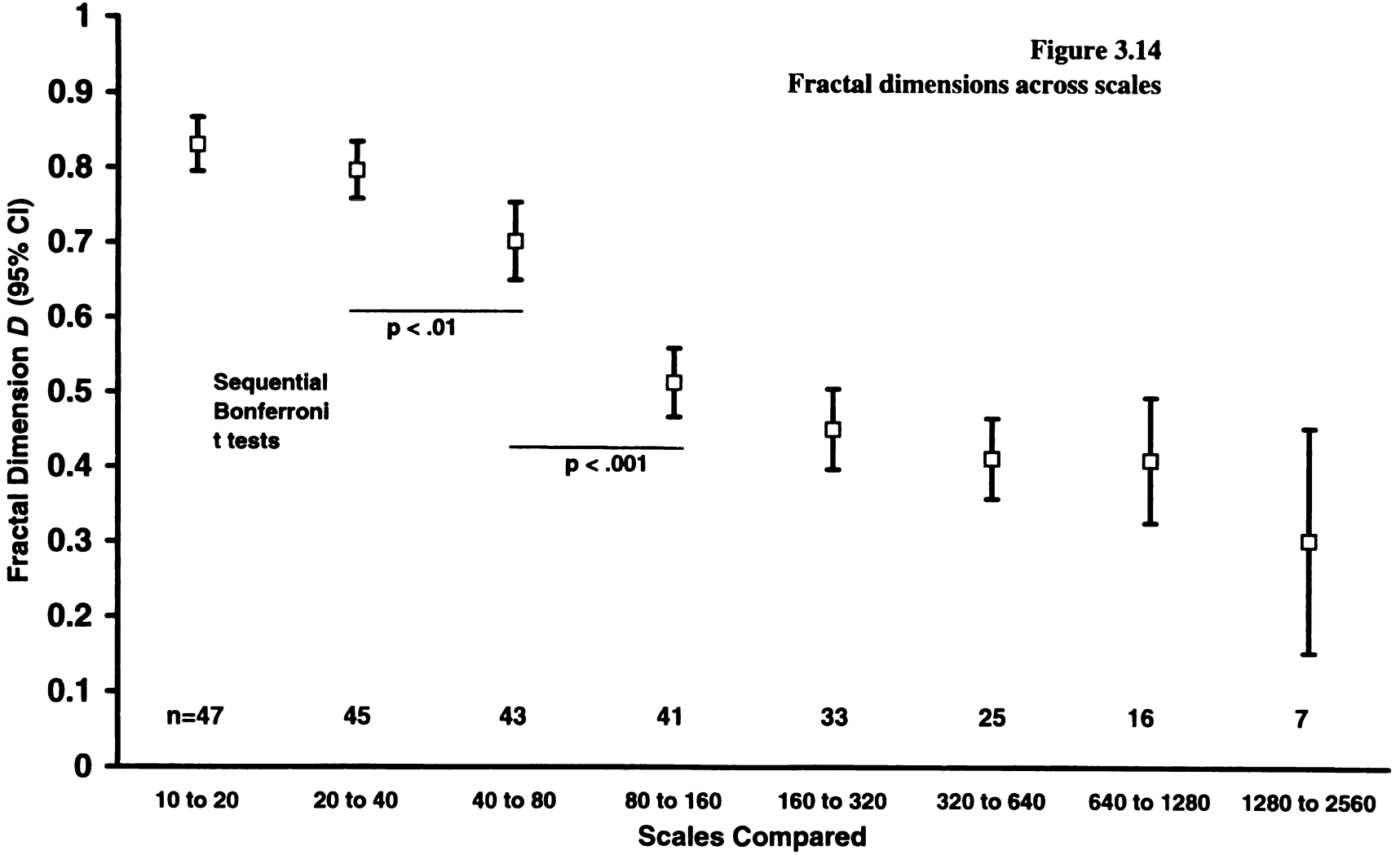


Table 3.10 Variation in species richness among cells for scales J = 10 km through 640 km. Mean, variance, and coefficient of dispersion are given for each scale.

Scale (*J*)	Species Richness																						
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**23**	**n**	***mean***	***var***	***CD***
10	2241	201	30																	2472	1.11	0.119	.11
20	1438	316	73	17	1	2														1847	1.29	0.367	.29
40	653	244	108	47	23	8	3													1086	1.69	1.16	.68
80	193	135	71	31	25	19	7	6	1	1										489	2.36	2.78	1.18
160	55	40	23	14	15	10	4	3	6	4	4		1							179	3.34	7.36	2.20
320	20	13	6	8	1	1	3	2	1	1	2	2		1		2		1		64	4.26	18.5	4.35
640	2	7		1	2			1	1				1	1				1	2	20	7.10	52.4	7.38

The largest numbers of species rich cells fall in Utah and Nevada. At the smaller scales they are predominantly found in Utah, whereas at the larger scales, Nevada has the greater number of species rich cells. Figures 3.15 and 3.16 show species richness in Utah at scales J = 40 and 80 km. Tabulation of species richness by state boundary, rather than grid cells, found 24 species located in Utah and 23 species in Nevada. Among the two states, 14 species are common to both, and together they contain 33 species, or 65% of the total number of species in the study group. Additionally, these two states have the majority of the 17 rare species (as defined above) in the group: 6 in Nevada, and 4 in Utah (see figure 3.10).

The region with the largest cluster of species rich cells is found in southern Utah, especially on and adjacent to the Utah Plateaus and in the area south extending toward the north rim of the Grand Canyon and extending east into the Pine and Bull Valley Mountains. A second area of high species richness lies on the eastern flanks of the Sierra Nevada Range in California, extending across the White Mountains and including the southern portion of the Toiyabe Range. As expected, the center points of maximum species diversity depend on the measurement area. They are nevertheless very near the most species rich cells.

3.4 DISCUSSION

Perhaps the most significant result from this study was the discovery of high levels of variation in the area of occupancy measure A due to variation in the placement of grids. The "Minimum Cell Count" procedure was developed to eliminate this arbitrary variation. A comparison of values derived from an arbitrarily placed grid versus placements that minimized A revealed large differences for species with small range size and/or a small number of localities. Other procedures might be employed to eliminate this variation,

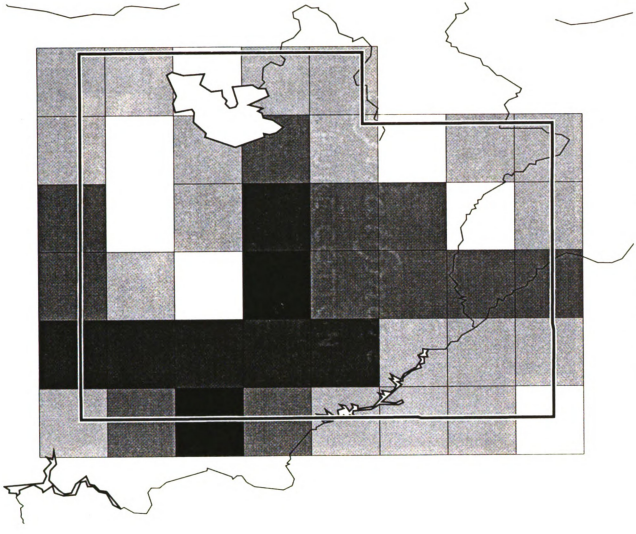


Figure 3.15 Utah species richness--80km scale

Figure 3.16
Utah
species
richness--
40km scale
Species/Cell
1
2
3
4
5
6
7

such as taking the mean of 10 random grid placements; however, sampling error due to estimating the mean will be influenced by the spatial pattern of a particular species and will thus vary among species.

These finding have important implications for studies that include species with highly divergent range sizes. Indeed, when area of occupancy is used for assigning rare status to species leading to listing for special protection, it is possible that some species may not attain status and listing by fixed grid methods whereas they would if a minimization procedure were employed. Given the importance of a sound and repeatable process for assigning special status to species for conservation protection, the arbitrary nature of fixed grid methods should be avoided. Furthermore, fixed grids should be avoided to reduce experimental error in studies of biogeography.

The effect of scale with respect to the area of occupancy measure is readily apparent when the scale of measure is large compared with the areas occupied. Large measurement scales, in effect, summarize variation at smaller scales and thus reduce information content. This highlights the need to use scales that correspond with species with the smallest area, especially for studies that focus on rare and more restricted species.

Rank abundances are also strongly influenced by changes in scale due to the interaction between a species' distribution, the scale in which the data was collected, and the scale in which the data is summarized. Nearly all species in the study changed rank position as scales changed, the extreme example being *Astragalus giganteus* which shifted from position 20 at the smallest scales to 33 at the largest scales. This suggests the need to choose scales carefully when employing ranks.

The use of fractal properties to mitigate the among scale effects discussed above appears to be problematic. Based on results in this study, species are not strictly fractal across the scales employed in accordance with the findings of others (Krummell, *et. al.* 1987; Allen and Hoekstra 1992).

The majority of species in the current study have fractal dimensions near the value of 1 between scales J = 10 and 20 km. Two possible explanations are offered: 1) The numbers at these scales may simply be a sampling artifact. If the average distance between sites is substantially greater than 10 km and sampling (collecting) was done systematically leading to over-dispersion, this would lead to high values of D at the lowest scales; and 2) the organisms themselves may be more widely distant than the sampling measure and/or the species may be systematically distributed due to ecological factors. Unfortunately, both of these effects can lead to higher values. Untangling the extent to which these factors affect the data set is difficult to elucidate.

