FLORISTIC PATTERNS ON LATE TERTIARY LACUSTRINE DEPOSITS IN THE ARIZONA SONORAN DESERT

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ABSTRACT

A chain of narrow basins in the Transition Zone lies across central Arizona at the northern edge of the Sonoran Desert. They contain recently exposed late Tertiary lacustrine deposits which are infertile compared to surrounding zonal soils, forming a sharp edaphic contrast. The dominant Sonoran Desert woody species, *Larrea tridentata* (creosotebush) and *Cercidium microphyllum* (foothill palo verde), are excluded from the infertile lacustrine soils. The escape from competition for soil moisture allows an opening for disjuncts, relicts, and endemics to survive, in many cases the taxa's only occurrences in the Sonoran Desert. Floristic analysis shows these taxa to be from noncontiguous floristic areas, the Colorado Plateau to the north and the present day Chihuahuan Desert to the southeast. *Lotus mearnsii* var. *equisolensis,* a new variety endemic to one of the basins, is described.

In central Arizona the northern edge of the Sonoran Desert overlaps the Transition Zone, a geological province of closely-spaced mountain ranges with narrow basins below the Mogollon Escarpment (Titley 1984). Most of the Sonoran Desert in Arizona, by contrast, lies within the Basin and Range Province of broad plains and isolated mountain ranges (Smiley et al. 1984). Block faulting and basin subsidence in central Arizona associated with the mid-Miocene Basin and Range Disturbance initially resulted in a series of closed basins (Fig. 1A–H) within which lacustrine deposits with interbedded ash flows were laid down into limy tuffs (Damon et al. 1984). Later, cessation of subsidence and increased precipitation during Pleistocene glacial periods caused stream throughflow between basins and erosion exposed the undeformed lacustrine deposits to plant colonization (Nations et al. 1982).

These limy tuffs were found to be comparatively infertile with very low levels of phosphorus and nitrogen (Anderson 1992). Infertile azonal soils (atypical of the surrounding common soils), including gypsum, limestone, and serpentine, have been shown to host many endemic and disjunct species by excluding the surrounding dominant species and reducing competition for soil moisture (Billings 1950; Kruckeburg 1969, 1986). The surrounding dominant shrubby species, in this case the recently arrived *Larrea tridentata* (DC) Coville (creosotebush) and *Cercidium microphyllum* (Torr.) Rose & Johnst. (foothill palo verde), have apparently not yet

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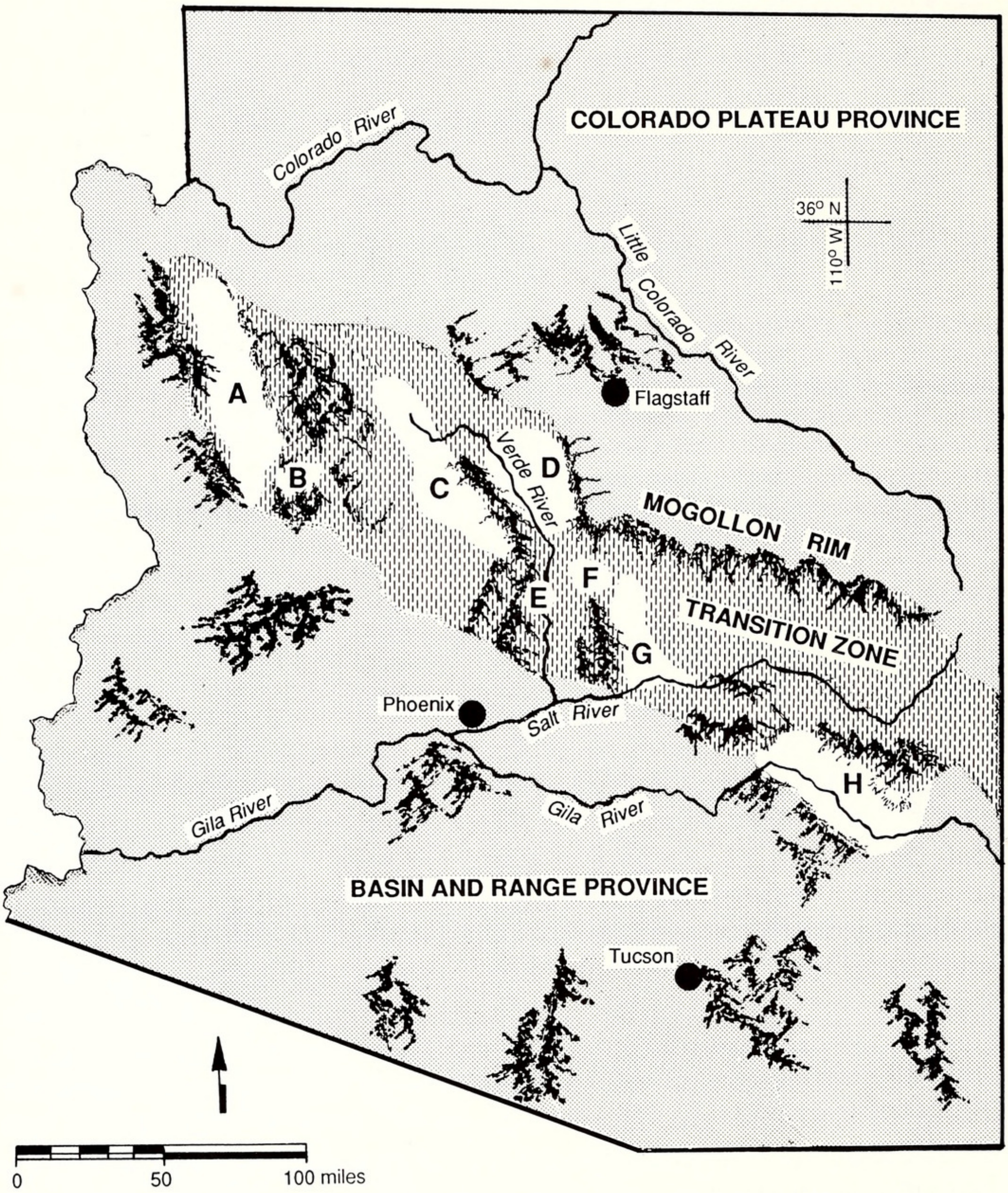
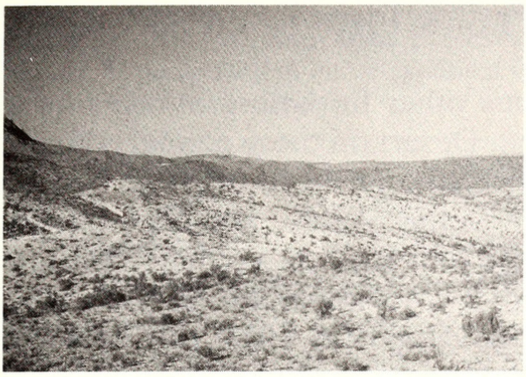
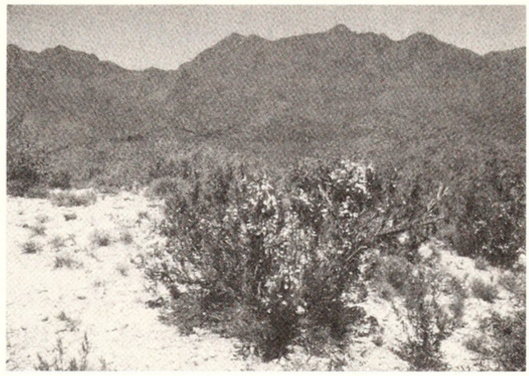


