

Distribution and Taxonomic Discussion of *Tetraneuris verdiensis*, an Apparently Rare Edaphic Endemic from the Verde Valley of Arizona

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Abstract: *Tetraneuris verdiensis* was first published in 1996. It appears to be closely related to *Tetraneuris acaulis* var. *arizonica*. The closest known location of *T. acaulis* var. *arizonica* is approximately 7 miles northwest of the known *T. verdiensis* locations, which are 5 miles east of Camp Verde. *Tetraneuris verdiensis* is significant in that no other entirely discoid populations, or series of populations, of *Tetraneuris* have been reported. *Tetraneuris verdiensis* populations are consistently discoid, which separates them from *T. acaulis* var. *arizonica*. The type locality is on the top of a low hill of a gypsum stratum of the Late Tertiary Verde Formation. Denham and Turner (1996) stated that additional populations occur on the tops of the adjacent small hills within this stratigraphic unit. Results of a survey of all of the similar gypsum hills and mesas in this area east of Camp Verde are presented, along with population sizes for each gypsum hill where this species occurs. The morphological similarities and differences between *T. verdiensis* and *T. acaulis* var. *arizonica* are discussed, as well as the taxonomic status of *T. verdiensis*.

During recent investigations of rare plant distributions for the Arizona Rare Plant Field Guide (in preparation), a recently named species from the Late Tertiary Verde Formation of central Arizona was first investigated by this author. *Tetraneuris verdiensis* R. A. Denham & B. L. Turner is a dwarf scapose perennial species with densely pilose basal leaves and discoid yellow flower heads (Figure 1). At the time of its discovery in the winter of 1993–1994, this species was known only from the tops of a few small localized gypsum hills within the lacustrine limestone deposits of the Verde Formation. It has been well documented that the lacustrine deposits of the Verde Valley contain several species of endemic, disjunct, and relict plants from different floristic communities (Anderson 1996, Denham and Turner 1996).

To understand the floristics of the Verde Valley's lacustrine deposits, it is important to look at the geologic and climatic history of that region. The Verde Valley is in an area of central Arizona where the northern limits of the Sonoran Desert come into contact with the Transition Zone. The Transition Zone is a relatively narrow geologic province below the Mogollon Escarpment that consists of closely spaced mountain ranges with narrow basins (Anderson 1996, Titley 1984). Approximately 15 million years ago, this geologic province was formed during the mid-Miocene Basin and Range Disturbance, which initially resulted in the formation of a series of sub-Mogollon enclosed basins through tectonic uplifting and subsidence, as well as volcanic activities. During the Late Tertiary period, these enclosed basins

subsequently filled with large quantities of water, where lacustrine deposits with interbedded ash flows were laid down into limy tuffs (Anderson 1996, Damon et al. 1984, Denham and Turner 1996). The Late Tertiary Verde Formation was created during this process, as well as several other geologic lacustrine formations in disjunct sub-Mogollon basins (Anderson 1992, 1996). See Figure 2 for a map of the Transition Zone and the formerly enclosed basins, where lacustrine deposits formed during the Late Tertiary Period.

During the Pleistocene glacial periods that occurred approximately 11,000 years ago, as subsidence ceased and precipitation increased, stream throughflow between basins increased and caused erosion to occur. In the Verde Valley area, this erosional activity exposed the undeformed lacustrine deposits of the Late Tertiary Verde Formation, allowing plant species to colonize the area (Anderson 1996, Nations et al. 1982). Floristic communities within these deposits vary drastically with changes in the substrates of this formation. The upper portion of this formation, near Cottonwood, consists of narrow interbedded layers of limestones, mudstones, and marls. The lower end of the formation, from near Camp Verde and extending to the south and east, was formed in the deepest parts of the prehistoric lake. This area consists primarily of larger limestone deposits and evaporites, such as gypsum and deposits of salts (Anderson 1992, Denham and Turner 1996). In this portion of the Verde Valley, numerous narrow bands of peculiar soils running in a northeast-southwest direction are exposed. In this area one



Figure 1. *Tetraneuris verdiensis*.