Recent work by Kunin (1998) made use of fractal properties to predict areas of occupancy of scarce plant species at scales finer than the scale at which data was collected. Kunin did not quantify the fractal properties of the species he studied, however; rather, he assumed the distributions were fractal and used this assumed property to derive predicted values. Predicted values were generally greater than a second set of observed data collected separately at the fine scale. He concluded that either undersampling occurred at the fine scale or that species are not strictly fractal over the range of scales employed. Given the results from the current study, Kunin's later suggestion is clearly supported. His first suggestion may also be simultaneously influencing the outcome.

These findings raise concerns about using fractal dimensions for estimating the abundance of a species at scales smaller than the scale for which data has been collected. However, given the effect of variation introduced by using fixed grids, there may yet be hope for refining a procedure similar to that of Kunin (1998).

Regarding findings on species richness, because values were derived from fixed grids, the largest values found were not the maximum possible. Indeed, an informal search for higher maximum species richness counts at scales 160 and 320 km netted higher values than with the fixed grids—17 species versus 13 for the former, and 21

species versus 18 for the later. Procedures to optimize species richness values were not undertaken due to the computational difficulty and the lack of a rationale for doing so.

One of the more interesting aspects of the findings on species richness is that high values correspond with the boundaries of the Great Basin Floristic Province (Barneby 1989) (see figure 3.17). Indeed, a ridge of species richness contours (not shown) runs parallel east of the boundary from central Utah, continuing south and curving to the west in southern Utah. The high level contours coincide with the Utah Plateaus.

Two explanations are offered for these patterns. The first rests with the logical consequences of how floristic regional boundaries have been determined. Boundaries are defined by areas with high rates of change in species assemblies and/or areas of regional endemism. Floristic traits such as these lead to higher species richness values near boundaries.

Perhaps a more encompassing explanation for these correspondences derives from the underlying topographic heterogeneity along the boundaries. Not only do the topographic features act as barriers to dispersal, but the topographic complexity may lead to higher rates of diversification (Cracraft 1985). Topographic discontinuities also have large impacts on local climate patterns, which further create environmental heterogeneity. Thus, for both ecological and evolutionary reasons, it is not surprising that high levels of species richness are found in south-central Utah and east-central California.

During the search for the best possible source(s) of biogeographic data for this study, the large databases maintained by state governments and nonprofit organizations were seriously considered. Indeed, I held lengthy discussions about the attributes and availability of these data with a number of individuals involved in rare plant monitoring.

Several matters became clear following these discussions and are worthy of mention. First, because each state or regional unit maintains its own data, the effort required to retrieve and organize the data would be enormous; further there would be no guarantee of obtaining all the data desired due to varying policies of dissemination. Further

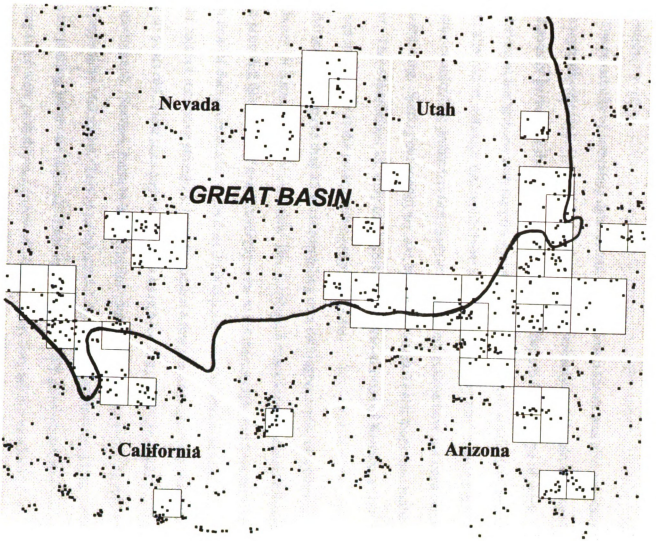


Figure 3.17
High species richness cells--
40 & 80 km scales

complicating matters is the fact that each unit stores data in different formats and uses different criteria for measuring and categorizing the species they monitor. Thus, there is great variation within and among the data sets attributable to the various individuals and the specific agencies and organizations involved. Sorting through this quagmire would have required more effort than a single individual could accomplish in a reasonable amount of time. For these reasons, use of data from these sources was dropped early in this study.

The possibility of compiling data directly off herbarium sheets was also entertained but eventually rejected. It would be impractical, and probably inadvisable, to have thousands of herbarium sheets sent to one's home herbarium for this type of work. Visitations at the herbaria with the principal *Astragalus* collections would have been a better alternative, although that would have been costly and very time consuming. Another contributing problem is that many *Astragalus* collections have not been curated for some time. Sorting out synonymy, etc. would have added even more time to the effort. These limitations left only one viable alternative—the use of Barneby's (1964) monographic work as the source of biogeographic data.

Barneby spent more than 25 years compiling data on biogeographic and other attributes of *Astragalus* in N. America. His distribution maps are exceptional because: 1) he provided dot maps for nearly every species in his monograph, and 2) he provided a great deal of data, estimated at more than 20,000 points, for the whole monograph.

In spite of the above strengths, his data contain a few weaknesses. First, the data are now 30 years old. New sites and new species have been discovered since publication of his monograph. Second, Barneby's distribution maps were constructed using different map projections and scales. This required careful digitizing to overcome. Third, error rates for plotting points are difficult, if not impossible, to fully ascertain because specific plotting rules were probably not followed. If they were, they are not described and remain unknown. Even with these weaknesses, however, the data set is exceptional.

The number and location of sites ***S*** were taken directly from Barneby's monograph; thus, the quality of his distribution maps affects both the area of occupancy ***A*** and geographic extent ***E*** measures. For both these measures, the accumulation of error resulting from plotted maps and from digitizing is mitigated by the summary procedure of converting points to areas. Furthermore, the summarization procedure diminishes any underrepresentation of the true number of sites. The difference between actual versus measured occupancy diminishes as the area of measure increases to the overall extent of the species.

Collecting bias also affects some of Barneby's data. For example, southern Nevada, which includes the inaccessible areas of the Nevada Test Site and Nellis Air Force Base, has a dearth of sites. This is not surprising considering most of Barneby's work corresponds with some of the most intense periods of nuclear testing in these areas.

Regardless of these reservations, it is satisfying that there is close correspondence between the categories of rarity applied to data presented in this study and the listing of rare species in the IUCN Red list. Among the 17 "rare" species categorized in this study, 14 appear on the Red List. *Astragalus helleri* is not on the Red List, quite possibly because data from Mexico did not include it—in spite of its obvious rarity. *Astragalus subvestitus* did not make the Red List either, although it is on the California Native Plant Society's (CNPS) *Inventory of Rare and Endangered Vascular Plants of California* (Skinner and Pavlik 1994). A California endemic, this species is not vulnerable at this time but is rare according to CNPS. The classification used in this study places this species in the R3 and R3 categories—somewhat rare for both ***A*** and ***E***. *Astragalus lutosus* also did not make the Red List for unknown reasons; Barneby (1989) suggests that this species should be closely monitored because of its potential endangerment.

Four species in this study group made the Red List but did not meet the R2 requirement in at least one category for this study. These include *A. cymboides* and *A. leucolobus*, both classified as an R3-R3 in this study; *A. musiniensis,* classified as an

R3 for ***A*** but common for ***E***; and *A. shortianus*, classified as "common" for both measures. This latter species' native range lies east of the Rockies and corresponds to a large extent with the Denver metropolitan area. This species is probably becoming rare due to human activity.

The principal aim of the work presented in this chapter was to quantify the biogeographic distributions of the 51 species of the Large-flowered Piptoloboid group of *Astragalus*. Data from this study were also used in the study discussed in Chapter 4.

In the interest of obtaining the most robust results possible, an exploration of area of occupancy measure ***A*** with respect to two methods of determination (fixed grid and minimization) and the effect of measurement scale on resulting quantities were undertaken. As predicted, these factors had large effects on the resulting quantities. Results led to the use of the minimization procedure to reduce arbitrary variation in the area of occupancy measure ***A*** and to the use of the 10 km scale to reduce information loss. The geographic extent measure ***E,*** which is far less subject to the vagaries of grid placement and scale, was also determined because it is typically used for rarity classification. Using these results, species were categorized into rarity classes as per IUCN's criteria.

Additional analysis, secondary to the principal aims of this study, included assessment of the fractal properties of the species distribution to test the possibility of using fractal dimensions as a scale-independent distributional attribute. Results show that distributions are generally not fractal. Further analyses are required to elucidate the underlying mechanism generating the curvilinear fractal relationships uncovered for most species.

Finally, a brief analysis of patterns of species richness of the 51 study species revealed high levels of diversity in the Great Basin and the Utah Plateaus to the east.

Specific regions of high diversity depended on the scale of measure and underscore the need for choosing measurement scales with reason when undertaking diversity studies.

4

Phylogenetic Patterns of Rarity in the Argophyllean Clade of *Astragalus* L.

