To the Graduate Council:

I am submitting herewith a thesis written by Thomas Charles Paison entitled "A Biogeographic Review of the Spider Genus *Agelenopsis* (Araneae: Agelenidae)." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

Susan E. Riechert, Major Professor

We have read this thesis
and recommend its acceptance:

Accepted for the Council:

Associate Vice Chancellor and
Dean of The Graduate School

A BIOGEOGRAPHIC REVIEW OF THE SPIDER GENUS *AGELENOPSIS* (ARANEAE: AGELENIDAE)

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Thomas Charles Paison
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DEDICATION

This thesis is dedicated to my parents

Lee Franklin Paison

and

Frieda Lucille Paison

who taught me the value of hard work

and whom I love dearly.

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I would like to thank the many people I have encountered at the University of Tennessee who made my time here educational and enlightening. Particularly, I would like to thank those faculty members, graduate students, and staff from the Department of Ecology and Evolutionary Biology who generously gave me the benefit of their expertise and friendship. I am deeply indebted to my Thesis committee, Susan Riechert, Arthur Echternacht, and Paris Lambdin for their support and encouragement. I cannot thank them enough for their time and other sacrifices they have made to help me complete this work.

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ABSTRACT

This study is a review of the biogeography of the North American spider genus *Agelenopsis* (Giebel) (Araneae: Agelenidae). Previous theoretical and empirical work provides support for the hypothesis that many North American taxa have been subject to disjunction and divergence due to the effects of Late Pleistocene glacial/interglacial cycles. A summary of the current knowledge of the biology and ecology of the 13 *Agelenopsis* species is developed and new distribution maps for each species are generated from published collections. A reconstructed phylogeny for the genus is created based on the adult sexual morphology of the species. A detailed hypothesis for the historical biogeography of the genus is developed combining information from the late Pleistocene history of North America, the reconstructed phylogeny and the current distributions of the species. It is concluded that the available information strongly supports the hypothesis that Late Pleistocene glacial/interglacial cycles were the driving force behind the origin and modern distributions of *Agelenopsis* species.

PREFACE

Questions of how species arise and attain their modern distributions on the face of the Earth are central to historical biogeography. Both Darwin and Wallace were asking these types of questions when they formulated their theories of evolution by natural selection Historical biogeography still maintains a close association to evolutionary theory in which biogeographic patterns may spur theoretical developments and theoretical developments may be examined using biogeographic data. This relationship has been fruitful in the past and the application of new techniques in biogeography should keep it fruitful in the future. It was exposure to the vast explanatory potential of the theories of Darwin that lead the author to study biology and eventually to the basic questions addressed by biogeography.

It was exposure to Robert Mengel's theory on glacier driven avian speciation in North America that interested the author in the complex interaction of geology, climate, and the biota. It seemed reasonable that some of the amazing diversity of the Arthropoda might also be explained by the recent glacial/interglacial cycles of the late Pleistocene. Having had some exposure to spiders of the genus *Agelenopsis* under Dr. Susan Riechert, who uses *A. aperta* as a model animal, the author decided to carry out a biogeographic analysis examining the hypothesis that glaciation drove speciation in this group.

Chapter One provides a review and synthesis of the theoretical background and geologic and climatic history supporting biogeographic hypotheses involving glacial/interglacial cycles. The chapter also includes a review of the results of studies on a

wide variety of animals that support the importance of glacial/interglacial cycles. Although a fair amount of work had been done on insects, studies of the biogeographic history of spider taxa were few and proved the need for additional work on these animals.

Chapter Two is a review of the available information on the biology and ecology of the 13 species in the genus *Agelenopsis*. Distribution maps for the species are also presented in the chapter, none have been published for this genus previously. Although there was good information on a few of the species, the biology and ecology of the majority of species is poorly known and in need of more in depth study. The distribution maps from this chapter were used in the development of the historical biogeography hypothesis in Chapter Three.

Chapter Three presents the phylogeny the author generated for *Agelenopsis* and the detailed historical biogeography hypothesis that was developed using this phylogeny and the information from the preceding chapters. The biogeographic hypothesis is presented in sufficient detail that predictions could be made from it and tested. It is meant to be a blueprint for the type historical biogeographic hypothesis that is consistent with speciation driven by glacial/interglacial cycles.

Chapter Four is a summary of the study, it recapitulates the main points of the thesis and provides a synthesis of the conclusions.

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CHAPTER I

INTRODUCTION AND BACKGROUND

Introduction

This thesis is a biogeographic review of the funnel web spiders belonging to the North American genus *Agelenopsis* (Araneae: Agelenidae). The hypothesis that the origin and current distribution of the species in this genus was determind by the glacial/interglacial cycles of the late Pleistocene is developed and examined. *Agelenopsis* exhibits all of the characteristics that make a taxon susceptable to speciation through vicariance during the recent ice ages. The members of the genus have broad ranges vulnerable to disjunction, they have poor long distance dispersal abilities, and they have the r-selected reproductive strategy that may make fast evolution and divergence possible.

This chapter covers first the general and specific theoretical background for the hypothesized historical biogeography of the genus presented in chapter three. A history of the geology, biota, and climate of North America follows. This provides the specific background on which the reconstruction of the history of the genus is built. A review of the biogeographic literature bearing on the proposed hypothesis wraps up the chapter.

Biogeography

Historical Biogeography

Biogeography is the study of the patterns of distribution of organisms in time and space (Cox et al. 1973). Historical biogeography is specifically concerned with the reconstruction of the sequence of events that generated present day biotic distributions and ultimately with those factors that lead to the divergence of taxonomic groups (Myers & Giller 1988). It is generally assumed that most speciation occurs following the disjunction of a species' range. For speciation to occur gene flow must be prevented or significantly reduced between populations for a length of time sufficient for them to diverge to the extent that they become genetically differentiated (i.e. allopatric speciation). Hypotheses accounting for such range disjunctions fall into two categories, dispersal and vicariance (Pielou 1979).

Dispersal hypotheses could be more accurately called jump dispersal hypotheses, as they refer to dispersal events across existing barriers that lead to the subsequent founding of populations that are genetically isolated from source populations (Myers and Giller 1988). On the other hand, vicariance hypotheses propose the development of barriers which separate once continuous ranges of species populations. Such barriers might result from physical, climatic, or biotic changes which would prevent dispersal between populations. Following either type of disjunction the populations may diverge to the subspecies, species or higher level depending on the evolutionary forces operating on the populations and the length of time they are separated (Watts 1984).

Dispersal Versus Vicariance

Although there has been considerable controversy over which mechanism of disjunction predominates, the available evidence makes it very clear that both dispersal and vicariance have had roles in the history of Earth's biota. Jump dispersal, for example, is applied to speciation and distribution patterns observed for the biota of oceanic islands. This is based on the assumption that dispersal has occurred across open ocean. On the other hand, the break up of the supercontinent Gondwanaland is an example of a major vicariance event, effecting a significant portion of the fauna and flora of the southern continents (Pielou 1979).

Despite evidence for both of these mechanisms of speciation, a strictly probabilistic point of view indicates that successful establishment of a viable population by jump dispersal is much less likely than the establishment of a viable population by vicariance. In order for jump dispersal to establish a viable population in a new area, it has to be assumed that the organism survived crossing a significant existing barrier to its dispersal and did so in numbers sufficient to establish a new population. Vicariance hypotheses only require the assumption that the organism occupied the habitat available to it and that at some subsequent time that habitat was fragmented by the development of a barrier. Vicariance explanations are thus more parsimonious in general than are jump dispersal explanations. Particularly, vicariance should be the default hypothesis in cases where the organisms in question have poor long distance dispersal abilities and for which the

development of a potentially isolating barrier can be garnered from independent evidence (Erwin and Adis 1982).

Glaciation in North America as a Taxon Generating Cycle

Mengel's Original Hypothesis

In 1964 Robert Mengel published a detailed vicariance hypothesis accounting for the diversification of wood warblers in North American. The analysis included six species groups from three genera with two to five species per group. His general hypothesis starts in the Pliocene with a parental species broadly distributed in the deciduous forests of the eastern United States and extending along the Gulf coast. Subsequently, the expansion of the Laurentide glacier during the Nebraskan glacial period compresses the species' range into the southeastern United States. The following interglacial period (the Aftonian) witnesses the expansion of the species' range north coincident with the expanding deciduous forest as well as north and northwest within the expanding boreal forest. It is assumed that this species was able to adapt and expand into the boreal forest habitat at a time when the deciduous and boreal forests were compressed together during the glacial period. However, during the following glacial period (the Kansan), this new transcontinental boreal range was effectively divided in two by the creation of a new barrier, an advancing ice sheet. The species was thus divided into southeastern and western refugia by this advance and the divergence of the parental species would have occurred by vicariance. With the next interglacial period (the Yarmouth), the eastern and

western species might both expand to inhabit the transcontinental boreal forest belt and thus stage themselves for disjunction and possible speciation with the coming of the next glacial period (the Illinoian). This cycle could have occurred at least one more time with the coming of the Sangamon Interglacial and Wisconsin Glacial periods which immediately preceded the current interglacial. It was also proposed that a new species might have budded off from the parental population in the east by habitat disjunction along the Gulf coast during one of the glacial periods. The hypothesized pattern of speciation events would account for a minimum of four species (one eastern "parental" and three western "derivative" species), though more species could result if the western derivatives reinvaded the east and speciated or if Gulf coast disjunction occurred one or more times Each of these two variants on the general pattern were seen in at least one of the six species groups Mengel examined.

Mengel's Extension of the Hypothesis

Mengel (1970) later extended his hypothesis to 100 avian species and subspecies in 34 species complexes. His analyses indicate that bird species in the New World that occupy boreal habitats during the summer show the essential characteristics of the hypothesized pattern described for wood warblers, while the non-migratory boreal birds of Old World origin do not. It seems that many of these non-migratory boreals have migrated to North America across the Bering land bridge, and may have persisted during glaciations in the Alaskan and northeastern Canadian refugia. A more truly northern, boreal climate prevailed during the glacial period in these refugia. The use of these

northern refugia would give the non-migratory boreal inhabitants a different biogeographic history and pattern from that described for the migratory species.

During the course of this latter study Mengel noted a number of variations on the basic vicariance speciation pattern. He found evidence that some species did not undergo speciation during each glaciation. There were also groups that show diversification beginning as early as the Pliocene and continuing into the Pleistocene. Evidence from this study confirmed that reinvasion of the east by western species during interglacials and subsequent disjunction and speciation during glacial periods has happened, though not very frequently among the bird taxa studied. It was also discovered that speciation has occurred within the western region of North America that appears to correspond with habitat shifts associated with the western mountain ranges during the glacial/interglacial cycle. Mountain glaciers may have isolated populations on the opposite sides of ranges during glacial periods. It is also possible that populations spread from the foothills of one range to those of another using altitudinally depressed vegetation corridors and were isolated when the vegetation moved up slope during an interglacial period. This may partly explain the high number of endemic species in the northwestern United States.

Glaciation and Speciation in Non-Avians

Hypotheses of glaciation effects on both patterns of species distribution and speciation events have been proposed for insects (Howden 1969), amphibians (Blair 1965), and small mammals (Hibbard 1970) It is thought that range expansion during glacial retreats may have primed species genetically for rapid speciation in the event of a

subsequent disjunction (Sage & Wolff 1986, Hewitt 1993). A species expanding its range will have sequentially recolonized the newly opened habitat behind the retreating ice. The populations at the leading edge of the range provide migrating individuals which will occupy the new habitat during each stage of the expansion in a stepping stone fashion These populations thus go through a series of bottlenecks followed by a period when lost genetic variation is regained by migration of individuals coming up from behind. If the range expansion is rapid, the populations farthest from the central cluster of species populations may diverge genetically to a significant degree. It is assumed that the next glacial advance separates the now genetically distinct populations from the rest of the species' populations. Then genetic differentiation already in place thus becomes the basis for divergence to the species level.

Geological, Climate and Vegetation History of North America

Underlying evidence for the biotic importance of the late Pleistocene comes from the obvious and massive alterations in the geology, climate, and vegetation during the period. The extent of these changes have forced biogeographers to consider the ice ages as a possible driving force behind speciation. The sources of information used to reconstruct paleohistory are derived from a wide variety of disciplines. Geological studies of land forms, plate tectonics, and the nature of base materials underlying soils provides information on how and when the basic land features of North America arose. Studies of erosion patterns, sediments, ice cores, and soil formation have been used by

paleoclimatologists in the reconstruction of past climate regimes. Additionally, microfossils (pollen and tiny organisms) and macrofossils (plant and animal parts) have been used to study past climate regimes and their effects on the biota. Due to the tendency of geological processes to slowly destroy the traces of earlier ages, the information available concerning the history of Earth's surface becomes increasingly more vague and tenuous the further into the past one inquires. However, we do have a fairly accurate picture of the timing and extent of glaciation events which occurred in the more recent past.

The Distant Past

Fortunately, only the changes since the break up of the single supercontinent Pangaea in the mid to late Triassic (~200-180 million years ago or m.y.a.) are considered relevant to the study of the distribution and evolution of modern taxa. This is due to the fact that most modern taxonomic families appear to have originated no earlier than the Triassic. Table 1 provides an overview of the geological periods of North America. The history of North America began when it, as part of Laurasia (made up of Eurasia, Greenland & North America), broke away from Gondwanaland (made up of South America, Africa, Australia and Antarctica). This event occurred during the break-up of Pangaea. North America then split off of Laurasia in the late Cretaceous (~80 m.y.a) (Pielou 1979). At this stage the biogeographically relevant history becomes more detailed.

Table 1. A Timeline of Geological Eras (Cox 1973, Pisias and Moore 1981).

Era	Period	Epoch	Glacials & Interglacials	Beginning (m.y.a.)
Mesozoic	Triassic			225
	Jurassic			190
	Cretaceous			136
Cenozoic	Tertiary	Paleocene		65.0
		Eocene		53.5
		Oligocene		37.5
		Miocene		22.5
		Pliocene		5.0
	Quaternary	Pleistocene		2.5
			Nebraskan Glacial	0.39
			Aftonian Interglacial	0.32
			Kansan Glacial	0.3
			Yarmouthian Interglacial	0.23
			Illinoian Glacial	0.19
			Sangamon Interglacial	0.12
			Wisconsin Glacial	0.08
		Holocene	Recent Interglacial?	0.018

Setting the Stage for the Pleistocene

In the late Cretaceous, North America was bisected by a shallow mid-continental seaway extending from the Gulf of Mexico to the Canadian Arctic. At the same time there was a major marine transgression on the east and Gulf coasts of the continent that left portions of the coast and all of the southeastern states west to the middle of Texas and north to Illinois submerged. The retreat of these inland waters began in the Paleocene (~65 m.y.a.) and was completed in the Miocene epoch (~22.5 to 5 m.y.a.) (Rosen 1978). From the Cretaceous to the Eocene epoch (~53.5 to 37.5 m.y.a.), the climate of North America was tropical to warm temperate. The climate became more equable throughout the continent over this period and reached an optimum in the Eocene. At this time, the tropical and temperate vegetation belts had extended far north of their current positions and had mixed widely in a broad ecotone occupying much of the United States (Daubenmire 1978). With the onset of the Oligocene epoch (~ 37.5 to 22.5 m.y.a.) the climate began to "deteriorate" across much of the continent (Matthews 1979).

During the Paleocene and Eocene epochs, the western half of North America was mostly a level plain dominated by forest. The Oligocene epoch saw the onset of the tectonic uplift of the west. This activity continued into the Pliocene epoch (~5 to 2.5 m.y.a.), creating the mountainous terrain of the western region. The mountain building activity produced a progressively cooler and drier climate over much of the continent as the mountain ranges grew (West 1988). Increasing aridity subsequently led to the establishment of arid adapted plants across the southwest by the middle of the Miocene (Keely and Keely 1988). The continental cooling trend further led to a southward shift of

North American tropical and subtropical zones. For example, by the Miocene the flora of the southeastern coastal plain had shifted from a tropical to a more subtropical formation (Christensen 1988). By the middle to late Miocene the East Antarctic Ice Sheet and North American mountain glaciers were in evidence. This was followed by the formation of ice sheets in the northern hemisphere by the late Pliocene (~3 m.y.a.) (Elliott-Fisk 1988). The development of these ice sheets presaged the ice ages to come in the Pleistocene epoch (~2.5 to 0 m.y.a.).

The Pleistocene in North America

The climate of the Pleistocene was dominated by large cyclic variations that culminated in a relatively regular 100,000 year cycle of glaciation and deglaciation over the last 900,000 years. It has been theorized that this cycle was generated by changes in the amount of heat received from the sun as a result of regular fluctuations in the Earth's orbit due to gravitational interactions with the moon and other planets (Pisias and Moore 1981, Bennett 1990). It is thought that a 500 meter increase in the elevation of the North American landmass between the Eocene and Pliocene made local climates more responsive to such variations in solar radiation (Daubenmire 1978). There is evidence of up to 20 ice ages during the Pleistocene, increasing in intensity toward the present (Mix 1987).

Of the seven ice ages occurring during the last 900,000 years, the last four (covering about 500,000 years) are thought to have been particularly extreme (Pisias and Moore 1981). These are, from oldest to most recent: the Nebraskan glacial with the Aftonian interglacial, the Kansan glacial with the Yarmouthian interglacial, the Illinoian

glacial with the Sangamon interglacial, and the Wisconsin glacial with the Holocene (or Recent) epoch (Matthews 1979). In the past there has been considerable controversy over the dating and reality of these periods, but recent developments in the study of oxygen-isotope ratio found in deep-sea sediment cores provides strong evidence placing four distinct ice ages in the last half million years (Mix 1987). Due to the ravages of time and the nature of the radical climate ages in the Pleistocene, the most detailed accounts of the climate and vegetation dynamics of the glacial/interglacial cycles come from the Wisconsin/Holocene cycle. Even so, the fragmentary information available about earlier glaciation cycles implies that these were generally similar to the Wisconsin/Holocene cycle (Delcourt and Delcourt 1991).

During the Wisconsin glacial maximum, North America was covered by a thick ice sheet extending across northern Washington and Montana in the west, midway through Iowa, Illinois, Indiana, and Ohio in the midwest and into northeastern Pennsylvania in the northeast (Bowen 1978). Figure 1 shows the extent of glaciation and the distribution of major habitat types in North America during the Wisconsin glacial maximum. At its maximum extent the ice altered the movement of air masses and thus effected the climate of the entire North American continent. In particular, the arctic airmass was kept from intruding over North America south of the ice and this lead to a generally more moderate (less seasonally extreme) climate in areas away from the ice margin (Delcourt and Delcourt 1987). North America can be divided into four general regions when describing the effects of glaciation on the climate and vegetation of the continent: the east, mid-continent, northwest, and southwest.

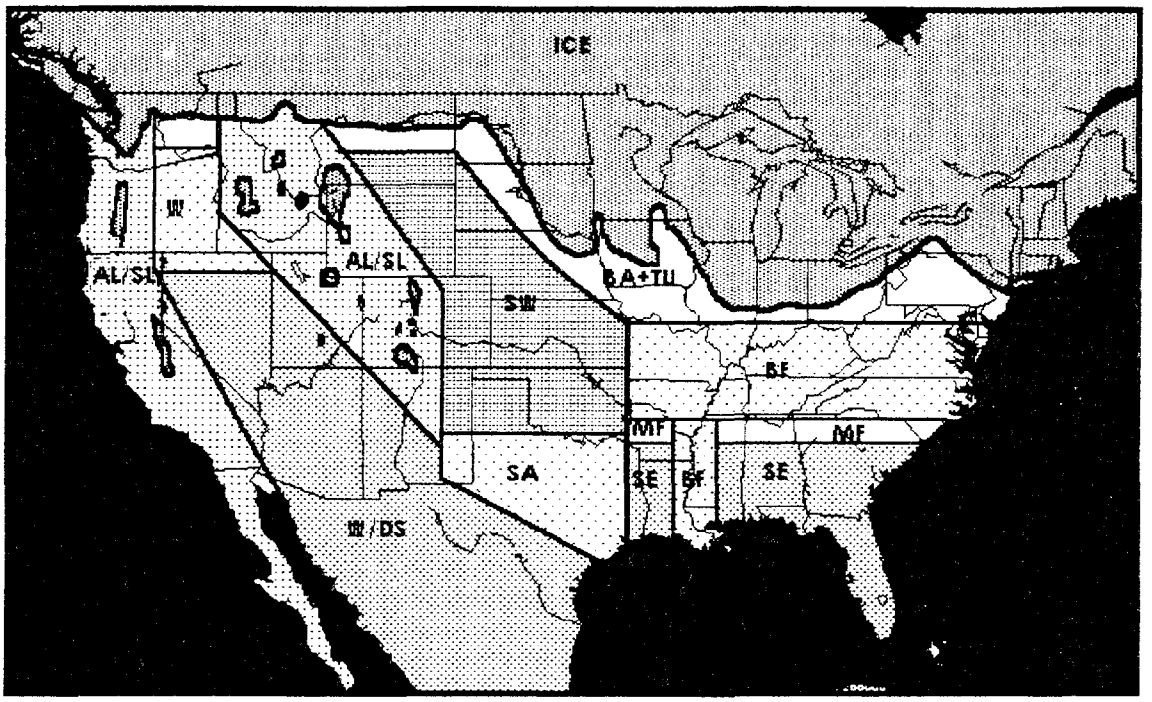


Figure 1. A Map of the Approximate Distribution of Major Vegetation Types During the Wisconsin Glacial Maximum (BF=boreal forest, MF=mixed forest, SE=southeastern deciduous & evergreen forest, SA=savannah, SW=spruce woodland, BA= bare area, TU=tundra, AL=alpine, SL=subalpine, W=woodlands, DS=desert scrub).

The Ice Ages in Eastern North America

During glaciation, the east experienced a compression of broadly defined vegetation belts southward ahead of the ice with some fragments of tundra persisting along the ice margin. The boreal forest belt extended across the region from about 40°N to 34°N latitude. It's canopy was relatively open in the eastern, western and northern edges of the belt. There was also a southward extension of boreal forest within the lower Mississippi alluvial valley that reached close to the Gulf coast. A mixed forest ecotone occurred between 34°N and 33°N latitudes on both sides of the Mississippi embayment. South of this ecotone, southeastern evergreen forest dominated on sandy uplands. Deciduous forest here existed in the fire-protected mesic habitats with rich soils. Peninsular Florida was dominated by sand dune fields with open scrub vegetation (Delcourt and Delcourt 1987). Plant species responded to the climate changes of the Pleistocene individually rather than as communities. During glacial periods, this led to the creation of plant communities composed of species that are not normally found in the same communities. Much of this mixing appears to have been driven by the reduction in seasonality during the glacial periods (Webb et al. 1993).

The Ice Ages in Mid-Continental North America

The mid-continental region of North America was dominated by the prairie during interglacial periods (Kapp 1970). On the other hand, during the glacial periods the prairie did not exist as a large, continuous biome in the plains. The northern and middle part of the plains south of the ice was instead dominated by spruce woodland with sedge and

forbs in the understory (Jacobson et al. 1987). The change in vegetation to woodland may have been due to the lower summer temperatures and higher moisture levels experienced in the plains during glacial periods (Lafontaine 1982, Delcourt and Delcourt 1987).

The Ice Ages in Northwestern North America

Northwestern North America can be divided into two areas, the mountains and the intermontane region. During glacial periods the intermontane regions experienced increased precipitation resulting in the development of extensive lakes which are present today as arid basins and dry lakebeds (Thompson et al. 1993). This lake formation combined with the lowering of altitudinal belts led to the constriction of aridlands vegetation and the growth of woodlands in the basins of the northwest (West 1988). In the mountains, alpine glaciers expanded to below 2800 meters in some ranges. This corresponded to climate shifts which promoted the movement of alpine and subalpine vegetation to lower altitudes (Thompson and Mead 1982).

The Ice Ages in Southwestern North America

The climate of arid southwestern North America is very sensitive to changes in the general circulation of the atmosphere. As a result the formation of vast continental ice sheets capable of distorting the movement of airmasses can effect the climate of this area far removed from the glaciers themselves (Van Devender et al. 1987). Climate in the southwest was cooler overall, evaporation was reduced, summer precipitation decreased, and winter precipitation increased. This led to an overall increase in effective moisture

and an increase in the extent and persistence of pluvial lakes (Spaulding et al. 1983). Forests and woodlands grew up to 1200 meters lower than they do today and replaced desert scrub vegetation in many places (Van Devender et al. 1987).

The geological, climatic and vegetation histories of North America provide the backdrop for examining possible explanations for the current distributions and origins of the continent's taxa. Correlations between this history and the distribution and origin of species have been widely noted and examined.

Biogeographic Studies of North American Taxa

It is clear that the glacial periods must have had a large effect on the distribution's of taxa as many occupy areas which were entirely covered by massive ice sheets during the last glacial maximum. Large scale climatic changes during the glacial periods have also been documented. The difficulty biologists have is in establishing a cause and effect relationship between these physical phenomena and the evolution of many of the modern species of North America. The use of biogeographical techniques that bring together the phylogenies and distributions of a wide range of taxa complete the case for the Pleistocene glaciations as generating vicariance speciation events. A brief overview of the biogeographical literature on this subject for birds, mammals, reptiles, amphibians, and arthropods follows. Arthropods are emphasized due to the great volume of literature on this speciose group and because this thesis concerns the biogeography of an arthropod

taxonomic group, funnel web spiders belonging the North American genus *Agelenopsis* (Araneae: Agelenidae).

Birds

Mengel's (1964,1970) hypothesis for the origin some of the North American wood warblers (Parulidae) has been generalized to other groups of North American birds and even to avian species on other continents. Livezey (1986) applied Pleistocene vicariance to explain a morphological phylogeny of South American steamer-ducks. Indications of extensive habitat fragmentation in the southwest U.S. during glacial periods led to similar hypotheses of cyclical speciation for aridlands bird species groups such as the Crissal Thrasher complex, Curve-billed Thrasher complex, Brown Towhee complex, and Scaled Quail complex (Hubbard 1973).

Various molecular techniques have been applied in preparing phylogenies for studying these hypotheses and attempting to directly date the age of speciations using molecular clocks. For instance, Gutierrez et al. (1983) used allozyme analysis to establish a molecular phylogeny for New World quail. The timing of the splits in this phylogeny were established from the molecular data using a calibration directly from the fossil record. Gutierrez et al. (1983) concluded that three east-west disjunctions over the last 13 million years accounted for the origin of the quail genera and that divergence of species within at least genus dates to the late Pleistocene. Another example come from Johnson and Zink's (1983) electrophoretic analysis of a sapsuckers phylogeny. Some of the

species in this group were found to have diverged during or since the Pleistocene either as a result of east-west or western intermontane population disjunctions

Independent evidence of speciation events in birds is available from genetic distance estimates. Avise & Aquadro (1982) thus determined the age of an average pair of parulid bird species to be between 5000 to about 1 million years old. Such estimates are rather broad, but fall primarily within the late Pleistocene era of ice ages. Gill et al. (1993) concluded that North American chickadees diverged in the early Pleistocene or somewhat earlier, where as Zink (1994) placed the initial branching within the fox sparrows at or before 500,00 years ago. Intermontane speciation appears to dominate in the fox sparrows (genus *Passerella)*, but at least one disjunction across the mid-continental region (between nearctic *iliaca* and the common ancestor of three northwestern species) is implied in the phylogeny of the group.

A direct test of Mengel's hypothesis using mtDNA techniques on North American wood warblers concluded that while the time frame is correct, the hypothesized pattern of speciation should be revised to allow for the greater possibility of intermontane speciation in the west (Bermingham et al. 1992). The research on mtDNA based molecular clocks indicates mtDNA evolves at heterogenous rates across at least some taxa and several other factors lead to a large degree of uncertainty around any specific clock calibration (Avise 1994). Given these problems in calibration, it would seem that the consistent placement of divergence time for the above bird species in the Pleistocene epoch should be considered evidence in support of Mengel's Pleistocene speciation hypothesis.

Mammals

The mammalian fossil record is the most complete record of any of the major animal groups. The fossil record clearly shows that North American mammal species responded to the climate changes of the ice ages by shifting their ranges in an individualistic manner. This individualistic response resulted in the formation of many communities with no exact modern analogs during glacial periods (Graham and Mead 1987). This record shows that modern mammalian species are generally of Pleistocene origin and that some 18 genera and subgenera of North American mammals might have originated as recently as the early Pleistocene (Hibbard et al. 1965).