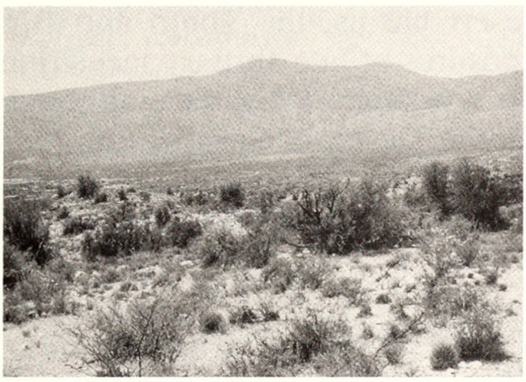
FIG. 1. Transition Zone Basins across central Arizona. A—Big Sandy Basin, B—Burro Creek, C—Chino Valley, D—Verde Valley, E—Lower Verde River (Horseshoe Reservoir), F—Payson Basin, G—Tonto Basin, and H—San Carlos Basin.

evolved ecotypes adapted to these infertile soils, but are more competitive, probably at the seedling stage, on the zonal soils (Yeaton et al 1977). There is an abrupt vegetative change across the edaphic ecotone which provides a synecological opening on the azonal soils for the less competitive disjunct, endemic, and relictual species (Fig. 2–5).

The chain of basins across central Arizona containing contrasting late Tertiary lacustrine deposits is isolated by fifty to one hundred







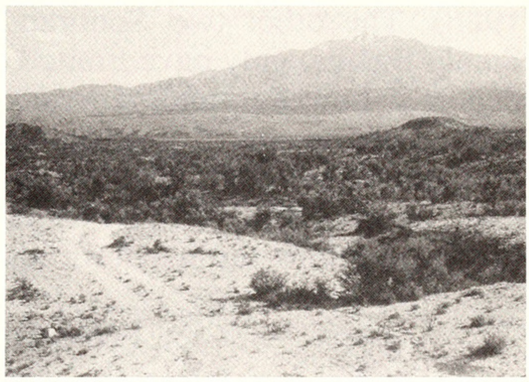


FIG. 2. (upper left) Burro Creek with late Tertiary lacustrine deposit in foreground and Aquarius Mts. in background, Mohave County. Note sharp edaphic contrast between lacustrine deposit and surrounding common soil, but similarity of lacustrine deposits in four basins in Figures 2–5.

FIG. 3. (lower left) Verde Valley with late Tertiary lacustrine deposit (Verde Formation) in foreground and Mingus Mt. in background, Yavapai County.

FIG. 4. (upper right) Lower Verde River (Horseshoe Reservoir) with late Tertiary lacustrine deposit in foreground and Humboldt Mt. in background, Maricopa County. Note *Purshia subintegra* in full bloom in foreground.

FIG. 5. (lower right) San Carlos Basin with late Tertiary lacustrine deposit in foreground and Gila River and Mt. Turnbull in background, Graham County.

miles from each other (Nations et al. 1981) and provide a similar setting for endemics and disjuncts within the Sonoran Desert (Anderson 1986). From northwest to southeast the six basins in the Sonoran Desert (Fig. 1) are the Big Sandy Basin (A) at 630 m along the Big Sandy River, small local basin deposits along Burro Creek (B) at 770 m (Fig. 2), the Verde Valley (C) at 1030 m (Fig. 3) and the Lower Verde River–Horseshoe Reservoir (E) at 630 m (Fig. 4) along the Verde River, the Tonto Basin (G) at 770 m along Tonto Creek, and the San Carlos Basin (G) at 850 m along the middle Gila River (Fig. 5). (Two other Transition Zone basins at higher elevations, the Chino (D) and Payson (F) Basins at 1300–1400 m with plains grassland (Brown and Lowe 1980) lie outside the Sonoran Desert).