4.1 INTRODUCTION

In the introduction of this dissertation, several questions were raised regarding the relationship between rare status and the processes of evolution. Among the many vantage points for addressing the nature of this relationship, work presented in this chapter focuses on the role evolution may play in explaining the origins of rare species.

Considerable evidence suggests that the majority of speciation in higher plants occurs locally—either via peripatric speciation or via chromosomal reorganization (Levin 1993). Indeed, it has also been suggested that peripatric speciation is the most common mode among animals (Brooks and McLennan 1991). Diversification by local processes leads to rarity of at least one sister lineage during the early stages following a cladogenic event, unlike allopatric speciation which takes place within large regional or continental areas without the necessity of rare status.

To the extent that a lineage has undergone a shift toward higher rates of diversification, we might expect to see a larger proportion of rare species in that lineage compared to its sister lineage or compared to a more inclusive and larger group within

which it is found. If this scenario is true, macroevolutionary patterns of rarity are likely and may be discernible with a well resolved species level phylogeny.

The aim of the work presented here was to explore patterns of rarity among species within a monophyletic assembly. Specifically, the following hypothesis was tested: Lineages undergoing higher net rates of diversification, when coupled with local speciation, generate a disproportionate number of species with small range sizes compared to lineages with lower net rates of diversification. If this hypothesis is true, the following features are expected within the group: 1) evidence of diversification rate variation; 2) phylogenetic clustering of rare species in the region of high diversification; and 3) a preponderance of newly derived rare species. Testing the generality of this hypothesis requires study of many groups and is beyond the scope of this study. Here, a single group will be used as a case study.

Using the Argophyllean clade of *Astragalus*, identified during the phylogenetic study presented in chapter 2, and results from the biogeographic study of the group presented in chapter 3, the following questions are addressed: 1) Is there evidence of diversification rate variation among lineages? 2) Do rare species cluster in the phylogeny? 3) Are newly derived rare species more frequent than expected by chance?

4.2 METHODS

The Argophyllean clade of 47 species was identified during a morphological cladistic study of the Large-flowered Piptolobi of *Astragalus* (presented in chapter 2) and was used as the study system. The 12 most parsimonious trees recovered were very similar and resulted in a highly resolved strict consensus tree. Furthermore, all branches leading to single rare species were fully resolved. A randomly chosen tree among the 12 most

parsimonious trees was used for this study and is shown in figure 4.1. Extensive preliminary testing using alternative trees among the 12 revealed nearly identical results.

Range size and classification of rarity for the 47 Argophyllean species were taken from results presented in chapter 3. Log values for the minimum area of occupancy ***A*** based on the number of 100 km^2 grid cells occupied and log values for geographic extent ***E*** were used. Rare species were defined following criteria used for the *1997 Red List of Threatened Plants* (Walter and Gillett 1998) and are indicated on the phylogeny in figure 4.1.

Evidence of diversification rate variation within the clade was assessed using Kirkpatrick and Slatkin's (1993) phylogenetic tree asymmetry test. Average internal node distances from the inferred common ancestors to terminal taxa were tabulated for each subclade with eight or more species—19 in all. Results were compared with confidence intervals based on data provided by the authors. Average internal node distances above confidence intervals provide evidence to reject the null hypothesis that the subclade is not asymmetrical.

A preliminary assessment of rare species clustering was attained by plotting the number of rarest species versus the total number of species for each of the 46 subclades within the study group. For purposes of this plot, both "Very Rare" and "Rare" species, as defined in section 3.2.5, were combined into a single category comprising the rarest species. Among the 47 species in the group, 17 (36%) met this criteria.

The Mantel procedure (Sokal 1979; Manly 1997) was adapted to statistically test for the clustering of rare species within the phylogeny. Specifically, the association between topological distance as measured by internal node distances and dissimilarity in log range size was tested. Two tests were conducted, one using log area of occupancy ***A*** and one using log geographic extent ***E***. The two half-matrices used in each procedure contained the following data: 1) pairwise internal node distances among species and 2) pairwise differences of log ***A*** and again of log ***E***. Figure 4.2 shows how these data were

Figure 4.1
Phylogeny of the Argophyllean clade of *Astragalus* used for analysis in chapter 4 with area of occupancy *A* and geographic extent *E* categories indicated for each species. Values correspond with those in table 3.5.

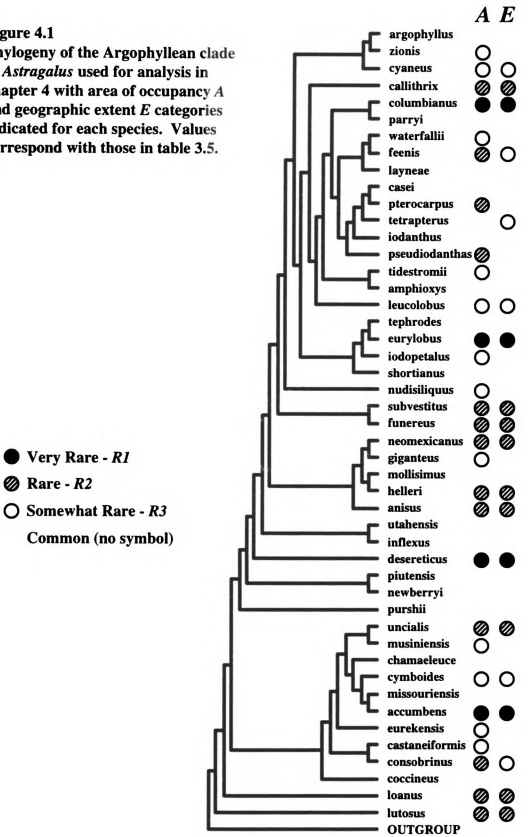
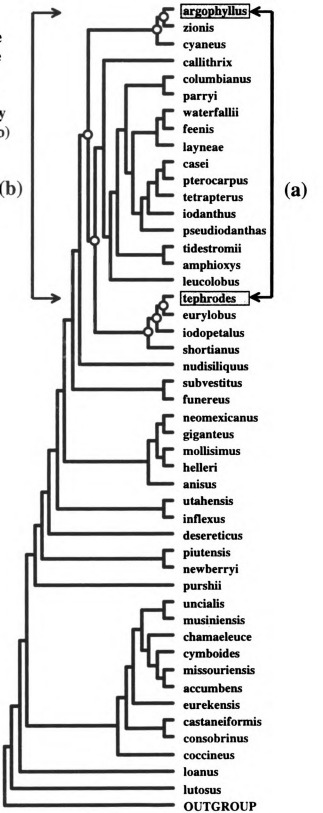


Figure 4.2
Phylogeny of the Argophyllean clade of *Astragalus* with an example of one set of pairwise data used for the phylogenetic clustering test: (a) The dissimilarity of log area of occupancy *A* is 0.2 (data from chapter 3); and (b) the topological distance is 7.



determined for this procedure. Corresponding matrix values were multiplied and summed to determine the Mantel coefficient observed values. The null hypothesis, that there is no association between topological distance and dissimilarity in log range size, was tested by comparing the observed value with a reference distribution of 1000 coefficients derived from the randomization of the first matrix with respect to the second.

A test for the preponderance of newly derived rare species was conducted by first counting the number of the rarest 17 species among the 14 terminal pairs in the phylogeny. Figure 4.3 shows the position of the terminal pairs and the rarest species used for this test. Next, the null hypothesis, that the number of rare species among terminal pairs is not different than expected by chance, was tested by comparing the observed value of 11 with a reference distribution of 200 values obtained by randomization of species placement in the phylogeny.

4.3 RESULTS

Among the 19 subclades within the Argophyllean clade tested for asymmetry, 11 were found to be significantly asymmetrical. Results are charted in figure 4.4. Significantly asymmetrical subclades are indicated on the phylogeny in figure 4.5. An unbroken internal node link with significant asymmetry begins at the base of the phylogeny and extends to the node which includes *A. nudisiliquus*. Continuing up the phylogeny, the node with *A. callithrix* is also significantly asymmetrical while the two nodes below it are marginally not symmetrical. Results provide strong evidence, given the phylogeny, that net diversification rates vary significantly within the group. The region of the phylogeny with the highest net rate of diversification is indicated by an asterisk (*) in figure 4.5.

Figure 4.3
Phylogeny of the Argophyllean clade of *Astragalus* with positions of the 14 terminal pairs and the 17 rarest species.

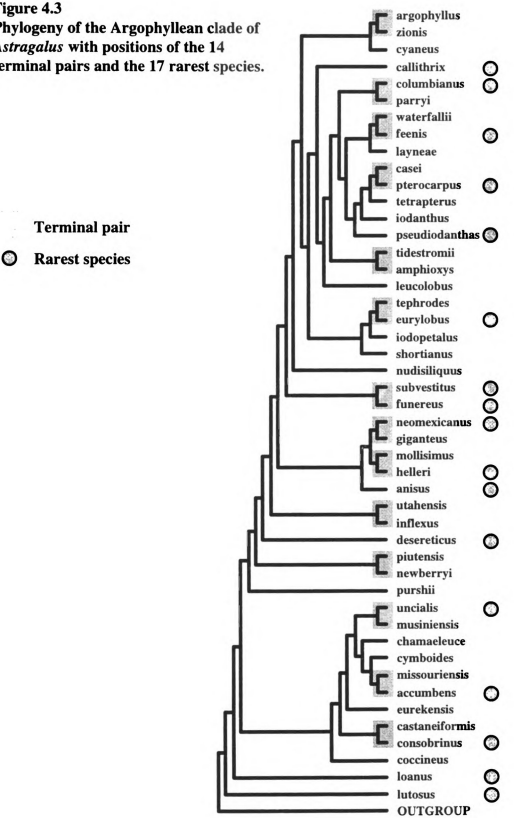


Figure 4.4
Asymmetry tests of the 19 subclades within the Argophyllean clade of *Astragalus*. Subclades with significant asymmetry are plotted as diamonds.