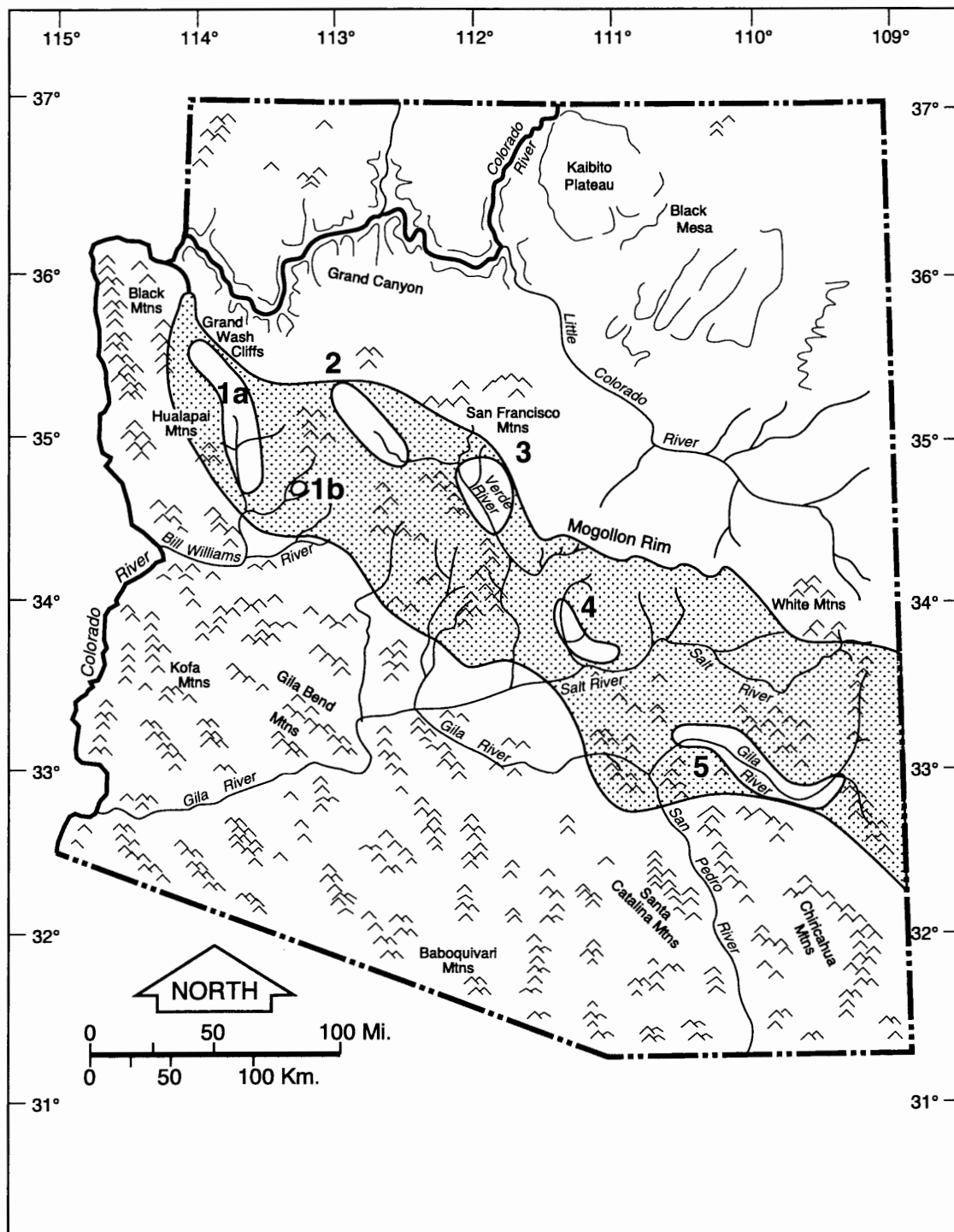


Figure 2. The Transition Zone geologic province of Arizona (shaded area). 1a = Hualapai Valley, 1b = Burro Creek, 2 = Chino Valley, 3 = Verde Valley, 4 = Tonto Valley, 5 = San Carlos Basin.

can go from areas of limestone to areas of gypsum and marl, and eventually to areas of volcanic tuff. Each of these substrates accommodates a unique floristic community. *Tetranneuris verdiensis* apparently occurs only on these gypsum marl soils of the lower end of the Verde Formation.

The Verde Valley is approximately 300–450 m higher in elevation than any of the other Transition Zone basins and is the closest of these basins to the Mogollon Rim. As in all of the other Transition Zone basins, the climate is more equable than the surrounding desert areas. This equable climate exhibits a biseasonal precipitation pattern of 25 cm or more of annual precipitation, a moderate mean annual temperature, and a relatively small difference between the annual high and low temperatures as compared to other areas in the surrounding deserts (Raven and Axelrod 1978, Axelrod 1979, Anderson 1996). The combination of these climatic characteristics causes the climate to be similar to the more mesic climate of the Miocene in the Southwest (Axelrod 1979, Anderson 1996).