Biogeographic studies of the mammals of North America have yielded a number of examples of speciation within this group during the ice ages. Praire dogs (genus *Cynomys*) have undergone some speciation in the southwest during the late Pleistocene and climate change is implicated in the speciation pattern (Goodwin 1993). Moose (genus *Alces*) underwent an east-west continental disjunction during the Wisconsin glacial period that led to the divergence of the endemic species *Alces scotti* from the parental species, *Alces latrifrons* (Lister 1993). A number of genera of smaller mammals have groups or pairs of species that have distribution patterns consistent with speciation due to one or more glacial disjunctions between the Great Plains and Great Basin as well. Some of the genera with this pattern are *Vulpes* (kit and swift foxes), *Spilogale* (western and eastern

spotted skunks), *Perognathus* (3 species of pocket mice), *Sorex* (shrews, *cinerus* group), and *Spermophilus* (ground squirrels, *richardsii* complex) (Hoffman and Jones 1970).

Recent molecular studies have reinforced the importance of the glacial/interglacial cycles of the late Pleistocene in the generation of modern mammalian species. For instance, an allozyme study completed on the Dall sheep of Alaska indicates that its populations have very low genetic variability. This finding is in accord with previous work indicating that northern species occupying formerly glaciated areas have significantly lower average genetic heterozygosities than southern species This has been hypothesized to result from allele loss due to the serial recolonizations and cyclic range alterations associated with glacial cycles (Sage and Wolff 1986). A mtDNA study applied to the historical biogeography of grasshopper mice (genus *Onychomys*) indicates that genetic differentiation occurred during the pluvial glaciation periods in five regions of the southwest U.S.: 1) the Mohavean, Sonoran, and Sinaloan areas; 2) the Columbia Basin and Great Basin; 3) the Wyoming Basin, Interior Plains, and Colorado Plateaus; 4) the Gulf Coastal Plain; and 5) the Chihuahuan area (Riddle and Honeycutt 1990). These studies established that range fragmentation and genetic divergence occurred during the ice ages in at least some mammals. The future use of modern molecular genetics techniques will allow empirical examination of hypothesized refugia and areas of endemism.

Amphibians and Reptiles

Fossil evidence indicates that while diversification in the amphibians had reached the levels of family, genus, and species group long before the beginning of the Pleistocene, the midcontinental drying and grassland formation during the Pliocene acted as a major barrier for most genera of urodeles (salamanders) and a few anurans. North/south disjunctions, probably resulting from range shifts south during glacial periods and relict populations left behind by northern shifts during interglacials, have created a series of northern and southern sibling species of anurans and urodeles. In addition, some anuran genera have relict species in the southwest that reflect broader distributions during the pluvial conditions of the glacial periods. Common intermontane speciation in both western anurans and urodeles may have resulted from a cycle of range expansions and contractions connecting and isolating mountains during Pleistocene climate changes (Blair 1965).

The reptile fauna of North America was also very modern by the Pliocene. Only a few good reptile fossils exist from the Pliocene, but several have been identified as members of modern species. The Pleistocene was a period of taxonomic stability for this group of animals during which there is little evidence of speciation and only records of a few extinctions, unlike some other groups of animals (Holman 1995).

Arthropods

It is generally hypothesized that the origin of modern insect species and their current distributions are most often the result of the Pleistocene ice ages. This is based on the synthesis of theoretical developments in biogeography in the second half of this century arising from accumulating information about the changes in climate, geology, flora and faunal distributions of that period (Howden 1969, Ross 1965). An examination of the recent insect fossil record, primarily Coleoptera, indicates that many modern species are older than the onset of the Pleistocene and perhaps as old or older than the Miocene (Elias 1994). Even though it appears that few new beetle species arose during the Pleistocene, there is ample evidence of divergence of isolated populations to at least the level of distinct subspecies (Elias 1994, Ball and Nimmo 1983, Graves et al. 1988). It is also clear that rates of phenotypic evolution can be highly variable between taxa (Avise 1994).

A recent review and synthesis of the insect biogeography literature, including 22 genera distributed among eleven families and six orders, discovered ten zones in North America and Mexico that separate allopatric sister taxa. At least six of these zones (Fig. 2) may have been intermittent, cycling between presence and absence in correspondence with past geologic and climatic events (Noonan 1988). The first cyclic zone runs north-south in the middle of the continent from far into Canada all the way down to the Gulf coast of Texas. This zone was the most commonly found (fourteen genera in seven families and five orders) area of disjunction; it separates eastern North America from western North America and Mexico biogeographically (Noonan 1988). Additional taxa

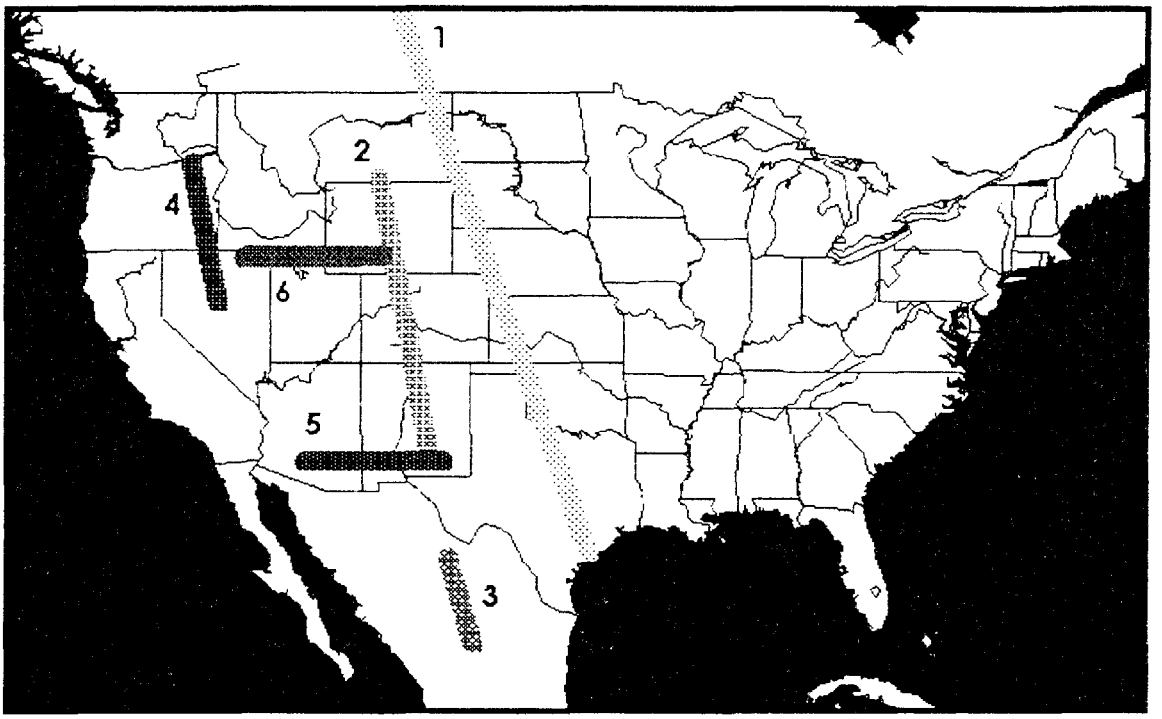


Figure 2. The Six Major Zones of Disjunctions for Arthropods. The zones are numbered as they are in the text. (adapted from Noonan 1988).

showing disjunction across this zone are from the lepidopteran genera *Papilio* (Sperling 1987) and *Euxoa* (Lafontaine 1982); the dipteran genus *Efferia* (Bullington and Lavigne 1984); the hemipteran genera *Parabrochymena* (Lariviere 1994) and *Acalypta* (Froeschner 1976), and the coleopteran genera *Cicindela* (Graves et al. 1988), *Polyphylla* (Young 1988), and *Pelidonota* (Hardy 1975).

The second cyclic zone runs along the spine of the Rocky Mountains in the United States. The third cyclic zone of disjunction runs north-south in the middle of northern Mexico and corresponds the combined barrier created by the Sierra Madre Occidental and Sierra Madre Oriental Mountains. Both zones separate sister taxa found directly to the east and west of the mountains (Noonan 1988). Additional taxa showing the second disjunction zone are the hemipteran genus *Parabrochymena* (Lariviere 1994) and lepidopteran genus *Euxoa* (Byers and Hinks 1978). Zone three disjunctions are found in the orthopteran genus *Neobarretia* (Cohn 1965) and coleopteran genus *Pelidnota* (Hardy 1975).

The xeric lowlands of the Great Basin appear to correspond to the fourth cyclic disjunction zone, separating sister taxa in the Rocky and Cascade Mountains (Noonan 1988). The lepidopteran genus *Euxoa* has two pairs of sister species demonstrating this type of intermontane disjunction (Lafontaine 1982). The Pacific Northwest insect fauna is diverse and has many endemic forms. This appears to be related to the physiographic and climatic complexity of the region, which may provide a variety of smaller areas separated by diverse barriers of different strength for different taxa. The beetle genus *Nebria* has 49

species and a number of subspecies restricted to the northwest. Because these species are poor fliers, they appear to have diverged as a result of vicariance due to a combination of the complexity of the region and climate fluctuations during the Pliocene and Pleistocene (Kavanaugh 1988).

The fifth zone circumscribes the desert of Arizona and New Mexico. This zone appears to have isolated more mesic adapted sister taxa in coastal and montane regions west of the desert southwest, the mountains of Mexico, and highlands and mountains within the desert during dryer periods (Noonan 1988). Taxa demonstrating this zone are the lepidopteran genus *Euxoa* (Lafontaine 1982) and the coleoptera genera *Cicindela* (Graves et al. 1988) and *Polyphylla* (Young 1988). This zone, along with zone two, appears to correspond to the disjunction between the Chihuahuan region and the Wyoming Basin, Interior Plains, and Colorado Plateaus region detected for grasshopper mice (Riddle and Honeycutt 1990).

The sixth and final zone separates sister taxa in the northern or middle Rockies from those in the southern Rockies. This zone corresponds to the Wyoming Basin, which is similar in climate to the aridlands mentioned above and were probably effected by changes in moisture regimens like those areas. This is the least common of the cyclical disjunction zones (Noonan 1988). Zone six appears to correspond to the disjunction between the Columbia and Great Basin areas and the Mohavean, Sonoran, and Sinaloan areas detected for grasshopper mice (Riddle and Honeycutt 1990).

There may be additional cyclic disjunction zones not discussed above. The apparent origin of the wolf spider *Geolycosa pikei* complex in the southeastern United States by isolation as a result of sea level changes during the ice ages could be one of these (McCrone 1963). A variety of insect taxa, in fact, are reported to show apparent disjunction zones that are difficult to explain (Noonan 1988). For example, the trichopteran genus *Hesperophylax* has a complex biogeographic pattern that may be accounted for by speciation resulting from some of the above six disjunctions during the ice ages. However, the predicted distribution patterns may have been obscured by range expansions which brought these species into sympatry after disappearance of the barriers (Parker and Wiggins 1985). In other cases, range shifts and the creation of relict populations could have led to disjunctions and divergence. The coleopteran *Cicindela sexguttata* species group in eastern North America shows a pattern of distribution consistent with relict population divergence (Kaulbars and Freitag 1993).

Two orthopteran subspecies of the genus *Chorthippus* are known to have reestablished contact following the retreat of glaciers from the Pyrenees Mountains. Although there has been approximately 9000 generations of contact between the subspecies, there has been little introgression. Such low levels of hybridization are common and could allow subspecies to remain distinct during secondary contact long enough to be isolated by the next glacial advance with their genetic identities intact (Hewitt 1993). This would allow repeated isolations of subspecies by glacial periods that could lead to divergence at the species level. In fact, sexual selection in animals which

have ornate and species-specific genitalia may act rapidly and cause the divergence of isolated populations for these traits. Many arthropods have such genitalia and this could account for low rates of hybridization among subspecies making secondary contact (Eberhard 1985). A mtDNA study of periodical cicadas (genus *Magicicada*) determined that the 13-year cicadas were derived from 17-year cicadas through a switch in life cycle, possibly as a result of population bottlenecking and genetic drift. The genetic structuring of the populations and their distributions is most easily explained by the impact of range shifts and restriction to refugia due to Pleistocene ice ages (Martin and Simon 1990). This molecular work supports the hypothesis that some arthropods have undergone significant divergence during the Pleistocene.

Summary

In the reconstruction of historical processes it is necessary to use inductive reasoning as direct observation is not possible. One way to establish the validity of a vicariance hypothesis is to demonstrate that the proposed barrier effected a variety of taxa. The above review demonstrates that at least some genera of birds, mammals, amphibians, and arthropods show divergence of subspecies or species in North America during the Pleistocene. This is necessary but not sufficient evidence to establish the hypothesis that Pleistocene glaciations generated vicariance barriers.

One of the main patterns predicted for glaciation driven speciation is the existence of sister taxa separated by the mid-continental region of North America. There are examples from all four classes of animals showing this pattern. Particularly, there are a great number of examples from the birds, amphibians, and arthropods. It is also predicted that a number of other common disjunctions from this time period should correspond to areas where climate change was sufficient to fragment the ranges of some animals. The intermontane region of the northwestern U.S. and the aridlands of the southwestern U.S. both meet this criteria. Thus, multiple examples from different taxa have been established with the proper time frame and general pattern proposed by the biogeographic hypothesis.

Biogeography of a Spider

The topic of this thesis is the biogeography of the North American agelenid spider genus *Agelenopsis*. The central hypothesis of the thesis is that the species in this genus arose and attained their current distributions as a result of vicariance events produced by the glacial/interglacial cycles of the Pleistocene. This hypothesis was derived as a result of the low level of morphological divergence between species, their poor dispersal abilities, and because their current distributions are consistent with having arisen from cyclical vicariance events. *Agelenopsis* shows a pattern Mengel's hypothesis would predict for ice age driven speciation.

CHAPTER 2

THE BIOLOGY, ECOLOGY AND DISTRIBUTION OF *AGELENOPSIS* (GIEBEL)

Introduction

The spider genus *Agelenopsis* is a widely distributed North American representative of the funnel web spiders (Araneae: Agelenidae). All *Agelenopsis* build horizontal sheet webs with vertical scaffoldings that knock airborne prey down onto the web-sheets. Attached silk funnels extend into the substrate and serve as refuges for the spiders when they are not attacking prey or engaging in territorial contests (Riechert 1991). The spiders of this genus are relatively large, up to 20 mm in length at maturity (Kaston 1953).

According to the taxonomy of Roth and Brown (1986), the genus *Agelenopsis* is composed of 13 species. This taxonomy is consistent with Chamberlin and Ivie's (1941) earlier summary of the genus, with the exception that Roth and Brown (1986) do not assign subspecific status to Mexican populations of the desert species *A. aperta* as did Chamberlin and Ivie. Excluded from the discussion here are another four species considered initially to belong to the genus *Agelenopsis*, but which are now thought to be a

species group derived from the genus. Roth and Brown (1986) have assigned these four species to the genus *Barronopsis* on the basis of their distinctive genitalia.

It is possible to examine the historical biogeography of *Agelenopsis* in a way which is not normally possible for many spider taxa because no species in this genus exhibit dispersal by ballooning (S.E. Riechert pers. comm.). Ballooning is a form of aerial dispersal. The spider is carried aloft by updrafts and other wind movements with the assistance of silk threads it releases from its spinnerets. These threads provide greater surface area for the generation of lift (Foelix 1984). Ballooning can carry young spiders to great altitudes and for long distances under favorable wind conditions (Foelix 1984). Because of spider ballooning behavior vicariance explanations cannot generally account for the pattern of distribution of most species. But for those spider taxa which are non-ballooning, such as *Agelenopsis*, vicariance hypotheses may be able to explain the origin and current distributions of species.

In order to explore the historical biogeography of *Agelenopsis*, it is first necessary to create distribution maps for the component species, as none have been previously published. An extensive literature review was carried out to obtain the available data concerning the locations of collections or observations of specimens of *Agelenopsis* species in the wild. These data are compiled into tables in appendix A, one table per species. The first column of these tables contains a longitude and latitude map coordinate derived from each of the reported locations using an atlas (Hammond 1982). The tables also contain the specific locality information used to derive the map coordinates and the citations for these in the second and third columns. The map coordinates were used to

place the location markers on the distribution maps for the species (Figs. 3-14) using the computer program, Expert Maps for Windows Gold Edition (Expert Software).

Summary of the Biology and Ecology of Each Species

Agelenopsis actuosa (Gertsch & Ivie)

Chamberlin and Ivie (1941) report an adult body size of 10.7 mm for males and 12 mm for females of *Agelenopsis actuosa*. Adult *A. actuosa* have been captured as early as April or May and as late as October (Doane and Dondale 1979). However, the main reproductive season begins in late July (Wickland 1993). This species does not appear to be winter active, as it was only collected during snow-free months (Aitchison-Benell and Dondale 1990).

Agelenopsis actuosa has been collected in a variety of habitats: an apple orchard (Dondale 1956), a wheat field and field border (Doane and Dondale 1979), a non-forested lake margin (Wickland 1993), and in prairie vegetation (Muma and Muma 1949). It builds its webs in both grasses and deciduous foliage at heights of 2 to 20 centimeters (Aitchison-Benell and Dondale 1990, Wickland 1993). Figure 3 shows that *Agelenopsis actuosa* is a northern species with the greatest number of reported collections from south central Canada.

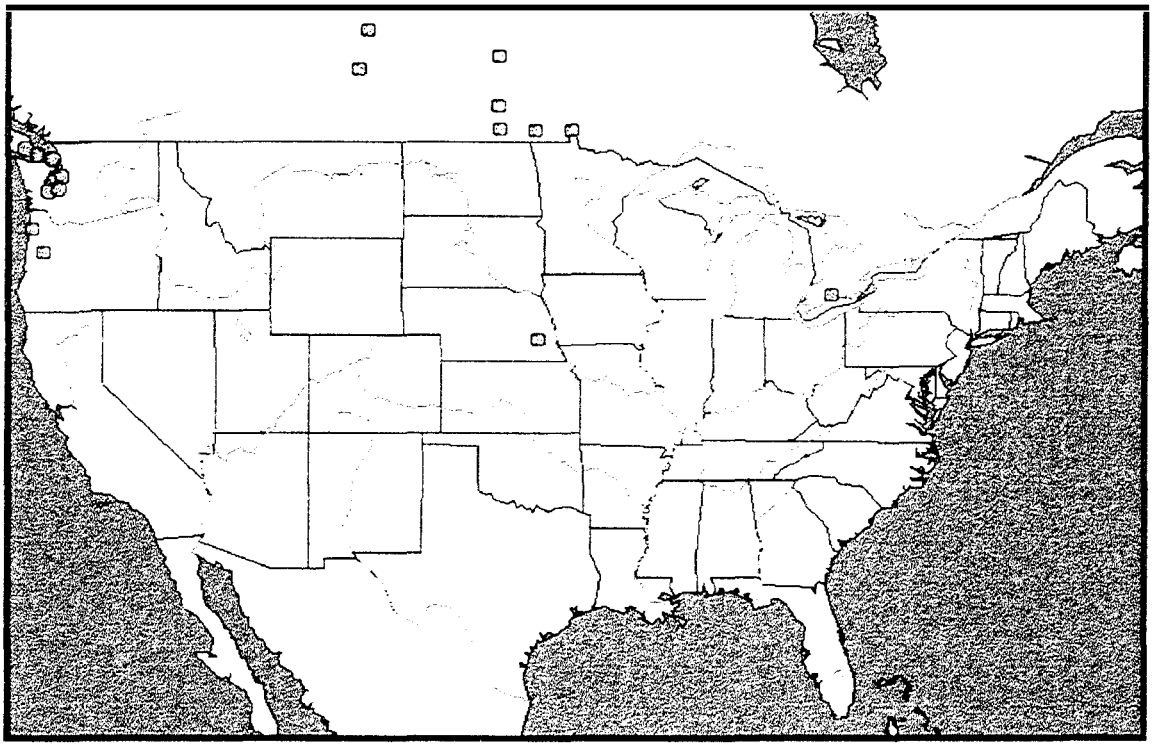


Figure 3. The Distribution of *Agelenopsis actuosa* (source data in appendix A, Table A-1).

Agelenopsis aleenae (Chamberlin & Ivie)

Agelenopsis aleenae is known from only one male found under a rock on a dry hillside in New Mexico (Chamberlin and Ivie 1941). Inspection of its genitalia indicates that this animal may be a hybrid between two of the other southwestern species of *Agelenopsis*, *A. aperta* and *A. spatula*. Its genitalic design is intermediate and the specimen was collected in an area where the ranges of the two species overlap. With only one specimen collected, little is known about *A. aleenae*.

Agelenopsis aperta (Gertsch)

Agelenopsis aperta is a highly successful aridlands inhabitant showing a broad distribution in the western United States and Mexico (Fig. 4). Kaston (1953) reports adult body lengths as 10 mm to 19 mm for females with males only slightly smaller. Adults have been collected from late April (in California) to late December (in Arizona) (Chamberlin and Ivie 1941, Ali and Hartin 1988).

Agelenopsis aperta is found in a variety of habitats such as: mixed grassland, lava bed shrub vegetation (Gertsch and Riechert 1976), and a California Christmas tree farm (Ali and Hartin 1988). While the majority of this spider species' range lies in the aridlands of the southwest, comparison of the distribution of *A. aperta* (Fig. 4) to that of aridland vegetation (Kuchler 1985) indicates that the spider may be associated with vegetation that provides significant shading and thus better microhabitats. This agrees with the finding by Gertsch and Riechert (1976) that *A. aperta* selects those microhabitats offering greater cover.

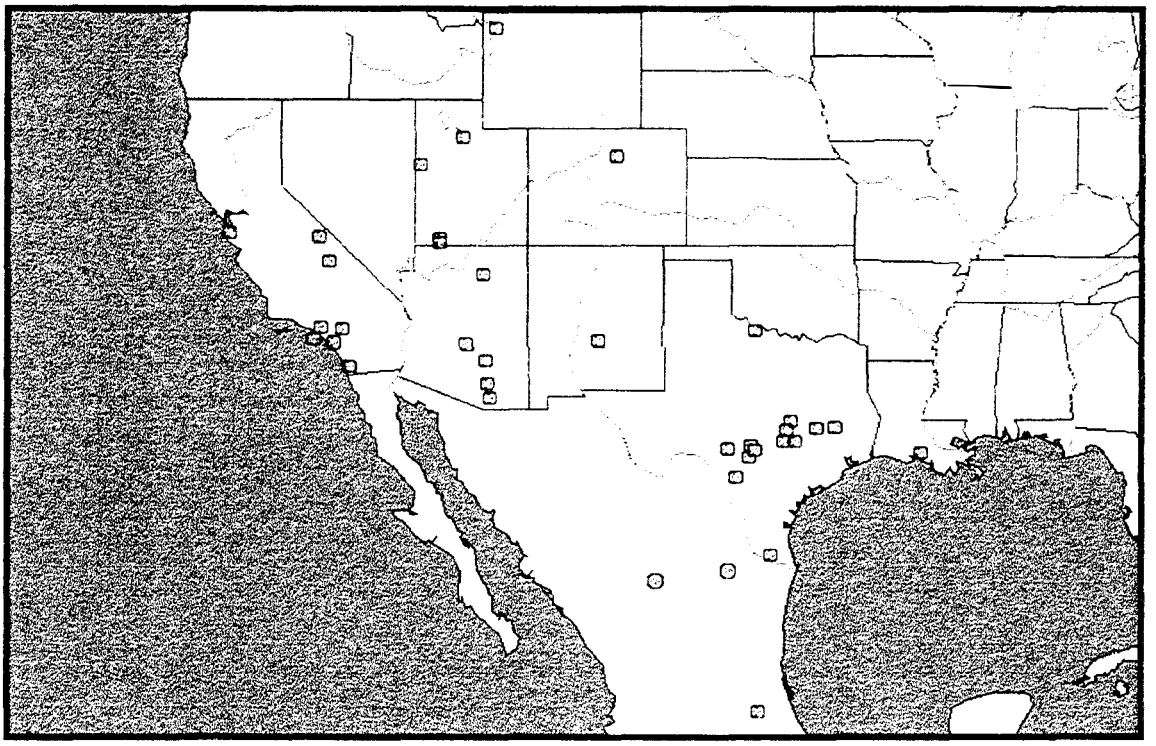


Figure 4. The Distribution of *Agelenopsis aperta* (source data in appendix A, Table A-2).

Agelenopsis emertoni (Chamberlin & Ivie)

Agelenopsis emertoni is slightly smaller on the average than most species in this genus (Muma 1945), but Chamberlin and Ivie (1941) report highly variable adult body sizes ranging from 8.60 mm to 11.70 mm for males and 7.30 mm to 15.30 mm for females. Spiderlings hatch in September and then overwinter in the egg sac. Maturity is usually reached starting in mid-July of the following year (Gibson 1947)

Agelenopsis emertoni inhabits a variety of habitats including open areas associated with river terrace forest (Gibson 1947), prairie (rarely) (Muma and Muma 1949), cotton fields (Whitcomb and Bell 1964), old fields (Drew 1967), lawn (Branson 1966), and piedmont forest and stream valleys (Uetz 1976). Muma (1945) found *A. emertoni* webs on the sides of houses and trees and with its funnel extending under stones and boards. Figure 5 shows the range of *A. emertoni* as limited to the eastern United States. Comparison of the distribution of *A. emertoni* to that of the vegetation of the eastern U.S. (Kuchler 1985) indicates that this species' range is correlated with the locations of assemblages dominated by or containing a significant proportion of oak.

Agelenopsis kastoni (Chamberlin & Ivie)

Kaston (1948) reports adult body lengths of 8 mm to 9 mm for males and 9 mm to 11 mm for females of *Agelenopsis kastoni*. This spider matures late in the spring (May and June) with an early fall die off (Kaston 1948).

Agelenopsis kastoni webs have been found on the ground in open places (Chamberlin and Ivie 1944), in soybean foliage (LeSar and Unzicker 1978), and in a

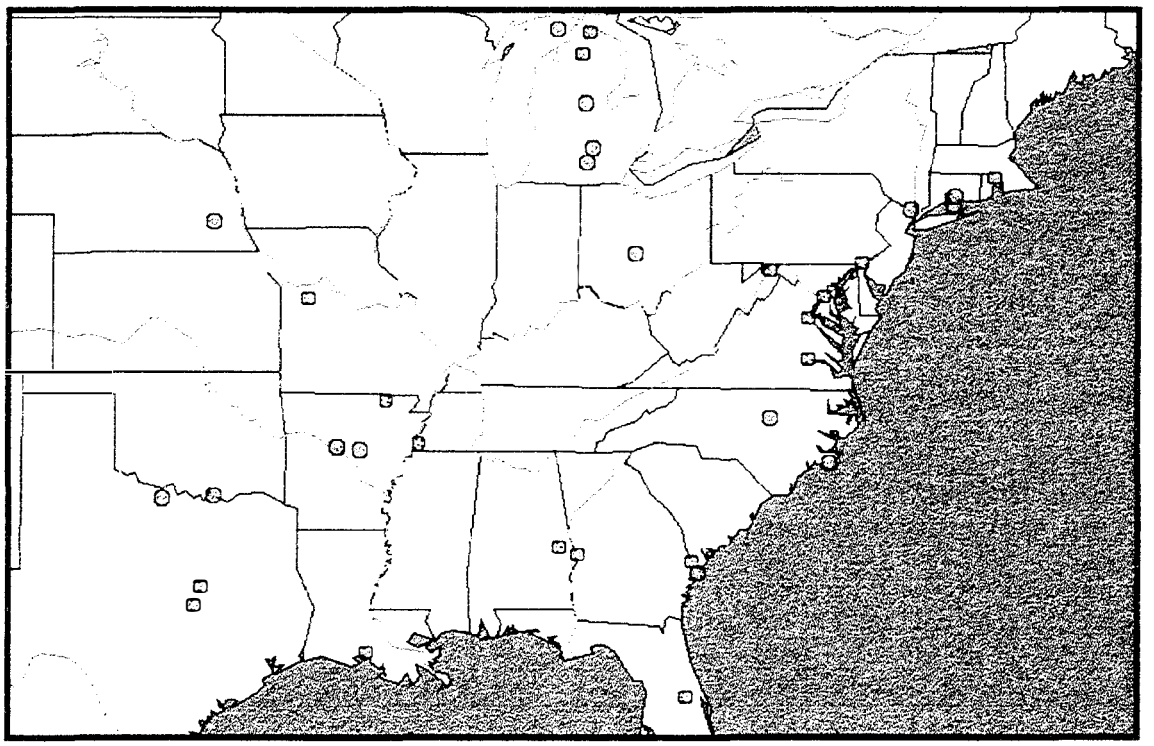


Figure 5. The Distribution of *Agelenopsis emertoni* (source data in appendix A, Table A-3).

burned old field (Haskins and Shaddy 1986). Figure 6 shows the range of *A. kastoni* to center around the middle latitudes of the eastern United States. Comparison of the distribution of *A. kastoni* to that of the vegetation of the eastern U.S. (Kuchler 1985) indicates that the range of this species is correlated with the locations of oak-hickory dominated assemblages.