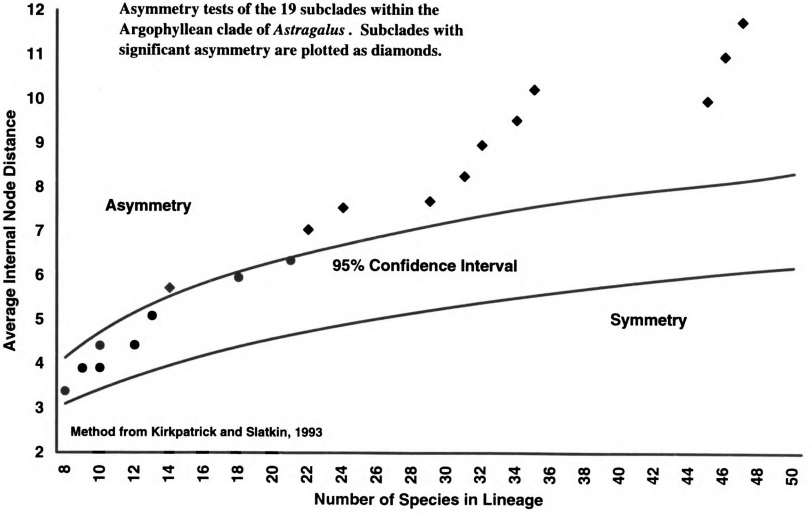
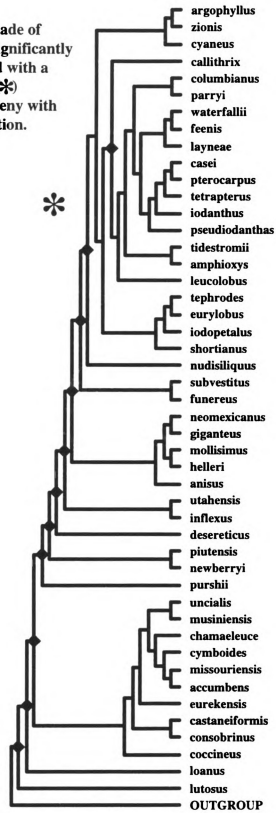


Figure 4.5
Phylogeny of the Argophyllean clade of *Astragalus* with the positions of significantly asymmetrical subclades indicated with a black diamond ◆. The asterisk (✻) indicates the region of the phylogeny with the highest net rate of diversification.



The preliminary assessment of rare species clustering is shown in figure 4.6. Each point on the bivariate plot represents the relative proportion of rare species in each of the 46 subclades with respect to the expected proportion of 0.36, indicated by a line. Points above the line represent subclades with higher proportions of the rarest species compared to the expected value. Inspection of this plot reveals points that are not far from the expected values. The statistical properties of this assessment are not known.

Results from the phylogenetic clustering test using the log area of occupancy ***A***, shown in figure 4.7, returned a probability ($p = .089$) and points toward an association between topological distance and area of occupancy ***A*** but does not meet standard significance levels. Results using log geographic extent ***E*** returned a probability ($p = 0.25$) and does not indicate an association. This latter result is shown in figure 4.8.

Of the 17 rarest species in the study group, 11 were found among the 14 terminal pairs. The 200 trees with randomized placement of species averaged 9.8 rare species among the pairs. The distribution of these values is shown in figure 4.9. Although the observed number of rare species is greater than the expected value, it is not significantly different ($p = .32$) from that expected by chance.

4.4 DISCUSSION

The principle aim of the research undertaken for this dissertation has been to explore patterns of rarity from a phylogenetic viewpoint The discussion of this undertaking will first focus on the basic findings presented in this chapter. Next, implications of these findings will be discussed and will include some results presented in earlier chapters. Potential limitations of this study will also be addressed. Finally, a summary, including a few speculations about the nature of rarity in the Argophyllean clade, will be offered.

Figure 4.6
Bivariate plot of rarest species versus total species for each of the 46 subclades in the phylogeny.

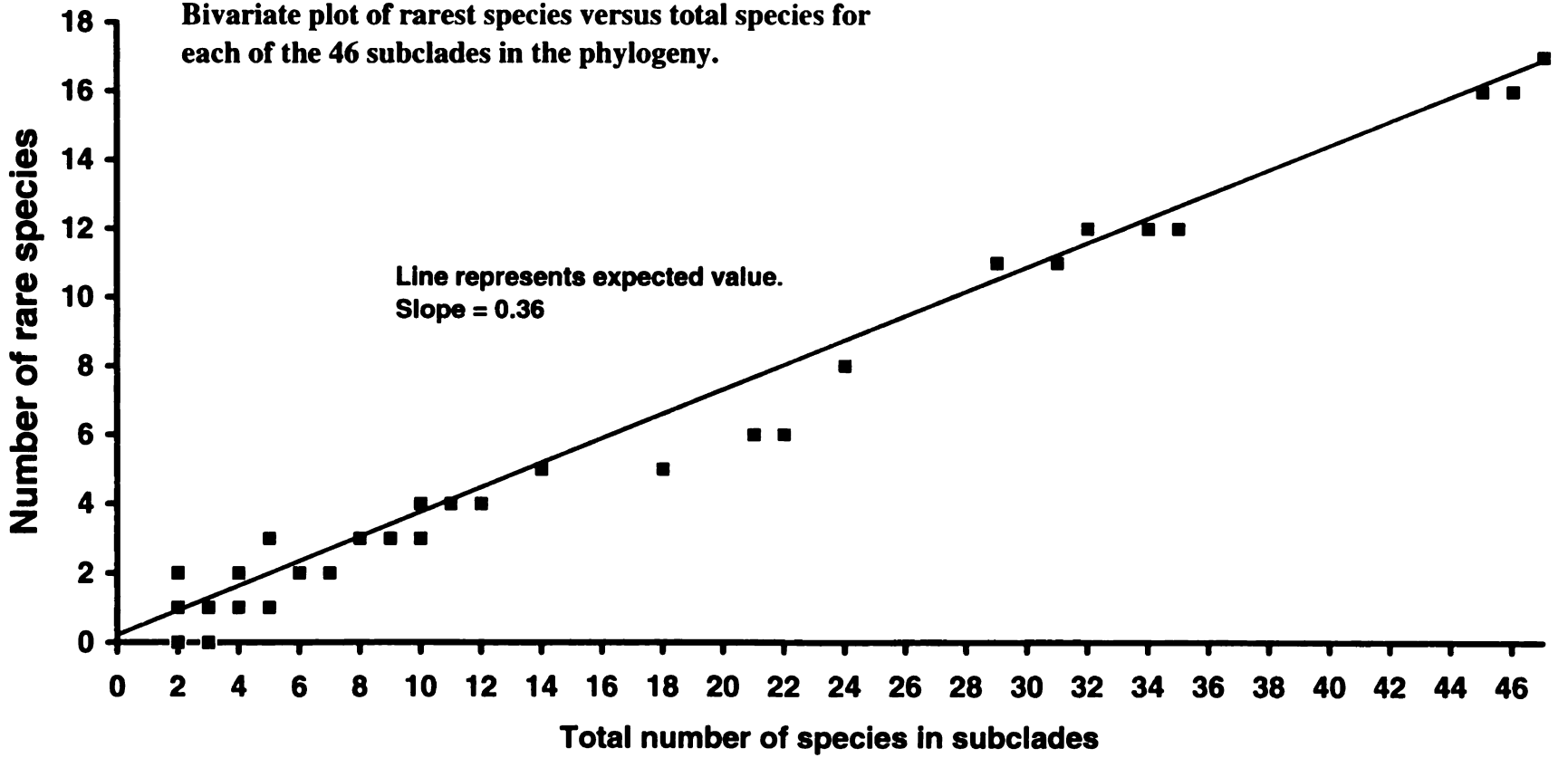


Figure 4.7
Result of the phylogenetic clustering test:
Area of occupancy *A* and internode distance