The Verde Valley Transition Zone basin is located within the *Larrea tridentata*–*Canotia holacantha* series of the Arizona Upland Subdivision of the Sonoran Desertscrub biotic community (Brown 1994). However, the relatively infertile soils of the lacustrine deposits within the Verde Valley form a sharp edaphic contrast and generally exclude species that are typically dominant in this biotic community, including *Larrea tridentata* (DC) Coville, *Parkinsonia microphylla* Torr., and *Canotia holacantha* Torr. This opens the way for the occurrence of disjunct, endemic, and relict species by reducing competition for soil moisture. The number of elevationally and geographically disjunct species, as well as endemic and relict species, is higher in the Verde Valley than in any of the other Transition Zone basins (Anderson 1996). Apparently, the sharp edaphic contrast of the lacustrine deposits compared to the typical volcanic and metamorphic soils found in the Sonoran Desert has been the most important factor in the establishment and continued existence of the endemic, disjunct, and relict species that are found there (Gankin and Major 1964, Anderson 1996).

Climatic changes in the Southwest have provided the sources of these floristic curiosities in the Verde Valley area. Through studies of pack rat middens, it has become clear that the Verde Valley contained pine-oak-juniper woodland with chaparral as recently as the Late Tertiary period. This vegetation arrived in that area as a result of Pleistocene glacial cycles, which caused pinyon-juniper

woodlands to extend southward into the lower elevation deserts of the Southwest, including areas that today contain the modern Sonoran and Chihuahuan Deserts (Betancourt 1986, Van Devender 1977, Van Devender and Spaulding 1979, Van Devender and King 1971, Lanner and Van Devender 1981). At the end of the most recent Wisconsin glaciation, approximately 11,000 years ago, the climate of the Southwest became warmer and drier, causing pinyon-juniper woodland to retreat from these lower deserts (Anderson 1992). The relatively infertile soils of the Verde Valley's lacustrine limestone deposits have apparently offered refugia for many genera that historically occurred in the area. Because of the biseasonal precipitation pattern and relatively equable climate, and the fact that many of the species dominant in the modern Sonoran Desert do not grow on these infertile soils, the lack of competition for soil moisture has enabled genera typically associated with pinyon-juniper vegetation to remain in the Verde Valley (Anderson 1992, 1996). The genus *Tetranneuris* is no exception, as it typically occurs at higher elevations in the Great Plains, Great Basin, and Rocky Mountains (Denham and Turner 1996).

Distribution of *Tetranneuris verdiensis*

The distribution of *Tetranneuris verdiensis* and the sizes of each population segment of this apparently rare plant were investigated and documented during this study. This research was conducted in May of 1999 and 2000. Based on Denham and Turner's (1996) description of the habitat and distribution of this species and on personal observations of the habitat of the type location, all suitable and similar habitats within a 3-mile radius of the type locality were surveyed for this species. This habitat consists of the tops of low chalky hills composed of gypsum crystals, gravel, and marl, occupied by a dwarf sub-shrub community of numerous perennial species (Figure 3). The dominant species of the type location include edaphic endemic species, such as *Eriogonum ericifolium* Torrey & A. Gray var. *ericifolium*, *Salvia dorrii* (Kell.) Abrams subsp. *mearnsii*, and *Lesquerella cinerea* S. Wats., as well as *Hymenopappus filifolius* Hook., *Penstemon thompsoniae* (Gray) Rydb., *Krameria erecta* Willd. ex J. A. Schultes, *Melampodium leucanthum* Torr. & A. Gray, *Townsendia incana* Nutt., *Thymophylla acerosa* (DC) Strother, *Frasera albomarginata* S. Wats., *Houstonia rubra* Cav., and *Castilleja chromosa* A. Nels. Other less dominant species present at the type location include *Arenaria eastwoodiae* Rydb. var. *adenophora* Kearney