Agelenopsis longistylus (Banks)

This is one of the smallest species in the genus: Chamberlin and Ivie (1941) report adult body sizes of 6.50 mm for males and 6.35 mm to 7.70 mm for females of *Agelenopsis longistylus*. Adults of this species have been collected in late August and early September (Chamberlin and Ivie 1941).

Gertsch and Riechert (1976) studied *Agelenopsis longistylus* in a rangeland habitat of gravel pavement covered with sand and sparse clumps of bush muhly and herbs. The area has low vegetative cover and lacks depressions for funnel webs to be built in, it thus has little well sheltered microhabitat. Figure 7 shows the range of *A. longistylus* to be restricted to southwestern North America. Comparison of the distribution of *A. longistylus* to that of aridlands vegetation (Kuchler 1985) indicates that the range of this species is correlated with the locates of shrub savanna, shrubsteppe, and steppe assemblages in the North American aridlands. This agrees with the finding of Gertsch and Riechert (1976) that *A. longistylus* both tolerates and thrives in less sheltered aridland habitats than *A. aperta*.

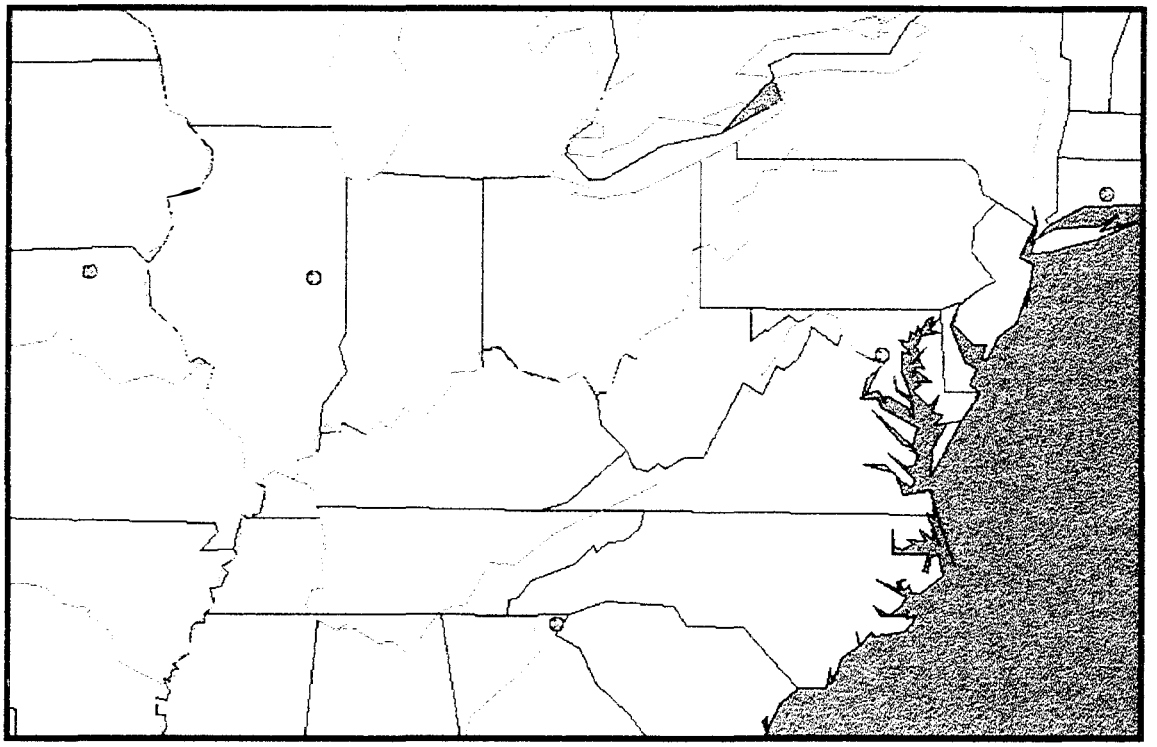


Figure 6. The Distribution of *Agelenopsis kastoni* (source data in appendix A, Table A-4).

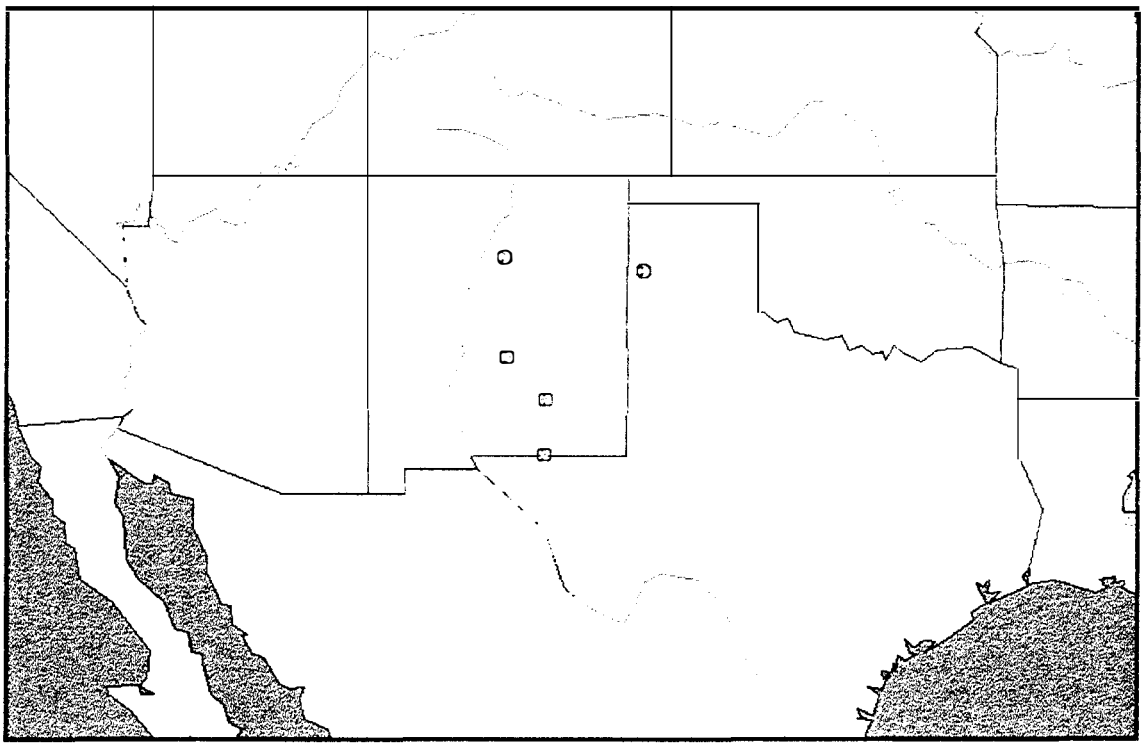


Figure 7. The Distribution of *Agelenopsis longistylus* (source data in appendix A, Table A-5).

Agelenopsis naevia (Walckenaer)

Kaston (1948) reports Adult body lengths of 13 mm to 17 mm for males and 16 mm to 20 mm for females of *Agelenopsis naevia*, making it the largest species in the genus. Maturity is usually reached around mid-July (Gibson 1947).

Agelenopsis naevia appears to have broad habitat requirements, although Jones (1941) determined that it must be exposed to a humidity above fifty percent for at least a short period each day in order to have normal growth and development. It is found abundantly in woodlands (Fitch 1963) but is also common in cultivated areas, meadows and grassland (Gibson 1947) and forest-field ecotones and old fields (Young et al. 1989). It builds its webs in small shrubs, on the sides of houses and trees (Muma 1945), among stones (Kaston 1948), and in herbs and grass 0.5 to 2.0 m above the ground (Young et al. 1989). Jones (1941) found that younger *A. naevia* build their webs close to the ground (1-2 inches) and older spiders show some variation in web height, building them up to 3 to 4 feet above the ground. This species has its highest densities in areas where ground litter and low vegetation are abundant (Fitch 1963).

Figure 8 shows *Agelenopsis naevia* to have a range restricted to the eastern United States. Comparison of the distribution of *A. naevia* with that of the vegetation of the eastern U.S. indicates a broad correlation between the range of this species and forest vegetation. *Agelenopsis naevia* does not appear to have been collected in areas without significant forest stands of some type (U.S. Forest Service 1987).

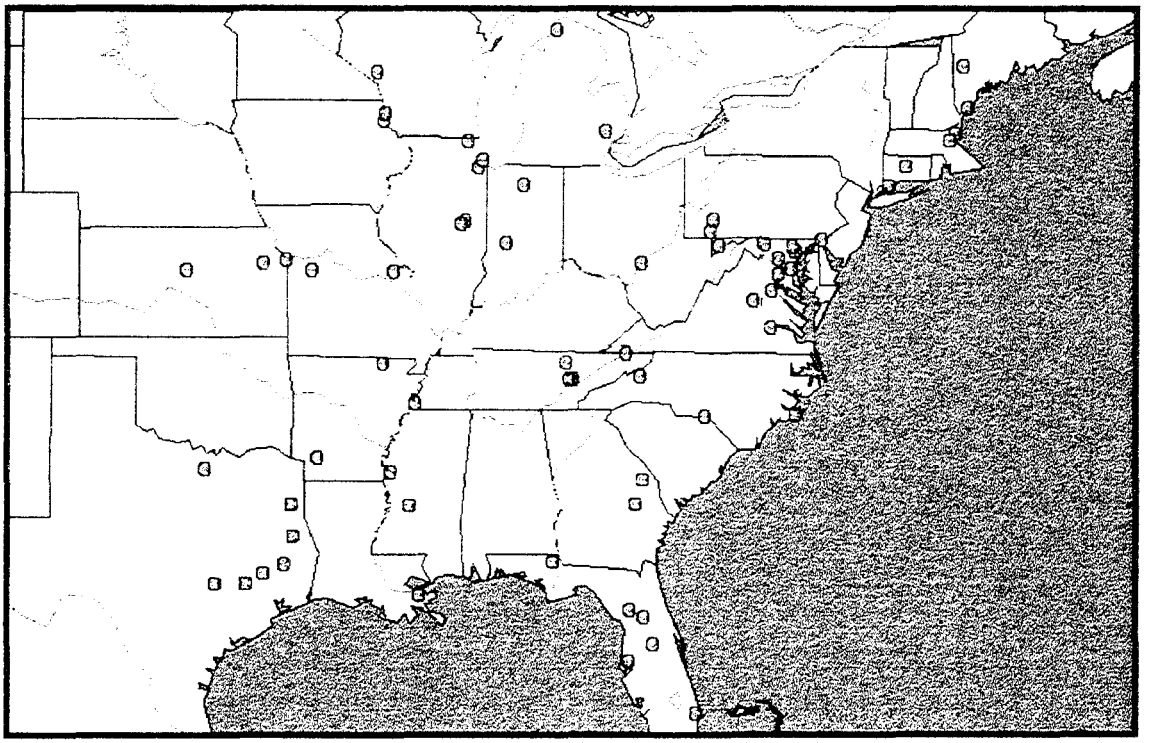


Figure 8. The Distribution of *Agelenopsis naevia* (source data in appendix A, Table A-6).

Agelenopsis oklahoma (Gertsch)

Chamberlin and Ivie (1941) report adult body sizes of 6.50 mm for males and 6.35 mm to 7.70 mm in females of *Agelenopsis oklahoma*. This spider is abundant between early August and early November. Females mature in June and mature males and females survive until October (Muma and Muma 1949).

Muma and Muma (1949) found *Agelenopsis oklahoma* to be very common in the prairie around Lincoln, Nebraska. It is most common in high prairie, but it is also found in tall grasses and occasionally in shrubs. Figure 9 shows *A. oklahoma* to have a range restricted to the mid-continent in the middle and northern latitudes of the United States. A comparison of the distribution of *A. oklahoma* to that of the vegetation of the Great Plains (Kuchler 1985) indicates that the range of the species is correlated with the locations of tall grass prairie vegetation and the shrub steppe vegetation of the Wyoming basin. It may be that the short grass prairie, abutting the foothills of the Rocky Mountains to the west, is too harsh a habitat for *A. oklahoma*.

Agelenopsis oregonensis (Chamberlin & Ivie)

Chamberlin and Ivie (1941) report an adult body length of 9.50 mm for males and 10.60 mm for females of *Agelenopsis oregonensis*. Mature *A. oregonensis* have been collected from early August to mid-September (Chamberlin and Ivie 1941).

Agelenopsis oregonensis occupy open and disturbed areas that are neither meadow nor have significant vegetation much above ground level. Parsons et al. (1991) found *A. oregonensis* to be very common in the Cascade Mountain Range of northeastern Oregon.

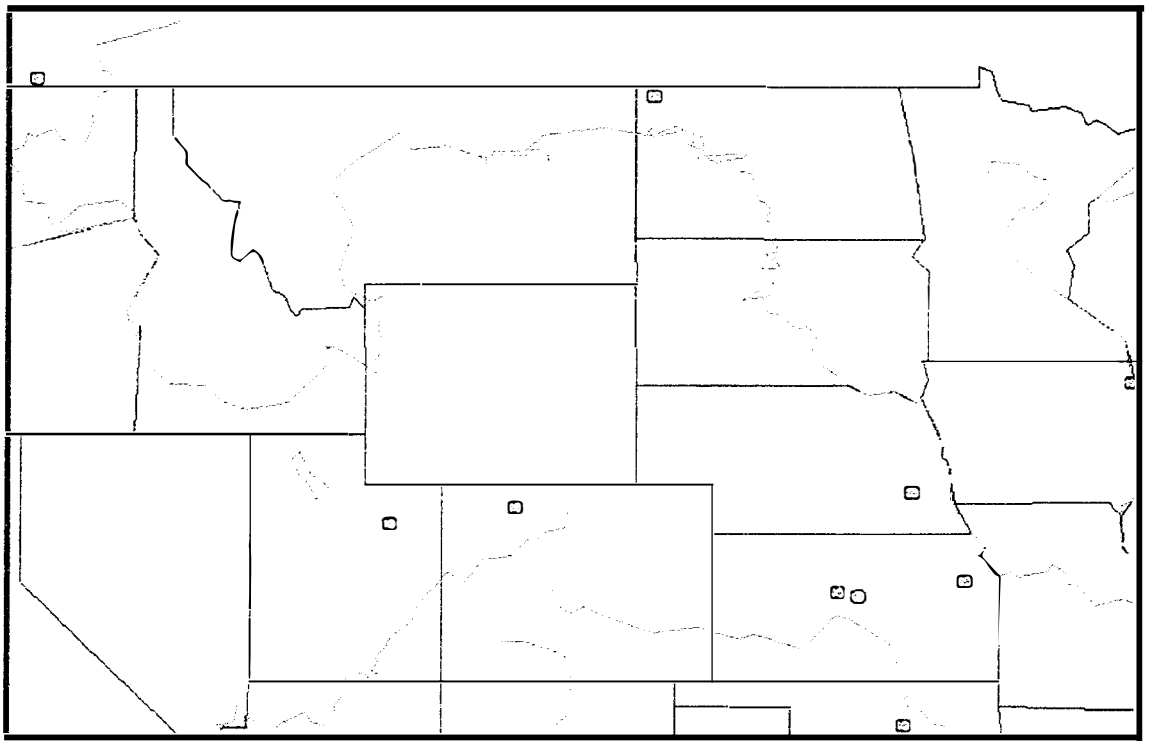


Figure 9. The Distribution of *Agelenopsis oklahoma* (source data in appendix A, Table A-7).

Figure 10 shows *Agelenopsis oregonensis* to have a range restricted to the vicinity of the Cascade Mountain Range. Comparison of the distribution of *A.* oregonensis to that of the vegetation of the northwestern U.S. (U.S. Forest Service 1987) indicates that the range of this species is correlated with the locations of non-coastal coniferous forests of Oregon and Washington. It appears as if this species inhabits gaps and edges associated with these forests.

Agelenopsis pennsylvanica (C.L. Koch)

Chamberlin and Ivie (1941) report adult body lengths of 8.80 mm to 13.00 mm for males and 6.70 mm to 17.00 mm for females of *Agelenopsis pennsylvanica.* Maturity is reached beginning in mid-July (Gibson 1947). Fitch (1963) observed *A. pennsylvanica* mating in late September. *Agelenopsis pennsylvanica* deposits its egg sac under loose bark in the fall (Kaston 1953).

Agelenopsis pennsylvanica inhabits areas around buildings more frequently than any other member of the genus (Muma 1945). It has also been collected in black oak and beech-maple dune communities (Lowrie 1948); cultivated areas, meadows or grassland associated with river terrace forest (Gibson 1947); open woods (Kaston 1948); cotton fields (Whitcomb et al. 1963); woodland and brushy fields (Fitch 1963); damp areas with old field and crop vegetation (Branson and Batch 1970); coastal salt marsh (Uetz 1976); and in the prairie and forested fens of a plateau in the Ozark Mountains (Bultman 1992). Levi and Field (1954) found *A. pennsylvanica* to be abundant wherever it occurs.

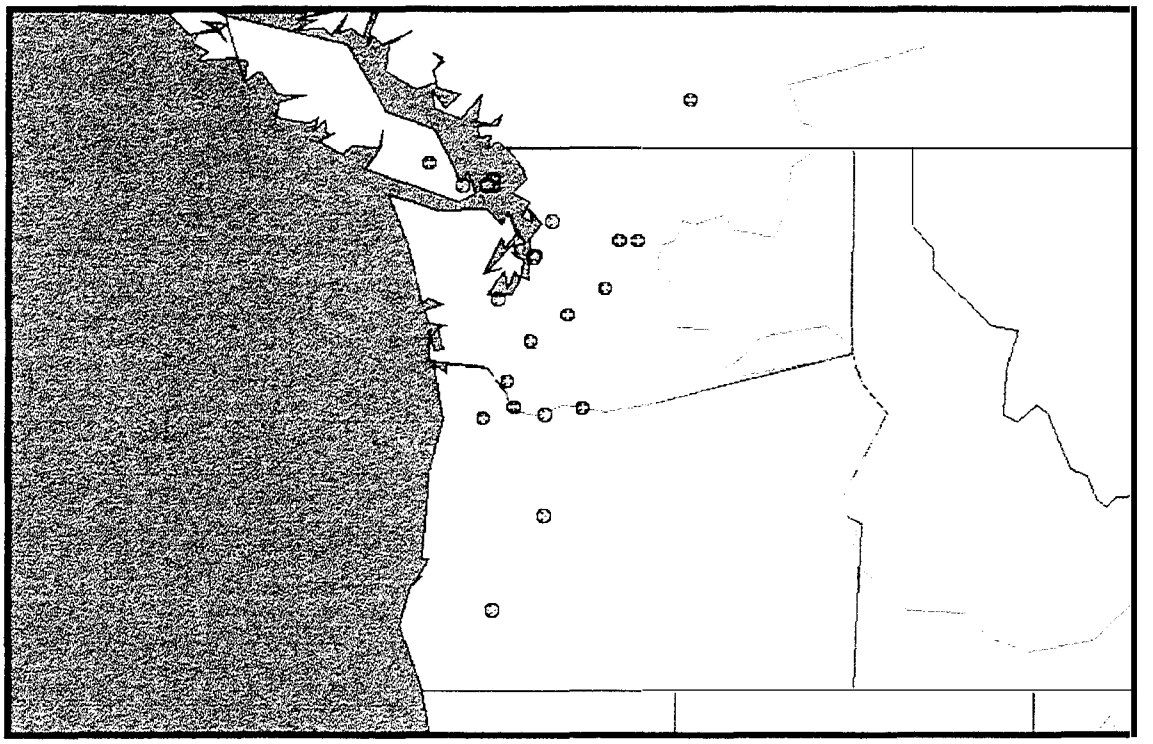


Figure 10. The Distribution of *Agelenopsis oregonensis* (source data in appendix A, Table A-8).

Figure 11 shows *Agelenopsis pennsylvanica* to have an apparently disjunct range. The species is broadly distributed in the eastern United States and more narrowly distributed in the northwestern United States. These two apparent disjuncts may be connected by populations along river corridors that cross the plains (Kaul et al. 1988). Comparison of the distribution of *A. pennsylvanica* to that of the vegetation of the United States (Kuchler 1985) indicates that the range of this species is correlated with areas of high water availability such as floodplain forests and other habitats close to bodies of water. Humidity may be a key factor in the distribution of *A. pennsylvanica*.

Agelenopsis potteri (Blackwall)

Chamberlin and Ivie (1941) report highly variable adult body lengths ranging from 7.30 mm to 12.70 mm for males and 6.70 mm to 16.00 mm for females of *Agelenopsis potteri*. Females of this species create egg sacs and places them under loose bark during October (Harrington 1978).

Agelenopsis potteri is commonly found around buildings (Chamberlin and Ivie 1941). This spider has a broad habitat tolerance. Earnshaw (1973) found that *A. potteri* occurs in both open meadow and deciduous woodland, but is most numerous in the ecotone between the two. The webs of this species are found on trees, shrubs, grass, herbaceous plants, rock piles and buildings (Drew 1967, Turnbull 1965, Aitchison-Benell and Dondale 1990). It is fairly heat tolerant, able to survive temperature up to 30 degrees centigrade for significantly longer than *A. utahana*. Juvenile *A. potteri* are sensitive to humidity, but the adults do not appear to be (Earnshaw 1973).

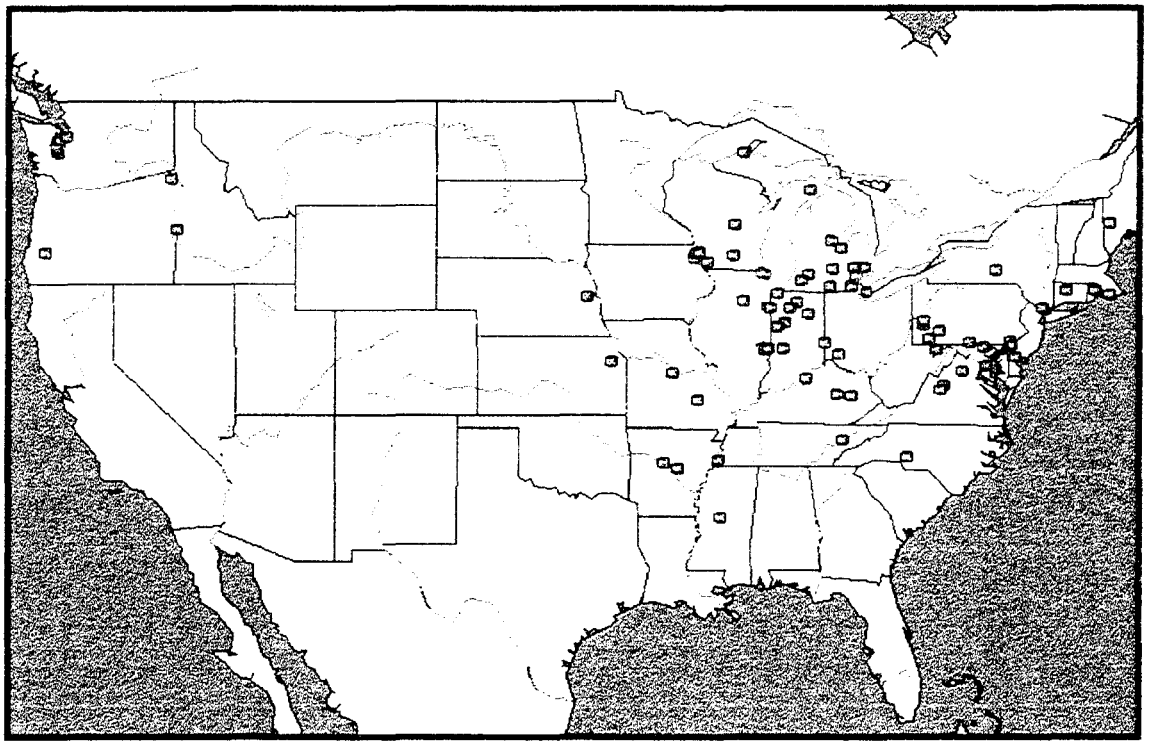


Figure 11. The Distribution of *Agelenopsis pennsylvanica* (source data in appendix A, Table A-9).

Figure 12 shows *Agelenopsis potteri* to have an apparently disjunct distribution. The distribution of *A. potteri* occupies the northern United States and southern Canada east and west of the Great Plains and Rocky Mountains. This species appears to be most concentrated in the Pacific Northwest and Great Lakes regions, both of which are northern areas of high humidity. It may be a combination of the low temperature and high humidity regimes of these regions that defines the habitat requirements of the species. A comparison of the distribution of *A. potteri* to that of the vegetation of the U.S. (Kuchler 1985) provided no clear correlation between the range of the species and any specific vegetation type.

Agelenopsis spatula (Chamberlin & Ivie)

Chamberlin and Ivie (1941) report an adult body length of 13.0 mm for males and 13.5 mm for females of *Agelenopsis spatula*. Adults of this species have been collected from mid-August to early September (Chamberlin and Ivie 1941).

Figure 13 shows *Agelenopsis spatula* to have range restricted to the southern Great Plains and Rocky Mountains. Comparison of the distribution of *A. spatula* with that of the vegetation of the southwestern U.S. (Kuchler 1985) indicates that this species occupies aridlands in the southern plains bordering the short grass prairie. Though *Agelenopsis spatula* appears to be an arid adapted animal, it may be that the species is not sufficiently arid adapted to survive in the full rain shadow of the Rocky Mountains in a vegetation type which offers little shade.

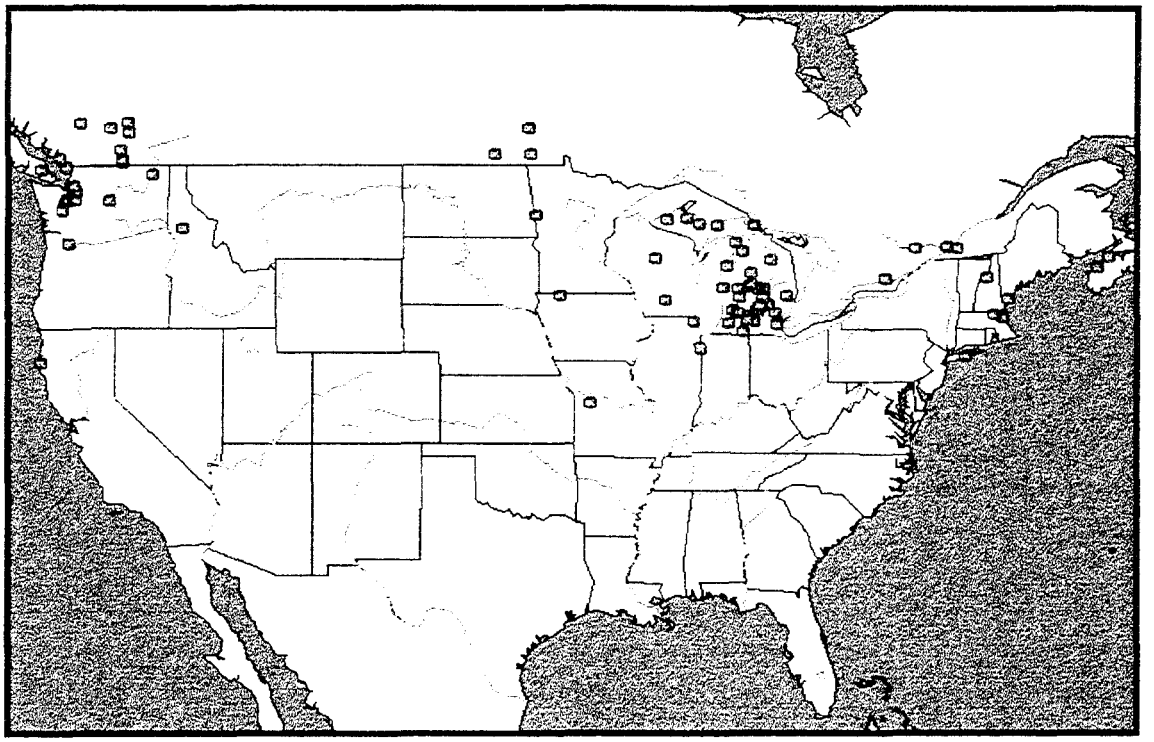


Figure 12. The Distribution of *Agelenopsis potteri* (source data in appendix A, Table A-10).