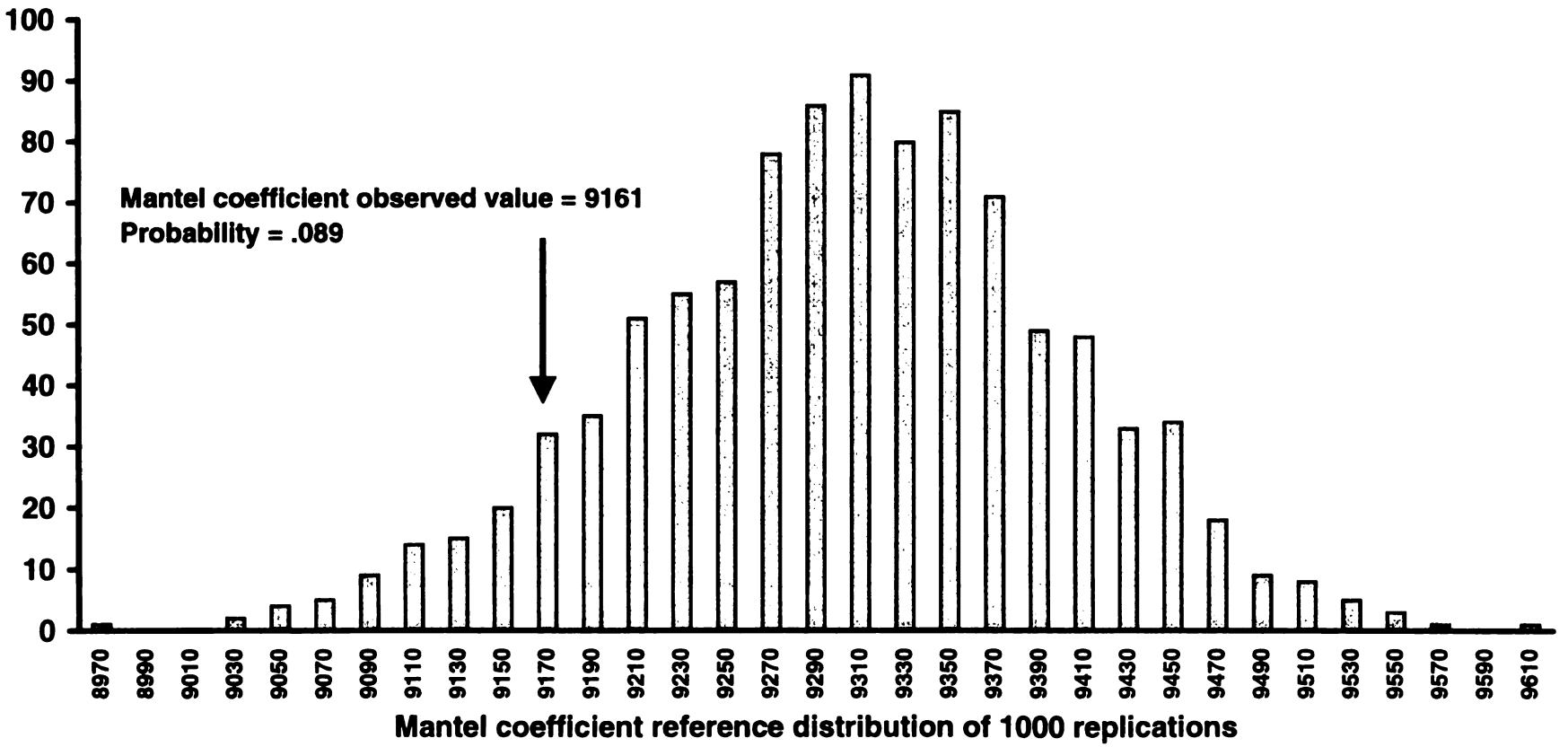


Figure 4.8
Result from the phylogenetic clustering test:
Geographic extent E and internode distance

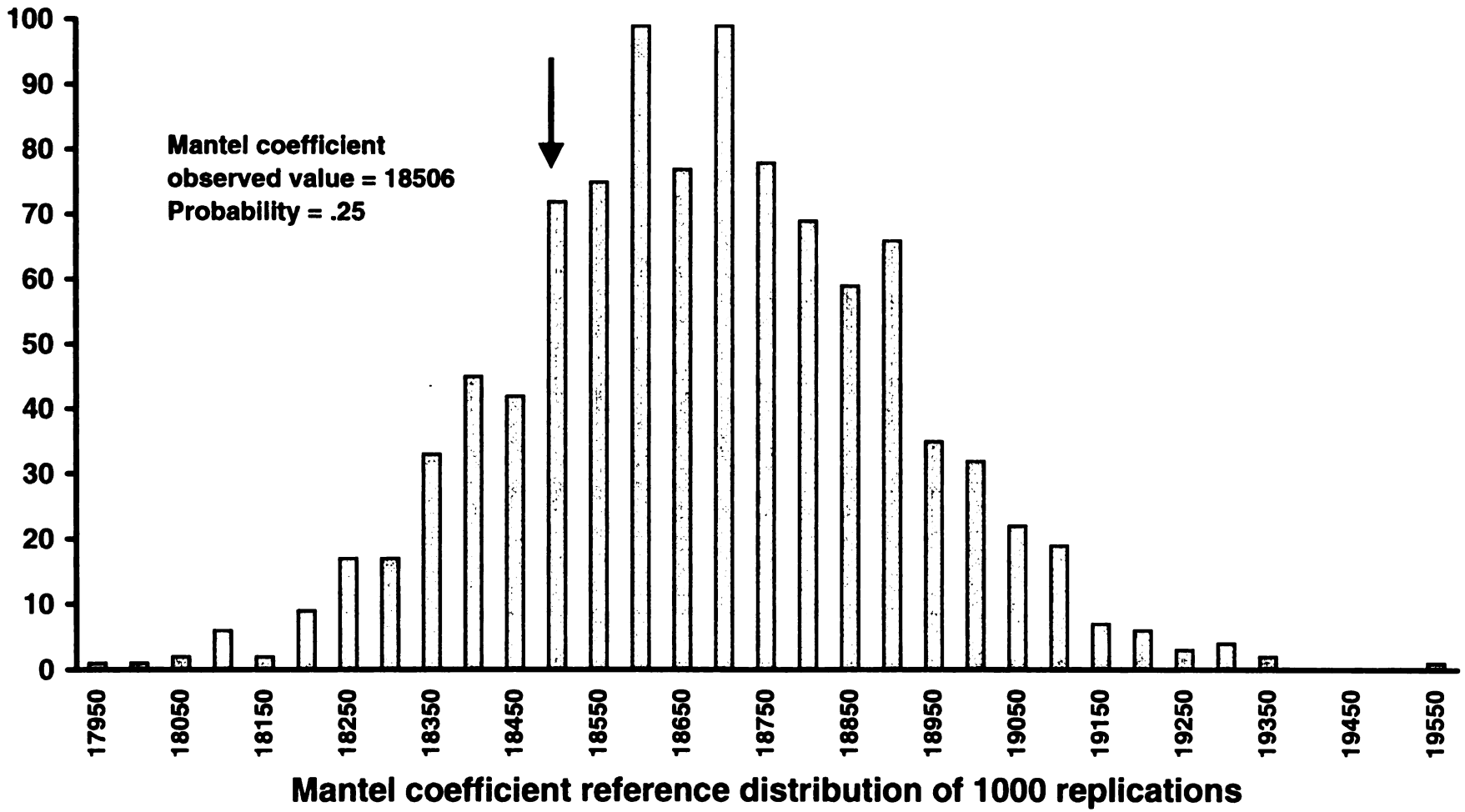
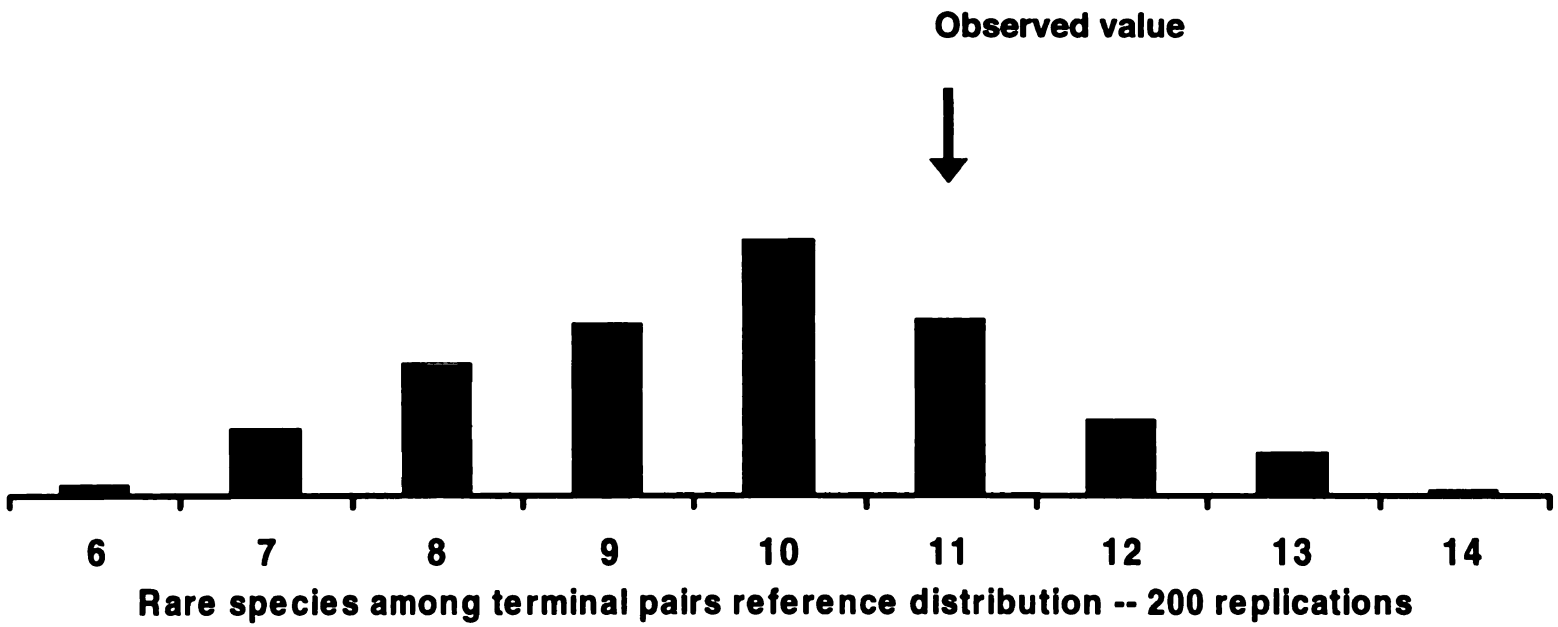