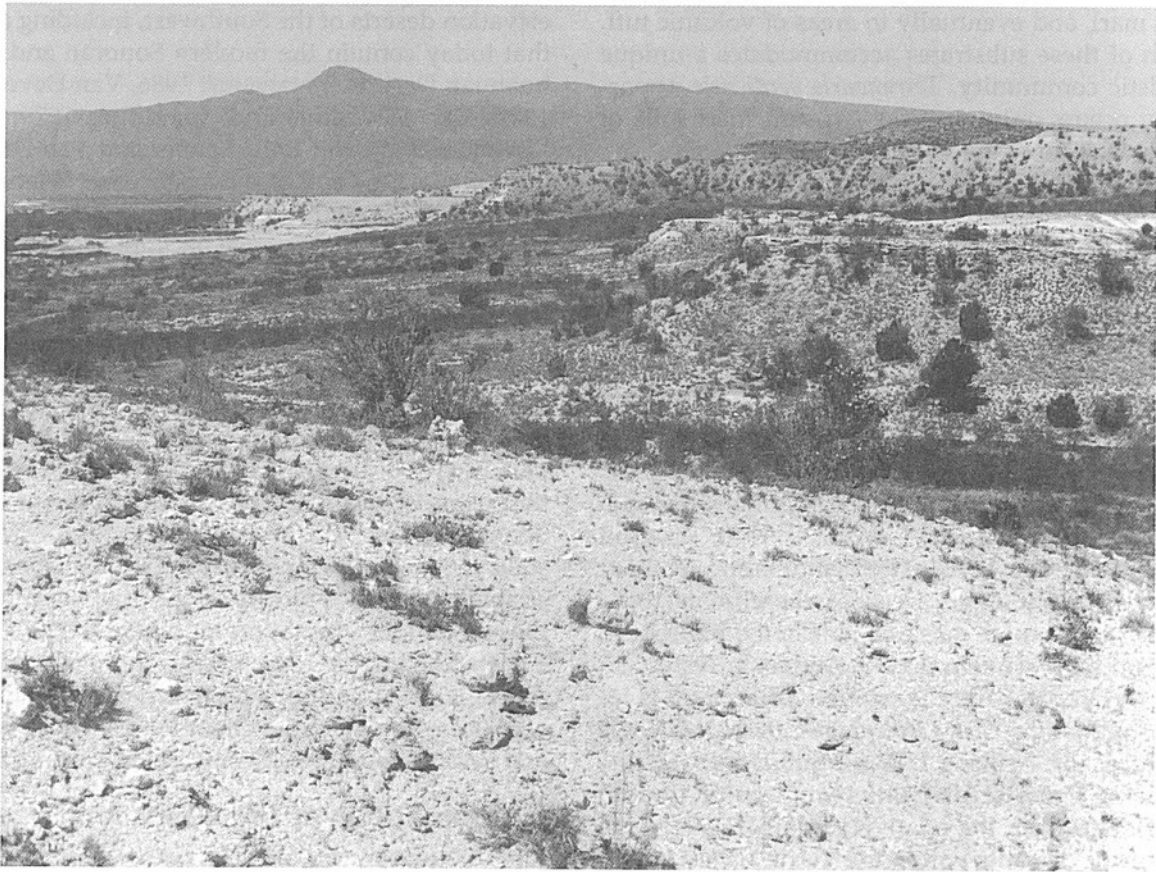


Figure 3. *Tetraneuris verdiensis* habitat.

& Peebles *Polygala alba* Nutt., *Ceanothus greggii* Gray, *Echinocereus engelmannii* (Parry ex Engelm.) Lem., *Ephedra torreyana* S. Wats., *Lepidium* sp., *Purshia stansburyana* (Torr.) Henrickson, *Rhus trilobata* Nutt., and *Juniperus coahuilensis* (Martinez) Gausson ex R. P. Adams.

In total, 18 low hills and mesas in the nearby area were searched for the presence of this species, based on soil characteristics and the presence of similar vegetation. Each of these areas contained sub-shrub communities with many of the same species found at the type location. Of the 18 study areas, only 10 appeared to contain the same mix of gypsum, marl, and gravel substrates as the type location. These unique gypsiferous soils of the type location are limited to the southeastern portion of the Verde Valley, where the deepest portions of the ancient lake were located.

Tetraneuris verdiensis was found only on the tops of four low hills: the type location and three

low hills adjacent to it. The distribution of this species was patchy, and primarily limited to the tops of the hills or on gently sloping areas at the edges of the tops. Steeper sides of these hills, and areas at the base of these hills with very similar soils and sub-shrub communities, were conspicuously lacking this species. In addition, this species was not found in areas on the same hilltops where thicker shrub communities and more gravelly or cobbly soils were present.