A number of species from various other floristic provinces have their only occurrences in the Sonoran Desert on these azonal edaphic sites where they are disjunct between two or more of these basins: Burro Creek, Verde Valley, Lower Verde Valley, and San Carlos. The resultant floristic patterns at these four sites thus contain unusual combinations of species that normally occur in different floristic provinces and may serve as phytogeographical clues to document past plant migrations, community types, and speciation (Anderson 1986). The other two Sonoran Desert basins, the Tonto and Big Sandy Basins, only have limited exposures of late Tertiary lacustrine deposits, however, and generally do not support disjuncts although each contains one of just three Sonoran Desert occurrence of *Stanleya pinnata* (Pursh) Britt. [*Anderson 86-37* (ASU) and *Butterwick and Hillyard 4577* (ASU) respectively], a species from the mountains and plains farther north and west.

Floristic Analysis

The Transition Zone basins in the Arizona Sonoran Desert lie within the *Larrea tridentata-Canotia holocantha* (creosotebush-crucifixion thorn) series of the Arizona Upland Subdivision (Brown 1982). But, the absence of the usually dominant creosotebush and foothill palo verde on the infertile lacustrine soils provides a synecological opening for the disjuncts, endemics, and relicts to occur. Other desert shrubs present in typical low densities on two or more of the basin lacustrine deposits are *Canotia holocantha* Torr., *Krameria parviflora* Benth., *Gutierrezia sarothrae* (Pursh) Britt., *Ziziphus obtusifolia* (Hook. ex Torr. & A. Gray) A. Gray, *Fouquieria splendens* Engelm., *Dalea formosa* Torr., *Melampodium leucanthum* Torr. & A. Gray, *Eriogonum fasciculatum* Benth., *Simmondsia chinensis* (Link) Schneid., *Aloysia wrightii* (A. Gray) Heller, *Parthenium incanum* H.B.K., and *Dyssodia acerosa* DC. Species disjunct, endemic, and relict on the late Tertiary lacustrine deposits and their floristic affinities are listed in Table 1. Representative collections and author citations are listed in Appendix 1.

Colorado Plateau. Many of the disjuncts and endemics on the late Tertiary lacustrine deposits in the Transition Zone basins have floristic affinities to the north with the main portion of their range in the Colorado Plateau Floristic Area (McLaughlin 1986, 1989), also described as the Great Basin Desertscrub and Conifer Woodland (Brown 1982). Endemic taxa are marked with an asterisk; their affinities are with the respective typical varieties or presumed most closely related species (Reveal 1969, 1976; Isely 1983; Strachen 1982). These include *Arenaria eastwoodiae, Astragalus calycosus*

TABLE 1. SPECIES DISJUNCTS AND ENDEMICS ON LATE TERTIARY LACUSTRINE DEPOSITS IN CENTRAL ARIZONA AND THEIR FLORISTIC AFFINITIES. Chihuahuan Desert, Colorado Plateau, Mohave Desert, and elevational (various floristic affinities from surrounding mountains). * = endemics.

Species and Floristic Affinities	Transition Zone Basins in the Sonoran Desert			
	Burro Creek	Verde Valley	Lower Verde River	San Carlos Basin
Chihuahuan Desert				
Anulocaulis leisolenus		X		
Polygala macradenia			X	X
Polygala scoparioides		X	X	X
Purshia subintegra	X	X	X	X
Thamnosma texana		X	X	X
Colorado Plateau				
Arenaria eastwoodiae	X			X
Astragalus calycosus var. *scaposus*		X	X	X
Astragalus newberryi var. *aquarii**	X			
Astragalus newberryi var. *newberryi*		X		
Astragalus praelongus		X		
Atriplex confertifolia				X
Cordylanthus parviflorus	X	X		
*Eriogonum apachense**				X
Eriogonum ericifolium var. *ericifolium**		X		
Eriogonum ripleyi		X	X	
Glossopetalon spinescens var. *aridum*		X		X
Hymenoxys acaulis var. *arizonica*		X		
Penstemon thompsonae		X		X
Petradoria pumila		X		
Physaria newberryi				X
Polygala rusbyi		X	X	
Salvia dorrii var. *mearnsii**		X		
Streptanthus cordatus	X	X		X
Mohave Desert				
Phacelia parishii	X			
Elevational				
Astragalus tephrodes var. *chloridae*			X	
Eriogonum hieracifolium				X
Lesquerella cinerea	X	X	X	
Lotus mearnsii var. *equisolensis*			X	
Lotus mearnsii var. *mearnsii*		X		
Senecio neomexicana		X	X	

var. *scaposus, Astragalus newberryi* var. *aquarii*, Astragalus newberryi* var. *newberryi, Astragalus praelongus, Atriplex confertifolia, Cordylanthus parviflorus, Eriogonum apachense*, Eriogonum ericifolium* var. *ericifolium*, Eriogonum ripleyi, Glossopetalon spinescens* var. *aridum, Hymenoxys acaulis* var. *arizonica, Penstemon thompsonae, Petradoria pumila, Physaria newberryi, Polygala rusbyi, Salvia dorrii* ssp. *mearnsii**, and *Streptanthus cordatus.*

The Verde Valley (Fig. 3), which is closest to the Mogollon Rim and 300–450 m higher in elevation than the other basins, has the largest number of the northern disjuncts. At this higher elevation several of these taxa are not totally restricted to the Verde Formation limestone and gypsum, but have scattered occurrences along the north end of the Verde Valley: *Astragalus calycosus* var. *scaposus, Astragalus praelongus, Cordylanthus parviflora, Glossopetalon spinescens* var. *aridum, Hymenoxys acaulis* var. *arizonica, Lesquerella cinerea,* and *Senecio neomexicana.*