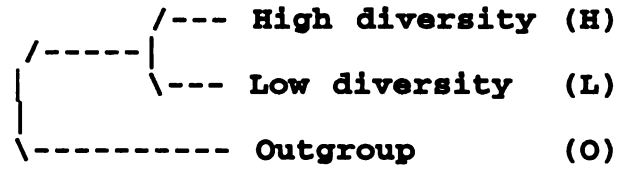
Figure 4.9
Number of the rarest species among terminal pair species. The count of 11 rarest species among the terminal pairs is not significantly different from the expected value of 9.8 (p=.32).



4.4.1 Basic findings

The clearest finding from the work presented in this chapter is that the Argophyllean clade of *Astragalus* is significantly asymmetrical. Eleven of the 19 tested subclades were found to be asymmetrical, clearly indicating diversification rate variation within the Argophyllean clade. Estimates of the direction of change were not possible, however, without data in which to estimate the timing of events in the phylogeny. Furthermore, because diversification rate is the net result of the speciation rate minus the extinction rate, inferences regarding changes in these two rates are also not possible (Sanderson and Donoghue 1996).

Two scenarios might explain the diversification rate variation as illustrated within the example below. Consider the following phylogeny:



With respect to the outgroup (O) lineage, the above pattern might be explained by:

SCENARIO 1: Diversification rate increase in clade H is due to either:

(a) an increase in the speciation rate in clade H or

(b) a decrease in the extinction rate in clade H.

SCENARIO 2: Diversification rate decrease in clade L is due to either:

(a) a decrease in the speciation rate in clade L or

(b) an increase in the extinction rate in clade L.

Of course, more than one of these rate changes may occur simultaneously.

The Argophyllean clade is obviously more complex than the above three-taxon system. As such, it is reasonable to suppose that its diversification rates may have varied in more complex ways as well. Evidence from the asymmetry tests supports this. Furthermore, Wojciechowski *et.al.* (1993) speculate that the rate of diversification within Neo-Astragalus (also called the aneuploid groups), a well supported monophyletic assembly of nearly 500 species and the clade in which the Argophyllean clade is nested, may also have been heterogeneous based on their results. They suggest that "Groups that diverged early may have remained depauperate while those splitting off later radiated rapidly generating the bulk of diversity now evident within the aneuploid groups." Indeed, among the 93 sections that constitute what is now called Neo-Astragalus, one section, *Argophylli*, accounts for 10% of the species (Barneby 1964).

Regarding the potential clustering of rare species in the phylogeny, the bivariate plot of the number of rarest species versus the total number of species (figure 4.6) and results from the phylogenetic clustering test suggest that rare species are not significantly clustered within the phylogeny. A few qualifications should be noted, however. In the case of the test based on area of occupancy ***A***, the p-value of 0.89 is low, which may indicate a tendency toward clustering in the phylogeny. In the absence of a power analysis, it is not known how large a sample size is required to detect a significant difference. Therefore, failure to reject the null hypothesis should not mean acceptance of the null hypothesis.

Another issue affecting the interpretation of these results is that this test included all taxa, not just the rarest. The clustering of some common or widespread species could also lead to lower probabilities. Of course, if all the common and widespread species were clustered, the rare ones would necessarily be clustered as well.

Other findings are consistent with the conclusion of "no significant clustering," namely from results presented in chapter 3. The locations of the rarest 17 species are not

clustered geographically, as can be seen in figure 3.10 (chapter 3). Indeed, the two geographical pairs that overlap in their geographic extent ***E*** are not closely related species. *Astragalus callithrix* and *A. uncialis* of Nevada are very distantly related, and *A. loanus* and *A. consobrinus* of Utah are intermediately related.

One small clade of five species, *A. neomexicanus, A. giganteus, A. mollisimus, A. helleri,* and *A. anisus*, does appear to have a cluster of rarity (see figure 4.1). Three of the five species are rare and one is somewhat rare. *Astragalus mollisimus* is widespread. All five species are either regionally sympatric or are in close proximity to one another. Having offered this observation, it is also unlikely that this clade has a significant level of clustering or had much influence on the overall clustering test for the whole group owing to the small sample size of five.

Another interesting finding is that Argophyllean rare species do not appear to be disproportionately newly derived. They appear both ancestral and newly derived, based on the sister group relationships. No direct estimation of time since divergence, from findings presented here, was attempted because this requires: 1) estimates of absolute time for at least one node in the tree, preferably at the base, 2) estimates of branch lengths, and 3) estimates of evolutionary rates among branches.

In the case of the Argophyllean clade, the assumption of homogeneous evolutionary rates throughout the tree would be contrary to the evidence (significant asymmetry). Moreover, the use of branch lengths to assess evolutionary rates along the branches is difficult to support with morphological data that are inherently homoplasious. For these reasons, no assumptions were made with respect to evolutionary rate homogeneity among branches.

An approximation of the relative timing of cladogenic events was assessed by considering the size of sister lineages. Among the 17 rare species, 11 are considered newly derived because their sister lineage size is one. They are thus members of terminal

pairs on the phylogeny. The ancestral rare species have sister lineage sizes of 46, 45, 31, 13, 4, and 4; the latter two are probably best considered somewhat newly or intermediately derived. Although 65% of the rarest species are members of the 14 terminal pairs, this is not significantly more than would be expected by chance according to the randomization test (p=.32). This is because 28 of the 47 terminal positions (60%) are part of the terminal pairs.

Another important finding is that the Argophyllean clade of *Astragalus* has a disproportionate number of rare species, at least when viewed from the perspective of the genus as a whole. Among the 47 species in the lineage, 17 (36%) are rare by internationally accepted criteria. This percentage is substantially larger than *Astragalus* as a whole (14%), its sister lineage *Oxytropis* + the Coluteoid clade (8%), and the Fabaceae (17%). More importantly, however, is that Neo-Astragalus, the clade in which the Argophyllean clade is nested, is not substantially different in its proportion of rare species (30%). These conclusions are drawn from comparisons of current findings with results and data from Sanderson and Wojciechowski (1996) and Walter and Gillett (1998) and are presented in figure 4.10.

Sanderson and Wojciechowski (1996) also found evidence of a shift toward higher diversification rates at the base of the *Astragalus* + *Oxytropis* + the Coluteoid clade (known collectively as the Astragalean clade) but did not find statistically significantly higher rates for *Astragalus* compared to *Oxytropis* or the Coluteoid clade, both of which are also quite diverse. They did not test for diversification rate variation within *Astragalus*.

In a separate study, Wojciechowski, *et. al.* (1999) applied a simplistic molecular clock model to nuclear ribosomal ITS sequence data and crudely estimated the age of *Astragalus* at around 11 million years and Neo-Astragalus at around 4-5 million years.