This taxon occurred in seven distinct population segments on these four low hills. The number of plants present in each of these population segments was estimated (Table 1), and each population segment was sampled with 5 m wide transects of variable length. Five transects were sampled in each of the smaller population segments, which covered nearly the entire distribution of the segments and the very specific habitat each occurred in. In the two largest population segments, where

Table 1. Population estimates for each population segment of *Tetraneuris verdiensis*.

Population segment no.	No. transects sampled	No. plants per sq m	Size of area sampled in sq m	Estimated no. plants
1	8	0.39	4,621	1,808
2	5	0.08	532	43
3	5	0.11	550	62
4	8	0.28	2,148	602
5	5	0.36	926	341
6	5	0.07	789	58
7	5	0.31	1,224	384
Totals			10,790	3,298

the amount of suitable habitat was more abundant, eight transects were surveyed for this species and approximately half of the area in those population segments was sampled. The average number of plants per square meter was determined for these transects, and a population estimate was made based on the total area covered by the population segment and the total number of plants per square meter in the sampled transects.

The total number of plants is approximately 3,298. It should be noted that the exact number of plants is difficult to determine with this species, as multiple underground stems are commonly associated with one plant. The estimated total area of suitable habitat occupied by this species was 10,790 sq m (1.08 hectares). Based on the transects sampled for this study, the overall average of plants per square meter is estimated to be 0.23. By far, the largest population segment can be found at the type location, where approximately 1,808 plants occur. Several of the population segments occurred on small patches of suitable habitat, which supported less than 100 plants. Only in the largest population segment was the phenology of this species examined. An estimated 51% of plants within that population segment were blooming. The only insect pollinator observed was a bee fly (Family Bombyliidae).

Taxonomic Discussion of *Tetraneuris verdiensis*

The genus *Tetraneuris* was first described in 1898 by E. L. Greene and is part of the *Hymenoxys* complex (Asteraceae: Helenieae). In the past century, various botanists have encountered difficulties when attempting to understand generic delimitation within the *Hymenoxys* complex. In light of these challenges, several different treatments of this group have been published. This complex includes taxa referable to *Dugaldia* Cass., *Hymenoxys* Cass., *Macdougalia* A. Heller, *Phileozer*

Buckley, *Picradenia* Hook., *Plummera* A. Gray, *Rydbergia* Greene, and *Tetraneuris* Greene. Various taxonomic treatments have recognized *Tetraneuris* at the generic level, including Rydberg (1914), Robinson (1981), Bierner (1994), and Bierner and Jansen (1998). Others have submerged the genus *Tetraneuris* into *Hymenoxys* (Turner and Powell 1977, Kearney and Peebles 1960, Lehr 1978).

After analysis of the chromosome numbers, chemical characters, and morphological characters of taxa within the *Hymenoxys* complex, Bierner (1994) determined that a reasonable case could be made for either submerging all of the genera in this complex into *Hymenoxys* or for splitting them into the eight genera mentioned above. More recent studies of DNA restriction site variation in *Hymenoxys* and *Tetraneuris* taxa have clearly separated the taxa referable to *Tetraneuris* into a separate branch of the DNA phylogenetic tree from all of the other taxa that were evaluated within the *Hymenoxys* group. These findings were consistent within the taxa studied, with the exception of *Hymenoxys texana*, which produced a phenogram that placed it with *Tetraneuris* (Bierner and Jansen 1998, Spring et al. 1994). Although *Tetraneuris* is a genus closely related to *Hymenoxys*, Bierner and Jansen (1998) discovered that the taxa referable to *Tetraneuris* that they studied formed a monophyletic clade supported by the presence of 40 shared characters and a boot strap value of 100%. This research appears to merit recognition of *Tetraneuris* at the generic level.