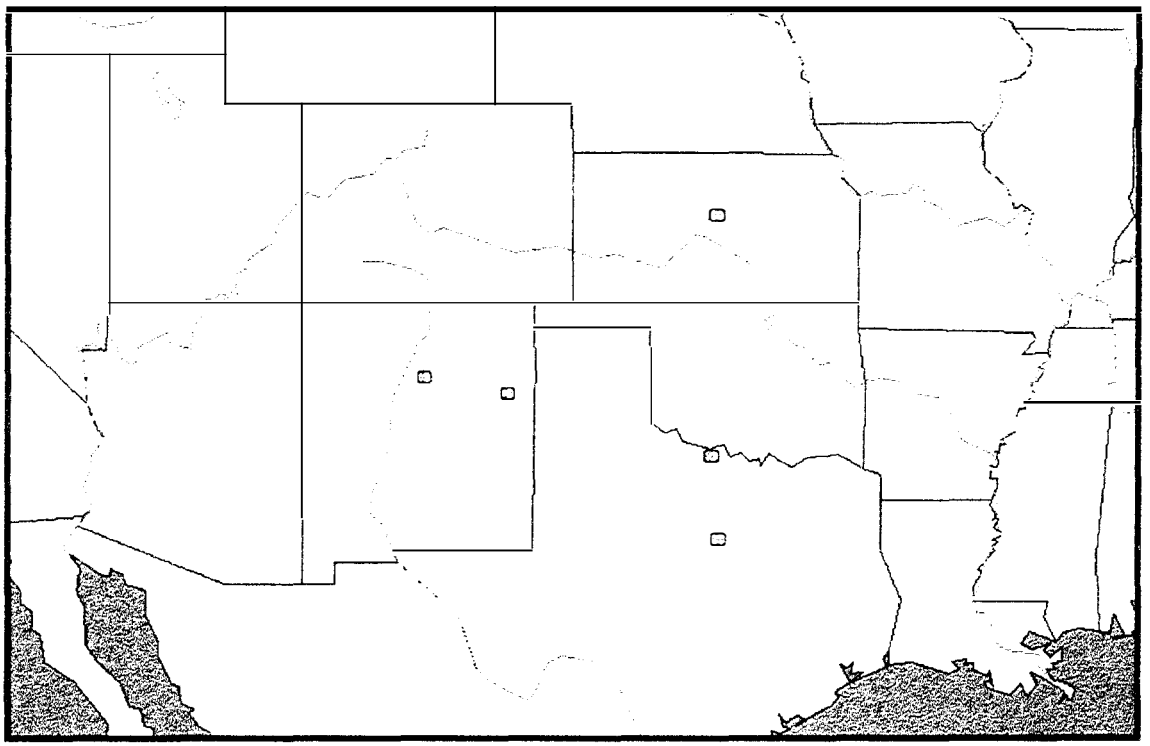


Figure 13. The Distribution of *Agelenopsis spatula* (source data in appendix A, Table A-11).

Agelenopsis utahana (Chamberlin & Ivie)

Kaston (1948) reports adult body lengths of 8 mm to 10 mm for males and 9 mm to 12 mm for females of *Agelenopsis utahana*. *Agelenopsis utahana* produces egg sacs in the fall. Earnshaw (1973) found that the egg sacs overwinter below the snow line enclosed in a leaf. Spiderlings emerge from the egg sac in the spring and take two years to develop to full maturity (Earnshaw 1973). Maturity is reached beginning in late July of the second year of life (Hackman 1954).

Agelenopsis utahana is recognized as a woodland species (Earnshaw 1973). Aitchison-Benell and Dondale (1990) describe it as a Nearctic species found in boreal forest, aspen parkland, mixed woods, bogs, and on jackpine ridges, usually building its webs in grass. The webs of *A. utahana* are also found on herbs and stumps in woods (Kaston 1948) and among debris in areas strongly influenced by man (Hackman 1954).

Earnshaw (1973) found the optimal temperature for the growth and development of *A. utahana* to be 18°C. This optimum is consistent with adaptation to the colder habitats found at higher latitudes and altitudes. Levi and Levi (1955) found *A. utahana* at altitudes between 4200 feet and 5100 feet in northwestern Montana. Earnshaw (1973) concluded that the two year life cycle of this animal may be due to the lower temperatures it lives in and the lower prey density available in the woods compared to more open habitats.

Figure 14 shows *Agelenopsis utahana* to have a transcontinental range that appears most concentrated around the U.S.-Canadian border. The distribution of this spider species has some extensions further south into the mountainous regions of the

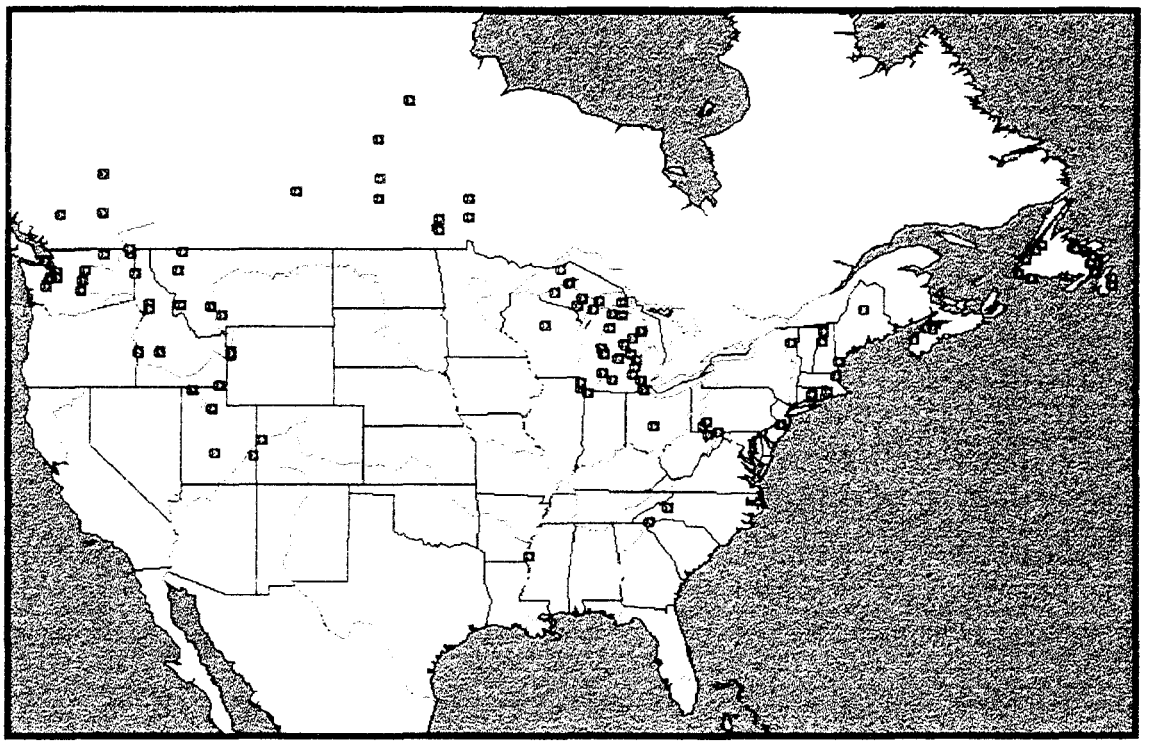


Figure 14. The Distribution of *Agelenopsis utahana* (source data in appendix A, Table A-12).

eastern and western United States. The distribution of *A. utahana* clearly seems to be correlated with the locations of the alpine and northern boreal forests of North America (U.S. Forest Service 1987). This is consistent with the woodland habitat preference and cold tolerance of this species.

Summary

Most of the species of the spider genus *Agelenopsis* have fairly extensive ranges. They also appear to be habitat generalists that tolerate different local climates and habitats. What appears to distinguish the species ecologically is not how broad their tolerances are, but where along a rather large spectrum of environmental regimes these tolerances lie. Though there is extensive overlap in tolerances and habitat utilization patterns among species the distributions of the species of *Agelenopsis* are suggestive of Pleistocene disjunctions.

CHAPTER 3

A PHYLOGENY AND HISTORICAL BIOGEOGRAPHY OF *AGELENOPSIS*

Introduction

In order to examine the hypothesis that speciation within the genus *Agelenopsis* has been driven by the Pleistocene glacial/interglacial cycles, it was necessary to develop a phylogeny that could be examined in terms of the patterns of species distributions as presented in Chapter Two. A phylogeny is a reconstruction of the evolutionary history of a taxon. There are two philosophies on the generation of phylogenies, phenetics and cladistics. Phenetics utilizes overall similarity based on measurement guided by defined rules and using as many traits as possible. Cladistics defines the branches of a phylogeny by grouping the taxa by shared traits derived from a common ancestor (i.e. monophyletic groups). Cladistics focuses on the branch-splitting portion of phylogeny construction rather than the branch length component (Avise 1994). Cladistics is the method most commonly used in conjunction with historical biogeography due to its emphasis on the identification of the evolutionary branch points that define related taxonomic groups (Humphries et al. 1988).

A phylogeny can serve as a basis for specific reconstruction of the biogeographical history of a taxon. It establishes how the lineages within a group of taxa are related and the order of the splits that produced them. Without this information, it would be impossible to propose that specific vicariance barriers effected specific lineages. This is particularly true in the case of barriers which might act in a cyclic fashion, such as those produced by glacial/interglacial cycles of the Pleistocene.

Methods

Phylogeny

Because the relationships between the genera in the Family Agelenidae have not been well studied, it was impossible to select an adequate outgroup for *Agelenopsis* that would allow for a highly rigorous designation of traits as either ancestral or derived. Thus I used the qualitative technique of Platnick and Shadab (1981), which utilizes morphological similarity, in generating a phylogeny for the 13 species. The technique tests for degree of similarity between the adult sexual structures of species in determining the branching pattern of the phylogeny. The traits were unweighted under this technique. The sexual structures are used because they are highly species-specific in spiders and the only reliable way in which closely related spider species may be distinguished from one another morphologically (Chamberlin and Ivie 1941). The complex and species specific genitalia of spiders is thought to result from the action of runaway sexual selection which may rapidly alter the morphology of the selected sexual characters (Eberhard 1985).

Thus, the complex structures of the genitalia serve as stimulators that increase reproductive fitness by direct effect on copulation and fertilization rates. This interpretation is supported by Gering's (1953) study of *Agelenopsis* gentalia in which he found poor evidence for the lock and key explanation for genitalic complexity.

Differences in the size, shape and relative location of components of the genitalia were the traits used to develop a phylogeny for *Agelenopsis* (listed in Table 2). The specific traits utilized were chosen based on similarity to the type used by Platnick and Shadab (1979, 1981) for phylogeny construction within the spider family Gnaphosidae. These traits may be applied to agelenid spiders because all spider genitalia have the same basic set of components. The genitalia of *Agelenopsis naevia* are illustrated in Figure 15; the structures used in the phylogeny are labeled on the drawings. Drawings of the genitalia of the other 12 species can be found in Appendix B (Figs. B-1 to B-12). The traits chosen were used as a presence/absence test for grouping the species first into sister species, then into progressively more inclusive subsets of the genus. Trait A1 is considered present if the embolus is thick along its entire length and absent if the embolus is otherwise. The coded traits are the shared characters that define the lineages following them as monophyletic groups. The subsets defined the order in which branches were placed in the phylogeny. This method for generating the phylogeny is admittedly crude, but the phylogeny does not need to be exceptionally accurate for it to be useful in the exploration of the general biogeographical hypothesis put forth here.

Table 2. Key to the Morphological Traits Underlying the Proposed Phylogeny for the Genus *Agelenopsis*.

Lineages	Morphological Traits Used to Distinguish Between Sister Lineages
A1	The embolus is thick over its entire length.
A2	The embolus is thinner and tapers off in thickness from the base to the tip.
A3	The tip of the embolus is broadened.
A4	The conductor is blunt.
A5	The tip of the embolus is distinctly elongated and slender.
A6	The tip of the embolus is interiorly directed and tapers to a point.
A7	The tip of the embolus is clearly spatulate
A8	The anterior lip of the posterior pouch of the vulva has a distinctive double arch appearance.
A9	The vulva is flaired out posteriorly.
A10	The conductor is distinctly shortened

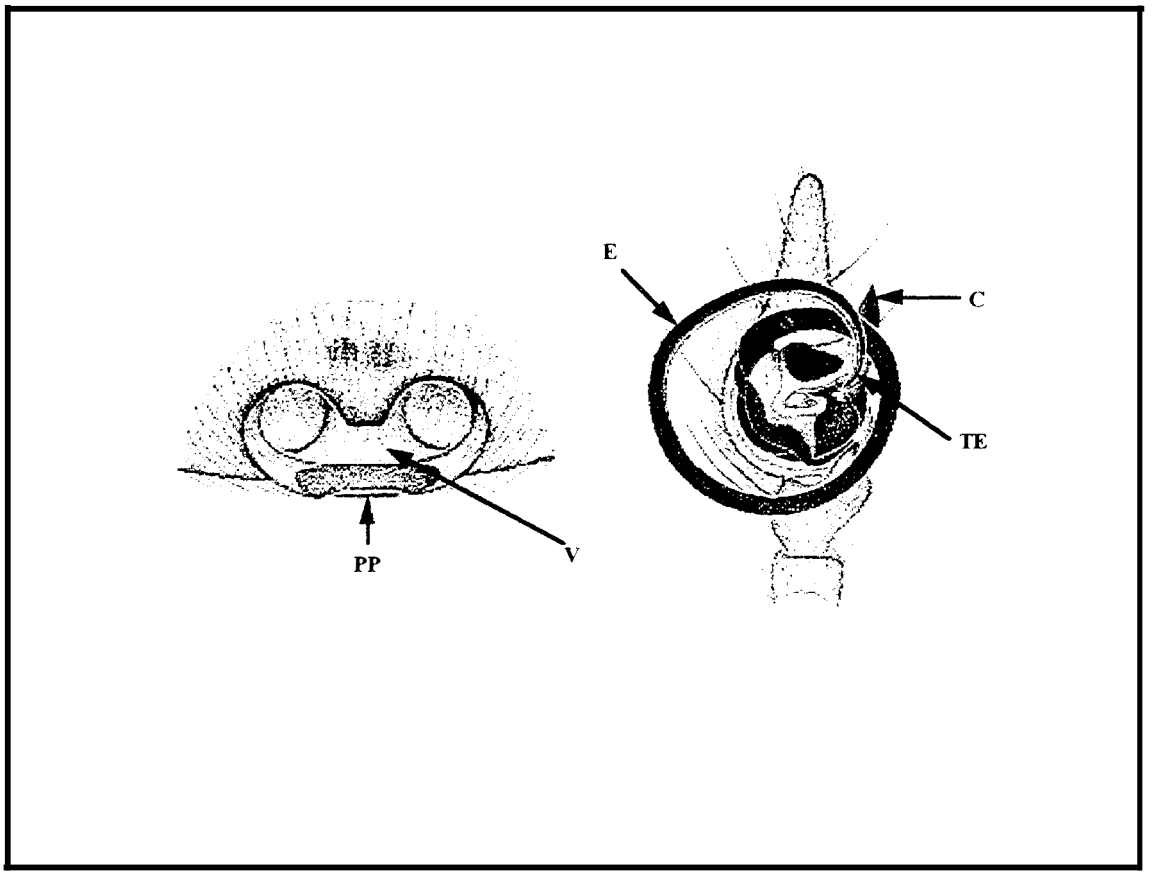


Figure 15. The Epigynum (left) and Left palpus (right) of *Agelenopsis naevia*, labelled to identify the genitalic structures utilized in the phylogeny (PP=posterior pouch of the vulva, V=vulva, E=embolus, C=conductor, TE=tip of the embolus) (Modified from Chamberlin & Ivie 1941).

Historical Biogeography

This phylogeny was analyzed in combination with the distribution maps for the 13 species (from Chapter Two) and the Pleistocene history of North America (detailed in Chapter One) in order to develop a specific biogeographic hypothesis of the pattern of distribution shifts and disjunctions that resulted in the origin and current distributions of the *Agelenopsis* species. Specifically, the maps of the modern distributions of *Agelenopsis* species were used as the end-point the hypothesized series of events had to achieve, where as the phylogeny was used to determine the order in which speciation events occurred and which lineages were involved in specific speciation events. Finally, the climate and vegetation history of North America was used to decide where the hypothesized distribution shifts and range disjunctions occurred. Using this information, a series of figures (17-25) was prepared to demonstrate the proposed speciation pattern using the Expert Maps for Windows Gold Edition from Expert Software and the Microsoft Windows Paintbrush program.

Results

Phylogeny

The phylogeny lists each modern species as terminus of a lineage (Fig. 16). Ancestral lineages prior to those leading to modern species are coded A to A10. These designations are used in Table 2 to identify the trait used to differentiate a given lineage

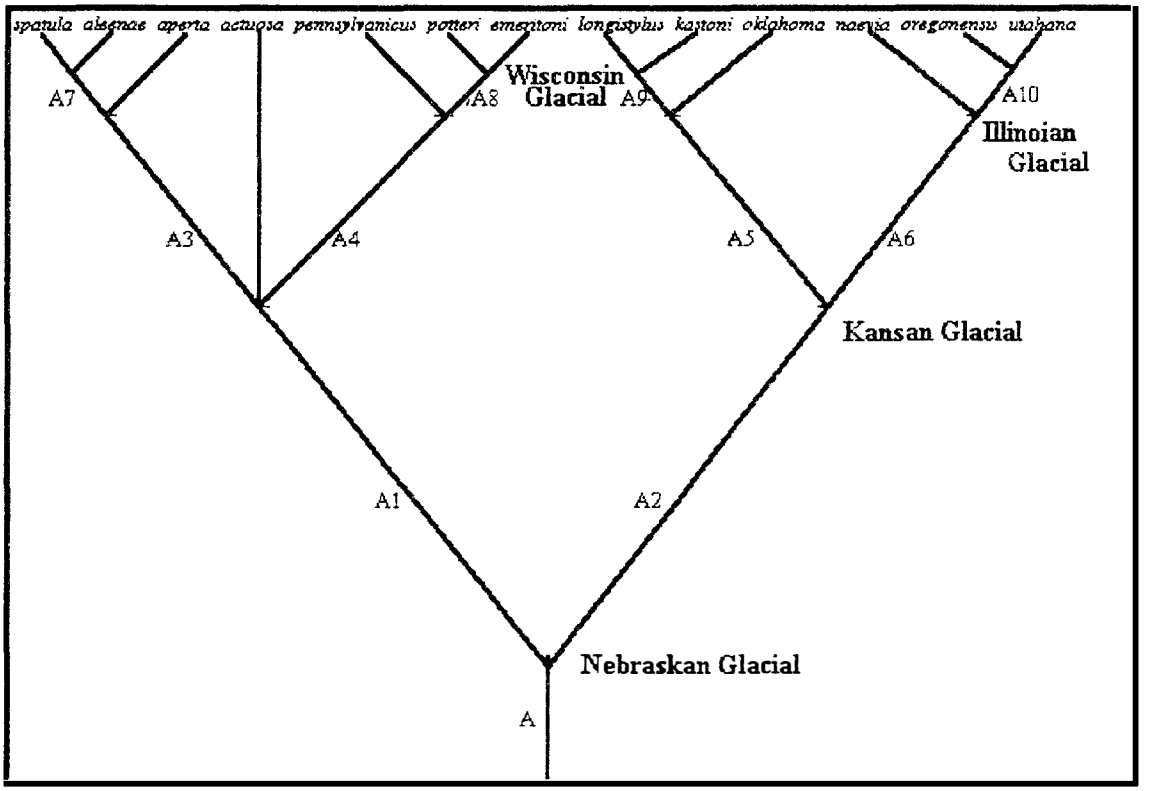


Figure 16. Proposed Phylogeny for the Genus *Agelenopsis*, the key to the lineage distiguishing traits is found in Table 2. The names of the glacial periods hypothesized to correspond to the four levels of splitting in the phylogeny are included on the figure.

from its sister lineage. The four levels of branching in the phylogeny have labels next to them indicating the specific glacial period hypothesized to have caused them.

The construction of the phylogeny began with the identification of 4 pairs of sister species by the unique traits they share that occur in no other species in *Agelenopsis*. The first pair, *A. spatula* and *A. aleenae*, are highly similar in the overall structure of their male genitalia (palps) and share the unique trait of having the tips of their emboli distinctly spatulate (defining lineage A7). This in fact may be due to *A. aleenae* being a hybrid as suggested in Chapter 2. Even so, *A. aleenae* is included in the analysis because there is no way to establish the actual nature of this species from the available information. The second pair, *A. potteri* and *A. emertoni*, are highly similar in their overall sexual morphology and share the unique trait of having a double arch shape along the anterior lip of the posterior pouch of the vulva (defining lineage A8). The third pair, *A. longistylus* and *A. kastoni*, both have the lateral outer edges of the vulva flared out to a point, which is a trait unique to these species (defining lineage A9). The fourth pair of sister species are *A. oregonensis* and *A. utahana*. Both the male and female genitalic morphology are highly similar in these species and they share a uniquely shortened conductor compared to the rest of the *Agelenopsis* species (designating lineage A10).

The next step in the construction of the phylogeny entailed determining which of the remaining species and newly defined lineages shared unique morphological traits. *Agelenopsis aperta* was grouped with lineage A7 to create lineage A3 based on possession of a broadened embolus tip by all three species. Likewise, *A. pennsylvanica* was joined with lineage A8 to generate lineage A4 due to the possession of a blunt

conductor by these three species and none of the others in the genus. Lineage A9 was combined with *A. oklahoma* to create lineage A5 utilizing their sharing a distinctly elongated and slender tip on their embolus. Finally, *Agelenopsis naevia* was grouped with lineage A10 to generate lineage A6 based on the fact that the tip of the embolus in all three species is directed toward the middle-line of the palp and tapers to a sharp point. Of the 13 *Agelenopsis* species, only *A. actuosa* remains unincorporated into an ancestral lineage at this stage.

The final stage in building the phylogeny was to link the four ancestral lineages and *A. actuosa* into more inclusive and more ancient lineages. Only *A. actuosa* deviates from the dichotomous branching pattern in this phylogeny. *Agelenopsis actuosa* is part of a three way split involving the ancestral lineages A3 and A4. This is either a true three-way split in the phylogeny or it may result from the inability of the method used being to clearly resolve which of the two other lineages *actuosa* is more closely related to. Lineages A3 and A4 and *A. actuosa* arise from lineage A1 which includes all species possessing an embolus which is thick over its entire length. Lineages A5 and A6 were combined to create lineage A2, based on the common possession of a thinner embolus which tapers off in size from base to tip. Once lineages A1 and A2 were generated the next step was automatic; assuming the genus is monophyletic, these two lineages must have arisen from the original ancestral lineage for entire genus (lineage A).

Historical Biogeography

In order to explore the general hypothesis that the series of glacial periods in the Pleistocene explains the origin and current distribution of *Agelenopsis* species, the relationship between glaciation patterns and the phylogeny based on the morphology of the genitalia was examined (Figs. 17-25). The specific types of habitat changes which correpond to the glacial/interglacial cycles were discussed in detail in Chapter 1.

Figure 17 shows the hypothesized range of lineage A in the southeastern United States and along the Gulf coast during the Pliocene in semitropical forest. Lineage A was divided into a southeastern (A2) and southwestern (A1) lineages during the Nebraskan glaciation as shown in Fig. 18. This may have been due to either the replacement of once continuous coastal forest by savannah or the strengthening of the Mississippi embayment as a boreal forest barrier between non-boreal forests to the east and west of it. Figure 19 show that lineage A1 expanded its range back into the east and through the taiga into the northwest as the glaciers retreated during the Aftonian interglacial. Lineage A2 expanded during this period to occupy a range similar to that of lineage A.

Figure 20 show that during the Kansan glaciation, lineage A1 was divided into northwestern (*A. actuosa)*, southeastern (A4), and southwestern (A3) lineages. The *A. actuosa* lineage was isolated in the northwest by the division of the northern boreal forest into eastern and northwestern refugia by the continental glaciers. Lineage A3 was probably isolated from lineage A4 in the same way that A1 and A2 were separated during the Nebraskan. During the Kansan glacial period lineage A2 was similarly divided into lineages A5 and A6 in the southwest and southeast, the disjunction was probably due to

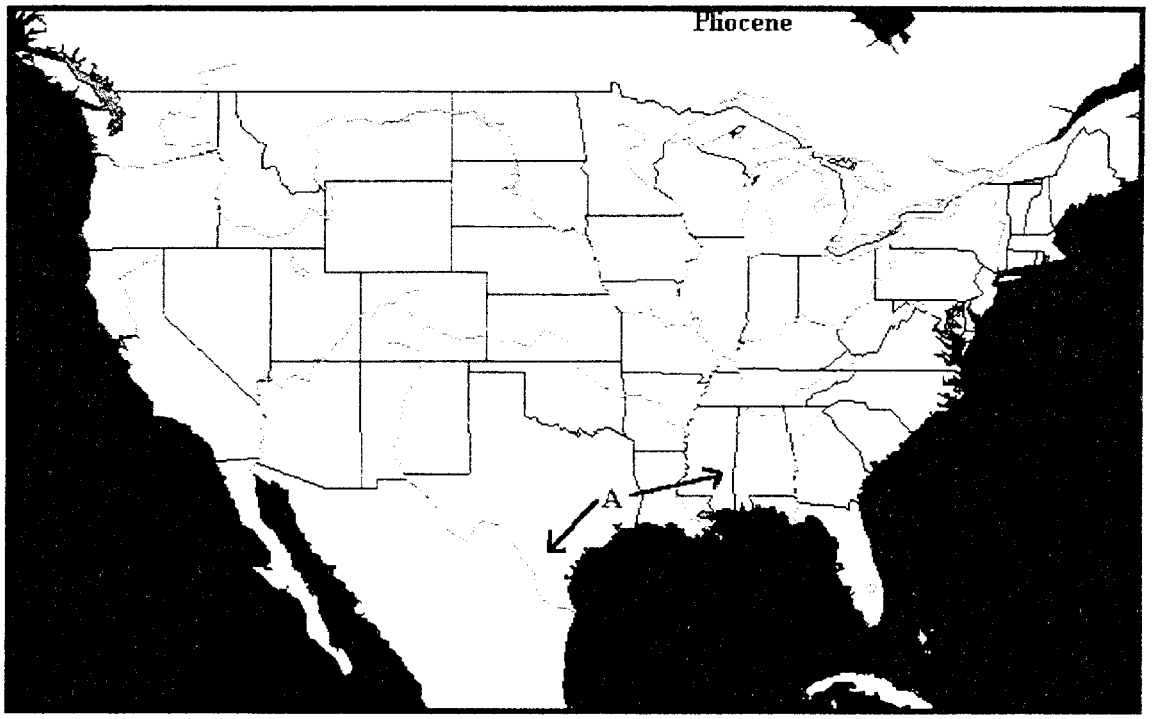


Figure 17. Ancestral *Agelenopsis* During the Pliocene The letter-number code refers to an ancestral species that corresponds to a branch arm bearing the same designation in the phylogeny. The arrows indicate range expansions, dispersal events, or range shifts.