Several of the Colorado Plateau species are found all the way to the southeast on the San Carlos Basin lacustrine deposits (Fig. 5): *Arenaria eastwoodiae, Astragalus calycosus* var. *scaposus, Eriogonum apachense* (endemic), *Glossopetalon spinescens* var. *aridum, Penstemon thompsonae, Physaria newberryi,* and *Streptanthus cordatus.* The San Carlos Basin lacustrine deposit also contains the only Sonoran Desert occurrence of *Atriplex confertifolia,* a Great Basin desertscrub species (shadscale) of alkaline soils, although it is also disjunct farther east and south into Texas (Benson and Darrow 1981). There are pollen records of *Atriplex confertifolia* from late Pleistocene packrat middens in present day Sonoran Desert mountain ranges of western Arizona documenting its southward migration during glacial periods (King and Van Devender 1977).

Chihuahuan Desert. One group of disjuncts has the main portion of their present range in the warm temperate Chihuahuan Desert in southeastern Arizona, New Mexico, Texas, and Mexico (Brown 1982). *Polygala macradenia, Polygala scoparioides,* and *Thamnosma texana,* which are scattered in southeastern Arizona, become disjunct and reach the northwestern margin of their ranges at the lacustrine sites along the Verde River, the former at the Lower Verde River and the latter two at the Verde Valley. None reach the Burro Creek outcrops. (There are also historical records of *Polygala scoparioides* [*Collom 714* (ASC)] and *Thamnosma texana* [*Collom 401* (ARIZ)] from the Payson Basin). *Anulocaulis leisolenus* is the most widely disjunct taxa, from southern New Mexico to the Verde Valley, the only one of the late Tertiary basins in which it has been found. Conversely, it does not reach its northwestern margin there as the above mentioned species do, but is then disjunct even farther northwest from the Verde Valley to limestone strata at the south rim of the Grand Canyon and gypsum beds of the Muddy Mountains in southern Nevada (Knight 1983).

Purshia subintegra, which is endemic to the late Tertiary lacustrine deposits at all four basins: the San Carlos Basin, the Verde River sites, and Burro Creek, is a vicariant species with *Purshia ericifolia,* a Chihuahuan Desert species from over 500 miles away in the Big Bend Region of Texas and adjacent Mexico (Anderson 1992). *Purshia ericifolia* occupies a similar ecological setting there on limestone in the succulent-scrub upland of the Chihuahuan Desert (Brown 1982).

Mohave Desert. The Burro Creek site (Fig. 2) which is the smallest in size and the farthest from these floristic sources has the fewest disjuncts. It does support the only Arizona occurrence of *Phacelia parishii,* a rare annual species disjunct from the Mohave Desert in Nevada and California.

A few taxa, *Eriogonum hieracifolium, Lesquerella cinerea, Lotus mearnsii* var. *mearnsii,* and *Senecio neomexicana,* are disjunct in elevation by 300–1200 m lower to one or more of the Sonoran Desert basins from their primary distribution in the Rocky Mountain Montane Conifer Forests directly north on the Mogollon Rim or west in the Bradshaw Mountains (Brown 1982), also described as the Apachian Floristic Element of McLaughlin (1989). A new variety of *Lotus mearnsii* is described below that is endemic to the lowest elevation basin at the Lower Verde River (Fig. 4). It is related to the typical variety mentioned above. Another taxon from the Lower Verde River, *Astragalus tephrodes* var. *chloridae,* is disjunct lower from the interior chaparral in the surrounding Mazatzal Mountains; this variety also extends northwest to the higher elevation Mohave Desert between the Cerbat Mountains in Arizona and the adjacent Newberry Mountains in Nevada.

New Variety Description

The discovery during this study of a disjunct population of *Lotus mearnsii* from the Lower Verde River near Horseshoe Reservoir in the Sonoran Desert that differed from specimens of previously known populations led to the recognition of a new variety. It differs from typical *L. mearnsii* in longer peduncles, larger flowers, larger pods, and shorter internodes with a more compact growth habit. It is endemic to lacustrine deposits near Horseshoe Reservoir for which it is named var. *equisolensis* (horseshoe) and is separated geographically by 80 km (50 miles) from the nearest populations of *Lotus mearnsii* var. *mearnsii* in the Verde Valley.

Lotus mearnsii (Britt.) Greene var. **equisolensis** J. Anderson, var. nov.—TYPE: USA, Arizona, Maricopa County, (Lower) Verde

River, S of Horseshoe Reservoir, 0.3 miles W of road to reservoir on Forest Service Road 205, growing on white lacustrine outcrop, 2100 feet elevation, T17N, R6E, S3, with *Purshia, Canotia, Dodonea, Eriogonum, Nolina, Encelia,* Sonoran Desert, 3 April 1987, *J. L. Anderson 87-21* (holotype, ASU; isotypes ARIZ, BYU, ISC, NY).

A var. *mearnsii* foliolis grandioribus latioribusque late obovatis minus quam duplo longioribus quam latioribus, pedunculis longioribus longitudine 25–75 mm, floribus longioribus longitudine 14–20 mm, leguminibus grandioribus 25–35 mm longis et 4–7 mm latis, internodis brevioribus et habitu condensatiore differt.