The apparently closely related taxon, *Tetraneuris acaulis* (Pursh) Greene var. *arizonica* (Greene) K. L. Parker also occurs in the Verde Valley, where it can be found on the lacustrine limestone deposits and adjacent Mesozoic sandstones. This taxon, common in northern Arizona and southern Utah, reaches the southernmost extent of its range in the Verde Valley, where it has been documented by Denham and Turner (1996) near the town of

Cottonwood and in the Middle Verde Road area by Anderson (1996). The Middle Verde Road population is approximately 7 miles from the known locations of *Tetranneuris verdiensis* but the two have not been documented as occurring together, possibly because of the lack of suitable habitat between them. The most important characteristic distinguishing these two species is the consistently discoid flower heads of *Tetranneuris verdiensis*. Denham and Turner (1996) also stated that *T. verdiensis* differs from *T. acaulis* var. *arizonica* in its dwarf habit, long pilose vestiture, and relatively short broad leaves. However, observations of the latter species in the Middle Verde Road area reveal a population of *T. acaulis* var. *arizonica* that does exhibit a dwarf habit, long pilose vestiture, and relatively short broad leaves (Figure 4). Although the degree of hairiness in this population of *T. acaulis* var. *arizonica* is not as severe as it is in *T. verdiensis*, the characters that these plants exhibit appear to provide evidence of intergradation and intermediate forms between the two taxa.

Discoid individuals have been documented elsewhere in taxa referable to *Tetranneuris*, such as in the case of populations of *Tetranneuris acaulis* Greene var. *acaulis* in Wyoming. There, discoid individuals have been documented within the population as isolated individuals that only differed from the typical form of this species in their rayless condition. Those plants were the basis of *T. eradiata* A. Nelson, but are currently considered to be deviant forms of *T. acaulis* var. *acaulis* (Denham and Turner 1996). Other than *T. verdiensis*, no completely discoid populations or series of populations have been documented within this genus.

Discussion

The results of this research indicate that *Tetranneuris verdiensis* has a severely limited range and very specific habitat requirements. Of 18 hills searched, this species was documented only on the tops of four adjacent hills in the Verde Valley, occurring in seven distinct subpopulations. A total population estimate of 3,298 plants, covering approximately 10,790 sq m (1.08 hectares), was revealed during this study. This taxon is apparently very sensitive to slight changes in soil characteristics, degree of slope, and competition from other plants. Even on the same hills as known populations, this species was not found in areas of more dense shrub cover or in more gravelly-cobbly situations. On the steeper slopes of the sides of these hills, where soils and sub-shrub communi-

ties appeared to be very similar, this species could also not be found. Some very small patches of seemingly similar habitat on nearby hills were not occupied by this species at the time of this study, and appear to be available for colonization by this species in the future.

Taxonomically, this species appears to be very closely related to *Tetranneuris acaulis* var. *arizonica*. The two taxa both occur in the Verde Valley, but known locations of these two taxa are separated by a distance of 7 miles and occur in different habitats. The nearest location of *T. acaulis* var. *arizonica* occurred on gently sloping areas in the bottom of the valley, where somewhat more dense shrub communities with less gypsiferous soils were present. Meanwhile, *T. verdiensis* occurred only on the tops of low hills. The entirely discoid flower heads of *T. verdiensis* were consistently observed in all plants and all sub-populations, and not as isolated individuals. In addition, all plants observed in the nearest *T. acaulis* var. *arizonica* population contained ray flowers. However, the long pilose vestiture and dwarf habit of plants within the nearest location of *T. acaulis* var. *arizonica* appeared to be intermediate between the degree of those characters found in *T. verdiensis* and the typical more northern form of this taxon.

Recent genetic studies of the genus *Tetranneuris* by Bierner (1994) and Bierner and Jansen (1998) did not include *T. verdiensis*. To further understand the taxonomy of the species, genetic studies appear to be necessary. It appears possible that *T. verdiensis* would be best treated as a discoid variety of *T. acaulis*. However, without genetic analysis of this taxon, that recognition cannot be made at this time.

Currently, all known occurrences of this species are located on lands owned by the Coconino National Forest. However, privately owned land can be found directly south of the hills occupied by *T. verdiensis*, and some of the hills on that land are currently being mined for gypsum. Although at least one of the hills containing this species is accessible to all-terrain vehicles, the degree of disturbance within the occupied habitat is currently minimal. Protection of these hills would not only benefit *T. verdiensis*, but would also benefit other edaphic endemic species (*Eriogonum ericifolium* var. *ericifolium*, *Salvia dorrii* subsp. *mearnsii*, and *Lesquerella cinerea*) as well as populations of several disjunct species. Simply by retaining these lands under the current Coconino National Forest ownership and management regime, this unique taxon and the rare combination of substrates and



Figure 4. *Tetraneuris acaulis* var. *arizonica*.

vegetation that makes up its specific habitat will be protected. It is possible that more populations are present that were not detected during this survey. Further investigations into the distribution of this plant within the Verde Valley may uncover new populations in the future.

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