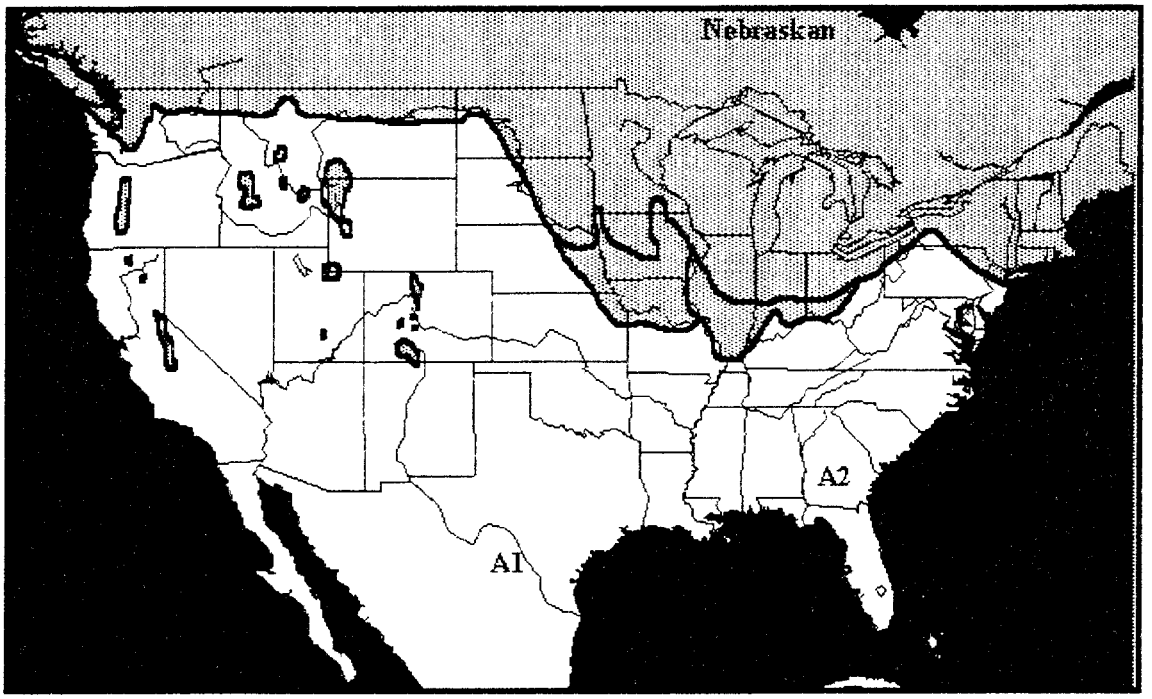


Figure 18. Ancestral *Agelenopsis* During the Nebraskan Glacial Maximum. The gray shaded and outlined areas indicated the regions covered by glaciers. The letter-number code refers to an ancestral species that corresponds to a branch arm bearing the same designation in the phylogeny. The arrows indicate range expansions, dispersal events, or range shifts.

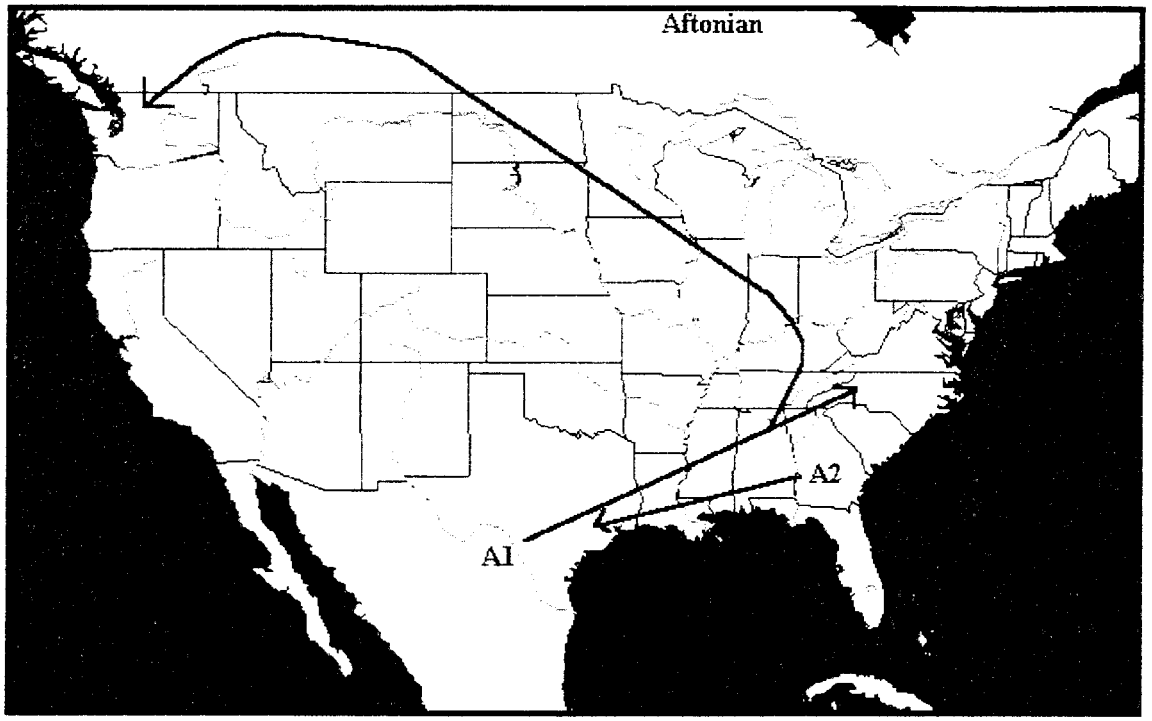


Figure 19. Ancestral *Agelenopsis* During the Aftonian Interglacial. The letter-number code refers to an ancestral species that corresponds to a branch arm bearing the same designation in the phylogeny. The arrows indicate range expansions, dispersal events, or range shifts.

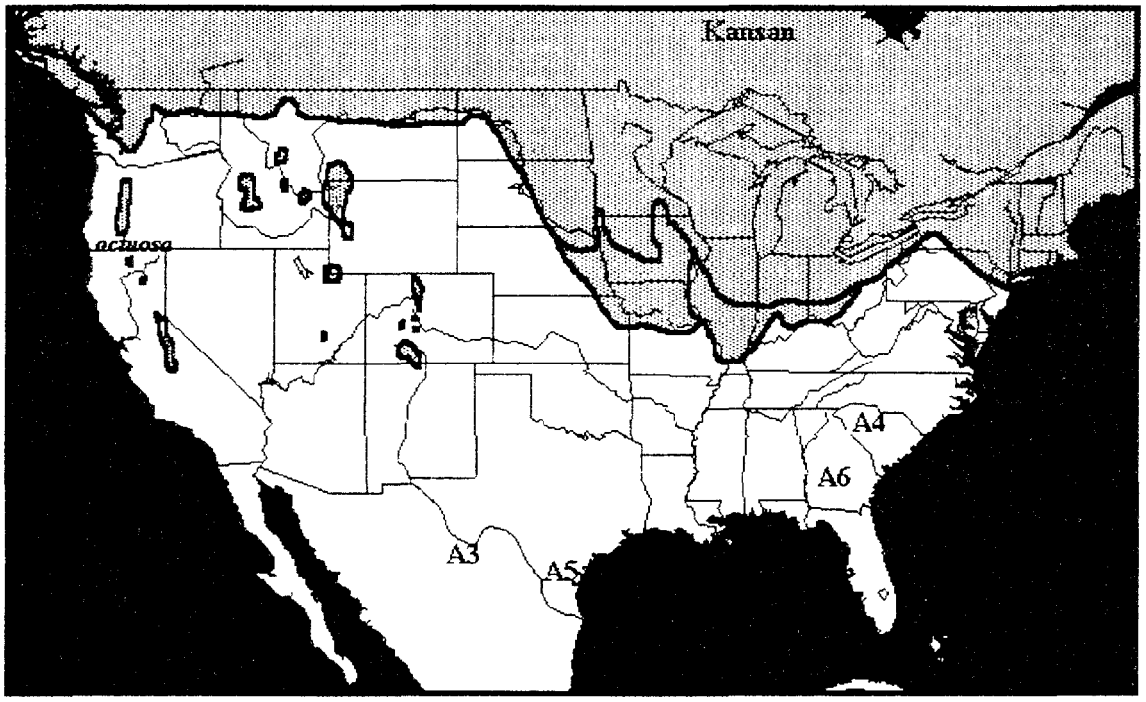


Figure 20. Ancestral *Agelenopsis* During the Kansan Glacial Maximum. The gray shaded and outlined areas indicated the regions covered by glaciers. The letter-number code refers to an ancestral species that corresponds to a branch arm bearing the same designation in the phylogeny. The arrows indicate range expansions, dispersal events, or range shifts.

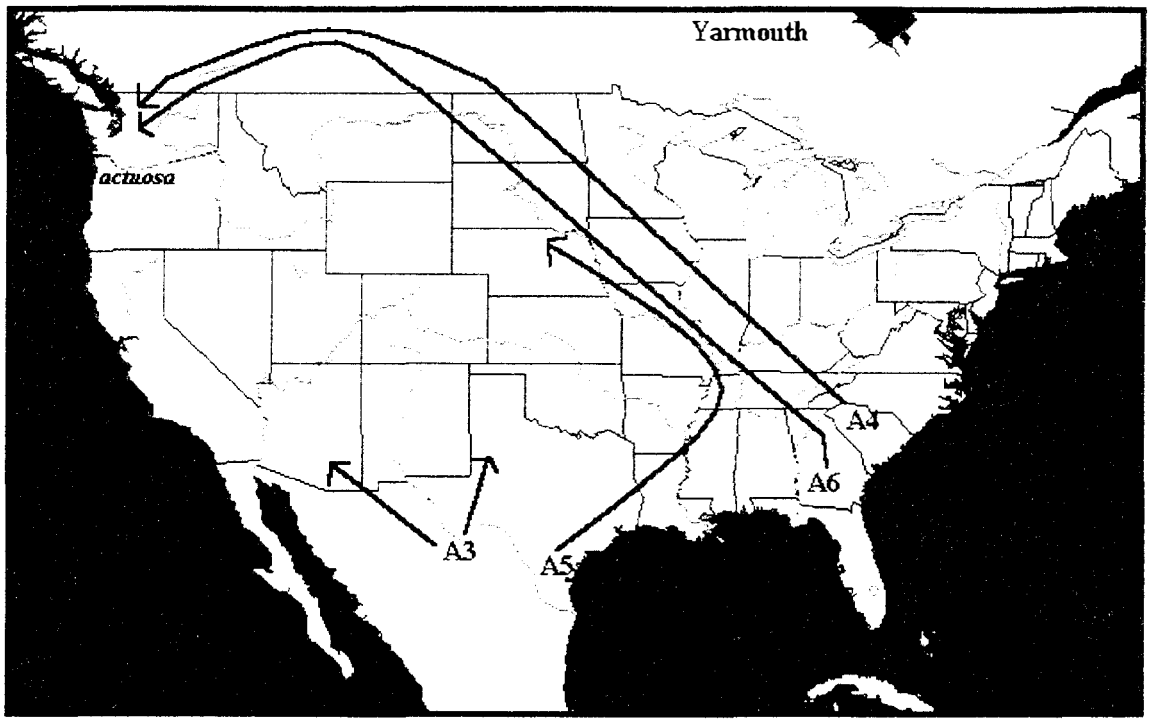


Figure 21. Ancestral *Agelenopsis* During the Yarmouth Interglacial. The letter-number code refers to an ancestral species that corresponds to a branch arm bearing the same designation in the phylogeny. The arrows indicate range expansions, dispersal events, or range shifts.

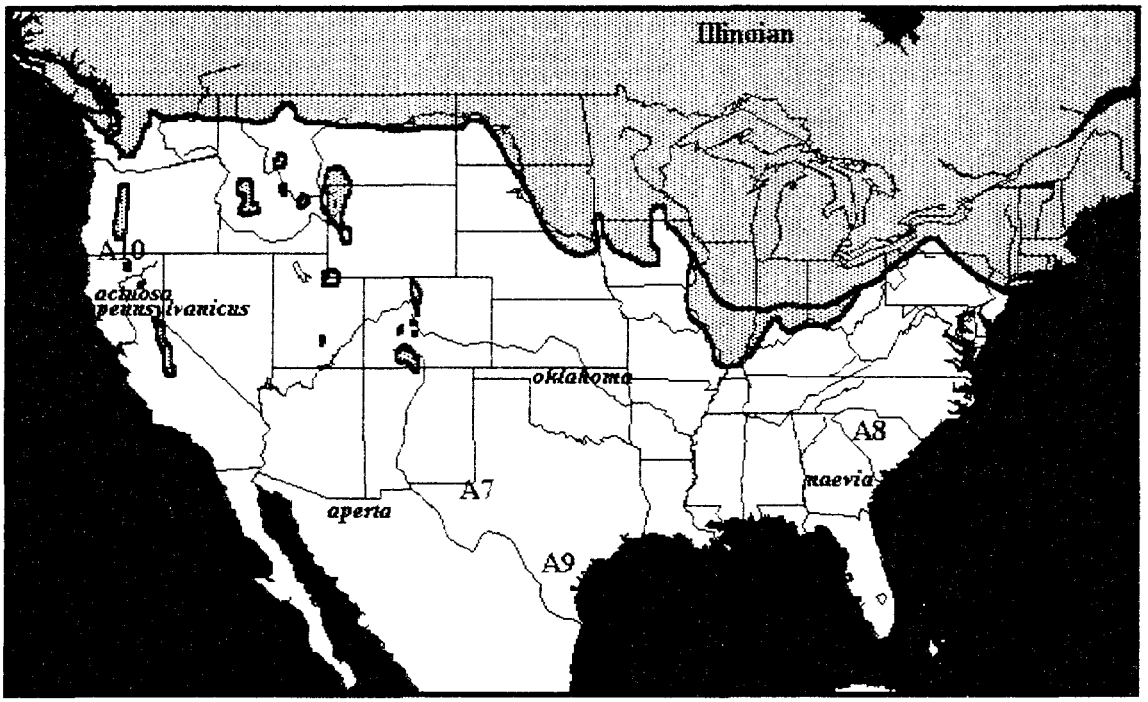


Figure 22. Ancestral *Agelenopsis* During the Illinoian Glacial Maximum. The gray shaded and outlined areas indicated the regions covered by glaciers. The letter-number code refers to an ancestral species that corresponds to a branch arm bearing the same designation in the phylogeny. The arrows indicate range expansions, dispersal events, or range shifts.

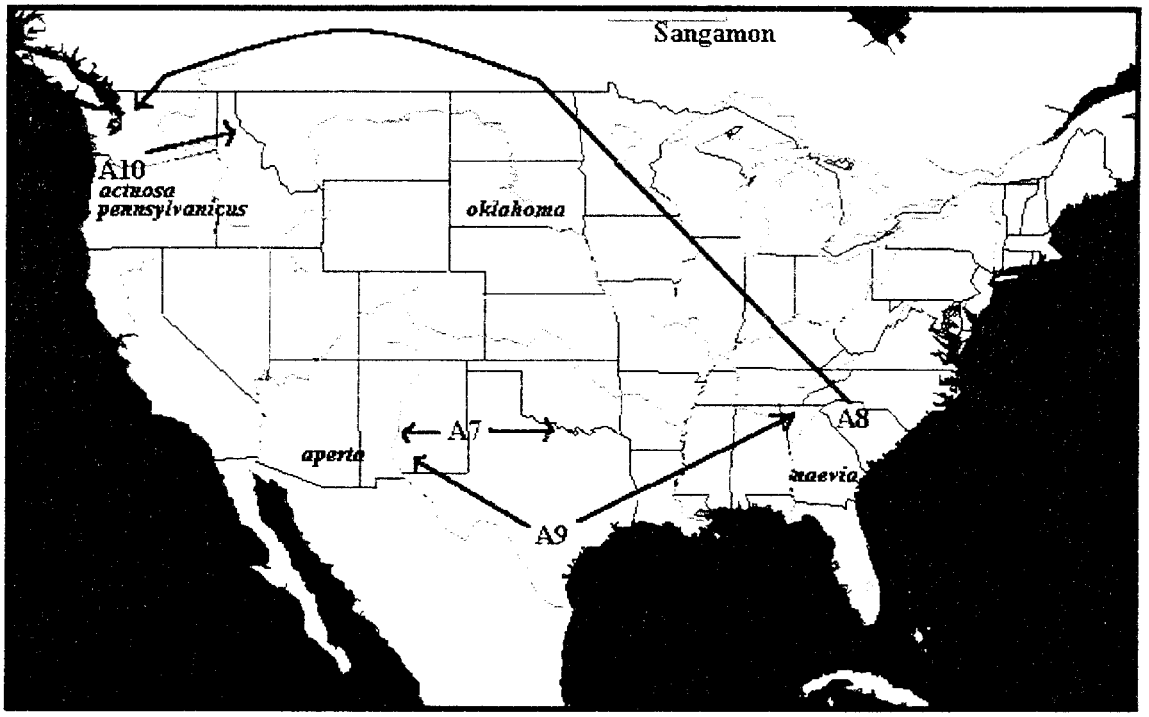


Figure 23. Ancestral *Agelenopsis* During the Sangamon Interglacial. The letter-number code refers to an ancestral species that corresponds to a branch arm bearing the same designation in the phylogeny. The arrows indicate range expansions, dispersal events, or range shifts.

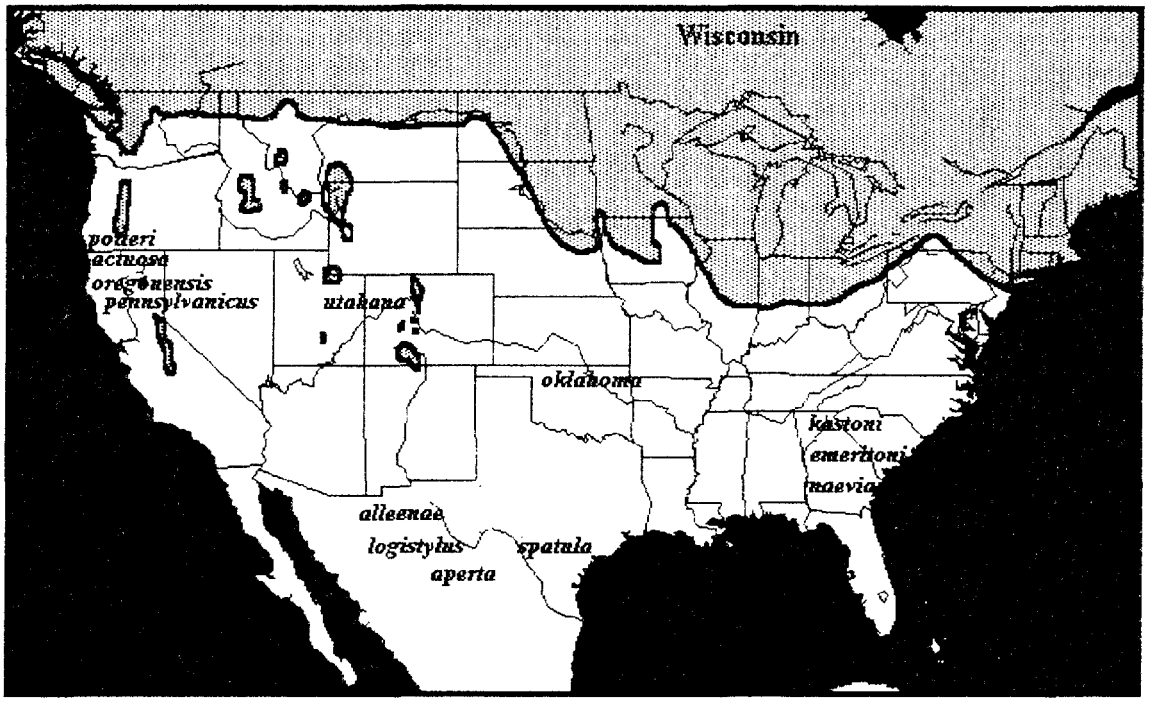


Figure 24. Ancestral *Agelenopsis* During the Wisconsin Glacial Maximum. The gray shaded and outlined areas indicated the regions covered by glaciers. The letter-number code refers to an ancestral species that corresponds to a branch arm bearing the same designation in the phylogeny. The arrows indicate range expansions, dispersal events, or range shifts.

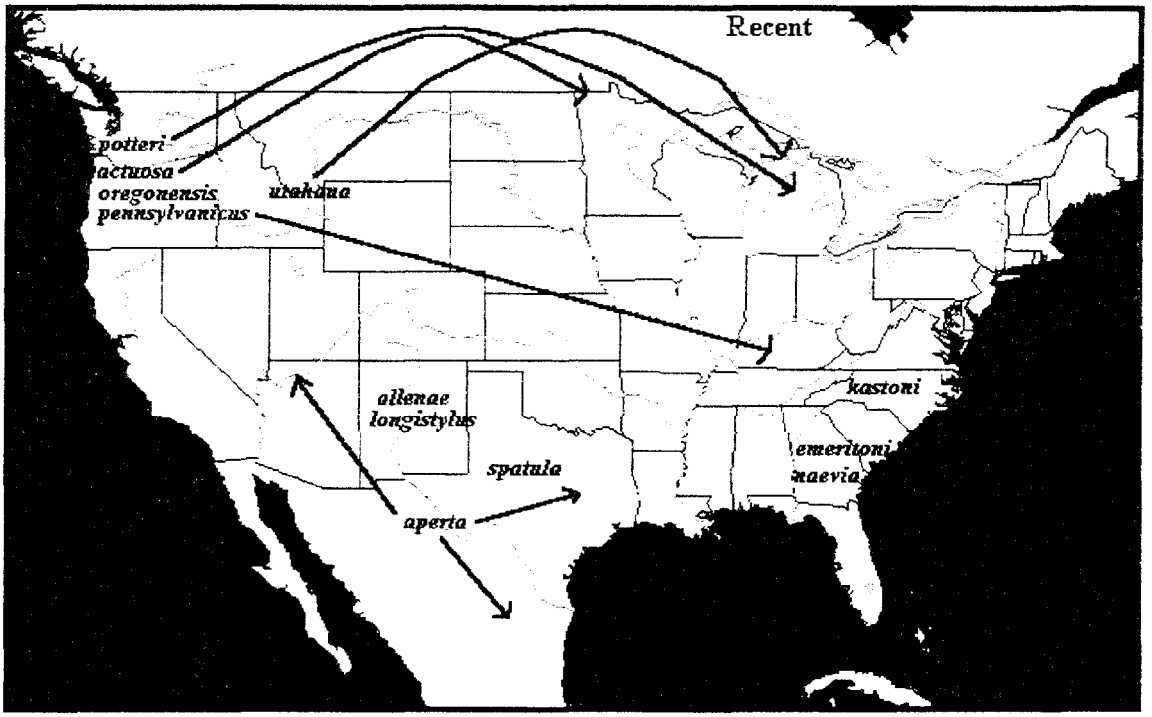


Figure 25. The Redistribution of the Modern Species of *Agelenopsis* Since the Last Glacial Period. The letter-number code refers to an ancestral species that corresponds to a branch arm bearing the same designation in the phylogeny. The arrows indicate range expansions, dispersal events, or range shifts.

the Mississippi Embayment boreal forest or degeneration of forest along the Texas coast to savanna.

With the onset of the Yarmouth interglacial the four lineages may have expanded their ranges as shown in Fig. 21. Lineage A3 expanded into the desert areas of the southwest and the southern plains. Lineages A4 and A6 expanded their ranges from the southeast to the northwest to occupy a transcontinental range. Lineage 5 expanded its range to occupy the tall grass prairie all along the eastern side of the Great Plains during the Yarmouth interglacial.

Figure 22 shows the areas in which *Agelenopsis* lineages may have been isolated and diverged during the Illinoian glacial period. Lineage A3 split into the ancestors of *A. aperta* and lineage A7 across the barrier of the Rocky Mountains as altitudinal zones lowered and made many passes inhospitable. The disjunction of the northern boreal forest by glaciers split lineage A4 into the *A. pennsylvanica* and A8 lineages. Likewise, the A6 lineage was split into the *A. naevia* and A10 lineages. Most of the A5 lineage was forced south by the intrusion of spruce woodland into the northern and middle plains, but a remnant survived in limited prairie refugia that persisted in the north. The northern isolate diverged into the *A. oklahoma* lineage and the southern into lineage A9.

During the Sangamon interglacial the lineages developed in the Illinoian altered their ranges as shown in Fig. 23. Thus, lineage A7 expanded its range west across the southern Rocky Mountains. Lineage A9 expanded its range toward the Rocky Mountains and into the eastern United States. Another of the transcontinental range expansions through the northern boreal forest was demonstrated by lineage A8. Lineage A10

expanded its range from the Coastal Mountain ranges eastward into the Rocky Mountains through the taiga linking them to the north.

The lineages leading directly to all of the modern species of *Agelenopsis* were restricted to the regions shown in Fig. 24 during the Wisconsin glacial period. The divergences that occurred during this glacial period are due to east/west disjunctions resulting either from the division of the boreal northern forest into eastern and western refugia or the barrier of the much colder and often glaciated Rocky Mountains. Figure 25 shows the modern species expanding their ranges to occupy their current pattern following the retreat of the glaciers and a return to an interglacial climate.

Discussion

The specific hypothesis developed here assumes that the provided phylogeny is correct. A different phylogeny would, by definition, imply a different specific pattern of speciation. Though, it should be noted, it is possible for different phylogenies to still be consistent with the glaciation vicariance hypothesis in its general form. The major requirement of the general vicariance hypothesis is that the branching points in the phylogeny correspond to a division of the ancestral lineage's range across one of the disjunction zones attributed to the effects of Pleistocene ice ages.

Clearly, much of what I have presented here is highly speculative. The goal of this paper was not to prove a biogeographical hypothesis, but to propose one that might

account for how the species of *Agelenopsis* arose and acquired their modern North American distributions. It is also more broadly suggestive of how the distribution of any North American arthropod species group lacking a "reliable" form of long distance dispersal might have been influenced by Pleistocene glaciations.

In terms of the relevance and testability of my speculations, both the specific phylogeny proposed for the genus and the hypothesis concerning the importance of glaciation to the pattern of speciation are testable by molecular techniques for generating phylogenies. A molecular phyogeny for this genus could be prepared and compared to the one presented here. Even if the molecular phylogeny turns out significantly different, it may still be consistent with the hypothesis relating branching events to glacial advances. If the molecular techniques are used that provide information about the approximate timing of branching events, it could be determined whether or not glacial advances in the Pleistocene were likely to have been major forces driving speciation in this genus of spiders. Additionally, an examination of the subfossil record of spider carapaces, similar to that done with beetles and other arthropods, could determine whether or not the species in this genus are older than predicted here (Elias 1994).

CHAPTER 4

SUMMARY AND CONCLUSIONS

Summary

For some time it has been generally accepted that most modern animal species originated relatively recently, during the Pliocene or Pleistocene epochs. Robert Mengel has developed a hypothesis which explains speciation in a variety of North American avian genera as the result of the cyclic application of vicariance barriers caused by climate changes associated with the glacial/interglacial cycles of the late Pleistocene. Changes accompanying the glacial advances that may have caused range disjunctions in some species are the formation of mountain glaciers, changes in precipitation patterns, reduction of seasonality, and massive alterations in the distributions of plant communities. The effects of the glacial/interglacial cycles were not limited solely to birds; mammal, amphibians, and arthropods from North America also show patterns of speciation and distribution which indicate the influence of the cycles.

Among the arthropods, the species of the North American spider genus *Agelenopsis* show a pattern of distribution that is consistent with glacial/interglacial cycle driven speciation. These species are particularly good candidates for undergoing the hypothesized types of vicariance because it has poor long distance dispersal abilities,

several of the species have Nearctic ranges prime for disjunction as a result of glaciation, and they are generalists with broad habitat tolerances that would be more likely to survive and diverge in ice age refugia.

A reconstructed phylogeny was developed based on the sexual morphology of the *Agelenopsis* species. The branching points in the phylogeny imply a specific series of speciation events. This series was combined with knowledge of the Pleistocene history of North America and the distribution of the modern species to construct a hypothesis of the historical biogeography of the genus. The effects of the glacial/interglacial cycles appear to be sufficient to explain the origin and current distributions of the modern *Agelenopsis* species.

Conclusions

The generality of vicariance hypotheses like Mengle's can only be established by demonstrating that the proposed barriers created disjunctions in multiple taxa during the prescribed time frame. This study offers an example of one more North American taxon which shows a pattern of distributions consistent with glacial/interglacial driven vicariance. It adds to the mounting evidence that the massive changes in the geology, climate and vegetation of North America that occurred as a result of the ice ages were driving forces behind the speciation and subspeciation that produced the modern fauna of the continent.