Spreading to prostate perennial herb arising from subterranean caudex; stems clustered, procumbent, 1–3 dm long; pubescence silvery to less dense at distal end of stems, sericeous; leaves shorter than to as long as internodes, subpinnate to palmate, sericeous on both surfaces, petiole 2–5 mm, leaflets 3–5, broadly obovate or obcordate, 6–16 mm long, 4–12 mm wide, length to width ratio less than 2; peduncles prolonged beyond the leaves, 25–75(95) mm long; umbels with 2–7 flowers, 14–20 mm long; calyx tube narrowly campanulate, 4–7 mm long, teeth 2–4 mm long; corolla bright yellow, petals subequal; ovary pubescent, ovules 16–20; pod erect to ascending, oblong, 25–35 (40) mm long, 4–6 mm wide, subpersistent, dehiscent, valves strigulose, coriaceous; seeds few.

PARATYPES: same locality, 9 April 1986, *J. L. Anderson 86-33* (ASU, BYU).

Because the morphological differences between *Lotus mearnsii* var. *equisolensis* and the typical variety are quantitative rather qualitative, this new taxon has been named at the varietal level. *L. m.* var. *equisolensis* is endemic to the Lower Verde River in the Sonoran Desert at 840 m (2100 ft), whereas the range of the typical variety is separated geographically 80-240 km (50–150 miles) to the northwest, from the Verde Valley (the type locality of the typical variety (Britton 1889)), to the Bradshaw Mountains and the Chino Valley; and its habitat is described as "... limestone plateau, dry rocky grasslands, ca 3000–7000 ft ..." (Isely 1981) and "... 3,000–7,000 feet, grassland and dry mesas and slopes ..." (Kearney et al. 1960). Thus, the new variety is geographically isolated and largely ecologically distinct from the typical variety. Because of this populational integrity (rather than representing simply the end of a cline), taxonomic recognition of the Lower Verde River population is warranted. The varietal level is also appropriate since plants of the typical variety that are transitional to *L. m.* var. *equisolensis* occur in the Verde Valley which is intermediate in elevation and habitat between the Lower Verde River and the Chino Valley (Isely 1981). This taxonomic situation is paralleled by *Astragalus newberryi* from the Colorado Plateau which has the geographically isolated low elevation endemic variety, *A. n.* var. *aquarii,* at the Burro Creek site and transitional plants of *A. n.* var. *newberryi* in the Verde Valley (Isely 1983).

Discussion

The many floristic migrations across Arizona caused by the great climatic and topographic variability in the late Tertiary and Pleistocene have resulted in the different floristic sources of the disjuncts, relicts, and endemics occurring on the Transition Zone lacustrine basins which were formed by the late Tertiary Basin and Range Disturbance (Damon et al 1984) and which now serve as refugia as ". . . the edaphic environments stand as either selecting agents, or barriers imposed across the path of a migrating flora . . ." (Mason 1946). Sharp edaphic boundaries can produce sharp discontinuities in plant species distribution (Gankin and Major 1964; Kruckeberg 1969). The inclusion of various types of infertile or otherwise azonal soils, for example, gypsum (Turner and Powell 1979), limestone (Wentworth 1981), and serpentine (Kruckeberg 1954; Whittaker 1954), within the surrounding, but contrasting, normal soils, can form edaphic islands that act as refugia for disjuncts, relicts, and endemics (Kruckeberg 1986). However, it is the existence of a sharp edaphic contrast itself that is more important than the specific nature of the soil differences (Gankin and Major 1964). Since Sonoran Desert soils are mainly derived form volcanics and metamorphics, limestone soils (such as the late Tertiary lacustrine deposits in the Transition Zone) form a sharp edaphic contrast here (Whittaker and Neiring 1968).

In addition, the Sonoran Desert basins along the Transition Zone contain a more equable climate compared to surrounding desert areas. The equable climatic parameters combine a moderate mean annual temperature, a small difference between mean annual high and low temperature, and a biseasonal precipitation pattern of 25 cm or more annual precipitation (Raven and Axelrod 1978; Axelrod 1979); these are the climatic parameters which are most similar to the mesic Miocene paleoclimates in the Southwest (Axelrod 1979; Brown 1882). This comparatively more mesic ecological setting at the northern edge of the Arizona Sonoran Desert is a climatic refugia similar to the Sonoran Desert/coastal chaparral ecotone in Baja California Norte at the southwestern edge of the Sonoran Desert described by Raven and Axelrod (1979) as ". . . an ecotonal region of equable climate that [is] inhabited by many endemics, both ancient and recently derived." Cain (1944) has termed such sites ". . . regions of compensation where the local conditions of microclimate or soil allow them to resist, for a time at least, the climatic pressure and the competition from the surrounding vegetation . . . relicts are likely to occupy the most favorable sites in a region at least with respect to temperature and moisture conditions".

In the Miocene the equable paleoclimate and low topographic relief across the Southwest supported a diverse pine-oak-juniper woodland (Axelrod 1979). Also, there was a contiguous physiographic connection of the paleoflora between central Arizona and southwestern New Mexico as the Verde and eastern Gila River drainage systems flowed eastward into New Mexico with possible connections of the Verde Valley with the Payson and Tonto Basins and the San Carlos Basin with New Mexico through the Pliocene, the opposite of their present westward courses across Arizona (Kottlowski et al. 1965; Pedersen and Royce 1970). The Pliocene uplift of the Sierra Nevada in California and the Mexican Plateau in Sonora and Chihuahua caused a rainshadow from the west and east respectively across the Southwest, resulting in a less equable climate overall with increased aridity, less summer precipitation, and a more continental climatic condition of temperature extremes (Axelrod 1979; Smiley 1984). The vegetative history of southern Arizona in the late Tertiary has reflected this progressive climatic deterioration as the pine-oak-juniper woodland has given way to the arid Sonoran Desert and Chihuahuan Desert vegetation present today (Gray 1960a, b; Axelrod 1979; Northington et al. 1981).