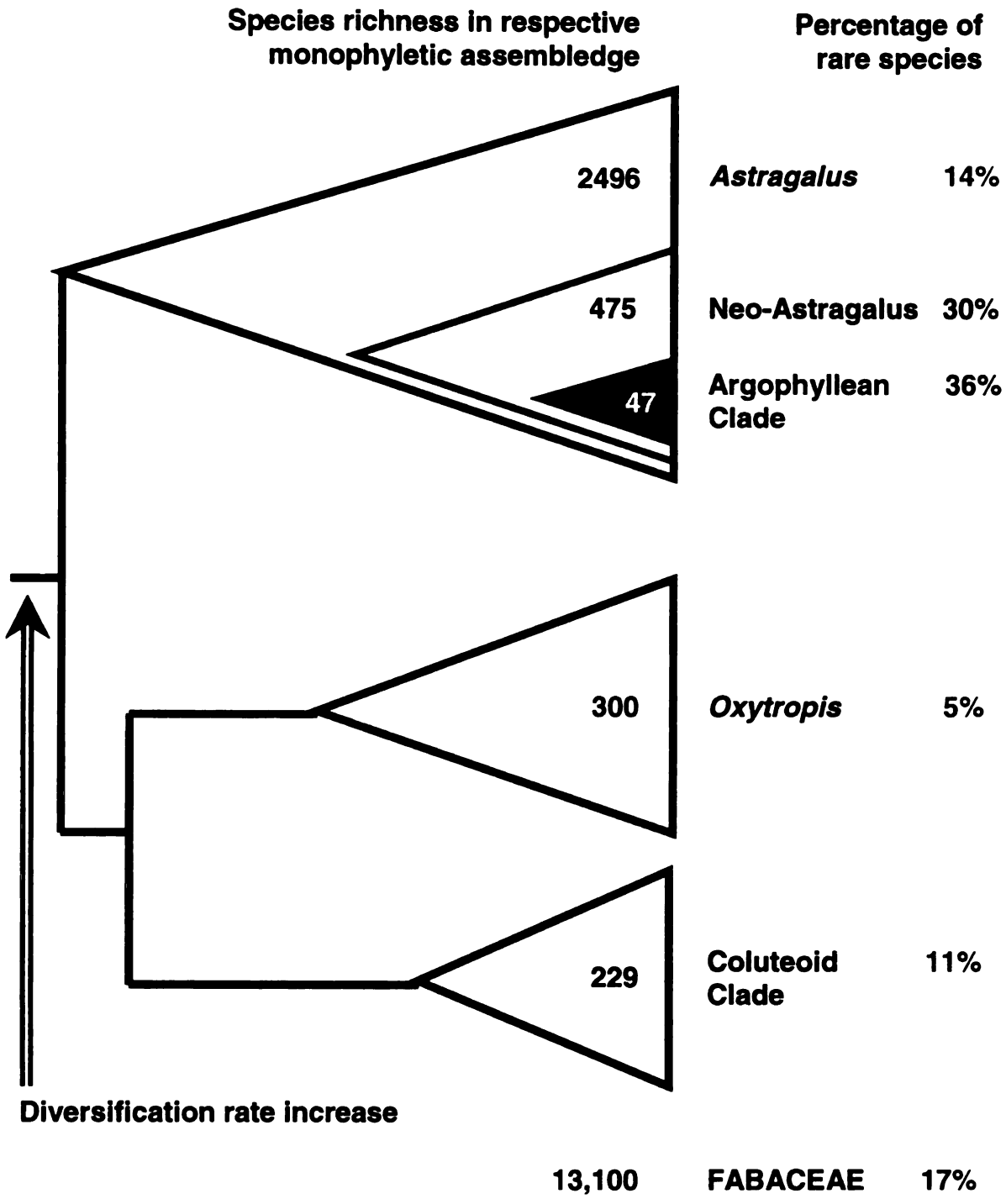


Figure 4.10
Proportion of rare species within monophyletic groups related to the Argophyllean clade. Diagram after Sanderson and Wojciechowski (1996). Rarity data from Walter and Gillett (1998).

With these estimates, net diversification rates can be estimated using a standard exponential model that assumes homogeneous rates:

$$N(t) = e^{rt} \qquad (4.1)$$

where N(t) represents standing diversity at time t, and r is net diversification (speciation minus extinction). This equation can be rearranged to give:

$$r = \ln N/t \qquad (4.2)$$

Given the estimated age of *Astragalus* and Neo-Astragalus, the following rates are obtained (Wojciechowski, *et. al.* 1999):

Astragalus	0.71 species/Myr
Neo-Astragalus	1.48 species/Myr

These finding suggest that Neo-Astragalus is diversifying at least twice as fast as *Astragalus* as a whole and perhaps faster, given that Neo-Astragalus is nested within *Astragalus* and thus adds a boost to the rate for the genus. Furthermore, this would put an age for the Argophyllean clade at 2.5 million years. This latter estimate is also a rough approximation especially in light of the evidence of heterogeneous evolutionary rates in the clade.

4.4.2 Implications of findings

What are the implications of this work regarding the causes of rarity in the Argophyllean clade? First, there is no suggestion that genealogical traits are correlated with rare status.

Correlations are used to estimate the phylogeny, and any phylogenetic correlations with rare status should result in the clustering of rare species in the phylogeny. Even if clustering were apparent, assessment of a possible correlation would require testing with an appropriate comparative method (Harvey and Pagel 1991) to establish the significance of the correlation.

The phylogeny was reconstructed using morphological traits and, to the extent that they have tracked diversification events of the group, we would expect to see clustering of rarity, if those traits were correlated with rare status. There is no suggestion of this. Even if other genealogical traits, such as root biochemical or physiological traits, are correlated with rare status, we should see clustering if the phylogenetic hypothesis is robust. Given the high levels of homoplasy in the group (as well in Astragalus generally), it is also possible that correlated traits with rare status are homoplasious and therefore do not cluster.

Another implication of this work is that the genesis of rare species probably occurs more commonly via peripatric speciation. This conclusion rests on two lines of evidence. First, the Argophyllean clade is significantly asymmetrical. Recent investigations by Chan and Moore (1999) on the effects of mode of speciation on tree symmetry led them to conclude that asymmetry increases when significant time lags are built into modeling the branching process. The rationale for time lags under the peripatric speciation mode rests on the assumption that the likelihood of speciation increases with range size. Newly derived species are less likely to speciate because they are inherently small in range size. Time is required for their ranges to expand and lead to increased probability of speciation.

Second, many biogeographic patterns among species pairs with rare species are consistent with a peripatric mode of speciation. Most of the recently derived rare species are adjacent to or nested within the range of their sister species (data not shown). Among the 11 rare species in terminal pairs, 7 are adjacent to their sister species. Two species, *A. funereus* and *A. subvestitus*, are each other's sister species and are in close proximity

to each other, similar to the seven species. The rare *A. uncialus* of Nevada is somewhat distant from its sister species, *A. musiniensis*, found in eastern Utah. The most extreme disjunction is the rare species *A. columbianus* of Washington, whose sister species, *A. parryi*, is found in Colorado and southeast Wyoming. Taken together, most of the rare species are geographically located consistent with peripatric speciation.

Because peripatric speciation leads to the emergence of new species that are rare, shifts toward higher speciation rates may lead to a proportional increase in the number of rare species. Speciation rate variation may result from either intrinsic or extrinsic causes or both. Intrinsic causes include genealogical traits that either forestall extinction and thus provide greater opportunities for speciation to occur or result in higher absolute rates of speciation. Speciation rates might also increase for extrinsic reasons, such as climate change or radiation of lineages into regions with greater topographic complexity and/or habitat heterogeneity (Cracraft 1986). Speciation rate variation can thus be lineage specific or episode specific.

We know from geological and climate studies that North America has undergone great climate changes during the last 100,000 years, plenty of time for new species to evolve via peripatric speciation. Indeed, during the Pleistocene, large areas of the Great Basin—the center of Argophyllean diversity—were inundated with inland lakes and its mountain ranges were covered with glaciers (Tierney 1995). Many of these areas are now inhabited by Argophyllean species. It remains to be seen whether new species occupy areas that were unavailable in recent times. Nevertheless, climate change has been an influential factor for the Argophyllean species. Although it is likely that significant episodes of climate change can cause speciation rate variation across time, it is difficult to assess the degree to which episodic speciation has occurred in the group because of the problems of timing.

In spite of some evidence suggesting increased diversification as a possible explanation for the rarity in this study group, the effect of extinction due to demographic

decline cannot be ignored. Indeed, extinction processes are likely to affect a number of rare species in the group. Unfortunately, little is know about extinction events because no fossil record exists for the group.

Among the four ancestral rare species in the group, as measured by the size of the sister lineages, two species, *A. loanus* and *A. desereticus* are found in habitats common for other *Astragalus* species and species of other genera. Given that they are rare in a common habitat and are relatively old based on time since divergence, these two species may be going extinct and may be the last descendants of a more widespread species or a more diverse lineage from the past.

The two other species, *A. lutosus* and *A. callithrix*, are found in unusual habitats and are not, therefore, likely to be rare because they are going extinct, although they are probably very vulnerable to extinction because of their small range size. These two species probably adapted to their unique habitats far in the past and have continued to persist as rare species. They were probably never widespread and are less likely to have been part of a more species rich lineage of the past that is now going extinct.

Finally, results presented in this chapter, taken with the work of others, strongly suggest that elucidating the reason for the high proportion of rare species in the Argophyllean clade is best studied from within the Neo-Astragalus clade. This simple conclusion rests on the fact that the proportion of Neo-Astragalus species that are rare is very similar to that of the Argophyllean clade and because of the evidence of a diversification rate shift toward higher rates in Neo-Astragalus. If genealogical traits do exist that are correlated with rare status, they may have evolved before the evolution of the Argophyllean clade. Furthermore, many other questions will be easier to test statistically with a larger study group. Indeed, if the whole Neo-Astragalus clade were used, the sample size would increase approximately tenfold.

4.4.3 Summary

In summary, evidence for the hypothesis that high rates of diversification and local speciation have led to high proportions of rare species in the Argophyllean clade is equivocal. Significant clustering of rare species and a significant preponderance of newly derived rare species were not found. However, these results are not sufficient to reject the hypothesis because alternative explanations may account for these findings. The existence of specific attributes leading to rarity in the Argophyllean clade also remains an open question. Nevertheless, several conclusions can be drawn from the present work and are offered below.