Future work utilizing molecular techniques should expand the depth of the evidence supporting more detailed reconstructions of the historical biogeography of the

North America fauna. These techniques can provide additional traits for phylogeny construction, genetic estimates of divergence times, and identify population structuring within species that can provide clues concerning past patterns of gene flow. Future developments in the arthropod fossil record could provide independent estimates of the age of those species that can be identified from the gross or microscopic morphology of the sclerotized body parts that are preserved in Quaternary sediments

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APPENDICES

APPENDIX A

SOURCE DATA FOR DISTRIBUTION MAPS

Table A-1. Source Data for the *Agelenopsis actuosa* Distribution Map (Figure 3).

Coordinates	Location	Source
W 81°15': N 42°45'	St. Thomas, Ontario	Chamberlin & Ivie 1941
W 122°55': N 47°5'	Olympia, Washington	Chamberlin & Ivie 1941
W 122°20': N 47°35	Seattle, Washington	Chamberlin & Ivie 1941
W 122°40': N 48°20'	Oak Harbor, Washington	Chamberlin & Ivie 1941
W 123°30': N 48°30'	W. side Saanich Inlet, Vancouver Is.	Chamberlin & Ivie 1941
W 123°25': N 48°35'	Sidney, Vancouver Island	Chamberlin & Ivie 1941
W 123°59': N 45°32'	Cape Meares, Oregon	Chamberlin & Ivie 1941
W 123°15': N 44°30'	Corvallis, Oregon	Chamberlin & Ivie 1941
W 65°: N 45°	Annapolis Valley, Nova Scotia	Dondale 1956
W 106°25': N 52°	Clavet, Saskatchewan	Doane & Dondale 1979
W 105°56': N 53°37'	Saskatoon, Saskatchewan	Wickland 1993
W 96°50': N 40°50'	9 mi. NW of Lincoln, Nebraska	Muma & Muma 1949
W 99°: N 49°30'	Manitoba, Canada	Aitchison-Benell & Dondale 1990
W 97°: N 49°30'	Manitoba, Canada	Aitchison-Benell & Dondale 1990
W 95°: N 49°30'	Manitoba, Canada	Aitchison-Benell & Dondale 1990
W 99°: N 50°30'	Manitoba, Canada	Aitchison-Benell & Dondale 1990
W 99°: N 52°30'	Manitoba, Canada	Aitchison-Benell & Dondale 1990
W 122°40': N 47°7'	Fort Lewis, Washington	Crawford 1988

Table A-2. Source Data for the *Agelenopsis aperta* Distribution Map (Figure 4).

Coordinates	Location	Source
W 105°8': N 40°4'	Valmont, Colorado	Chamberlin & Ivie 1941
W 111°: N 32°15'	Tucson, Arizona	Chamberlin & Ivie 1941
W 110°30': N 44°30'	Yellowstone Pk., Wyoming	Chamberlin & Ivie 1941
W 111°: N 33°	Junction Mesa, Arizona	Chamberlin & Ivie 1941
W 111°45': N 33°30'	Salt Rivers, Arizona	Chamberlin & Ivie 1941
W 111°: N 36°	Houserock, Arizona	Chamberlin & Ivie 1941
W 111°55': N 40°45'	Salt Lake City, Utah	Chamberlin & Ivie 1941
W 113°: N 37°15'	Zion Park, Utah	Chamberlin & Ivie 1941
W 113°: N 37°	Motaqua, Utah	Chamberlin & Ivie 1941
W 113°45': N 39°45'	Trout Creek, Utah	Chamberlin & Ivie 1941
W 117°10': N 32°45'	San Diego, California	Chamberlin & Ivie 1941
W 117°45': N 33°30'	Laguna Beach, California	Chamberlin & Ivie 1941
W 117°55': N 36°25'	West side Owens Lake, California	Chamberlin & Ivie 1941
W 118°35': N 33°45'	San Pedro, California	Chamberlin & Ivie 1941
W 118°15': N 34°5'	Los Angeles, California	Chamberlin & Ivie 1941
W 118°20': N 37°10'	Big Pine, California	Chamberlin & Ivie 1941
W 122°15': N 37°25'	Stanford, California	Chamberlin & Ivie 1941
W 95°30': N 30°45'	Huntsville, TX	Chamberlin & Ivie 1941
W 96°20': N 30°40'	Brazos Co., TX	Chamberlin & Ivie 1941
W 97°15': N 30°10'	Bastrop, TX	Chamberlin & Ivie 1941
W 97°45': N 30°15'	Austin, TX	Chamberlin & Ivie 1941
W 97°40': N 30°40'	Georgetown, TX	Chamberlin & Ivie 1941
W 97°30': N 31°	Belton, TX	Chamberlin & Ivie 1941
W 99°: N 21°	South of Valles, Mexico	Chamberlin & Ivie 1941
W 98°15': N 26°20'	Edinburg, TX	Chamberlin & Ivie 1941
W 98°55': N 34°	Electra, TX	Chamberlin & Ivie 1941
W 99°7': N 29°55'	South of Kerrville, TX	Chamberlin & Ivie 1941
W 99°20': N 29°45'	Bandera Co., TX	Chamberlin & Ivie 1941
W 99°15': N 30°5'	Kerrville, TX	Chamberlin & Ivie 1941
W 100°15': N 25°45'	Monterrey, Mexico	Chamberlin & Ivie 1941
W 100°: N 29°	Montell, TX	Chamberlin & Ivie 1941
W 100°15': N 30°	Rock Springs, TX	Chamberlin & Ivie 1941
W 103°30': N 25°30'	Lerdo, Mexico	Chamberlin & Ivie 1941
W 110°45': N 31°45'	Greaterville, AZ	Chamberlin & Ivie 1941
W 117°20': N 34°5'	Grand Terrace, San Bernardino Co., CA	Ali & Hartin 1988
W 91°45': N 29°50'	Iberia Parish, Louisiana	Hensley et al. 1961
W 105°50': N 33°45'	N of Carrizozo, Lincoln Co., New Mexico	Gertsch & Riechert 1976

Table A-3. Source Data for the *Agelenopsis emertoni* Distribution Map (Figure 5).

Coordinates	Location	Source
W 71°25': N 41°50'	Providence, Rhode Island	Chamberlin & Ivie 1941
W 74°10': N 41°5'	Ramsey, New Jersey	Chamberlin & Ivie 1941
W 77°25': N 37°15'	South St. Petersburg, Virginia	Chamberlin & Ivie 1941
W 77°25': N 38°20'	Fredricksburg, Virginia	Chamberlin & Ivie 1941
W 78°40': N 35°50'	Raleigh, North Carolina	Chamberlin & Ivie 1941
W 81°20': N 28°45'	Sanford, Florida	Chamberlin & Ivie 1941
W 85°30': N 32°35'	Auburn, Alabama	Chamberlin & Ivie 1941
W 91°10': N 36°15'	Imboden, Arkansas	Chamberlin & Ivie 1941
W 97°28': N 31°4'	Belton, TX	Chamberlin & Ivie 1941
W 97°10': N 31°30'	Waco, TX	Chamberlin & Ivie 1941
W 98°30': N 33°50'	Wichita Falls, TX	Chamberlin & Ivie 1941
W 83°: N 40°	Ohio(Seyler)	Chamberlin & Ivie 1941
W 85°34': N 45°40'	Beaver Island, Michigan	Drew 1967
W 91°45': N 29°50'	Iberia Parish, Louisiana	Hensley et al. 1961
W 92°: N 35°	Throughout Arkansas	Whitcomb et al. 1963
W 96°45': N 33°50'	Willis, Marshall Co., Oklahoma	Branson 1966
W 84°30': N 45°30'	Cheboygen Co., MI	Snider 1991
W 84°40': N 43°50'	Clinton Co., MI	Snider 1991
W 84°25': N 42°40'	Ingham Co., MI	Snider 1991
W 85°35': N 42°20'	Kalamazoo Co., MI	Snider 1991
W 85°45': N 45°	Leelanau Co., MI	Snider 1991
W 76°40': N 34°45'	Beaufort, Carteret Co., North Carolina	Barnes 1953
W 90°5': N 35°10'	Memphis, Tennessee area	Gibson 1947
W 75°40': N 39°50'	Pike Creek Valley, NE of Newark, DE	Uetz 1976
W 96°50': N 40°50'	9 mi. NW of Lincoln, Nebraska	Muma & Muma 1949
W 81°15': N 32°5'	8 mi. W of Savannah, Georgia	Chamberlin & Ivie 1944
W 81°5': N 32°2'	3 mi. SE of Savannah, Georgia	Chamberlin & Ivie 1944
W 84°55': N 32°20'	Fort Bennin, Georgia	Chamberlin & Ivie 1944
W 92°50': N 35°5'	7 mi. SW of Morrilton, Arkansas	Whitcomb & Bell 1964
W 72°50': N 41°17'	Branford, Connecticut	Kaston 1948
W 72°35': N 41°22'	Killingworth, Connecticut	Kaston 1948
W 72°43': N 41°16'	Leete's Island, Connecticut	Kaston 1948
W 78°40': N 39°35'	Allegahney Co., Maryland	Muma 1945
W 39°: N 76°35'	Anne Arundel Co., Maryland	Muma 1945
W 76°50': N 38°50'	Prince Georges, Maryland	Muma 1945
W 93°45': N 38°45'	Warrensburg, Johnson Co., Missouri	Peck 1966

Table A-4. Source Data for the *Agelenopsis kastoni* Distribution Map (Figure 6).

Coordinates	Location	Source
W 72°31': N 41°28'	Haddam, Connecticut	Chamberlin & Ivie 1941
W 92°35': N 40°15'	Kirksville, Missouri	Haskins & Shaddy 1986
W 88°10': N 40°10'	Champaign Co., Ill.	LeSar & Unzicker 1978
W 83°25': N 34°50'	Clayton, Georgia	Chamberlin & Ivie 1944
W 77°: N 39°	Maryland	Muma 1945
W 72°50': N 41°17'	Branford, Connecticut	Kaston 1948
W 72°31': N 41°28'	Haddam, Connecticut	Kaston 1948
W 72°7': N 41°20'	Waterford, Connecticut	Kaston 1948

Table A-5. Source Data for the *Agelenopsis longistylus* Distribution Map (Figure 7).

Coordinates	Location	Source
W 105°: N 33°	White Mountains, New Mexico	Chamberlin & Ivie 1941
W 105°: N 32°	Camp May White, New Mexico	Chamberlin & Ivie 1941
W 105°55': N 35°30'	10 mi. South Santa Fe, New Mexico	Chamberlin & Ivie 1941
W 102°40': N 35°15'	Adrian, TX	Chamberlin & Ivie 1941
W 105°50': N 33°45'	N of Carrizozo, Lincoln Co., NM	Gertsch & Riechert 1976

Table A-6. Source Data for the *Agelenopsis naevia* Distribution Map (Figure 8).

Coordinates	Location	Source
W 70°53': N 42°33'	Salem, MA	Chamberlin & Ivie 1941
W 70°35': N 43°15'	Wells, Maine	Chamberlin & Ivie 1941
W 70°45': N 44°25'	Bethel, Maine	Chamberlin & Ivie 1941
W 71°5': N 42°22'	Boston, MA	Chamberlin & Ivie 1941
W 73°25': N 41°7'	Norwalk, Connecticut	Chamberlin & Ivie 1941
W 77°25': N 37°15'	South St. Petersburg, Virginia	Chamberlin & Ivie 1941
W 77°25': N 38°20'	Fredericksburg, Virginia	Chamberlin & Ivie 1941
W 77°5': N 38°45'	Mt. Vernon, Virginia	Chamberlin & Ivie 1941
W 77°45': N 39°40'	Hagerstown, Maryland	Chamberlin & Ivie 1941
W 78°: N 38°	Amissville, Virginia	Chamberlin & Ivie 1941
W 79°50': N 34°45'	Cheraw, South Carolina	Chamberlin & Ivie 1941
W 80°5': N 26°35'	Lake Worth, Florida	Chamberlin & Ivie 1941
W 82: N 29°15'	Ocala Forest, Florida	Chamberlin & Ivie 1941
W 82°30': N 28°	Tampa, Florida	Chamberlin & Ivie 1941
W 82°35': N 29°50'	High Springs, Florida	Chamberlin & Ivie 1941
W 82°30': N 29°25'	Welliston, Florida	Chamberlin & Ivie 1941
W 82°20': N 32°20'	Oakpark, Georgia	Chamberlin & Ivie 1941
W 82°5': N 35°50'	Sprucepine, North Carolina	Chamberlin & Ivie 1941
W 82°35': N 36°35'	Kingsport, Tennessee	Chamberlin & Ivie 1941
W 82°: N 39°	Rockbridge, Ohio	Chamberlin & Ivie 1941
W 84°30': N 35°50'	Kingston, TN	Chamberlin & Ivie 1941
W 84°40': N 35°50'	Rockwood, TN	Chamberlin & Ivie 1941
W 84°45': N 36°20'	Burrville, TN	Chamberlin & Ivie 1941
W 85°15': N 30°45'	Mariana, Florida	Chamberlin & Ivie 1941
W 86°50': N 39°35'	4 mi. east of Putnamville, IN	Chamberlin & Ivie 1941
W 90°5': N 29°55'	New Orleans, Louisiana	Chamberlin & Ivie 1941
W 90°15': N 32°20'	5 mi. east of Jackson, Mississippi	Chamberlin & Ivie 1941
W 90°50': N 38°50'	14 mi. east of Wright City, Missouri	Chamberlin & Ivie 1941
W 91°15': N 36°15'	Imboden, Arkansas	Chamberlin & Ivie 1941
W 93°35': N 33°35'	Hope, Arkansas	Chamberlin & Ivie 1941
W 94°45': N 30°45'	7 mi. east of Livingston, TX	Chamberlin & Ivie 1941
W 94°30': N 31°30'	8 mi. north of Lufkin, TX	Chamberlin & Ivie 1941
W 94°30': N 32°20'	7 mi. NE of Henderson, TX	Chamberlin & Ivie 1941
W 94°35': N 39°10'	Kansas City, Kansas	Chamberlin & Ivie 1941
W 95°30': N 30°30'	6 mi. south of Huntsville, TX	Chamberlin & Ivie 1941
W 96°10': N 30°10'	Hemstead, TX	Chamberlin & Ivie 1941
W 97°15': N 30°10'	Bastrop, TX	Chamberlin & Ivie 1941
W 97°30': N 33°15'	Decatur, TX	Chamberlin & Ivie 1941
W 98°15': N 38°45'	Ellsworth, Kansas	Chamberlin & Ivie 1941
W 86°10': N 41°10'	Talma, Indiana	Parker 1969
W 81°40': N 28°30'	17 mi. east of Orlando, Florida	Corey & Taylor 1989
W 91°: N 33°15'	Washington Co., Mississippi	Young et al. 1989
W 85°: N 45°30'	Emmet Co., MI	Snider 1991
W 83°20': N 42°40'	Oakland Co., MI	Snider 1991

Table A-6 (continued).

Coordinates	Location	Source
W 88°10': N 42°20'	Volo, Illinois	Kaston 1955
W 87°40': N 41°50'	Chicago, Illinois	Kaston 1955
W 87°50': N 41°40'	Palos Park, Illinois	Kaston 1955
W 88°15': N 40°10'	Urbana, Illinois	Kaston 1955
W 91°10': N 43°5'	Prairie du Chien, Wisconsin	Levi & Field 1954
W 91°10': N 42°55'	Wyalusing State Park, Wisconsin	Levi & Field 1954
W 91°20': N 44°15'	Perrot State Park, Wisconsin	Levi & Field 1954
W 76°40': N 34°45'	Beaufort, Carteret Co., NC	Barnes 1953
W 90°5': N 35°10'	Memphis, Tennessee area	Gibson 1947
W 75°45': N 39°43'	White Clay Creek, N of Newark, DE	Uetz 1976
W 95°30': N 39°	Douglas Co., Kansas	Fitch 1963
W 82°: N 33°	Burke Co., Georgia	Chamberlin & Ivie 1944
W 82°20': N 32°20'	Oak Park, Georgia	Chamberlin & Ivie 1944
W 76°40': N 39°30'	Baltimore Co., Maryland	Muma 1945
W 76°37': N 39°20'	Baltimore City, Maryland	Muma 1945
W 79°15': N 39°30'	Garrett Co., Maryland	Muma 1945
W 77°10': N 39°7'	Montgomery Co., Maryland	Muma 1945
W 76°50': N 38°50'	Prince Georges Co., Maryland	Muma 1945
W 77°: N 38°55'	Washington D.C.	Muma 1945
W 79°40': N 39°55'	Fayette Co., Pennsylvania	Vogel 1968
W 79°25': N 40°15'	Westmoreland Co., Pennsylvania	Vogel 1968
W 88°30': N 40°5'	White Heath, Illinois	Jones 1941
W 72°45': N 41°45'	Common throughout Connecticut	Kaston 1948
W 93°45': N 38°45'	Warrensburg, Johnson Co., Missouri	Peck 1966

Table A-7. Source Data for the *Agelenopsis oklahoma* Distribution Map (Figure 9).

Coordinates	Location	Source
W 97°4': N 36°7'	Stillwater, OK	Chamberlin & Ivie 1941
W 98°15': N 38°45'	Ellsworth, Kansas	Chamberlin & Ivie 1941
W 98°50': N 38°50'	Russel, Kansas	Chamberlin & Ivie 1941
W 103°30': N 48°50'	Divide Co., North Dakota	Chamberlin & Ivie 1941
W 107°20': N 40°30'	Hayden, Colorado	Chamberlin & Ivie 1941
W 110°25': N 40°10'	Duchesne, Utah	Chamberlin & Ivie 1941
W 91°10': N 43°5'	Prairie du Chien, Wisconsin	Levi & Field 1954
W 96°50': N 40°50'	9 mi. NW of Lincoln, Nebraska	Muma & Muma 1949
W 95°30': N 39°	Douglas Co., Kansas	Fitch 1963
W 119°40': N 49°10'	Oliver, British Columbia	West et al. 1984

Table A-8. Source Data for the *Agelenopsis oregonensis* Distribution Map (Figure 10).

Coordinates	Location	Source
W 121°30': N 45°45'	Hood River, Oregon	Chamberlin & Ivie 1941
W 121°45': N 46°50'	Mt. Ranier, Washington	Chamberlin & Ivie 1941
W 122°12': N 45°33'	Latourell Falls, Columbia River, Oregon	Chamberlin & Ivie 1941
W 122°45': N 45°40'	10 mi. north of Vancouver, Washington	Chamberlin & Ivie 1941
W 122°20': N 47°35'	Seattle, Washington	Chamberlin & Ivie 1941
W 122°55': N 47°5'	Olympia, Washington	Chamberlin & Ivie 1941
W 122°: N 48°	Larabee Park, Washington	Chamberlin & Ivie 1941
W 123°: N 43°	Comstock, Oregon	Chamberlin & Ivie 1941
W 123°10': N 45°30'	Forest Grove, Oregon	Chamberlin & Ivie 1941
W 123°: N 48°35'	Friday Harbor, Washington	Chamberlin & Ivie 1941
W 123°30': N 48°30'	West side Saanich Inlet, Vancouver Is.	Chamberlin & Ivie 1941
W 122°11': N 44°14'	Willamette National Forest, Oregon	Parsons et al. 1991
W 124°5': N 48°45'	Cowichan Lake, British Columbia	West et al. 1984
W 119°40': N 49°35'	Summerland, British Columbia	West et al. 1984
W 122°48': N 46°	W 122°48': N 46°	Crawford 1988
W 122°24': N 46°30'	W 122°24': N 46°30'	Crawford 1988
W 121°12': N 47°12'	W 121°12': N 47°12'	Crawford 1988
W 122°18': N 47°36'	W 122°18': N 47°36'	Crawford 1988
W 120°42': N 47°48'	W 120°42': N 47°48'	Crawford 1988
W 120°54': N 47°48'	W 120°54': N 47°48'	Crawford 1988
W 123°: N 48°30'	W 123°: N 48°30'	Crawford 1988
W 123°6': N 48°30'	W 123°6': N 48°30'	Crawford 1988

Table A-9. Source Data for the *Agelenopsis pennsylvanica* Distribution Map (Figure 11).

Coordinates	Location	Source
W 70°45': N 44°25'	Bethel, Maine	Chamberlin & Ivie 1941
W 70°55': N 41°37'	New Bedford, MA	Chamberlin & Ivie 1941
W 71°25': N 41°50'	Providence, Rhode Island	Chamberlin & Ivie 1941
W 74°10': N 41°5'	Ramsey, New Jersey	Chamberlin & Ivie 1941
W 76°30': N 42°25'	Ithaca, New York	Chamberlin & Ivie 1941
W 77°45': N 39°40'	Hagerstown, Maryland	Chamberlin & Ivie 1941
W 78°5': N 38°45'	Mt. Vernon, Virgina	Chamberlin & Ivie 1941
W 80°: N 40°25'	Pittsbug, Pennsylvania	Chamberlin & Ivie 1941
W 82°50': N 41°40'	Put-in-Bay, South Bass Island, Ohio	Chamberlin & Ivie 1941
W 85°50': N 38°15'	New Albany, IN	Chamberlin & Ivie 1941
W 83°55': N 35°55'	Knoxville, TN	Chamberlin & Ivie 1941
W 86°50': N 39°35'	4 mi. east of Putnamville, IN	Chamberlin & Ivie 1941
W 87°35': N 39°25'	8 mi. east of Marshall, Illinois	Chamberlin & Ivie 1941
W 88°50': N 41°20'	Ottawa, Illinois	Chamberlin & Ivie 1941
W 90°30': N 42°45'	Platteville, Wisconsin	Chamberlin & Ivie 1941
W 96°30': N 41°30'	Fremont, Nebraska	Chamberlin & Ivie 1941
W 116°55': N 44°	Fruitland, Idaho	Chamberlin & Ivie 1941
W 122°55': N 47°5'	Olympia, Washington	Chamberlin & Ivie 1941
W 122°20': N 47°35'	Seattle, Washington	Chamberlin & Ivie 1941
W 123°20': N 43°15'	Roseburg, Oregon	Chamberlin & Ivie 1941
W 90°: N 33°	Mississippi	Chamberlin & Ivie 1941
W 92°: N 35°	Arkansas	Chamberlin & Ivie 1941
W 89°: N 40°	Illinois(Keyserling)	Chamberlin & Ivie 1941
W 83°: N 40°	Ohio(Seyler)	Chamberlin & Ivie 1941
W 91°: N 37°30'	Reynolds Co., Missouri	Bultman 1992
W 85°34': N 45°40'	Beaver Island, Michigan	Drew 1967
W 85°30': N 40°50'	Huntington, Indiana	Parker 1969
W 86°45': N 40°30'	Americus, Indiana	Parker 1969
W 86°40': N 41°5'	Winamac, Indiana	Parker 1969
W 86°10': N 41°10'	Talma, Indiana	Parker 1969
W 87°15': N 40°20'	Attica, Indiana	Parker 1969
W 92°: N 35°	Throughout Arkansas	Whitcomb et al. 1963
W 83°30': N 37°45'	Pine Ridge, Wolfe Co., Kentucky	Branson & Batch 1970
W 84°15': N 37°45'	Big Hill, Madison Co., Kentucky	Branson & Batch 1970
W 84°40': N 41°50'	Hillsdale Co., MI	Snider 1991
W 88°50': N 47°	Houghton Co., MI	Snider 1991
W 84°25': N 42°40'	Ingham Co., MI	Snider 1991
W 85°35': N 42°20'	Kalamazoo Co., MI	Snider 1991
W 82°55': N 42°40'	Macomb Co., MI	Snider 1991
W 84°25': N 43°40'	Midland Co., MI	Snider 1991
W 83°30': N 41°55'	Monroe Co., MI	Snider 1991
W 83°20': N 42°40'	Oakland Co., MI	Snider 1991
W 84°: N 43°20'	Saginaw Co., MI	Snider 1991
W 86°: N 42°15'	Van Buren Co., MI	Snider 1991

Table A-9 (continued).

Coordinates	Location	Source
W 83°20': N 42°15'	Wayne Co., MI	Snider 1991
W 87°50': N 42°20'	Waukegon, Illinois	Kaston 1955
W 87°45': N 39°25'	Marshall, Illinois	Kaston 1955
W 91°: N 43°10'	Eastman, Wisconsin	Levi & Field 1954
W 91°10': N 43°5'	Prairie du Chien, Wisconsin	Levi & Field 1954
W 89°20': N 43°5'	Madison, Wisconsin	Levi & Field 1954
W 91°10': N 42°55'	Wyalusing State Park, Wisconsin	Levi & Field 1954
W 90°30': N 42°45'	Platteville, Wisconsin	Levi & Field 1954
W 89°15': N 44°10'	Wautoma, Wisconsin	Levi & Field 1954
W 84°10': N 39°20'	Morrow, Ohio	Bultman & Uetz 1982
W 87°10': N 41°40'	Dune Acres, Indiana	Lowrie 1948
W 87°35': N 41°5'	Kankakee Co., Pembroke Twp., Illinois	Lowrie 1948
W 84°50': N 39°45'	Lewis Woods, Richmond, Indiana	Lowrie 1948
W 92°25': N 38°35'	12 mi. east of Jefferson City, Missouri	Dowdy 1950
W 90°5': N 35°10'	Memphis, Tennessee area	Gibson 1947
W 75°45': N 39°40'	Univ. Woodlot, S of Newark, DE	Uetz 1976
W 75°40': N 39°50'	Pike Creek Valley, NE of Newark, DE	Uetz 1976
W 75°35': N 39°48'	Thompson's Bridge, N of Wilmington, DE	Uetz 1976
W 75°35': N 39°50'	Talleyville, DE	Uetz 1976
W 75°40': N 39°40'	Coochs Bridge, DE	Uetz 1976
W 75°25': N 39°15'	Bombay Hook Nat. Wildlife Refuge, DE	Uetz 1976
W 95°30': N 39°	Douglas Co., Kansas	Fitch 1963
W 92°50': N 35°5'	7 mi. SW of Morrilton, Arkansas	Whitcomb & Bell 1964
W 76°37': N 39°20'	Baltimore City, Maryland	Muma 1945
W 77°: N 39°35'	Carrol Co., Maryland	Muma 1945
W 79°15': N 39°30'	Garrett Co., Maryland	Muma 1945
W 76°50': N 38°50'	Prince Georges Co., Maryland	Muma 1945
W 77°: N 38°55'	Washington D.C.	Muma 1945
W 79°15': N 37°55'	Steels Tavern, Virginia	Wheeler & McCaffrey 1984
W 79°5': N 38°10'	Staunton, Virginia	Wheeler & McCaffrey 1984
W 80°50': N 35°15'	Charlotte, North Carolina	Wheeler & McCaffrey 1984
W 80°: N 40°30'	Allegheny Co., Pennsylvania	Vogel 1968
W 79°40': N 39°55'	Fayette Co., Pennsylvania	Vogel 1968
W 72°45': N 41°45'	Common all over Connecticut	Kaston 1948
W 79°15': N 40°15'	Ligonier Valley, Westmoreland Co., Penn.	Vogel 1966
W 117°12': N 46°	W 117°12': N 46°	Crawford 1988
W 122°48': N 47°	W 122°48': N 47°	Crawford 1988

Table A-10. Source Data for the *Agelenopsis potteri* Distribution Map (Figure 12).