Along with climatic deterioration, southern Arizona and southern New Mexico were separated by uplift of the Continental Divide through southwestern New Mexico with the reversal of drainage patterns to the west across central Arizona with the westward connection of the basins and exposure of the lacustrine deposits (Nations et al. 1982). Species from the pine-oak-juniper woodlands migrated to the southeast into the present day Chihuahuan Desert of New Mexico, Texas, and Mexico; however, some left behind vicariant species pairs of paleoendemics in *Canotia, Castela, Colubrina,* and *Tetracoccus* between the Sonoran and Chihuahuan Deserts (Axelrod 1979), and including *Purshia subintegra* and *P. ericifolia* (Van Devender 1986).

A similar vicariant pattern has been documented between the Transition Zone basins in the genus *Sophora* section *Calia* (Berland) Rudd by Northington et al. (1977). *Sophora arizonica* Watson, an interior chaparral shrub called mescal bean, is disjunct between the two most widely separated basins (but in the non-limestone foothills), the Big Sandy Basin (Fig. 1A) and the San Carlos Basin (Fig. 1H), at a distance of over 300 km; it also has a few disjunct populations in southeastern Arizona mountain ranges on limestone. *Sophora arizonica*'s nearest relative is *S. gypsophila* Turner and Powell, a rare Chihuahuan Desert species of west Texas (Northington

1976). This vicariant pair is thought to be the arid remnants of a widespread mesic progenitor from the late Tertiary pine-oak-juniper woodlands with present relatives in the pine-oak-juniper woodlands of Mexico (Northington et al. 1977). Those taxa listed in Table 1 with Chihuahuan Desert floristic affinities are thus thought to really be relicts or their descendents of the late Tertiary Southwestern pine-oak-juniper woodlands which presently occur in the Chihuahuan Desert, similar to the *Sophora arizonica/S. gypsophila* pattern described above (Anderson 1986).

More recently, floristic migrations in Arizona have been between the south and north, rather than east and west. The presence of desert vegetation here has been interrupted by the Pleistocene glacial cycles with their colder climates that pushed pinyon-juniper woodlands and sagebrush scrublands south from the Colorado Plateau into southern Arizona as recently as 11,000 years ago, as evidenced by packrat midden studies (Van Devender 1977; Van Devender and Spaulding 1979; Betancourt 1987). Floristic remnants of the southern migration of the pinyon-juniper woodlands and sagebrush scrublands, as well as Joshua tree woodlands (Van Devender 1987), during the last Wisconsin glaciation were left behind with their subsequent retreat northward during the Holocene. These northern disjuncts have survived on the edaphic refugia of the Transition Zone Basins in various combinations, but do not occur anywhere else in the Sonoran Desert. Also, the Transition Zone receives the highest amounts of winter rainfall in the Sonoran Desert, simulating the paleoclimate of increased winter precipitation during glacial times (Van Devender 1977). Because of the parallel distribution pattern of several northern disjuncts between the Transition Zone Basins, their occurrences are probably the remnants of parallel migrations during glacial times, rather than a result of several, independent long range dispersals resulting in similar distributions (Anderson 1986). The presence of elevational disjuncts from the surrounding mountains or the Mogollon Rim onto the Sonoran Desert basins is similarly a result of the lowering of vegetation zones during the Wisconsin glaciation.

With the subsidence of southwestern Arizona during the late Tertiary Basin and Range Disturbance, these relicts have been restricted progressively northward from the lower elevations of the Sonoran Desert to the more equable climates of the basins. There they survive only on refugia of azonal edaphic islands of Late Tertiary lacustrine deposits where they also escape competition from the surrounding dominant vegetation (Anderson 1986).

Substrate switching, whereby a population disjunct from the main range of a species exhibits a different soil preference at the edge of the species' range, is well documented (Pigott and Walters 1953; Raven 1972; Mansberg and Wentworth 1984; Neely and Barkworth

1984). In a famous example, several long range disjuncts with no preference for calcareous soils elsewhere are calciphiles in Convict Basin in the Sierra Nevada where limestone soils act as an ecological island within the predominately granitic Sierra Nevada and provide a sharp edaphic contrast (Major and Bamberg 1963). Similarly, the late Tertiary lacustrine disjuncts and endemics are mostly indifferent to calcareous soils throughout their main ranges, but are calciphiles here at the edge of their range in the Sonoran Desert, for example (Kearney et al. 1960, pp. 298, 428, 459, 467, 494, 499, 501, 741, and 791; Vines 1960, pp. 426, 593, and 606).

Conclusions

In the Transition Zone basins on the northern edge of the Sonoran Desert, each set of disjuncts is independently derived and the particular combination of disjuncts and endemics is a product of the vagaries of the unique environmental history of that basin within the overall vegetative history of the Southwest. What is unusual is the resultant mix of members of normally widely separated floristic areas, the Colorado Plateau and the Chihuahuan Desert, in these climatic and edaphic refugia within another floristic area, the Sonoran Desert. Other ecotonal margins of the Sonoran Desert at the xeric/mesic boundary characterized by a more equable climate of biseasonal rainfall, the interior foothills of the Peninsular Ranges in southern California on the west and the coastal foothills of the Sierra San Pedro Mártir in northern Baja California on the southwest are also characterized by endemics and relicts (Raven and Axelrod 1978; Stebbins and Major 1965). There are more disjuncts with northern affinities because they can extend farther south wherever moisture conditions are sufficient, but frost sensitive southern species are limited sooner to the north by freezing temperatures (Shreve 1936).