First, some lineages of the Argophyllean clade have experienced higher net rates of diversification than other lineages in the group. Moreover, the clade is nested within two larger assemblies, the Neo-Astragalus and Astragalean clades, which have experienced rate shifts toward higher diversification (Sanderson and Wojciechowski 1996; Wojciechowski *et. al.* 1999)

Second, peripatric speciation is probably the most common mode of speciation in the group, given the highly asymmetrical topology of the phylogeny. Asymmetrical phylogenies are consistent with peripatric speciation tree branching models. Also, biogeographic evidence presented in chapter 3 is consistent with peripatric speciation.

Third, the Argophyllean clade clearly has a higher proportion of rare species compared to *Astragalus* and the Fabaceae; however, the clade does not have a higher proportion of rare species compared to Neo-Astragalus. Clade specific attributes of Neo-Astragalus may account for the high proportion of rare species in the group. The Argophyllean clade of 47 species (10% of Neo-Astragalus) is most likely too small to uncover the presumed patterns in the phylogeny. At the phylogenetic scale of the Argophyllean clade, the position of rare species is likely to appear random, which might

explain the lack of significant clustering of rarity in the group and that newly derived rare species are not more frequent than expected by chance.

Forth, extinction is most probably contributing to rarity in concert with rapid local diversification. The effect may be somewhat smaller in the Argophyllean clade compared to Neo-Astragalus.

Finally, although it is evidently "not necessary to seek explanations for the 'exceptional' diversity of *Astragalus*" (Sanderson and Wojciechowski 1996), explanations for the high proportion of rare species within the Neo-Astragalus and Argophyllean clades remain a mystery and are worthy of further investigation.

APPENDICES

Appendix A.

Table A.1 Species codes, Barneby numbers, A_{10} rank, and A and E rarity. Codes used in tables 3.3, 3.8, and 3.9. Barneby's number from Barneby (1964). Asterisk indicates species revised from variety status since Barneby (1964). See chapter 2 for details. Species sorted beginning with rarest as measured by their area of occupancy A_{10}. See section 3.2.5 for details about A and E rarity.

Astragalus epithet	Code	Barneby number	A_{10} Rank	A Rarity	E Rarity	*Astragalus* epithet	Code	Barneby Number	A_{10} Rank	A Rarity	E Rarity
desereticus	dese	195	1	1	1	*castaneiformis*	cast	220	27	3	C
columbianus	colu	201	2	1	1	*eurekensis*	eure	210	28	3	C
eurylobus *	eury	197.7	3	1	1	*tidestromii*	tide	202	29	3	C
accumbens	accu	226	4	1	1	*tetrapterus*	tetr	247	30	3	C
uncialis	unci	206	5	2	2	*piutensis*	piut	194	31	3	C
funereus	fune	215	6	2	2	*casei*	case	245	32	C	C
loanus	loan	208	7	2	2	*megacarpus*	mega	241	33	C	C
helleri	hell	234	8	2	2	*coccineus*	cocc	211	34	C	C
callithrix	call	196	9	2	2	*parryi*	parr	219	35	C	C
subvestitus	subv	214	10	2	2	*chamaeleuce*	cham	221	36	C	C
pterocarpus	pter	246	11	2	3	*shortianus*	shor	199	37	C	C
neomexicanus	neom	205	12	2	2	*layneae*	layn	232	38	C	C
lutosus	luto	244	13	2	2	*inflexus*	infl	218	39	C	C
consobrinus *	cons	220.7	14	2	3	*tephrodes*	teph	197	40	C	C
anisus	anis	227	15	2	2	*utahensis*	utah	216	41	C	C
pseudiodanthas	pseu	291	16	2	C	*iodanthus*	ioda	290	42	C	C
feenis	feen	204	17	2	3	*oophorus*	ooph	242	43	C	C
cyaneus	cyan	200	18	3	3	*argophyllus*	argo	192	44	C	C
leucolobus	leuc	213	19	3	3	*beckwithii*	beck	243	45	C	C
iodopetalus	iodo	198	20	3	C	*amphioxys*	amph	222	46	C	C
giganteus	giga	235	21	3	C	*newberryi*	newb	209	47	C	C
musiniensis	musi	207	22	3	C	*missouriensis*	miss	225	48	C	C
cymboides	cymb	224	23	3	3	*mollisimus*	moll	233	49	C	C
waterfallii	wate	203	24	3	C	*purshii*	purs	212	50	C	C
zionis	zion	193	25	3	C	*lentiginosus*	lent	289	51	C	C
nudisiliquus	nudi	217	26	3	C						

Appendix B

GridPoly Avenue Program--*ArcView GIS 3.x*

This program creates a grid of square polygons which are added as a theme to the active view. A dialog box appears requesting cell size, array size (number of row cells and the number of column cells), and the location of the left and bottom of the grid. Note that the row and column input fields are reversed in the dialog box. Units are the same as those for the active theme. This program was conceived by Jeffrey W. White and written by the programming staff of Environmental Systems Research Institute, Inc.

```
'--------theView = av.GetActiveDoc

'If a theme in the view is being edited, Stop Editing it before creating new theme
editThm = theView.GetEditableTheme
if (editThm <> nil) then
  doSave = MsgBox.YesNoCancel("Save edits to "+editThm.GetName+"?","Stop
Editing",true)
  if (doSave = nil) then
    return nil
  end
  if (editThm.StopEditing(doSave).Not) then
      MsgBox.Info("Unable to Save Edits to "
                  + editThm.GetName +
                 ", please use the Save Edits As option", "")
      return nil
  else
      theView.SetEditableTheme(NIL)
  end
end

def = av.GetProject.MakeFileName("theme", "shp")

def = FileDialog.Put(def, "*.shp", "New Theme")
```

```
if (def <> nil) then
  tbl = FTab.MakeNew(def, Polygon)
  if (tbl.HasError) then
     if (tbl.HasLockError) then
        MsgBox.Error("Unable to acquire Write Lock for file " +
def.GetBaseName, "")
     else
        MsgBox.Error("Unable to create " + def.GetBaseName, "")
     end
     return nil
  end
  fld = Field.Make("ID", #FIELD_DECIMAL, 8, 0)
  fld.SetVisible( TRUE )
  tbl.AddFields({fld})
  theTheme = FTheme.Make(tbl)
  theView.AddTheme(theTheme)

end
theftab = tbl
theshpfld = theftab.findfield("shape")
theidfld = theftab.findfield("id")
theftab.seteditable(true)
labels = { "cell size", "left", "bottom", "num rows", "num columns" }
defaults = { "3", "0", "0", "10", "10" }
order = MsgBox.MultiInput( "Create Grid structure", "Enter values", labels,
defaults )
c = order.get(0).asnumber
ox = order.get(1).asnumber
oy = order.get(2).asnumber
oy2 = oy.clone

for each i in 1..order.get(3).asnumber
  for each j in 1..order.get(4).asnumber
    x = ox + c
    y = oy + c
    p = polygon.make({{ox@oy, ox@y, x@y, x@oy}})
    thePrj = theView.GetProjection
    if (thePrj.IsNull.Not) then
```

```
      p = p.ReturnUnprojected(thePrj)
    end
    r = theftab.addrecord
    theftab.setvalue(theshpfld, r, p)
    theftab.setvalue(theidfld, r, r)
    oy = oy + c
  end
oy = oy2
ox = ox + c
end
theftab.seteditable(false)
'-------
```

Appendix C

Minimum Cell Count Q-Basic Program

```
'Minimum Cell Count
'By Jeffrey W. White with programing assistance from David Wisner.

'This program is designed to determine the minimum number of square
'cells occupied in a grid which overlay points in a plane.
'Cell counts are proportional to area when generated from
'equal-area projections.

DIM SPECIES(1000), X(1000), Y(1000), GRIDX(1000), GRIDY(1000)
DIM COORD(1000), CHECK(1000), POSTN(1000)

OPEN "C:\QBASIC\SPECIES.TXT" FOR INPUT AS #1
OPEN "C:\QBASIC\SPECIES.OUT" FOR OUTPUT AS #2

CLS
I = 1
DO UNTIL (EOF(1))
   INPUT #1, SPECIES(I), X(I), Y(I)
   I = I + 1
LOOP
I = I - 1

INC = 10
FOR SIZE = 10 TO 320 STEP 10
    IF SIZE = INC THEN
       MINCOUNT = 1000
       FOR T = 0 TO (SIZE - 2) STEP 2
           FOR U = 0 TO (SIZE - 2) STEP 2
               FOR J = 1 TO I
                   GRIDX(J) = FIX((X(J) + T) / SIZE)
                   GRIDY(J) = FIX((Y(J) + U) / SIZE)
```

```
                NEXT J

                FOR J = 1 TO I
                    COORD(J) = (GRIDX(J) * -1000) + GRIDY(J)
                    CHECK(J) = 0
                NEXT J

                COUNT = 0
                FOR J = 1 TO I
                    IF CHECK(J) = 0 THEN
                       FOR K = J + 1 TO I
                           IF COORD(K) = COORD(J) THEN
                              CHECK(K) = 1
                           END IF
                       NEXT K
                       COUNT = COUNT + 1
                    END IF
                NEXT J
                IF COUNT < MINCOUNT THEN
                   MINCOUNT = COUNT
                END IF
            NEXT U
        NEXT T
        WRITE #2, SIZE, MINCOUNT
        INC = SIZE * 2
    END IF
NEXT SIZE

CLOSE #1
CLOSE #2
END
```

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