Coordinates	Location	Source
W 65°45': N 44°40'	Digby, Nova Scotia	Chamberlin & Ivie 1941
W 70°35': N 43°15'	Wells, Maine	Chamberlin & Ivie 1941
W 70°53': N 42°33'	Salem, MA	Chamberlin & Ivie 1941
W 70°55': N 42°33'	Peabody, MA	Chamberlin & Ivie 1941
W 71°22': N 42°37'	Chelmsford, MA	Chamberlin & Ivie 1941
W 71°45': N 44°15'	Franconia, New Hampshire	Chamberlin & Ivie 1941
W 73°30': N 45°30'	Montreal, Canada	Chamberlin & Ivie 1941
W 95°10': N 43°25'	Okoboji, Iowa	Chamberlin & Ivie 1941
W 96°45': N 46°50'	Fargo, North Dakota	Chamberlin & Ivie 1941
W 116°15': N 46°15'	Kamiah, Idaho	Chamberlin & Ivie 1941
W 122°55': N 47°5'	Olympia, Washington	Chamberlin & Ivie 1941
W 122°15': N 47°48'	Everett, Washington	Chamberlin & Ivie 1941
W 122°45': N 49°	Blaine, Washington	Chamberlin & Ivie 1941
W 124°25': N 40°30'	Mendocino, California	Chamberlin & Ivie 1941
W 85°34':N 45°40'	Beaver Island, Michigan	Drew 1967
W 65°: N 45°	Annapolis Valley, Nova Scotia	Dondale 1956
W 75°40': N 45°30'	Ottawa, Ontario	Barron 1987
W 74°: N 45°30'	Ste. Anne de Bellevue, Quebec	Barron 1987
W 86°30': N 46°30'	Alger Co., MI	Snider 1991
W 83°40': N 45°	Alpena Co., MI	Snider 1991
W 88°20': N 46°40'	Baraga Co., MI	Snider 1991
W 85°20': N 42°30'	Barry Co., MI	Snider 1991
W 84°: N 43°45'	Bay Co., MI	Snider 1991
W 86°: N 44°40'	Benzie Co., MI	Snider 1991
W 85°5': N 41°50'	Branch Co., MI	Snider 1991
W 85°: N 42°20'	Calhoun Co., MI	Snider 1991
W 85°: N 45°15'	Charlevoix Co., MI	Snider 1991
W 84°30': N 46°30'	Chippewa Co., MI	Snider 1991
W 84°40': N 43°50'	Clinton Co., MI	Snider 1991
W 84°50': N 42°30'	Eaton Co., MI	Snider 1991
W 83°45': N 43°	Genesee Co., MI	Snider 1991
W 84°25': N 42°40'	Ingham Co., MI	Snider 1991
W 84°50': N 43°40'	Isabella Co., MI	Snider 1991
W 84°30': N 42°15'	Jackson Co., MI	Snider 1991
W 85°35': N 42°40'	Kalamazoo Co., MI	Snider 1991
W 87°35': N 46°25'	Marquette Co., MI	Snider 1991
W 85°20': N 43°40'	Mecosta Co., MI	Snider 1991
W 84°25': N 43°40'	Midland Co., MI	Snider 1991
W 85°15': N 43°20'	Montcalm Co., MI	Snider 1991
W 83°20': N 42°40'	Oakland Co., MI	Snider 1991
W 86°15': N 43°40'	Oceana Co., MI	Snider 1991
W 89°20': N 46°40'	Ontonagon Co., MI	Snider 1991
W 84°40': N 44°20'	Roscommon Co., MI	Snider 1991
W 84°: N 43°20'	Saginaw Co., MI	Snider 1991

Table A-10 (continued).

Coordinates	Location	Source
W 82°45': N 43°25'	Sanilac Co., MI	Snider 1991
W 84°10': N 42°55'	Shiawassee Co., MI	Snider 1991
W 86°: N 42°15'	Van Buren Co., MI	Snider 1991
W 83°20': N 42°15'	Wayne Co., MI	Snider 1991
W 87°50': N 42°20'	Waukegon, Illinois	Kaston 1955
W 87°35': N 41°5'	Pembroke, Illinois	Kaston 1955
W 90°: N 45°	Very Common in Wisconsin	Levi & Field 1954
W 99°: N 49°30'	Manitoba, Canada	Aitchison-Benell & Dondale 1990
W 97°: N 49°30'	Manitoba, Canada	Aitchison-Benell & Dondale 1990
W 97°: N 50°30'	Manitoba, Canada	Aitchison-Benell & Dondale 1990
W 77°20': N 44°10'	Belleville, Ontario, Canada	Dondale 1971
W 89°25': N 43°5'	Lake Mendota, Wisconsin	Harrington 1978
W 73°: N 40°45'	Long Island, New York	Kaston 1948
W 93°45': N 38°45'	Warrensburg, Johnson Co., Missouri	Peck 1966
W 119°35': N 49°5'	Osoyoos, British Columbia	West et al. 1984
W 119°40': N 49°10'	Oliver, British Columbia	West et al. 1984
W 119°15': N 50°20'	Vernon, British Columbia	West et al. 1984
W 120°20': N 50°40'	Kamloops, British Columbia	West et al. 1984
W 119°15': N 50°45'	Salmon Arm, British Columbia	West et al. 1984
W 121°55': N 50°45'	Lillooet, British Columbia	West et al. 1984
W 119°40': N 49°35'	Summerland, British Columbia	West et al. 1984
W 124°5': N 48°45'	Cowichan, British Columbia	West et al. 1984
W 123°10': N 49°15'	Vancouver, British Columbia	West et al. 1984
W122°20': N 47°35'	Seattle, Washington	Crawford 1988
W 122°30': N 45°42'	W 122°30': N 45°42'	Crawford 1988
W 120°18': N 47°24'	W 120°18': N 47°24'	Crawford 1988
W 122°12': N 48°6'	W 122°12': N 48°6'	Crawford 1988
W 118°: N 48°36'	W 118°: N 48°36'	Crawford 1988

Table A-11. Source Data for the *Agelenopsis spatula* Distribution Map (Figure 13).

Coordinates	Location	Source
W 98°27': N 33°53'	Wichita Falls, TX	Chamberlin & Ivie 1941
W 98°15': N 38°45'	Ellsworth, Kansas	Chamberlin & Ivie 1941
W 103°45': N 35°10'	Tucumcari, New Mexico	Chamberlin & Ivie 1941
W 105°55': N 35°30'	10 mi. south of Sante Fe, NM	Chamberlin & Ivie 1941
W 98°15': N 32°15'	Stephensville, Erath Co., Texas	Agnew et al. 1985

Table A-12. Source Data for the *Agelenopsis utahana* Distribution Map (Figure 14).

Coordinates	Location	Source
W 70°53': N 42°33'	Salem, MA	Chamberlin & Ivie 1941
W 70°35': N 43°15'	Wells, Maine	Chamberlin & Ivie 1941
W 71°25': N 41°50'	Providence, Rhode Island	Chamberlin & Ivie 1941
W 71°45': N 44°15'	Franconia, New Hampshire	Chamberlin & Ivie 1941
W 72°: N 44°45'	Jaffrey, New Hampshire	Chamberlin & Ivie 1941
W 73°55': N 44°10'	Mt. Marcy, New York	Chamberlin & Ivie 1941
W 82°5': N 35°50'	Sprucepine, North Carolina	Chamberlin & Ivie 1941
W 97°: N 50°	Kettle Rapids, Manitoba	Chamberlin & Ivie 1941
W 108°45': N 39°15'	Loma, Colorado	Chamberlin & Ivie 1941
W 109°10': N 38°20'	LaSal Mts., Utah	Chamberlin & Ivie 1941
W 110°45': N 43°30'	10 mi. north of Jackson, Wyoming	Chamberlin & Ivie 1941
W 111°45': N 38°35'	Fish Lake, Utah	Chamberlin & Ivie 1941
W 111°55': N 40°45'	Wasatch Mts., near Salt Lake City, Utah	Chamberlin & Ivie 1941
W 111°25': N 42°	Fishaven, Idaho	Chamberlin & Ivie 1941
W 111°15': N 45°30'	Gallatin Gateway, Montana	Chamberlin & Ivie 1941
W 112°: N 46°	Blossburg, Montana	Chamberlin & Ivie 1941
W 113°10': N 41°57'	Clear Creek, Raft River Mts., Utah	Chamberlin & Ivie 1941
W 114°: N 46°	Ravalli Co., Montana	Chamberlin & Ivie 1941
W 114°15': N 47°50'	Flathead Lake, Montana	Chamberlin & Ivie 1941
W 115°30': N 43°45'	Boise River, Idaho(at North Fork)	Chamberlin & Ivie 1941
W 116°: N 46°10'	Kooskia, Idaho	Chamberlin & Ivie 1941
W 116°45': N 43°45'	Notus, Idaho	Chamberlin & Ivie 1941
W 116°: N 46°	Lawyer Creek, Idaho	Chamberlin & Ivie 1941
W 122°15': N 47°48'	Everett, Washington	Chamberlin & Ivie 1941
W 122°20': N 47°35'	Seattle, Washington	Chamberlin & Ivie 1941
W 122°55': N 47°5'	Olympia, Washington	Chamberlin & Ivie 1941
W 123°: N 48°35'	Friday Harbor, Washington	Chamberlin & Ivie 1941
W 152°: N 57°	Kodiak, Alaska	Chamberlin & Ivie 1941
W 74°30': N 40°	New Jersey(Exline)	Chamberlin & Ivie 1941
W 83°: N 40°	Ohio(Seyler)	Chamberlin & Ivie 1941
W 85°34':N 45°40'	Beaver Island, Michigan	Drew 1967
W 85°: N 45°45'	Waugoshance Point, MI	Drew 1967
W 83°10': N 35°	Buck Creek, Highlands Ranger Dist., NC	Coyle 1981
W 69°5': N 45°55'	NW of Millinocket, Piscataquis, Maine	Jennings et al. 1988
W 65°: N 45°	Annapolis Valley, Nova Scotia	Dondale 1956
W 65°45': N 44°20'	Marshalltown, Digby Co., Nova Scotia	Fox & Dondale 1972
W 64°40': N 45°	Hall's Harbour, Kings Co., Nova Scotia	Fox & Dondale 1972
W 106°25': N 52°	Clavet, Saskatchewan	Doane & Dondale 1979
W 91°: N 33°15'	Washington Co., Mississippi	Young et al. 1989
W 83°40': N 44°45'	Alcona Co., MI	Snider 1991
W 84°50': N 44°	Clare Co., MI	Snider 1991
W 87°50': N 46°	Dickinson Co., MI	Snider 1991
W 86°50': N 45°50'	Delta Co., MI	Snider 1991
W 84°25': N 42°40'	Ingham Co., MI	Snider 1991

Table A-12 (continued).

Coordinates	Location	Source
W 85°35': N 42°20'	Kalamazoo Co., MI	Snider 1991
W 88°5': N 47°25'	Keweenaw Co., MI	Snider 1991
W 89°: N 48°	Isle Royale, MI	Snider 1991
W 85°45': N 45°	Leelanau Co., MI	Snider 1991
W 85°: N 46°10'	Mackinac Co., MI	Snider 1991
W 87°35': N 46°25'	Marquette Co., MI	Snider 1991
W 86°15': N 44°	Mason Co., MI	Snider 1991
W 84°25': N 43°40'	Midland Co., MI	Snider 1991
W 83°30': N 41°55'	Monroe Co., MI	Snider 1991
W 85°15': N 43°20'	Montcalm Co., MI	Snider 1991
W 86°15': N 43°40'	Oceana Co., MI	Snider 1991
W 84°10': N 44°20'	Ogemaw Co., MI	Snider 1991
W 89°20': N 46°40'	Ontonagon Co., MI	Snider 1991
W 84°: N 43°20'	Saginaw Co., MI	Snider 1991
W 84°10': N 42°55'	Shiawassee Co., MI	Snider 1991
W 86°20': N 46°20'	Schoolcraft, MI	Snider 1991
W 83°50': N 42°15'	Washtenaw Co., MI	Snider 1991
W 110°40':N 43°45'	Grand Teton Nat. Park, Wyoming	Lowrie & Gertsch 1955
W 87°40': N 41°50'	Chicago, Illinois	Kaston 1955
W 87°45': N 42°10'	Glencoe, Illinois	Kaston 1955
W 90°: N 45°	Very common in Wisconsin	Levi & Field 1954
W 87°15': N 41°40'	Ogden Dunes, Indiana	Lowrie 1948
W 86°15': N 42°40'	Saugatuck, MI	Lowrie 1948
W 97°: N 49°50'	Manitoba, Canada	Aitchison-Benell & Dondale 1990
W 97°: N 50°30'	Manitoba, Canada	Aitchison-Benell & Dondale 1990
W 95°: N 50°30'	Manitoba, Canada	Aitchison-Benell & Dondale 1990
W 101°: N 51°30'	Manitoba, Canada	Aitchison-Benell & Dondale 1990
W 95°: N 51°30'	Manitoba, Canada	Aitchison-Benell & Dondale 1990
W 101°: N 52°30'	Manitoba, Canada	Aitchison-Benell & Dondale 1990
W 101°: N 54°30'	Manitoba, Canada	Aitchison-Benell & Dondale 1990
W 99°: N 56°30'	Manitoba, Canada	Aitchison-Benell & Dondale 1990
W 78°40': N 39°35'	Allegany Co., Maryland	Muma 1945
W 79°15': N 39°30'	Garrett Co., Maryland	Muma 1945
W 79°40': N 39°55'	Fayette Co., Pennsylvania	Vogel 1968
W 79°25': N 40°15'	Westmoreland Co., Pennsylvania	Vogel 1968
W 72°45': N 41°45'	Common throughout Connecticut	Kaston 1948
W 119°15': N 50°45'	Salmon Arm, British Columbia	West et al. 1984
W 121°55': N 50°45'	Lillooet, British Columbia	West et al. 1984
W 119°15': N 52°45'	Canoe, British Columbia	West et al. 1984
W 144°: N 48°45'	Glacier Nat. Park, Montana	Levi & Levi 1955
W 120°30': N 46°54'	W 120°30': N 46°54'	Crawford 1988
W 120°30': N 47°24'	W 120°30': N 47°24'	Crawford 1988
W 117°5':N 47°42'	W 117°5':N 47°42'	Crawford 1988
W 120°18': N 47°54'	W 120°18': N 47°54'	Crawford 1988

Table A-12 (continued).

Coordinates	Location	Source
W 119°: N 48°42'	W 119°: N 48°42'	Crawford 1988
W 117°18': N 48°48'	W 117°18': N 48°48'	Crawford 1988
W 117°18': N 48°54'	W 117°18': N 48°54'	Crawford 1988
W 59°: N 47°45'	South Branch, Newfoundland	Hackman 1954
W 58°30': N 48°30'	Stephensville Crossing, Newfoundland	Hackman 1954
W 58°15': N 47°25'	Grand Bruit, Newfoundland	Hackman 1954
W 52°55': N 47°10'	Cape Broyle, Newfoundland	Hackman 1954
W 58°: N 48°55'	Corner Brook, Newfoundland	Hackman 1954
W 57°30': N 49°10'	Deer Lake, Newfoundland	Hackman 1954
W 55°15': N 49°2'	Norris Arms, Newfoundland	Hackman 1954
W 55°25': N 49°5'	Lewisporte, Newfoundland	Hackman 1954
W 54°50': N49°	Glenwood, Newfoundland	Hackman 1954
W 54°30': N 48°55'	Gander, Newfoundland	Hackman 1954
W 54°15': N 48°15'	Gambo, Newfoundland	Hackman 1954
W 54°: N 47°50'	Come by Chance, Newfoundland	Hackman 1954
W 54°: N 48°15'	Shoal Harbor, Newfoundland	Hackman 1954

APPENDIX B

GENITALIA FIGURES FOR *AGELENOPSIS*

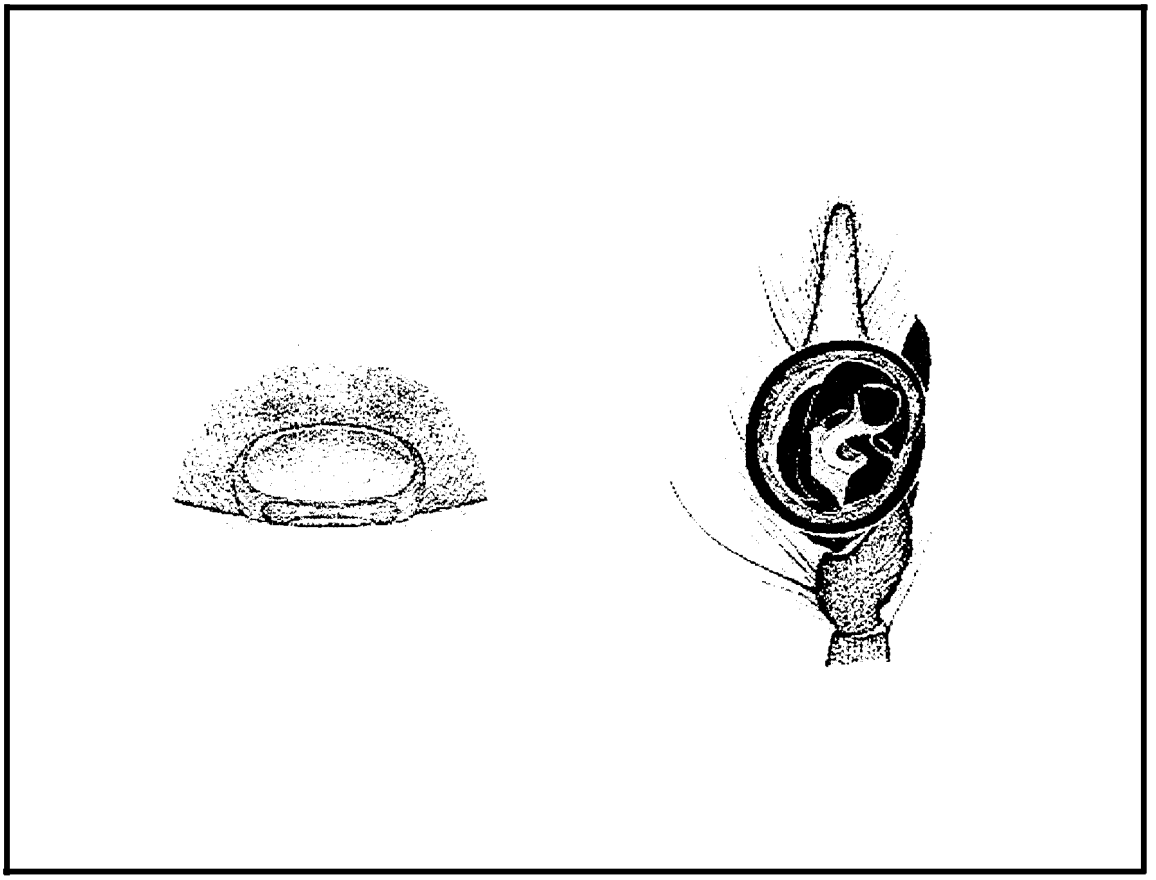


Figure B-1. The Epigynum (left) and Left Palpus (right) of *Agelenopsis actuosa* (drawings from Chamberlin & Ivie 1941).

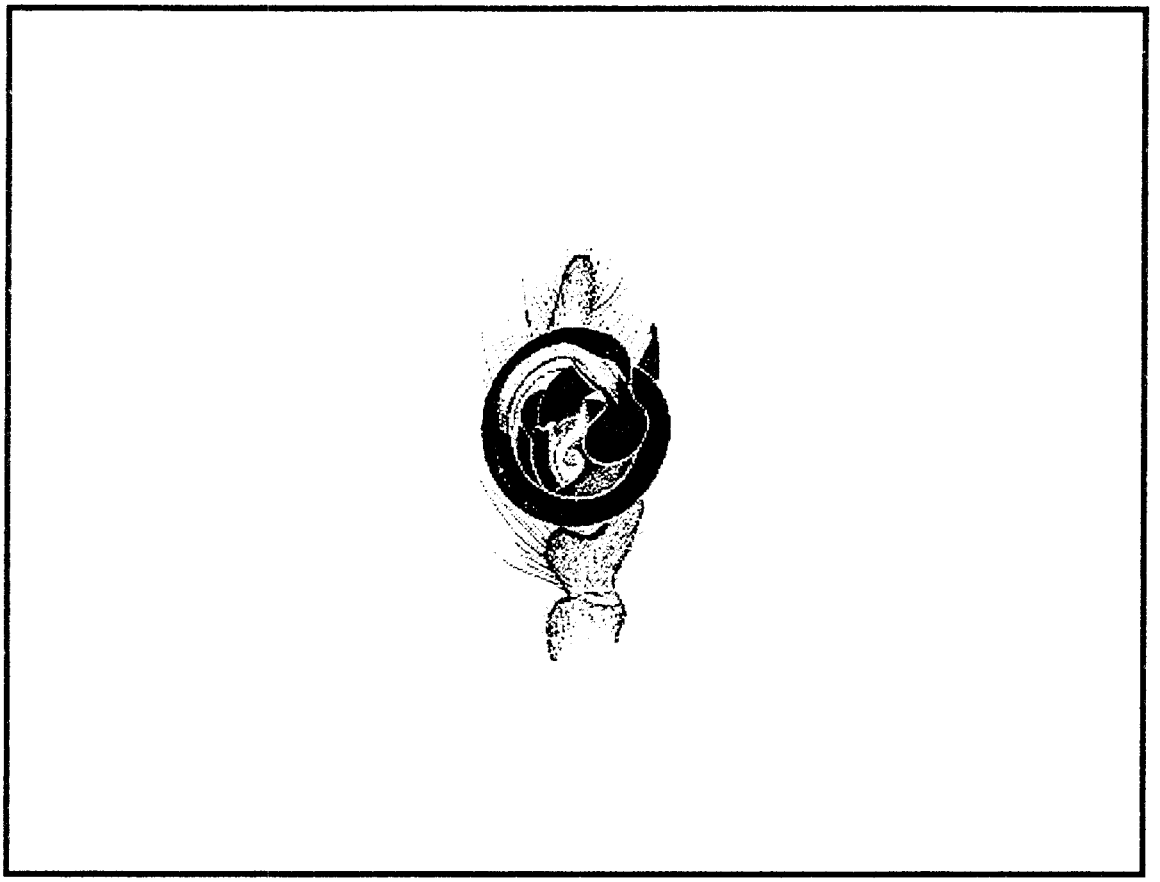


Figure B-2. The Left Palpus of *Agelenopsis aleenae* (drawings from Chamberlin & Ivie 1941).

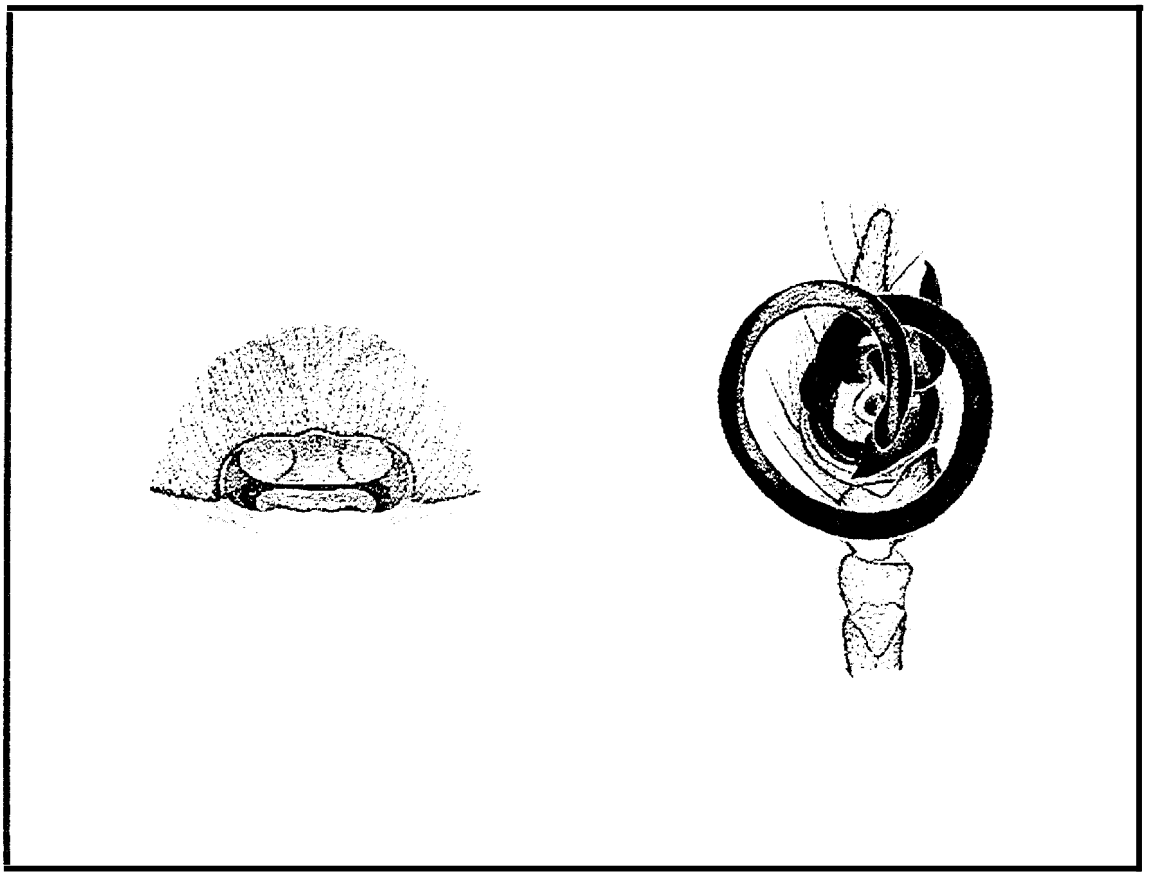


Figure B-3. The Epigynum (left) and Left Palpus (right) of *Agelenopsis aperta* (drawings from Chamberlin & Ivie 1941).

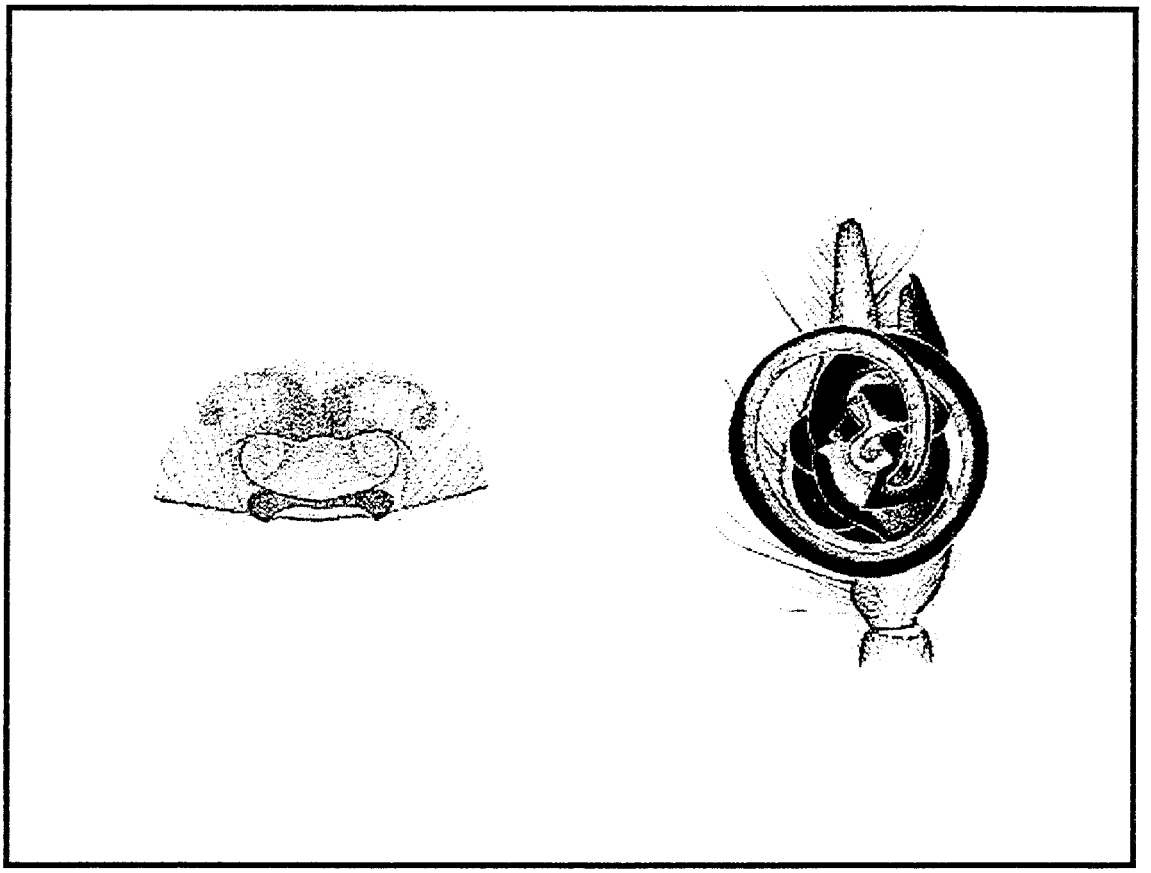


Figure B-4. The Epigynum (left) and Left Palpus (right) of *Agelenopsis emertoni* (drawings from Chamberlin & Ivie 1941).