A knowledge of floristic history can be used to predict where to search for other disjunct populations. For example *Anulocaulis leisolenus* might be expected on the lacustrine deposits in the San Carlos Basin or other limestones in the Chihuahuan Desert mountain ranges of southeastern Arizona, which are between its disjunct occurrences in New Mexico and the Verde Valley. A recently described species from dolomite soils in southern Nevada, *Porophyllum pygmaeum* Keil and Morefield, is postulated to be most closely related to a species from west Texas, *P. greggii* Gray (Keil and Morefield 1989). If either species occurs in Arizona, it would be expected on the late Tertiary lacustrine basin deposits.

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APPENDIX I.
SPECIMEN CITATIONS FOR DISJUNCTS AND ENDEMICS

Specimen citations are listed by basin location: Burro Creek, Verde Valley, Lower Verde River (Horseshoe Reservoir), and San Carlos Basin. More specific locality data are on the herbarium labels. All voucher specimens are deposited at Arizona State University (ASU) unless otherwise indicated.

ASTERACEAE

Hymenoxys acaulis (Pursh) K. F. Parker var. *arizonica* K. F. Parker. - Verde Valley, 8 June 1995, *Anderson 95-17.*

Petradoria pumila (Nutt.) Greene. - Verde Valley, 8 June 1995, *Anderson 95-18.*

Senecio neomexicanus Gray. - Verde Valley, 29 May 1981, *Van Devender et al. s. n.* (ARIZ); - Lower Verde River, 7 Apr 1986, *Anderson 86-18*; 9 Apr 1986, *Anderson 86-31.*

BRASSICACEAE

Lesquerella cinerea Rollins. - Burro Creek, 10 Apr 1947, *Darrow and Gould 4251* (ARIZ); 7 Apr 1984 *Anderson s. n.*; - Verde Valley, 10 May 1967, *Rollins 67111* (ARIZ); 29 Apr 1985, *Schaack and Morefield 1474* (ASC); - Lower Verde River, 7 Apr 1986, *Anderson 86-20.*
Physaria newberryi Gray. - San Carlos Basin, 5 June 1968, *Pinkava, Keil, and Lehto 13023*; 7 Apr 1969, *Pinkava, Keil, and Lehto 15590*; 18 Mar 1985, *Anderson 85-1*; 11 Apr 1985, *Anderson 85-7*; 14 Apr 1986, *Anderson 87-9.*
Streptanthus cordatus Nutt. ex T & G. - Burro Creek, 6 Apr 1986, *Anderson 86-3*; - Verde Valley, 11 May 1968, *Patten, Pinkava, and Keil 3381*; 18 Apr 1978, *Romminger 1743* (ASC); - San Carlos Basin, 7 Apr 1969, *Pinkava, Keil, and Lehto 15584*; 11 Apr 1985, *Anderson 85-6.*

CARYOPHYLLACEAE

Arenaria eastwoodiae Rybd. - Burro Creek, 10 Apr 1947, *Darrow and Gould 3695*; 6 Apr 1986, *Anderson 86-6*; 1 Apr 1987 *Anderson and Reichenbacher 87-1*; - San Carlos Basin, 7 Apr 1969, *Pinkava, Keil, and Lehto 15591*; 14 Apr 1986, *Anderson 86-45*; 2 May 1987, *Anderson and Reichenbacher 87-8.*

CHENOPODIACEAE

Atriplex confertifolia (Torr. & Frem.) S. Wats. - San Carlos Basin, 2 Sept 1993, *Anderson 93-17.*

CROSSOSOMATACEAE

Glossopetalon spinescens Gray var. *aridum* M. E. Jones. - Verde Valley, 2 Apr 1953, *Carter 3232 and Chisaki* (ARIZ); 16 Mar 1984, *Anderson 84-1*; San Carlos Basin, 19 Apr 1984, *Anderson s.n.*

FABACEAE

Astragalus calycosus Torr. var. *scaposus* (Gray) Jones. - Verde Valley, 10 Apr 1941, *Darrow s.n.* (ARIZ); 25 May 1947, *Goodding 5-47* (ARIZ); Lower Verde River, 8 Apr 1986, *Anderson 86-22*; - San Carlos Basin 14 Apr 1986, *Anderson 86-44.*
Astragalus newberryi Gray var. *aquarii* Isely. - Burro Creek, 18 Apr 1941, *Benson and Darrow 10898* (ARIZ); 20 Mar 1985, *Anderson 85-2.*
Astragalus newberryi var. *newberryi* Gray. - Verde Valley, 15 Apr 1977, *Lehto 25576, Pinkava, Parfitt, and Reeves*; 16 Apr 1978, *Gierisch 4184.*
Astragalus praelongus Sheld. - Verde Valley, 27 Mar 1959, *Deaver 5438a*; 14 Apr 1960, *Crosswhite 726.*
Astragalus tephrodes Gray var. *chloridae* (Jones) Barneby. - Lower Verde River, 3 Apr 1987, *Anderson 87-23.*
Lotus mearnsii var. *mearnsii* (Britt.) Greene. - Verde Valley, *Mearns 342* (Holotype: NY); 15 Apr 1978, *Lehto 22564, Pinkava, Parfitt, and Reeves*; 23 June 1979, *Ertter and Strachen 2937*; 29 Apr 1981, *Van Devender s.n.* (ARIZ); 7 May 1989, *Anderson 89-40.*
Lotus mearnsii (Britt.) Greene var. *equisolensis* J. Anderson. - Lower Verde Valley, 3 Apr 1987, *Anderson 87-21*; 9 Apr 1986, *Anderson 86-33.*