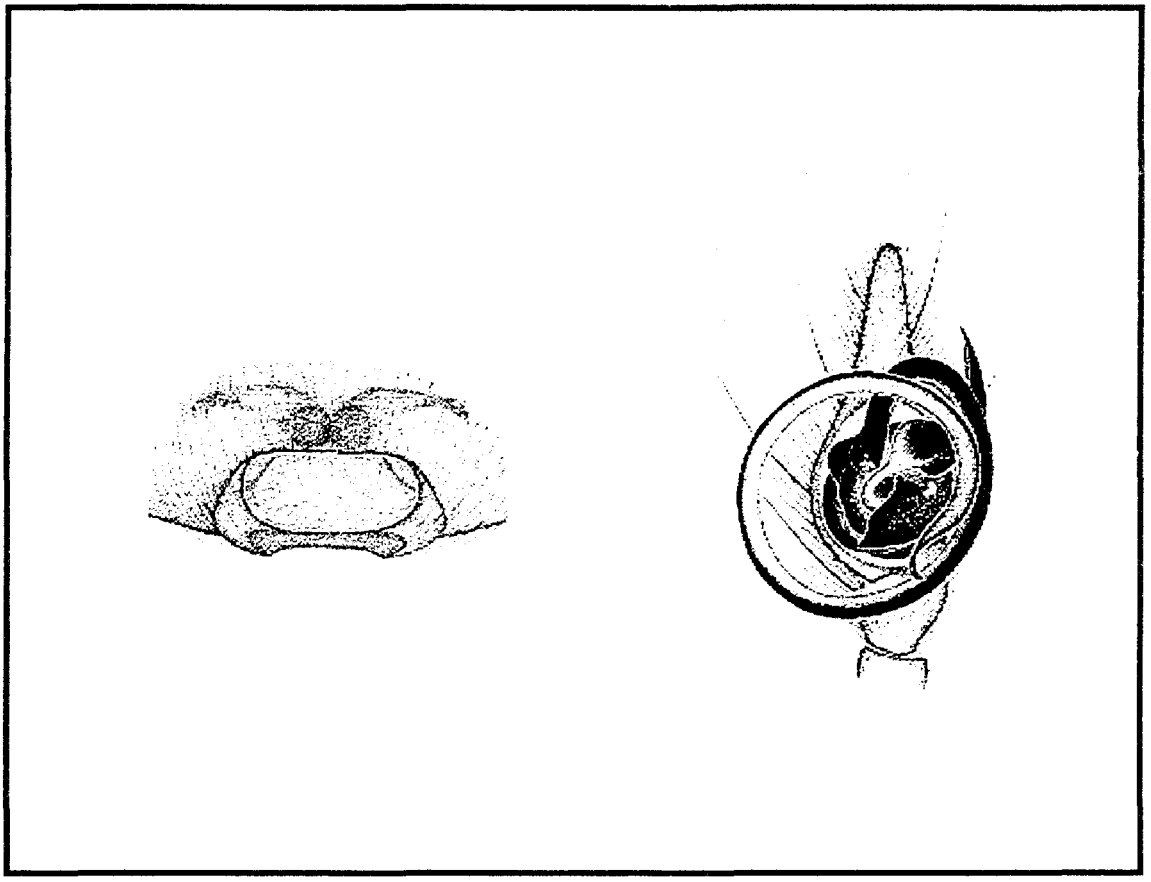


Figure B-5. The Epigynum (left) and Left Palpus (right) of *Agelenopsis kastoni* (drawings from Chamberlin & Ivie 1941).

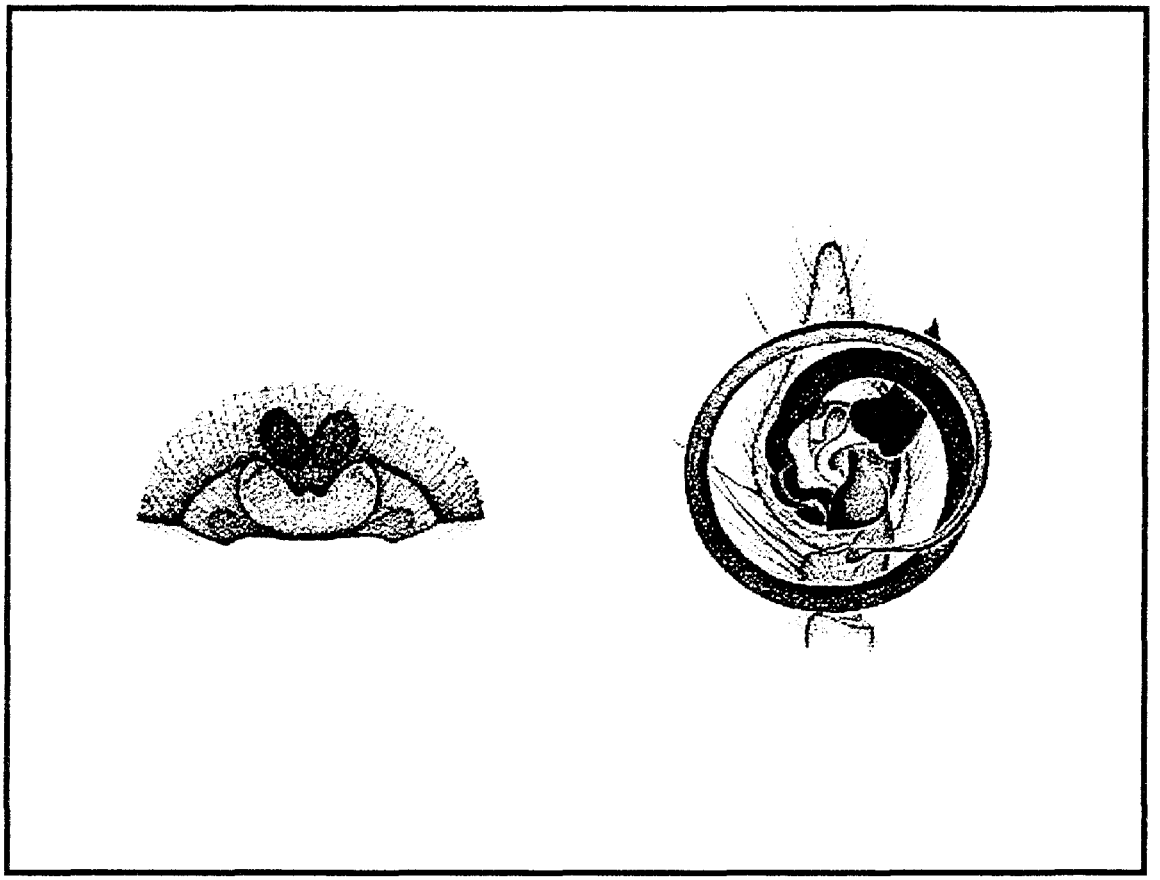


Figure B-6. The Epigynum (left) and Left Palpus (right) of *Agelenopsis longistylus* (drawings from Chamberlin & Ivie 1941).

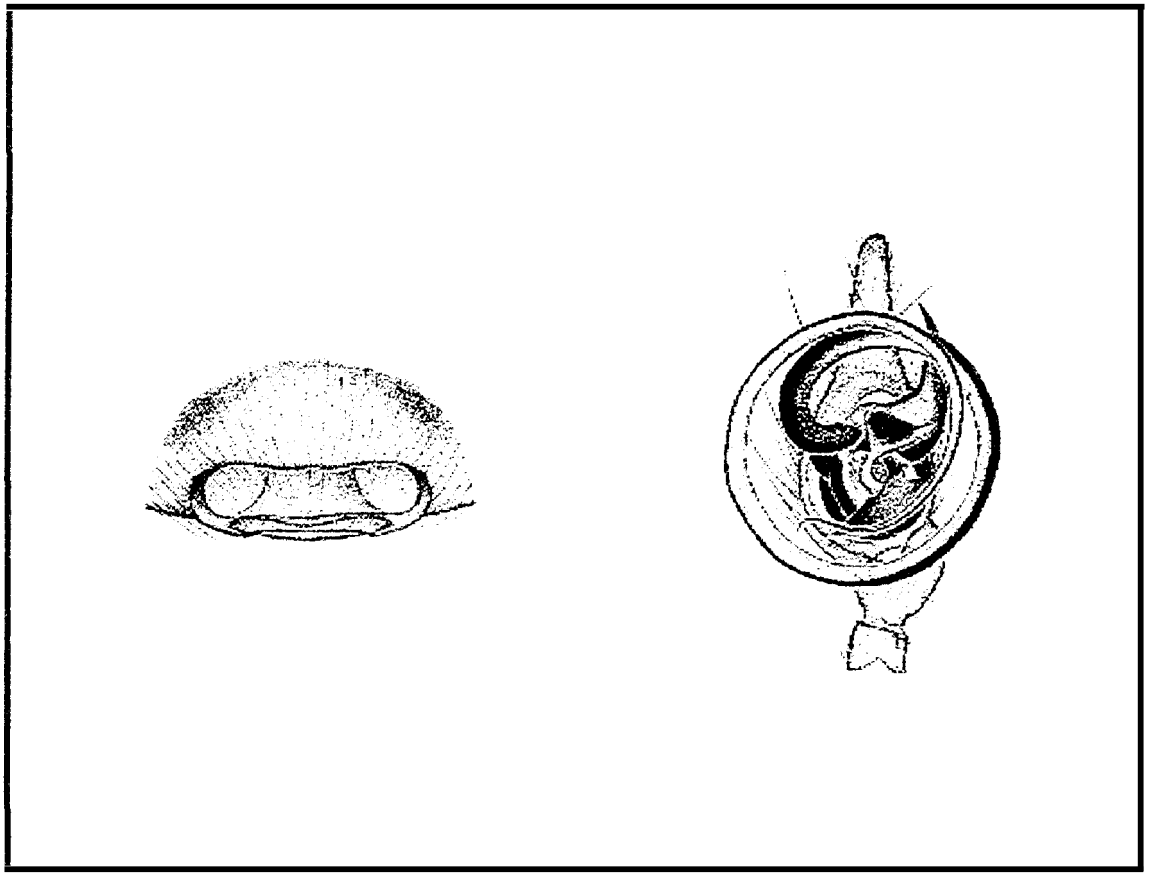


Figure B-7. The Epigynum (left) and Left Palpus (right) of *Agelenopsis oklahoma* (drawings from Chamberlin & Ivie 1941).

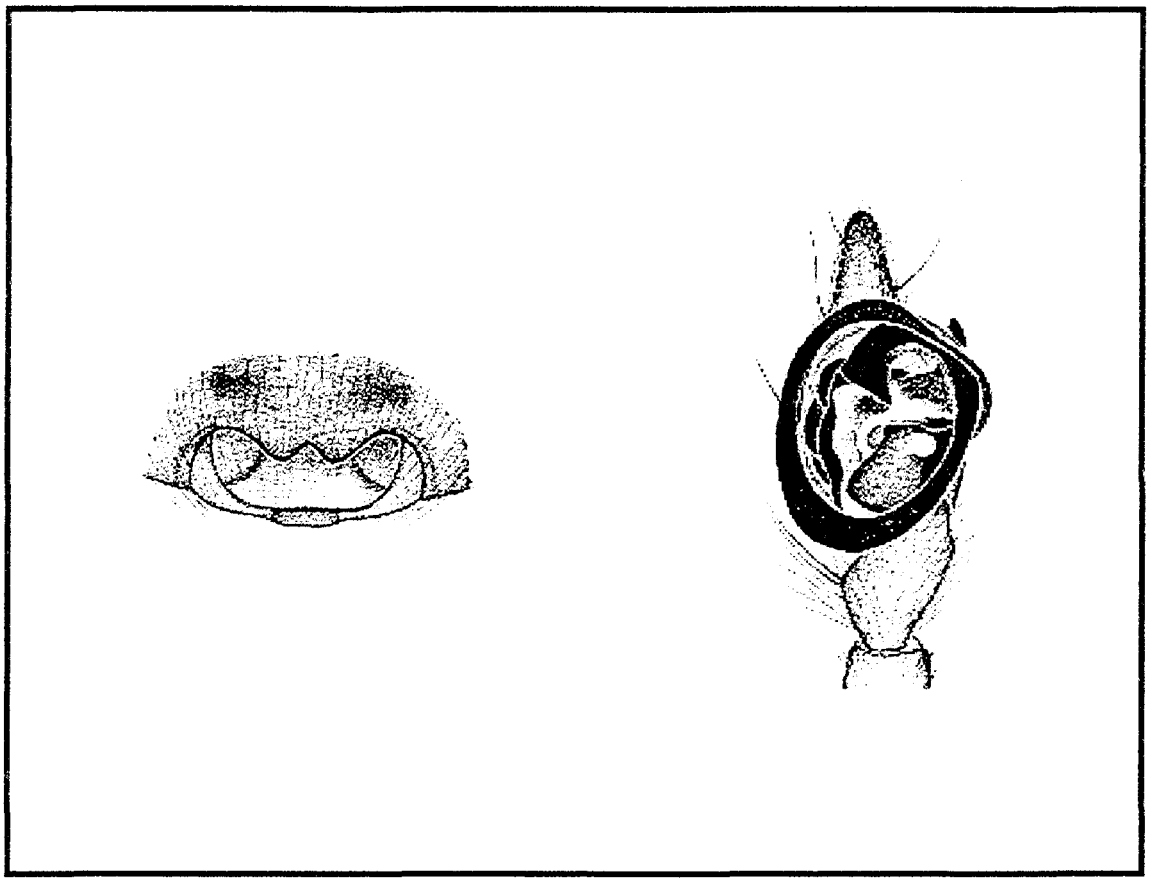


Figure B-8. The Epigynum (left) and Left Palpus (right) of *Agelenopsis oregonensis* (drawings from Chamberlin & Ivie 1941).

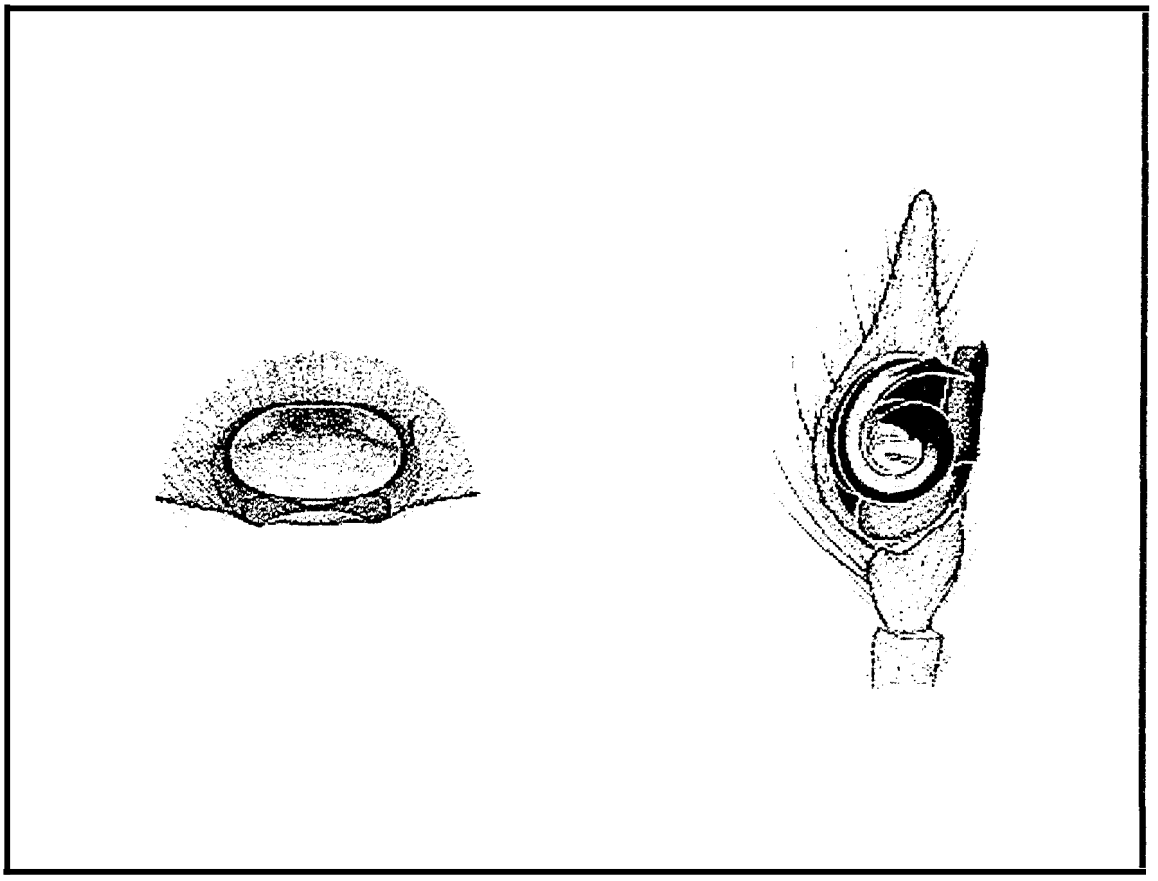


Figure B-9. The Epigynum (left) and Left Palpus (right) of *Agelenopsis pennsylvanica* (drawings from Chamberlin & Ivie 1941).

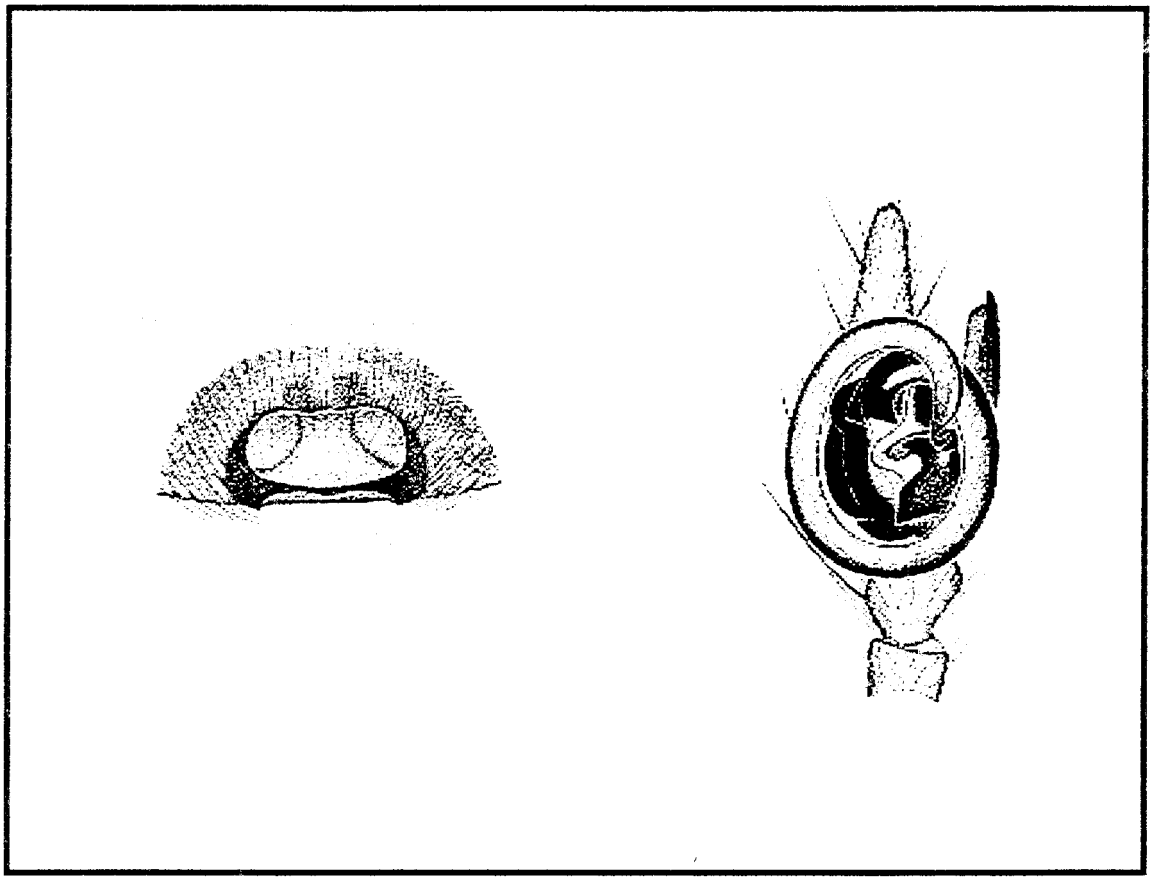


Figure B-10. The Epigynum (left) and Left Palpus (right) of *Agelenopsis potteri* (drawings from Chamberlin & Ivie 1941).

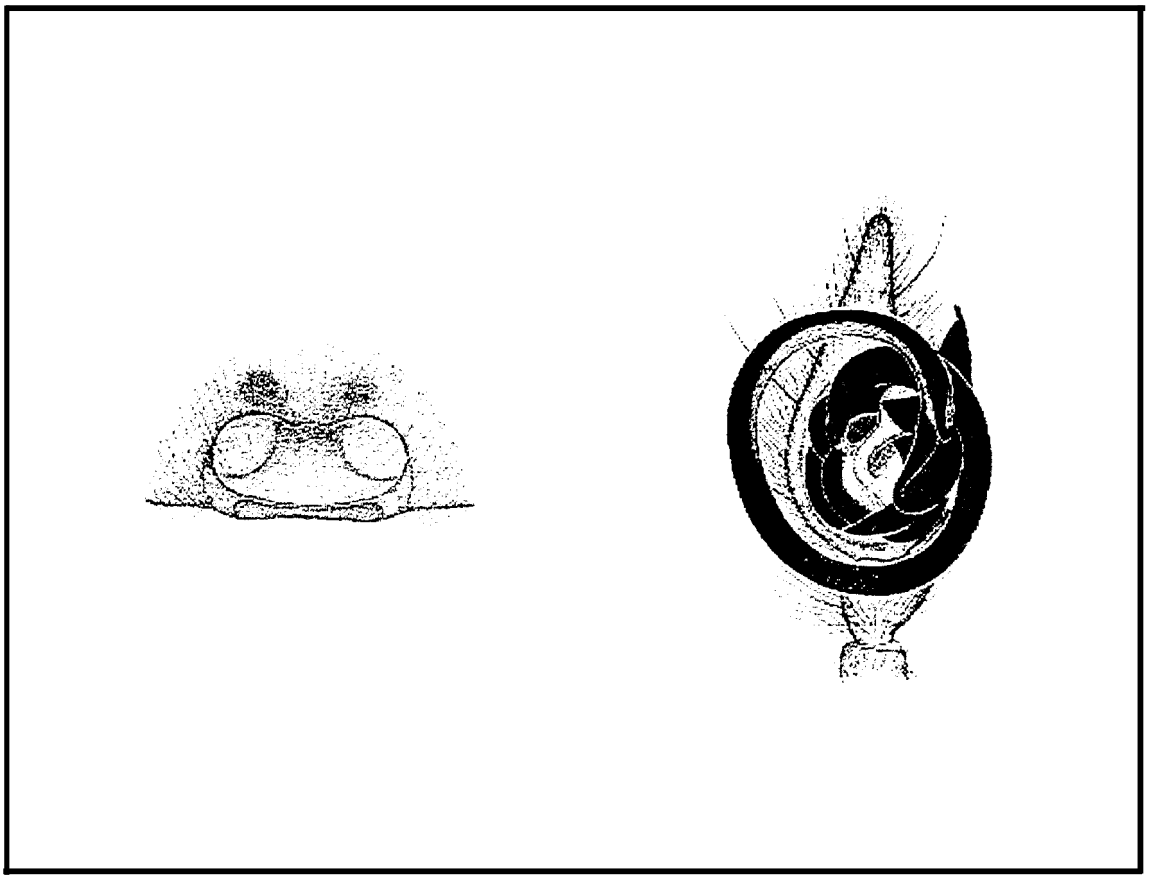


Figure B-11. The Epigynum (left) and Left Palpus (right) of *Agelenopsis spatula* (drawings from Chamberlin & Ivie 1941).

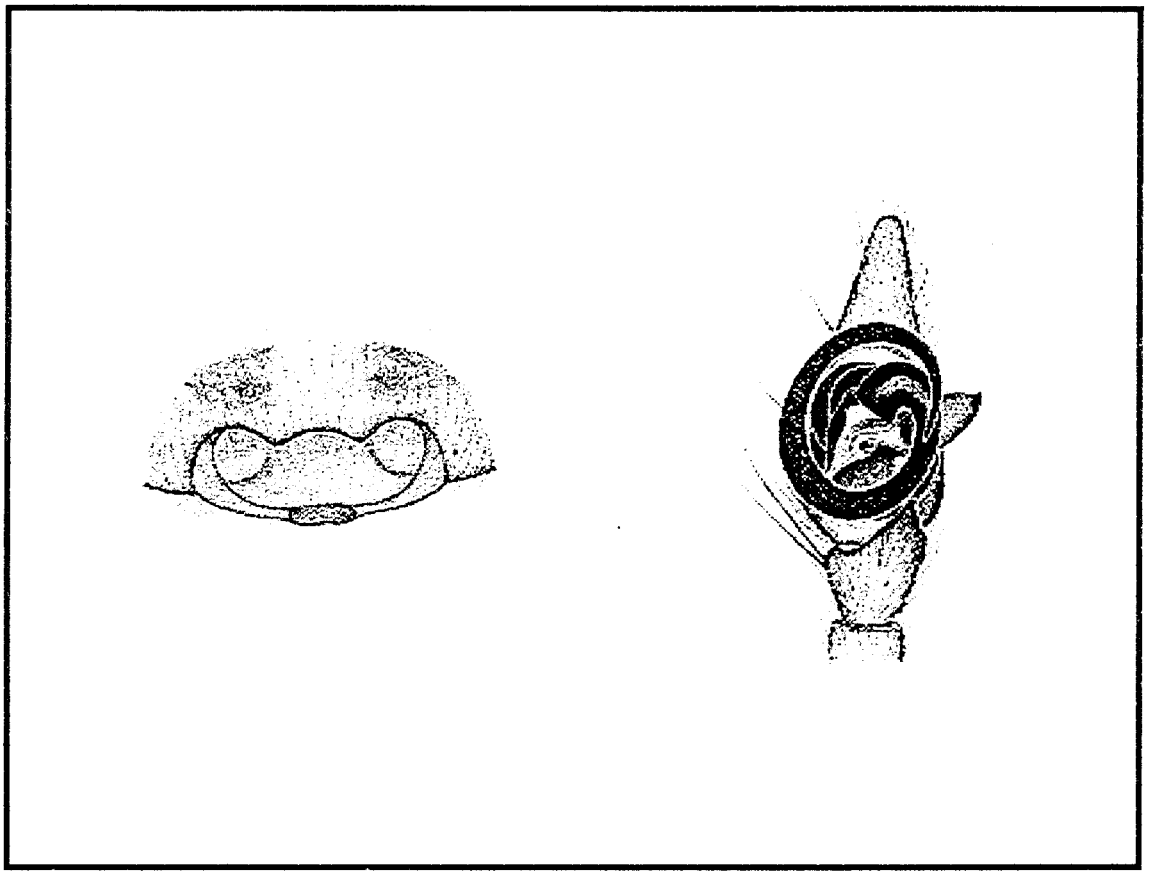


Figure B-12. The Epigynum (left) and Left Palpus (right) of *Agelenopsis utahana* (drawings from Chamberlin & Ivie 1941).

VITA

Thomas Paison was born in Dearborn, Michigan on July 17, 1969. He attended the public schools of the City of Dearborn and graduated from Edsel Ford High School in June, 1987. He entered Henry Ford Community College during September of 1987. He received Associate of Science and Associate of Liberal Arts degrees from the community college in May of 1990. In August of 1990 he entered the Bachelor of Science in Biology program at Michigan Technological University in Houghton. He was awarded that Bachelor's degree in February of 1993. He entered the Doctor of Philosophy program in Zoology at The University of Tennessee, Knoxville in August of 1993. He later transferred to the Master's program in Ecology in order to prepare himself to pursue a Master's degree and career in ecologically sound Landscape Architecture. The Master of Science in Ecology degree was received in August of 1997.