HYDROPHYLLACEAE

Phacelia parishii Gray. - Burro Creek, 2 June 1993, *Anderson 93-12.*

LAMIACEAE

Salvia dorrii (Kell.) Abrams ssp. *mearnsii* (Britt.) McClintock. - Verde Valley, 20 Apr 1985, *Schaack and Morefield 1457* (ASC); 17 May 1977, *Romminger 1629*

(ASC); 15 Apr 1978, *Parfitt 2537, Reeves, and Pinkava*; 24 June 1979, *Ertter and Strachen 2940*; 7 May 1989, *Anderson 89-42.*

NYCTAGINACEAE

Anulocaulis leisolenus (Torr.) Standl. - Verde Valley, 24 June 1939, *Peebles 14441* (ARIZ); 19 Sept 1976, *McGill and Lehto 20699*; 24 June 1979, *Ertter and Strachen 2943*; 29 May 1981, *Van Devender s.n.* (ARIZ); *Schaack, Romminger, and Morefield S1303* (ASC); 7 May 1989, *Anderson 89-38*; - Coconino Co., Havasupai Canyon, 27 Sept 1943, *Clover 7217* (ARIZ); Grand Canyon, Little Colorado stop, 30 Apr 1970, *Holmgren and Holmgren 15494* (ARIZ); Grand Canyon National Park, along River Trail, 1/2 mile W of Phantom Ranch, 7 June 1976, *Romminger 1569* (ASC); Nevada, Clark Co., 1 mile S of Glendale, *Spaulding, Van Devender, and Tessman s.n.* (ARIZ).

POLYGALACEAE

Polygala macradenia Gray. - Lower Verde River, 8 Apr 1986, *Anderson 86-25*; San Carlos Basin, 2 Apr 1987, *Anderson with Reichenbacher 87-11.*

Polygala rusbyi Greene. - Verde Valley, 5 May 1973, *Lehto, Brown, and Pinkava 11064*; 6 May 1978, *Lehto and Pinkava 22748*; 16 Apr 1985, *Schaack 1437* (ASC); - Lower Verde River, 11 May 1979, *Harris and Lehto s.n.*; 5 Apr 1986, *Schaack 1726* (ASC); 3 Apr 1987, *Anderson 87-22.*

Polygala scoparioides Chodat. - Verde Valley, 30 Apr 1977, *Pinkava and Lehto 21345*; 18 Apr 1978, *Romminger 1744* (ASC); 27 June 1979, *Ertter and Strachan 2920*; 7 May 1989, *Anderson 89-45*; - Lower Verde River, 8 Apr 1986, *Anderson 86-24*; - San Carlos Basin, 14 Sept 1967, *Keil, Pinkava, and Lehto 10112*; 24 May 1976, *Bingham 2234.*

POLYGONACEAE

Eriogonum apachense Reveal. - San Carlos Basin, 7 Apr 1968, *Pinkava, Keil, and Lehto 13400*; 27 May 1976, *Bingham 2242*; 18 Oct 1976, *Gierisch 3837.*

Eriogonum ericifolium Torr. & Gray var. *ericifolium* Torr. & A. Gray. - Fort Verde, *Mearns 179* (Holotype: NY); Verde Valley, 19 Sept 1976, *McGill and Lehto 20720*; 24 Aug 1977, *Gierisch 3981*; 5 Oct 1984, *Schaack 1374* (ASC); 19 Oct 1984, *Schaack 1386* (ASC).

Eriogonum hieracifolium Benth. in DC. - San Carlos Basin, 24 May 1976, *Bingham 2228*; 14 Apr 1989, *Anderson and Porter 89-46.*

Eriogonum ripleyi J. T. Howell. - Verde Valley, 20 Apr 1985, *Schaack and Morefield 1458*; - Lower Verde River, 8 Apr 1986, *Anderson 86-29*; 9 Apr 1986, *Anderson 86-34.*

ROSACEAE

Purshia subintegra (Kearney) Henrickson. - Burro Creek, 4 Apr 1938, *Darrow & Crooks 3,* 18 Apr 1941 (ARIZ); *Darrow and Benson 10891* (ARIZ); 18 Apr 1977, *Geirisch 3896*; 7 Apr 1984, *Anderson 84-5* and *84-6*; - Verde Valley, 16 Mar 1984, *Anderson 84-2*; 11 Apr 1984, *Anderson* 84-13; - Lower Verde River, 7 Apr 1986, *Anderson 86-15*; 9 Apr 1986, *Anderson 86-35* and *86-36*; - San Carlos Basin, 7 Sept 1968, *Pinkava, Keil, and Lehto 13397*; 9 Apr 1984, *Anderson 84-7, 84-8, 84-10, 84-11,* and *84-12*; 11 Apr 1985, *Anderson 85-5.*

RUTACEAE

Thamnosma texana (A. Gray) Torrey. - Verde Valley, 30 Apr 1977, *Pinkava and Lehto 21344*; 18 Apr 1978, *Romminger 1749* (ASC); - Lower Verde Valley, 3 Apr 1987 *Anderson 87-21*; - San Carlos Basin, 2 Apr 1987, *Anderson 87-10.*

SCROPHULARIACEAE

Cordylanthus parviflorus (Ferris) Wiggins. - Burro Creek, 5 Nov 1983, *Parfitt 3155*; - Verde Valley, 2 Aug 1969, *Hekard and Chuang 2362* (RSA).

Penstemon thompsonae (A. Gray) Rydb. - Verde Valley, 11 May 1968, *Patten, Pinkava, and Keil 3382*; 5 May 1977, *Lehto, Brown, and Pinkava 11082*; - San Carlos Basin, 4 Sept 1967, *Keil, Pinkava, and Lehto 13022*; 4 May 1973, *Holmgren and Holmgren 7064.*